WHERE BIRDS ARE RARE OR FILL THE AIR: THE PROTECTION OF THE ENDEMIC AND THE NOMADIC AVIFAUNAS OF THE KAROO

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Abstract

The primary objectives of this study were to assess the protected status of birds in the Succulent and Nama-Karoo, and to identify areas, using a GIS approach, where new protected areas could be established. The Karoo *sensu lato* lacks a distinctive avifauna, but is rich in species. A total of 407 bird species has been recorded in the Succulent and Nama-Karoo, of which 294 species are considered typical of the region. The Karoo is not particularly rich in bird species endemic to the region, and all Karoo endemic species occur in both biomes. The Nama-Karoo has an unusually high species richness of nomadic birds, and both the Succulent and Nama-Karoo have an unusually high species richness of larks (Alaudidae) compared with other biomes.

The Succulent and Nama-Karoo have stochastically low annual rainfall and generally low above-ground primary production. Rainfall is often highly localized and varies annually in amount and timing. The variability of the rainfall and long dry spells or severe droughts create a mosaic so that high and low resource areas occur as patches in the landscape. Resident species of birds tend to maintain low densities and wait for rainfall events, whereas nomadic species search for high resource patches scattered in time and space, so that their respective densities likewise vary temporally and spatially. Compared with other biomes in southern Africa, there is a high species richness of nomadic birds in the Karoo. The small nomadic larks are most common in areas of perennial and annual desert grasses, and they feed on grass seeds, whereas resident granivorous birds tend to feed on the seeds of forbs and shrubs. Clutch sizes of the nomadic larks birds are small, apparently selected for by the need for a short breeding cycle.

Threats to the diversity of the avifauna are mostly from domestic livestock. Grazing-induced changes in species richness of plants and structure of habitats appear to be important determinants of species richness of birds. The general pattern is that species richness of birds is highest on lightly grazed rangelands, intermediate on moderately grazed rangelands and lowest on the heavily grazed rangelands. Nest site preferences of ground-nesting and shrub-nesting birds may have been influenced by grazing mammals in Karoo shrublands, and birds tended to select sites in or under plants that are not preferred by mammals for food.

The Succulent and Nama-Karoo biomes are poor in protected areas compared with other biomes in southern Africa, and only 0.69% (2 481 km^2) of *ca* 359 707 km^2 of the Karoo *sensu lato* is protected from agricultural activities. Protected areas in the Karoo are markedly skewed to the higher rainfall areas, and are particularly inadequate for the protection of the endemic and nomadic species of birds. The major deficiency in protected areas is in the arid and semi-arid central and northwestern parts of the Karoo. Areas were identified and recommendations made for protected areas in those parts of the Succulent and Nama-Karoo in which there is a high species richness of birds endemic to the Karoo, nomadic birds and larks (Alaudidae). For dryland nomadic birds, areas to be protected should be selected in areas in which the probability of autumn rainfall is highest, and where the coefficient of variation in the rainfall is highest. In the context of protected areas in the Karoo, where the density of birds is low and the above-ground primary and secondary production of habitats highly variable, large areas may be more effective at preserving populations of certain species than small areas, simply because they contain more temporally asynchronous patches and more individual birds.

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Disclaimer

All parts of this thesis have benefitted from discussions with colleagues. Except for some of the raw data, where I have made use of databases compiled by various organisations, and for Chapter 3, parts of which were prepared as a book chapter in conjunction with C.J. Vernon, this thesis is my own work, and has not been submitted to any other university.

Signed by candidate

W. R. J. Dean

Chapter 1

General Introduction

> "The Great *Karro*, stretched out before me, presented, at this distance, no visible object to break the evenness of the plain, or relieve the eye. The rivers and their Thorn-trees, were lost in the vast extent, and were not to be distinguished as a feature in the landscape. The road we travelled might be traced for a few miles, in an undulating line across the desert, till it gradually lessened and vanished away. The Hangklip, in the second distance, constituted the only object; and by its projecting and overhanging crag, naturally gave a name to a spot where nothing else presents itself, that could suggest an appellation. In these solitary wilds, no moving being was to be seen, no sound to be heard" (Burchell, 1822).

Despite the emptiness described above, the southwestern arid zone of Africa is rich in plant and animal species, and in endemism (Gibbs Russell, 1985; Clancey, 1986; Vernon, 1986; Branch, 1988; Hilton-Taylor & le Roux, 1989). The arid zone includes the Namib and Kalahari deserts (Werger, 1978, 1985) and, the focal area of this thesis, the Succulent Karoo and Nama-Karoo biomes (Rutherford & Westfall, 1986). The Succulent Karoo, a dwarf shrubland, has an extremely high species richness of succulent plants, unparalleled anywhere else in the world (Hilton-Taylor & le Roux, 1989). The grassy shrubland vegetation of the Nama-Karoo, however, is not particularly species-rich or unique (Hilton-Taylor & le Roux, 1989), but it does include a high species richness of perennial desert grasses (Gibbs Russell *et al.*, 1990). Many of the animal species of the Nama-Karoo are shared with adjacent biomes, particularly savanna and grassland (Smithers, 1983; Branch, 1988; Maclean, 1993).

The Succulent Karoo and Nama-Karoo are rich in bird species (Winterbottom, 1968a; Vernon, 1986), but the avifauna, in general, is not distinctive or particularly rich in endemic species (Huntley, 1984; Clancey, 1986). However, there is an unusually high species richness of both resident and nomadic larks (Alaudidae) in the two biomes, especially in the Nama-Karoo (Dean & Hockey, 1989; Dean *et al.*, 1992). There is also an unusually high species richness of other nomadic bird species in the Nama-Karoo (Maclean, 1993). Avian species richness and density in the Karoo is spatially and temporally variable according to the distribution of rainfall (Winterbottom, 1968a; Vernon, 1986).

As in other arid and semi-arid ecosystems throughout the world (Noy-Meir, 1973), the Karoo *sensu lato* has stochastically low annual rainfall (Venter, Mocke & de Jager, 1986) and generally low primary production (Rutherford, 1978; Werger, 1985). Vegetation in the Succulent Karoo and Nama-Karoo varies in productivity and phenology in accordance with weather conditions (Werger, 1985). The variability of the rainfall and long dry spells or severe droughts (Tyson, 1987; Vogel, 1994) create a mosaic so that both high and low resource areas occur as patches across the landscape. These major driving forces have pushed the evolution of typical Karoo birds in two different directions.

Environments in which resources vary seasonally in abundance and availability, or are clumped in time and space, favour the evolution of migration and nomadism in animals (Sinclair, 1984). Nomadism is the unpredictable movements of animals to find high resource patches in the environment. It has evolved as a stable strategy in several groups of birds, including ratites (Sauer & Sauer, 1966; Davies, 1976) pteroclidiformes (Maclean, 1976a) and passerines (Maclean, 1970a; Davies, 1984). These provide examples of highly mobile elements of a fauna which has adapted to cope with stochastic variability of resources, while keeping a relatively specialized diet. The alternative strategy, also evolutionary stable, is for a species to be resident or locally nomadic within a landscape, and to have a relatively unspecialized diet.

In the context of the protection of biodiversity in the Karoo, the patchiness of resources and the mobility of part of the avifauna create a particular problem (Dean & Lombard, 1994). Since avian species richness and density varies in time and space over parts of the Karoo, present protected areas may not always contain the set of nomadic bird species for which they were designed. More importantly, present protected areas may not often provide suitable breeding habitat for the nomadic birds. Opportunities for breeding in the nomadic birds are patchy in time and space in the Karoo, and production of young, at least in the arid savanna, appears to vary considerably according to the duration, amount and timing of rainfall (Maclean, 1970a, 1970b). Production must exceed mortality in birds breeding in certain high-resource patches for the species to survive. It is these critical high-resource habitat patches, where there is a high probability of successful breeding (in terms of maximum production of surviving young), that are of primary importance in the protection of nomadic birds in the Karoo. Existing protected areas in the region may also be inadequate for the protection of other bird species and biodiversity in general. In this dissertation, "protected area" means an area that is fenced to exclude domestic livestock and where there are no croplands in current use, and where there are no other activities that are known to change the structure and diversity of natural habitats. Protected area categories, as approved by the IVth World Congress on National Parks and Protected Areas, are listed by McNeely (1994).

Land-use in the Karoo

Most of the Karoo is used for the ranching of small domestic livestock (sheep and goats), with wool, mohair and meat as important products. In general, the Karoo is not a highly altered system (Dean *et al.*, in press a), but secondary production appears to be decreasing (Dean & Macdonald, 1994). The vegetation in parts of the Karoo has changed (Acocks, 1953, 1964; Talbot, 1961; Leistner, 1979; Stock, Bond & le Roux, 1993; Bond, Stock & Hoffman, 1994). Both plant and animal species may have been lost through the selective overgrazing of rangelands (Leistner, 1979; Milton, 1992) and through transitions of rangeland vegetation to different states (Westoby, Walker & Noy-Meir, 1989; Walker, 1993; Milton *et al.*, 1994; Milton & Hoffman, 1994). The biodiversity of the Karoo is therefore threatened, not by major land transformation schemes, but by the inexorable nibbling of thousands of sheep.

The increasing pressure on agricultural resources (Downing, 1978) and the progressive change in the species composition and density of Karoo rangelands (reviewed by Novellie *et al.*, 1988) has possibly affected the avifauna. Rainfall may now be less effective, because of increased runoff as a result of reduced density of plant cover (Snyman & van Rensburg, 1986; Snyman & Fouché, 1986). Changes in fire regimes in the grassy eastern Nama-Karoo (Manry & Knight, 1986) has eliminated the Bald Ibis *Geronticus calvus* from these areas (Siegfried, 1966; Manry, 1985). Draining or ploughing of wetlands has eliminated the Wattled Crane *Bugeranus carunculatus* in the eastern Nama-Karoo (Brooke & Vernon, 1988).

The Khoi-San peoples, who were hunter-gatherers formerly widespread in the Karoo, and the Khoikhoin herders on the margins of the Karoo (Klein, 1986), probably contributed towards small-scale patchiness in habitats in the Karoo, by repeatedly using certain camp-sites (Sampson, 1986). The Khoi-San, through their hunting activities, would have contributed to the pool of food available for avian scavengers and raptors, and would also have created small and intermediate disturbances through their gathering activities. The large herds of antelope that were hunted by the Khoi-San and that formerly moved over the Karoo, particularly nomadic springbok *Antidorcas marsupialis* (Skead, 1980, 1987), probably had some influence on the avifauna of the Karoo, if only in creating small-scale patchiness in habitats through selective grazing. Domestic livestock, because of their different grazing behaviour and their confinement to paddocks (Talbot, 1961), are unlikely to simulate the same effects on the vegetation. The loss of the large herds of ungulates, and the intermediate disturbances caused by patch selective grazing, has almost certainly had a large effect on the avifauna. As much as 10% of the Karoo avifauna may have been affected in one or another way by the replacement of the large herds of ungulates by domestic livestock. The Egyptian Vulture *Neophron percnopterus*, for example, is now extinct in the Karoo, where it was formerly widespread (reviewed by Brooke, 1984). Other elements of the avifauna may represent the last survivors of species that were once widespread through the Karoo

Protected areas in the Karoo

There are more than 582 protected terrestrial areas in South Africa, Swaziland and Lesotho, covering about 6% of the land surface area (Siegfried, 1989). Biome representation in protected areas (mainly publicly owned "nature reserves") is markedly skewed to Fynbos, forest, and moist and arid savannas (Siegfried, 1989). Three biomes, Succulent Karoo, Nama-Karoo and grassland, although accounting for 61% of the surface area of South Africa, are poorly represented, and account for only 3.62% of all protected areas. The Karoo biomes are particularly poorly represented, and only 0.69% (2 481 km^2) of *ca* 359 707 km^2 is protected from agricultural activities (Hilton-Taylor & le Roux, 1989). Protected areas in the two Karoo biomes are disproportionate, with 1.2% of the total area in the smaller Succulent Karoo, and 0.5% of the total area protected in the larger Nama-Karoo. Furthermore, 33.2% (428 km^2) of the protected area in the Nama-Karoo is in so-called "False Karoo" types (Huntley, 1978), which are degraded grasslands thought to be only recently invaded by karroid shrubland vegetation (Acocks, 1953). The biota are generally under-represented in the few protected areas that have been established in the Karoo (Siegfried, 1989). It has been shown that endemic southern African bird species with the smallest populations in statutory protected areas are found in the Karoo or grassland biomes or both (Siegfried, 1992), so there is cause for concern.

In this context, the protection of biological diversity (Brussard, 1991) and the design and locality of protected areas has become increasingly important (Diamond, 1975; Simberloff & Abele, 1976a, 1976b; Diamond, 1976; Terborgh, 1976; Diamond & May, 1981; Margules, Higgs & Rafe, 1982; Soulé, 1986; Scott *et al.*, 1987; Quinn & Hastings, 1987, 1988; Bond, 1989; Cowling & Bond, 1991; Pressey, 1994). Conservation efforts in the past tended to be focused on the protection of single species or on large areas of land, regardless of species richness (Miller, 1983). Conservation biologists currently recommend the protection of species-rich areas as both cost-effective and efficient in preserving biological diversity (Scott *et al.*, 1987). Systems of protected areas (Margules, Nicholls & Pressey, 1988; Franklin, 1993), incorporating steep environmental gradients (Siegfried, 1989), or linking together separated elements of metapopulations (Thomas, 1994) may be more valuable in the longer-term protection of a maximum amount of biological diversity than a few isolated large and small protected areas.

An approach that I have taken *inter alia* in this dissertation is to review the adequacy of existing protected areas for the protection of birds, and to review the potential threats to the avifauna. Land-use in the Karoo has important consequences for the protection of birds (and biodiversity) in the Karoo. Most of the Karoo is privately owned (Anon, 1985a, 1985b, 1986). The management of Karoo rangelands is therefore vested in many individuals, and in a wide range of options.

sensu lato. Vultures, and certain eagles, formerly widespread in the Karoo, are now infrequent to rare in the region (Boshoff, Vernon & Brooke, 1983). This change can be attributed not only to the loss of the large ungulates and their attendant predators, but also to persecution and poisoning of the large raptors (Brooke, 1984; Allan, 1989; Boshoff, 1993).

No research has yet been done in the Karoo that has been specifically aimed at investigating the direct effect of sedentary grazers (domestic livestock) on the population size and breeding success of birds. It may be hypothesized that avian species richness and density in the Karoo are influenced by the effects of grazing by domestic livestock, as has been found elsewhere (Medin, 1986; Taylor, 1986; Bock & Bock, 1988; Tidemann, 1990; Baker & Guthery, 1990). Plant-granivore interactions may also be adversely affected by heavy grazing pressure on rangelands. This may result in the disruption of bird movement patterns or the loss of species from certain areas.

Thesis presentation

The specific objectives of the present study are to identify parts of the Succulent and Nama-Karoo that should, on the basis of their richness of particular species of birds or other attributes, be further examined to investigate their potential as protected areas. Priorities for protection include bird species endemic to the Karoo *sensu lato*, nomadic birds in the Karoo, and larks (Alaudidae). These objectives cannot be achieved without initially identifying areas of high avian species richness and endemism and areas in which there is a large proportion of nomadic bird species. The identification of potential protected areas will also be influenced by the factors affecting the distribution, breeding and species richness of resident and nomadic birds, the impact of land-use practices on birds in the Karoo, and the degree to which these areas of avian species richness, endemism and nomadism overlap with existing protected areas.

This thesis is presented in three sections, the first of which is descriptive and provides information on the Karoo region and on the ecology and distribution of birds in the Karoo. The second section leads on to more specific discussions on nomadic birds, and examines the results of two studies on the stability of avian species richness in the southern Karoo. The third section deals with land-use in the Karoo, with discussions on the possible impacts of land-use practices and concludes with the identification of areas that should be investigated for protected areas in the Karoo. To this end, extensive use has been made of Geographic Information System (GIS) analyses of spatial data, such as bird species distribution patterns, the localities of protected areas and other environmental information.

SECTION 1

Background:
Geographical Information Systems, a description of the Karoo and land-use in the Karoo, and the avifauna of the Karoo

Preface to Section 1: Geographical Information Systems

Among the new technologies available to ecologists, and particularly to landscape ecologists, Geographical Information Systems (GIS) are one of the powerful tools that enable users to analyze complex spatial information (Burrough, 1986; Haines-Young, Green & Cousins, 1993). For example, GISs have been used in many recent studies in landscape ecology (Bridgewater, 1993), the description and characterization of habitats for birds and foxes (Shaw & Atkinson, 1990; Haslett, 1990), the analysis of populations and extinction risk of a threatened mammal (Yonzon, Jones & Fox, 1991) and in conservation evaluation (Lombard, August & Siegfried, 1992; Scott *et al.*, 1993). One of the advantages of a computer-based GIS is the interactive nature of the analyses that can be performed. A GIS can be used to produce map compositions very quickly, and these in turn may be used for the production of thematic maps or may suggest new directions for analyses, or a new understanding of the spatial distributions of particular biota. Non-spatial attributes can be linked to spatial data in the GIS database so that specific and general questions can be asked of the database (Lombard *et al.*, 1992). In this way, the database can be passed through a series of sieves so that a small subset of the original database can be extracted and mapped or analyzed.

Many of the results and conclusions of this study are based on thematic maps, produced by integrating different spatial and non-spatial databases containing environmental information, and overlaying these on simple topographic maps of southern Africa, using a Geographical Information System. The results of the various analyses presented in different chapters have much in common, and in order to avoid repetition, a general overview of the Geographical Information System used and the method of producing thematic maps will be given here. Databases relevant to particular sections or chapters in this dissertation will be discussed and described more fully in the relevant chapters.

Geographical Information System

The GIS program used in this study is PC ARC/INFO 3.4D PLUS (Environmental Systems Research Institute, Redlands, California, U.S.A.) running on a 386 DX computer. PC ARC/INFO is a vector-based system that can map exact boundaries of map units of any size (see Haslett (1990) for further discussion). In the present case, the resolution of the topographic input data (15' x 15' cells, approximately 27.25 x 23.5 km (*ca* 640 km^2) at the latitudes and longitudes at which this study was completed) was fairly coarse, but this resolution does provide broad geographic patterns of the focal species' distributions and provides a base for more detailed studies at a finer scale. ARC/INFO is also capable of producing summary statistics, such as frequency distributions.

In order to produce thematic maps, my procedure was to computerize coded distribution data of climate, biomes, land-use, certain plant species and all avifauna currently recorded from the Karoo, and then to use ARC/INFO to generate coverages (integrated maps plotting the distribution of particular qualitative or quantitative data) to plot distributions and to identify specific areas or specific distributions of weather patterns, land-use, vegetation or birds. I used simple sorting programs, written as ARC/INFO macros, to extract specific subsets of data. The programming and procedure for generating GIS coverages are given in the ARC/INFO program manual and in various publications (e.g. Burrough, 1986) and will not be discussed here.

The various databases were all assembled in the same way, using codes for each 15' x 15' square as the reference point to which all other data were attached. The reference numbering system is that developed by Edwards & Leistner (1971) in which a one-degree square is given a reference number consisting of the degrees of latitude and longitude at the northwest corner of the square. The square is then divided into four, and each of the quarters is again divided into four, giving quarter- and one-sixteenth degree squares that are each coded A, B, C and D from west to east and from north to south. Any point within a one-sixteenth degree square is then defined by a combination of the reference number and a two-alpha code (see Leistner & Morris, 1976). Although these sub-divided squares are one-sixteenth of a degree in area, they are known universally among southern African biogeographers as "quarter-degree squares" (QDS), the length of each side being one quarter of a degree. This term is used throughout the present dissertation.

The base map used for all maps in this dissertation is a polygon coverage of southern Africa, compiled and digitized at the FitzPatrick Institute. A second polygon coverage, containing only those quarter-degree squares that included Succulent Karoo or Nama-Karoo vegetation according to the biome map of Rutherford & Westfall (1986), was used to generate coverages of all environmental data that were overlaid on the base map. All the databases used to generate overlay coverages have a common problem, and that is the presence of "holes" in the database (Lombard, 1993). In the present case, this means quarter-degree squares for which there are no data. When coverages are generated from the data, the holes in the resulting map may be interpreted as the absence of the phenomenon, giving a "false negative" (Lombard, 1993). The presence of these false negatives varies in different databases analyzed in this dissertation - the bird database is probably the most complete, and the mining database probably the most incomplete. Sources of error in the various databases include misidentifications of birds and mis-keyed code numbers in the two major bird databases, the patchy distributions of birds and plants as a result of poor coverage of parts of the Karoo by ornithologists or botanists, and the scale at which various land-uses were mapped. It was also difficult to decide on the northern and eastern boundaries of the Karoo. The "avifaunal Karoo" (Allan *et al.*, unpublished MS) differs in some ways from the "botanical Karoo", of which there are several versions (Acocks, 1953; Werger, 1978, 1985; Rutherford & Westfall, 1986). On the basis of bird distributions and the distribution of arid grassland and karroid shrubland, I used the Karoo boundaries defined by Rutherford & Westfall (1986) and ended the Karoo at 26° S in the north, and at 26° E in the east. Beyond this latitude and longitude, "savanna" species of birds become increasingly common, although many "Karoo" bird species are still present in the avifauna.

Chapter 2
The Succulent and Nama-Karoo

Part 1: Ecological characteristics of the Karoo

Introduction

The southwestern arid zone of Africa has traditionally been divided into three major areas: the Namib Desert, the southern Kalahari Desert and the Karoo (Werger, 1985). The Karoo *sensu lato* comprises two biomes (Rutherford & Westfall, 1986), the southern semi-arid and the western, arid succulent shrubland Karoo (Succulent Karoo), and the grassy central, upper and "false Karoo" (Nama-Karoo) (**Figure 2.1**). The two biomes share some plant and animal species but are generally regarded by botanists as clearly distinct. The vegetation of the winter-rainfall Succulent Karoo has some taxonomic affinities with the shrublands of the Cape Floral Kingdom in parts, whereas the vegetation of the summer-rainfall Nama-Karoo has affinities with savanna vegetation (Gibbs Russell, 1987). The vegetation of both biomes has some regional variation and is patchy on a landscape scale, with a number of distinct plant assemblages and high *beta* diversity in the Succulent Karoo (evident from data in Acocks, 1953; Milton *et al.*, in press). The Succulent and Nama-Karoo together occupy *ca* 369 946 km^2 (Huntley 1984) or *ca* 359 707 km^2 (Hilton-Taylor & le Roux, 1989) or approximately 32% of South Africa. Karroid shrubland extends into Namibia, where it is bounded by the Namib Desert to the west, the Khomas Hochland to the north and arid savanna to the east. Karroid vegetation also occurs on the perimeter of Lesotho (Rutherford & Westfall, 1986). For various reasons, chiefly a paucity of data on birds specifically from karroid habitats in the two countries, neither the Namibian Karoo nor the Lesotho Karoo will be discussed further here. The Richtersveld of the northwestern Cape Province, which has very low rainfall and sparse succulent vegetation (Werger, 1978, 1985) has been included in the Succulent Karoo for the purposes of this study. The two Karoo biomes have been treated as a single entity in many of the discussions that follow. This is partly because the two biomes do not have a clear boundary between them, and partly because earlier literature treated both as a single biome (Hilton-Taylor & le Roux, 1989).

The term "Karoo" is derived from a Hottentot word *!garob* signifying parched or desiccated (Talbot, 1961). Most of the western and central Karoo is an "interior continental desert", *i.e.* arid because of its distance away from maritime moist air and its position in the global wind system (Cloudsley-Thompson, 1977). With the exception of Burchell (1822) and a few others, who found much of interest in the Karoo, most travellers and early explorers found the vast plains of the Karoo to be fairly sterile (review by Kokot, 1948), rather than a highly diverse, well-adapted plant and animal assemblage (Werger, 1978, 1985). In comparison with other arid and semi-arid regions in the world, the Karoo has a high diversity of succulent plants (Danin, 1983; MacMahon & Wagner, 1985; Williams & Calaby, 1985; Hilton-Taylor & le Roux, 1989) and a rich reptile fauna, particularly tortoises (Branch, 1988). There is a wealth of potential study material in the Karoo, and there is a real need for basic research on climate, soils, vegetation changes, and plant and animal population dynamics. The Karoo Biome Project (Cowling, 1986) was set up to address this need, but despite the initiative and the theory that has emerged from the programme, ecological patterns and processes in the Karoo are still poorly understood, and there remains much basic research still to be done.

Geomorphology, geology and soils

The geomorphology of the Karoo is characterized by extensive plateaus, mainly at an elevation of 750-1250 m. The range in altitude in quarter-degree squares in the Succulent and Nama-Karoo is shown in **Figure 2.2**. Typically, the central, northern and eastern Nama-Karoo is a region of open plains and low rocky hills, whereas in the southern Succulent Karoo the influence of the Cape folded mountains is clearly seen and the landscape is more angular and geomorphologically complex. "Landscape", as used throughout this dissertation, has been defined by Turner (1989). The term refers to "the landforms of a region in the aggregate or to the land surface and its associated habitats at scales of hectares to many square kilometres" (Turner, 1989). Geomorphological features of the different parts of the Karoo are: (after Visser, 1986)

1. A narrow coastal plain along the west coast covered with Quaternary and Recent sands.

2. In the extreme south and west isolated strips of Karoo vegetation are found amongst the Cape folded mountains. These strips are underlain by Cretaceous and Cenzoic beds of the Nama, Table Mountain, Bokkeveld, Witteberg and Dwyka formations (**Figure 2.3**).

3. The central, northern, eastern and north-eastern parts of the Karoo are on a vast plateau, which consists of Dwyka, Ecca and Beaufort beds (**Figure 2.3**).

4. The north-western part of the Karoo is an inselberg landscape built by formations of the Namaqualand Complex.

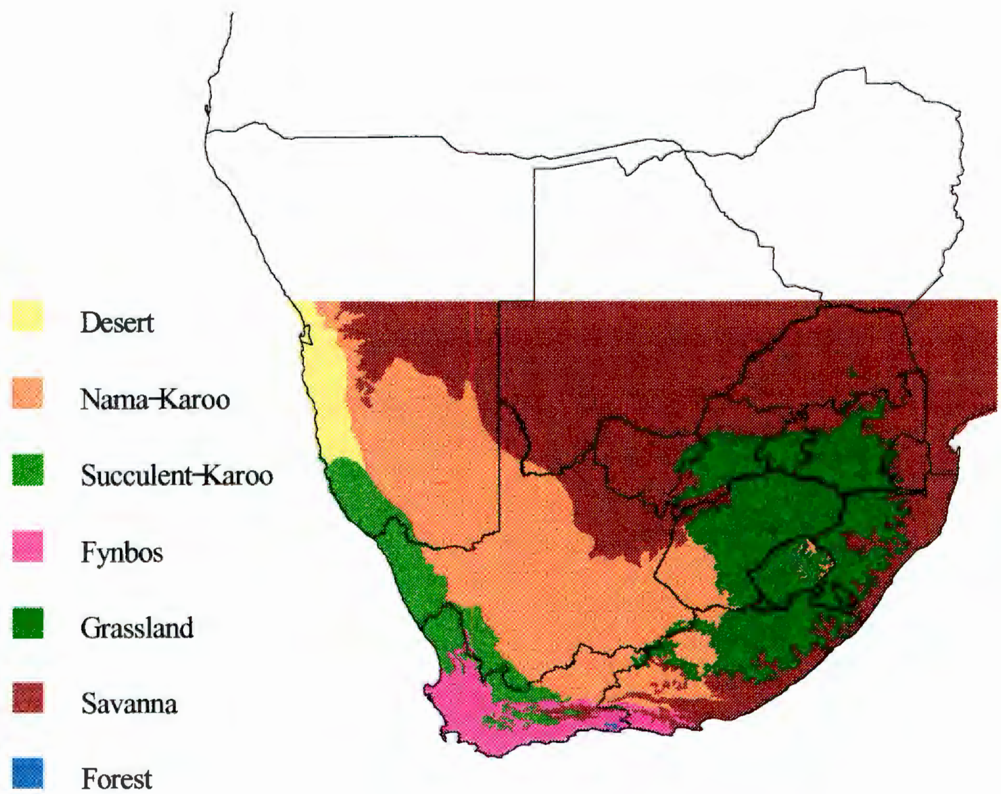

Figure 2.1. Biomes of Southern Africa (from Rutherford & Westfall, 1986).

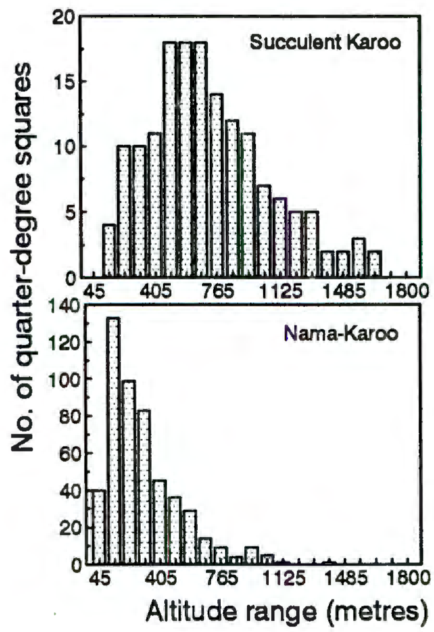

Figure 2.2. The range in altitude in quarter-degree squares in the Succulent and Nama-Karoo.

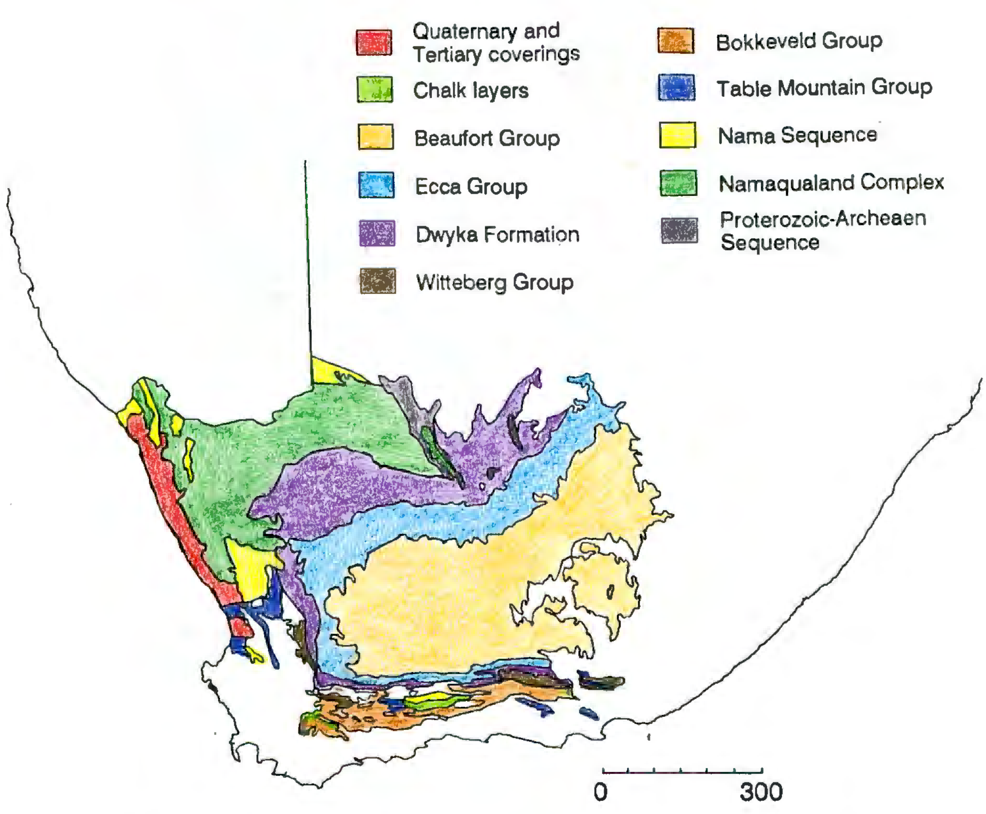

Figure 2.3. A generalized map of the geology of the Karoo (redrawn from Visser, 1986).

Much of the Karoo is constituted mainly from sedimentary rocks of the so-called Karoo sequence (Visser, 1986). The geology of the Karoo is complex (**Figure 2.3**), and the distribution of Karoo vegetation and animals is influenced by the geology, not only through the relationship of the geology to the geomorphology, but also by the influence of the geology on soil colour, soil particle size, soil nutrient status, infiltrability and water retention capacity of the underlying strata.

The greater part of the Karoo is covered by reddish-brown, greyish-brown or yellowish-brown weakly developed shallow calcareous sands and loams, mainly overlying calcrete, with other shallow brown to greyish-brown calcareous soils to the north (von Harmse, 1978). Some bird species (e.g. Karoo Lark *Certhilauda albescens*) show, among the various subspecies, a high degree of correlation between plumage colour and pattern, and soil colour, (Macdonald, 1953).

Climate

General

Three major climatic regions in the Karoo, characterized in terms of rainfall seasonality, have been recognized (Cowling, 1986). Most of the western, central and upper Karoo receives less than 250 mm rainfall annually (**Figure 2.4**). There is a gradient of decreasing rainfall from east to west, and a change in rainfall seasonality at about 22°E from summer in the east, through between-seasons rainfall in a broad transition zone, to winter rainfall in the west (**Figure 2.5**). Along the west coast, dry season precipitation occurs in the form of fog (Cowling, 1986). Fog banks may extend inland at times into Bushmanland (Schulze & McGee, 1978). Winter rain is generally associated with the deep penetration of cyclonic fronts into the interior (Cowling, 1986). Rutherford & Westfall (1986) used climate as the main factor separating the Succulent Karoo from the Nama-Karoo biomes. Mean annual rainfall in the Succulent Karoo is lower but more reliable than mean annual rainfall in the Nama-Karoo (Hoffman & Cowling, 1987) (**Figure 2.6**). Rainfall events in the Nama-Karoo are often highly localized, are variable in the duration and amount of rain that falls in a single event, and vary annually in amount and timing (Venter, Mocke & de Jager, 1986). General patterns and probabilities of rainfall in the Karoo are given by Tyson (1987) and Zucchini, Adamson & McNeill (1992). Prolonged droughts, with the total annual rainfall less than 60% of the long-term mean, are characteristic of many parts of the Karoo (Venter *et al.*, 1986). Wind may be an important ecological driving force in the Karoo, determining flowering and fruiting times for plants, and influencing nest-site selection by birds.

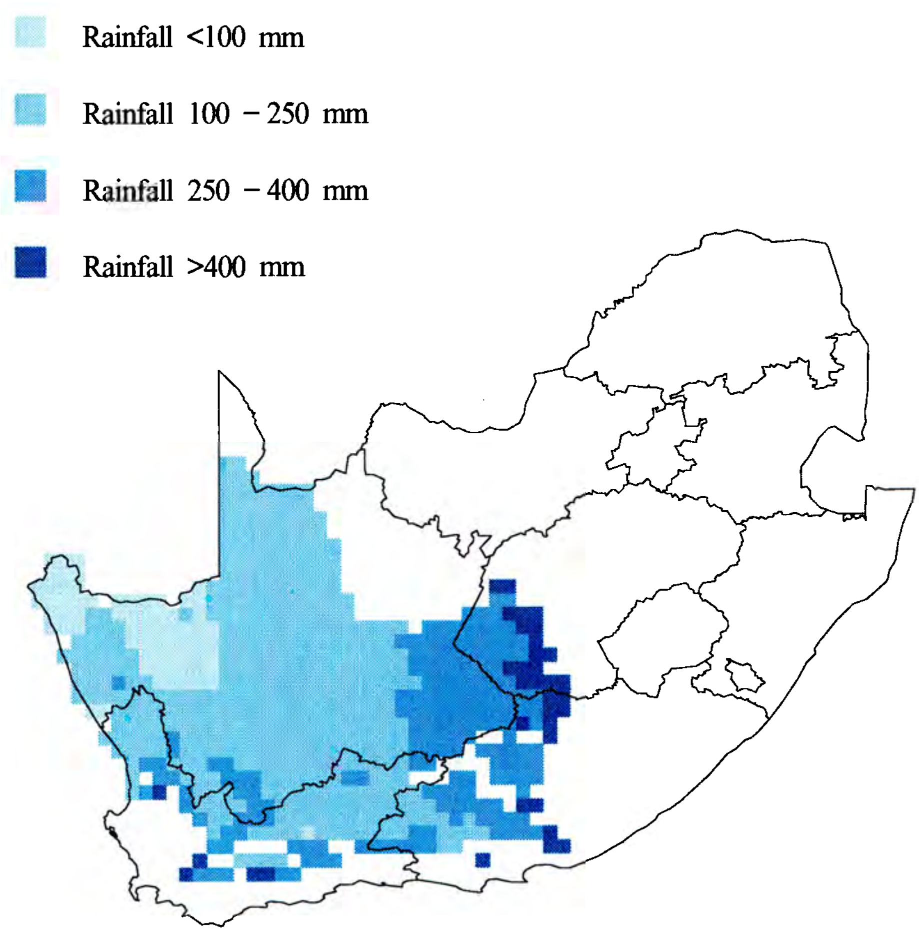

Figure 2.4. Mean annual rainfall in the Succulent Karoo and Nama-Karoo biomes in South Africa.

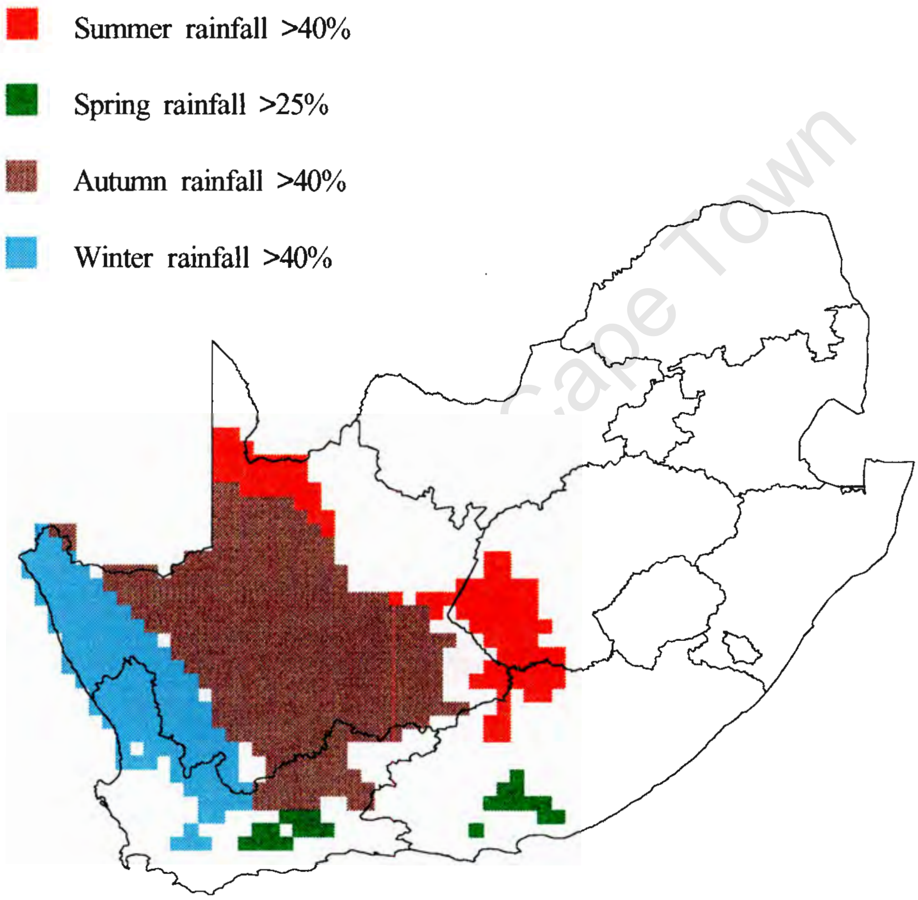

Figure 2.5. Rainfall seasonality in the Succulent Karoo and Nama-Karoo biomes.

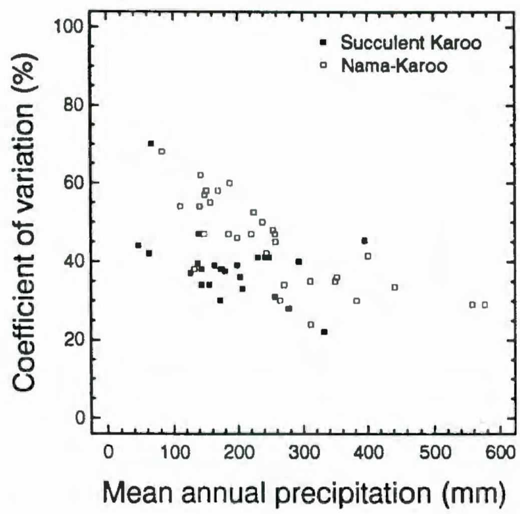

Figure 2.6. The relationship between the coefficients of variation and the mean annual rainfall for some weather stations in the Succulent and Nama-Karoo biomes (from Hoffman & Cowling, 1987).

Rainfall patterns

Data on the daily rainfall for 1988 - 1993 for all weather stations in the Succulent and Nama-Karoo were obtained from the Weather Bureau, Pretoria. There are 118 weather stations in the Succulent Karoo, and 329 weather stations in the Nama-Karoo that report rainfall data. Most weather stations are on the edges of the Karoo, with few stations and quite large gaps in coverage in the north-central and northwestern Nama-Karoo (**Figure 2.7, 2.8** and **2.9**). These figures show the total rainfall for January, April, July and October, for 1988, 1990 and 1993 respectively. These years were selected randomly. The amounts and areas in which rainfall was recorded differs markedly in all years, but the maps do show some significant patterns in the rainfall. These are: (1) that rain in January (summer rain) may be widespread across the Karoo; (2) that rain in April is widespread throughout summer, between-seasons and winter rainfall areas, and may be fairly dependable; and, (3) that rainfall is patchy on temporal and spatial scales, more so in the central Nama-Karoo than elsewhere in the Karoo.

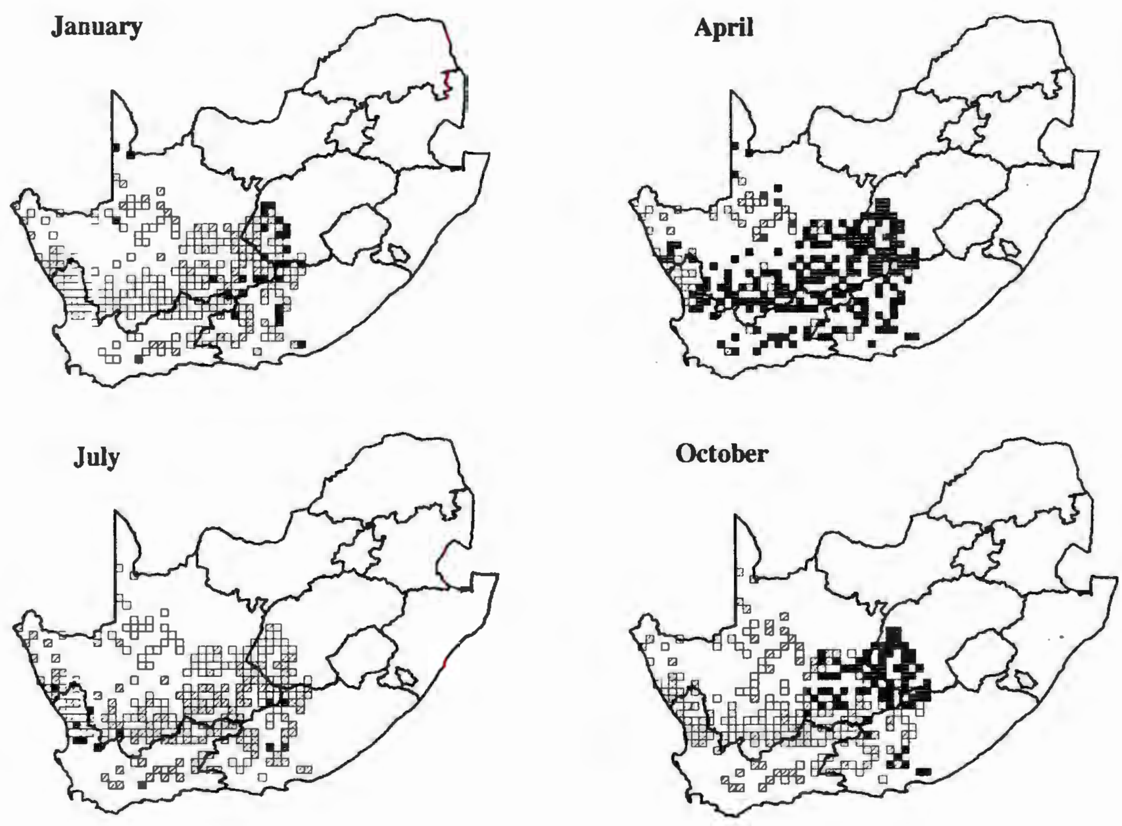

Figure 2.7. The rainfall recorded at weather stations throughout the Succulent and Nama-Karoo during 1988. Quarter-degree squares in which weather stations are situated are outlined. Open squares indicate stations that did not record any rain for the month, stippled squares received less than 20 mm of rainfall for the month, and solid black squares received more than 20 mm.

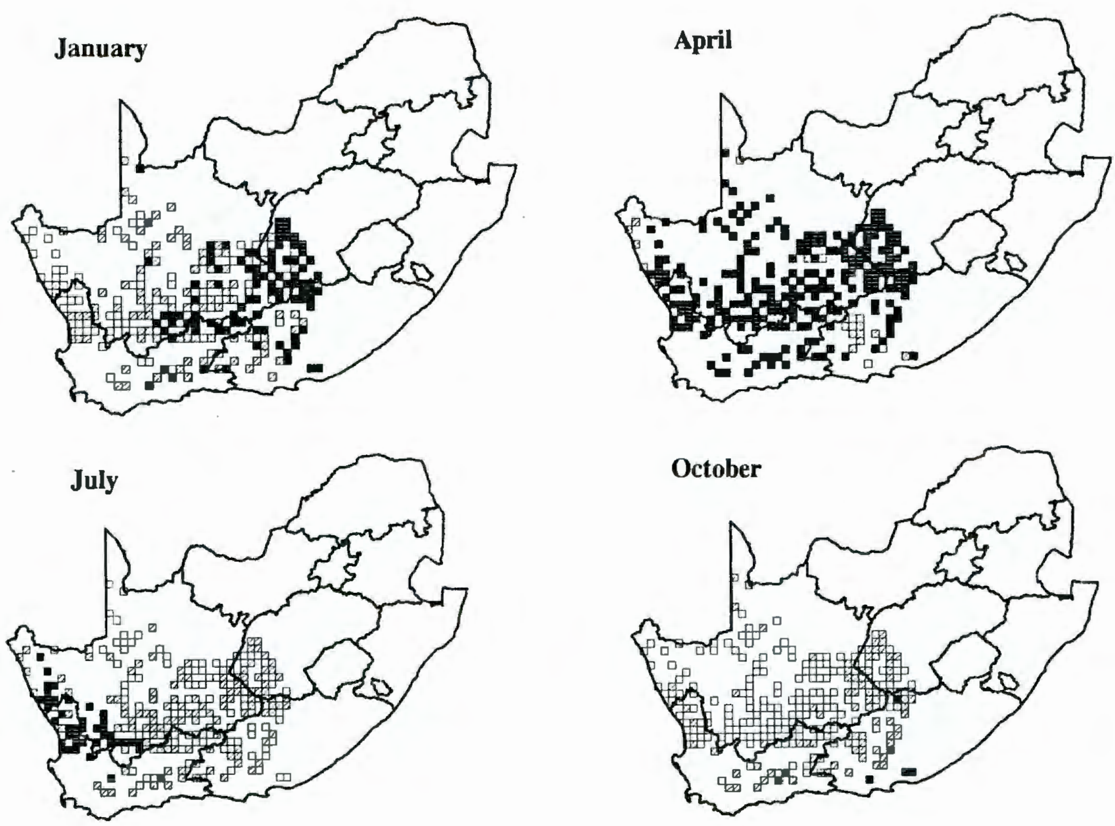

Figure 2.8. The rainfall recorded at weather stations throughout the Succulent and Nama-Karoo during 1990. Open squares indicate stations that did not record any rain for the month, stippled squares received less than 20 mm of rainfall for the month, and solid black squares received more than 20 mm.

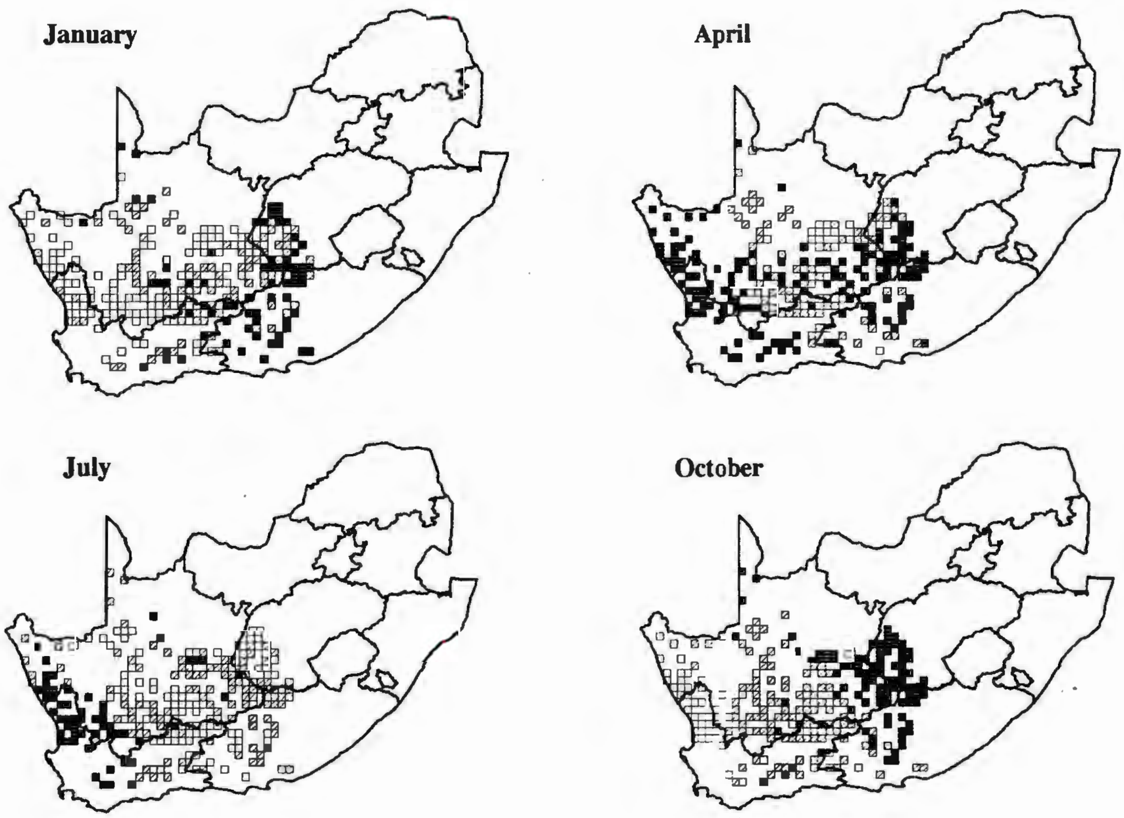

Figure 2.9. The rainfall recorded at weather stations throughout the Succulent and Nama-Karoo during 1993. Open squares indicate stations that did not record any rain for the month, stippled squares received less than 20 mm of rainfall for the month, and solid black squares received more than 20 mm.

Patchiness in rainfall is particularly marked in the central Nama-Karoo. Monthly rainfall totals for 1993 for adjacent stations in two degree squares, 3020 and 3121, in the central Nama-Karoo are shown in **Figures 2.10** and **2.11.** The rainfall shows considerable variation in amount and timing between stations, and even between stations in close proximity in the same month **(Figure 2.11)**, although the general pattern of rainfall is similar.

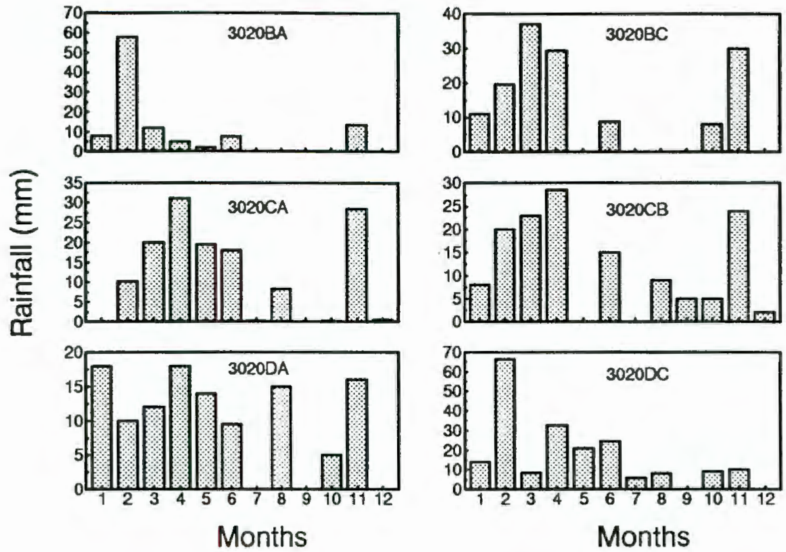

Figure 2.10. Monthly rainfall totals for 1993 for weather stations situated in the degree square 3020. The weather stations are: Bastiaanskolk (3020BA), Kraandraai (3020BC), Kans (3020CA), Enkeldoorn (3020CB), Retseh (3020DA) and Bleskrans (3020DC).

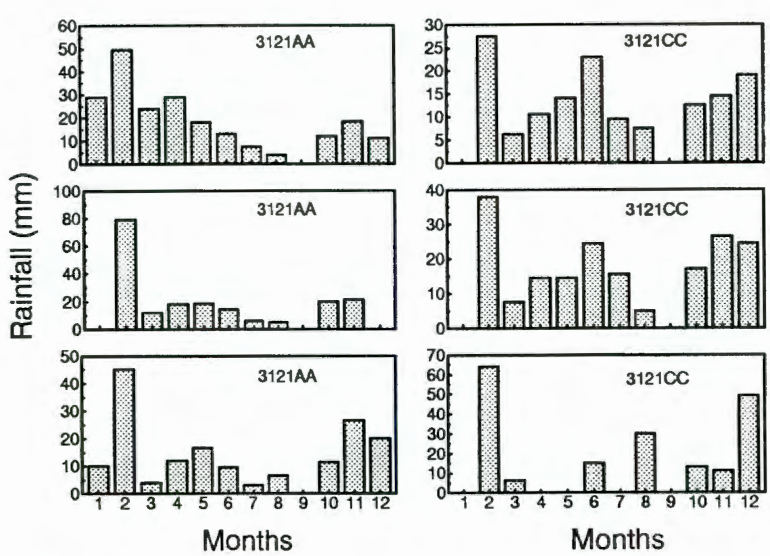

Figure 2.11. Monthly rainfall totals for 1993 for weather stations situated in the quarter-degree squares 3121AA and 3121CC. Weather stations are: Breekyster, Sandtuin and Grootfontein (3121AA), Sonop, Ploegfontein and Vondeling (3121CC).

Rainfall in the Succulent Karoo, however, is less variable between stations in the same month, although it may differ in amount (**Figure 2.12**). Rainfall in the eastern Nama-Karoo, generally a summer rainfall area, has a less erratic pattern (**Figure 2.13**), although there is some variation between amounts recorded at weather stations in close proximity (**Figure 2.14**).

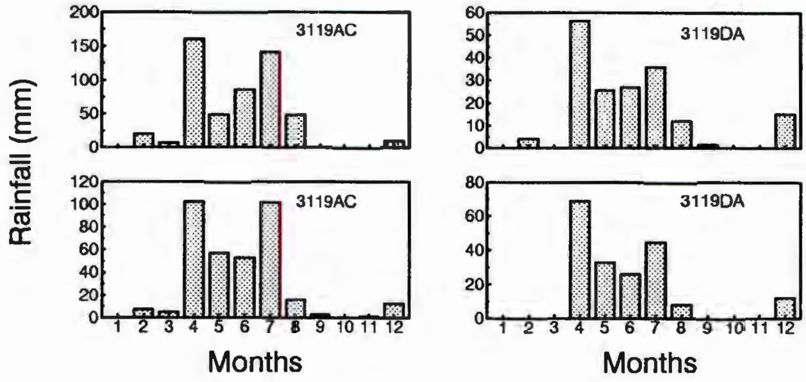

Figure 2.12. Monthly rainfall totals for 1993 for weather stations situated in quarter-degree squares 3119AC and 3119DA. Weather stations are: Cloudskraal and Niewoudtville (3119AC), Doega and Platberg (3119DA).

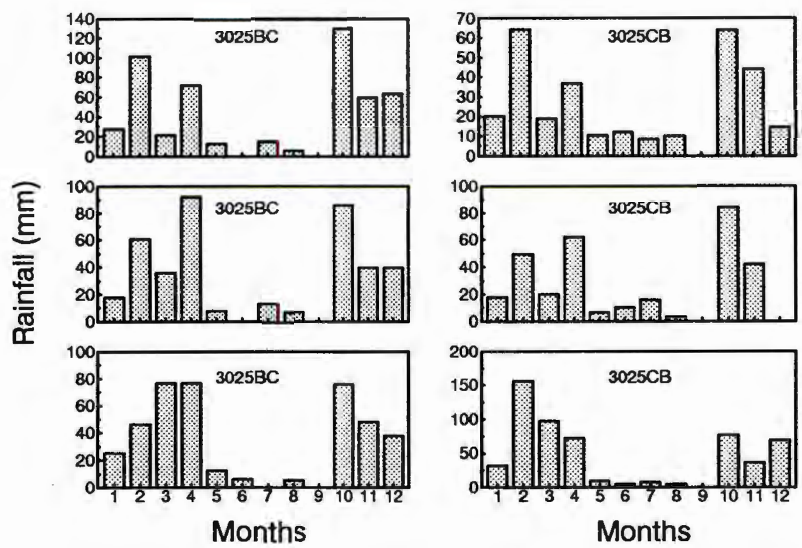

Figure 2.13. Monthly rainfall totals for 1993 for weather stations situated in the quarter-degree squares 3025BC and 3025CB.. Weather stations are: Oranje, Klipbanksfontein and Springfontein (3025BC), Agtertang, Tweefontein and Norvalspont (3025CB).

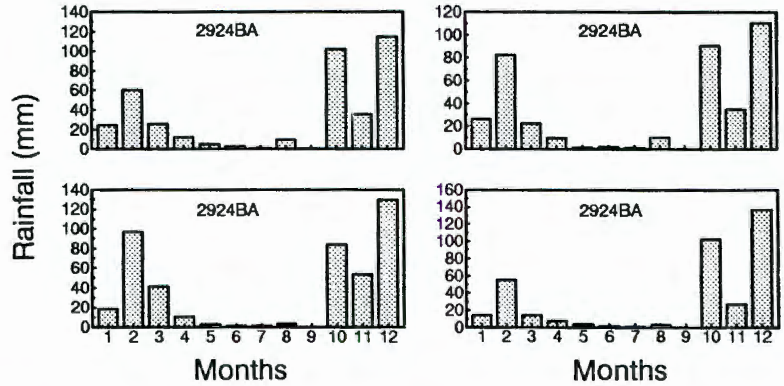

Figure 2.14. Monthly rainfall totals for 1993 for weather stations situated in the quarter-degree square 2924BA. Weather stations are: Holpan, Klipfontein, Klokfontein and Rietrivier.

Temperature

Temperatures throughout the Succulent and Nama-Karoo are extreme, with a wide daily and seasonal range. There is a high frequency of days with a maximum temperature exceeding 30° C in the northern Nama-Karoo, and a high frequency of days with a minimum below 0° C in the central Nama-Karoo (Venter *et al.*, 1986). Minimum temperatures in the Succulent Karoo are significantly higher than the Nama-Karoo (Cowling *et al.*, 1994).

The influence of temperature on the distribution patterns of birds in southern Africa is largely unknown. Rowan (1967) suggested that the distribution of the Speckled Mousebird *Colius striatus* appeared to be limited by the July mean minimum isotherm for 20° F (*ca* -5° C). However, in a later publication, Rowan (1971) suggested that temperature *per se* was unlikely to be the sole factor limiting distribution in several other bird species.

Vegetation

The vegetation of the Succulent Karoo biome is dominated by evergreen and drought-deciduous dwarf shrublands, often with a large succulent component (Werger, 1978, 1985). Deciduous and evergreen trees and thickets are present along drainage lines, and sparse bush clumps, taller than the surrounding vegetation, develop on termite mounds and nutrient-rich soil patches (known throughout the southern and western

Karoo as *heuweltjies*; see Lovegrove & Siegfried, 1989; Midgley & Musil, 1990; Milton & Dean, 1990a). In the northern and eastern parts of the Nama-Karoo biome, grasses are common, usually as patches along drainage lines within the dwarf shrublands, or as open steppe grassland on sands (Werger, 1978). Extensive grassy plains on fine gravels and sands occur in the north-central and north-western parts of the Nama-Karoo in Bushmanland. The grassiness of the eastern Nama-Karoo is ephemeral and is driven strongly by summer rainfall (Hoffman, Barr & Cowling, 1990) so that grassy habitats available for birds are patchy and unpredictable in occurrence. Dwarf shrublands in the northern and eastern Karoo generally have a larger component of narrow-leaved species and fewer succulents. In the south-east the Karoo merges into subtropical thicket, in the north-east into grasslands and in the north into open arid savanna on sands and calcretes. The transition zone in the north is particularly poorly defined, and patches of karroid vegetation are interspersed with patches of typical arid savanna vegetation along the southern edge of the transition. Similarly, karroid vegetation merges, without a clear edge, into subtropical thicket in the southeastern Nama-Karoo. Subtropical thicket was considered to be "Karoo" vegetation types by Acocks (1953) (Veld Types 23 and 24), but the avifauna of sub-tropical thicket apparently includes both forest and typical savanna bird species (Skead, 1967), as well as typical Karoo bird species. Subtropical thicket has not been included as a Karoo vegetation type in the present study.

Avian habitats

Terrestrial habitats

Acocks (1953) described 28 Karoo and "False Karoo" veld types, and these, with a few exceptions, were used by Winterbottom & Skead (1962), Winterbottom (1968a) and Vernon (1986) to define bird habitats in the Karoo. However, Acocks (1953) separated structurally-similar plant assemblages because of differences in plant species composition. The conventional wisdom is that no birds are confined to only one of Acocks' Veld Types in the Karoo, but Vernon (1986), using his own and data from Winterbottom (1968a), showed that most southern African endemic bird species in the Karoo are more frequently recorded in some of Acocks' Veld Types than in others. On a broad scale, Dean & Hockey (1989) related the distribution of larks (Alaudidae) to vegetation patterns in the Karoo. Recently, on the basis of bird distribution patterns, Allan *et al.* (unpublished MS) proposed that the Karoo should be divided into the Succulent Karoo, the Nama-Karoo and the Grassy Karoo. This division, however, may still be too simplistic, as the "Succulent Karoo" actually consists of a diversity of plant assemblages (Milton *et al.*, in press) and a diversity of bird habitats ranging from sparse succulent vegetation on gravel plains to tall succulent and woody vegetation on sands and silts.

It is evident that the fine scale relationship between bird distribution and plant assemblages in the Karoo requires further investigation. However, the distribution of birds in the Karoo is unlikely to be determined only by plant assemblages, and the geology, geomorphology, rainfall and rainfall seasonality appear to strongly influence bird distributions in the Karoo. The complex geomorphology has a strong influence on the local distribution of habitats in parts of the Karoo. For example, the strong east-west ridging of the Cape folded mountains influences the adjacent Dwyka tillite, Ecca and Beaufort shales, which in turn are strongly ridged, providing almost continuous bands of habitats across the southern Karoo as far north as the foot of the Nuweveldberge. More localized examples are found along the southern edge of the Nama-Karoo, at the interface with the Succulent Karoo, where folding by the tectonic movement of the strata has interspersed quartzites, shales and tillite. In this area, arid fynbos vegetation occurs on high ridges, interspersed with Karoo succulent vegetation in deep valleys. The birds show similar broken distribution patterns, with typical fynbos bird species (Cape Rockjumper *Chaetops frenatus*, Cape Sugarbird *Promerops cafer*, Orangebreasted Sunbird *Nectarinia violacea*) interspersed in patches of habitat between typical Karoo species such as Layard's Titbabbler *Parisoma layardi* and Rufouseared Warbler *Malcorus pectoralis*.

In the central and upper Karoo, dolerite intrusions and basement inselbergs tend to isolate islands of succulent and woody shrubs, surrounded by grassland on gravel or sandy plains. Or, conversely, where dolerite sands have settled in bottomlands, to isolate patches of grassland surrounded by shrubland. Species richness and amount of cover of grasses also seems to be an important determinant of avifaunal species richness in any area of the Nama-Karoo. Many species occur in more than one habitat, and some species (e.g. Cape Sparrow *Passer melanurus*, Pale Chanting Goshawk *Melierax canorus* and Yellow Canary *Serinus flaviventris*) apparently occur in all Karoo habitats. A list of avian habitats in the Succulent and Nama-Karoo is given in **Table 2.1**.

Table 2.1
Type and height of vegetation of avian habitats in the Succulent and Nama-Karoo.

Habitat type	Height (cm)
1. Arid, open dwarf succulent shrubland	5-20
2. Semi-arid, open dwarf shrubland	20-50
3. Semi-arid, tall closed shrubland	50-80
4. Semi-arid, non-succulent, grassy shrubland	30-60
5. Semi-arid, open grassy shrubland	30-80
6. Arid grassland	50-150
7. Arid and semi-arid drainage line woodlands	2-10 m

Terrestrial habitats for birds may be briefly described as follows:

1. **Figure 2.15.** Arid, open succulent dwarf shrubland, 5-20 cm in height, on shales, quartz gravels and limestones, cover fairly low (5-15%), with bare patches between plants, dominated by stemless, mat-forming Mesembryanthemaceae, with annual grasses and forbs appearing after rains. Nutrient-rich patches over termite nests (*heuweltjies*) occur throughout the area. This habitat type is mainly in the western Karoo. The climate is arid, and mean annual precipitation is low (< 125 mm) and falls in winter.

Figure 2.15. Arid, open succulent dwarf shrubland (1) 150 km north of Ceres, in the western Succulent Karoo (Tankwa Karoo), July 1994.

2. Semi-arid, open shrublands, 20-50 cm in height, including dwarf shrublands on plains (**Figure 2.16**) and taller vegetation on ridges (**Figure 2.17**). with variable amounts of succulents present and taller woody vegetation along drainage lines and well-drained patches on tillites, quartzites, shales, stony soils, clays and sands. The cover is fairly sparse (about 10-30%), and there are bare patches between plants (**Figure 2.16**). Vegetation on the ridges and tilted shales may be taller and more grassy than on the plains (**Figure 2.17**). *Heuweltjies* are common in the southern and western areas. The climate is semi-arid to arid in places, and the between-seasons rainfall averages 150-250 mm p.a. This is the habitat type that covers a large part of the southern and central Karoo. On the central plateau, particularly in the west, the shrubland is low and homogeneous, with very few emergent bushes or trees. Grasses, mainly *Stipagrostis ciliata*, occur in patches where there are dolerite outcrops and sandy soils.

Figure 2.16. Open dwarf shrubland (2) with few succulents on shales near Fraserburg, south-central Nama-Karoo, March 1994.

Figure 2.17. Taller, more dense vegetation (2) up to 2 m in height on a ridge south of Beaufort West, southern Nama-Karoo. The woody shrub is *Rhigozum obovatum*, October 1986.

3. Semi-arid, tall closed shrubland, 50-80 cm in height, on shales and sandy soils, with tall or bush-forming succulents, mainly Aizoaceae (Mesembryanthemaceae) and *Euphorbia* spp., but with a number of woody shrubs such as *Salsola* spp., *Pteronia* spp. and *Osteospermum* spp. also common (**Figure 2.18**). The cover is fairly dense (30-60%) and there are few grasses. Nutrient-rich patches (*heuweltjies*) are common and are important in increasing habitat heterogeneity in these shrublands, as are patches of renoster (*Elytropappus rhinocerotis*) shrubland. The climate is semi-arid and rainfall averages 250-300 mm p.a., and varies from between-seasons in the east to winter rainfall in the west. This is the type of habitat mostly encountered in the southern Succulent Karoo, from about Oudtshoorn west to Worcester.

Figure 2.18. Tall, closed shrubland (3) on sandy soils, with *Othonna* sp., *Nylandtia spinosa* and *Elytropappus rhinocerotis*. Near Touwsrivier, in the southern Succulent to Nama-Karoo transition, July 1994.

4. Semi-arid, dwarf, non-succulent, grassy shrublands, 30-60 cm in height, dominated by narrow-leaved species, with few succulents and many grasses, and taller woody vegetation along drainage lines; on shales, stony soils, fine-grained sandstones, granite gravels, sands and calcretes, occasionally on silts and floodplains (**Figure 2.19**). The cover is generally fairly high, (40-60%). This is the habitat type in the eastern and northeastern Karoo. From about Oudtshoorn east, taller sub-tropical thicket elements, such as *Pappea capensis*, *Euclea undulata*, *Carissa haematocarpa*, *Rhus longispina*, *R. undulata* and *Scotia afra* occur on hillsides or in patches along drainage lines and are really important here in increasing habitat heterogeneity. In the eastern Karoo this habitat type merges into grasslands and fairly dense sub-tropical thicket, and in the northeast into grasslands. The climate is semi-arid and rainfall averages 250-400 mm, and falls mainly in summer.

Figure 2.19. Non-succulent, grassy dwarf shrubland (4) with scattered trees and emergent grasses above *Pentzia incana* shrubs. Baroe, about 30 km east of Steytlerville, April 1994.

5. Open grassy shrublands, 30-80 cm in height, with large bare stony patches (**Figure 2.20**), tall woody shrubs and many grasses (**Figure 2.21**), on poorly drained silts and shallow sands or gravels overlying calcrete. The cover is generally fairly sparse (1-30%) but, particularly in the case of annual grasses, increases markedly after rains (up to 80% in a high rainfall year) (**Figure 2.22**). The climate is generally arid, and annual rainfall averages 150-200 mm p.a. Rainfall is aseasonal and patchy, with both heavy summer rains and light winter rains. This is the habitat type that covers most of the north-central Nama-Karoo, and is most prevalent in the area around Brandvlei.

Figure 2.20. Open, grassy shrubland on stony plains (5). Northwest of Brandvlei, north-central Nama-Karoo, March 1994.

Figure 2.21. Open, grassy, shrubland (5) on dolerite sands, south of Williston, central Nama-Karoo, March 1994.

Figure 2.22. Open, grassy shrubland on granite sands overlying calcretes (5), with a fairly dense cover of *Stipagrostis ciliata* after good rains in May 1988. The shrubs are *Rhigozum trichotomum* and *Lycium* sp. Near Brandvlei, north-central Nama-Karoo.

6. **Figures 2.23 and 2.24.** Arid grassland on granite gravel plains, sand plains or dunes. There are few woody shrubs and the grasses, usually 50-150 cm in height, range from short *Stipagrostis obtusa* to tall *S. ciliata*. Annual forbs are abundant among the grasses in years of high rainfall. There is a marked difference in cover between high and low rainfall periods, and cover can increase from 20% to 80% fairly rapidly. The rainfall is patchy and low (< 150 mm) and variable in timing, though it usually falls in autumn and spring. This is the habitat type that covers most of Bushmanland in the northwestern Karoo.

Figure 2.23. Arid open *Stipagrostis ciliata* grassland (6) on red sands. Aggeneys, northwestern Nama-Karoo, March 1994, following good rains.

Figure 2.24. Arid, open *Stipagrostis ciliata* grassland on sands, with a granite inselberg in the background. Brakputs, northwestern Nama-Karoo, May 1988, during a dry period.

7. Drainage line woodlands, and thicket woodlands, up to 10 m in height (averaging about 5 m), usually dominated by *Acacia karroo*, on poorly drained plains or basins, on silts and clays, and found in various forms in all other habitat types (**Figure 2.25**). The cover in these drainage line woodlands is usually fairly dense (60-100%). In the southern Succulent Karoo, in frost-free sites (e.g. Meiringspoort) this may develop into low diversity gallery forest with such species as *Ilex mitis*, *Cunonia capensis* and *Kiggelaria africana* present. In the southern and western Karoo, drainage line vegetation dominated by fairly dense *Tamarix usneoides* thickets and woodlands is occasionally present on sands.

Figure 2.25. Extensive drainage line woodland (mostly *Acacia karroo*) below the escarpment south of Fraserburg, south-central Nama-Karoo, March 1994.

Aquatic habitats

Inland water ecosystem types in South Africa are described by Noble & Hemens (1978). Most wetland areas in the Karoo are ephemeral river systems, which may flow for no more than 24 hours in an entire rainy season, or shallow endorheic saline pans, or areas of impeded drainage which often cover a large area. The Nama-Karoo probably has fewer large man-made impoundments than the Succulent Karoo (where the rainfall is generally lower but less variable: see **Figure 2.5**), and small reservoirs and dams are common in both biomes, often providing sufficient water area to support broods of

Egyptian Goose *Alopochen aegyptiacus* or South African Shelduck *Tadorna cana*. Sewage treatment ponds appear to be important for waterbirds in arid areas. Aquatic habitats in the Succulent and Nama-Karoo may be broadly classified as:

1. Ephemeral ponds and pans that form quickly after rains and may cover large areas, sometimes flooding perennial woody shrubs (**Figure 2.26**). The pans are usually sodic and support a large biomass of annual halophytic vegetation. This type of pan is more frequently found in the central and northeastern Nama-Karoo.

Figure 2.26. Ephemeral pan in dwarf shrubland on stony plains north of Brandvlei, north-central Nama-Karoo. February 1989.

2. Perennial streams and man-made impoundments with aquatic vegetation such as *Phragmites* and *Typha* sp., and thickets of water tolerant forbs such as *Epilobium* and *Conyza* spp. Perennial streams are restricted mainly to the Succulent Karoo.

Acocks (1976) concluded that the vegetation along perennial streams in South African semi-arid areas is similar regardless of veld type. However, differences in underlying geology and the local geomorphology may give rise to differences in soil type and vegetation, and this in turn can affect the species richness and numbers of birds in drainage lines (see, for example, Brooke, 1992). The river terraces and alluvial flood plains of the larger rivers in the southern Karoo that flow frequently or carry water underground have almost all been ploughed and planted, mostly in the late 1800s and early 1900s (Macdonald, 1989). Many of these old lands have now been abandoned, but few of them have been recolonized by the original plant and animal species (Dean & Milton, in press). Bird species assemblages along the larger rivers have possibly also changed as a result. The effects of the invasion of some of the river systems by alien *Prosopis* spp. (Stoltz & Zimmerman, 1994) and *Tamarix ramosissima* (R. K. Brooke, *in litt.*) is largely unknown, but is thought to adversely affect bird species richness by habitat modification.

Part 2: Land-use in the Karoo

Introduction

Southern Africa has a great diversity of climate, topography and soils, giving rise to a diversity of agricultural activities throughout the region (Schoeman & Scotney, 1987). Various agricultural activities, particularly crop farming, have the potential to transform, sometimes irreversibly, natural rangelands and other habitats (Macdonald, 1989). Surface and underground mining are also potential disturbances on a landscape scale. In a conservation context, where potential protected areas are being planned, and particularly if the objective of the investigation is the identification of potential protected areas, it is important to know which parts of the country (a) have high dryland agricultural production potential, (b) are important areas for the production of animal products without drought subsidies, and, (c) are being mined or that contain as yet unexploited deposits of economically viable minerals that are likely to be mined in the future.

Information on various land-use activities in the Karoo is presented here. Rangelands in the region are mainly used for forage for small domestic livestock, and the impacts of grazing on the rangelands and on the avifauna are discussed more fully in Chapters 7 and 8. The term "grazing", which means specifically "eating grass" has been used throughout this dissertation to denote the feeding activity of various herbivores in karroid shrublands. Much of this feeding activity is, strictly speaking, "browsing", since it refers to the removal of foliage from forbs, shrubs and trees.

The various agricultural and other activities carried out over a region as vast as the Karoo, cannot, for a variety of reasons, be documented in detail in a study such as this. However, it is possible to identify, on a broad scale, the relative density of domestic livestock, the areas that have high dryland agricultural potential and the areas that are being mined or may be mined in the future.

The database and sources of data on land-use

Agriculture

Assembling a database on agricultural activities was a difficult task. For the purposes of management and extension services, the Karoo *sensu lato* is divided into three or more regions by the Department of Agriculture (Anon, 1986). The eastern, northeastern and southwestern edges of the Karoo are covered by largely "non-Karoo" agricultural regions. It was not possible to obtain land-use data directly from the various regional head offices of the Department of Agriculture, so information on land-use was extracted from the various regional agricultural development programme publications (*Landbou-ontwikkelingsprogramme*: Anon, 1985a, 1985b, 1986). In some cases this information was available at a quarter-degree scale, while in other cases it was available only for specific "extension areas" (*voorligtingswyke*) within the agriculture region, or available only for "farming areas" (*boerderygebiede*) within the extension area. The three development programme reports that were used to extract information further differed in the way that the information was presented and in the quality, accuracy and type of information, so that it was extremely difficult to extract accurate data on land-use for the whole Karoo. Furthermore, the boundaries of the agricultural regions are political, not natural, so two of the agricultural regions cover parts of both the Succulent and Nama-Karoo. Nevertheless, a database on land-use was compiled that provides an indication of the major land-use in any particular district. This database, coupled with the data on stocking rates, extracted from Dean & Macdonald (1994), and the information on dryland agricultural potential and erodibility of soils presented by Schoeman & Scotney (1987), was also be used to assess the agricultural potential of an area. Information on stocking rates is given as the number of Large Stock Units (LSU) per 100 ha, one LSU being equivalent to one bovid weighing 420 kg (see Dean & Macdonald, 1994).

An ARC/INFO coverage giving the median annual primary production over southern Africa, compiled by the Department of Agricultural Engineering, University of Natal, Pietermaritzburg, (see Schulze *et al.*, 1990) was also used as an overlay on the land-use coverage to identify areas of low primary production.

Mining

Information on mining (mines in production) and the localities of kimberlite pipes and salt extraction works was extracted from the geological map of South Africa (Government Printer, Pretoria). This information, although accurately located on the geological map, was only mapped at a quarter-degree scale on the Karoo land-use map, so the impression given by the map is that mining is far more extensive than it actually is. The presence of economically viable deposits of minerals is particularly difficult to map without access to detailed geological survey data, and in any case much of the information regarding the localities of minerals is confidential. The information on mining that is presented here, with the exception of the kimberlite pipes, does not include many unworked deposits.

Land-use in the Karoo

Pastoral farming

In common with other semi-arid shrublands in the world, the Karoo is used mainly as grazing for small domestic livestock, and the region is an important source of fine wool, mohair and mutton (Anon, 1985a, 1985b, 1986). The distribution of the most common breeds of domestic livestock (Merino sheep, Dorper sheep and Angora goats, in numbers of animals in 640 km^2 blocks), in the Succulent and Nama-Karoo is shown in **Figures 2.27, 2.28 and 2.29.** Currently, wool sheep and Angora goats are the most common small livestock in the southern and eastern Karoo, and mutton sheep, Karakul sheep and Boer goats more frequent in the northern and north-western Karoo.

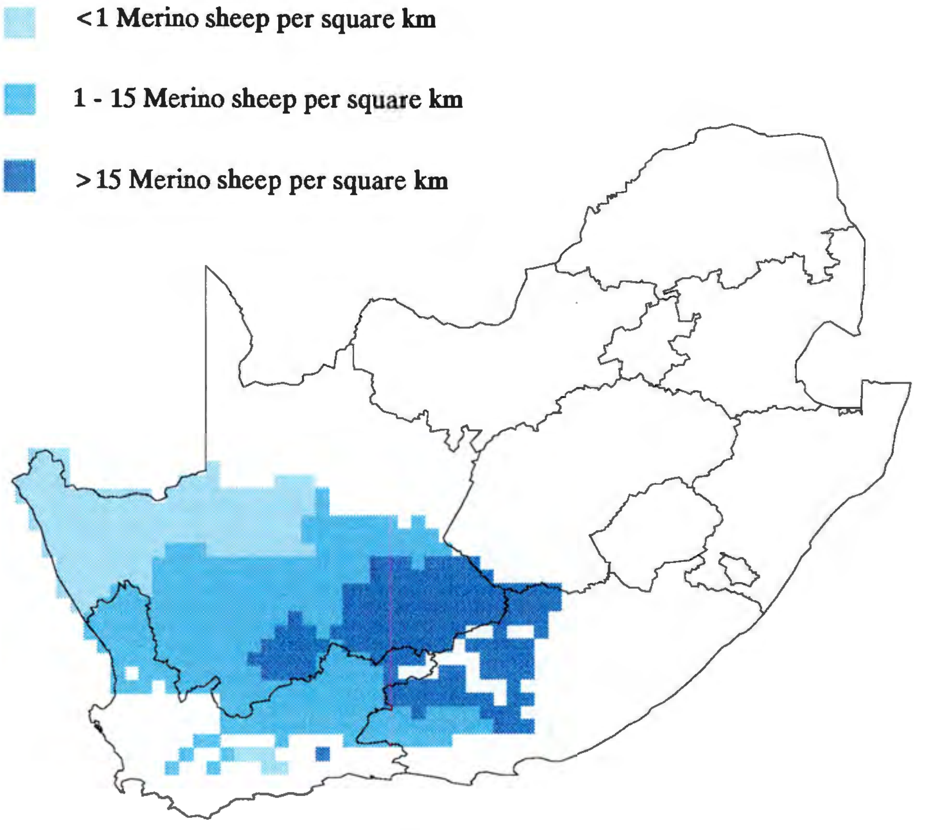

Figure 2.27. The distribution of Merino sheep in the Succulent and Nama-Karoo, shown as the number of sheep per square km in each quarter-degree square.

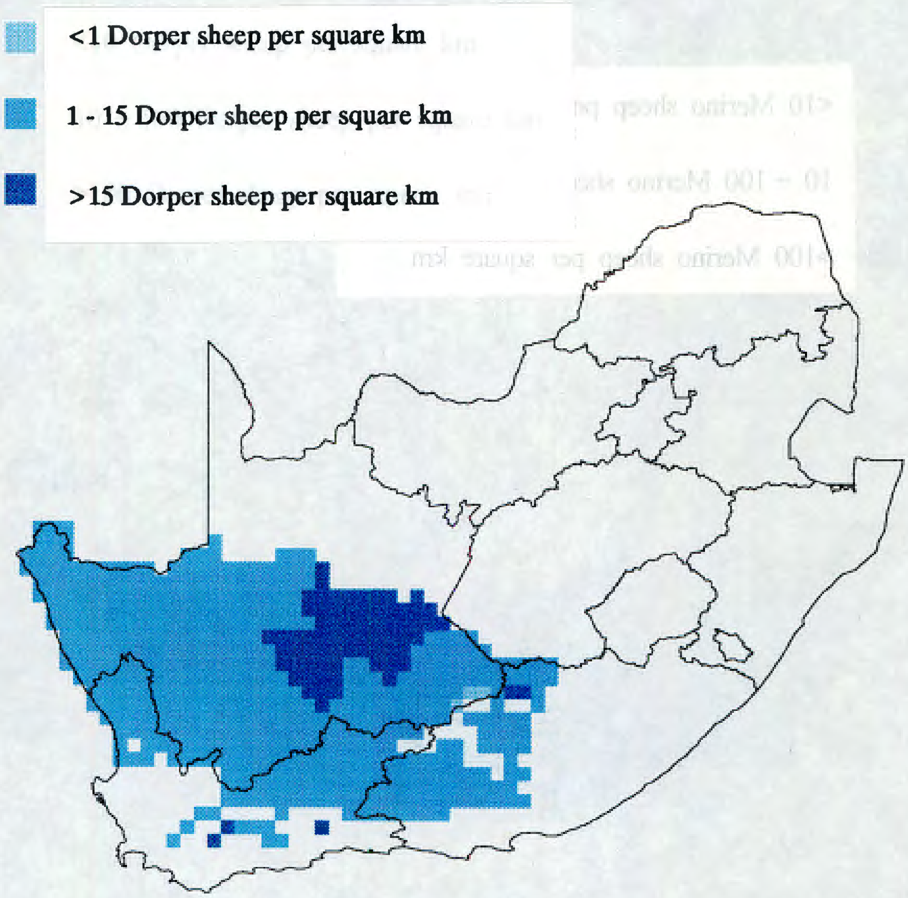

Figure 2.28. The distribution of Dorper sheep in the Succulent and Nama-Karoo, shown as the number of sheep per square km in each quarter-degree square.

Ostrich (*Struthio camelus*) farming is common in the eastern Succulent Karoo (the "Little" Karoo) from about Uniondale to Ladismith and is currently increasing in geographical area and number of birds (Anon, 1991; Claassen, 1991; Milton, Dean & Siegfried, 1994; Dean *et al.*, 1994). Ostriches are often the major farm animal in the Little Karoo but are usually kept in feed-lots rather than out on open rangelands. Cattle are ranched in the Karoo, but are relatively unimportant in the Succulent Karoo (except as dairy herds, usually on feedlots or planted pastures) and the arid western,

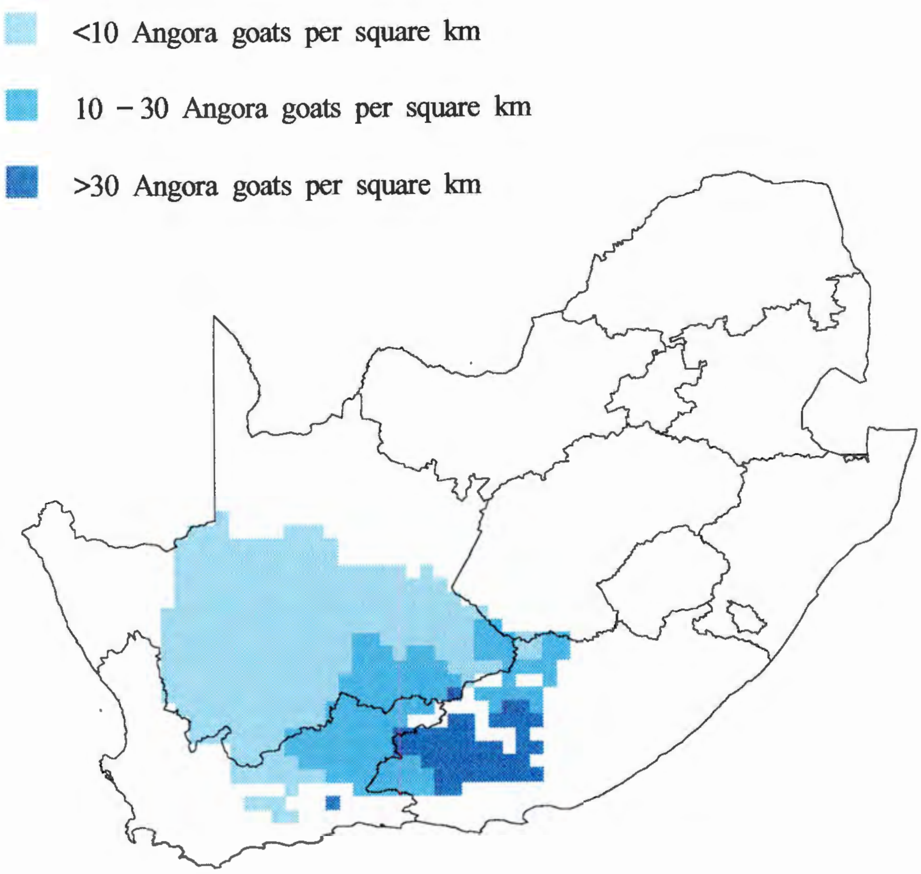

Figure 2.29. The distribution of Angora goats in the Succulent and Nama-Karoo, shown as the number of goats per square km in each quarter-degree square.

central and northern Nama-Karoo. The effects of grazing by domestic livestock and the state of rangelands in the Karoo is discussed further in Chapter 8.

Crop farming
At least 1920 km^2 (0.5%) of the Succulent and Nama-Karoo is currently cultivated, although only 200 km^2 is actually suitable for dryland crop production (Schoeman & Scotney, 1987). The Karoo *sensu lato* has low potential for dryland agriculture (**Figure 2.30**). Similarly, the potential for irrigated agriculture is low, given that water in the Nama-Karoo is available for irrigation only along the few major river systems.

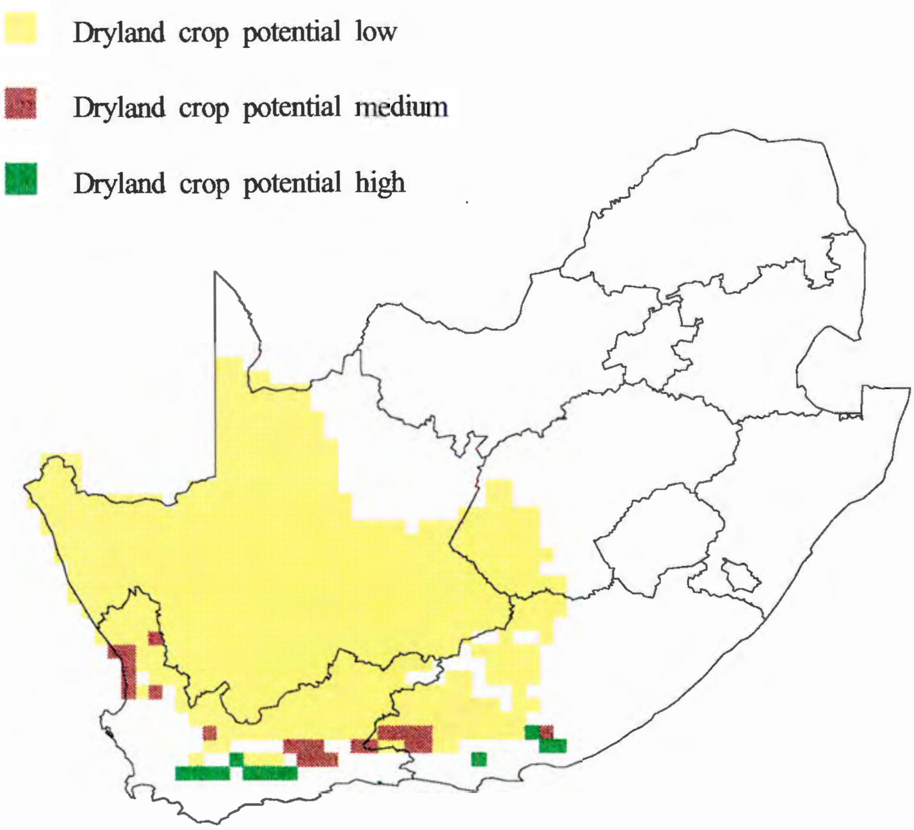

Figure 2.30. The potential for dryland agriculture in the Succulent and Nama-Karoo (from Schoeman & Scotney, 1987).

Nevertheless, 1410 km^2 is currently under irrigation in the Karoo *sensu lato*, with only 730 km^2 under regular irrigation (Macdonald, 1989). It is only along the Orange River in the northern and northwestern Karoo, at scattered localities in the western and southern Succulent Karoo, and in the eastern Karoo that irrigated agriculture is a major part of farm incomes (Anon, 1985a, 1985b, 1986). Irrigation schemes, such as the Sakrivier (Sak River, Williston-Calvinia), Oubaaskraal (Tankwa River, Calvinia), Gamka (Gamka River, Laingsburg) and Smartt (Ongers River, Britstown) have allowed irrigated agriculture to develop in the more arid parts of the central Karoo, but collectively these schemes only cover an area of 7500 ha (Anon, 1986).

There is extensive crop farming in parts of the Succulent Karoo, particularly where there are perennial rivers, and mostly on the fine soils of the interface between the Fynbos and Succulent Karoo biomes. The vegetation on bottomland soils in some places has been almost totally transformed, and landscapes are considerably fragmented as a result (**Figure 2.31**). The major impact of crop farming on the biota in the more arid Karoo, however, seems not to be from current croplands, but from "old lands". Large areas of semi-arid ecosystems have been cultivated in the past (Macdonald, 1989),

Figure 2.31. Intensive agriculture on Namibian Series limestone and shale bottomlands in the Matjies River valley, near Oudtshoorn, in the Succulent Karoo, showing almost total removal of the original bottomland *Elytropappus rhinocerotis* shrubland vegetation.

particularly along river terraces and alluviums in the southern Karoo (Dean & Milton, in press). The area occupied by old, and currently used dryland ploughed lands in unsuitable areas may be considerable, and 2449 km^2 (3.5%) of 68719 km^2 in the "Namaqualand agricultural region" was under cultivation by 1983, with only 180 km^2 under irrigation (Anon, 1985a). Many areas that have been ploughed and planted in the past have not recovered their original plant and animal assemblages, even after many decades of lying fallow (Macdonald, 1989; Dean & Milton, in press). There are no quantitative data available on the effects of irrigated pastures and croplands on the avifauna. Irrigated pastures and croplands possibly have a two-directional effect in that some bird species would be excluded from such areas, whereas other species may benefit from them and are possibly heavily dependant on such areas. Observations suggest that species such as Hadeda Ibis and Fantailed Cisticola *Cisticola juncidis* are dependent on irrigated pastures to the extent that they would not otherwise occur in the Karoo. The cultivation of plants specifically for fodder, such as prickly pears (*Opuntia* spp.) and old-man saltbush (*Atriplex nummularia*) is fairly widespread in the Nama-Karoo, and results in the transformation of large areas of bottomlands (**Figure 2.32**). Elsewhere in the Karoo *sensu lato*, native vegetation has been totally removed

Figure 2.32. A field of old-man saltbush (*Atriplex nummularia*) near Touwsrivier, in the transition zone between the Succulent and the Nama-Karoo, showing the total transformation of the bottomland vegetation, and invasion by alien grasses.

in places, allowing invasive alien shrubs such as *Atriplex lindleyi* var. *inflata* and alien grasses, such as *Bromus* spp. to successfully establish in the disturbance. The effects of these alien plant assemblages is unknown, but my own observations suggest that bird species richness decreases with an increase in alien vegetation. In parts of Namaqualand, alien annual grasses (*Bromus*, *Hordeum* and *Lolium* spp.) are abundant, widespread and even dominant, and are considered to be a threat to endemic plant species (Vlok, 1994). Alien vegetation is, however, not generally a problem in the Karoo (Macdonald, 1989), although, as noted earlier, the increase in the distribution and relative abundance of *Prosopis* spp. (Stoltz & Zimmerman, 1994) and *Tamarix ramosissima* (R. K. Brooke, *in litt.*) is becoming a cause for concern.

Mining

In general, the Karoo is poor in economically viable mineral deposits, and mining is largely restricted to the Namaqualand Complex in the northwest (**Figure 2.3**). Most of the mines in production in this part of the Karoo are underground and the disturbance caused by the actual mining is slight, although pollution caused by refining and slimes dams may become a problem in the future. There is some strip mining for gypsum and kaolin in the western Succulent Karoo, but the areas being stripped are small and restricted geographically. Quarter-degree squares in which there are mines in production, and in which there are kimberlite pipes and salt extraction works are shown in **Figure 2.33**. As shown on this map, the central Nama-Karoo is largely clear of any type of mining and apparently lacks sizable deposits of minerals.

Mining is not a major threat to the avifauna or, in general, to avian habitats in the Karoo *sensu lato*. Although surface diamond mining along the northern west coast has transformed 3-5% of the proclaimed mining area (Macdonald, 1989), these activities are restricted to the coastal strip and do not directly impact shrublands. Salt extraction works are frequent on high saline endorheic pans in the central and northern Nama-Karoo, but these generally have a low impact on the surrounding vegetation and animal communities, and furthermore may provide breeding habitat for species such as Greater *Phoenicopterus ruber* and Lesser Flamingo *Phoeniconaias minor*, Avocet *Recurvirostra avosetta* and Chestnutbanded Plover *Charadrius pallidus*. However, salt extraction often involves manipulating water levels in salt pans in order to collect the evaporites. The changes in water level and the disturbance associated with collecting salt can prevent birds from breeding successfully.

No study on the localized effects of surface strip mining or underground mining on birds in the Karoo has been done. Observations suggest that abandoned gypsum strip mines in the Knersvlakte near Vanrhynsdorp in the Succulent Karoo have not been recolonized by many birds, or many native species of plants (pers. obs). In the absence of census data for birds on the abandoned strip mines it is difficult to assess the impact of strip mining on the avifauna of the area. These areas, however, did not support a unique avifauna, and all the bird species that occurred there are common elsewhere. Strip mining has had a far greater impact on the endemic succulent flora of the area (Annelise le Roux, pers. comm.).

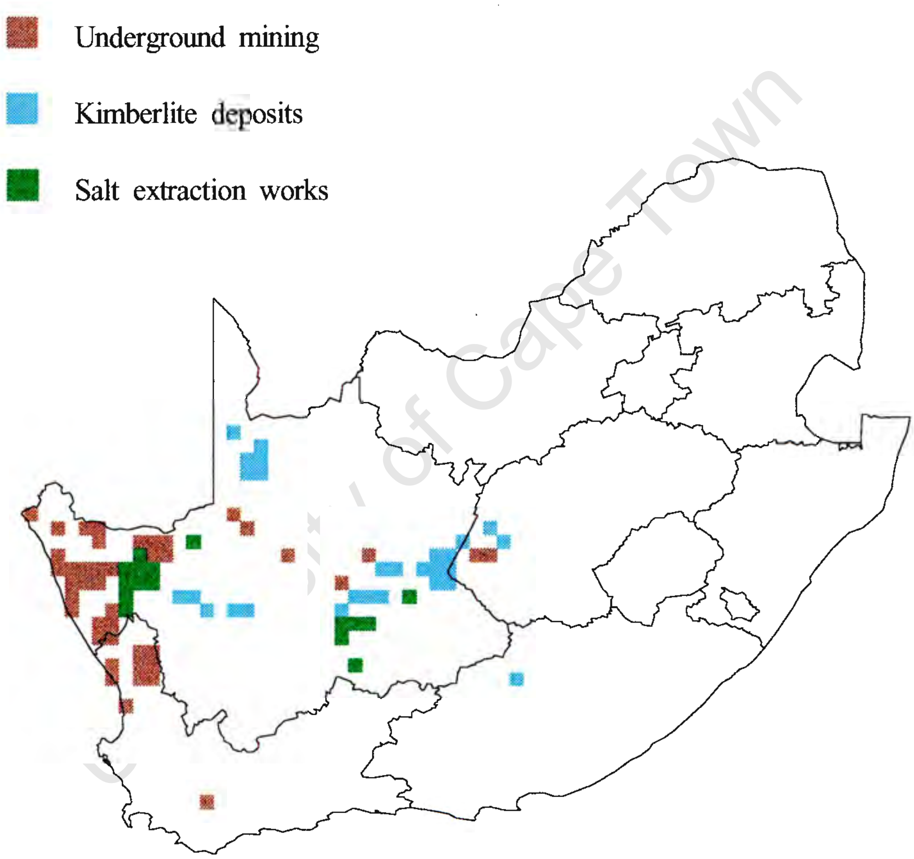

Figure 2.33. Quarter-degree squares in which there are mines in production, kimberlite pipes and salt extraction works in the Succulent and Nama-Karoo.

Chapter 3
The avifauna of the Karoo

Introduction

The Karoo (*sensu lato*) lacks a distinctive avifauna, but is rich in species (Winterbottom, 1968a; Vernon, 1986). In general, the biology of the avifauna is poorly known and few studies on individual species have been made in the region. The only report that deals with all the avifauna of the Karoo over the whole area is that of Vernon (1986), although Taylor (1957), Winterbottom & Rowan (1962), Winterbottom (1946, 1968a, 1968b, 1972, 1974, 1978), Kieser & Kieser (1978), Farkas (1981), Collett (1982), Martin, Martin & Martin (1986), Watkeys (1986, 1987) and Brooke (1992 & MS) have reported on the birds of parts of the Karoo. Studies of species assemblages, or of single species in the Karoo have been made by Siegfried (1968a), Frost & Vernon (1978), Brooke *et al.* (1980), Boshoff & Vernon (1980a, 1980b); Boshoff, Vernon & Brooke (1983); Boshoff & Palmer (1988), Boobyer (1989), Dean & Hockey (1989), Dean *et al.* (1991), Brooke & Dean (1991), Malan (1992) and Allan (1993).

Although the Succulent Karoo and the Nama-Karoo are now regarded as separate biomes, earlier literature (pre-1986) treated both the Succulent Karoo and the Nama-Karoo as a single biome (Hilton-Taylor & le Roux 1989). There are some important differences in the avifauna of the two biomes, chiefly in the numbers of grassland and savanna species that occur, and in the numbers of nomadic and locally nomadic species. Where possible, the Succulent Karoo and the Nama-Karoo will be discussed separately.

The Karoo is composed of a mosaic of habitats, determined by the geomorphology, the rainfall regime and the vegetation (Chapter 2). Shrublands in the winter rainfall area are generally succulent, between-seasons rainfall areas have narrow-leaved dwarf shrub vegetation and summer rainfall areas are grassy. Within these broad vegetation types, there is some variation in geological formations, soil type, rainfall amount and fine-scale patchiness of vegetation, providing a diversity of habitats for birds (Chapter 2). Superimposed on the habitat-rainfall mosaic is the variability of the system - rainfall events may be patchy in amount, timing and in space, and the response of the vegetation varies infinitely in accordance with environmental conditions (Hoffman, 1989; le Roux, Perry & Kyriacou, 1989; Milton & Dean, in press a; Milton, in press) and the response of the animal populations vary infinitely in accordance with the vegetation (Struck, 1992). Winterbottom (1968a, 1972) and Vernon (1986) have pointed out that there is a large difference between the density of birds in the dry season and densities after rain in the Karoo. It follows, then, that any area in the Karoo may thus support diverse bird species at an unusually high density for a short time, but that there is a certain measure of unpredictability about where these species rich areas will be.

Birds use a variety of tactics to live in the Karoo. Many of the resident species are "bet-hedgers" in terms of food, feeding on insects and seeds, often including juicy fruits in their diets. Other species, possibly less adaptable in terms of food, may move locally or widely, or aggregate in flocks in search of more productive patches. This chapter provides information on the distribution and diversity of birds of the Karoo, and discusses some of the tactics that birds use for survival in this harsh environment. Nomadism and seasonal movements in the birds in the Karoo are discussed later in this dissertation (Chapter 4).

Bird database

Specific names for all birds are given in the Appendices. Distributions of birds were plotted using ARC/INFO (Chapter 2: Preface), and the data on frequency of occurrence of various bird species were analyzed using the same program. I used simple programs (written as ARC/INFO macros) to sort and extract data on birds.

Source of distributional data

The main bird database used was that compiled by the Southern African Bird Atlas Project (SABAP) (Harrison, 1989, 1992). This has been supplemented by the bird distribution database compiled by Cape Nature Conservation and my own personal field records. The data consist of lists of birds entered on field cards, with separate field cards being completed for each month and locality. The field cards provide data on presence of species only, generally without any data on abundance or relative frequency of occurrence. I calculated a "reporting rate" (Harrison, 1989) that provides a "relative abundance index" for each bird species. The reporting rate is calculated by dividing the number of observations of the species by the number of field cards for the quarter-degree square. This probably gives an unrealistically high index for species in squares for which there are few cards (see **Figure 3.1**). However, in the absence of census data, this is the only way of evaluating the occurrence of species beyond simple presence or absence.

Precise coordinates for localities were not entered into the database and the locality information was entered as being within a 15' x 15' square (QDS), following the system described in the Preface to Chapter 2. Both the SABAP database and the CNC database have the same resolution. Harrison (1989, 1992) outlines some of the problems with the SABAP database, of which the major problem with respect to the Karoo is poor coverage of certain quarter-degree squares (**Table 3.1**). Less than 10% of the QDS in the Karoo can be said to have been adequately covered (*i.e.*, more than 50 cards for each QDS for the atlas period, 1987-1992).

Table 3.1
The number of field cards collected for quarter-degree squares in the Karoo *sensu lato*.

	No. of quarter-degree squares	
No. field cards	Succulent Karoo	Nama-Karoo
<11	62	272
11-20	39	137
21-30	20	41
31-40	10	21
41-50	6	7
51-75	17	21
76-100	3	6
101-125	2	5
126-150	1	0
>150	2	3
Total	4712	8791

Mean for Succulent Karoo = 28.9 (S.D. = 41.89) cards per QDS.
Mean for Nama-Karoo = 17.13 (S. D. = 23.01) cards per QDS.

Problems connected with the relatively coarse resolution of the database are that squares may include "non-Karoo" habitats, such as grassland, fynbos, savanna and forest, or they may include marine and estuarine habitats, so that species richness for these squares is boosted by "non-Karoo" species or vagrants from other habitats. Further difficulties, not mentioned specifically by Harrison (1992), but related to the poor coverage of quarter-degree squares, are that species numbers are curvilinearly related to the number of field cards (**Figure 3.1**). This implies that species richness has been underestimated for many of the squares that have been poorly covered by observers, and that at least 50 cards per square are required before species totals level out. For this study, I have considered QDS with 10 cards or more to have been covered sufficiently often for my purposes.

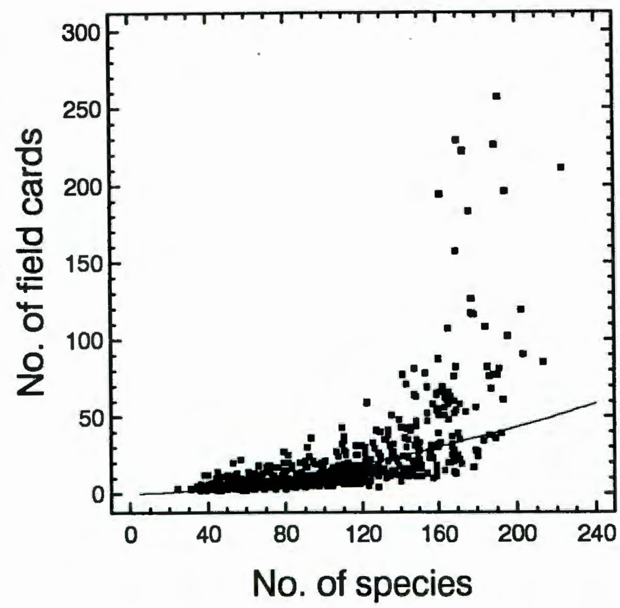

Figure 3.1. A regression of the number of field cards submitted for each quarter-degree square against the number of species recorded for that square. The line has the equation $y = x^{(0.72 + 0.017)}$, $r^2 = 0.65$, $p<0.0001$.

Both the SABAP and the CNC database were supplied in digital form, and were carefully checked for errors and mis-keyed data before the analyses were done. The database was initially passed through a sieve to remove all obvious misidentifications. Secondly, all marine species were removed from the database. Thirdly, all quarter-degree squares that contained marine or estuarine habitats, or that contained grassland, fynbos, savanna or forest, were temporarily removed from the database and 63 species occurring only in these squares were filtered out (**Appendix 1(d)**). A species list was then extracted from the remainder of the database and was further sieved to remove 31 species that occurred in less than 5 quarter-degree squares (species listed in **Appendix 1(c)**). The remaining species were finally sorted into two groups so that species occurrences in the Succulent Karoo and the Nama-Karoo could be listed separately. The final "Karoo" list consists of a large group (294 species) of species commonly recorded in the Karoo (**Appendix 1(a)**), and a smaller group of 82 species that have been recorded in more than four squares, but less than 25 squares in the Karoo (**Appendix 1(b)**). This latter group consists of species that are restricted to particular habitats or occur in the Karoo only during particular environmental circumstances. The species listed in Appendices 1(a) and 1(b) have been used in all the analyses of distribution patterns.

Species attribute data were added to the distributional database before ARC/INFO coverages were generated, so that species with particular attributes, such as endemics, or nomads, could be mapped. Attributes of Karoo species, *i.e.* those listed in Appendix 1(a), are given in **Appendix 2**; data on food, status, habitat and weight were taken from Maclean (1993) and my personal notes on birds.

Source of bird breeding data

A database of breeding data was compiled using records from the Southern African Ornithological Society (SAOS) nest record scheme files and the breeding data collected by observers who submitted field cards for the Southern African Bird Atlas Project. This was supplemented by records collected personally during the last eight years in the Karoo. No distinction was made between the Succulent and the Nama-Karoo biomes in the earlier SAOS nest record cards, so it was not possible to examine these earlier data (up to 1986) for seasonal or other differences in breeding patterns between the two biomes. However, it was possible to analyze the recent data for the two biomes separately using SABAP and my own data.

Biogeography and species richness of birds

Excluding marine and estuarine species, and the species listed in Appendix 1(d), a total of 407 species has been recorded in the Succulent and Nama-Karoo. The Succulent Karoo is less species-rich (269 spp.) than the Nama-Karoo (368 spp.), but the numbers of "Karoo" species recorded in each of these biomes is similar (**Table 3.2**). The distribution of species richness in the Succulent and Nama-Karoo is shown in **Figure 3.2**. Species richness tends to be highest in the eastern Nama-Karoo, and along transition zones with other biomes. Species richness in the Karoo *sensu lato* is significantly correlated with rainfall (**Figure 3.3**) ($r^2 = 0.45$, $y = 37.7 + 0.33x$, $p < 0.001$).

Table 3.2

Numbers of species that commonly occur both in the Karoo (and arid grassland) and in other habitats or biomes. Species given as "Karoo" species are either endemic or near-endemic to the Karoo, or appear to be more common in the Karoo than they are in other biomes. "Widespread" species are those that appear to be equally common in a number of biomes, and "commensal" species (both alien) are those that are almost entirely confined to villages and farmhouses.

	No. of species in:	
Distribution	Succulent Karoo	Nama-Karoo
Aquatic	74	83
Grassland	28	38
Karoo	40	43
Fynbos	9	5
Savanna	34	94
Forest	18	25
Widespread	6	7
Commensal	2	2

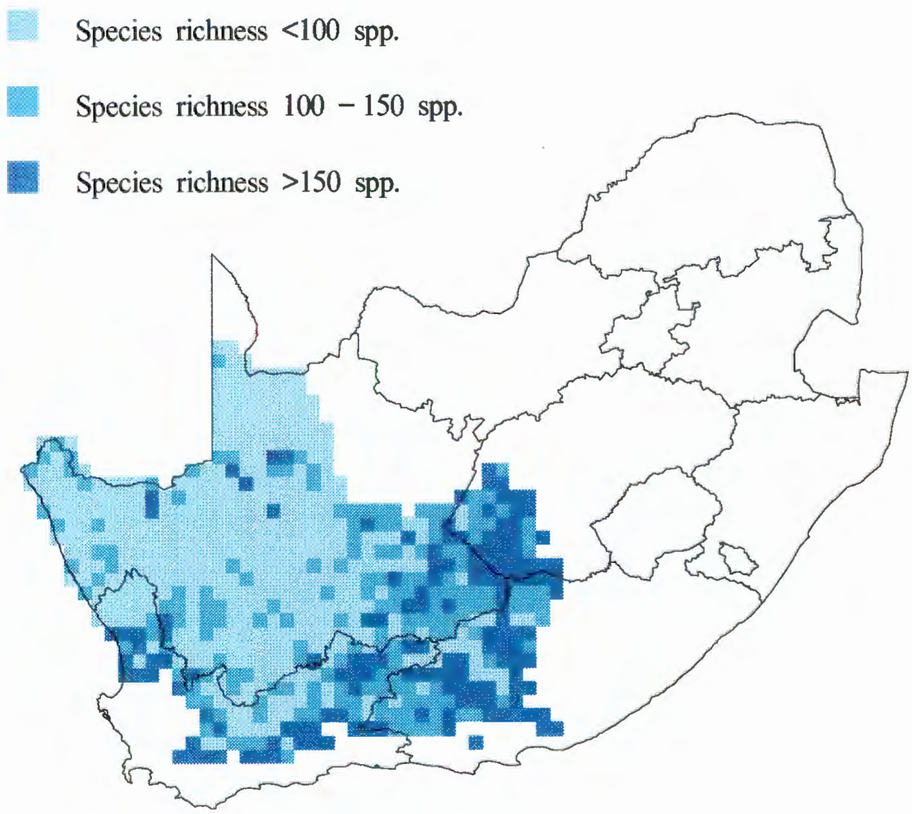

Figure 3.2. The distribution of avian species richness (all species) in the Succulent and Nama-Karoo.

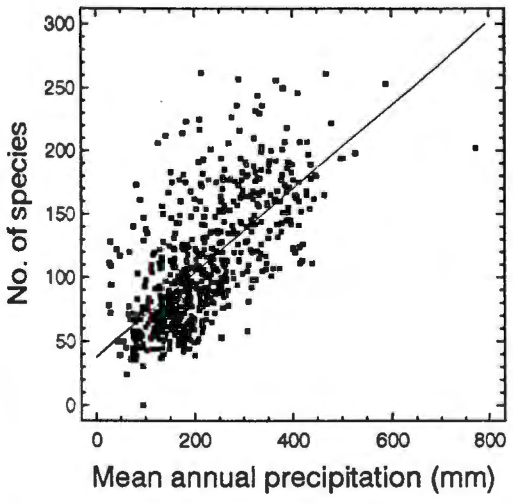

Figure 3.3. A regression of species richness in quarter-degree squares (*ca* 640 km^2 cells) against the mean annual precipitation in quarter-degree squares in the Succulent and Nama-Karoo.

The subset of 294 species (**Appendix 1(a)**) that are considered to be typical of the Karoo, are either widely distributed throughout the Karoo and also occur commonly or frequently in other biomes, or are commonly recorded in typical Karoo habitat on the edge of the region, or whose distribution is largely in the Karoo. Most "non-Karoo" species are savanna or grassland species, and relatively few fynbos species appear to be present in Karoo shrubland. Of the "Karoo" species, 252 have been recorded on more than 10% of the SABAP field cards in either the Succulent or the Nama-Karoo. Of these 252 species, 24 species were equally frequently recorded in both biomes, 135 species were more frequently recorded in the Succulent Karoo and 93 species were more frequently recorded in the Nama-Karoo (**Appendix** 3). The Succulent Karoo is thus the more species rich of the two biomes. The distribution of species richness of typical Karoo species is shown in **Figure 3.4.**

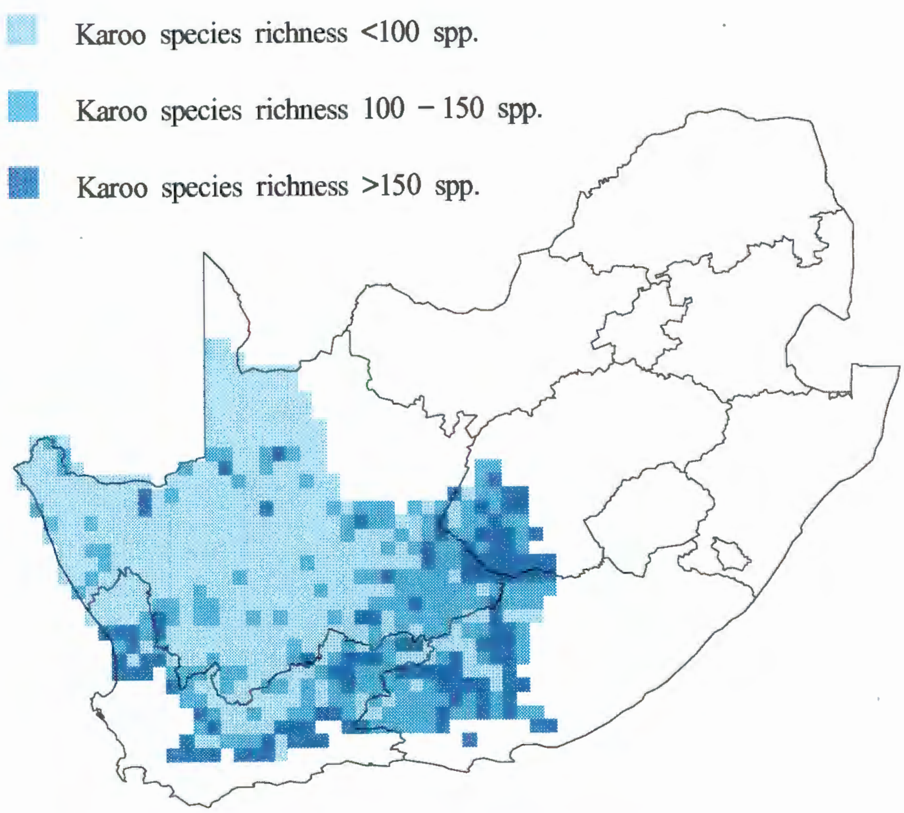

Figure 3.4. The distribution of avian species richness in quarter-degree squares (Appendix 1(a) species only) in the Succulent and Nama-Karoo.

Very few species of birds in the Karoo are considered to be "suffusively rare" (Schoener, 1987), i.e. rare throughout most of their geographic ranges. Most species that are rare in the Succulent and Nama-Karoo are common in substantial parts of their geographic ranges elsewhere ("diffusive rarity": Schoener, 1987). However, Red Lark *Certhilauda burra* and Sclater's Lark *Spizocorys sclateri*, whose distribution ranges are entirely within the Karoo, are considered rare (Brooke, 1984) and the Chestnutbanded Plover, whose range is fairly widespread, is considered generally rare throughout its range (Brooke, 1984). Cinnamonbreasted Warbler *Euryptila subcinnamomea* is locally common but mostly rare in its fairly restricted range in the Karoo, and the Karoo Eremomela *Eremomela gregalis* is fairly widespread, but sparse and not frequently recorded. One other species, Bradfield's Swift *Apus bradfieldi*, is considered by Brooke (1984) to be rare in the Karoo. However, this species is poorly known, and difficult to identify with certainty in the field, so it may be more abundant than present records suggest.

The relationship between the reporting rate and distribution of birds in the Karoo is shown in **Figure 3.5**. In both the Succulent and the Nama-Karoo there are a few species that are relatively abundant but not widely distributed. The majority of species, however, show a trend of increasing reporting rate with increasing geographical distribution. The results are not unexpected; widespread species tend to be frequently recorded whereas narrowly distributed species tend to be rare, with the exception of a few localized species. The regressions are significant (Succulent Karoo; $r^2 = 0.70$, $y = 0.05 + 0.024x$, $p < 0.001$: Nama-Karoo; $r^2 = 0.68$, $y = 0.09 + 0.078x$, $p < 0.001$). In general, more rare or narrowly distributed species occur in the Nama-Karoo, suggesting that these species are confined to particular habitats such as drainage lines or inselbergs.

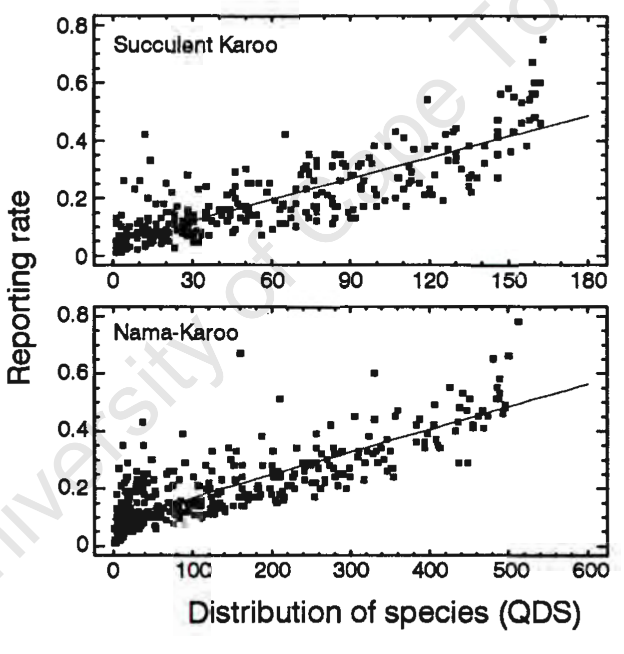

Figure 3.5. The relationship between the reporting rate for species and their distribution in quarter-degree squares in the Succulent and Nama-Karoo.

Endemic species

There are no families of birds peculiar to the Karoo, but members of the Alaudidae, Turdidae, Sylviidae (*sensu* Wetmore, 1960) and Fringillidae are well represented. The avifauna of the Karoo generally is distinctive at the species level but not at the genus level. There are two, possibly three, endemic genera (*Euryptila* and *Phragmacia*) and two near-endemic genera (*Malcorus* and *Stenostira*), all four monotypic. There is some evidence to suggest that the Red Lark belongs to the monospecific genus *Pseudammomanes* (Siegfried & Brooke, 1994). Of the 166 species, defined by Clancey (1986) as southern African endemics, 116 occur in the south west arid zone, and 80 occur in the Nama- and Succulent Karoo (**Appendix** 1). Only 25 endemic species have distributions that are largely within the Succulent and Nama-Karoo. The data shown in **Table 3.3** suggest that Karoo endemics are not commonly recorded in the region, and this is perhaps due to their relatively specialized habitat requirements. Crowe & Crowe (1982) show that their Karoo District (which differs somewhat from the Karoo as defined by Rutherford & Westfall, 1986) is not high in bird diversity, nor is it high in endemism (1% in non-passerines, 9% in passerines) compared with other biogeographic zones in Africa. Only one family, Alaudidae, has a high proportion of endemic species in the southwest arid zone with five species endemic or near-endemic to the zone out of a total of 19 species endemic to the southern African sub-region (Clancey 1986). For the purposes of this study, the Black Harrier *Circus maurus* has been considered endemic to the Karoo, although it also breeds in shrubland dominated by *Elytropappus rhinocerotis*, and in grassland. Similarly, the Fairy Flycatcher *Stenostira scita* has been considered endemic to the Karoo, since its breeding range is almost entirely confined to the Karoo and the south-central mountains of Lesotho (Maclean, 1993). Only the Red Lark, Sclater's Lark and Cinnamonbreasted Warbler are confined to the Karoo, with the Blackeared Finchlark *Eremopterix australis* and Namaqua Warbler *Phragmacia substriata* largely confined to the Karoo, but ranging into the southern Kalahari and high rainfall grasslands respectively. The distribution of species richness of southern African endemics is shown in **Figure 3.6** and the distribution of Karoo endemics in **Figure 3.7**.

Table 3.3
Endemic and near-endemic species of birds of the Karoo and their frequency of occurrence in quarter-degree squares in the Karoo. Specific names are given in Appendix 1.

	Percentage occurrence in:	
Species	Succulent Karoo	Nama-Karoo
Black Harrier	50.9 (83)	22.4(115)
Ludwig's Bustard	65.6 (107)	65.1(334)
Karoo Korhaan	50.9 (83)	75.4(387)
Karoo Lark	84.7 (138)	30.8(158)
Red Lark	1.8 (3)	8.4(43)
Sclater's Lark	1.2 (2)	13.5(69)
Thickbilled Lark	89.6 (146)	65.9(338)
Blackeared Finchlark	18.4 (30)	50.5(259)
Southern Grey Tit	81.0 (132)	44.4(228)
Tractrac Chat	46.6 (76)	52.6(270)

Table 3.3, continued

Species	Percentage occurrence in: Succulent Karoo	Nama-Karoo
Sicklewinged Chat	47.2 (77)	55.4(284)
Karoo Chat	96.9 (158)	74.7(383)
Karoo Robin	95.1 (155)	86.2(442)
Layard's Titbabbler	68.1 (111)	41.5(213)
Karoo Eremomela	38.7 (63)	25.7(132)
Cinnamonbreasted Warbler	17.2 (28)	7.6(39)
Greybacked Cisticola	92.6 (151)	69.0(354)
Namaqua Warbler	66.3 (108)	39.4(202)
Rufouseared Warbler	83.4 (136)	95.1(488)
Pririt Batis	57.7 (94)	53.2(273)
Fairy Flycatcher	67.5 (110)	58.3(299)
Palewinged Starling	77.9 (127)	49.9(256)
Dusky Sunbird	68.7 (112)	68.8(353)
Blackheaded Canary	89.6 (146)	68.4(351)
Whitethroated Canary	99.4 (162)	85.0(436)

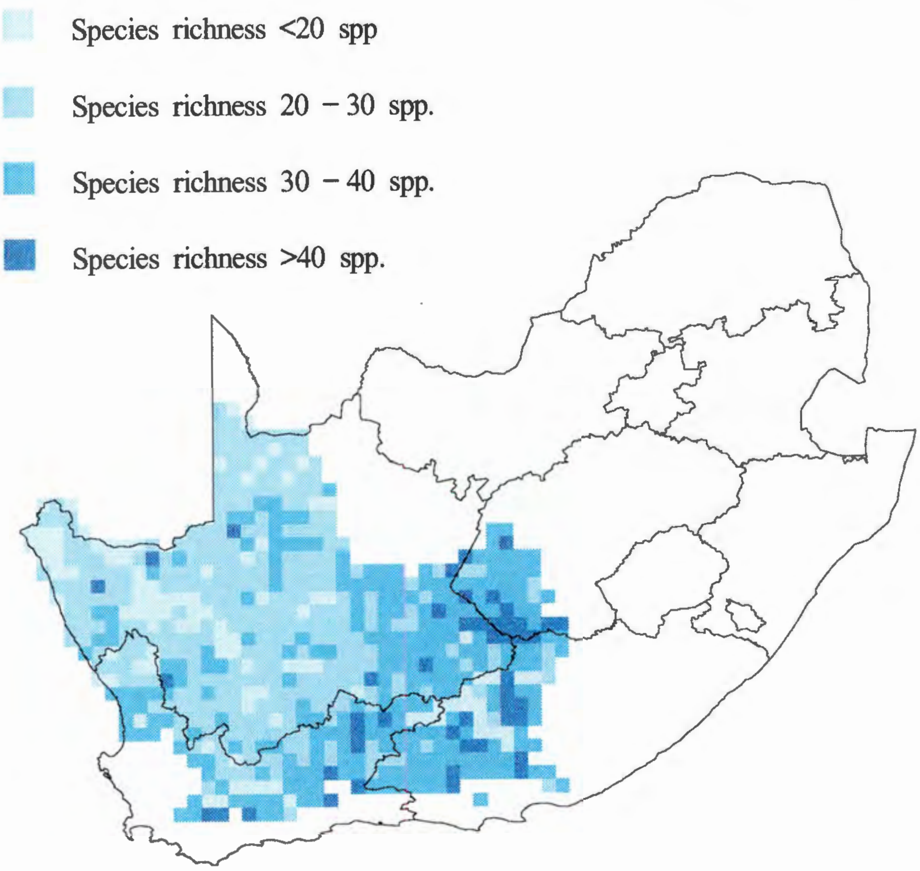

Figure 3.6. The distribution of southern African endemic avian species richness in the Succulent and Nama-Karoo.

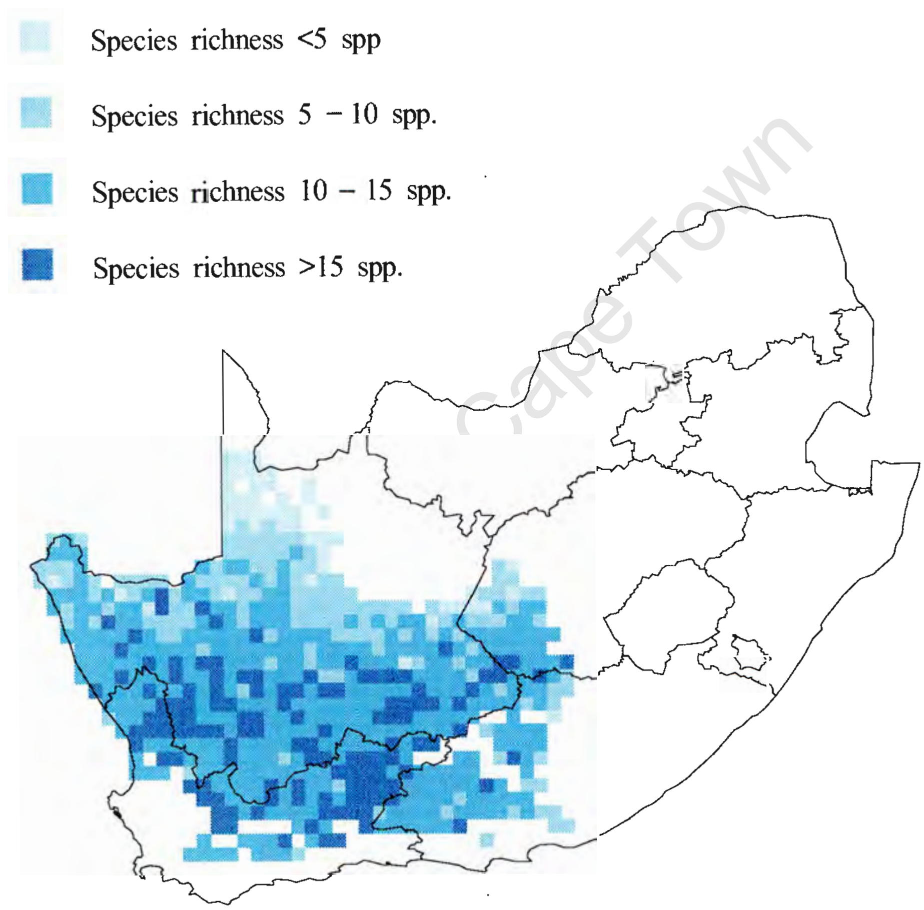

Figure 3.7. The distribution of species richness of "Karoo" endemic birds in the Succulent and Nama-Karoo.

The numbers of southern African endemic bird species that were recorded in the Succulent and Nama-Karoo are similar, but "Karoo" endemics were more frequently recorded in the Succulent Karoo (**Table 3.4**). Of interest is that no Karoo endemic species appears to be equally frequently recorded in both biomes. Also of interest is that several Karoo endemic species are confined to habitats on particular geological formations or geomorphological features in the Karoo. Thus the Red Lark is virtually confined to the coarse red sands of a relic dune system, the Cinnamonbreasted Warbler confined to granite and dolerite inselbergs, and Sclater's Lark to stony plains overlying beds of Beaufort Group shales.

Table 3.4
The frequency of species in the Succulent and Nama-Karoo that are widespread in southern Africa, or endemic to southern Africa, or endemic to the Karoo *sensu lato*. Common species have been recorded equally frequently in both biomes.

Status	Common	Succulent Karoo	Nama-Karoo
Widespread	18	94	60
S. African	6	27	28
Karoo	0	14	5

Aquatic species

Few bird species that are dependent on aquatic habitats are widespread through the Karoo, and most of the species that occur tend to be opportunistic and nomadic due to the aseasonal and unpredictable rainfall. Most species that feed in water use ephemeral habitats that may be either man-made impoundments or natural pans that hold water briefly after rain, or high-salinity pans that hold water for several months. Among the ducks, Egyptian Goose and South African Shelduck are widespread in the Karoo, using both natural waters and man-made impoundments. Yellowbilled Duck *Anas undulata*, Cape Teal *A. capensis* and Cape Shoveler *A. smithii* occur less frequently in the Nama-Karoo and tend to use ephemeral habitats in this biome (Winterbottom, 1968a; Maclean, 1993; Siegfried, 1970). Black Duck *A. sparsa* are locally nomadic along the southern edge of the Nama-Karoo and are apparently resident on permanent streams in the southern and eastern Succulent Karoo. The grebes, cormorants and large herons tend to occur only where there is permanent water, such as along the Orange River or at various large impoundments.

Temporary habitats are frequently used by the South African Shelduck and Cape Teal, while in years of exceptionally high rainfall in which many formerly dry areas are flooded, dense concentrations of Cape Shoveler occur in the Nama-Karoo (Siegfried, 1970). Species that use more saline waters, such as Greater and Lesser Flamingo, Chestnutbanded Plover, Avocet and Blackwinged Stilt *Himantopus himantopus* tend to be more common and widespread in the Nama-Karoo. For at least three species, South African Shelduck, Chestnutbanded Plover and Avocet, the Karoo is an important breeding/feeding area.

Density

The density of birds in the Karoo is unusually low compared with other biomes (e.g. savanna, Tarboton, 1980), but not unusually low compared with other shrublands in southern Africa (Siegfried 1983). The highest estimated density of birds in the Karoo is in shrubby grasslands on stony plains and hills, where densities varying from 28.7 birds/ha to 49.1 birds/ha were estimated by Farkas (1981). However, the estimated density calculated by Farkas (1981) is an order of magnitude higher than any other densities for birds in structurally similar habitats in the Karoo, and these estimates have not been included in any comparative analyses in this dissertation. Other published estimates of density range from 3.5 birds/ha in Succulent Karoo at Vanrhynsdorp to 7.6 birds/ha in Karroid Broken Veld at Robertson (Winterbottom, 1972, summarized by Siegfried, 1983) (**Table 3.5**).

Table 3.5
Estimates of density of birds in some localities in the Karoo.

Vegetation	Density (birds/ha)	Source
Karroid shrublands		
Succulent dwarf shrubland	3.5	Winterbottom (1968a)
Succulent dwarf shrubland	0.7-2.35	Winterbottom (1972)
Succulent dwarf shrubland	0.7	This study
Shrubland with many grasses	4.9	Winterbottom (1946)
Arid grasslands on sandy plains	<1.0	This study
Arid grasslands on sandy plains	3.4	This study
Arid grasslands on dunes, dry season	1.1	This study
Arid grassland on dunes, after rains	5.1	This study
Riverine woodland	59.2	This study (Chapter 6)
Other shrublands in southern Africa		
Strandveld	10.3-12.7	Siegfried (1983)
Coastal renosterveld	12.3	Siegfried (1983)
Coastal fynbos	2.4-2.9	Siegfried (1983)
Mountain fynbos	2.0-4.3	Siegfried (1983)
Fynbos	3.8-7.0	Winterbottom (1972)
Savanna woodlands in southern Africa		
Acacia woodland	9.2-16.0	Tarboton (1980)
Burkea africana woodland	3.9-9.0	Tarboton (1980)

In slightly less succulent dwarf shrubland near Klaarstroom, Winterbottom (1972) estimated that the density varied from 0.7 birds/ha to 2.35 birds/ha with rainfall. In structurally similar succulent dwarf shrubland at Tierberg, near Prince Albert, results from 446 counts in lightly grazed shrubland (the Tierberg study site itself) show an overall mean density of 0.72 birds/ha (mean biomass 80.4 ± 237.2 g/ha, range 0 - 2104 g) from 1988 to 1993 (**Appendix 4**). Results from all counts (n = 1034) at Tierberg (in lightly grazed, moderately grazed and heavily grazed shrubland) show an overall mean density of 32.7 ± 32.8 birds/km^2 (mean biomass 1593 ± 3031 g/km^2) suggesting very low average densities of birds. However, the density of birds in karroid shrublands and in other southern African shrublands is not unusually low compared to similar habitats in other parts of the world. In chenopod-dominated shrubland in north-central Nevada and south-central Oregon, U.S.A., Wiens (1991) calculated a density of 3.01 birds/ha (301 birds/km^2), and at a similar shrubland site in New South Wales, Australia, calculated a density of 1.57 birds/ha (157 birds/km^2). Data on densities of birds given by Szaro & Jakle (1985) suggest densities of 3.23 birds/ha (323 birds/km^2) and 2.97 birds/ha (297 birds/km^2) in desert upland shrubland in Arizona. A range of densities from <1 bird/ha (98 birds/km^2) to 1.15 birds/ha (115 birds/km^2) in Great Basin grassy shrublands in Utah is given by Medin (1986). All these densities lie within the range recorded for karroid shrublands.

Energy flow and nutrient cycling

A Field Metabolic Rate (FMR) that includes costs of basal metabolism, thermoregulation, locomotion, feeding, predator avoidance, posture, digestion, reproduction and growth (Nagy 1987), was calculated for birds for each of three sites, one in the Nama-Karoo, and two sites in the Succulent Karoo/Nama-Karoo transition. Crude energy budgets for the avifauna of these sites, grassy dwarf shrubland at Melton Wold, Victoria West (Nama-Karoo), and succulent dwarf shrublands near Klaarstroom and the Tierberg study site, both in Succulent Karoo/Nama-Karoo transition near Prince Albert, southern Karoo, were calculated using data presented by Winterbottom (1946, 1968b) and data collected during the present study (Chapter 6). Note that only the data for the 100 ha Tierberg study site (Chapter 6) were used to calculate the crude energy budget for this site. The FMR used in the present paper is:

$$\log FMR = 1.052 + 0.660 \log W$$

where W = weight of the bird in grams

Average metabolizable energy contents of food are: insects 18.0 kJ/g; seeds 18.4 kJ/g; nectar 20.6 kJ/g, and an intermediate value of 14 kJ/g for omnivores and frugivores (Nagy, 1987).

Results are summarized in **Table 3.6**. In the Melton Wold area, with 34 species, the biomass/km^2 was more than twice as great as that obtained at Klaarstroom, with 60 species. At the Tierberg study site, the biomass was just over half the biomass at Klaarstroom, and fewer species (48) were consistently recorded. Major contributors to the overall biomass in the three areas differed with the Karoo Korhaan *Eupodotis vigorsii* (1.35 kg) at Melton Wold, Ludwig's Bustard *Neotis ludwigii* (5.0 kg) at Klaarstroom, and the Kori Bustard *Ardeotis kori* (14.5 kg) at Tierberg being the largest contributors. Full species lists for **Table 3.6** are given in **Appendix 4**. The three areas are not directly comparable because Winterbottom (1946, 1968b) included riverine habitats in his counts, and thus sampled a generally more diverse, in terms of diet, avifaunal community. However, the lists of shrubland species from the three areas are similar, but also show the differences in the species assemblages of birds occurring in structurally different vegetation patches in the Karoo. Also of interest is that the range in species biomass increased inversely with decreasing density so that the site with the lowest density of birds had the largest weight range in species (**Appendix 4**). Bird assemblages tend to show varying relationships between density and weight within the niche space of communities (Telleria & Carrascal, 1994). The relationship between habitat structure, bird densities and bird weights has not been investigated in the Karoo.

Table 3.6

Species, biomass and crude energy budget for birds in succulent dwarf shrubland at Klaarstroom, Prince Albert area (Winterbottom, 1968b) and at Tierberg, Prince Albert (Chapter 6) and birds in grassy dwarf shrubland at Melton Wold, Victoria West (Winterbottom, 1946).

Locality	Overall biomass (g/km^2)	Metabolized energy ($kJ/day/km^2$)	Food intake ($g/day/km^2$)
Tierberg	8460	19199.7	1329.71
Klaarstroom	15115	24242.8	1605.09
Melton Wold	32183	64458.5	3957.13

The avian standing crop biomass (8.5-32 kg/km^2) is not unusually low for shrublands in southern Africa, and is similar to the biomass of 7.9-8.3 kg/km^2 for Coastal fynbos and the biomass of 3.1-14.1 kg/km^2 for Mountain fynbos calculated by Siegfried (1983). However, the biomass in Karoo shrublands is considerably lower than that of Strandveld (42.6-45.6 kg/km^2) and Coastal renosterveld (45.9 kg/km^2) given by Siegfried (1983). The avian standing crop biomass is likely to be more seasonally variable in Karoo habitats than in the coastal shrublands, and the movements of nomads and local nomads into areas may increase the biomass by orders of magnitude (Chapters 5 and 6). The approximate avian energy requirements given by Siegfried (1983) and the data presented here cannot be directly compared. Siegfried (1983) used the Lasiewski-

Dawson equation (Lasiewski & Dawson, 1967) and the results are not directly comparable to results obtained with the FMR equation of Nagy (1987).

The primary production of Karoo shrublands is generally low (Rutherford 1980; also suggested by the low carrying capacity for domestic livestock, Vorster 1985; Dean & Macdonald, 1994) and the energy available to birds is low for most of the time. Pulses in the productivity of the shrublands caused by localized rainfall events may increase available energy briefly. As a consequence of temporal and landscape patchiness in production, several species of birds in the Karoo are nomadic over large areas, while a number of other species move about locally in search of high resource patches (Chapter 4). Resident species apparently use different tactics for dealing with landscape patchiness since they tend to maintain low densities and wait for pulses. Many areas of the Karoo have long dry spells or severe droughts (Tyson, 1987; Vogel, 1994), when primary production may be very low. It has been suggested by Siegfried (1983) that there may be regular movements of birds from the Karoo into lowland fynbos, presumably caused by periods of low primary production in Karoo shrublands at these times.

Food

Birds in the Karoo, with the exception of the Ostrich, raptors, birds foraging in water, and the nomadic granivores, tend to have a mixed diet, feeding on invertebrates, seeds and small fruits (Maclean, 1993). Group-foraging species, such as Spikeheeled Lark *Chersomanes albofasciata*, Karoo Eremomela *Eremomela gregalis* and Rufouseared Warbler *Malcorus pectoralis* may also be relatively specialized in their diet (pers. obs.). The number of species in each of the broad diet food categories is given in **Table 3.7** for all species and in **Table 3.8** for the most frequently recorded species in each of the Succulent and Nama-Karoo biomes and equally common to both. The Succulent Karoo appears to be disproportionately species rich in raptors compared to the Nama-Karoo, but relative proportions of species in the various diet categories in the Succulent Karoo and Nama-Karoo biomes do not differ significantly.

A number of bird species in the Karoo feed on green vegetation in various forms, but the Ostrich, formerly distributed throughout the Succulent and Nama-Karoo, is the only truly herbivorous bird in southern Africa (Williams *et al.*, 1993; Maclean, 1993; Milton, Dean & Siegfried, 1994; Dean *et al.*, 1994). Several other species of birds that occur in the Karoo include flowers of shrubs and trees (Winterbottom, 1973; Milewski, 1978; Boobyer & Hockey, 1994), young leaves and basal nodes of grasses (Willoughby, 1971), unripe seed capsules of Mesembryanthema (pers. obs), seedlings of forbs and grasses (pers. obs) and the bulbs of geophytes when available (Broekhuysen, 1963; Boobyer & Hockey, 1994) in their mixed diet. Speckled, Whitebacked *C. colius* and Redfaced Mousebirds *Urocolius indicus* feed on leaves (Rowan, 1967), particularly at sunset before going to roost (Decoux, 1976; pers. obs).

Table 3.7
Species in each of the major diet groups in the Succulent and Nama-Karoo. The expected number of species in each category, calculated using a contingency table, is given in parentheses. Part-granivores include all those species that consistently have a mixed diet of seeds, insects and fruit. Herbivory, with 1 species, and aquatic species have been omitted from the table (data from Maclean, 1993)).

Diet group	Succulent Karoo	Nama-Karoo
Insectivores	105 (109)	145 (140)
Granivores	29 (31)	42 (40)
Part-granivores	38 (43)	61 (55)
Raptors	52 (40)	40 (51)
Frugivores	11 (12)	16 (15)
Nectarivores	8 (6)	7 (8)

Table 3.8
Most frequently recorded species in the Succulent and Nama-Karoo and common to both biomes, placed in major food categories.

Diet group	Common	Succulent Karoo	Nama-Karoo
Insectivores	6	48	43
Granivores	3	13	16
Part-granivores	2	17	20
Raptors	1	18	6
Frugivores	2	5	3
Nectarivores	1	4	0

Avian frugivory is widespread in the Karoo, but the frugivore species guild over most of the Karoo is relatively small. Species richness in this group increases along the southern and eastern edge of the Karoo, where species intrude into the Karoo from forests and subtropical thicket. However, despite the low numbers of specialized frugivorous species, frugivory as part of a mixed diet is fairly common among the birds of the Karoo, and many species include some fruit in their food in this region (Macleod, 1961; Penzhorn, 1973; Broekhuysen, 1973; Brooke & Dean, 1991).

There are few nectarivorous birds in the Karoo and only the Malachite Sunbird *Nectarinia famosa*, Lesser Doublecollared Sunbird *N. chalybea*, Dusky Sunbird *N. fusca* and the Cape White-eye *Zosterops pallidus* are regular flower visitors, and all are most common in the Succulent Karoo. The vegetation in Karoo shrublands generally is dominated by Asteraceae, Poaceae and Aizoaceae (Mesembryanthema) (Werger, 1985), all families in which there are few ornithophilous flowers (totally absent from Poaceae). Drainage line woodland, however, is rich in ornithophilous flowers, and such families as Loranthaceae, and such genera as *Aloe*, *Lycium*, *Cadaba* and *Rhigozum* are widespread, and likely to be important in sustaining and controlling the movements of nectarivore populations (Chapter 6).

Although bird species considered to be insectivores form the largest diet category in the Karoo, granivores and part-granivores are also numerous, and may be numerically superior to insectivores in any part of the Karoo, often present in large flocks (James 1921, 1929; Gill, 1931; Winterbottom, 1945, 1946, 1968a, 1968b, 1972, 1978; Maclean, 1970a, 1970b, 1974; Vernon, 1986).

There are few quantitative data on the amount of seed eaten by birds on a patch or community scale in the Karoo. In the shrublands and grasslands of the Karoo the families Asteraceae, Poaceae, Aizoaceae, Liliaceae and Scrophulariaceae are dominant and species rich (Werger, 1985) and all these plants produce small, dry seeds. In arid areas seeds may be abundant and van Rooyen & Grobbelaar (1982) found 10 000-40 000 seeds/m^2 in the upper 25 mm of soil on sandy plains in Namaqualand, and the numbers of seeds in the soil remained high for two years in the absence of good rains. In the central and northern Karoo, sandgrouse, doves, larks, canaries and buntings are the main granivores, taking the seeds of annual forbs and grasses, but in the southern Karoo, these birds feed on the seeds of perennial and annual Fabaceae (particularly annual *Lotononis* spp.), Asteraceae, and on the seeds of Mesembryanthema, which are released by the plants after rain. Individual birds may eat large numbers of seeds of a few plant species indicating preferences for particular plant families or species. At Tierberg, an estimated 215 kg of seed/year/km^2 is taken by birds (Milton *et al.*, 1989). This probably overestimates the actual off-take because granivorous birds often supplement their diet with fruits and insects. Furthermore, species such as Ludwig's Bustard, Namaqua Sandgrouse *Pterocles namaqua* and Greybacked Finchlark *Eremopterix verticalis* are visitors to the area only during the summer months, and are not present at Tierberg regularly during their visit. In drainage line woodland, where the bird populations are somewhat higher (Chapter 6), six common granivorous species probably take a maximum of 567 kg/km^2 of seed per year. The offtake of seed from dwarf shrubland at Tierberg is estimated at 4.7% of seed production (Milton *et al.*, 1989).

The raptor avifauna in the Karoo is neither diverse compared with savannas (e.g. Vernon, 1978), and with the exception of the Pale Chanting Goshawk which is widely distributed throughout the Karoo, the Booted Eagle *Hieraaetus pennatus*, which is probably most numerous in the Succulent Karoo, and the Pygmy Falcon *Polihierax semitorquatus*, which has a restricted distribution in the northern and northwestern Karoo (Maclean, 1993), nor is it distinctive. The commonest large raptor in the southern Karoo is probably the Black Eagle *Aquila verreauxii* (Boshoff & Vernon, 1980a; Boshoff & Palmer, 1988). The Martial Eagle *Polemaetus bellicosus* is widely, but thinly, distributed over the Succulent and Nama-Karoo (Boshoff & Vernon, 1980a). Both Rowan (1964) and Siegfried (1968b) have shown that migrant raptors are twice as common as residents in the Karoo during the summer, due mainly to the presence of small insectivorous Lesser Kestrels *Falco naumanni* and Eastern Redfooted Kestrels *F. amurensis*, but that raptors generally are not as frequently seen in the Karoo as in other parts of the Cape Province. Of interest is that Lesser Kestrels and Eastern Redfooted Kestrels were not widely recorded by observers during the atlas period (Appendix 1). This may support the hypothesis that the Lesser Kestrel has suffered a population decrease during recent years (Pepler, 1994), although regular census data is required before the situation can be properly assessed.

Reptiles are the most frequent vertebrate prey item taken by raptors in the Karoo (Table 3.7). Live mammalian prey larger than 1 kg is commonly taken only by the Black Eagle, Tawny Eagle *Aquila rapax*, Martial Eagle and Cape Eagle Owl *Bubo capensis*, and is most frequently the rock hyrax *Procavia capensis* or several species of lagomorphs (Boshoff & Palmer, 1980; Brown, Urban & Newman, 1982; Davies, 1994).

Table 3.7
Numbers of species feeding on different types of vertebrate prey in the Karoo.

Type of prey	No. of species
Carrion	9
Mammals >1 kg	4
Mammals <1 kg	24
Birds	18
Reptiles	30
Amphibians	18

A large number of species of mammals, birds and reptiles are killed on the roads in the Karoo (Siegfried, 1965a), providing food for a number of scavenging birds including eagles (Steyn, 1982), Jackal Buzzard *Buteo rufofuscus* (Steyn, 1982; Schmitt, Baur & von Maltitz, 1987), Pale Chanting Goshawk (Malan, 1992), Rock Kestrel *Falco tinnunculus* (Siegfried, 1965b), Black Crow *Corvus capensis*, Pied Crow *C. albus* and Whitenecked Raven *C. albicollis* (Siegfried, 1963; Winterbottom, 1975; Macdonald & Macdonald, 1985) and smaller species such as the Fiscal Shrike *Lanius collaris* (pers. obs).

Reproduction

There are few published data on the breeding success and productivity of Karoo birds. Farkas (1981) estimated breeding success at 65% in the northeastern Karoo. Compared with breeding success in the more stable savannas (Tarboton, 1979), this estimate is remarkably high.

Several resident dryland and nomadic aquatic species, in both the Succulent and Nama-Karoo, apparently breed at any time of the year (**Figures 3.8 and 3.9**) (breeding seasons of dryland nomadic species are dealt with in Chapter 4). Breeding in the Succulent Karoo, where the rainfall is lower but more reliable (Chapter 2), is more markedly seasonal than in the Nama-Karoo. There are regional differences in rainfall seasonality and amount across the Karoo (Chapter 2) that apparently influence the timing and duration of breeding seasons. For example, birds in the southwestern, southern and eastern Nama-Karoo appear to breed seasonally (James, 1921, 1929; Gill 1931; Beven & Chiazzari, 1942; Winterbottom, 1968a; Collett, 1982), but birds in the northwestern Succulent Karoo, and central and northern Nama-Karoo appear to be opportunistic to some extent (Maclean 1993). In the southern Kalahari, raptors and migrants are seasonal breeders regardless of rainfall and there are a number of opportunists that breed when conditions are suitable (Maclean, 1970b). Vernon (1986) pointed out that of the 13 species that are opportunistic nesters and common to both the Nama-Karoo and the Kalahari, 11 species tended to be seasonal breeders in the Nama-Karoo.

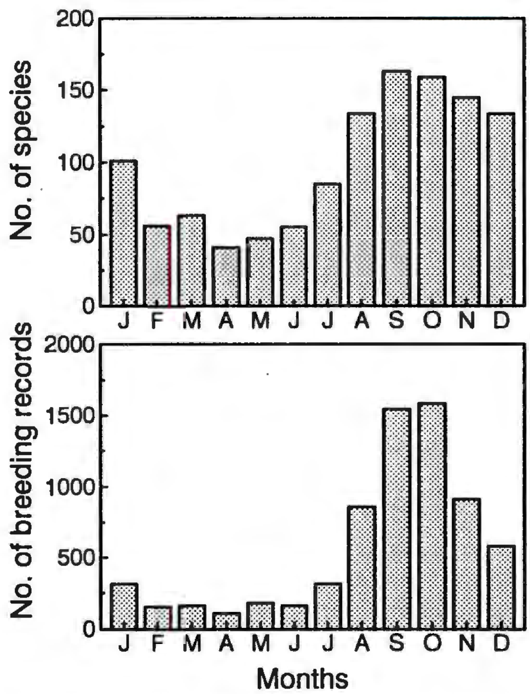

Figure 3.8. The number of species recorded nesting and the total number of breeding records in each month in the Succulent Karoo. These data include all species except nomads, local nomads and birds of aquatic habitats.

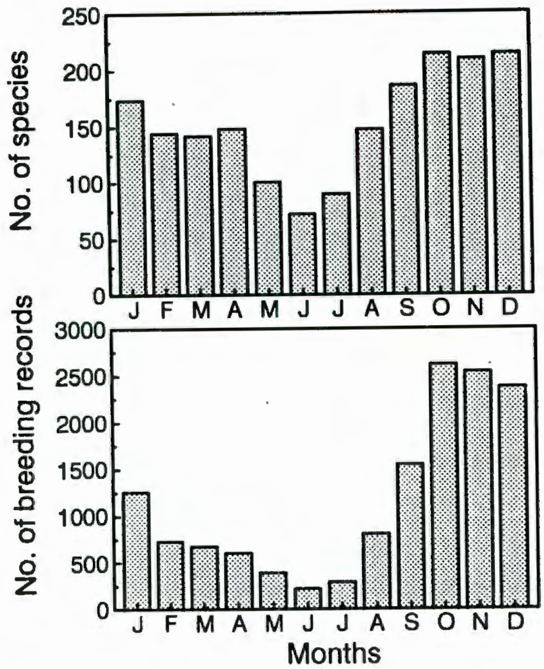

Figure 3.9. The number of species recorded nesting and the total number of breeding records in each month in the Nama-Karoo. These data include all species except nomads, local nomads and birds of aquatic habitats.

However, published data on a number of species breeding in different parts of the Karoo suggest that opportunistic breeding may be widespread in some years (Winterbottom, 1959; Winterbottom & Rowan, 1962; Macleod, 1961; Martin & Martin, 1970; Vernon, 1971; Broekhuysen, 1973; Martin *et al.*, 1986; Brooke, 1988), but not in others (pers. obs). It is apparent that birds breeding in the Karoo are opportunistic to some extent and that seasonal breeding may be modified to suit current environmental conditions. Maclean (1970b) noted that insectivorous birds have a more prolonged breeding season and begin to breed sooner after rain than granivores. A pattern noted in the breeding birds of the southern Karoo is that the insectivores may have two peaks in breeding, one immediately after the rain and another some weeks later. This may be correlated with the increase in invertebrate populations that have increased in response to rain, a hypothesis as yet untested. Observations in the southern Nama-Karoo suggest that group-foraging and co-operative breeding species (Whitebacked Mousebird (pers. obs), Spikeheeled Lark (Steyn, 1988), Karoo Eremomela (pers. obs)) have an extended breeding season, if not able to breed at any time of the year. From this I infer that group-foraging and co-operative breeding species are more successful at finding and using small patches at any time of the year, and as a result are less tied to markedly seasonal breeding.

Rainfall in the Karoo is often highly localized, with consequent localization of breeding activity by birds (Vernon, 1986). An important factor may be the amount of rain that falls in a single event, and Maclean (1970b) found that >25 mm of rain is needed to stimulate breeding in opportunistic species in the arid savanna. The development of a better understanding of the relationship between rain and the ecosystem processes that create suitable bird breeding habitat is a priority for research in the Karoo, a recommendation already put forward by others (Maclean, 1970c; Vernon, 1986).

There are few breeding records for aquatic nomads and four species (Chestnutbanded Plover, Avocet, Blackwinged Stilt and Whiskered Tern *Chlidonias hybridus*) have been consistently recorded breeding in the Karoo. Only the Avocet (recorded breeding in every month) and Blackwinged Stilt (recorded breeding every month except June) appear to commonly nest in both the Succulent and Nama-Karoo. Breeding records for locally nomadic aquatic species in the Karoo are sparse, and only Whitefaced Duck *Dendrocygna viduata* and Greyheaded Gull *Larus cirrocephalus* have been recorded. Both Greater and Lesser Flamingoes are likely to occasionally breed in the Nama-Karoo. There is suitable habitat for both species in high rainfall years in Bushmanland and the arid central Nama-Karoo. There are old records of Greater Flamingo breeding in the Nama-Karoo (cited by Brooke, 1984), and there is a recent reliable record in the SABAP database of Greater Flamingo breeding in the north-central Nama-Karoo (D. Allan, pers. comm.).

The number of species breeding and the number of breeding records for each month of all species associated with aquatic habitats in the Succulent and Nama-Karoo is given in **Figure 3.10** and **3.11**. Breeding peaks in October in the Succulent Karoo and in November in the Nama-Karoo, but in many species, breeding in both biomes by aquatic nomads and local nomads appears to be generally opportunistic, although this is not clear in the histogram.

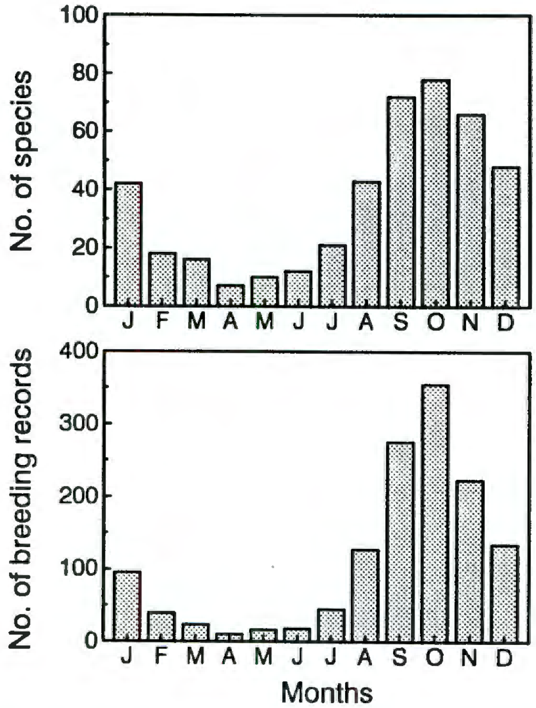

Figure 3.10. The number of species associated with aquatic habitats that have been recorded nesting and the total number of breeding records in each month for the Succulent Karoo.

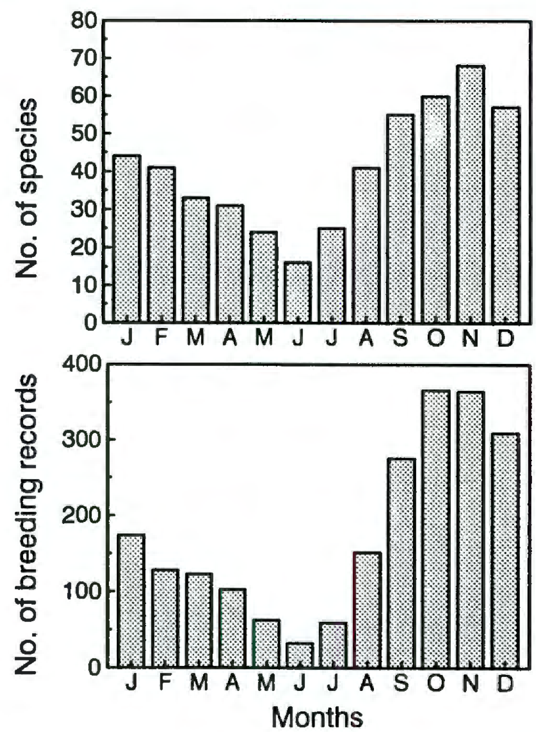

Figure 3.11. The number of species associated with aquatic habitats that have been recorded nesting and the total number of breeding records in each month for the Nama-Karoo.

Community interactions

Bird-plant interactions

Dispersal of seeds

The role of birds as dispersers of seeds in the Karoo, with the exception of mistletoes (Loranthaceae and Viscaceae) and *Galium tomentosum* (Rubiaceae) (Dean, Milton & Siegfried 1990; Dean & Milton, 1993), is not well known. Birds are thought to be important in dispersing the seeds of such genera as *Rhus*, *Lycium*, *Euclea*, *Diospyros*, *Protasparagus*, *Carissa*, *Pappea* and *Boschia*, but there is very little empirical evidence of the process from the southern Karoo. Observations show that Pied Barbets *Tricholaema leucomelas* and mousebirds disperse the seeds of mistletoes in the Karoo (Dean, Midgley & Stock, in press), but these birds are restricted to well developed drainage line woodlands and other taller trees by their nest site requirements. The Pied Starling *Spreo bicolor*, Redwinged Starling *Onychognathus morio* and Palewinged Starling *O. nabouroup* in the Succulent and Nama-Karoo, and Glossy Starling *Lamprotornis nitens* in the Nama-Karoo feed on a variety of juicy fruits and disperse seeds to sheltered germination sites below rocky outcrops or below tall trees on river banks and at watering points (pers. obs). Both Black and Pied Crows take fruits of alien *Opuntia* spp. in the Karoo (Milstein, 1966; Winterbottom, 1975) and other large fruits, and disperse seeds to favourable germination sites (Milton & Dean, 1987). Skead (1967) noted the recruitment of plant species bearing fleshy fruits at the bases of telegraph poles and below isolated *Acacia karroo* trees in "Eastern Cape Grassveld". Birds appear to be important in maintaining species richness of fleshy-fruited plants beneath large *Acacia erioloba* trees in the southern arid savanna. "Bird-dispersed" plants were significantly associated with large live *A. erioloba* trees and fleshy-fruited shrubs composed 84% of the sub-canopy vegetation (Milton & Dean, in press b). It is likely that birds similarly maintain the association of fleshy-fruited shrubs and large trees in drainage line woodland in the Karoo.

Small dry seeds, as well as the seeds of *Galium tomentosum*, appear to be most commonly dispersed by birds as nest material in the Karoo (Dean *et al.*, 1990; Dean & Milton, 1993) and secondarily dispersed by raptors (Dean & Milton, 1988).

Bird-other animal interactions

Commensalism and mutualism

Three kinds of commensalism may be distinguished among the birds of the Karoo: bird-other animal nesting associations, bird-other animal feeding associations and bird-man associations (which include nesting and feeding associations).

In general, bird-other animal nesting associations in the Karoo are not common. Anteating Chats *Myrmecocichla formicivora* dig nest holes in the sides or roofs of aardvark *Orycteropus afer* burrows (Maclean, 1993) which may be occupied at the time by aardvarks, porcupines *Hystrix africaeaustralis*, bat-eared foxes *Otocyon megalotis* or Cape foxes *Vulpes chama* (pers. obs).

Feeding associations between birds and other animals in the Karoo are scarce or seldom reported (see Dean & Macdonald, 1981). With the exception of birds foraging in aardvark diggings at dusk (Vernon & Dean, 1988) or in the early morning (pers. obs), most associations appear to be of birds gleaning ectoparasites from mammals (e.g. Penzhorn, 1981).

Apart from many species of birds foraging and feeding in croplands and farmyards (**Table 3.8**), or opportunistically using a walking man as a beater (Dean, 1993a), feeding associations between birds and man in the Karoo are equally scarce or seldom reported. The only important association is between man and the Greater Honeyguide *Indicator indicator*, that occurs in the eastern and southern Karoo (Collett, 1982; Winterbottom & Winterbottom, 1984; SABAP database) and guides man to bee-hives in these areas, as it does throughout much of its range (Friedmann, 1955). No data exist on associations between the Khoikhoin herders and birds or between the Khoi-San hunter-gatherers and birds in the Karoo. Greater Honeyguides (and perhaps Lesser Honeyguide *Indicator minor*) almost certainly fed on the remains of honey-combs taken out by Khoi-San gatherers.

A number of species use man-made installations such as houses, sheds, farm machinery, road bridges and transmission or telegraph poles as nest sites in the Karoo, or utilize farmyards, village gardens and irrigated lands and pastures as feeding and/or breeding sites (**Table 3.8**).

Table 3.8
Numbers of bird species that are commensal in the Karoo *sensu lato* and their modes of commensalism.

Mode of commensalism	No. of species
Nesting in association with other animals	2
Nesting on man-made structures	22
Nesting in farmstead gardens and village gardens	39
Nesting in plantations	2
Feeding in association with other animals (excluding man)	4
Feeding in association with man	3
Feeding in croplands and farmyards	62

Both the Black Eagle (Boshoff & Fabricius, 1986) and Martial Eagle (Boshoff, 1986, 1993) have been recorded nesting on man-made structures in the Karoo. The widespread planting of alien poplar *Populus deltoides* and *P. alba* groves in the Karoo have provided nest and foraging sites for the Redbreasted Sparrowhawk *Accipiter* *rufiventris* (Macdonald, 1986a) and the Hadeda Ibis *Bostrychia hagedash* (Macdonald, Richardson & Powrie, 1986).

Historical changes in species richness and density

While several commensal species appear to have expanded their ranges and increased in abundance in the Karoo, several other species appear to have decreased markedly in density or distribution in the Karoo. There is very little published historical data on numbers of birds in the Karoo. However, changes in the frequency of occurrence of particular species have been inferred from the information in early accounts that are largely anecdotal (e.g. Hare, 1915; James, 1921, 1929). The commensal species that appear to have expanded their distribution ranges are either birds that lived in the Karoo prior to pastoral farming or birds that lived on the edge of Karoo (Vernon, 1986)). Thus the Redwinged Starling and the Palewinged Starling, that now co-exist along the southern margin of the Karoo, and feed on orchard fruits and nest on buildings (Vernon, 1986; Maclean, 1993) have probably only recently come into contact, after range expansions northward by Redwinged Starlings and southward by Palewinged Starlings. The Pied Barbet has probably expanded its range in the Karoo by the use of alien vegetation (Macdonald, 1986b) and the Redbreasted Sparrowhawk is almost certainly a recent arrival in the Karoo (Macdonald, 1986a). Other relatively recent arrivals in the Karoo are the Hadeda Ibis, that forages in irrigated pastures (Macdonald *et al.*, 1986), and the Redeyed Dove *Streptopelia semitorquata* that forages in town and farm gardens in the eastern Nama-Karoo (Collett, 1982) and Succulent Karoo (Winterbottom & Winterbottom, 1984).

Several species, chiefly raptors, have decreased markedly in numbers in the Karoo within the last 100 years (**Table 3.10**), but small, carrion-feeding raptors, such as *Milvus* spp. kites (Brooke, 1974) and both Black and Pied Crows appear to have increased markedly in numbers in the Karoo (Siegfried, 1963; Macdonald & Macdonald, 1985). Hare (1915) notes that Black and Pied Crows, and the Whitenecked Raven were resident in the Philipstown district, but were not often seen. Black and Pied Crows are now common in the Karoo (Appendix 1(a)). This increase in numbers of crows has been ascribed to a reduction in the numbers of solitary scavengers such as the Egyptian Vulture *Neophron percnopterus*, Hooded Vulture *Necrosyrtes monachus*, Lappetfaced Vulture *Torgos tracheliotus*, Whiteheaded Vulture *Trigonoceps occipitalis* and Bateleur *Terathopius ecaudatus* in the Karoo (Macdonald & Macdonald, 1985). The reduction in numbers of these and other raptors in the Karoo has been attributed

Table 3.10
Species that have declined in numbers in the Karoo in recent times. ^ = some decrease, ^^ = marked decrease, ? = uncertain, but anecdotal evidence suggests a decrease. Specific names for all species are given in Appendix 1.

Species	Comments
Southern Ostrich	(only a small relic population in a wild state)
Bald Ibis	(no longer occurs in the Karoo)
Bearded Vulture^^	
Egyptian Vulture^^	(no longer occurs in the Karoo, possibly extinct in South Africa)
Hooded Vulture^^	
Cape Vulture^	
Lappetfaced Vulture^^	
Whiteheaded Vulture	
Tawny Eagle^	
Bateleur^^	
Wattled Crane	(no longer occurs in the Karoo)
Kori Bustard^?	
Ludwig's Bustard^?	
Blackwinged Pratincole^?	

References: Boshoff *et al.* (1983), Brooke (1984), Macdonald & Macdonald (1985), Vernon (1986), Brooke & Vernon (1988) and Maclean (1993).

to the annihilation of the wild ungulates and predators with concomitant changes in the availability of food (Boshoff & Vernon, 1980b; Macdonald & Macdonald, 1985). It is probable that the virtual extinction of the hunter-gathering Khoi-San peoples from the Karoo (Humphreys, 1987) also had some effect on the availability of food for avian scavengers and raptors.

Not only raptors appear to have decreased in abundance. The Southern Ostrich *Struthio camelus australis* no longer occurs in the Karoo as a wild bird, and populations of the larger bustards may have been reduced or the birds exterminated from parts of their range in the Karoo.

Hare (1915) notes that both Montagu's Harrier *Circus pyargus* and Pallid Harrier *Circus macrourus* were "fairly numerous" in the Philipstown district in the early 1900s. This is supported by Boshoff *et al.* (1983) who show numerous records for the two species throughout the Karoo for the period 1700-1969. These distinctive harriers were recorded recently only in two and three widely scattered QDS respectively during the atlas period, suggesting that these birds are now less frequently seen in the Karoo. Similarly, distribution maps for both Montagu's and Pallid Harriers for the period 1970-1979 in Boshoff *et al.* (1983) show very few records for the Karoo. The cause of this decrease in numbers of these harriers could be due to habitat destruction in the Palaearctic range of these species, and a general decline in numbers (as noted by

Maclean, 1993). However, it is equally possible that grazing induced changes in shrublands (Chapter 7) have altered the suitability of the habitat for these species in the Karoo, as suggested by Hare (1937). Grazing induced changes in shrubland vegetation cover has also been implicated in changes in the reporting rate of Crowned Plover *Vanellus coronatus*, Burchell's Courser *Cursorius rufus* and Doublebanded Courser *Smutsornis africanus* in the eastern Nama-Karoo (Collett, 1982). This may be due to heavy grazing by domestic livestock, or it may be due to changes in the way in which the vegetation is now grazed, and the loss of closely cropped patches created by wild ungulates.

Although Brooke (1984) shows very few past records of breeding by Greater and Lesser Flamingoes in the Karoo, it is likely that itinerant breeding by both these species was more widespread in the Karoo than it is at present. Suitable breeding habitat for these species is now sparse in the Karoo, due to disrupted drainage and other disturbances in saline endorheic pans.

SECTION 2

Nomadism in birds and fluctuations in the density and species richness of birds in the Karoo

Chapter 4
The distribution and biology of nomadic birds in the Karoo

Introduction

Movements in animals may be either seasonal and predictable ("migration"), directional one-way movements ("emigration") (Sinclair 1984) or dispersal (Greenwood 1984). Dispersal usually refers to one-way movements from high-resource areas, where survival and reproduction may be relatively high, and is considered to be an adaptation to avoid inbreeding and to reduce competition between relatives (Greenwood 1984). Nomadism, in which the movements are irregular and where destinations may differ from year to year is a form of emigration (Sinclair 1984) and is considered to be an adaptation to use resources that are patchy in space and time. Unlike dispersal, all members of a nomadic species may leave an area, and move together to another patch, so that competition between individuals is not necessarily reduced and inbreeding not necessarily avoided. Nomadic species may return to the same area to breed, or they may move to other areas, depending on environmental conditions.

The evolution of nomadism in animals is favoured by unpredictable patchiness or clumping of resources in space and time (Sinclair 1984). Arid and semi-arid ecosystems are characterized by low and unpredictable annual rainfall (Noy-Meir 1973) and rainfall events are often highly localized so that patches of vegetation at different phenological stages are scattered across the landscape. Birds that are able to move quickly and efficiently to these patches may enjoy abundant food and shelter (nest sites) and a lack of intense competitive interactions, so that selection would favour local and regional movements by birds. Nomadism appears to be most prevalent among granivorous birds inhabiting arid or semi-arid ecosystems (Maclean 1974; Davies 1984). Arid, and to some extent, semi-arid environments, tend to have only residents or nomads among the avifauna (Maclean, 1974), although such migrant species as European Swallow *Hirundo rustica* and Willow Warbler *Phylloscopus trochilus* occur regularly throughout the semi-arid Karoo. Palaearctic migrants and intra-African migrants may be "resident" in one area for the period of their stay, or they may be nomadic, moving about the Karoo in the same way as the Karoo nomadic species. Vernon (1986) hypothesized that there should be fewer residents, and greater nomadism and aseasonal breeding with decreasing rainfall in the Karoo.

The objectives of this chapter are to identify the part of the Karoo most commonly occupied by nomadic birds and to examine the factors affecting the distribution, breeding and species richness of nomadic birds. There are two categories of nomadic birds; those that are nomadic on a regional scale (nomads) and those that are nomadic on a landscape scale (local nomads). Local nomads tend to vary in numbers of individuals present at a locality; nomads vary both in number of individuals and in species richness. Noy-Meir (1973) makes the point that the inclusion of nomads in ecosystem models requires modelling at the regional, rather than the local scale. Although local nomads are briefly discussed, this chapter is essentially concerned with those species that are nomadic on a regional scale and that use dryland habitats. Key questions are: (1) where in the Karoo are nomadic birds most common?; (2) can their distribution be related to particular weather patterns?; and, (3) can their distribution be related to particular vegetation types?

As a primary requisite for the conservation and protection of avian species richness in the Karoo, particularly the conservation of nomadic birds, species rich areas need to be identified and classified. There is also the need to identify what qualities a potential protected area must have in order to offer protection to nomadic birds. This is essentially a review chapter in which I examine the attributes of nomadic birds and their habitat requirements.

Methods and database

I categorized all bird species in the Succulent and Nama-Karoo as residents, nomads or local nomads on the basis of published accounts of their biology (Maclean, 1993) and my personal knowledge of their behaviour in the Karoo. Distributions of nomadic birds were mapped with ARC/INFO (see Section 1: Preface), using the bird distribution and breeding database described in Chapter 3. These data were supplemented by my own records of food of nomadic birds (mainly stomach and crop contents) and breeding records collected over the period 1986 - 1993 in the Karoo. Data on the food of granivorous birds were from road casualties picked up in various parts of the Karoo and from birds collected during the course of other studies (e.g. Transvaal Museum collections; Dean *et al.*, 1991). Seeds from stomachs and crops were examined under a 40x binocular microscope and where possible were identified to genus using a reference collection of seeds from identified plant specimens.

The structural heterogeneity of habitats was classified using Acocks (1953). All habitats in the Succulent and Nama-Karoo were placed in one of five classes, one being relatively homogeneous (e.g. sparse grassland), and five being relatively structurally heterogeneous (e.g. arid savanna woodland). The distributions of grasses were taken from Gibbs Russell *et al.* (1990),Zacharias (1990) and van Breda & Barnard (1991).

Data on the relative abundance of plant growth forms were taken from an unpublished manuscript entitled "Veld types of the western half of the Republic of South Africa" by J. P. H. Acocks (National Botanical Institute, Kirstenbosch). This manuscript gives various plant growth forms as a percentage of all growth forms in each Veld Type (Acocks, 1953).

Biogeography and species richness of nomadic birds

Nomadic and locally nomadic species in the Karoo are given in **Table 4.1**. There is some conjecture that Sclater's Lark may not be as nomadic as other small larks (P.G. Ryan, pers. comm.). Several species, particularly the sunbirds, may be more sedentary in other biomes. Movements in some of the columbids are also not well known. Rock Pigeon *Columba guinea*, Turtle Dove *Streptopelia capicola* and Laughing Dove *S. senegalensis* appear to be resident in the Karoo, but there may be local movements in all three species. Table 4.1 does not include aquatic species, although all aquatic species in the Karoo are nomadic to some extent.

Table 4.1.
Nomadic and locally nomadic species of birds in the Karoo and their frequency of occurrence in quarter-degree squares (out of 676 possible squares). Data from Maclean (1993) and personal observations. Specific names are given in Appendix 1.

Nomadic species

Species	Frequency
Tawny Eagle	10.4 (70)
Namaqua Sandgrouse**	84.2 (569)
Burchell's Sandgrouse*	4.3 (29)
Redcapped Lark	71.2 (481)
Pinkbilled Lark*	10.5 (71)
Sclater's Lark**	10.5 (71)
Stark's Lark*	16.3 (110)
Chestnutbacked Finchlark	3.7 (25)
Greybacked Finchlark*	75.9 (513)
Blackeared Finchlark**	42.8 (289)
Wattled Starling	54.3 (367)
Scalyfeathered Finch	30.5 (206)
Blackheaded Canary**	73.5 (497)
Larklike Bunting*	91.4 (618)

Table 4.1, continued

Locally nomadic species

Species	Frequency
Blackbreasted Snake Eagle	18.3 (124)
Lanner Falcon	41.6 (281)
Ludwig's Bustard**	65.2 (441)
Burchell's Courser*	17.2 (116)
Doublebanded Courser	41.0 (277)
Namaqua Dove	94.2 (637)
European Swift	22.9 (155)
Sentinel Rock Thrush*	5.3 (36)
Anteating Chat*	89.2 (603)
Yellowbellied Eremomela	77.1 (521)
Fantailed Cisticola	26.9 (182)
Chat Flycatcher*	80.6 (545)
Fairy Flycatcher**	60.5 (409)
Malachite Sunbird	48.7 (329)
Lesser Doublecollared Sunbird*	45.6 (308)
Greater Doublecollared Sunbird*	6.5 (44)
Dusky Sunbird**	68.8 (465)
Black Sunbird	5.3 (36)
Redbilled Quelea	33.0 (223)
Redheaded Finch*	38.5 (260)
Blackthroated Canary	39.6 (268)
Yellow Canary*	92.0 (622)
Whitethroated Canary*	88.5 (598)
Streakyheaded Canary	14.3 (97)
Rock Bunting	16.4 (111)

* Southern African endemic (Clancey, 1986)
** Karoo endemic

Nomadic bird species (including local nomads), as a proportion of all species in a biome in southern Africa, is highest in the arid grassland and Karoo (**Figure 4.1**). Two species, Pinkbilled Lark *Spizocorys conirostris* and Chestnutbacked Finchlark *Eremopterix leucotis* do not occur in the Succulent Karoo, and Sclater's Lark is rare in the Succulent Karoo (Appendix 1(a), but there is otherwise no difference in species richness of nomadic birds between the Succulent Karoo and the Nama-Karoo biomes.

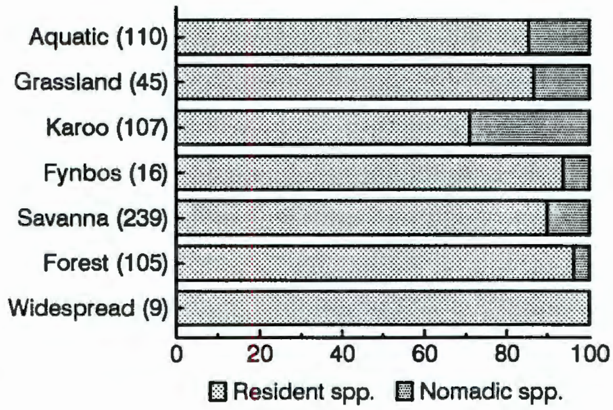

Figure 4.1. The percentage nomadic and locally nomadic species of birds in terrestrial biomes in southern Africa. The total number of non-migratory breeding species is given in parentheses after the name of the biome, and species have been placed in their most typical habitat.. Numbers of species are from Maclean (1993). The Succulent Karoo and the Nama-Karoo have not been separated. Marine and estuarine species have been excluded from the table.

The distribution of nomadic species, showing their occurrence relative to all species recorded in a quarter-degree square, is given in **Figure 4.2**. The distribution of locally nomadic species is shown in **Figure 4.3**. Nomadic birds, of which the most widespread species is the Greybacked Finchlark (**Appendix 1(a)**), are most frequently observed in the north-central and northwestern Nama-Karoo, whereas locally nomadic species appear to be more frequently observed in the eastern Nama-Karoo. The reporting rate of nomadic species is inversely, and significantly correlated with species richness of all species in the Karoo (**Figure 4.4**) ($r^2 = 0.09$, $y = 0.17 - 0.005x$, $p < 0.001$). Since the distribution of nomadic birds in the Karoo also appears to be mainly in areas where rainfall is patchy, low and aseasonal, this supports the idea that fewer species are able to cope with resources that become unpredictable in time and space, and that there has been selection for nomadism in the species that are able to use patchy environments. The distribution of nomadic birds in the Karoo appears to be mainly in areas where the mean annual precipitation is below 250 mm (**Figure 4.5**) and

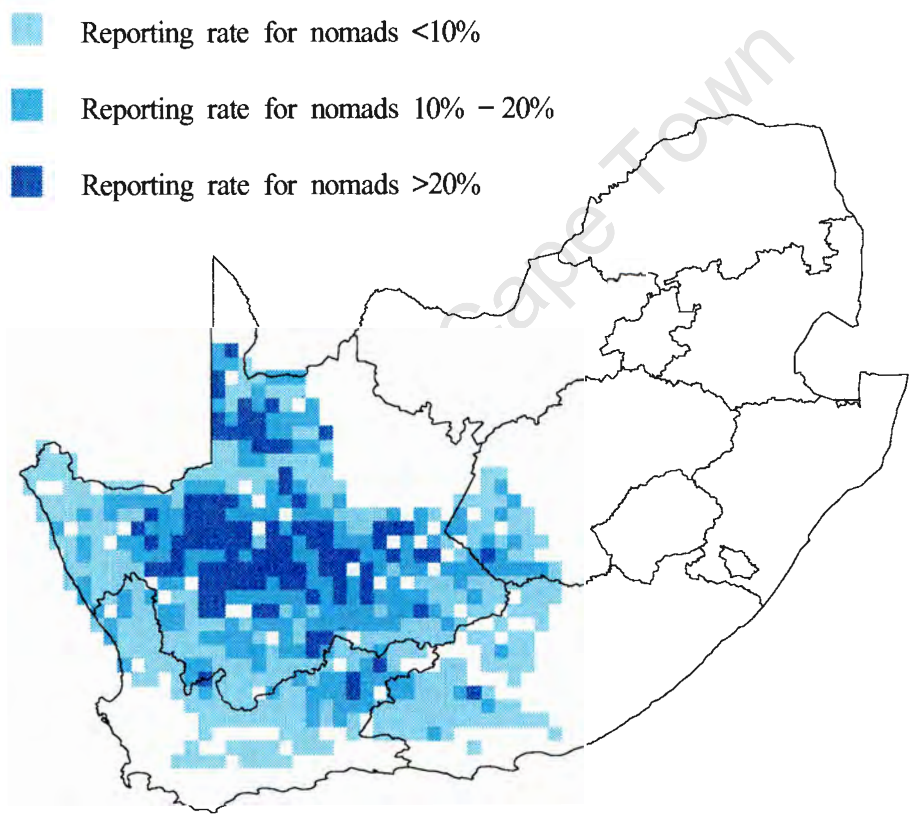

Figure 4.2. The relative frequency of nomadic bird species in the Karoo. The map shows the occurrence of nomadic species as a proportion of all species recorded on each field card for each quarter-degree square.

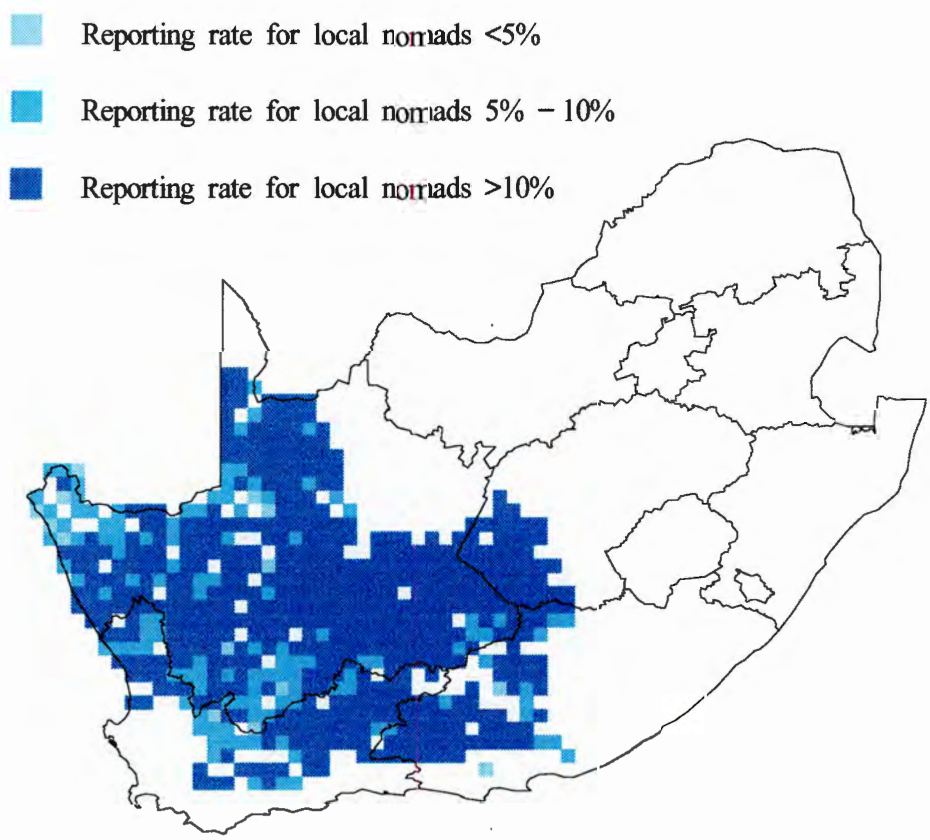

Figure 4.3. The relative frequency of locally nomadic bird species in the Karoo as a proportion of all species recorded on each field card for each quarter-degree square.

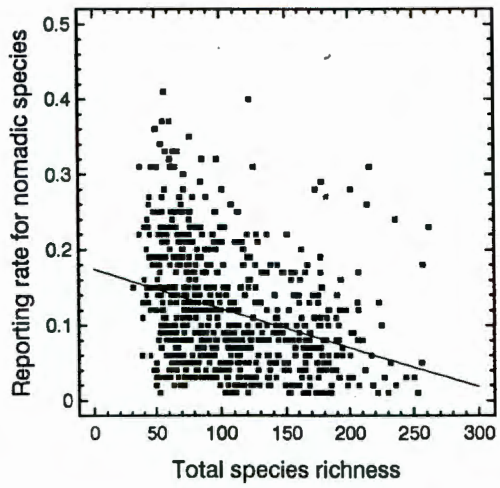

Figure 4.4. A regression of the reporting rate of nomadic species in each quarter-degree square against total species richness in the Karoo *sensu lato*.

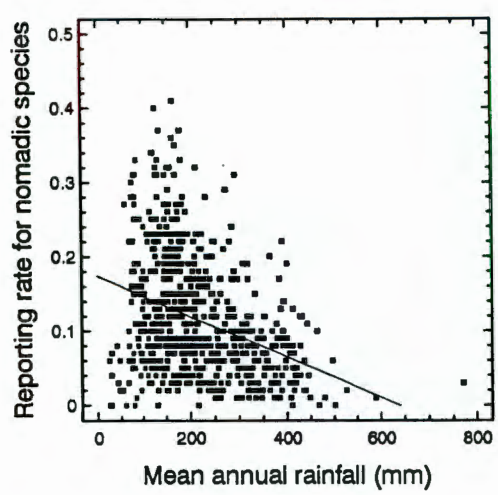

Figure 4.5. A regression of the reporting rate of nomadic species in each quarter-degree square against mean annual precipitation in the Karoo *sensu lato*.

is significantly and negatively correlated with rainfall amount (r^2 = 0.11, y = 0.17 - 0.02x, p <0.001). The reporting rate of individuals and of species richness of nomadic birds is significantly and positively correlated with the coefficient of variation of the rainfall (**Figure 4.6**) (r^2 = 0.21, y = -0.03 + 0.02x, p <0.001) and where the rainfall is usually between seasons (March-April and August-September as peak rainfall periods)

(Figure 4.7). **Similarly, the reporting rate of individuals and of species richness of nomadic birds is significantly correlated with autumn rainfall, and is highest in those parts of the Karoo that receive more than 40% of the total annual rainfall in autumn ($r^2 = 0.23$, $y = -8.33x^{1.61}$, $p < 0.001$).**

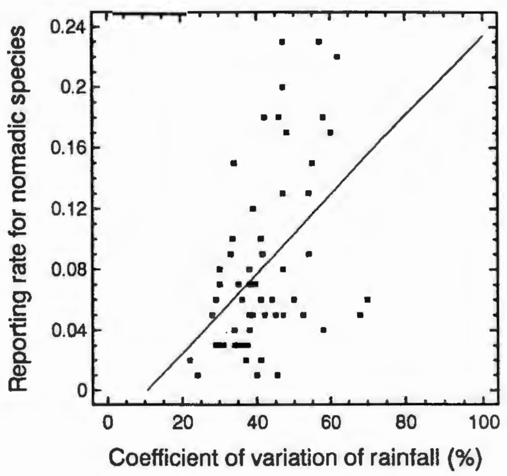

Figure 4.6. A regression of the reporting rate of nomadic species against the coefficient of variation in rainfall in the Karoo *sensu lato*.

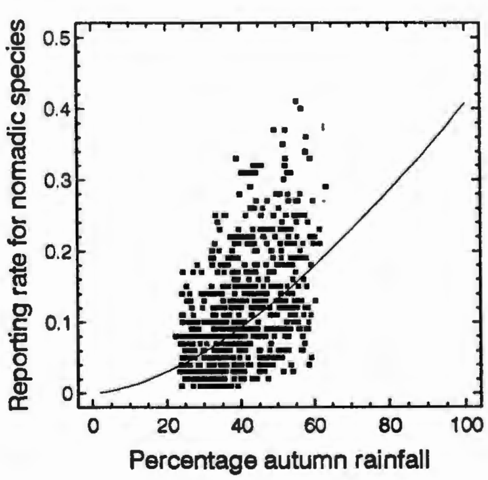

Figure 4.7. A regression of the reporting rate of nomadic species against the amount of autumn rainfall in the Karoo *sensu lato*.

Nomadic birds occur in most habitats in the Succulent and Nama-Karoo, but they are much less common on rocky slopes, inselbergs and mountains, and they tend to

avoid the relic fynbos patches on mountain tops. The reporting rate of nomadic birds is inversely and significantly correlated with altitude range; nomadic species are most frequently recorded in habitats that are fairly flat, and are most common where the range in height is less than 200 m over a quarter-degree square (**Figure 4.8**) (Succulent Karoo: $r^2 = 0.18$, $y = 0.1 - 5.45x$, $p < 0.001$; Nama-Karoo: $r^2 = 0.2$, $y = 0.18 - 0.001x$, $p < 0.001$). Plains shrubland and arid grassland (habitat types 4, 5, 6 in Chapter 2) appear to be the habitats in which all nomads have been most frequently recorded.

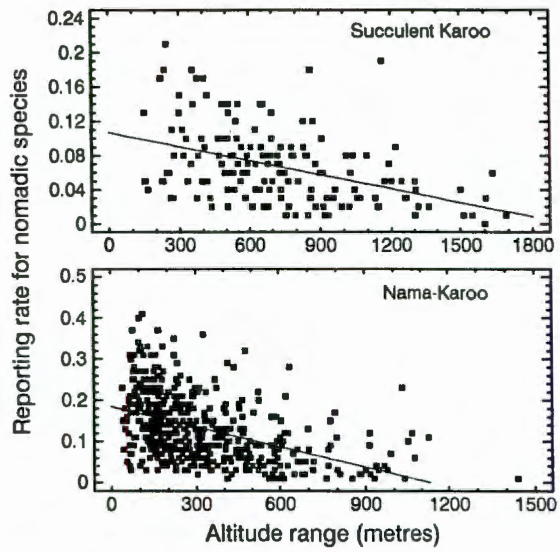

Figure 4.8. A regression of the reporting rate of nomadic species against altitude range in each quarter-degree square in the Succulent and Nama-Karoo.

Dryland nomadic species tend to be most abundant in habitats with the least structural heterogeneity in the Karoo (**Figure 4.9**). The regression is significant ($r^2 = 0.02$, $y = 0.13 - 0.08x$, $p < 0.001$). This is supported by **Figure 4.10**, that shows the reporting rate of nomadic species to be highest in arid grasslands and sparsely vegetated dwarf shrublands in the central northern Nama-Karoo. The occurrence of nomadic species is also correlated with certain plant growth forms. The reporting rate of nomadic species is significantly correlated with the percentage annual forbs (**Figure 4.11**), annual grasses (**Figure 4.12**) and all grasses (including annual grasses) (**Figure 4.13**) in the vegetation. Perennial desert grasses are important components of the habitat and diet of small nomadic granivores, and also provide nest sites and nest material for the birds. Small (<25g) nomadic granivorous birds (Pinkbilled Lark, Sclater's Lark, Stark's Lark *Eremalauda starki*, Greybacked Finchlark, Blackeared Finchlark and Larklike Bunting *Emberiza impetuani*) in the Karoo appear to be most frequently recorded where perennial and annual desert grasses occur (**Figure 4.14**). The areas of relatively high

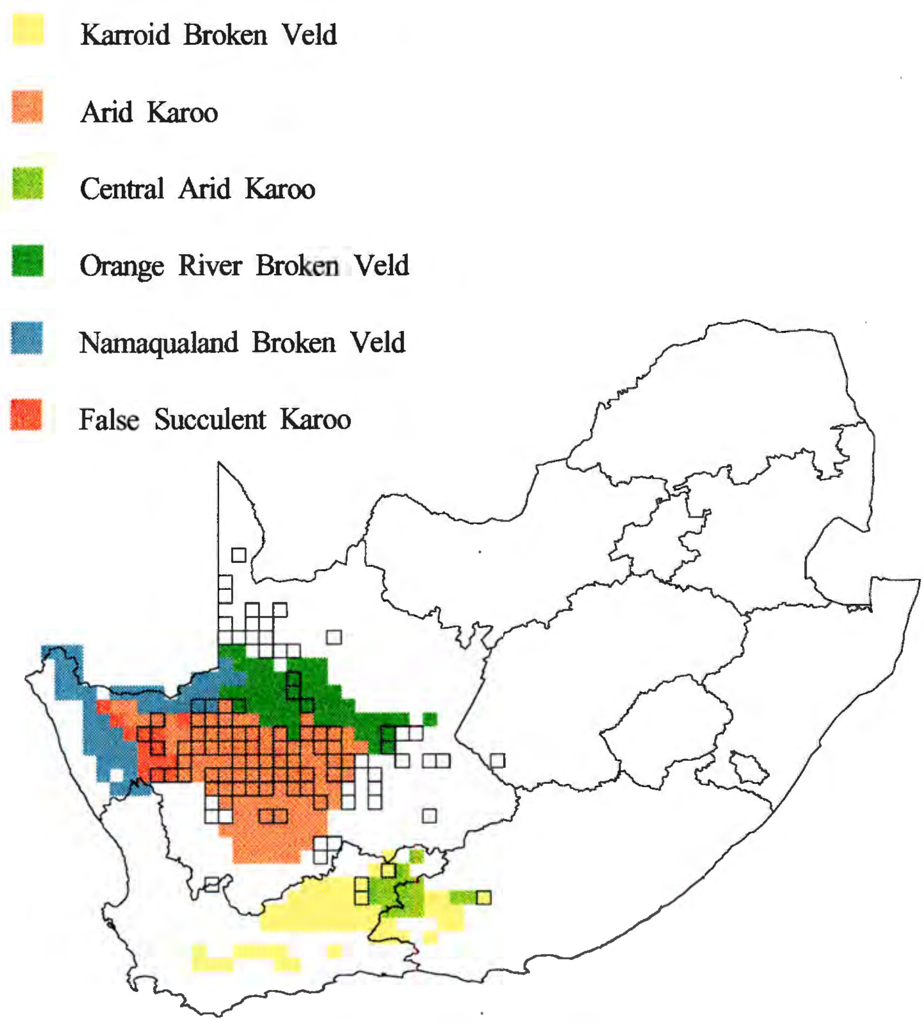

Figure 4.10. The distribution of arid and "False Karoo" veld types (Acocks, 1953). The black squares show quarter-degree squares where the reporting rate of nomadic species exceeds 20%.

species richness and high reporting rate of this group overlaps the distribution of the annual grass *Schmidtia kalihariensis*, and perennial grasses *Stipagrostis brevifolia*, *S. ciliata* and *S. obtusa*. The widespread and common desert perennial grass *S. uniplumis* var. *uniplumis* is often the dominant plant in nomadic bird breeding habitats in the Namib Desert, but appears to be relatively uncommon in the north-western Nama-Karoo. The small granivorous larks and bunting are not confined to *Stipagrostis* spp. grasslands, and in some years are abundant in other grassland and shrubland habitats. For example, in high rainfall years Pinkbilled Lark and Greybacked Finchlark may be abundant in the eastern Nama-Karoo (James, 1921, 1929; Collett, 1982) in grassy patches in which *Aristida* spp., *Eragrostis* spp. and *Themeda triandra* are common. Other desert annual grass species can provide suitable habitat at times, and both Greybacked Finchlarks and Larklike Buntings were present in large numbers in ripening *Stipa capensis* grassland at Vanrhynsdorp in September 1994 (pers. obs).

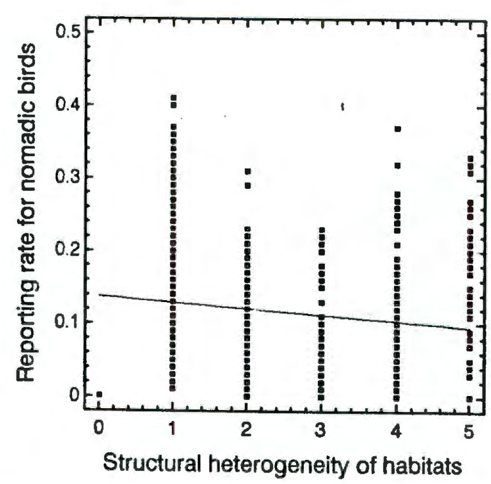

Figure 4.9. A regression of the reporting rate of nomadic species against habitat heterogeneity in each quarter-degree square in the Succulent and Nama-Karoo.

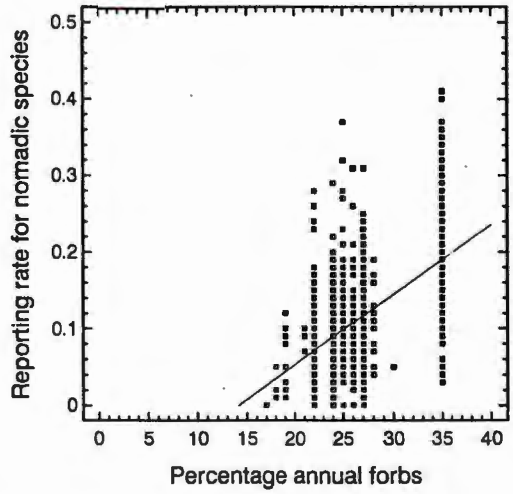

Figure 4.11. A regression of the reporting rate of nomadic species against the percentage annual forbs in the vegetation. The equation is $y = -0.12 + 0.09x$, $r^2 = 0.27$, $p<0.001$.

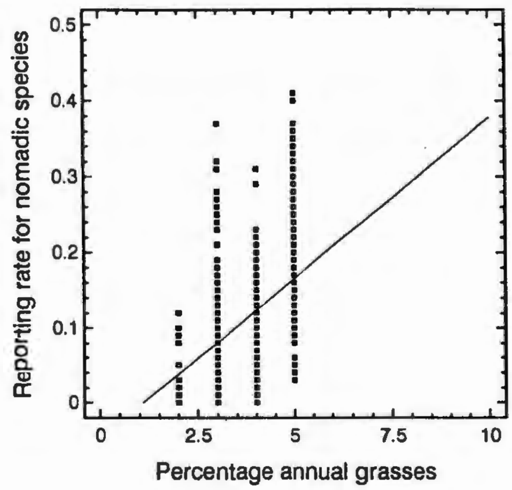

Figure 4.12. A regression of the reporting rate of nomadic species against the percentage annual grasses in the vegetation. The equation is $y = -0.04 + 0.042x$, $r^2 = 0.18$, $p<0.001$.

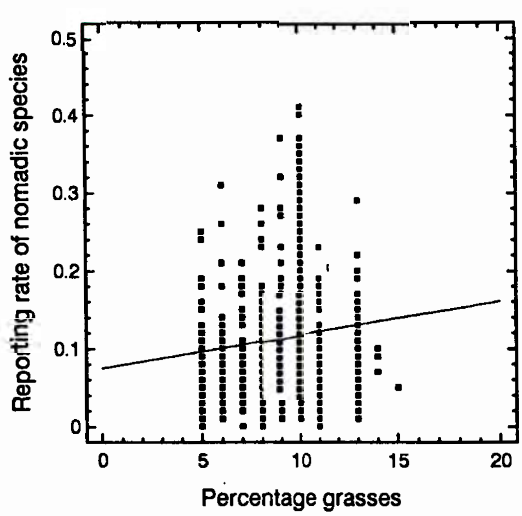

Figure 4.13. A regression of the reporting rate of nomadic species against the percentage of all grasses (including annual grasses) in the vegetation. The equation is $y = 0.07 + 0.042x$, $r^2 = 0.01$, $p = 0.001$.

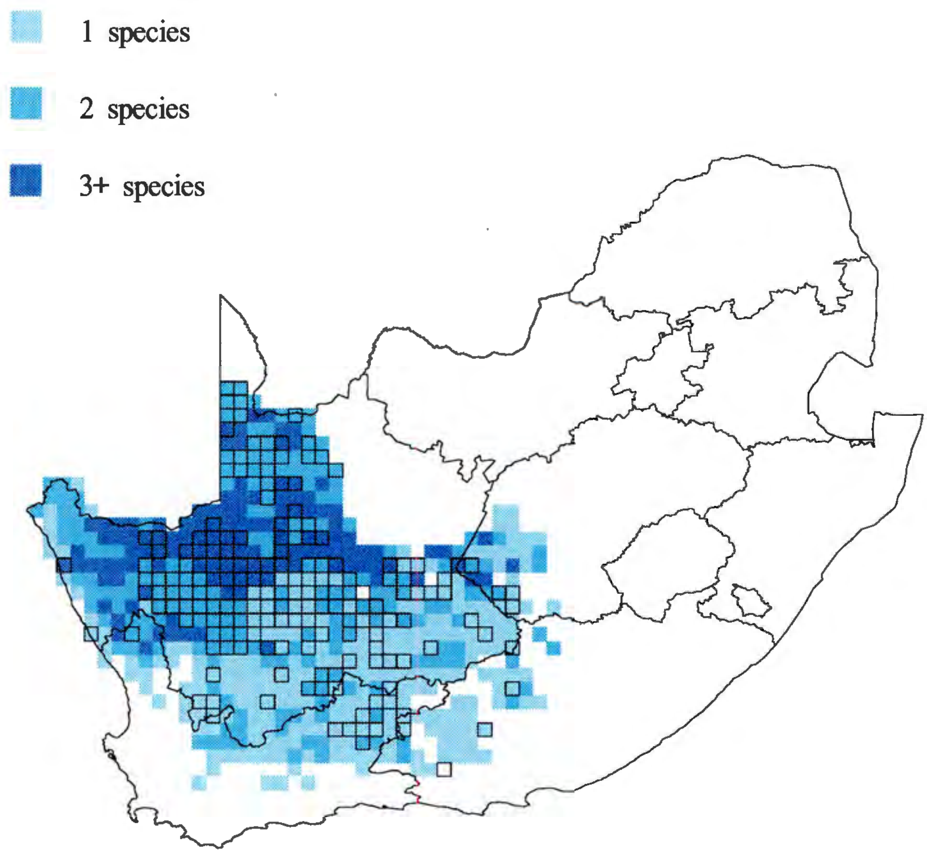

Figure 4.14. The distribution of nomadic birds in the Karoo (square marker) in relation to the species richness of a small set of annual and perennial desert grasses commonly used as food or nest material by the birds. Only those squares in which nomadic species were relatively abundant (>20% occurrence) are shown.

Food of dryland nomadic birds

Most nomadic bird species in semi-arid regions throughout the world are granivorous (Maclean, 1974; Davies, 1984). Regional nomads in the Karoo are mainly granivorous, whereas local nomads tend to be mainly insectivorous (**Table 4.2**). There are also a number of locally nomadic species that are granivorous and nectarivorous. The relative proportion of granivory in nomads is significant (Fisher's Exact Test, $p = 0.007$). Similarly, the relative proportion of insectivores among the local nomads is significant (Fisher's Exact Test, $p = 0.007$).

Table 4.2
Number of nomadic or locally nomadic species of birds in each of the major diet groups. Data from Maclean (1993).

Status	Aquatic	Raptor	Inverts.	Seeds	Nectar
Nomad	6	1	1	12	0
Local nomad	2	2	10	8	5

A discriminant function analysis of the food of all ground-foraging birds for which I have detailed stomach contents analyses shows that there is some overlap in the food of residents, local nomads and nomads (**Figure 4.15(A)**). The food data were log transformed for the tests. Both discriminant functions are significant, although the status is well defined by the first discriminant function alone (relative percentage 84.7%, Wilks-Lambda = 0.522, Chi-square = 118.96, $p < 0.001$). To remove the possible influence of phylogenetic position on these results, a discriminant function analysis using data only for larks (Alaudidae) was done. There are no locally nomadic larks, so the species were grouped into savanna species, Karoo shrubland species and arid grassland species. The arid grassland species are all nomads. The plot is shown in **Figure 4.15(B)**. Both discriminant functions are significant (relative percentage 87.4, Wilks-Lambda = 0.441, Chi-square = 116.57, $p < 0.001$), so differences in diet are fairly well defined. The arid grassland species show very little overlap in diet with the shrubland species, whereas the savanna species overlap considerably in diet with both grassland and shrubland species. The results of both tests, in general, suggest that arid grassland larks differ from shrubland larks in their diet, and that there is a similar difference between nomads and residents. From this I infer that nomads differ markedly in diet from residents.

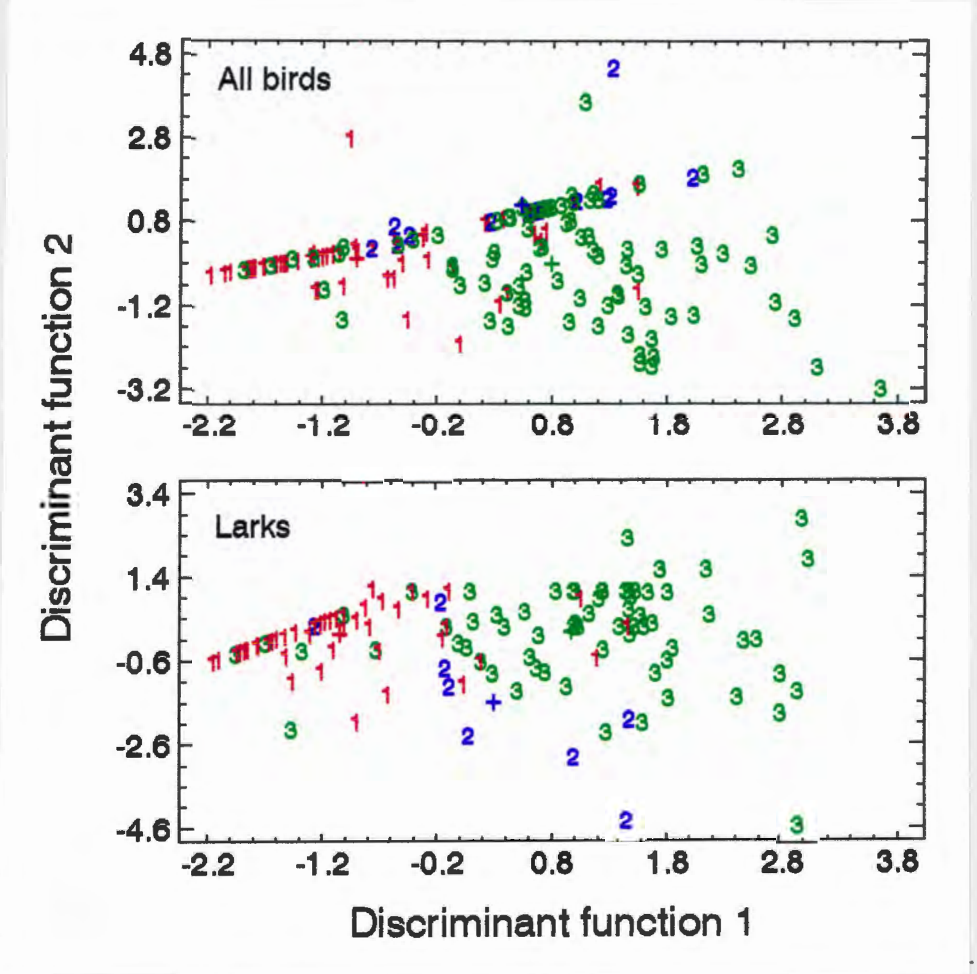

Figure 4.15(A: All birds): Plot of a discriminant function analysis of the food of nomadic species (1), locally nomadic species (2) and resident species (3). **(B: Larks):** Plot of a discriminant function analysis of the food of larks (Alaudidae). Arid grassland species (1), savanna species (2) and shrubland species (3).

There is some difference in the kinds of seeds that are eaten by resident, nomadic and locally nomadic avian granivores in the Karoo. Summarized data on the seed components of the food of 25 resident, nomadic and locally nomadic species from the Karoo is presented in **Table 4.3**. Resident species feed on the seeds of forbs, shrubs and legumes. The small nomadic larks and buntings feed mainly on the seeds of perennial and annual grasses (*Centropodia glaucum*, *Stipagrostis* spp. and *Schmidtia kalihariensis*), occasionally on the seeds of ephemeral Asteraceae and occasionally legumes, whereas the Namaqua Sandgrouse feeds largely on legumes **(Table 4.3)**. Locally nomadic species feed mainly on the seeds of forbs and shrubs. Nomadic species eat a significantly larger proportion of grass seeds (Kruskal-Wallis test, $p = 0.016$) than do locally nomadic species or residents.

Table 4.3
The proportion of different kinds of seeds in combined stomach and crop contents of granivorous or partly-granivorous birds in the Karoo. Only the seed component of the diet of individual birds is given here. Specific names are given in Appendix 1.

Residents

Species	Weight	n	Grass	Others	Legumes	Total seeds
Fawncoloured Lark	23	2	0.54	0.46	0	270
Sabota Lark	25	9	0.69	0.27	0.04	99
Longbilled Lark	50	3	0	1	0	15
Karoo Lark	31	33	0.13	0.77	0.10	3501
Red Lark	37	12	0.27	0.73	0	832
Spikeheeled Lark	27	8	0	0.97	0.03	252
Redcapped Lark	26	2	0.02	0.98	0	64
Thickbilled Lark	44	4	0.04	0.93	0.03	295
Cape Sparrow	27	1	0	1	0	5
Masked Weaver	26	1	0	1	0	29
Cape Canary	15	2	0	1	0	40
Cape Bunting	21	1	0	1	0	53

Local nomads

Species	Weight	n	Grass	Others	Legumes	Total seeds
Namaqua Dove	40	3	0	1	0	6843
Yellow Canary	17	6	0.05	0.95	0	263
Whtthroated Canary	27	7	0	1	0	242
Rock Bunting	15	1	1	0	0	32

Nomads

Species	Weight	n	Grass	Others	Legumes	Total seeds
Namaqua Sandgrouse	180	4	0	0.63	0.37	16067
Sclater's Lark	20	6	0.99	0	0.01	157
Stark's Lark	19	16	0.90	0.10	0	377
Greybckd Finchlark	17	30	0.99	0.01	0	869
Blkeared Finchlark	15	8	0.67	0.33	0	360
Scalyfthrd Finch	11	1	1	0	0	63
Blkheaded Canary	12	3	0.85	0.15	0	200
Larklike Bunting	15	6	0.91	0.09	0	138

Small birds (<25 g) eat significantly more grass seeds than larger birds in the Karoo (Mann-Whitney *U*-test: z = -2.925, p <0.003). The samples in Table 4.4 are too small to test differences in the proportion of legume seed eaten by resident and nomadic birds. Legumes appear to be important only for some of the resident larks and the nomadic Namaqua Sandgrouse. Dixon & Louw (1978) found that Namaqua Sandgrouse

in the Namib Desert feed almost exclusively on legume and forb seeds. Lists of carefully identified seeds from stomachs and crops of many of the granivorous species in southern Africa are not available, so the conclusions drawn from the above analysis are tentative. The results also support Morton & Davies (1983), who found that small birds (<100 g) in the Australian arid zone eat proportionately more grass seeds than other seeds. It would be of interest to test the generality of these findings in all arid ecosystems.

The advantages of eating grass seeds, particularly for nomadic birds, are that the seeds are often abundant after rain, the seeds are easily harvested and handled, and they lack the tannins and alkaloids often present in the seeds of forbs and shrubs (Watt & Breyer-Brandwijk, 1962). Seeds of grasses are produced relatively quickly after rain (*ca* 4 weeks from rain to seeding in *Stipagrostis ciliata* (pers. obs). There are few data available for the Karoo on numbers of grass or shrub seeds on the soil surface. A study in progress suggests that forb and shrub seeds may be abundant (up to 6 g/m^2) on sandy soils in the northern Nama-Karoo (Lloyd, Little & Crowe, 1994).

Reproduction in nomadic birds

Rainfall and its effects apparently initiate breeding in birds in the southern African arid zone (reviewed by Maclean, 1976b, 1990). Although this has been stated many times, there has been very little, if any, research on the ecosystem processes involved and the length of time various processes take to ultimately provide the resources that add up to suitable breeding habitat for birds. Although some birds may start nesting within seven days of rain (Maclean, 1976b), there is likely to be a longer lag between rain and the time that granivores can begin nesting than between rain and when insectivores begin nesting. In the northwestern and northern Karoo, the small nomadic granivores (Pinkbilled Lark, Sclater's Lark, Stark's Lark, Greybacked Finchlark, Blackeared Finchlark and Larklike Bunting) line their nests with the awns of *Stipagrostis* spp. grasses (usually *S. ciliata*) (pers. obs) (Dean *et al.*, 1992). Awns of these grass species are 40-50 mm long, and are fluffy and white. The seeds are wind dispersed (Gibbs Russell *et al.*, 1990). A common occurrence in the central and northern Nama-Karoo some weeks after rain has fallen is the wind-drifted heaps of *Stipagrostis* spp. awns that collect against obstructions. There may be a direct correlation between the productivity of the grassland and the extent to which the sand has been carpeted with awns. The small nomadic granivorous birds all gather nest material from these drifted heaps. These drifts of awns, which are extremely obvious, may provide clear visual evidence of the relative amount of primary production (*i.e.* the 'quality') of a patch.

Resident species in the Succulent Karoo breed markedly seasonally (**Figure 4.16**), whereas resident species in the Nama-Karoo tend to have a longer breeding season, less clearly defined (**Figure 4.17**). Opportunities for resident species to nest in the Nama-Karoo may be irregular because of spatial and temporal variability in resources. Resident species in the Nama-Karoo may be adapted for persistence, living at a low density and using every benefit that their territories may offer (such as eating fruit or geophytes if need be, Chapter 3).

Dryland nomadic species are less constrained by the seasons, and in both the Succulent (**Figure 4.18**) and Nama-Karoo (**Figure 4.19**) can breed throughout the year, without a clearly defined "season". The nomadic species may have fewer opportunities to breed than residents and probably have higher productivity from a successful breeding event, but the constraints of a nomadic existence together with relatively high expenditure on reproduction may shorten their life expectancies. Locally nomadic species appear to conform to resident species in general in their breeding, although less markedly seasonal (**Figures 4.20 and 4.21**).

A different breeding strategy is unique to the Doublebanded Courser, which is insectivorous, locally nomadic, breeds frequently and at any time of the year, and lays a single egg (Maclean, 1967).

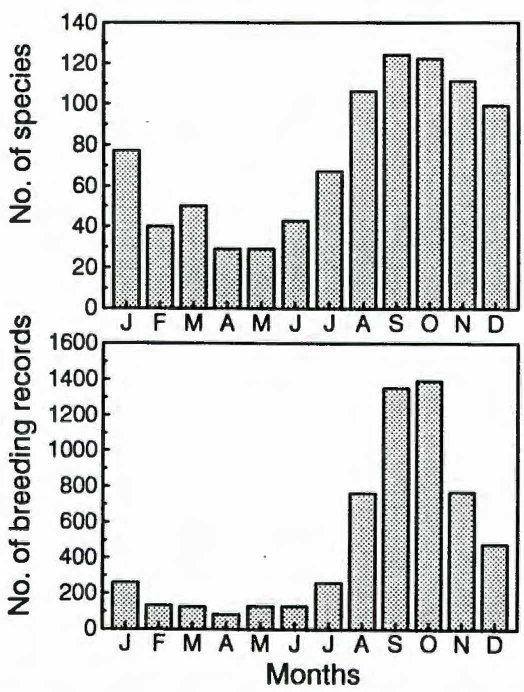

Figure 4.16. Numbers of resident species breeding and the number of nest records each month for the Succulent Karoo.

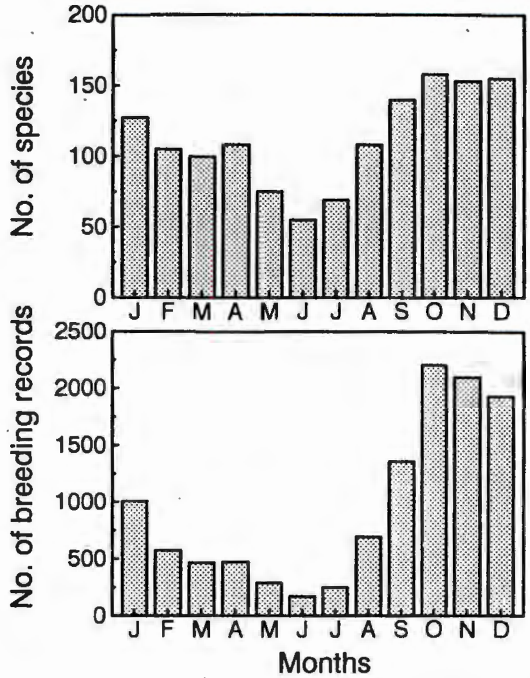

Figure 4.17. Numbers of resident species breeding and the number of nest records each month for the Nama-Karoo.

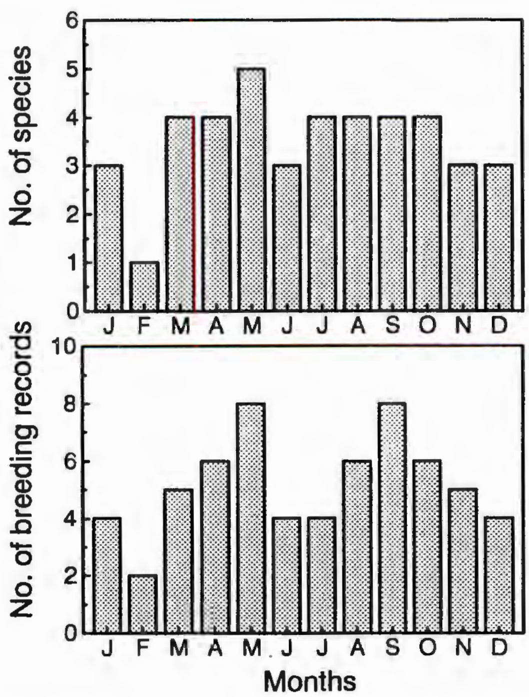

Figure 4.18. Numbers of nomadic species breeding and the number of nest records each month for the Succulent Karoo.

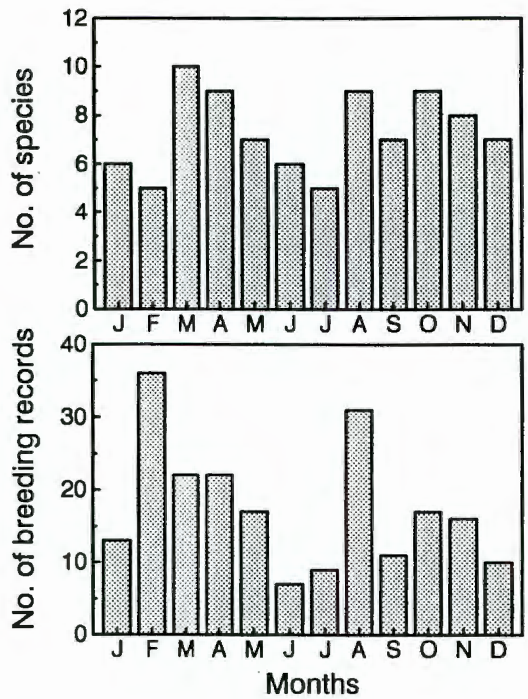

Figure 4.19. Numbers of nomadic species breeding and the number of nest records each month for the Nama-Karoo.

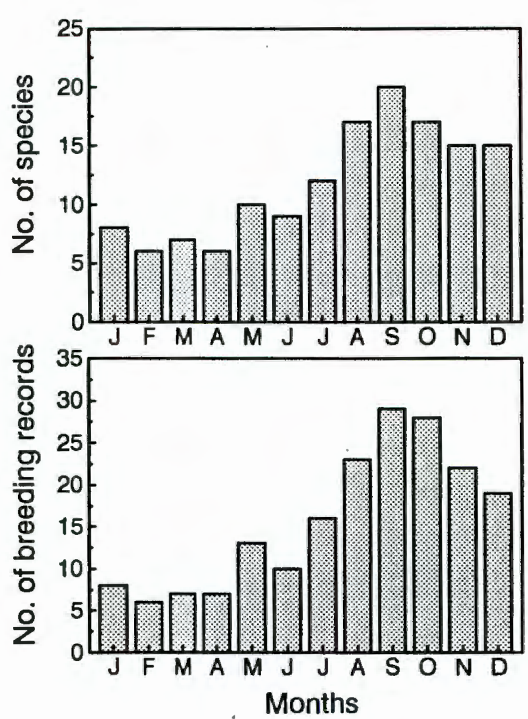

Figure 4.20. Numbers of locally nomadic species breeding and number of nest records each month for the Succulent Karoo.

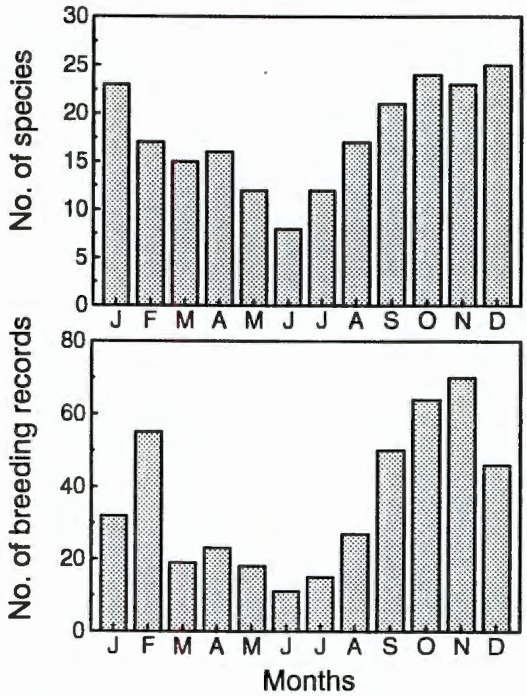

Figure 4.21. Numbers of locally nomadic species breeding and number of nest records each month for the Nama-Karoo.

Clutch sizes in nomadic larks: selection for a small clutch and short breeding cycle

It has been suggested that, as a general principle, instability of environmental conditions should favour an increase in clutch size in birds, *i.e.* that clutch sizes are inversely proportional to the climatic stability of the environment (Cody, 1966, 1971; Lack, 1968). The most apparent variation in clutch size is the relationship of clutch size with latitude (Ricklefs, 1980). In the northern hemisphere clutch size increases with increasing latitude (Klomp, 1970). A similar trend is evident in the southern hemisphere (Moreau, 1944; Yom Tov, 1987; Ford, 1989) although clutch sizes in southern South Africa are significantly smaller than clutch sizes in Israel at approximately the same latitude (Yom Tov, 1994). Ashmole (1963) accounted for this trend by hypothesizing that reproductive rate should depend on both resource levels and population density during the breeding season. This hypothesis was examined by Ricklefs (1980), who found that winter production was correlated with clutch size in birds, and concluded that variation in the seasonality of resources is the single most important cause of geographical patterns in clutch size.

A recent review of life-history styles in southern African birds (Siegfried & Brooke, 1989) showed that there is some evidence for larger clutch sizes in small insectivorous and granivorous passerine birds in the arid regions of South Africa compared with the same species in more mesic habitats. However, in reviewing adaptations in arid-zone birds, Maclean (1974) concluded that clutch size in most arid zone birds is determinate and small, usually of two to three eggs, and sometimes only one.

Average clutch sizes do not differ significantly between resident and all nomadic species in the Karoo (mean clutch size, residents, 3.1 eggs, range 1 - 10; nomads, 2.5, range 1 - 4, p = 0.08, Mann-Whitney *U*-test). However, clutch size in several small granivorous lark species, probably the most nomadic of all the birds in the Karoo, is significantly smaller than similar-sized, locally nomadic granivorous canaries and buntings, and significantly smaller than the highly nomadic Larklike Bunting. The species are Sclater's Lark, Stark's Lark, Greybacked Finchlark and Blackeared Finchlark.

These larks breed opportunistically following rainfall on arid grassy plains in the northwestern Cape Province and Namib Desert (Maclean, 1970a, 1970b; Willoughby, 1971) and lay small determinate clutches (Maclean, 1970b). They therefore have reproductive tactics which do not accord with general theories of clutch size for birds in climatically stochastic habitats.

All four species may breed in the same area at the same time, but Sclater's Lark is usually separated from the other three by different nesting and foraging substratum requirements. Sclater's Lark nests on gravel plains (Hockey & Sinclair, 1981; Dean *et al.*, 1992) or on gravel patches in poorly-drained, sparsely vegetated shrublands (Steyn & Myburgh, 1989). Stark's Lark nests on sandy desert grassland plains, Greybacked Finchlark in shrublands and grasslands on sandy and gravel plains, and the Blackeared Finchlark in shrublands and grasslands, usually on sands (Maclean, 1970a, 1970b, 1993; Willoughby, 1971; Dean *et al.*, 1992). The populations breeding in any one area when environmental conditions are favourable are fairly well synchronized (Maclean, 1970c). Pre-breeding displays in Stark's Lark and Greybacked Finchlark are similarly synchronized, hundreds of males calling and performing simultaneous aerial displays (Maclean, 1970a, 1970b; Willoughby, 1971). Social stimulation and interaction may be extremely important here in synchronizing reproductive state in the larks (see, for example, Lewis & Orcutt, 1971).

The need for synchrony in nesting is related to the brief pulse in food abundance that follows rain. Most of the net primary production on the arid plains is by grasses and annual forbs, neither of which will provide a sustainable seed resource on the soil surface (O'Connor, 1991). Net primary production in the Namib Desert (Louw & Seely, 1982) and other arid areas in southern Africa is low (Werger, 1985) and most of it occurs immediately after rain (Rutherford, 1980; Louw & Seely, 1982). The young larks are fed on insects, mainly harvester termites *Hodotermes mossambicus* and grasshoppers (Dean *et al.*, 1992). Harvester termites increase foraging activity on the soil surface when grass growth increases, and reduce foraging activity when grass becomes scarce (Coaton, 1958), so, like the seeds, they are abundantly available only for a short time after rain. Maclean (1970b) showed that Greybacked Finchlarks responded quickly to rain, and that the duration of the breeding "season" varied according to the amount of rain; in one case the breeding season lasted only three weeks (see Table 3 in Maclean, 1970b). Breeding by the larks must therefore be done in the shortest possible time. This leads to a high degree of synchrony in the breeding and a concentration of breeding birds in one area. The abundant seed presumably reduces inter- and intra-specific competition and this allows at least three species to breed together in the same habitat at the same time. A high degree of synchrony in the breeding population plus the ephemeral nature of the resource gives little time for the development of a large clutch of eggs and the provisioning of a large brood of young. As shown in **Table 4.4**, the small granivorous larks lay smaller clutches than similar-sized breeding granivorous canaries and buntings in the same habitat. Thus, selective pressure on the birds that track fairly ephemeral high-resource patches to reduce total nesting time would have operated to reduce clutch size, since each egg represents an additional 24 hours spent at the nest or in the breeding area (see Williams, 1966). Additional selective pressure to reduce total nesting time is suggested by Willoughby (1971), who found that larks breeding in the Namib Desert must complete breeding in the shortest possible time so that their post-breeding moult could take place while food resources were still available.

Table 4.4

Breeding data for four species of nomadic granivorous larks and for similar-sized small granivorous passerines. Average weight in grams for the species is given in parentheses after the species name, average clutch size with range in parentheses, incubation period as average or range and the nestling period as average or range for each species. Data from Maclean (1993) and Dean *et al.* (1992). *Egg weight calculated using Bergtold's equation (Romanoff & Romanoff, 1949).

Species	Clutch mean (range)	Incubat. (days)	Nestling (days)	Mean egg size	Egg as % ad weight*
Sclater's Lark (20)	1 (1)	*c*.13	?	21.1 x 14.4	11.3
Stark's Lark (19)	2.3 (2-3)	12-13	*c*.10	19.7 x 14.3	11.8
Greybckd Finchlark (17)	2.1 (2-3)	12-13	7-10	19.3 x 13.9	11.7
Blkeared Finchlark (15)	2.1 (2-4)	12-13	7-10	18.3 x 13.4	12.0
Yellow Canary (17)	3.0 (2-4)	*c*.12	14	18.0 x 13.2	10.3
Whitethrted Canary (27)	3.3 (2-4)	13	17	19.8 x 14.3	8.1
Larklike Bunting (14)	2.9 (2-4)	13	12-13	17.8 x 13.2	11.4

Apart from the rapid decrease in food availability, predation on eggs and young in the lark breeding areas is likely to be high. Maclean (1970b) notes that Bat-eared Foxes *Otocyon megalotis* take eggs and young and infers that foxes may have considerable impact on a breeding population of larks. Bat-eared Foxes live and forage in groups (Smithers, 1983). Maclean (1974) suggests that "a small determinate clutch is an economy measure in the face of high predation rates" - it being less costly to replace a small clutch than a large clutch. It may be significant that the eggs of the larks are no larger relative to body size, despite smaller clutches. Even Sclater's Lark, which lays only one egg, does not lay a larger egg than would be predicted by allometry (Western & Ssemakula, 1982; Kemp, 1985). Incubation period in the nomadic granivorous larks and buntings is not at or near minimum (Nice, 1953; cf. Redbilled Quelea *Quelea quelea*, Ward, 1965).

There has been, however, a marked reduction in nestling time in the larks compared with other small granivorous passerines (Table 1). Siegfried & Brooke (1989) noted a trend for small arid-zone granivorous passerines to have significantly shorter nestling periods (14.2 ± 4.9 days) than mesic-zone passerines (17.5 ± 3.7 days). In the small larks, this has been reduced to 7-10 days (Table 1). In Stark's Lark and the finchlarks, young leave the nest before they can fly, and almost before they can walk properly (Maclean, 1970b; Willoughby, 1971). There is no conclusive evidence either way that each of the pair from a nest takes charge of one nestling in Stark's Lark and the Greybacked and Blackeared Finchlarks. Clutch records (Maclean, 1970b) and nest records (S. A. O. S. Nest Record Card scheme) for the arid parts of the Cape Province show that the Greybacked Finchlark frequently lays clutches of three eggs (17.2% of 214 clutches). However, there are no records of more than two young in 13 nest records for which follow up data are available. This implies that a clutch of three eggs seldom, if ever, produces three fledglings. Maclean (1970a) notes that incubation in the Greybacked Finchlark and Blackeared Finchlark begins with the first egg. The consequence of this is that the third chick to hatch in a three-egg clutch may be seriously disadvantaged compared with its older siblings and has less chance of survival. One- or two-egg clutches in the finchlarks may be more successful in terms of number of young produced per egg than larger clutches. This is as yet untested. Morgan & Palfery (1987) hypothesized that a two-egg clutch in the Black-crowned Finchlark *Eremopterix nigriceps* is the optimal size, and note that incubation begins with the second egg, regardless of whether there are two or three eggs.

It may be that more than two young cannot be cared for satisfactorily by the adults, as suggested by Morgan & Palfery (1987) for the Black-crowned Finchlark in Saudi Arabia. These authors noted that once the chicks had been led from the nest, each under the care of one parent, the family group spent about 24 hours together before separating and that there was no further contact between the two halves of the brood. There are no comparative published data on post-nestling parental care after 24 hours in Stark's Lark and the Greybacked and Blackeared Finchlarks.

If each adult in a pair takes charge of one chick, this may confer an advantage to the young in that it then has the undivided attention of one parent and, perhaps, a greater chance of survival. Selection would thus favour a clutch of two eggs or fewer in individuals in this group of larks. Clutch size in Sclater's Lark, with a full clutch of one egg, has thus evolved to the point where time spent on egg-laying, incubation and care of the nestling has been minimized, and parental care of the chick has been maximized.

The small clutch size of these small nomadic larks implies a low reproductive rate. Breeding success (flying young produced per breeding event) is generally low (Maclean, 1970a, 1970b) and support the notion that these small larks must breed more than once in a favourable year. The brief breeding period does allow the birds to breed opportunistically (Figures 4.15 and 4.16) and to use fairly narrow "windows" of favourable environmental conditions to breed. If a low reproductive rate also means that the birds must breed often to maximize the production of young, the availability of suitable breeding habitat is a critical factor in their continued survival. The larks must be able to find high resource patches in order to nest (and maximize the production of young). It is likely that high resource patches are preferentially grazed by domestic livestock, possibly affecting the breeding success of the nomadic larks. For this reason, areas protected from domestic livestock may be extremely important in the breeding economy of the nomadic larks.

Nomadism as an evolutionary stable strategy

What are the advantages of nomadism? Why should a bird decide to move to a new patch? Or to remain on the old patch? The advantage of an individual bird moving or staying really depends on the variability of the productivity of the environment (Andersson, 1980; Davies, 1984) and on what other members of the population are doing (Sinclair, 1984). If all individuals were resident, then any individual that moved to a new patch would have an initial advantage over the rest of the population, provided that the new patch offered more abundant, or better quality resources. The first birds to move would enjoy less competition from conspecifics, more food, and perhaps escape a build-up of predators at the old patch. The advantage would be short-lived, and would only last until other birds moved to the same patch. The advantage of moving also depends on environmental conditions. In a high rainfall year, when patches are numerous and the probability of finding a high resource patch is high, then moving to a new patch is to the advantage of an individual bird. There is likely to be less competition at the new patch since the total population will be dispersed in many patches. In a low rainfall year, when patches are few and of poor quality, optimal foraging theory predicts that individuals should move only when resource levels are depleted and only when the probability of finding a better patch exceeds the probability of improvement in the current patch. In years when the rainfall is neither high nor low, the probability of improvement in the patch that an individual is occupying is probably equal to the probability of finding a better patch. Furthermore, if rain patches are randomly distributed in time and space, the probability of finding a patch on which rain has recently fallen is equal to the probability of rain falling on the current patch, and there is no advantage in moving regardless of the amount of rain. The decision to stay or move would also be influenced by the numbers of birds that had already moved to or from a patch. As birds leave a patch, there is less competition on the patch, and relatively more food available for the birds that remain, so the probability that the patch will improve increases. Similarly, as birds move into a patch, the probability that the patch will deteriorate increases and the probability of finding a better patch elsewhere will increase.

Nomadism therefore becomes an evolutionary stable strategy for individual species only when extremes in environmental conditions are frequent enough, and unpredictable enough, to maintain movements to high resource patches or to maintain dispersal away from low resource patches. If high rainfall years are too infrequent, or peaks in fluctuations in the environment too low, or rainfall patches are randomly distributed, nomadism would not be maintained as part of the individual behaviour pattern. If environmental fluctuations are too frequent and regular, the predictability of events would impose regularity in the movements of individuals. Frequent (annual) cyclic fluctuations in the environment will select for migratory, rather than nomadic, movements in birds. The advantage in nomadism really lies in an individuals ability to make the correct decision, on its ability to find a better patch, and its ability to get there ahead of the rest of the population.

It has been suggested by Andersson (1980) that the relative merit of nomadism in birds is higher with cyclic, rather than random, fluctuations in food abundance. Andersson's model indicates that large clutch size, high juvenile survival and low adult survival favour nomadism, and that adult nomadism is favoured as the interval between successive good years increases. Some bird species in the Karoo may fit Andersson's model. With random food production, no particular year is more likely than any other to be "good" and several good years, or several poor years may occur in succession. In this situation, there are advantages for the birds in being resident, since the probability of finding a better patch than the one that they are in is low. Results from the model thus suggest that cyclic fluctuations in food production will favour the evolution of nomadism in species, whereas random fluctuations will favour site tenacity. Andersson's model, however, is based on assumptions that may be unrealistic, such as that a genotype has the same survival rate whether it is nomadic or resident. The model is further based on a constant ratio between juvenile and adult survival, and does not take into account differential survival in different years. It would be of interest to test the generality of Andersson's model using data for the nomadic larks in the Karoo, but data on survival rates are lacking for this group. There is some evidence that the small granivorous larks in the Nama-Karoo would not fit the present model; clutch sizes in this group are small (Appendix 6) and breeding success is low (Maclean, 1970a).

If there are advantages in being nomadic, why then should some species choose to be resident, or at least relatively sedentary? Nomadic species are generally gregarious, feed mainly on a narrow range of seeds, with some insects (mainly termites), and tend to occur in fairly circumscribed habitats. Resident species tend to be solitary, or in pairs, and to have a fairly mixed diet of insects, seeds and fruit, and to occur in a fairly wide range of habitats. So the answer might lie partly in diet and partly in the relative ability of the two groups of species to tolerate fluctuations in habitat quality. The social organization of the two groups of species is more likely to be a consequence of nomadism or of residency than a preadaptation. There is evidently selection for gregariousness in individual nomadic species, but this varies among species (**Table 4.5**). There may be advantages in searching for high resource patches by flocks, rather than by single birds. This group foraging behaviour is also shown by such resident species as Whitebacked and Redfaced Mousebirds, Karoo Eremomela and Rufouseared Warbler. The energetic cost of moving to find a better patch may be high, and the probability for a solitary bird, or a pair of birds, of finding a new patch may be lower than for a group of birds (Cody, 1971). There are also predation risks which are greater for a solitary

Table 4.5
Average size ($\pm$ standard deviation) of flocks of various nomadic bird species in the southern Karoo. Specific names are given in Appendix 1.

Species	n	Av. flock size
Namaqua Sandgrouse	41	6.8 (3.93)
Redcapped Lark	28	8.4 (7.57)
Greybacked Finchlark	105	35.3 (68.81)
Blackeared Finchlark	39	39.8 (40.23)
Larklike Bunting	113	30.5 (50.23)

bird than a group (Kenward, 1978). The advantages of not moving for a sedentary species might be that a resident would have knowledge of favourable places for foraging and nesting, and would know where the predators were and, presumably, would have some knowledge of predator hunting patterns in its home range (Hinde, 1956). The longer a resident bird remains on its home range, the more its knowledge of the area will improve (Andersson, 1980), and the more costly, in terms of abandoning this knowledge, it is for it to move.

Why do individual birds not adopt the strategy of being nomadic during the good years and resident during the poor years? There is some evidence that all nomadic birds do not move to or from an area (Kieser & Kieser, 1978; Collett, 1982), and there is some evidence that there are regular movements by nomadic or locally nomadic species in southern Africa (James, 1929; Maclean, 1970a, 1970b; Liversidge, 1980; Collett, 1982; Siegfried, 1983; Allan, 1993; Malan, Little & Crowe, 1994). A recent model (Switzer, 1993) that investigated site fidelity suggests that individuals should be "site faithful" in unpredictable habitats. Furthermore, the success of two decision rules ("always stay" and "win-stay: lose-switch") suggests that the always stay strategy does well in unpredictable habitats, and that the win-stay: lose-switch strategy does best in predictable habitats (Switzer, 1993). Ultimately, the decision to move or to stay in any locality really depends on what benefits an individual bird will gain. The species and individuals of the nomadic birds in the Karoo may be using different tactics in different years according to the productivity of the environment. If the localities of high resource patches in the Karoo are not randomly dispersed, or are predictable in certain years, then individual nomadic birds are likely to return to them regularly.

Chapter 5
Responses of birds to rainfall and seed abundance in the southern Karoo

Introduction

Seasonal changes in habitat structure and food abundance potentially influence the species richness of birds in most terrestrial environments (reviewed by Wiens, 1989). Changes in local species richness of birds may be due to regular seasonal movements by part of any avian species assemblage in any environment that has marked seasonal changes in resource abundance. Where changes in resource levels are not so closely linked to seasonal changes, movements in birds are less regular, and species richness may be less predictable. Clear evidence of close tracking of resources has been found in many species of birds from different dietary guilds (Wiens, 1989). Changes in species richness and numbers of granivorous birds with changes in seed abundance in semi-arid habitats have been shown in Chaco, Argentina (Capurro & Bucher, 1982), in the Chihuahuan and Sonoran Deserts, southwestern U.S.A. (Brown *et al.*, 1986; Thompson, Brown & Spencer, 1991) and in Kenya, the U.S.A., Brazil and Argentina (Schluter & Repasky, 1991). It follows that nomadic granivorous birds should track resources closely, and that there should be a correlation between nomadic bird density and local seed abundance.

The variability of avian species richness and density in semi-arid habitats in South Africa has been observed and discussed by Winterbottom (1968a, 1972), Maclean (1970a, 1970b, 1970c, 1970d, 1974), Liversidge (1980), Vernon (1986) and in Chapter 4. One of the features of semi-arid shrublands, particularly karroid shrublands, is the variance in species richness and in the number of birds present in the shrubland (Winterbottom, 1968a, 1968b, 1972); this is thought to be related to local changes in resource quality or quantity. There is little seasonal change in habitat structure in shrublands in the Karoo but long dry periods and irregular rainfall probably affect the local abundance of food and local avian species richness. Bird populations in these patches may be limited by resources, and the local species richness of birds may vary in accordance with local shortages or abundances of food (see Wiens, 1989). Since these deficits or surpluses in food are likely to be of short duration, the appropriate response by the avifauna would be emigration or immigration, thus changing the species richness and the density of birds at a patch. The long-term response, in an environment where resources are relatively stable, is that sedentary or resident populations should expand until they became resource-limited. Whether resources are available for extended periods, or whether they are available ephemerally, the structure of avian communities should be such that the overall resource base is exploited most efficiently (Wiens, 1989).

In order to examine the hypothesis that patchiness in species richness in birds in the Karoo is related to changes in the abundance of food, S.J. Milton and I regularly collected information on seed abundance, soil surface microarthropods and bird species richness and abundance at a number of sites in the southern Karoo. In a conservation context, it is important to know whether small areas could serve as refugia for birds inhabiting Karoo shrublands. The present study provides information on the species richness of karroid shrublands, both at the landscape level and at the patch level. Pastoralism is an integral part of present-day Karoo ecosystems, and the effects of different kinds of domestic livestock and the extent to which the shrublands are browsed in a patch may shape the available resources for birds and thus influence the species of birds that occur in a patch. Although not discussed further here, relevant data on the browsing and grazing effects of domestic livestock on vegetation and birds were collected during the present study and will be addressed later in this thesis (Chapter 7).

Study sites

Data were collected at 40 sites (**Table 5.1**) on an east-west transect through karroid shrublands east of Prince Albert, southern Karoo (**Figure 5.1**). The sample sites were on rangelands at 5 km intervals along a roughly oval 200 km route from the Tierberg study site (fully described by Milton, Dean & Kerley, 1992), east to Rietbron and back to Tierberg along different roads. The first site was selected by driving 5 km from Tierberg, and then walking 25 m into the shrubland on the left hand side of the road. The second site was selected by driving 5 km from the first site, and so on until 40 sites had been selected. Some sites chosen in this way were not suitable for various reasons (mostly because of proximity to unusual landscape features, such as an impoundment or farmhouse) and at these sites we drove a further 1 km and marked our sample site. Sites 1-10, and 31-40 were in the (generally) between seasons rainfall area, and were in the watershed of the Gamka River. The remainder of the sites were in the (generally) summer rainfall area, and in the watershed of the Sundays River.

Table 5.1
Sampling sites in the southern Karoo. Site 1 is 5 km east of Tierberg farm house, and site 20 just west of Rietbron.

Western sites

Site	Topography	Soil	Vegetation, cover (%), ht (cm)
1	plain	silt	dwarf shrubland, 35, <50
2	plain	silt	dwarf shrubland, 35, <50
3	plain	silt	dwarf shrubland, 40, <50
4	plain	silt	dwarf shrubland, <40, <50
5	plain	sandy	dwarf shrubland, <40, <30
6	flat ridge top	shale	dwarf shrubland, <20, <20
7	gentle slope	shale	dwarf shrubland, <20, *ca* 20
8	gentle slope	shale	dwarf shrubland, 30, *ca* 30
9	gentle slope	shale	dwarf shrubland, 30, *ca* 40
10	stony plain	shale	dwarf shrubland, 20, *ca* 30
31	gentle slope	shale	dwarf shrubland, 25, 40-50
32	plain	silt	dwarf shrubland, 15, *ca* 40
33	undulating	sandy	dwarf shrubland, 20, *ca* 30
34	plain	sandy	dwarf shrubland, 25, *ca* 35
35	stony ridge	shale	dwarf shrubland, 25, *ca* 30
36	stony ridge	shale	dwarf shrubland, 30, *ca* 30
37	plain	sandy	dwarf shrubland, 35, *ca* 30
38	plain	sandy	dwarf shrubland, 35, *ca* 25
39	gentle slope	sandy	dwarf shrubland, 25, *ca* 30
40	plain	sandy	dwarf shrubland, 20, *ca* 40

Eastern sites

Site	Topography	Soil	Vegetation, cover (%), ht (cm)
11	flat ridge top	shale	dwarf shrubland, 30, *ca* 30
12	plain	shale	dwarf shrubland, 35, *ca* 30
13	gentle slope	shale	dwarf shrubland, 20, 20-100
14	undulating	shale	dwarf shrubland, 30, 40-60
15	plain	shale	dwarf shrubland, 20, 20-60
16	plain	sandy	grassy dwarf shrubland, 40, <50
17	plain	sandy	dwarf shrubland, 30, *ca* 20
18	flood plain	clay	shrubland, 25, 1-3 m
19	plain	shale	dwarf shrubland, 30, *ca* 40
20	plain	shale	dwarf shrubland, 40, *ca* 40
21	plain	silt	dwarf shrubland, 20, ~25
22	plain	sandy	dwarf shrubland, 30, *ca* 40
23	plain	sandy	dwarf shrubland, 10, *ca* 40
24	plain	sandy	dwarf shrubland, 25, *ca* 40
25	plain	shale	grassy dwarf shrubland, 25, *ca* 30
26	plain	shale	grassy dwarf shrubland, 15, *ca* 20
27	plain	shale	grassy dwarf shrubland, 25, *ca* 40
28	plain	sandy	dwarf shrubland, 15, *ca* 20
29	plain	silt	dwarf shrubland, 25, *ca* 20
30	stony plain	sandy	dwarf shrubland, 20, *ca* 15

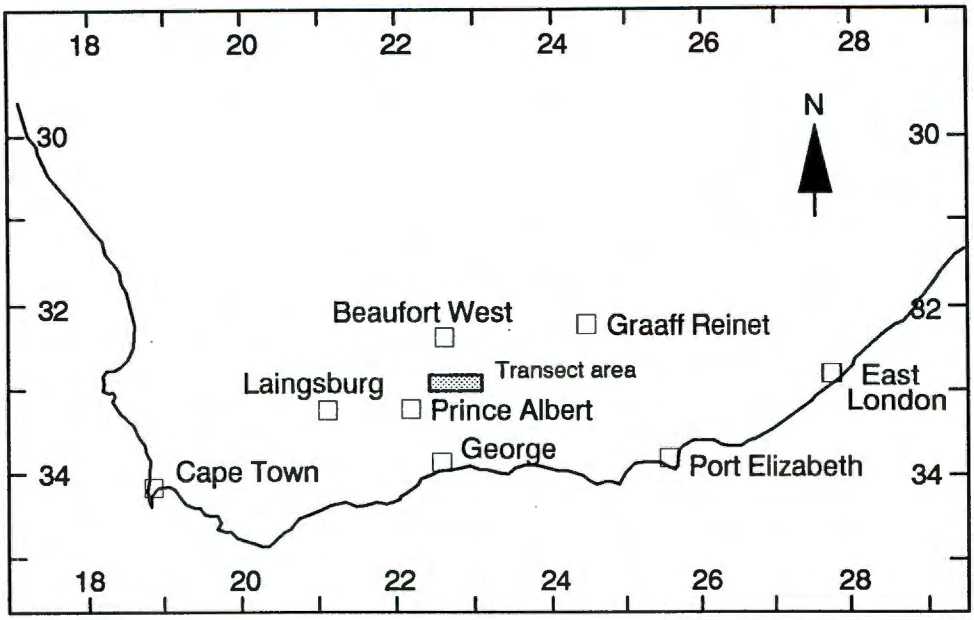

Figure 5.1. Southern South Africa, showing the area (stippled block north and east of Prince Albert) where the study was done.

Methods

The current herbivory by domestic livestock on each site was initially estimated (a subjective estimate of whether heavily grazed, moderately grazed or lightly grazed; discussed further in Chapter 7), basing the evaluation of current grazing or browsing effects on the extent to which grass and shrubs had been hedged. The dominant plant species were identified, plant cover was estimated and average plant height was measured at each site. Thereafter, on one day of each month from January 1988 to December 1990 (with the exception of October 1989), I identified all birds within a radius of 50 m of the site, and for 5 minutes counted all individuals of all species of birds within that area. All bird species were classified as either resident, nomadic or transient (see Results).

Seeds on the soil surface were sampled by running a 12 volt vacuum cleaner (with mouth 33 mm wide x 5 mm deep) for 30 seconds across the soil in the open between shrubs and for a further 30 seconds across the soil below the canopy shadow of shrubs. This provided a measure of the density of seeds and of microarthropods on the soil surface. The samples collected in this way were about 15 g of a soil/seed/microarthropod mixture per 30 second sweep, and for the whole transect an average of 23.6 ± 4.6 g of soil/seed mixture per site per month was collected and sorted.

The species richness and abundance of ephemeral plants was observed and estimated at each site, and the phenology of perennial and short-lived perennial plants was sampled by examining a variety of species and classifying them as dormant, growing, flowering or fruiting.

Data on rainfall for weather stations close to our sites were obtained from the Weather Bureau, Pretoria. I divided the rainfall stations into five groups according to their localities in relation to the sites. For groups that contained more than one rainfall station, the mean rainfall for the group was used. Rainfall data collected at the Tierberg study site (Milton *et al.*, 1992) and at the nearby Tierberg farm house were used for sites 1-4 and 36-40 (**Table 5.2**).

These data were analyzed statistically using regressions to correlate the numbers of both resident and nomadic birds at each site with rainfall, and the abundance of microarthropods, seeds and ephemeral plants. The possible relationship between rainfall and seeds, and rainfall and bird abundance was tested in two ways. A series of regressions using current rainfall ($Rain_1$) was run, and this was followed by a second set of regressions using a one-month lag in the rainfall ($Rain_2$).

Table 5.3
Total annual rainfall for sites along the transect

Locality	Total annual rainfall(mm) 1988	1989	1990	Sites
Tierberg farm	270.0	252.5	156.2	1-4, 36-40
Tierberg site	286.0	245.5	193.3	1-4, 36-40
Rondawel	138.8	157.5	116.2	5-9, 34-35
Aardoorns	167.5	166.5	179.5	10-15, 21-27
Klipkrans	173.5	299.9	105.3	10-15, 21-27
Rietbron	192.5	249.8	122.0	10-15, 21-27
Rietfontein	186.6	245.2	220.9	10-15, 21-27
Lammerkraal 1	168.2	211.5	133.0	16-20
Lammerkraal 2	148.5	212.2	150.5	16-20
Knapdraai	185.2	147.4	130.6	28-33

Results

Species richness, numbers and biomass of birds

Total species richness, including residents, nomads and transient species, ranged from 20 to 46 bird species per site (mean species richness 30.05 ± 5.31 per site). Less than half of the species recorded at most sites were considered to be resident at that site, with nomads and transients making up the remainder. The species considered resident at the study sites or nomads foraging or breeding at the study sites are given in **Table 5.3**

(a) and transient species are detailed in **Table 5.3 (b)**. Although a number of species were only sporadically recorded at any particular site, they have been classified as resident or nomad, either because they were recorded nesting at or near the study site, or they were present in groups and foraging on the site. Nomadic species are listed in Appendix 2, and in Chapter 4, Table 4.1. Species considered to be transients were those that were either recorded once only during the three years of the study, or species that were only observed flying over the site or species that have large territories, of which the site may have been a small fraction. Species that had large territories and that were present at many of the sites include Pale Chanting Goshawk, Greater Kestrel, Karoo Korhaan, Black Crow and Pied Crow. Transient species were excluded from all site analyses of abundance and biomass.

Table 5.3 (a)

Species considered to be resident, nomadic (*) or locally nomadic (**) at the study sites, ranked in order of frequency of occurrence at all study sites (no. of sites). The average frequency of occurrence at each study site out of a total of 35 samples, with the range in parentheses is given. Species recorded breeding at a study site or near (within 100 m) of a site are in bold type.

Species	No. of sites	Frequency
Rufouseared Warbler	40	16 (6-27)
Karoo Chat	40	15 (4-27)
Longbilled Lark	40	12 (3-26)
Spikeheeled Lark	40	10 (1-18)
Cape Sparrow	39	6 (2-23)
Yellow Canary**	38	6 (1-15)
Larklike Bunting*	38	5 (1-23)
Thickbilled Lark	36	13 (1-25)
Blackheaded Canary*	32	3 (1-13)
Redcapped Lark*	30	4 (1-19)
Greybacked Finchlark*	30	4 (1-11)
Chat Flycatcher**	30	4 (1-13)
Whitethroated Canary**	30	3 (1-12)
Bokmakierie	29	4 (1-11)
Namaqua Sandgrouse*	27	2 (1-5)
Fiscal Shrike	27	2 (1-4)
Tractrac Chat	22	2 (1-3)
Grassveld Pipit	21	2 (1-7)
Karoo Lark	20	6 (1-18)
Cape Bunting	20	4 (1-15)
Greybacked Cisticola	17	4 (1-11)
Karoo Eremomela	16	3 (1-6)
Redfaced Mousebird	16	2 (1-7)
Southern Grey Tit	16	2 (1-3)
Spotted Prinia	14	4 (1-10)

Table 5.3 (a), continued

Species	No. of sites	Frequency
Cape Penduline Tit	14	1 (1-2)
Cape Turtle Dove	13	3 (1-8)
Namaqua Dove**	12	2 (1-5)
Anteating Chat	10	4 (1-12)
Dusky Sunbird**	10	3 (1-9)
Pied Barbet	10	2 (1-3)
Familiar Chat	10	2 (1-10)
Yellowbellied Eremomela**	10	2 (1-3)
Pied Starling	9	3 (1-7)
Blackeared Finchlark*	9	1 (1-2)
Malachite Sunbird**	9	1 (1-2)
Masked Weaver	8	2 (1-4)
Lesser Doublecollared Sunbird**	7	2 (1-2)
Karoo Robin	6	4 (1-9)
Titbabbler	6	3 (1-5)
Longbilled Crombec	5	2 (1-5)
Plainbacked Pipit	5	1 (1-2)
Wattled Starling*	5	1 (1)
Doublebanded Courser**	4	3 (1-5)
Diederik Cuckoo	4	1 (1)
Pririt Batis	3	2 (2)
Fairy Flycatcher**	3	2 (2)
Scalyfeathered Finch*	3	2 (1-4)
Redheaded Finch*	3	1 (1)
Layard's Titbabbler	2	1 (1)
Redeyed Bulbul	2	1 (1)
Mountain Chat	2	1 (1)
Whitebacked Mousebird	2	2 (1-3)
Greyheaded Sparrow	2	1 (1)
Redbilled Quelea*	2	2 (1-3)

Table 5.3 (b)

Species considered to be transient on sampling sites, ranked in order of frequency of occurrence at all study sites (no. of sites), and in order of frequency of occurrence at each study site (frequency).

Species	No of sites	Frequency
Karoo Korhaan	40	10 (2-21)
Black Crow	40	7 (2-18)
Ludwig's Bustard	33	2 (1-6)
European Swallow	32	2 (1-5)
Pale Chanting Goshawk	20	2 (1-9)
Greater Kestrel	19	3 (1-5)
Pied Crow	10	2 (1-3)
European Swift	8	1 (1)
Rock Kestrel	7	1 (1-3)

Table 5.3 (b), continued

Species	No. of sites	Frequency
Kori Bustard	7	1 (1-3)
Rock Pigeon	7	1 (1-2)
Black Korhaan	6	3 (1-8)
Lesser Kestrel	4	1 (1)
Crowned Plover	4	2 (1-3)
Greater Striped Swallow	4	3 (1-6)
Rock Martin	4	1 (1)
Martial Eagle	3	1 (1)
Little Swift	3	1 (1)
Alpine Swift	3	1 (1-2)
European Bee-eater	3	1 (1)
Whiterumped Swift	2	2 (1-2)
Egyptian Goose	2	1 (1)
Yellowbilled Duck	2	1 (1)
Secretarybird	2	1 (1)
Avocet	2	1 (1)
Spotted Dikkop	2	1 (1)
Black Eagle	1	1 (1)
Redbreasted Sparrowhawk	1	1 (1)
Threebanded Plover	1	1 (1)
Blackwinged Stilt	1	1 (1)
Burchell's Courser	1	1 (1)
Redeyed Dove	1	1 (1)
Speckled Mousebird	1	1 (1)
Hoopoe	1	1 (1)
Clapper Lark	1	1 (1)
Sclater's Lark	1	1 (1)
Whitethroated Swallow	1	1 (1)
Brownthroated Martin	1	1 (1)
Whitenecked Raven	1	1 (1)
Capped Wheatear	1	1 (1)
Sicklewinged Chat	1	1 (1)
Fiscal Flycatcher	1	1 (1)
Palewinged Starling	1	1 (1)
Red Bishop	1	1 (1)

The species richness, numbers and biomass of birds varied at most sites, both among resident species (**Figure 5.2**) and nomadic species (**Figure 5.3**). Resident species were both more abundant and showed more variation in numbers and biomass at the western sites (Sites 1-9, 34-40) than at the eastern sites, but there was generally more variation in the numbers and biomass of nomads at the eastern sites. Nomads usually far out-numbered residents and generally made up the bulk of the biomass at most sites where they occurred. The majority of sites had a relatively high variance both in residents and in nomads, suggesting that there are local movements in species considered to be resident and that the species richness (and biomass) of the avifauna in these shrublands is not static. However, resident species did not show the extreme pattern of fluctuating abundance on the sites that was shown by the nomads, and there was no correlation between the numbers of residents and the number of nomads at all sites (resident insectivores vs nomads, r^2 = 0.01; resident granivores vs nomads, r^2 = 0.026, both n.s.) suggesting that the two groups were responding to different environmental cues. It was also noted that some sites always had very few birds and were seldom, if ever, visited by the flocks of nomads that were frequently observed at other sites.

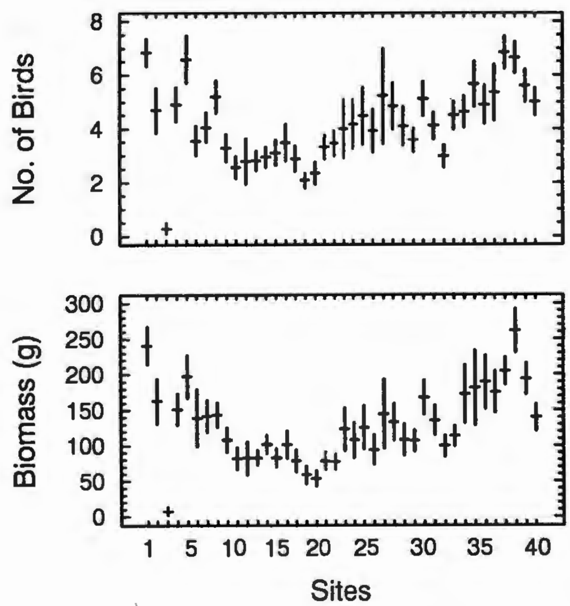

Figure 5.2. Average numbers and biomass of all resident birds at study sites. The average number is shown by the horizontal bar, while the vertical bar shows ± 1 standard error (s. e.).

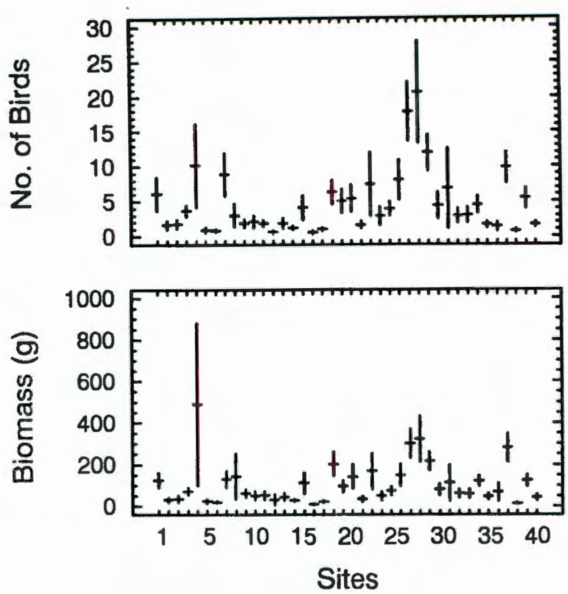

Figure 5.3. Average numbers and biomass (± 1 s. e.) of all nomadic species at study sites.

Resources, bird numbers and rainfall

The seasonal pattern in the rainfall over the three years was not very marked, although rain events tended to occur during the autumn and spring in the western sites and in summer in the eastern sites. Rainfall in both the western and eastern sites was highly variable from month to month and from year to year (**Figure 5.4, Table 5.2**). Total rainfall during the three years differed within and between sites, and showed a general trend of decreasing annual rainfall from 1988 to 1990 (**Table 5.2**).

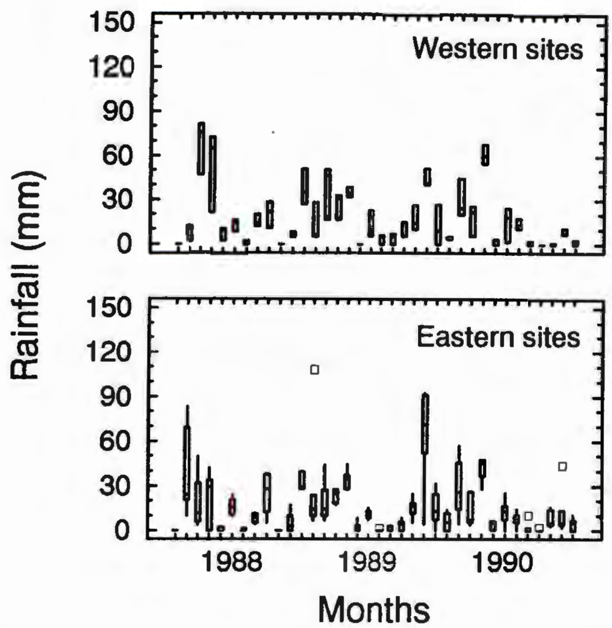

Figure 5.4. A "box-and-whisker" plot showing the average rainfall each month for sites in the western and eastern parts of the transect. The "box" covers the central 50% of the values, and the "whiskers" show the range of the data.

There was no correlation between the number of arthropods collected per sweep and current rainfall ($Rain_1$: $r^2 = 0.001$). However, the number of arthropods was significantly correlated with the amount of rain during the previous month ($Rain_2$: $r^2 = 0.02$, $p < 0.001$).

There was a weak, though statistically significant, correlation between the number of seeds on the soil surface and rainfall ($Rain_1$: $r^2 = 0.008$, $p < 0.001$; $Rain_2$: $r^2 = 0.007$, $p = 0.01$). The number of seeds collected per plot was variable, but in general seeds were more abundant (with a higher variance) in the eastern sites (**Figure 5.5**). Seeds showed a general pattern of highest abundance over the whole area of the study in late winter and spring, 1988 (**Figure 5.6**).

Similarly, there was also a weak, though significant, correlation between the number of resident birds and rainfall ($Rain_1$: $r^2 = 0.008$, $p = 0.01$; $Rain_2$: $r^2 = 0.02$, $p < 0.001$), but no significant correlation between nomadic birds and rainfall ($Rain_1$: $r^2 = 0.002$; $Rain_2$: $r^2 = 0.0002$).

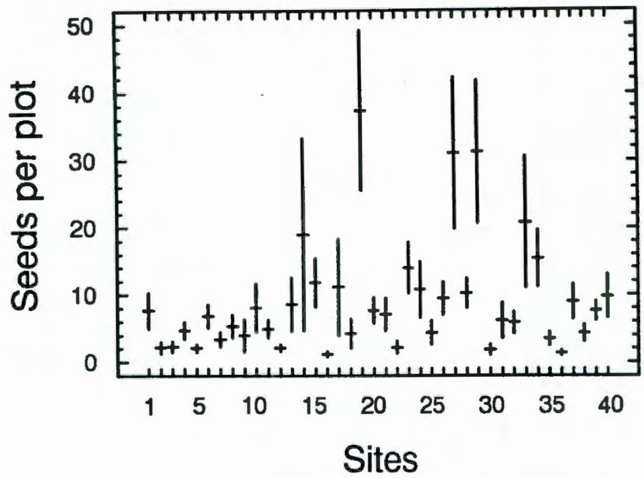

Figure 5.5. The average (± 1 s. e.) of seeds collected per sweep at each study site during 1988 - 1990.

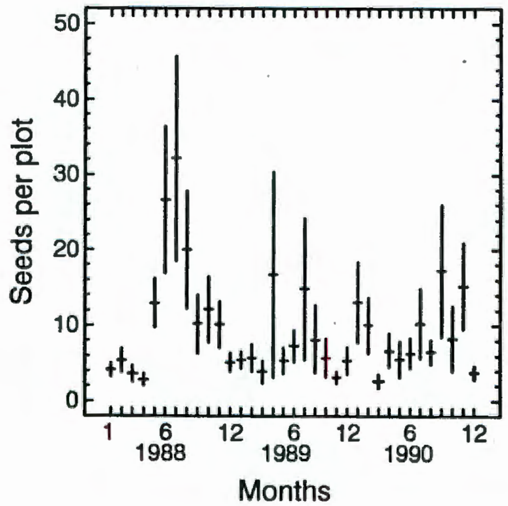

Figure 5.6. The average (± 1 s. e.) of seeds collected each month from 1988 - 1990, all sites combined.

Drainage line woodland

The major drainage line that was regularly censused for birds lies to the east of the study site and is not enclosed within the Tierberg study site boundary. The vegetation in this drainage line is up to 6 m high, and dominated by *Acacia karroo* and *Rhus* spp., with several fleshy-fruited species (*Diospyros* spp. and *Lycium* spp.) being common. The woodland is about 50 m wide at its widest point, but for much of the length of the drainage line it does not exceed 25 m in width.

Animals of the study site

A list of all invertebrate and vertebrate species (including birds) that have been recorded at the Tierberg study site was given by Milton *et al.* (1992). The full bird list will not be repeated here, and only species counted during censuses are included in the results.

Methods

From January 1988 to December 1993, I counted birds on walked fixed transects of 1 km through the shrubland and counted all birds in a fixed 1 km section of the woodland in a major drainage line. I attempted to do a series of counts (5 x shrubland counts, 1 x drainage line woodland count) once a week, but usually managed to do only about three series of counts per month for the whole period. Two transects were across the Tierberg study site, two transects were in moderately browsed and grazed rangeland to the north and south of the Tierberg study site respectively, and one transect was in heavily browsed and grazed rangeland to the west of the Tierberg study site. The results from all shrubland transects were pooled and analyzed as a single sample. In shrubland, all birds encountered on the transect line or within 50 m of the line, or that were foraging in the air over the transect area were counted. In drainage line woodland, all birds seen or heard within the woodland in a 1 km stretch were counted.

The density of birds in the shrubland was computed simply by extrapolation of the area counted and is expressed in birds per km^2. To compensate for possible overcounting, I considered that I had counted an area twice as large (*i.e.* 20 ha) as the area I actually counted on each transect (10 ha). The number of birds counted on each transect was then multiplied by five to give an estimated density of birds per km^2. This gave an estimated density that appeared to be close to the real density of birds in shrubland (determined by observations and mapping of approximate territory boundaries). More sophisticated methods of estimating bird populations, for example, the program DISTANCE (Buckland *et al.*, 1993) gave results with large variances that were intuitively unrealistic. The density of birds in the drainage line woodland is expressed in numbers of birds per km. These data were analyzed statistically using regressions to correlate the numbers of birds with both current rainfall ($Rain_1$) and rainfall in the previous month ($Rain_2$). A series of regressions was run to test the relationship between birds and plant phenology in the shrubland and in the drainage line, using data on plant phenology collected by S.J. Milton. I calculated the proportion of plants that were flowering, fruiting, with new leaves or with new shoots, and tested whether the presence of flowers, fruits, new leaves or shoots were correlated with bird numbers using stepwise linear models (Statgraphics 5.0). Sorenson's index was used to calculate the index of similarity in species composition between shrubland and woodland habitats.

Results

Species richness, numbers and biomass of birds in shrubland

A total of 69 species was recorded on counts through shrubland (**Table 6.1**), of which only 29 species were recorded on more than 1% of the counts. Species recorded once only (13 species) have been omitted from Table 6.1 and are not included in analyses. The Karoo Chat was the most frequently encountered species and was recorded on more than 50% of the counts (**Table 6.1**). The total estimated density of birds in shrubland was 32.7 ± 32.8 (S.D.) birds/km^2, and an average of 5.28 ± 5.4 (S.D.) birds were counted on each transect. The large standard deviation indicates that the numbers of birds encountered on transects varied considerably, suggesting some local movements by birds in the area. The average density of resident birds was 24.4 ± 21.0 birds/km^2, and the average number of resident birds counted on all shrubland transects was 5.1 ± 4.2 birds/transect. Nomad densities were generally low, and the estimated density averaged 1.9 ± 11.7 birds/km^2, while the average number of nomads counted was 0.5 ± 2.5 birds/transect. The average density of local nomads was estimated at 6.3 ± 20.1 birds/km^2, and the number of local nomads counted was 1.2 ± 3.9 birds/transect. The standing crop biomass of all birds calculated from all transect data was estimated to average 1593.8 ± 3031.8 g/km^2, of residents 1171.0 ± 2443.3 g/km^2, of nomads 67.9 ± 265.2 g/km^2 and of local nomads to average 354.8 ± 1657.6 g/km^2. However, resident species were fairly stable, both in numbers and in biomass (**Figure 6.2**), nomadic species were highly unstable (**Figure 6.3**) and local nomads (**Figure 6.4**) were fairly stable with occasional influxes into the area. The large numbers of local nomads were due to largely itinerant flocks of Yellow and Whitethroated Canaries encountered occasionally on the transects.

Table 6.1

Species and percentage frequency of occurrence of birds in shrubland at Tierberg, ranked in order of most frequently recorded species. The number of counts on which the species was recorded is given in parentheses. Species found nesting in the shrubland (not necessarily on transects) are in bold type.

Species	Frequency
Karoo Chat	96.3 (996)
Spikeheeled Lark	46.8 (484)
Rufouseared Warbler	44.4 (459)
Yellow Canary	28.3 (293)
Longbilled Lark	26.3 (272)
Tractrac Chat	17.1 (177)
Whitethroated Canary	14.8 (153)
Karoo Lark	12.1 (125)
Thickbilled Lark	11.9 (123)
Karoo Korhaan	8.1 (84)
European Swallow	8.0 (83)
Namaqua Sandgrouse	7.5 (78)
Greybacked Finchlark	6.8 (70)
Cape Sparrow	6.0 (62)
Fiscal Shrike	5.3 (55)
Greybacked Cisticola	5.2 (54)
Plainbacked Pipit	3.7 (38)
Black Crow	2.9 (30)
Karoo Eremomela	2.8 (29)
Doublebanded Courser	2.6 (27)
Ludwig's Bustard	2.5 (26)
Blackheaded Canary	2.0 (21)
Blackeared Finchlark	1.6 (17)
Rock Martin	1.3 (13)
Cape Bunting	1.3 (13)
Kori Bustard	1.2 (12)
Alpine Swift	1.2 (12)
Larklike Bunting	1.2 (12)
Cape Penduline Tit	1.0 (10)
European Swift	0.9 (9)
Greater Striped Swallow	0.9 (9)
Bokmakierie	0.9 (9)
Cape Turtle Dove	0.8 (8)
Redcapped Lark	0.8 (8)
Pale Chanting Goshawk	0.7 (7)
Whiterumped Swift	0.7 (7)
Grassveld Pipit	0.7 (7)
Malachite Sunbird	0.7 (7)
Common Quail	0.6 (6)
South African Shelduck	0.4 (4)
Black Harrier	0.4 (4)
Rock Pigeon	0.4 (4)
Capped Wheatear	0.4 (4)

Table 6.1, continued

Species	Frequency
Wattled Starling	0.4 (4)
Redwinged Starling	0.4 (4)
Dusky Sunbird	0.4 (4)
Secretarybird	0.3 (3)
Rock Kestrel	0.3 (3)
Black Swift	0.3 (3)
Redfaced Mousebird	0.3 (3)
Masked Weaver	0.3 (3)
Black Korhaan	0.2 (2)
Titbabbler	0.2 (2)
Spotted Prinia	0.2 (2)
Lesser Doublecollared Sunbird	0.2 (2)

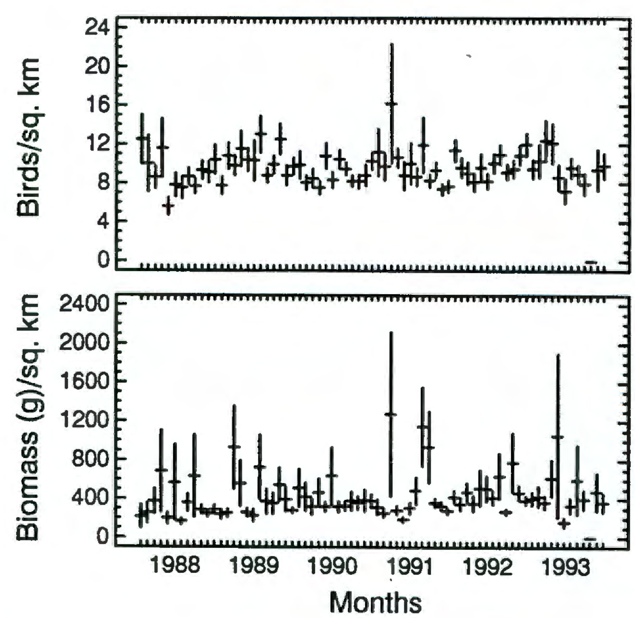

Figure 6.2. Average numbers and biomass of all birds in shrubland at Tierberg. The average number is shown by the horizontal bar, while the vertical bar shows ± 1 standard error (s. e.).

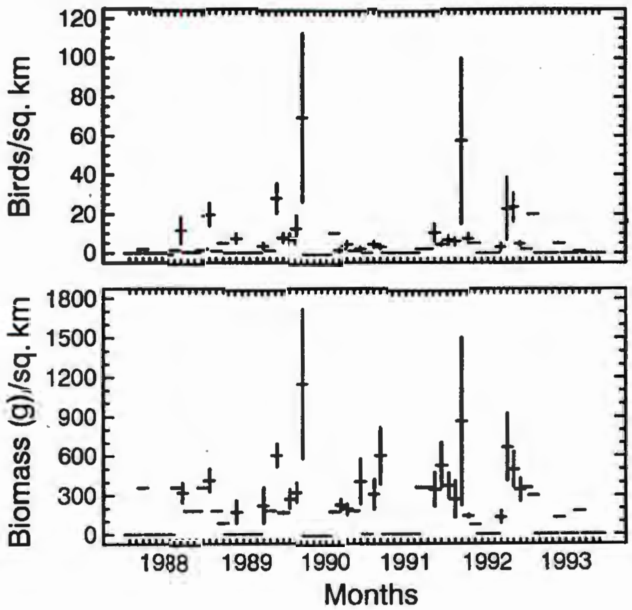

Figure 6.3. Average numbers and biomass (± 1 s.e.) of all nomads in shrubland at Tierberg.

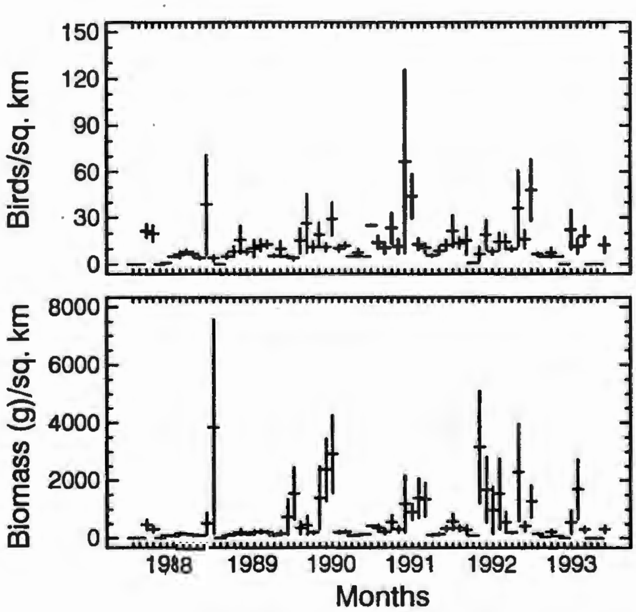

Figure 6.4. Average numbers and biomass (± 1 s.e.) of all local nomads at Tierberg.

The influence of rainfall on bird density in shrubland

The average monthly rainfall measured at the Tierberg site is given in **Figure 6.5**. There was no correlation between total bird numbers and $Rain_1$, nor, in general between total bird numbers or total bird biomass and $Rain_2$. Numbers and biomass of residents, nomads and local nomads were not individually correlated correlated with either $Rain_1$ or $Rain_2$. Numbers and biomass of nomads showed the strongest, though not significant, correlations with $Rain_2$. However, a stepwise model using $Rain_2$ as one of the variables shows that $Rain_2$ and plant phenology are significant correlates of nomad numbers. The total annual rainfall appeared to influence the density of birds in the shrubland, although the correlations were not significant.

Shrubland plant phenology and bird density

A stepwise model, using bird numbers or biomass as the dependent variable, and $Rain_2$ and plant phenology (flowering, fruiting, new leaves, shoots) as the independent variables, showed that there was no correlation between total bird numbers and plant phenology, but there was a weak, though significant, correlation between total bird

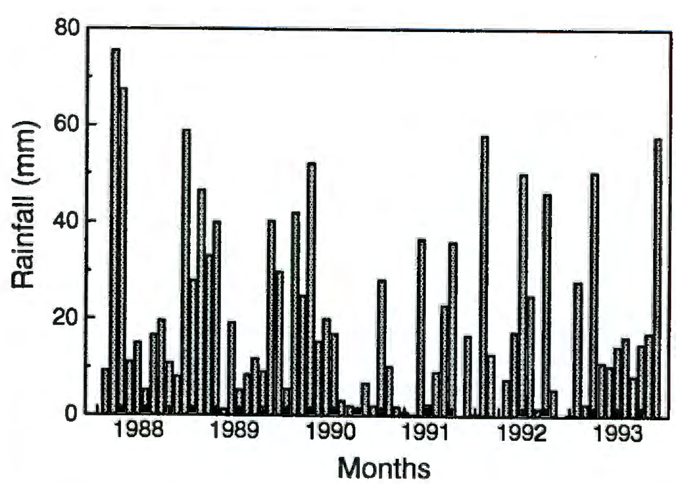

Figure 6.5. Total monthly rainfall recorded at the Tierberg study site from 1988 to 1993.

Table 6.4
Species of birds recorded only in drainage line woodland at Tierberg.

Species
Egyptian Goose
Namaqua Dove
Diederik Cuckoo
Spotted Eagle Owl
Speckled Mousebird
Whitebacked Mousebird
Hoopoe
Pied Barbet
Greater Honeyguide
Cardinal Woodpecker
Pearlbreasted Swallow
Southern Grey Tit
Olive Thrush
Familiar Chat
Cape Robin
Karoo Robin
Layard's Titbabbler
Barthroated Apalis
Longbilled Crombec
Chat Flycatcher
Fiscal Flycatcher
Pririt Batis
Fairy Flycatcher
Southern Tchagra
Cape White-eye
Common Waxbill

Discussion

At the beginning of this chapter I posed three questions: (1) do nomadic species have regular seasonal movements to the same area every year, differing only in relative abundance, (2) how stable are populations of resident species within a small area, and, (3), what is the contribution of drainage line woodlands to the species richness of the southern Karoo?

On the plains, some nomadic species appear to have regular seasonal movements to the same area every year, but their relative abundance differs markedly from year to year, and this is probably related to the patchiness, both in time and space, of certain resources. For example, high numbers of Namaqua Sandgrouse at Tierberg during 1991 and 1992 were during a period when an annual legume (*Lotononis* sp., Fabaceae) was extremely prolific in the study site (and in the general area) for the first time since 1987. Although no crop or stomach contents of Namaqua Sandgrouse were obtained, the birds were observed consistently feeding among the plants, strongly supporting the idea that the presence and abundance of sandgrouse was due to the prolific seed crop of this single legume species. Other nomadic species appear to be less regular in their movements in the southern Karoo. Driving forces controlling movements of Greybacked Finchlarks, Blackeared Finchlarks and Larklike Buntings in the southern Karoo are unclear, especially as the three species may be responding to different environmental stimuli (Chapter 5). The movements of small granivorous nomadic birds at Tierberg appear to be even more irregular than movements of nomads on the Tierberg-Rietbron transect (Chapter 5) and this may be due to the lack of grass on the Tierberg study site. Small granivorous nomads apparently feed mainly on grass seeds (Chapter 4) and are likely to occur more frequently and predictably at sites where grasses are common.

Resident species appear to be constant in terms of species richness, but less stable in terms of density. The patterns of presence on the Tierberg site are not dissimilar to the results obtained in the Tierberg-Rietbron transect (Chapter 5). There may be some movement by resident species on the Tierberg site to high resource patches or away from low resource patches, but whether these movements are local or on a landscape scale is not clear. It is also unclear whether the increases and decreases in the density of resident birds is due to the dispersal or immigration of young. The possibility also exists that the increases and decreases in the numbers of residents are due to the rearrangement of territories. Theory predicts that resident species should remain on their territories in unpredictable environments, when the average quality within a territory may be equal to all other territories (Switzer, 1993). However, it may be hypothesized that territories in strongly territorial species such as the Karoo and Tractrac Chats change according to the dispersion of patches of high resource density in the area. Populations of different insects, for example, occur in high densities at different scales in different years. Cicadas (*Quintillia* spp.) were abundant in some years in patches ranging from <1 ha to >1 km^2 (Dean & Milton, 1991, 1992; Milton & Dean, 1992), while chrysomelids may be abundant in some years in patches of <1 m^2 (Milton, 1993; S.J. Milton, pers. comm.). It is likely that at times of abundant prey there is some local movement by resident birds, and there may also be breakdowns in territorial barriers so that there is a high degree of overlap in space and in diet by resident birds. For example, an increase in density and species richness, in response to seasonally abundant cicadas, together with a high degree of overlap in diet and space, has been recorded in the birds of desert riparian communities in the southwestern U.S.A. (Rosenberg, Ohmart & Anderson, 1982). Very high quality patches are probably also undefendable.

The annual variation in numbers of resident birds on the Tierberg site suggests that the total annual rainfall may be more important than the monthly rainfall in influencing the density of birds in the following year. Changes in bird density might not be as tightly linked to short-term changes in local primary and secondary production as to the production status of the whole system. This might explain why correlations between current or the previous month's rainfall, plant phenology and birds at Tierberg are so poor. Unlike the results of other studies in semi-arid habitats (e.g. George *et al.*, 1992), there was a negative correlation between the total number of birds in the shrubland and the total annual rainfall. This may be due to larger flocks, or local aggregations of birds on the Tierberg site encountered on transects during the dry years, resulting in unusually high estimates of total numbers of birds on the site. Cody (1971) showed that flock sizes of small granivorous birds increased in the Mojave Desert in dry years when there were local shortages of food (seeds). Studies have shown that there are substantial reductions in bird density and species richness during dry years in semi-arid grasslands (George *et al.*, 1992).

Drainage line woodlands in the southern Karoo contribute substantially to the species richness of areas, as they do in semi-arid and arid habitats in other parts of the world (Szaro & Jakle, 1985). In view of the number of species common to both woodland and shrubland, drainage line woodlands may provide refuges for shrubland species in times of extreme drought or other landscape-level disturbances. The species richness of drainage line woodlands at Tierberg was fairly stable but it may be influenced to some extent in the short term by climatic events up- or downstream, and in the long term by the removal of large trees or heavy browsing of undergrowth by domestic livestock. The importance of large trees, as distinct from all trees, has been discussed by Milton & Dean (in press b). The species richness of drainage line woodlands may also be influenced to an even greater extent by events in the surrounding shrubland, such as severe hail storms that defoliate shrubs, or fire (rare in the Karoo, see Edwards, 1984). The density and species richness of birds in drainage line woodlands was positively correlated with total annual rainfall, and may indicate the movement by shrubland species into woodland during higher rainfall periods. Species overlaps between the shrubland habitat and the woodland habitat, particularly species nesting in both habitats, may also be due to the availability of particular types of nest sites that are common to both habitats. For example, Greybacked Cisticolas nested in both shrubland and drainage line woodland, and in both habitats nested in the grass *Stipagrostis namaquensis* and in thorny *Berkheya* spp.

In the context of protected areas, both shrublands and adjacent drainage line woodlands in the Karoo have unique component species. At least 23% of the total avian diversity of the plains shrubland, and 30% of the total avian diversity of drainage line woodland only occurs in one or other habitat. Preserving both habitats, at least in the southern Karoo, maximizes the potential to conserve considerably more species than protecting either shrubland or drainage line woodland alone. It is unlikely that either of these habitats would be preserved without the other, but the possibility exists that they may be managed differently. For example, firewood may be harvested from drainage line woodland, even in a so-called "nature reserve", leading to changes in the structure of the woodland (Acocks, 1976) and possible changes in the species richness and abundance of insects (Gess & Gess, 1993a, 1993b).

In general, the more structurally diverse woodland had more species, more breeding species and higher numbers of birds than the structurally homogeneous shrubland, supporting the findings of many other studies in desert (Tomoff, 1974; Vander Wall & MacMahon, 1984; Szaro & Jakle, 1985; Parker, 1986) and other habitats (reviewed by Wiens, 1989; Telleria & Carrascal, 1994). The density of birds in drainage line woodland was an order of magnitude higher than the density of birds in shrubland so the contribution by the woodland community to the total bird biomass of the ecosystem is considerable.

Conclusions

The most important finding from this study is that total bird density, both in numbers and in biomass, varies locally in time and space, but species richness, at least in the resident species, is fairly constant. The implications of this for the protection of birds in the Karoo is that the size of protected areas should be calculated on the density of the rarest resident. This would ensure that the protected area is large enough to protect all resident species at all times. The size of a protected area should be determined by a "worst-case scenario" and should then be large enough to contain the minimum viable population of residents in the driest years. It is essential to protect both shrublands and adjacent drainage line woodlands in the Karoo. By preserving both habitats, at least in the southern Karoo, more than twice as many bird species would be offered some protection than if one habitat alone was protected.

Chapter 7
The effects of domestic livestock on the avifauna and the state of rangelands in the Karoo

Part 1: The effects of heavy grazing on species richness and abundance of birds

Introduction

Although ecologists have expressed concern about the apparent progressive loss of secondary productivity and species richness of the biota of arid and semi-arid rangelands in southern Africa over the past century (reviewed by Milton *et al.*, 1994), shifts in the abundance of plant species other than those palatable to domestic livestock, or losses of native animals as a result of grazing has received less attention. Although no specific study in the Karoo has demonstrated that heavy grazing by domestic livestock has led to the extinction of animal species and the loss of species richness from an area, several studies have shown that changes in habitat diversity caused by grazing can affect some animal species (Milton & Dean, 1992, 1993; Milton *et al.*, 1994; Dean *et al.*, in press a, b; Dean, Milton & du Plessis, in press c).

Karoo rangelands lack stability but are apparently strongly resistant (see Pimm, 1986). It has been suggested elsewhere that changes in the vegetation and soil of Karoo rangelands proceeds in measurable stages, with shifts in the relative abundance of plants (Milton *et al.*, 1994; Milton & Hoffman, 1994). Rangelands that have shifted through transitions to new states may not return to their original state even when rested for decades (Westoby *et al.*, 1989; O'Connor, 1991; Milton *et al.*, 1994). Problems in protecting biodiversity, especially avian diversity, in the arid parts of South Africa have recently received attention (Siegfried, 1989; Hilton-Taylor & le Roux, 1989) and it is of interest to examine which avian species groups are affected by changes in rangeland condition. Preliminary findings suggest that, with heavy grazing, changes in the relative abundance of some species with may lead to cascade effects and the disruption of seed dispersal and other mutualistic relationships (Dean *et al.*, in press b).

There are few published studies on the effects of vegetation change on the diversity and relative abundance of animal communities in semi-arid and arid areas in South Africa (Novellie *et al.*, 1988). Avian species richness and density throughout the

Karoo may be influenced by the effects of grazing by domestic livestock, as has been found in semi-arid ecosystems elsewhere (Medin, 1986; Taylor, 1986; Bock & Bock, 1988; Tidemann, 1990; Baker & Guthery, 1990; Reid & Fleming, 1992). Vegetation change (as a result of grazing by domestic livestock) is implied by Hare (1937) to be a factor affecting birds locally in the northeastern Karoo. A study of the Red Lark and its habitat suggested that grazing by domestic livestock and resulting vegetation change on dune grasslands can affect the local abundance and distribution of the lark (Dean *et al.*, 1991). Plant-avian granivore interactions are most likely to be adversely affected by heavy grazing pressure on rangelands. For example, the seeds of small legumes are eaten by many birds in the Karoo (Chapter 4), and legumes are among the first plants to be eradicated when grazing pressure is high (McCabe, 1987).

The major land-use practices in the Karoo were described and discussed briefly in Chapter 2 (Part 2: Land-use). The objective of the present chapter is to examine the possible effects of grazing by domestic livestock on the avifauna of the Karoo. In Part 1, the results of two studies that examined the differences between the species richness and numbers of birds occurring on lightly grazed, moderately grazed and heavily grazed shrublands in the southern Karoo are presented. Data collected during the Tierberg-Rietbron transect study (Chapter 5) and at Tierberg (Chapter 6) were examined to discover whether there were clear differences in the avifauna of sites that were heavily grazed compared with sites that were moderately, or lightly grazed. The effects of grazing on other biota at these sites is discussed by Dean *et al.* (in press b).

Tierberg-Rietbron transect study

Methods and study sites

Methods of counting seeds and birds on the transect study, and a brief description of the sites are given in Chapter 5. Bird species were classified as resident or nomadic, and insectivores or granivores. Analyses of patterns of occurrence of birds on the different sites were done using these groups, and not using the data for individual species. A subjective, independent estimate by two observers of current herbivory on the 40 sites that were studied is given in **Table 7.1**.

Table 7.1

Current herbivory on study sites on the Tierberg-Rietbron transect.

Herbivory	No. of sites
Lightly-grazed	3
Moderately-grazed	19
Heavily-grazed	18

Results

The number of seeds on the soil surface at all study sites is shown in **Figure 7.1.** Although there is little difference in mean numbers, the data show a trend towards increasing numbers of seeds on the soil surface as grazing pressure increased. Surface seed assemblages in lightly grazed sites were dominated by perennial shrubs, whereas seed assemblages in heavily grazed sites were dominated by annual forbs and annual grasses.

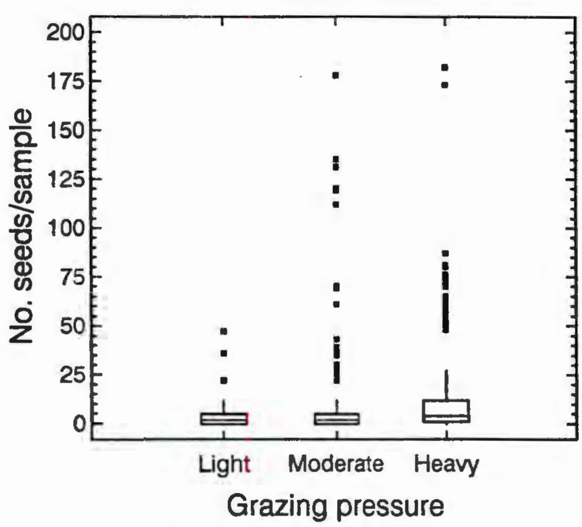

Figure 7.1. The number of seeds on the soil surface at all study sites.

Species richness (total number of species observed over three years) of birds was highest on the heavily grazed sites (58 species), intermediate on the moderately grazed sites (53 species) and lowest on the lightly grazed sites (47 species). However, the average number of species recorded in each sample on the sites was highest on lightly grazed sites (4.8 species per sample), suggesting that species richness on these sites is more stable. There was little difference between the species numbers on moderately grazed and heavily grazed sites (3.7 and 3.8 species respectively). The difference in species numbers between lightly grazed and heavily grazed sites is significant (ANOVA: $F_{2,1422} = 11.53$, $p < 0.001$). There was no difference in the mean numbers of all birds recorded at each site, but there was most variation in numbers on the heavily grazed sites (**Figure 7.2**). Numbers of insectivores and granivores showed a similar pattern, with little difference in average numbers between sites, and most variation in the heavily grazed sites (**Figure 7.3, 7.4**). The differences are not significant.

Average numbers of residents were highest on the lightly grazed sites (**Figure 7.5**). The difference is significant (ANOVA: $F_{2,1319} = 5.17$, $p = 0.005$) although the variance in the data suggests that patterns of occurrence of residents are not entirely clear. Nomads showed a clear pattern of occurrence and were most frequently recorded on heavily grazed sites, although there is little difference in average numbers of nomads between the three classes of sites (**Figure 7.6**), and the differences are not significant (ANOVA: $F_{2,382} = 2.36$, $p = 0.09$).

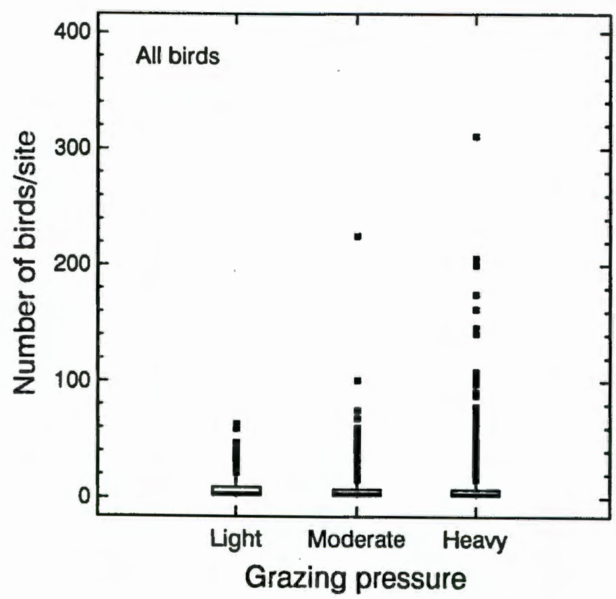

Figure 7.2. Numbers of all birds recorded at sites between Tierberg and Rietbron.

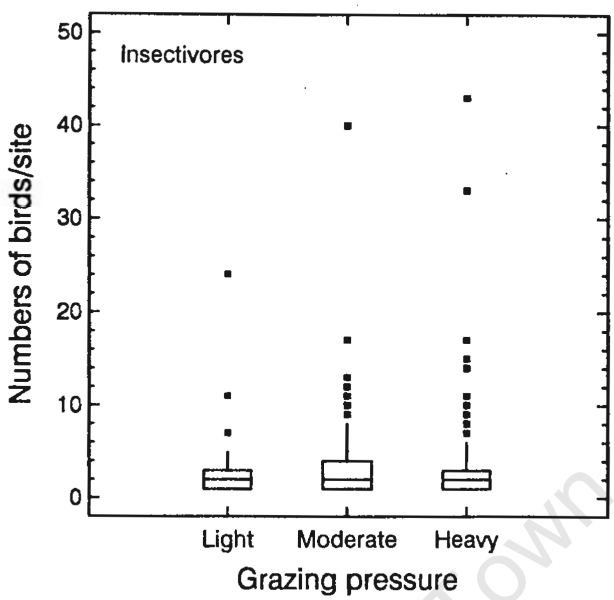

Figure 7.3. Numbers of insectivorous birds recorded at sites between Tierberg and Rietbron.

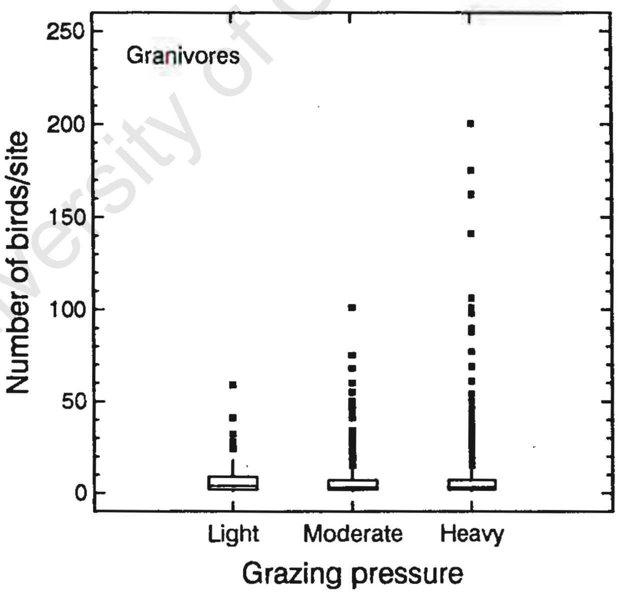

Figure 7.4. Numbers of granivorous birds recorded at sites between Tierberg and Rietbron.

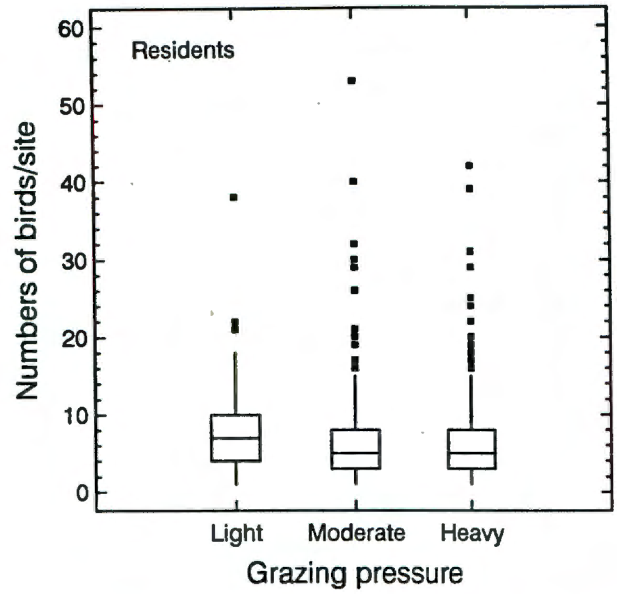

Figure 7.5. Numbers of resident birds recorded at sites between Tierberg and Rietbron.

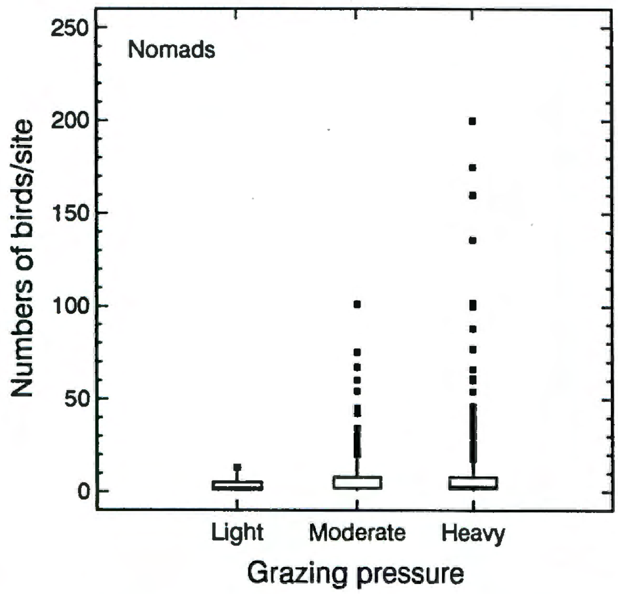

Figure 7.6. Numbers of nomadic birds recorded at sites between Tierberg and Rietbron.

Tierberg study

Methods and study site

Three sites at Tierberg Karoo Research Centre were intensively sampled. The study area is briefly described in Chapter 6, and fully described by Milton *et al.*, (1992). The study sites at this locality were (1) the Tierberg study site, which is a fenced exclosure 1 km^2 from which all domestic livestock have been excluded for the last 7 years, and currently lightly grazed by wild herbivores, (2) moderately grazed rangeland immediately adjacent to the Tierberg site on which Merino sheep have been stocked at 1 sheep per 6 ha for the past 40 years, and (3) adjacent rangeland that has a history of overstocking and heavy grazing by ostriches, wool and mutton sheep until about 1960, and subsequently less heavily stocked.

On all three Tierberg sites, during the period January 1990 to December 1993, I counted all birds seen within 50 m either side of a 1 km transect line, so an area of 10 ha in each grazing treatment was effectively sampled. Two transects each were done in lightly grazed and moderately grazed sites, but only one transect was done in the heavily grazed site. As in the transect study, bird species were classified as resident or nomadic, and insectivores and granivores, and analyses were done in a similar way.

Results

Numbers of species of birds (total number of species observed over six years) showed clear trends with the highest numbers of species on the lightly grazed sites (50 species), intermediate numbers of species on the moderately grazed sites (48 species) and lowest numbers of species on the heavily grazed site (36 species). The average number of species seen per transect was also highest on the lightly grazed sites (3.8 species) and lowest on the moderately grazed sites (2.6 species), with the heavily grazed sites intermediate with 3.2 species. The differences are significant (ANOVA: $F_{2,1028} = 64.83$, $p < 0.001$).

The average numbers of all birds seen on each transect was similar on both the lightly grazed and heavily grazed sites, but at all sites there was considerable variation in the count data (**Figure 7.7**). Numbers of insectivores increased with decreasing grazing pressure and average numbers were highest on both lightly grazed and moderately grazed sites (**Figure 7.8**). Average numbers of granivores were similar in all sites, but showed most variation in the heavily grazed sites (**Figure 7.9**). Neither insectivore numbers, nor granivore numbers differ significantly between sites.

The numbers of resident birds were highest on the lightly grazed sites (**Figure 7.10**). The difference is significant (ANOVA: $F_{2,998} = 31.87$, $p < 0.001$). Average numbers of nomadic birds were similar at all sites, but was highest and showed most variation at heavily grazed sites, possibly as a result of influxes of groups of nomadic granivores (**Figure 7.11**). The number of nomadic birds on heavily grazed sites was significantly higher (ANOVA: $F_{2,139} = 3.21$, $p = 0.04$).

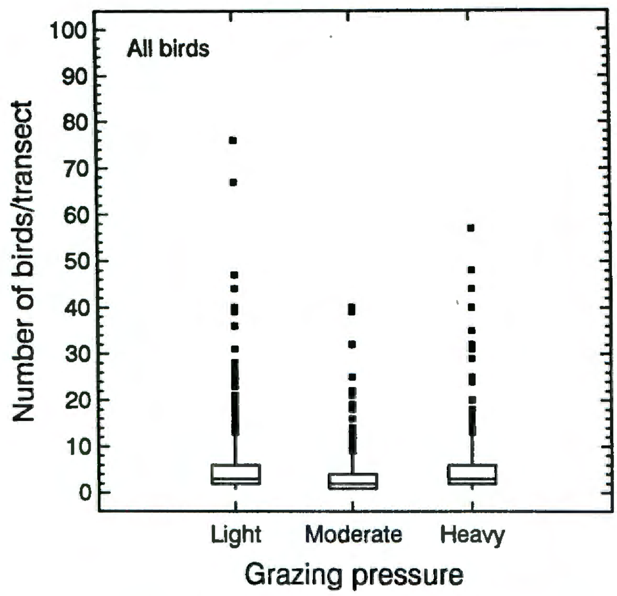

Figure 7.7. Numbers of all birds seen on transects on Tierberg.

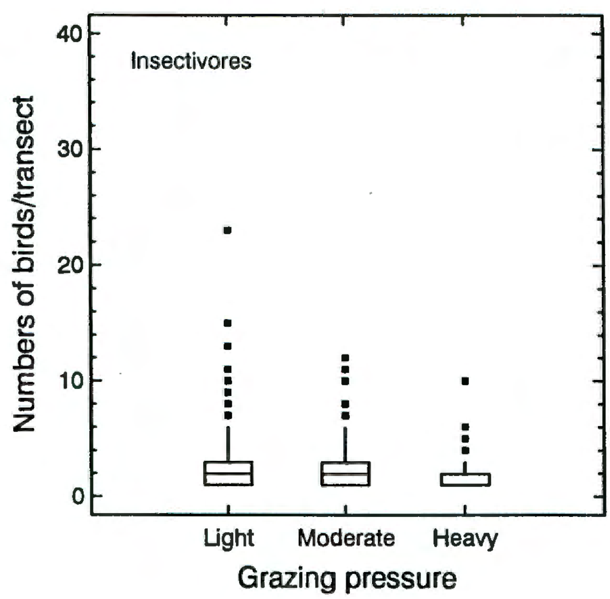

Figure 7.8. Numbers of insectivorous birds counted on transects on Tierberg.

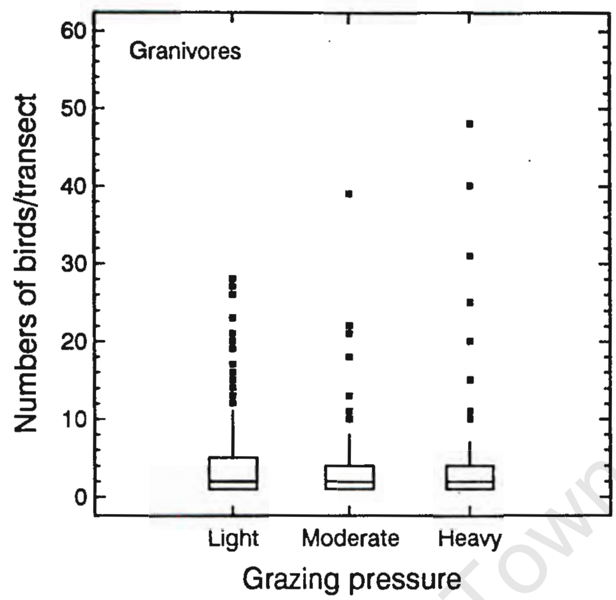

Figure 7.9. Numbers of granivorous birds counted on transects on Tierberg.

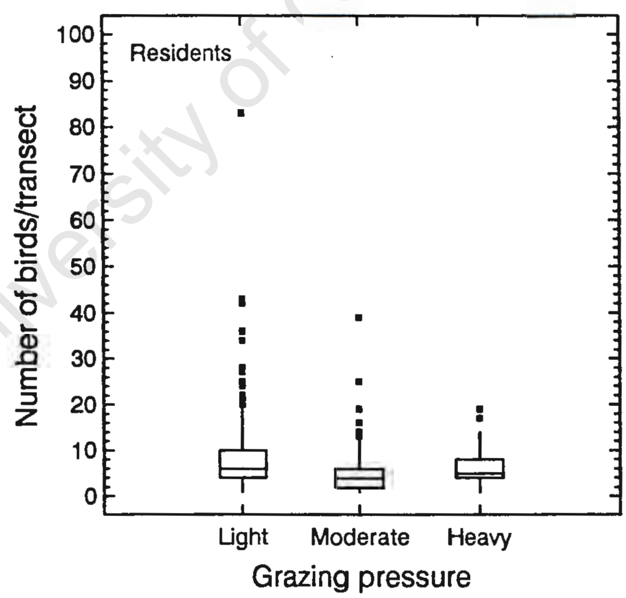

Figure 7.10. Numbers of resident birds counted on transects on Tierberg.

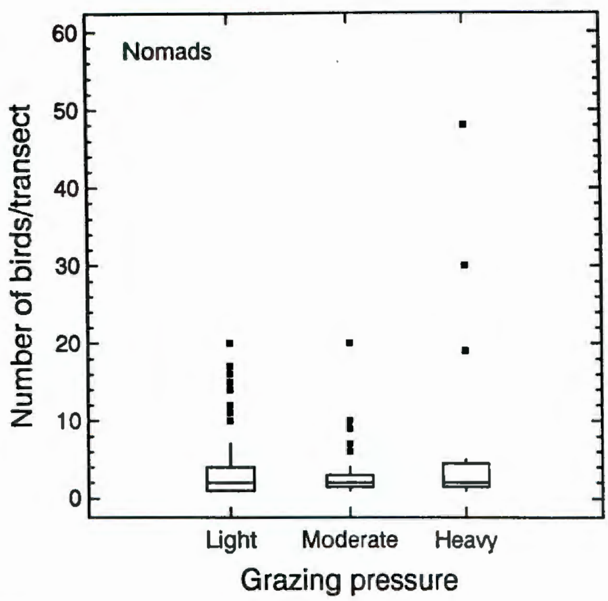

Figure 7.11. Numbers of nomadic birds counted on transects on Tierberg.

Discussion of both studies

Although the patterns of occurrence of different groups of birds are not entirely clear, there are trends in the data that indicate the consequences for the avifauna of heavy grazing in Karoo shrubland. The relative abundance of members of bird foraging guilds apparently changes with grazing pressure. Granivorous birds appear to increase in numbers with increasing grazing pressure, a pattern also found by Baker & Guthery (1990) in southern Texas, but contrary to the findings of Tidemann (1990) who found that granivorous birds (grass-finches) were negatively affected by cattle grazing in northern Australia. On heavily grazed rangelands in the southern Karoo, it appears that there are also increases in the numbers of such nomadic species as granivorous larks and buntings that feed on the seeds of ephemerals (Chapter 4, 5). This increase in the number of nomads indicates a lack of stability in seed resources, supported to some extent by the high variance of the samples obtained in the seed sweeps (Chapter 5).

The total canopy cover of perennial plants was generally lower in all sites with a history of heavy grazing (Milton, 1994; Dean *et al.*, in press b). In the hot summer months, many shrubs were leafless and the intershrub gaps were bare. After autumn rains, the intershrub gaps on heavily grazed rangeland were colonized by annual grasses (*Enneapogon*, *Aristida* and *Karoochloa* spp.) and forbs (*Galenia*, *Leysera*, *Trianthema*, *Tribulus* and *Gazania* spp). The densities and compositions of these ephemeral assemblages differed greatly from year to year. A decrease in perennial biomass or cover and an increase in ephemeral biomass has been observed elsewhere in arid rangelands that have been heavily grazed (Andrew & Lange, 1986). Temporal fluctuations in ephemeral cover influence both forage flow for domestic livestock and the availability of resources for granivores.

Certain insects benefit from the resources provided by both ephemeral and perennial plants of heavily grazed sites (Dean *et al.*, in press b). Seed-harvesting ants apparently take the most abundant, most available seed, and are not constrained by the toxicity of the plant. For example, nest-mounds of the harvester ant *Messor capensis* appear to increase in density in karroid shrublands with grazing regimes that favor medium- to large-seeded plants (Milton & Dean, 1993). However, in semi-arid grassland, Vorster, Hewitt & van der Westhuizen (1992) found that the number of harvester ant *M. capensis* nests was correlated with grazing pressure, and that the lowest nest density was found on "continually overgrazed" sites.

These preliminary data suggest that, with increasing grazing pressure on rangelands, changes in the ratio of ephemeral to perennial plants and concomitant changes in seed abundance cause a cascade that runs through the granivore community, resulting in increased variability in populations (Pimm, 1986). This will influence both the value of the area as a rangeland and its potential for protection and restoration. In natural, lightly grazed rangelands, the biomass and composition of vegetation varies with stochastic rainfall. The avifauna is largely resident, with fluctuations in the numbers and species richness of nomadic birds with particular rainfall events or at particular times of the year. At the next stage, reductions in the recruitment of palatable plants allows populations of unpalatables to increase (Milton *et al.*, 1994) and produce abundant seed. This allows harvester ants to increase in abundance, increasing the number of nutrient patches (Dean, 1991; Dean & Yeaton, 1993) and providing germination sites for seedlings (Dean & Yeaton, 1992). Since unpalatable species produce more seed per unit area than palatable plant species in heavily grazed rangelands (Milton & Dean, 1990b), they tend to produce more seedlings (Milton, in press), resulting in further increases in the number of unpalatable plants through lottery competition. Plant species that fail to recruit are lost, or drastically reduced in numbers, together with mutualistic relationships with animals and other plants (for example, nurse and nursed plants). With continued heavy grazing on the rangelands, the biomass and productivity begins to fluctuate as ephemeral plants benefit from the loss of perennial cover, and the number of nomadic seed-eating birds increases disproportionately. Rangelands finally reach a stage where vegetation is largely absent, seed numbers have been markedly reduced and few animals of any species are evident (Milton *et al.*, 1994).

The response of granivorous birds, particularly nomadic larks and canaries, to different grazing treatments should be further investigated, because it relates both to the conservation of birds and to the conservation of shrublands. Although not investigated in this study, it is likely that alien plants producing abundant seed, such as

Atriplex lindleyi and *Chenopodium* spp., are important in the food economy of small nomadic granivores. If this is the case, heavily grazed rangelands, or road verges that have been invaded by alien plants are probably optimal foraging habitat for small nomadic granivores, although such habitats may offer very little in the way of nest sites for these species.

Part 2: Nest site selection in ground-nesting birds in Karoo shrublands: Is there selection for defended plants?

Introduction

Nests of birds situated on the ground or low down in shrubs in semi-arid rangelands are usually well concealed or cryptic (Maclean, 1993), but are still exposed to many hazards. Small mammals, such as cats, foxes and mongooses (Smithers, 1983), and reptiles, such as *Varanus* spp. lizards and snakes, particularly *Dasypeltis* spp., eat eggs and nestlings (Branch, 1988). Apart from predators, birds' nests placed in low shrubs or on the ground in rangelands grazed by herbivorous mammals face an additional hazard; trampling of the nest or severe browsing of the shrub used as a nest site. However, not all plants are grazed or browsed for several reasons. Palatable plants may be defended by spinescence, reducing the amount of foliage that can be easily removed, or plants may be distasteful or toxic due to the presence of herbivore deterrent compounds (Huntly, 1991).

I hypothesized that, in rangelands grazed or browsed by herbivorous mammals, nest sites should be in plants that are unpalatable or well defended in other ways and generally not eaten by mammals. An alternate hypothesis could then be that birds select for a certain size, shape or structure in plants used as nest sites and that plants' defences are of secondary importance.

I examined the first hypothesis for nests of small passerine birds nesting in Karroid dwarf shrubland in the southern Karoo. The questions I asked were, (1) what plant species are used most commonly as nest sites (including nests built at the base or against the stem of a plant)?, and, (2) is there selection for certain types of plants by birds for nest sites?

Study area

The study was undertaken at the Tierberg Karoo Research Centre, near Prince Albert during 1992. The study area is briefly described in Chapter 6, and in Part 1 above, and fully described by Milton, Dean & Kerley (1992). The study site is a 1 km square area of dwarf shrubland, fenced in 1987 to exclude domestic livestock. Four types of habitat occur on the study site: plains cover 77,7% of the area, minor washes cover 16,6% and major drainage lines cover 2,5%. *Heuweltjies*, (nutrient-rich mounds averaging 13 m in diameter with more vegetation cover than the plains), occupy 3,2% of the study site.

Methods

For all birds nests encountered on the Tierberg study site, I recorded the plant species in which the nest was situated. For ground nests, I recorded the species of plants that were against or over the nest. Bird species commonly nesting >1 m above ground on the Tierberg site (mousebirds *Colius* spp., Fiscal Shrike *Lanius collaris*, Cape Sparrow *Passer melanurus* and Whitethroated Canary *Serinus albogularis*) were excluded from the data set because such nests are generally out of reach of small herbivorous mammals (<20 kg body weight) and small domestic livestock (sheep and goats).

All plants occurring on the study site were classified according to various characteristics: firstly, whether spiny, toxic, distasteful or palatable, secondly, whether a shrub, succulent or forb, and, thirdly, into height classes. A preference (or selection) index for each plant species in which nests were found was calculated. The index is a dimensionless statistic that indicates preferences for particular species or species characteristics, and is calculated as the percentage occurrence of nests in a particular plant species or type of plant divided by the percentage occurrence of the plant or type of plant in the environment (Petrides, 1975). The frequency of plant species in the study site was calculated according to the percentage occurrence of each species in 10 x 10 m plots (n = 150). Preference indices were calculated for plant species eaten by small antelope (steenbok *Raphicerus campestris* and grey duiker *Sylvicapra grimmea*) on the Tierberg study site and for plant species eaten by Merino sheep on the adjacent rangeland (S. J. Milton, unpublished data).

Results

Bird species breeding, the number of nests found at Tierberg and usual nest sites are listed in **Table 7.2.** A total of 96 nests of 14 species are included in the data set. Several birds nested on the ground under or against clumps of several plant species (shelter sites), so that the total number of plants (114) used by the birds is greater than the number of nests. With the exception of Karoo Robin *Erythropygia coryphaeus* and Greybacked Cisticola *Cisticola subruficapilla* that nested on the edges of drainage lines, all nests were in plains habitat.

Table 7.2
Bird species found nesting on the Tierberg study site, the number of nests found, and the usual nest site of the species.

Species	No. nests	Nest site
Longbilled Lark	2	On ground, at base of shrub
Karoo Lark	2	On ground, at base of shrub
Spikeheeled Lark	6	On ground, at base of shrub
Thickbilled Lark	2	On ground, at base of shrub
Greybacked Finchlark	3	On ground, at base of shrub
Tractrac Chat	3	On ground, at base of shrub
Karoo Chat	47	On ground, at base of shrub
Karoo Robin	1	On ground, at base of shrub
Karoo Eremomela	3	Well concealed in shrub
Greybacked Cisticola	4	Well concealed in shrub
Rufouseared Warbler	11	Well concealed in shrub
Plainbacked Pipit	2	On ground, at base of shrub
Yellow Canary	8	Well concealed in shrub
Cape Bunting	1	Well concealed in shrub

Of the 55 most common perennial plant species, 23 were used as nest or shelter sites (**Table 7.3**). Species of plants, their use as nest sites or shelter sites and the relative frequency in which they occurred on the Tierberg site are given in **Table 7.4(a)** & **7.4(b)**. Neither the species of plants used as nest sites by birds or their use of spiny, toxic, distasteful or palatable plants was statistically significant overall. However, ground-nesting species (**Table 7.2**) showed a significant preference for toxic plants (Kruskal-Wallis test statistic = 7.87, $p < 0.05$) and shrub-nesting species showed a marked, but not significant, preference for spiny shrubs (Kruskal-Wallis test statistic = 7.09, $p = 0.068$) (**Table 7.5(a), 7.5(b)** & **7.5(c)**).

Table 7.3

A list of the plant species on the Tierberg study site that contribute to >0.025% plant cover, taken from Milton, Dean and Kerley (1992). Plant characteristics (type) are: S = spinescent, Tx = toxic, X = distasteful (plants that are saline or contain chemical compounds that are distasteful to many mammalian herbivores), P = palatable (plants that are eaten by domestic livestock). The percentage frequency of each species in the shrubland is given, together with the number of nests found in each species, and the nest site preference index.

Family Species	Type	Frequency		Nest Preference
		Shrubland[1]	Nest	
Poaceae				
Stipagrostis namaquensis	S	0.04	2	45.4
Liliaceae				
Aloe variegata	S	0.30	0	0.0
Protasparagus recurvispinus	S	1.26	1	0.7
P. retrofractus	S	0.08	0	0.0
Santalaceae				
Thesium lineatum	P	0.38	0	0.0
Chenopodiaceae				
**Atriplex lindleyi*	P	0.69	2	2.6
Kochia salsoloides	P	0.08	0	0.0
Salsola cf. aphylla	P	0.22	0	0.0
S. tuberculata	P	0.43	0	0.0
Aizoaceae				
Aizooideae				
Galenia africana	Tx	0.34	0	0.0
G.fruticosa	P	7.31	17	2.1
Aptenioideae				
Aridaria noctiflora	P	2.14	0	0.0
Brownanthus ciliatus	X	5.63	0	0.0
Psilocaulon utile	X	1.04	1	0.9
Sphalmanthus bijliae	X	0.16	0	0.0
S. brevifolius	X	1.95	0	0.0
S. nitidus	X	0.95	0	0.0
Tetragonioideae				
Tetragonia cf. fruticosa	P	0.13	0	0.0
T. spicata	P	3.07	0	0.0
Ruschioideae				
Delosperma cf. subincanum	P	0.34	0	0.0
Drosanthemum cf.hispidum	P	2.03	0	0.0
D. lique	P	2.39	0	0.0
D. montaguense	P	5.24	6	1.0
D. uniflorum	P	1.30	0	0.0
Ruschia approximata	X	3.78	1	0.2
Ruschia spinosa[2]	S	7.02	6	0.8
Hereroa latipetala	X	4.80	0	0.0

Table 7.3, continued

Family Species	Type	Frequency Shrubland[1]	Frequency Nest	Nest Preference
Malephora lutea	X	5.04	2	0.4
Rhinephyllum cf.graniforme	X	2.40	0	0.0
R. macradenium	X	3.86	0	0.0
Trichodiadema cf. *bulbosa*	P	0.95	0	0.0
Crassulaceae				
Tylecodon reticulatus	Tx	0.26	1	3.4
Fabaceae				
Melolobium candicans	P	0.41	0	0.0
Zygophyllaceae				
Zygophyllum gilfillanii	P	0.65	0	0.0
Z. retrofractum	P	0.26	0	0.0
Augea capensis	X	1.83	4	1.9
Polygalaceae				
Polygala leptophylla	P	0.56	0	0.0
Euphorbiaceae				
Euphorbia caterviflora	P	1.24	0	0.0
Asclepiadaceae				
Microloma massonii	P	0.38	0	0.0
Asclepias buchenaviana	P	0.08	0	0.0
Solanaceae				
Lycium spp	S	1.54	0	0.0
Bignoniaceae				
Rhigozum obovatum	P	0.60	1	1.5
Asteraceae				
Pteronia cf.empetrifolia	P	3.86	6	1.4
P. glauca	P	0.60	0	0.0
P. pallens	Tx	7.40	7	5.6
P. viscosa	P	1.16	1	0.8
Felicia filifolia	P	1.37	1	0.6
F. muricata	P	0.38	0	0.0
Chrysocoma ciliata	Tx	2.09	1	0.4
Rosenia humilis	P	0.38	1	2.4
Eriocephalus ericoides	P	0.60	1	1.5
E. spinescens	P	0.30	0	0.0
Pentzia incana	P	0.63	0	0.0
Osteospermum sinuatum	P	7.03	8	1.0
Berkheya spinosa	P	1.08	4	3.3

[1]Weighted frequency (see methods)
[2]Includes *Eberlanzia* cf.*macroura* and *E.* cf.*vulnerans*

Table 7.4(a)
The number of plant species with particular characteristics that contribute >0.025% of the vegetation cover at Tierberg

	No. of species of plants that are:			
	Spinescent	Toxic	Distasteful	Palatable
In shrubland	8	4	12	31
As nest sites	5	3	4	11

Table 7.4(b)
The total percentage cover of plants and percentage use as nest sites in each category on the Tierberg study site

	Total cover (%) of plants that are:			
	Spinescent	Toxic	Distasteful	Palatable
Shrubland	11.6	10.0	31.8	46.5
Nest sites	11.4	42.9	7.0	38.5

Table 7.5(a)
Average nest plant preferences for all species sampled according to plant characteristics

Characteristics	No. nests	Average preference
Spinescent	13	6.26
Toxic	48	2.35
Distasteful	8	0.47
Palatable	44	0.28

Table 7.5(b)
Average nest plant preferences by ground-nesting birds

Characteristics	No. nests	Average preference
Spinescent	5	0.10
Toxic	38	2.70
Distasteful	8	0.37
Palatable	34	0.36

Table 7.5(c)
Average nest plant preferences for shrub-nesting birds

Characteristics	No. nests	Average preference
Spinescent	8	24.11
Toxic	11	1.28
Distasteful	0	0
Palatable	10	0.77

The frequency of use and the preference indices for shrubs (including the only grass, *Stipagrostis namaquensis*), succulents and forbs is not significant, although the number of nests in shrubs is high (**Table 7.6(a)**). There was a stronger preference for sites in plants that are usually >0.75 m high, but this was not significant (**Table 7.6(b)**).

A comparison between the preference indices for plant species used as nest sites and the plant species eaten by antelope and sheep shows some overlap in species use. However, highly preferred nest species were generally not preferred as food by herbivorous mammals (**Figure 7.12**). Similarly, highly preferred food species generally had low nest preference indices.

Table 7.6(a)
Average nest plant preferences according to plant growth form

Plant growth form	No. nests	Average preference
Shrub	102	2.11
Succulent	10	0.35
Forb	2	1.28

Table 7.6(b)
Average nest plant preferences according to plant height

Plant height (m)	n	Average preference
0.2	3	0.05
0.3	1	0.28
0.4	31	1.26
0.5	70	0.72
0.75	9	5.08

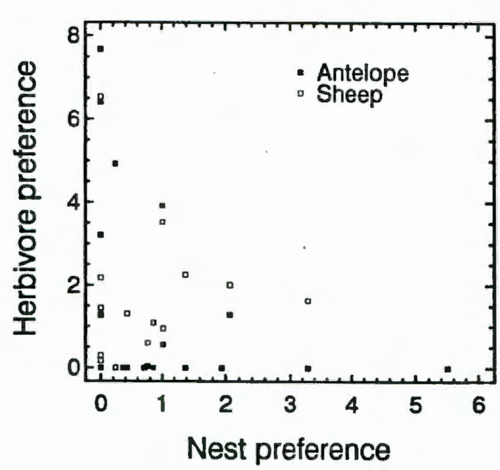

Figure 7.12. Preference indices for plants eaten by mammalian herbivores plotted against preference indices for plants used as nest sites by birds at Tierberg, Prince Albert.

For the seven bird species for which there are >5 records of plant species, individual preferences for particular plant characteristics are stronger than the overall preferences. However, only in Greybacked Cisticola was there a statistically significant preference for spinescent plants (Kruskal-Wallis test statistic = 11.82, $p < 0.001$). Mean preference indices for bird species nesting in plants with particular characteristics are given in **Table 7.7.** Preferences for individual plant species as nest sites by individual bird species are given in **Table 7.8.** The only species for which there is a large sample of data, Karoo Chat, used 10 different plant species, but had a marked preference for *Pteronia pallens*, a toxic species that was also used by 10 other bird species, but is not eaten by antelope or sheep. *Pteronia pallens* sheltered or supported 41.2% (47) of all nests, followed by *Galenia fruticosa*, a palatable species eaten by antelope and sheep (**Table 7.3**).

Table 7.7
Average preferences by birds for nest sites in or under plants with particular characteristics. Only bird species for which there are >5 data points are included.

Average preference for plants that are:				
Species	Spiny	Toxic	Distasteful	Palatable
Longbilled Lark	0.35	1.36	0	0.21
Spikeheeled Lark	0.59	0.28	0.18	0.22
Tractrac Chat	0	0.68	0	0.39
Karoo Chat	0	2.05	0.53	0.48
Greybacked Cisticola*	7.17	0.03	0	0.02
Rufouseared Warbler*	1.22	1.23	0	0.22
Yellow Canary*	0	2.55	0	1.03

* Shrub-nesting species

Table 7.8
Plant species that are preferred as nest sites by bird species (for which there are >5 data points)

Species	Plant species	Preference
Longbilled Lark	*Pteronia pallens*	5.44
Spikeheeled Lark	*Galenia fruticosa*	6.89
Tractrac Chat	*Galenia fruticosa*	5.51
Karoo Chat	*Pteronia pallens*	7.22
Greybacked Cisticola*	*Stipagrostis namaquensis*	55.63
Rufouseared Warbler*	*Berkheya spinosa*	8.51
Yellow Canary*	*Rhigozum obovatum*	21.14

* Shrub-nesting species

Discussion

This study has not unequivocally supported the hypothesis that, in general, nest sites of birds on or close to the ground in rangelands grazed or browsed by herbivorous mammals should be under or in plants that are spiny, toxic or distasteful. The vegetation of the southern Karoo appears to have evolved without much influence from mammalian herbivores (Milton, Siegfried & Dean, 1990) suggesting that herbivore density was never very high, and therefore unlikely to have exerted much selective pressure on birds and their nest sites. However, the results do indicate that birds tend to select plant species for nest sites that are not preferred by mammals as food. Sheep and other small domestic livestock may be too recent in the region to shape bird behaviour and nest site selection, and this is supported by my observations that there is more similarity between preference indices for plant species eaten by sheep and plant species used as nest sites by birds than there is between plants eaten by antelope and nest sites of birds (**Figure 7.12**). Further support for the hypothesis that grazing may influence nest site selection is provided by the observations that no nests were found in the taller and more dense vegetation on *heuweltjies* in the study site. *Heuweltjies* are highly disturbed sites (Milton & Dean, 1990a) and attract herbivores (Armstrong & Siegfried, 1990), including herbivorous rodents such as *Parotomys brantsii* that browse toxic species (du Plessis, 1989).

The alternate hypothesis, that birds select for a certain size, shape or structure in plants for nest sites similarly lacks unequivocal support. High variances in the derived preference indices tend to obscure the picture. Birds appear to have a marked preference for certain plant species as nest sites, but the criteria used for the selection of such sites are not clear. For example, the microclimate inside or under shrubs, or particular configurations of branches and foliage may influence the selection of a particular plant species and site in the southern Karoo. Although the findings are somewhat equivocal, I suggest that grazing by herbivorous mammals is one of the factors influencing the selection of nest sites by birds in the southern Karoo. Herbivorous mammals may benefit birds to some extent by increasing the relative abundance of less preferred (for food) but more preferred (for nests) plant species in shrubland. This shrubland state would be maintained by light to moderate grazing. Heavy grazing, however, would push the shrubland into a new state where recruitment of plants is low and plants are reduced in numbers, and finally to a state where vegetation (and nest sites) are largely absent (Milton *et al.*, 1994). If birds are selecting nest sites to avoid the possible destruction of nests in palatable shrubs, a testable hypothesis is that nests in vegetation that was protected from grazing would be equally distributed in both palatable and unpalatable shrubs, provided that both types of shrubs offered the same goods and services.

Part 3: The state of rangelands in the Karoo

Introduction

Selective grazing by domestic livestock is probably the major threat facing rangelands in the Karoo *sensu lato* (Roux & Vorster, 1983). Stocking rates have decreased markedly throughout the Succulent Karoo and Nama-Karoo biomes over the past 75 years (Dean & Macdonald, 1994). Decreases in stocking rates generally reflect decreases in the carrying capacity/secondary productivity of rangelands (Le Houérou, 1989) and this may be one of the symptoms of desertification (Mabbutt, 1984). In a protected area context, and particularly if areas are to be identified as worthy of protection, it is important to know the general condition of the available material. When protected areas are created, they are usually in areas that are themselves not pristine (May, 1994). It is of interest to know how much of the Karoo is "not pristine", and in order to justify the need for protected areas, the state of the rangelands and possible threats to biodiversity need to be examined.

The major land-use practices in the Karoo were described and discussed briefly in Chapter 2 (Part 2: Land-use). The objective of the present paper is to examine the present state of rangelands in the Karoo. I first discuss herbivory on rangelands in the Karoo in general and then focus on stocking rates of domestic livestock. This is followed by a review of the state of rangelands in the Karoo, using the results of a survey of the perceptions of agricultural extension officers, followed by a brief review of desertification and vegetation change in the Karoo.

Herbivory on rangelands in the Karoo

Despite the aridity of the region, large herds of springbok *Antidorcas marsupialis*, black wildebeest *Connochaetes gnou*, blesbok *Damaliscus dorcas* and the extinct quagga *Equus quagga* formerly occurred over most of the northern and eastern parts of the Karoo (Skead, 1980, 1987), but by the late 1800s had been largely replaced by domestic livestock (Talbot, 1961). Although springbok may cause extensive bare patches on sodic soils (Milton, Dean & Marincowitz, 1992), the effects of wild mammalian herbivores are generally considered to be less deleterious to the shrubland vegetation of the Karoo than the effects of domestic livestock (Davies, Botha & Skinner, 1986; Davies & Skinner, 1986). Patch selective grazing by wild herbivores may be instrumental in creating vegetation mosaics that benefit other animals, as has been suggested for certain mammals in Australia (Short & Turner, 1994).

Although some of the indigenous peoples of the Karoo, particularly the western Succulent Karoo, had been herding sheep for the past 2000 years (Schweitzer & Scott, 1973), it was only when South Africa was colonized by Europeans that pressure on the grazing resources of the Karoo increased markedly. European settlement of the Karoo apparently began with nomadic graziers moving slowly into the interior of South Africa with their flocks of sheep (Talbot, 1961). Many sheep farmers in the Karoo were essentially nomadic until the end of the 19th century (Penn 1986), although many others had settled areas of rangeland and established homesteads by this time (Talbot, 1961).

Grazing pressure on Karoo vegetation is generally high (Novellie *et al.*, 1988) and changes in vegetation over time have been reviewed by Brown (1875), Shaw (1875), Acocks (1953), Huntley (1978), Roux & Vorster (1983) Roux & Theron (1987) and Hoffman & Cowling (1990a). Local changes in species composition and the effects of herbivores have been shown by Milton (1994), Milton & Dean (1992, 1993), and changes in stocking rates and losses in secondary productivity have been discussed by Downing (1978) and Dean & Macdonald (1994).

It is estimated that the current carrying capacity of the Karoo is exceeded by 40%, or three million small stock units (Anon, 1986). Current stocking rates are shown in **Figure 7.13**) and recommended stocking rates are shown in **Figure 7.14**). These maps suggest that overstocking in the Karoo, particularly in the more arid western and central parts of the Karoo, is not particularly widespread. However, areas that have a low carrying capacity, and where the carrying capacity appears to have decreased markedly are still being stocked beyond their capacity. **Figure 7.15** shows the districts in the Succulent and Nama-Karoo where there has been a change in stocking rate of domestic livestock over the past 75 years (data from Dean & Macdonald, 1994). Grazing trials in the Karoo have shown that grazing can be a major determinant of vegetation composition, depending on intensity and season (Roux & Vorster, 1983). State-and-transition models suggesting that karroid vegetation is shifted to new states by inappropriate management of rangelands have been discussed by Milton *et al.* (1994) and Milton & Hoffman (1994). It may be hypothesized that heavy grazing on Karoo shrublands influences the bird community by the removal of seeds and fruits together with foliage and changes in plant community structure (by the reduction of some species relative to others) and disturbance, but this remains to be directly tested.

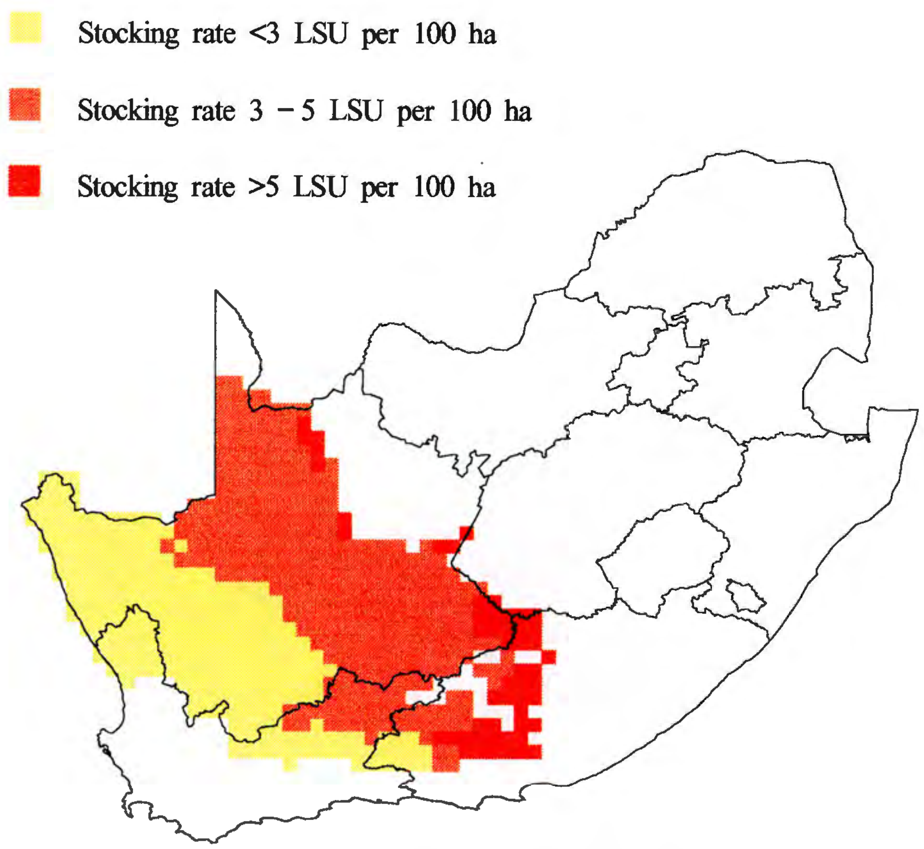

Figure 7.13. Current stocking rates in the Karoo (Anon, 1985a, 1985b, 1986). The data show the number of Large Stock Units (LSUs) in each quarter-degree square.

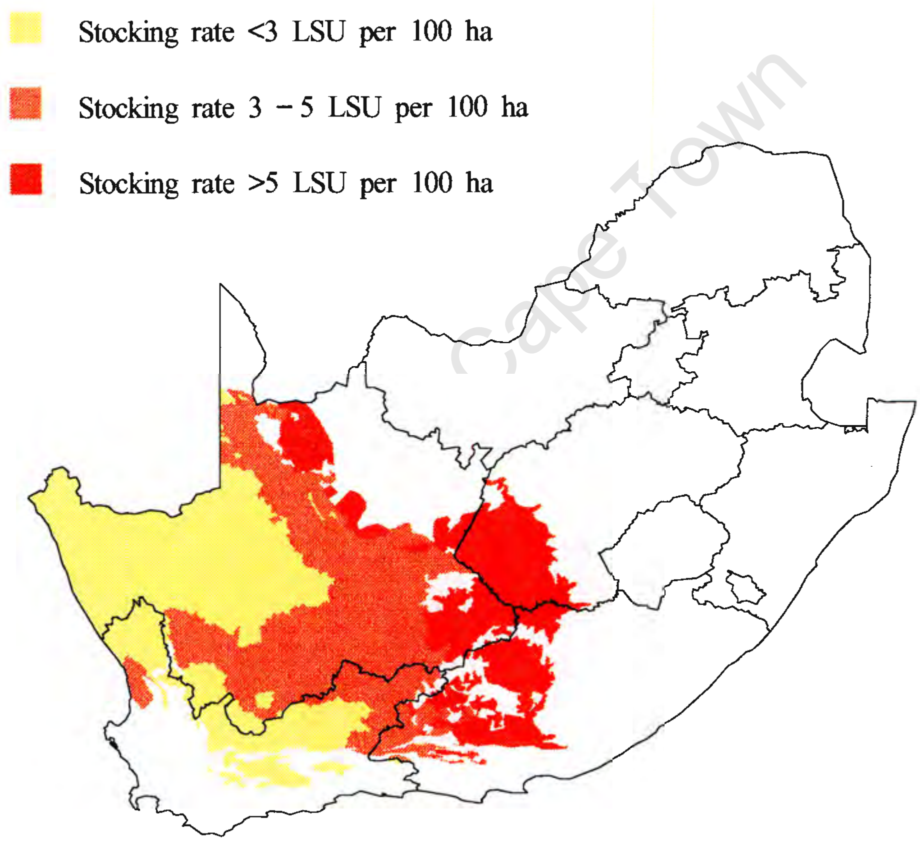

Figure 7.14. Recommended stocking rates in LSUs for the Karoo (data from Resource Conservation Section, Department of Agriculture).

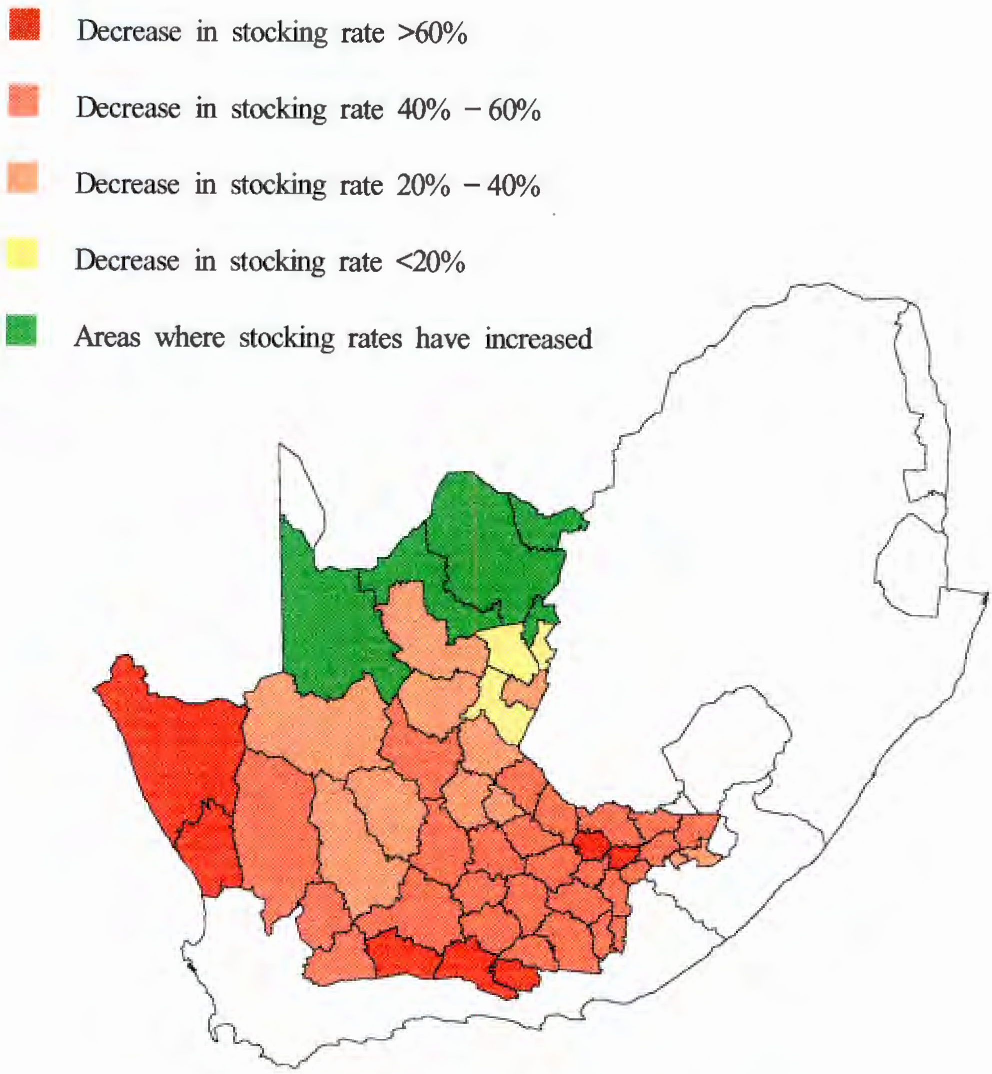

Figure 7.15. Magisterial districts in the Karoo where stocking rates have decreased or increased since 1900 (data from Dean & Macdonald, 1994).

The state of rangelands in the Karoo

Perceptions of agricultural extension officers

A questionnaire survey was used to obtain rough categorical information on the status of semi-arid and arid rangelands in the Karoo and southern Kalahari. Questionnaires were sent to extension officers of the Department of Agriculture, and the officers were asked to rank the condition of the rangeland in their extension districts on a 3 or 5-point scale. The questionnaire also obtained information on the experience of the extension officer, vegetation types, livestock ratios, farm sizes, water points and area-selective grazing, as well as data on changes in the status of alien plants and native birds and mammals. Only the data on the state of rangelands in the Karoo, and the effects of different rangeland management on plant and animal groups are presented in this dissertation.

Agricultural extension officers rated 35% of the semi-arid rangelands in the Karoo and southern Kalahari as being in poor condition. The percentage of the district that was rated by the extension officers as being in poor condition has been plotted against the percentage decrease in stocking rate for that district given by Dean & Macdonald (1994) (**Figure 7.16**). In general, with the exception of two points, where there has been no change in stocking rate, there was congruency between the perceived condition of the agricultural extension district and the percentage that the stocking rate had decreased. However, extension officers tended to rate rangelands as being in rather better condition than the stocking rates data suggest. Of interest is that a recent study (Düvel & Scholtz, 1992) shows that farmers in semi-arid parts of South Africa generally view their rangelands in a more favourable light than do local extension officers, so the potential for overstocking rangelands is high.

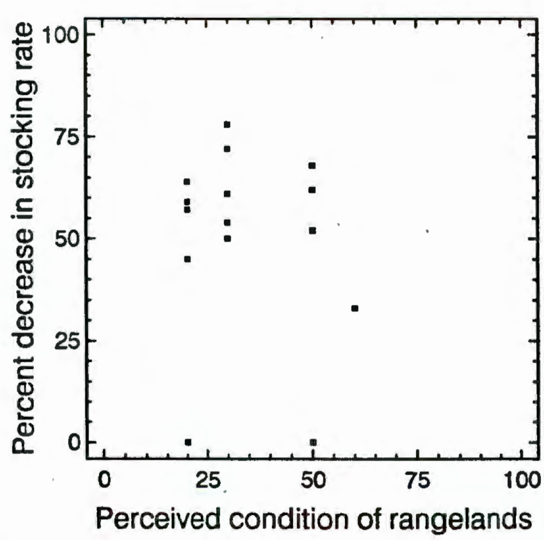

Figure 7.16. Changes in stocking rates plotted against the perceived condition of farms in the Karoo.

The extension officers were asked to score, on a scale of 1 to 10, the plant groups that they considered most threatened by rangeland management in their agricultural district. The results are given in **Table 7.9**. Predictably, grasses were rated as being the most threatened group of plants, but it is surprising that succulent plants did not score higher, given their vulnerability and sensitivity to trampling by domestic livestock.

Table 7.9
Average scores given to plant groups by agricultural extension officers, ranked in decreasing order from most to least threatened. The "n" is the number of extension officers who responded to the question.

Plant group	n	Average score
Grasses	29	7.8
Annual plants	23	4.9
Succulent plants	23	3.9

Extension officers were asked to rank, on a scale of 1 to 6, the causes of poor rangeland condition in their districts. Overgrazing in the past was considered to be the most important cause of present day rangeland condition, followed by present overstocking of rangelands (**Table 7.10**). Drought, and selective grazing were also perceived to be important in causing poor condition of rangelands.

Table 7.10
Average scores given to possible causes of poor rangeland condition by agricultural extension officers, ranked in decreasing order of perceived importance. The "n" is the number of extension officers who responded to the question.

Cause of poor condition	n	Average score
Overgrazing in the past	30	5.4
Present overstocking	30	4.1
Drought	30	3.7
Selective grazing	30	3.0
Unsuitable livestock	30	1.6
Burning	30	0.5
Present understocking	30	0.3

Agricultural extension officers were also given a prescribed list of animal groups and asked to score, on a scale of 1 to 10, what they considered to be the groups most threatened by rangeland management in their district (**Table 7.11**). As the generally low scores show, there was a diversity of opinion among the extension officers, but in general antelope were considered more threatened by rangeland management than mammalian carnivores and avian raptors, and bustards, gamebirds and tortoises were all perceived to be at risk by rangeland management.

Table 7.11
Average scores given to groups of animals by agricultural extension officers, ranked in decreasing order from most to least threatened. The "n" is the number of extension officers who responded to the question.

Animal group	n	Average score
Antelope	27	4.7
Carnivores	26	4.6
Raptors	27	4.3
Bustards	25	4.0
Termitivores	27	3.9
Gamebirds	25	3.5
Tortoises	24	3.1
Primates	26	2.9
Snakes	19	2.0
Insects	21	2.1
Songbirds	26	2.0
Lizards	19	1.6
Frogs	19	0.7

The desertification debate

The nature, extent, rates and mechanisms of post-colonial vegetation change in the Karoo have been frequently debated (Acocks, 1953; Jarman & Bosch, 1973; Hoffman & Cowling, 1990a; Dean & Macdonald, 1994; Dean *et al.*, in press a). It was thought that a pre-colonial eastern Karoo was dominated by perennial grasses such as *Sporobolus fimbriatus* and *Themeda triandra* (Acocks, 1953; Roux & Theron, 1987) and it has been generally assumed that overstocking in the recent past has largely been responsible for the dwarf shrubland evident today. It has been suggested that some changes in the vegetation of the Karoo occurred prior to European colonization, and were a function of phases of climatic shifts and the impacts of both *Khoi San* hunter-gatherers and *Khoikhoin* herders (Sampson, 1986; Sugden, 1989).

This issue is likely to remain incompletely resolved for some time (Dean *et al.*, in press a). The idea of a grass-dominated Karoo forms an important part of current semi-arid rangeland management philosophy, and suggests that the Karoo should support more perennial grasses than it currently does. The nature of vegetation change in the Karoo has attracted much interest. Models focussing on the dynamics, rates and broad patterns of vegetation change in the Karoo have been constructed (Acocks, 1953; Jarman & Bosch, 1973; Hoffman & Cowling, 1990b) and these are discussed briefly below.

It has been suggested that the Karoo has expanded northeastwards along a broad front in a wave into the more productive grasslands (Acocks, 1953). This perception has had considerable influence on pastoral management policy in South Africa, and led to various stock reduction schemes, of which the most recent is the National Grazing Strategy of the RSA (Bruwer & Aucamp, 1991).

A second model suggests that vegetation change in the Karoo occurred as the result of the coalescence of degraded patches over extensive regions through time. When rangeland degradation is examined more closely, the patchiness of the process appears evident. Rangeland condition appears to differ between and within farms. Patchiness in the vegetation within farms is associated with vegetation clearing and ploughing (Dean & Milton, in press), with localized overgrazing (Fuls, 1992) and with areas where animals congregate. The latter include water points (Roux & Opperman, 1986; Bosch & Gauch, 1991), pans (Milton, Dean & Marincowitz, 1992), and holding camps and feed lots.

A third model suggests that the edge of the Karoo is dynamic, and that shifts in Karoo vegetation are between dominance by shrubs and dominance by grasses, but that the overall direction of vegetation change is towards decreased productivity.

In general, these are models and views that are largely untested (Dean *et al.*, in press a). However, recent studies on the use of stable carbon isotope ratios to determine C_3 and C_4 grass fractions in soil organic matter (Stock, Bond & le Roux, 1993; Bond, Stock & Hoffman, 1994), have shown that grasses were once more abundant in the Nama-Karoo than they are now.

The perceptions of agricultural officers, published reports on the Karoo (Anon, 1985a, 1985b, 1986), the progressive decrease in stocking rates in the Karoo (Dean & Macdonald, 1994) and studies showing that there have been recent changes in the cover and composition of the vegetation of the Karoo (reviewed by Dean *et al.*, in press a) all support the notion that the future for the biota of Karoo rangelands outside of protected areas is bleak.

In some of the semi-arid and arid parts of the Karoo, peak densities of domestic livestock were reached in the late 19th century (Christopher, 1982), and have since shown a marked decrease in numbers of domestic livestock supported on rangeland. Stocking rate data presented by Dean & Macdonald (1994) suggest that those parts of the Karoo, particularly the Succulent Karoo, that are both arid and succulent have been more heavily damaged by overgrazing than the more mesic areas. Although karroid shrublands are strongly resistant, it is likely that they are not at equilibrium and have shifted to new states. At the root of these shifts is a perception by the early settlers (of European origin) that the rangelands were more productive than they actually were, and that drought years were exceptional, rather than the norm (Talbot, 1961). For many years livestock production in the Karoo has apparently exceeded the carrying capacity of the natural environment (Roux & Vorster, 1983; Roux & Opperman, 1986; Dean & Macdonald, 1994), with the result that the vegetation in the Karoo has moved through transitions to new states. There seems little doubt that there have been recent changes in the secondary production of Karoo rangelands (Downing, 1978; Roux & Opperman, 1986; Dean & Macdonald, 1994). Whether these changes are irreversible or not remains an open question. The available evidence suggests that the passive rehabilitation of Karoo rangelands requires a long time (Milton *et al.*, 1994; Milton & Hoffman, 1994) and is seldom economically viable. The effects of changes in rangeland vegetation on processes, and particularly on the avifauna of the Karoo, are poorly known, and should be a priority for research in semi-arid rangelands in South Africa in the future.

Differential changes in plant assemblages/bird habitats in the Karoo at the landscape level
Changes in plant assemblages have not been evenly distributed at the patch or landscape level (e.g. bottomlands, plains, drainage lines, upper and lower slopes, hilltops) in the Karoo *sensu lato*. The most transformed bird habitats are the bottomlands (Chapter 2: Part 2), that were drained, ploughed and planted, and then abandoned for various reasons, one of which in the more arid Karoo may be salinization of the soil (du Plessis & van Veelen, 1991). There are very few patches of alluvium or river terraces, or semi-permanent marshes in the Karoo that have not been ploughed and planted (pers. obs). Many of these river terraces and alluviums were ploughed and planted in the late 1700s. For example, a painting of Kweekvallei (Prince Albert) from about 1790 clearly shows extensive ploughed lands and a flood irrigation system (Raper & Boucher, 1988), that is still operating today.

Drainage lines have also been severely impacted by the removal of large *Rhus lancea* trees (for fence posts), by the construction of barrages and water diverting systems, and by increased runoff from heavily grazed plains. In areas in which sheep are the most common domestic livestock, it is likely that the vegetation of upper and lower slopes and hilltops has not been markedly affected by grazing, but in areas where Angora or Boer goats are farmed, hillsides (and in some cases, hilltops) have been severely impacted by grazing (pers. obs). The selective removal of spekboom *Portulacaria afra* from hillsides can clearly be seen in the southeastern Nama-Karoo.

These differential grazing effects have implications for the avifauna. There is very little empirical evidence to show that the bird assemblages of the more severely transformed areas have changed, but anecdotal evidence suggests that there has been shifts in the species richness of bird assemblages in bottomlands (C.J. Vernon, pers. comm.). This is supported by the only two cases for which there are data; the loss of the Wattled Crane and the Bald Ibis from the eastern Nama-Karoo as a result of draining and ploughing of wetlands and changes in the burning and grazing regime of bottomlands (Siegfried, 1966; Manry, 1985; Brooke & Vernon, 1988).

Aridification of the Karoo

One of the symptoms of "ecosystem rundown" may be manifested by a fall in the watertable that is not related to changes in rainfall amount. Data presented in Dean & Macdonald (1994) show that the number of stock water points increased over the period 1910-1960 in most Karoo districts. In selected examples, the increase in the number of stock water points was negatively correlated with stocking rates (Dean & Macdonald, 1994). Since most of these stock water points are supplied from boreholes, I infer from these data that supplies of underground water are becoming more difficult to obtain. The depletion of underground water may be at two levels; firstly, water is being removed from underground storage at a rate faster than it can be recharged (Hodgson, 1986), and secondly, poor infiltration, salinization, soil compaction and accelerated runoff is preventing water from percolating underground (Görgens & Hughes, 1986).

There are no empirical data on the effects that a lowering of the watertable in the Karoo might have had on the birds, and there is very little data on the effects that a drop in the watertable might have had on ecosystem functioning in the Karoo. Lowering of the watertable can cause the mortality of deep-rooted woody plants (Macdonald, 1989). The available evidence suggests that the Karoo is now "drier" than it was, *i.e.* that rainfall is now less effective, and that this is unrelated to changes in rainfall amount (Vogel, 1988a, 1988b). If this is indeed the case, ecosystem processes may have been disrupted or damaged, with the possibility that the entire Karoo has shifted to a new, more arid state.

Chapter 8
The protection of avian diversity in the Karoo

Introduction

The avifauna of the Karoo is not, in general, rare or threatened, and it has been said that it is not in need of special protection. To paraphrase Graber & Graber (1976) in reply to the question of why be concerned with the loss of populations of widely distributed birds from threatened habitats, there are at least two important reasons why all Karoo birds should be protected. One is that threats to the avifauna of the Karoo are not unique and are also present, often at a higher intensity, elsewhere in southern Africa. Secondly, the conservation of species should comprise the protection of the genetic breadth of the entire population. The avifauna of the Karoo may include, among species that are widespread in the region and elsewhere, particular genotypes or cryptic genera (Siegfried & Brooke, 1994) that are present only in Karoo populations.

The objectives of this chapter are to identify parts of the Succulent Karoo and the Nama-Karoo that should, on the basis of their richness of particular species or other attributes, be further examined to investigate their potential as protected areas. Although conservation biologists currently recommend the protection of species-rich areas as both cost-effective and efficient in preserving biological diversity (Scott *et al.*, 1987), this approach may not be successful in protecting the rarer endemics in the Karoo, many of which tend to occur in unique habitat in the less (avian) species rich western and northwestern Karoo (Chapter 3). In many cases, areas rich in a particular endemic or rare species are also rich in other species, but not necessarily so.

I have selected three groups of species in the Karoo as priorities for protection. These groups are the Karoo endemics, particularly those species that are fairly narrowly distributed, the nomads because they form a uniquely large component of the avifauna in the arid Karoo, and the larks (Alaudidae). The larks should form part of the focal conservation priority species assemblage because of their uniquely high species richness and relative abundance in the Nama-Karoo. Most larks are common and widespread in the Karoo *sensu lato*, and do not appear to be in need of special protection. However, some lark species have a number of well-differentiated subspecies occurring in different parts of the Karoo, and this genetic diversity should be protected. Most of the species in the groups given above are common or widespread in the Karoo, but may be inadequately protected under the present protected area system (Siegfried, 1992).

The need for protected areas

The paucity of extensive protected areas in the Karoo has often been pointed out (Huntley, 1978; Siegfried, 1989; Hilton-Taylor & le Roux, 1989). A question that arises is whether or not protected areas are necessary to protect avian diversity in the Karoo. Given that there are more than 500 "threatened" plant taxa in the Karoo (Hall, 1989; Hilton-Taylor & le Roux, 1989), that the semi-arid rangelands are generally regarded to be in poor condition (Macdonald, 1989; Chapter 7), and that at least two endemic bird species (Red Lark, Sclater's Lark) mostly occur outside of any protected area, there is certainly a need for protected areas for the conservation of biodiversity in the Karoo *sensu lato*. However, the question remains of whether protected areas are necessary for the protection of avian diversity. Alternatively, does the present use of Karoo rangelands threaten avian diversity in any way?

The principal ecological change in the Succulent and Nama-Karoo is probably in small-scale patch dynamics and the loss of intermediate disturbances. Although the smaller solitary antelope (duiker *Sylvicapra grimmea*, steenbok, and klipspringer *Oreotragus oreotragus*), large solitary antelope (kudu *Tragelaphus strepsiceros*) and springbok (in small captive herds) are still widespread in the Karoo, many species of large herbivore no longer occur in a wild state in the region. More than 15 species, including black rhinoceros *Diceros bicornis*, quagga (now extinct), mountain zebra *Equus zebra*, warthog *Phacochoerus aethiopicus*, gemsbok *Oryx gazella* and eland *Taurotragus oryx* were formerly widespread in the Karoo (Skead, 1980), but were eliminated from the region during the late 1800s. Only the black rhinoceros, mountain zebra and eland have been reintroduced and are present in isolated protected areas in the Karoo. Springbok occurred throughout the Karoo in large herds that periodically "migrated" through the region (Skead, 1980), and that must have had a large impact on the vegetation of the bottomlands during these movements. Warthog, now extinct in the Karoo, were probably particularly important in creating small-scale disturbances, since some of their food is obtained by rooting (Cumming, 1975). Both Karoo *Cercomela schlegelii* and Familiar Chats *C. familiaris* are adept at foraging in newly-turned earth (pers. obs). The loss of the wild herbivores may have had effects on the avifauna that go far beyond the documented changes in the large raptor assemblages (Boshoff *et al.*, 1983; Brooke, 1984; Macdonald & Macdonald, 1985). Although there is no evidence to show that small-scale disturbances caused by wild herbivores were important to the birds of the Karoo, the loss of this type of disturbance may have changed certain avian habitats in the Karoo.

There has been one other significant change in the Karoo that has often been overlooked by biologists. Stone tools, fragments of ostrich egg-shell water-carriers and paintings in rock shelters show that hunter-gatherer peoples (the Khoi-San) occurred throughout the Karoo, but the herders (the Khoikhoin) occurred only on the southern and western edges (Klein, 1986). The hunter-gatherer peoples in the Karoo were virtually wiped out when the interior of the country was settled, probably with the advance of the trekboers of the 1700s (Humphreys, 1987). The Khoi-San were efficient hunters and gatherers (Smith, 1986) who had a significant impact on the vegetation (through camp-sites) in certain areas of the Nama-Karoo (Sampson, 1986), and probably a significant impact on some prey animals. It is likely that small disturbances caused by the Khoi-San in their hunting and gathering activities could have benefitted birds, particularly digging for roots or bulbs, taking honey from bee-hives in rocks or hunting. The uneaten remains of large animals killed by the Khoi-San for food would have been consumed by scavenging birds of prey. Changes in the raptor and scavenger avifauna of the Karoo may have begun even before the large herds of ungulates were eliminated by the European settlers. The loss of the Khoi-San from the Karoo, as major predators in the ecosystem, must have been almost as important for the avifauna as the loss of the large herds of ungulates and the loss of the large non-human predators.

There is evidence to show that avian habitats in the Karoo are threatened, not by major land transformation schemes, but by small changes in the composition of plant assemblages and changes in plant cover brought about by heavy- or over-grazing (Acocks, 1953; Roux & Vorster, 1983; Chapter 7: Part 1). Although dryland or irrigated crop farming has a far more severe effect on bird habitats, the area covered by current use or old croplands in the Karoo is relatively small (Chapter 2: Part 2). Much of the Nama-Karoo has low agricultural potential (Chapter 2: Part 2) and many of the areas that could be used for dryland crop production have been ploughed and planted in the past. Dryland agriculture in the Nama-Karoo is particularly costly to the environment, since natural vegetation and soil biotic systems are destroyed in the process. Many of these croplands are subsequently abandoned because of the unpredictability of the rainfall (Hilton-Taylor & le Roux, 1989) or salinization of the soil as a result of irrigation (du Plessis & van Veelen, 1991).

It is clear from the results and discussion in Chapter 7 that the avifauna in the Karoo is affected to some extent by grazing by domestic livestock. Grazing by domestic livestock causes shifts in the ratio between annual and perennial plants, which may favour certain species of birds in the short-term. However, in the longer term it is likely that heavy grazing pressure on rangelands can lead to cascades that run through granivore and insectivore assemblages, resulting in increased variability in populations (Pimm, 1986) and a loss in biodiversity (Milton *et al.*, 1994; Fleischner, 1994). The potential for "blurry catastrophes" (Janzen, 1986), in which poorly known or undescribed species are wiped out or reduced to fragments of their former populations under such conditions is high. Areas under management by conservation authorities and protected from grazing by domestic livestock are not necessarily invulnerable, but are at least free from short-term financial incentives to overstock, plough and generally overexploit the available resources, including surface and underground water (Archer, 1994).

Elements of the avifauna of the Karoo present particular conservation problems (Dean & Lombard, 1994). The nomadic, granivorous larks and buntings are one such case; the localized endemics, such as the Red Lark and Cinnamonbreasted Warbler, possibly fragmented into metapopulations are another, while more widespread endemic species using fairly specialized habitats in the Karoo may be a third case. Not only certain bird species, but certain avian habitats in the Karoo should also be protected. The arid grasslands on red sand plains and dunes in the northwestern Karoo (Bushmanland) are unique to the area and should be included in any conservation initiative. The vast poorly drained shallow saline pans of the central northern Karoo, particularly the "*vloere*" in the Brandvlei area, should be protected. Although the birds that occur on these shallow saline pans are not particularly rare (with the possible exception of the Chestnutbanded Plover) or threatened, the habitat is unique in South Africa. Many of the pans in the Kenhardt-Brandvlei-Vanwyksvlei area have supported short-lived salt extraction schemes, and in addition have been ploughed, trenched, diked, fenced and driven across. In some cases causeways have been built across these shallow pans to carry roads and railway lines and drainage and water movement has been severely disrupted.

Databases and methods

Extensive use was made of GIS technology (Section 1: Preface), using the databases described in Chapters 2 and 3, and the protected areas database described below, to identify geographic areas that matched various criteria.

Protected areas database

The full protected-areas database was compiled at the Percy FitzPatrick Institute of African Ornithology, University of Cape Town. It consists of information for all publicly-owned areas in South Africa that provide refuges for the biota, whether or not they are owned by nature conservation authorities, and includes South African Defence Force training areas, ammunition dumps and missile ranges. The database includes the Republic of South Africa and the kingdoms of Lesotho and Swaziland, and former self-governing territories within South African borders. For the purposes of this study, only the data on protected areas falling within the Succulent and Nama-Karoo biomes were extracted. Details of protected areas in the Succulent and Nama-Karoo are given in **Appendix 5**, and summarized in **Table 8.4**. Land under the control of the South African Defence Force has been discarded from this database because such land is likely to be redistributed to small farmers (Anon, 1994). State forest reserves and mountain catchment areas were also discarded from the database, so that only "Karoo" protected areas remained. All the information on these Karoo protected areas was checked using Greyling & Huntley (1984).

Birds in protected areas

Checklists of birds recorded in protected areas were obtained from the relevant conservation authorities. Checklists are not available for some of the smaller protected areas, and in these cases I have *not* assumed that all the species recorded in the quarter-degree squares in which the protected areas are situated also occur in the protected area.

Land values database

I compiled a database containing the selling prices of farms in the Karoo. This information was taken from the small advertisements in issues of the *Landbouweekblad* for 1994 only, and included such details as locality, mean annual precipitation for the area, the size of the farm, whether or not electricity was supplied by ESCOM (Electricity Supply Commission) and whether or not there were irrigated lands or dryland croplands.

Gross margins for various small stock were computed using an equation presented by van den Berg (1983) for grazing capacity (in small stock units = SSUs) relative to rainfall. One SSU was assumed to be equal to one Merino sheep. Data on gross margins for various small stock were obtained from the Department of Agriculture, and converted to Rands per SSU per mm of rainfall, and then fitted to the curve given by van den Berg. Using the conversion table presented in Dean & Macdonald (1994), these curves were adjusted for each of the small stock types.

The identification of potential protected areas

There are several possible methods of identifying areas that could be investigated for potential protected sites. The method used here was to identify the particular quarter-degree squares in which the highest priority species was relatively abundant, and then to add squares to include the next priority species and so on. A priority list was drawn up by ranking all Karoo endemic species according to their relative rarity. Rarity was assumed on the basis of the number of squares in which the species had been recorded, and the reporting rate (Chapter 3, **Figure 3.5**).

The database that I used was the main bird database described in Chapter 3. I merged this database with the protected areas and land-use databases, and removed all quarter-degree squares in which there are statutory protected areas greater than 10 km^2, and all squares in which there are extensive irrigated croplands, extensive old croplands or particularly degraded rangelands. Squares in which there is underground mining were not taken out of the dataset because such mines usually occupy a small part of the surface area of a QDS and may be quite compatible with the protection of the avifauna.

The misidentification of rare species is a potential problem. The probability of bird species misidentifications is species-dependent and low in most cases, and is most likely to be only one record of the species in a particular square. Because my interest is in identifying those areas where the species are most abundant, I selected only those areas where the individual species had a high reporting rate. This index is sensitive to some extent to the number of surveys that have been made (Chapter 3), so I attempted to obtain squares with high indices and >10 cards. This effectively barred all marginal species and most of the possible misidentifications from being selected.

The steps that I used to identify QDS for further investigation were to sieve out, species by species, the QDS in which the rarest Karoo endemic species were most abundant. From this set, I selected one QDS in which each species was most abundant and had preferably been recorded on >10 field cards, combined all QDS into a single database and removed all duplicate squares. This provided the least number of QDS in which each species was well represented at least once. I subjectively sorted this set into first, second and third-tier priorities on the basis of their species richness and the reporting rate of species, and on their locality and proximity to other protected areas in the Karoo.

Priority species for protection

The priority endemic species are listed in **Table 8.1**. This group of species contains both sedentary (resident) and nomadic species, and contains both rare and common, widely-distributed species. Bradfield's Swift has been included in the group of Karoo endemic species, although it is a southern African endemic species not confined to the Karoo. However, this species is generally rare and poorly known and an evaluation of its conservation status would be useful. Furthermore, it was not included by Robertson (1993) in his review of the distribution and status of some Namibian endemic species. Red Lark, Cinnamonbreasted Warbler and Sclater's Lark, on the basis of reporting rate and distribution, are the highest priorities among the Karoo endemic species.

Table 8.1
Karoo endemic and southern African endemic species considered to be priorities for protection in the Succulent and Nama-Karoo, ranked in order of priority. The number (and percentage of the total) of quarter-degree squares in which each species has been recorded in each biome is given. Nomadic species are marked *.

Species	Frequency in Succulent Karoo	Frequency in Nama-Karoo
Bradfield's Swift	10 (6.1)	17 (3.3)
Red Lark	3 (1.8)	43 (8.4)
Cinnamonbreasted Warbler	28 (17.2)	39 (7.6)
Sclater's Lark*	2 (1.2)	69 (13.5)
Karoo Eremomela	63 (38.7)	132 (25.7)
Black Harrier	83 (50.9)	115 (22.4)
Blackeared Finchlark*	30 (18.4)	259 (50.5)
Karoo Lark	138 (84.7)	158 (30.8)
Namaqua Warbler	108 (66.3)	202 (39.4)
Layard's Titbabbler	111 (68.1)	213 (41.5)
Tractrac Chat	76 (46.6)	270 (52.6)
Southern Grey Tit	132 (81.0)	228 (44.4)
Sicklewinged Chat	77 (47.2)	284 (55.4)
Pririt Batis	94 (57.7)	273 (53.2)
Palewinged Starling	127 (77.9)	256 (49.9)
Fairy Flycatcher	110 (67.5)	299 (58.3)
Ludwig's Bustard	107 (65.6)	334 (65.1)
Dusky Sunbird	112 (68.7)	353 (68.8)
Karoo Korhaan	83 (50.9)	387 (75.4)
Thickbilled Lark	146 (89.6)	338 (65.9)
Blackheaded Canary*	146 (89.6)	351 (68.4)
Greybacked Cisticola	151 (92.6)	354 (69.0)
Karoo Chat	158 (96.9)	383 (74.7)
Karoo Robin	155 (95.1)	442 (86.2)
Whitethroated Canary	162 (99.4)	436 (85.0)
Rufouseared Warbler	136 (83.4)	488 (95.1)

A list of priority dryland nomadic species is given in **Table 8.2 (a)**. Most nomadic species are widespread in the Karoo and are probably in little need of formal protection. The list includes species that are only marginal in the Karoo, such as Tawny Eagle, Burchell's Sandgrouse and Pinkbilled Lark, that could probably be more efficiently protected in other ecosystems. The Tawny Eagle has been included in this group because it occurs over a fairly wide area of the northern and northeastern Nama-Karoo, and formerly nested in many parts of the Nama-Karoo from which it is now absent (Boshoff *et al.*, 1983). The Redbilled Quelea has been omitted from the table because its presence in the Karoo is probably recent, and is almost certainly as a result of available food in the form of cereal crops.

Aquatic species are listed separately (**Table 8.2 (b)**). The aquatic species could probably be more effectively protected in less arid ecosystems than the Karoo, but they are included here because the habitats they use in the Karoo are themselves a priority for protection.

Table 8.2

Nomadic species considered to be priorities for protection in the Succulent and Nama-Karoo. The number (and percentage of the total) of quarter-degree squares in which each species has been recorded in each biome is given. Southern African endemics (Clancey, 1986) are marked *.

(a) **Dryland nomadic species**

	Frequency in	
Species	Succulent Karoo	Nama-Karoo
Tawny Eagle	1 (0.6)	69 (13.5)
Namaqua Sandgrouse*	136 (83.4)	433 (84.4)
Burchell's Sandgrouse*	0	29 (5.7)
Redcapped Lark	135 (82.8)	346 (67.4)
Pinkbilled Lark*	0	71 (13.8)
Stark's Lark*	9 (5.5)	101 (19.7)
Greybacked Finchlark*	100 (61.3)	413 (80.5)
Wattled Starling	77 (47.2)	290 (56.5)
Scalyfeathered Finch*	5 (3.1)	201 (39.2)
Larklike Bunting*	125 (76.7)	493 (96.1)

(b) **Aquatic nomadic species**

	Frequency in	
Species	Succulent Karoo	Nama-Karoo
Greater Flamingo	22 (13.5)	81 (15.8)
Lesser Flamingo	13 (8.0)	31 (6.0)
Chestnutbanded Plover	8 (4.9)	17 (3.3)
Avocet	84 (51.5)	228 (44.4)
Blackwinged Stilt	79 (48.5)	267 (52.0)
Whiskered Tern	12 (7.4)	29 (5.7)

The larks are listed in **Table 8.3**. Some of the species are associated with particular habitat types that are not widespread in the Karoo, and all the species differ in their conservation status in southern Africa. Of the species less frequently recorded in the Karoo, Melodious Larks are uncommon and threatened by habitat destruction outside the Karoo (Maclean, 1993), Rufousnaped Larks are generally common in open savanna woodlands and grasslands, and the Chestnutbacked Finchlark is common in savanna woodlands in northeastern and northern southern Africa north to the Sahara (Dean *et* *al.*, 1992). Both the Rufousnaped Lark and the Chestnutbacked Finchlark occur in marginal habitats in the Karoo, and neither would be as adequately protected in the Karoo as in other ecosystems. Nevertheless, protected areas in suitable habitats in the southeastern or northeastern Nama-Karoo could include one or both of these species.

Table 8.3

Larks (Alaudidae) considered to be priorities for protection in the Succulent and Nama-Karoo. The number (and percentage of the total) of quarter-degree squares in which each species has been recorded in each biome is given. Southern African endemics are marked *.

	Frequency in	
Species	Succulent Karoo	Nama-Karoo
Melodious Lark*	0	25 (4.9)
Rufousnaped Lark	0	34 (6.6)
Clapper Lark*	73 (44.8)	247 (48.1)
Fawncoloured Lark	0	145 (28.3)
Sabota Lark*	17 (10.4)	289 (56.3)
Longbilled Lark*	120 (73.6)	393 (76.6)
Spikeheeled Lark*	122 (74.8)	485 (94.5)
Chestnutbacked Finchlark	0	25 (4.9)

The distribution of existing protected areas in the Succulent and Nama-Karoo

There are 26 permanently protected areas (state and semi-state owned "nature reserves") in the Nama-Karoo, covering about 2217 km^2 (0.5% of the biome) and 16 permanently protected areas in the Succulent Karoo, covering about 1144 km^2 (1.2% of the biome) (**Appendix 5, Table 8.4**). These protected areas vary in size from 0.02 to 824 km^2 in the Nama-Karoo and from 0.1 to 340 km^2 in the Succulent Karoo. Average protected area size in the two biomes is similar: 85.2 ± 166.49 km^2 in the Nama-Karoo, and 71.5 ± 99.74 km^2 in the Succulent Karoo. The total protected area given for the Succulent Karoo does not include the Richtersveld National Park (1624 km^2), which is the largest protected area in the biome, but is fairly atypical in geology and vegetation (Werger, 1985) and in that it includes a pastoralist community and domestic livestock.

The smaller protected areas, particularly those below 10 km^2, and particularly those in the more arid parts of the Nama-Karoo, are probably ineffective at protecting all but small populations of small (<20 g) resident species of birds. Very small protected areas (<1 km^2) in the Karoo that are surrounded by totally transformed habitats probably have no function as protected areas for birds. Six of the protected areas in the Succulent Karoo, and 12 of the protected areas in the Nama-Karoo are below 10 km^2, and in both biomes are several protected areas that are <1 km^2 in area (**Table 8.4**).

Table 8.4

Statutory protected areas in the Succulent and Nama-Karoo, excluding state forests and catchment reserves and S.A.D.F. areas. The number of bird species for protected areas for which lists of birds are available is given.

Succulent Karoo

Protected area name	Size (km^2)	Species numbers
Akkerendam Nature Reserve	23.01	87
Anysberg Nature Reserve	340.51	184
Bokkeveld Nature Reserve	0.1	
Dassieshoek Nature Reserve	8.65	121
Dries Le Roux Nature Reserve	25.75	
Eeufees Nature Reserve	0.11	
Gamkapoort Nature Reserve	80.02	169
Goegap Nature Reserve	148.64	93
Ladismith-Klein Karoo Nature Reserve	27.66	41
Marloth Nature Reserve	112.69	113
Nababiep Nature Reserve	109.84	
Nieuwoudtville Nature Reserve	0.66	
Oorlogskloof Nature Reserve	50.7	144
Ramskop Nature Reserve	0.54	
Richtersveld National Park	1624.45	195
Tankwa Karoo National Park	270.64	
Villiersdorp Nature Reserve	5.08	84
Vrolijkheid Nature Reserve	20.27	183

Nama-Karoo

Protected area name	Size (km^2)	Species numbers
Aberdeen Nature Reserve	5.74	
Appie van Heerden Nature Reserve	7.62	
Augrabies Falls National Park	824.15	168
Bosberg Nature Reserve	35.21	92
Boshof Townlands Nature Reserve	6.85	
Commando Drift Nature Reserve	59.83	194
De Aar Nature Reserve	0.51	
Die Bos Nature Reserve	0.6	
Doornkloof Nature Reserve	87.65	142
Hendrik Verwoerd Dam Nature Reserve	112.37	
Kalkfontein Dam Nature Reserve	1.62	
Karoo National Park	327.92	169
Karoo Nature Reserve	142.7	214
Mountain Nature Reserve	4.13	
Mountain Zebra National Park	65.36	203
Oviston Nature Reserve	130.0	141
Prieskakoppie Nature Reserve	0.32	
Rolfontein Nature Reserve	69.38	144
Spitskop Nature Reserve	27.4	
Strydenburg-Aalwynprag Nature Reserve	0.02	
Thomas Baines Nature Reserve	10.03	241
Tierberg Nature Reserve	0.77	
Tussen-die-Riviere Game Farm	210.0	126
Victoria West Nature Reserve	4.28	
Wuras Dam Nature Reserve	2.62	

Overlap between existing protected areas and areas rich in priority bird species: how well protected are the endemic and nomadic birds?

A list of all Karoo bird species and their presence in existing statutory protected areas is given in **Appendix 6**. Most species are represented in more than one large protected area in both the Succulent and the Nama-Karoo. Several of the species listed as priorities for protection (**Tables 8.2 - 8.4**) however, have not been recorded in protected areas. Chestnutbanded Plover, for example, together with Burchell's Sandgrouse, Melodious, Fawncoloured, Pinkbilled, Sclater's, and Stark's Larks have not been recorded in protected areas in the Nama-Karoo, and only Stark's Lark of this group has been recorded in the Succulent Karoo. A number of other species that are frequent to common in the Karoo, and not considered as priorities for protection in this dissertation, have not been recorded in protected areas. However, bird lists from protected areas are often not complete lists for the area, and lists were not obtained for all protected areas, so the representation of species in protected areas may be better than the picture presented in **Appendix 6**. There may be misidentifications, particularly of larks, in the protected area bird lists that may bias the apparent species representation either way. There are few data on breeding status or movements of many of the birds listed for protected areas, and no information on population sizes, so the data available at present for birds in protected areas are very limited.

Overlap between existing protected areas and avian species richness generally in the Karoo

The question arises of how effective existing protected areas in the Succulent and Nama-Karoo are to adequately protect avian species richness in general. **Figure 8.1** shows all QDS that contain protected areas in the Succulent and Nama-Karoo, with an overlay of all species-rich (>150 spp.) quarter-degree squares. **Figure 8.2** shows the same data for the protected areas with and overlay of Karoo (**Appendix 1(a)**) species richness, and **Figure 8.3** shows the same protected area distribution with an overlay of southern African endemic species richness. **Figures 8.4 - 8.6** show overlays of the distribution of endemic, nomadic and lark species richness relative to the parts of the Karoo where there are no protected areas larger than 10 km^2.

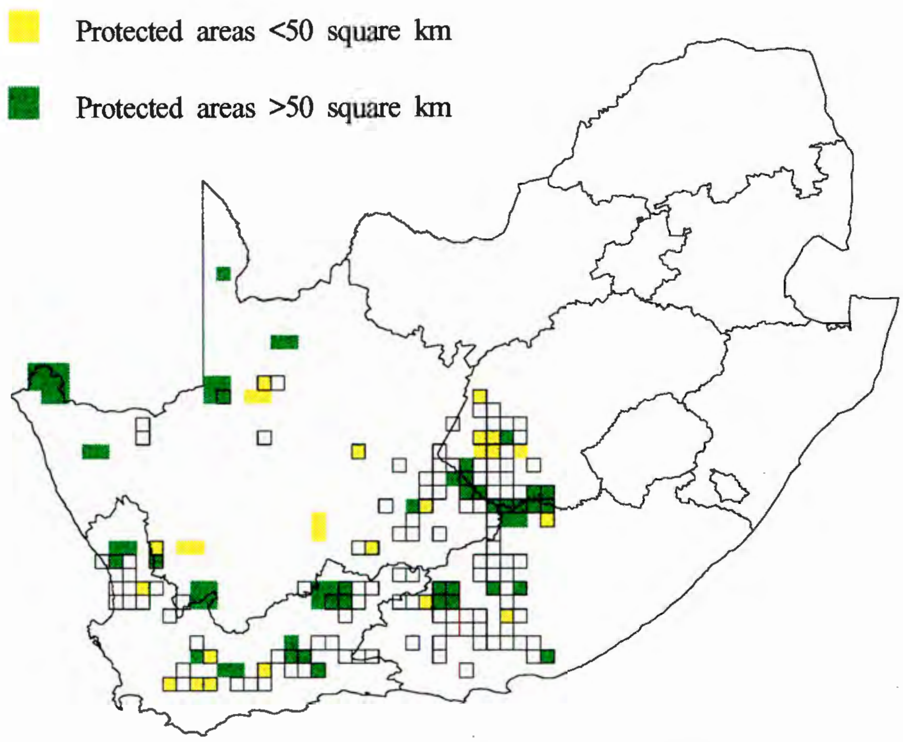

Figure 8.1. Quarter-degree squares that contain statutory protected areas in the Karoo. Squares with reserves smaller than 50 sq. km are shown in yellow and with reserves larger than 50 sq. km in green. Quarter-degree squares with species richness above 150 spp. are outlined in black.

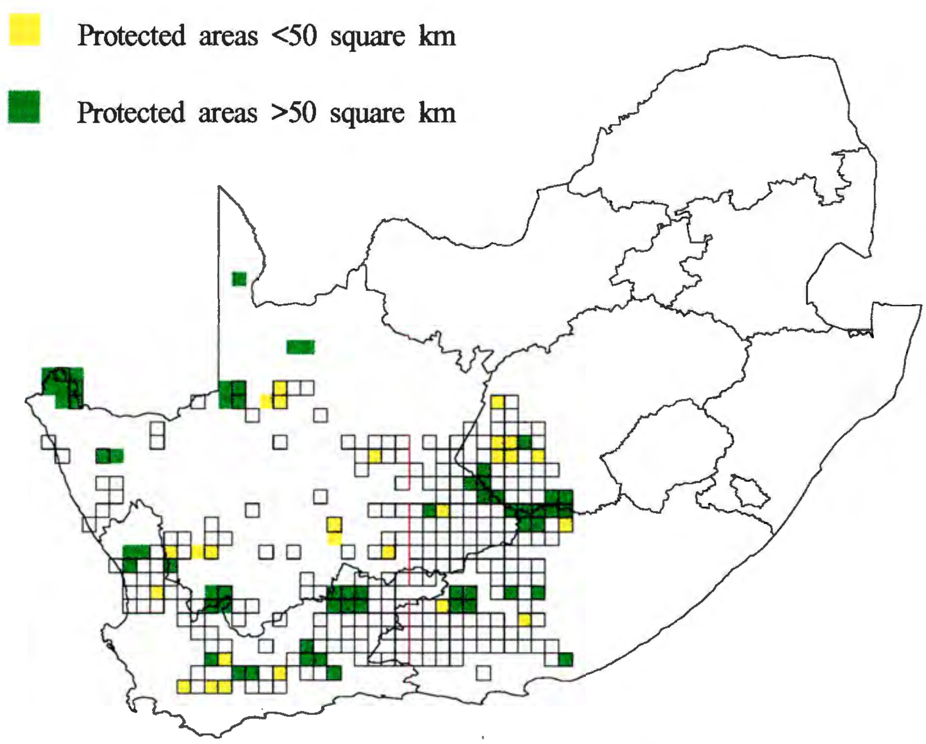

Figure 8.2. Quarter-degree squares that contain statutory protected areas in the Karoo. Squares with reserves smaller than 50 km2 are shown in yellow and with reserves larger than 50 km2 in green. Quarter-degree squares with Karoo (Appendix 1(a)) species richness above 100 spp are outlined in black.

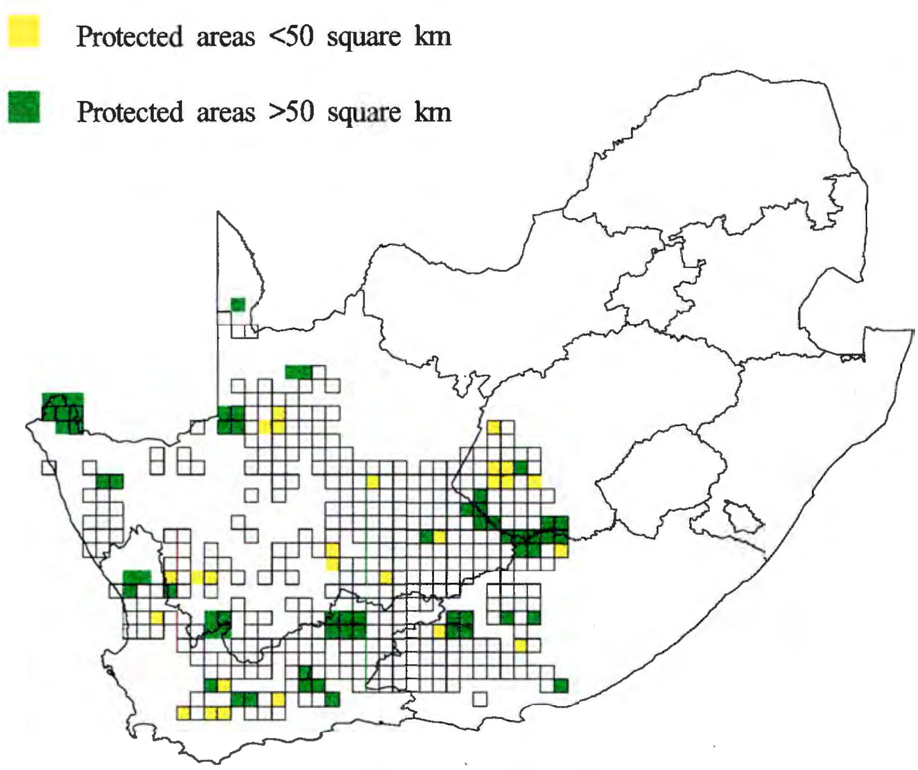

Figure 8.3. Quarter-degree squares that contain statutory protected areas in the Karoo. Squares with reserves smaller than 50 km2 are shown in yellow and with reserves larger than 50 km2 in green. Quarter-degree squares with southern African endemic species richness above 25 spp are outlined in black.

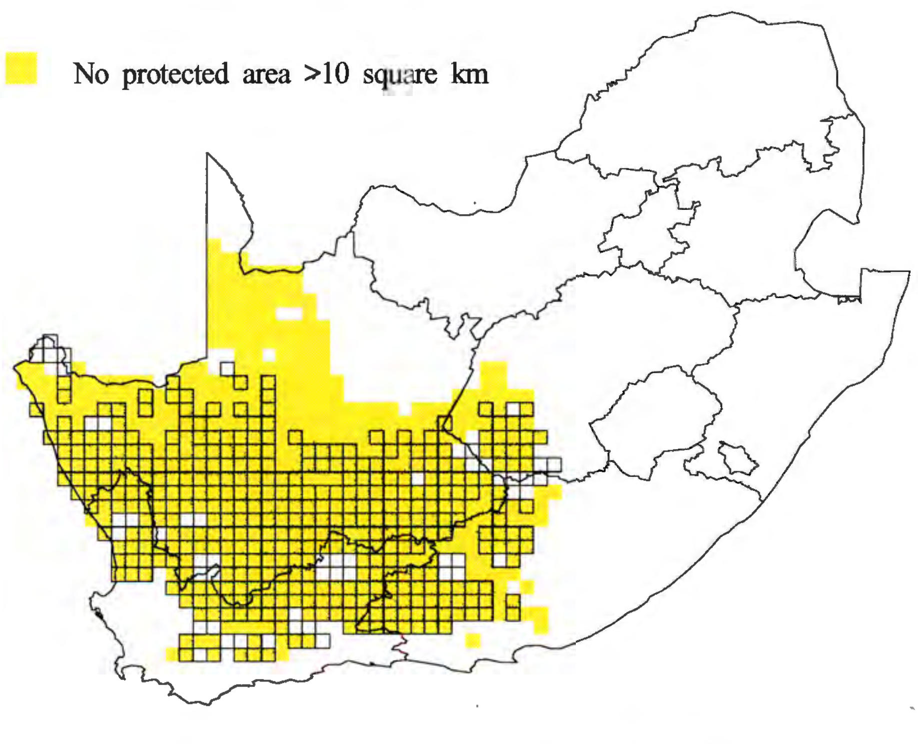

Figure 8.4. Quarter-degree squares where there is no statutory protected area larger than 10 km2 in yellow. Quarter-degree squares with species richness of Karoo endemic species above 10 spp. are outlined in black.

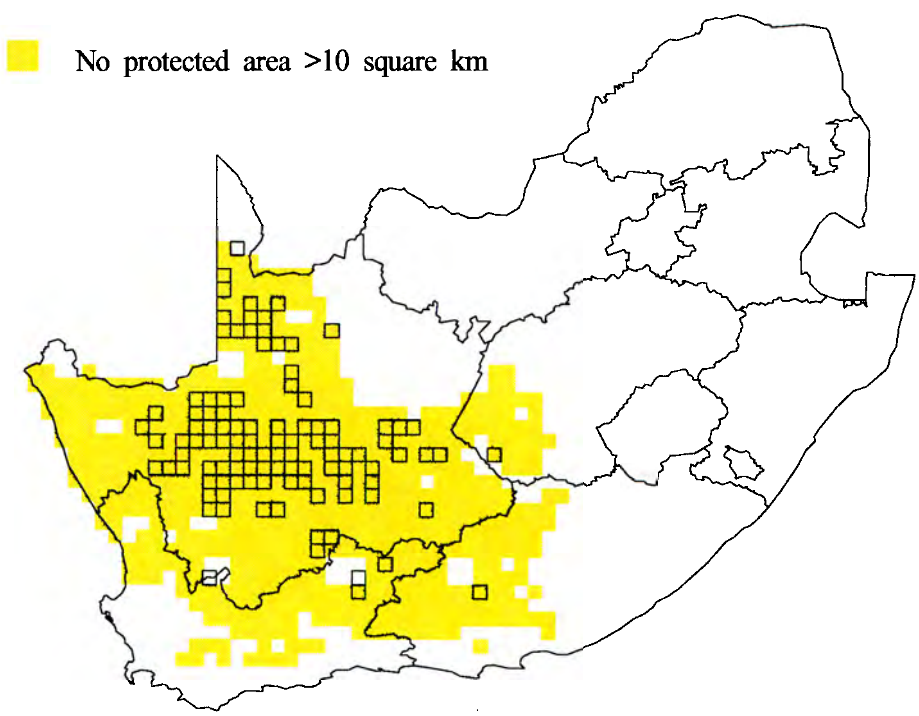

Figure 8.5. Quarter-degree squares where there is no statutory protected area larger than 10 km2 in yellow. Quarter-degree squares where the reporting rate of nomadic species above 20% are outlined in black.

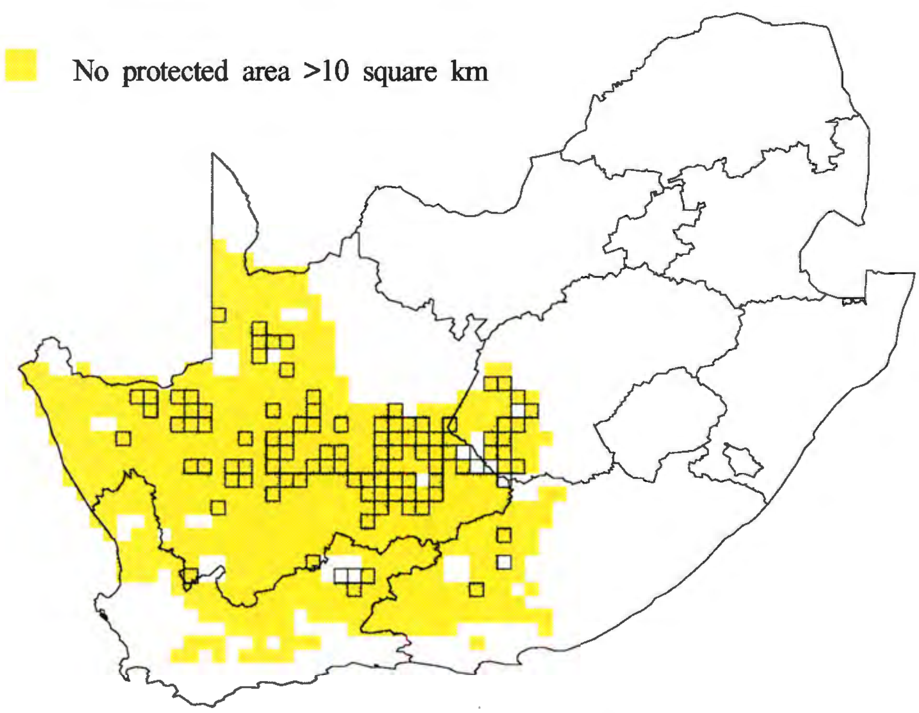

Figure 8.6. Quarter-degree squares where there is no statutory protected area larger than 10 km2 in yellow. Quarter-degree squares with species richness of larks (Alaudidae) above 8 spp. are outlined in black.

There are several protected areas in the Succulent and Nama-Karoo that are in species rich areas and that probably adequately serve to protect most of the avian diversity in the two biomes (**Figures 8.1 - 8.3**). However, the distribution of protected areas in both biomes is markedly skewed to the higher rainfall areas (Chapter 2, **Figure 2.3; Figure 8.1**). Although there are small protected areas in the more arid parts of both biomes, the central, northern and northwestern parts of the Nama-Karoo, and the more arid parts of the Succulent Karoo (with the exception of the Richtersveld) generally lack protected areas, and appear to be particularly inadequate in the central Karoo and Bushmanland where species richness and abundance of nomadic birds is highest (**Figures 8.4** and **8.5**).

Suggestions for improved protection of avian diversity

From the bird distribution database I identified 15 quarter-degree squares (first-tier priorities) in which all priority species occur at relatively high abundances (**Table 8.5**). In selecting these squares I accepted squares towards the centre of the Karoo in preference to edge squares. This group of squares could be reduced to six squares that contain all priority species using an algorithm to select squares that have minimum overlap in species (squares in bold type in Table 8.6). Since the objectives of the present study are to identify areas that could be further investigated, it is probably more useful to present the widest, rather than the narrowest selection of squares, and to investigate all of them if possible. Details (major town or city, vegetation, state of the rangelands) for each of these quarter-degree squares are given in **Appendix 7**.

Table 8.5
Summary statistics, giving priority species richness (Tables 8.2 - 8.4), total species richness and the number of Karoo endemic and southern African endemic species for the first-tier quarter-degree squares identified for further investigation.

QDS	Priority spp.	Total spp.	Karoo endemic	Sth Afr. endemic
2918BB	37	158	20	40
2918BD	44	173	21	38
2920DC	28	73	15	30
2921AC	32	162	12	36
3020AA	23	66	14	24
3020DB	25	79	13	22
3022AC	27	81	12	28
3024AA	38	215	17	44
3025BC	30	175	14	40
3123BB	34	173	17	42
3125CB	31	178	13	40
3221BB	30	160	18	38
3222DA	34	214	19	40
3223AA	36	187	17	40
3319BB	33	167	17	35

The distribution of these quarter-degree squares is shown in **Figure 8.7**. Included in this figure is an additional 11 quarter-degree squares (second-tier priorities) that were part of the penultimate set of squares, but were not finally selected. All of these squares need further studies to identify areas within them that could serve to protect avian diversity, and this requires an integrated, multidisciplinary approach. The bird database from which these QDS were identified does not contain any information on population sizes of birds within the squares, nor any indication of habitat "quality", and this information can only be acquired by extensive field studies. Parts of the area within one of the selected squares, and in one of the adjacent squares in the northwestern Nama-Karoo have already been the subject of a preliminary investigation (du Plessis, 1992). Similar preliminary studies are required for all of the squares listed in **Table 8.5**, particularly as co-operative or joint investigations with botanists and entomologists.

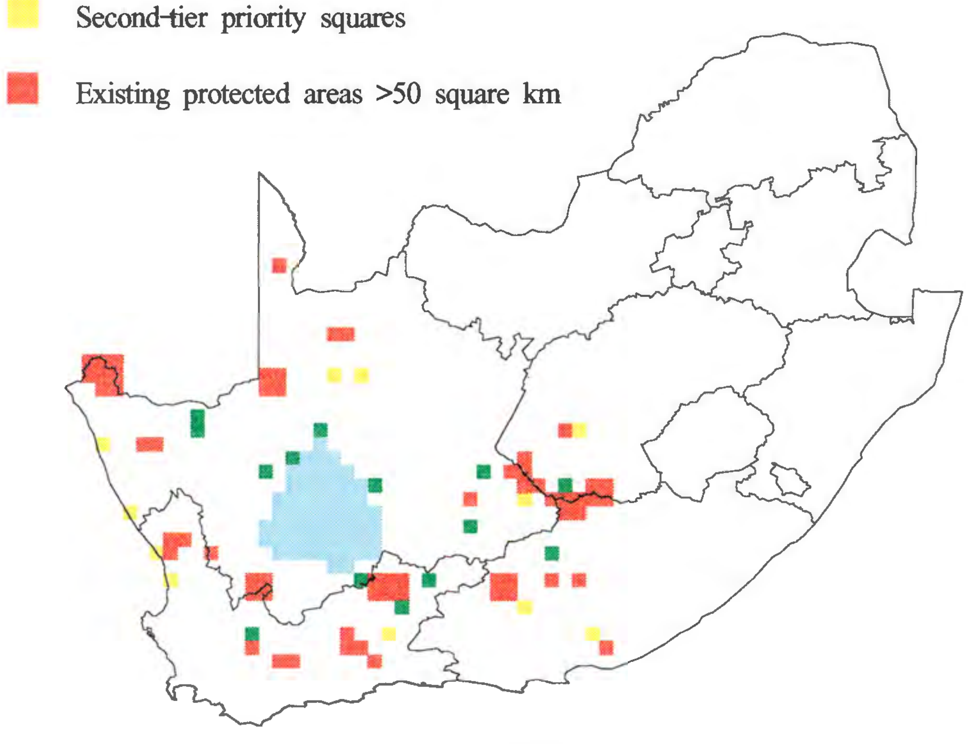

Figure 8.7. First and second tier priority quarter-degree squares for further investigation for protected area sites. The pale blue squares indicate an area of the Nama-Karoo that should be investigated for possible protected areas.

The highest priority species among the endemic birds is the Red Lark. For this species, protection of the remaining habitat is especially urgent. There is some evidence to show that the Red Lark is threatened by domestic livestock in its optimal habitat and that numbers have been reduced by overgrazing (Dean *et al.*, 1991). Although this species is listed for Goegap Nature Reserve, it is unlikely that a viable population could be maintained there, as there is very little suitable habitat for the species in the protected area. Populations of the Red Lark are fragmented within the present distribution range of the species. Any protected area that had as the primary objective the protection of Red larks should include *Stipagrostis brevifolia*, *S. ciliata* and *Centropodia glaucum* grassland on red sands, and preferably should include dunes and sparse *Parkinsonia africana* woodland. The quarter-degree square in which the Red Lark is most abundant (2918BD) has a comprehensive bird checklist, compiled by observers at Black Mountain Mine, and is also where some studies on disturbance and dynamics of dune grasslands have been carried out (S.J. Milton and W.R.J. Dean, in preparation). This area is also a centre of diversity of Mesembryanthemaceae (H.E.K. Hartmann, pers. comm.). A protected area that included suitable habitat for the Red Lark should also serve to protect most other species in Table 8.2. If such a protected area also included such diverse habitats as plains grassland, granite inselbergs and drainage lines, all species in Table 8.3 (with the possible exception of Tawny Eagle and Wattled Starling) would also be afforded protection. Protection of the priority species, not only the endemics, should focus on obtaining as much area as possible in the northwestern Nama-Karoo (Bushmanland). In this respect, the recommendations by du Plessis (1992) to establish a system of protected areas in the northwestern Nama-Karoo should be seriously considered.

The highest priority Karoo endemic and nomadic species is Sclater's Lark. A protected area in the north-central Nama-Karoo that included suitable habitat for this species and a diversity of other habitats would serve to protect other endemic, nomadic and rare species of birds. The protection of nomadic species generally, however, is complicated by the movements of the birds and the dispersion of suitable breeding habitat in the landscape (Chapter 4). No single protected area is likely to serve to protect all nomadic species all of the time. One system of protected areas for nomadic birds would be to have several small and large reserves scattered across a large area. Fahse (1994) has shown by means of a spatially explicit model that the optimal number of protected areas for nomadic larks within a 30 625 km^2 (175 x 175 km) region in the central northern Nama-Karoo is 25. More protected areas within this region would not provide any more breeding habitat for nomadic larks, and fewer protected areas would not ensure the survival of the species if they were confined only to protected areas. The assumptions for the model are that rainfall patches are 13 km^2 in area, that nomadic larks breed an absolute maximum of three times a year, produce 0.6 surviving young annually, have a mean life expectancy of four years, and are confined to protected areas for breeding. Only the last assumption is unrealistic.

Dryland nomadic birds appear to be most abundant in the parts of the Nama-Karoo that receive a large proportion of annual rainfall in autumn (Chapter 4), and most abundant in areas where there are both annual (*Schmidtia kalihariensis*) and perennial desert grasses (*Stipagrostis* spp.) (Chapter 4) on sandy and gravel plains. Areas to be selected for protection should have a high probability of autumn rainfall, and a high coefficient of variation in the rainfall. There is some evidence that the nomadic larks and buntings repeatedly breed in the same general area (pers. obs) and these "hot-spots" should be integrated into protected areas or form the nuclei for establishing new protected areas or conservancies.

Additional priorities for protected areas

There are limits to the degree of objectivity that can be used in making decisions about areas in the Karoo that should be further investigated for protected areas. Certain quarter-degree squares in the Karoo contain habitats that are not rich in bird species, but are unique in southern Africa. The arid grasslands on sands derived from granites and gneisses are one example; the extensive stony flats and poorly drained plains in the arid north-central Nama-Karoo are another, and the extensive shallow saline pans in the Kenhardt-Brandvlei-Vanwyksvlei area yet another. Only the arid grasslands are retained in any selection process that sorts the database on bird species richness or reporting rate of species alone. Quarter-degree squares (third-tier priorities) within the rectilinear figure formed by a line between Calvinia, Brandvlei, Kenhardt, Vanwyksvlei, Carnarvon, Williston and Calvinia (**Figure 8.7**) should be further investigated for potential protected sites, since this area contains extensive stony plains and many of the largest shallow endorheic saline pans. Both dryland and aquatic nomadic birds (Chapter 4: Table 8.3) occur at a relatively high abundance within this area.

Minimum size of protected areas in the Succulent and Nama-Karoo

There are no published data on species-area relationships at a landscape or larger scale for birds of Karoo habitats. Species-area regressions calculated using the SABAP atlas data for quarter-degree squares suggest that the relationship between species richness (in 640 km^2 blocks) and area differs according to rainfall in both the Succulent and Nama-Karoo (**Figure 8.8** and **8.9**), but does not differ significantly between the two biomes. Density data calculated for patches (*ca* 1 km^2) and presented by Winterbottom (1972) and in Chapters 3 and 6, shows that the overall density of birds in plains habitats in the Karoo is low and variable in time and space. Density also varies within and between species of birds (Chapter 6), and within and between habitats in the same landscape, so an area that may be large enough for one species is too small for another.

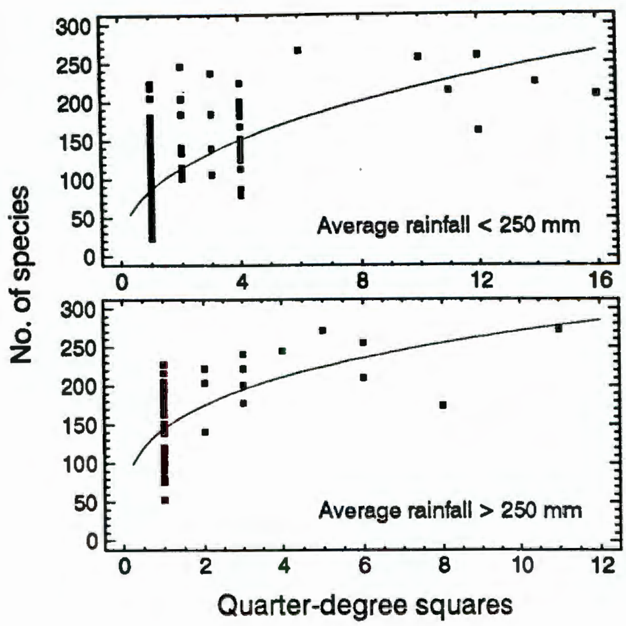

Figure 8.8. Species-area curves for birds in the Succulent Karoo. For rainfall <250 mm, $r^2 = 0.30$, $y = 4.45x^{0.403}$, $p < 0.001$; for rainfall >250 mm, $r^2 = 0.23$, $y = 4.98x^{0.26}$, $p < 0.001$.

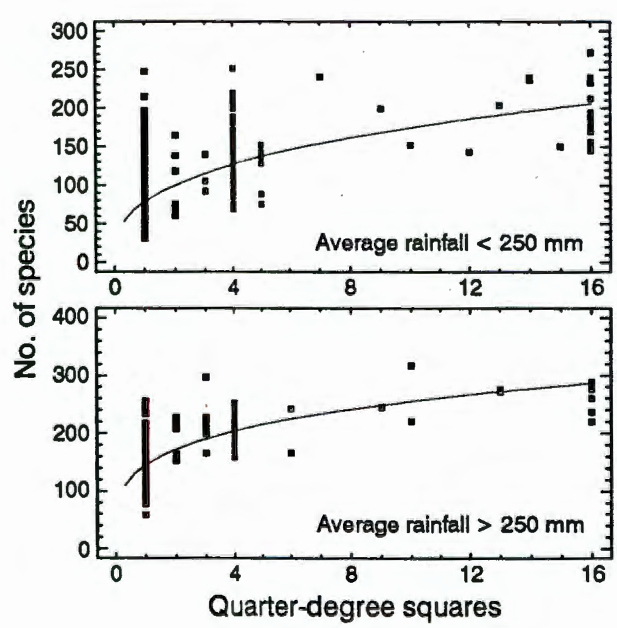

Figure 8.9. Species-area curves for birds in the Nama-Karoo. For rainfall <250 mm, $r^2 = 0.35$, $y = 4.36x^{0.34}$, $p < 0.001$; for rainfall >250 mm, $r^2 = 0.35$, $y = 4.9x^{0.24}$, $p < 0.001$.

Any protected area must be large enough to protect a minimum viable population of all resident species throughout all population and environmental fluctuations. Theoretically, the calculation of the size of any protected area should be simple. But there is no "magic number" to indicate the size of the minimum viable population that is universally applicable to all species (Gilpin & Soulé, 1986), so there is no equation that can be applied to calculating a minimum sized protected area.

In ecosystems such as the Succulent and Nama-Karoo, where there is both spatial and temporal heterogeneity in bird habitats, "larger" protected areas may be more effective than "smaller" protected areas in sustaining avian diversity, but this does not answer the question of what size a "larger" protected area should be. The size of any protected area should be calculated both on the mean density of birds and on the above-ground, and below-ground primary production potential of the area. Primary productivity is related to rainfall (Rutherford, 1980), and nutrient status of soils (Bell, 1982). The minimum size of protected areas should therefore be calculated according to the mean annual rainfall and coefficient of variation of the rainfall, and nutrient status and texture of soils. This implies that protected areas on sandy soils in the arid Karoo (mean annual rainfall <250 mm) should be larger than protected areas in the semi-arid Karoo if the objectives are to protect similar numbers of birds, and larger still if the objective is to protect similar numbers of species (**Figures 8.8** and **8.9**).

However, the relationship between primary production and the density of birds calculated using average density and average primary production data for the Karoo is meaningless. Instead, a range of criteria (density of particular bird species, general condition of the vegetation and soils, and past land-use, for example) should be used to select protected areas. Primary production, secondary production and density of birds are likely to vary according to environmental conditions. Furthermore, different types of shrubland habitats and high-resource patches within fairly homogeneous landscapes (with, presumably, similar primary productivity) have different densities of birds (Chapters 4, 5 and 6). Densities of birds in shrublands in the Succulent and Nama-Karoo vary from 70 to 350 birds/km^2, and in arid grasslands in the Nama-Karoo densities vary from <100 to 500 birds/km^2 (Chapter 3). These numbers, however, are for all species combined. The density of individual species is usually considerably less. Data presented in Chapter 6 and in Appendix 4 show that the density of individual species varies both between species (of similar biomass) and between areas in the Karoo.

In the absence of any "hard" data on minimum population sizes for birds in the Karoo, and for the purposes of this study, I have set the minimum sized population of any species at 500 individuals (following Siegfried, 1992, but Lawton, cited in Dhondt & Matthysen (1993), suggests that animals of 100 g or less need a population size of 5000 or more individuals in order to persist). Thus the area, in km^2, required to protect a population of 500 Karoo Chats in the southern Nama-Karoo is 500/average density per

km^2. The average density of Karoo Chats at Tierberg is 16.57 per km^2 (Chapter 6), which gives 500/16.57 = 30 km^2. The area required to protect a similar sized population of Rufouseared Warblers is 80 km^2 (again using the density data presented in Chapter 6). For larger species, there is a disproportionate rise in area needed to protect a viable population. For Kori Bustards the minimum sized area of homogeneous habitat needed to protect 500 individuals in the southern Nama-Karoo is *ca* 5000 km^2, and for such large raptors as the Martial Eagle, the area needed is *ca* 71000 km^2, assuming a minimum territory size of 284 km^2 per pair (Boshoff, 1993). Furthermore, because of patchiness in habitats generally in the Karoo, any area set aside to protect large species with low densities would have to be very much larger than the size estimated by simply extrapolating density. But protected areas in the Karoo are unlikely to be islands in a sea of vastly different habitats, so size of the protected area, above a certain minimum, is not as critical as, for example, an oceanic island (Gilpin & Diamond, 1980) or a forest or fynbos reserve (Hilton-Taylor & le Roux, 1989; Rebelo, 1991). There are exceptions; species such as the Cinnamonbreasted Warbler (Hockey *et al.*, 1989) and the Red Lark (Dean *et al.*, 1991) presently inhabit what are essentially islands of suitable habitat. There may be little or no interchange of genetic material between the birds of these habitat patches, so in these cases the dispersion, size and status of patches and protected areas may be critical (Hanski, 1994). I suggest that a protected area should be no smaller than 100 km^2 in either the Succulent or the Nama-Karoo to maximize habitat heterogeneity, species richness and to accommodate the variability in density of individual species. A protected area in the arid Nama-Karoo should ideally be about 1000 km^2. A protected area of this size is likely to be capable of maintaining some of those ecological processes that are most incompatible with current land-use in the Karoo. It would also include many of the smaller mammalian predators and would have sufficient area to support small populations of the large raptors and bustards. Any protected area should contain the full suite of evolutionary factors with which the birds evolved, but it would have to be very large to contain predator-prey interactions between large predators and prey, avian and mammalian scavengers and large-scale movements by large ungulates (Novellie, 1993).

To be realistic, very large protected areas are probably not attainable, even in the arid Nama-Karoo, because of sociological and financial constraints. South Africa is at the beginning of a new era, and land redistribution is highly likely to happen in many parts of the country. In the Western Cape, for example, 11216 km^2 that is presently under the control of conservation authorities, and a further 15394 km^2, under the control of various other statutory bodies, could be made available for smallholdings (Anon, 1994). It is almost certain that no decision to acquire land for conservation in South Africa will be made outside of a consultative process within a socioeconomic framework (S.A.N.F. internal report, 8 April 1994). There is a strong possibility that pastoral farming on quite small units of rangeland may be encouraged. It is unlikely, however, that subsistence crop farming in the more arid parts of South Africa will be sanctioned by the Resource Conservation section of the Department of Agriculture. Nevertheless, there is little chance that land solely for the protection of plants and animals will be easily acquired, even in the arid and semi-arid Karoo. It is also likely that some areas that are currently protected from grazing by domestic livestock and from agricultural mismanagement will be made available to small farmers. It is rumoured, for example, that all the land currently used by the South African Defence Force for training and for military manoeuvres, and that serves to protect some biodiversity (if only by benign neglect), will be redistributed. For these reasons, potential protected areas should be selected from the less productive parts of the Karoo, and should be selected particularly from those parts of the Karoo where drought subsidies have supported a pastoral farming industry that should never have existed (see, for example, Vorster, 1994).

The selection of specific sites for protected areas

The report by du Plessis (1992) containing specific proposals for the acquisition of certain farms in the northwestern Nama-Karoo provides useful information on a system of protected areas in Bushmanland. Similar reports at a landscape and at a patch scale must be drawn up for all the quarter-degree squares listed in **Table 8.6.** On the basis of these reports, several widely separated protected areas should be established (optimally 25 such areas over an area of 30 000 km^2 or more), especially in places where there is a high species richness of other taxa. The protection of high species richness of endemic plants and nomadic birds, however, is not always compatible. Plant species richness tends to be highest in areas where the geology and geomorphology is complex (Hilton-Taylor & le Roux, 1989), whereas nomadic bird species richness appears to be highest on sandy plains where there are relatively simple plant assemblages consisting mainly of grasses, annual forbs and legumes, and perennial shrubs. For endemic birds, however, "combination" reserves may work very well.

Another option for protected areas for nomadic birds would be to establish strip reserves, consisting of a 50 - 100 m wide road verge, along main and secondary roads throughout the core area in which nomadic birds occur. Road verges in this area are usually not "managed" in any way, or grazed by domestic livestock, and typically consist of a high cover of desert perennial grasses and shrubs **(Figure 8.10).** The photograph shows a clear difference between the grass cover of the road verge and adjacent rangelands. Stark's Larks, Greybacked Finchlarks, Blackeared Finchlarks and Larklike Buntings were nesting in the road verge, but not in the adjacent rangeland at the time that the photograph was taken (March 1994).

Although this road verge protected area would not be selected for particular qualities, such as a high incidence of particular bird species, it would serve to protect breeding habitat for both resident and nomadic birds. Such a road verge protected area would also protect reptiles, rodents, insects and plant diversity, particularly of geophytes, and would also be a reserve for seeds of plants that are heavily grazed in the adjacent rangelands. There are problems with road verges as protected areas, including traffic, alien plants, spills of toxic materials and discarded plastic bags.

Figure 8.10. Arid, open *Stipagrostis ciliata* grassland on the edge of the Loop 10 road between Aggeneys and the Sishen-Saldanha railway line, north-central Nama-Karoo, March, 1994.

The areas identified using the available data on bird distribution in the Karoo are fairly general, but suggestions for further steps in the selection of suitable specific protected areas can be made. For the Karoo endemic birds and aquatic nomads, the first step would be to select those quarter-degree squares where the representativeness (both reporting rate and species richness) of the priority species is high. Step two would be to identify patches or areas of suitable habitat of the priority species in the field and compile lists of plant and animal species for specific habitat patches. Birds should be repeatedly censused, if possible, in wet and dry periods.

The third step would be to integrate the census and inventory data and to select the richest areas. (It is expected that badly eroded, strip mined or heavily overgrazed areas would have already been eliminated). The fourth step would be to identify specific suitable farms to be purchased for protected areas, selecting them on the basis of whether they were fenced or not, whether the condition of the adjacent rangeland was good, whether the farm included attractive or unusual landscape features, what the price was and whether the area would attract ecotourists. All these steps could be built into an expert systems model, but most of the data to build the model would still have to be collected in the field.

For dryland nomadic species the selection process would be the same from step two onwards, but step one would be replaced by a series of smaller steps. The first step for nomadic species would be to select those quarter-degree squares where the reporting rate of the priority species is high, and where the rainfall is mainly in autumn and has a high coefficient of variation. In the field, select areas where the landscape is relatively flat, and identify places where there is a good cover of annual forbs, and annual and perennial desert grasses. From this point, the selection process would be the same as the process for areas for Karoo endemics.

It is important that potential protected areas are carefully and thoroughly studied before they are purchased. The objectives for protected areas should be not only to protect the priority bird species, but also to protect the maximum amount of biodiversity to be found in the area. Other objectives for any protected area in the Karoo are ecotourism (see below) and long-term research. There is a real need for long-term research sites and projects in the southwestern arid zone of southern Africa (Dean *et al.*, in press d). A protected area could easily fill the dual roles of protecting the avifauna and providing a secure site for long-term research projects investigating, *inter alia*, the effects of weather patterns on processes and population dynamics of birds.

Economic analysis

A critical component of any proposal to protect parts of the landscape is the cost of the land, and the loss to the local community and the country as a whole if the land is taken out of agricultural production.

Land values in the Karoo are variable, and do not appear to be entirely related to carrying capacity or potential income. The carrying capacity of Karoo rangelands is related to rainfall (Vorster, 1985). In order to generate the same amount of income from small livestock on a farm, regardless of locality in the Karoo, there must be an increase in farm size with decreasing rainfall (**Figure 8.11**). This relationship is significant ($y = 14.65x^{-1.19}$, $r^2 = 0.29$, $p < 0.001$) and shows that farm sizes are disproportionately larger in the more arid parts of the Karoo. The relationship between carrying capacity and rainfall is not linear (van den Berg, 1983). Rainfall is more variable and the probability of "disastrous" drought higher in the arid parts of the Karoo (Zucchini *et al.*, 1992). Carrying capacity thus tends to be disproportionately less in more arid parts of the Karoo.

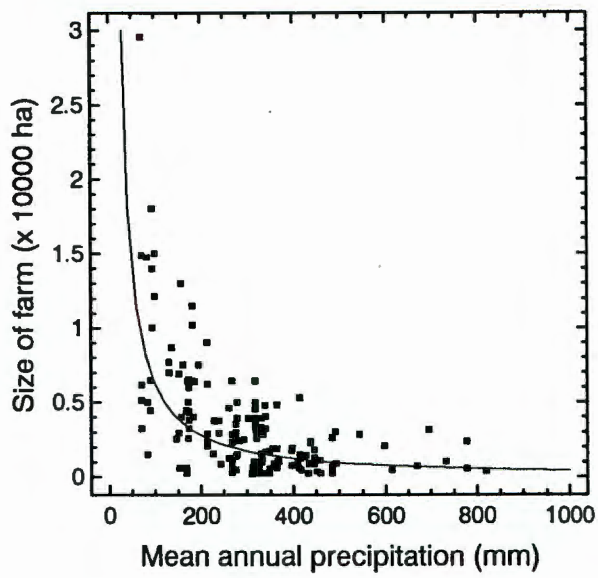

Figure 8.11. The relationship between the size of farms and rainfall in the Karoo.

Because of the high probability of drought, it is logical to assume that ranching small domestic livestock is more risky in arid regions, and that this risk would be reflected in land values; the greater the risk, the lower the price.

Land prices in the Karoo appear to vary according to the size of the farm and the amount of land under irrigation. A regression of all farm prices per ha against mean annual precipitation is not significant (r^2 = 0.06) and there are numerous outliers in the data. If all farms on which there are irrigated croplands are removed from the equation, the correlation coefficient is stronger (r^2 = 0.09). If all farms that are smaller than 1000 ha are removed from the equation, r^2 = 0.17. If a dataset of all farms that have no irrigated croplands and are larger than 1000 ha is used, the correlation is highly significant ($y = -34.2 + 0.73x$, $r^2 = 0.54$, $p < 0.001$). (**Figure 8.11**). Farmland is therefore relatively more expensive if the farm is small, and if there are irrigated

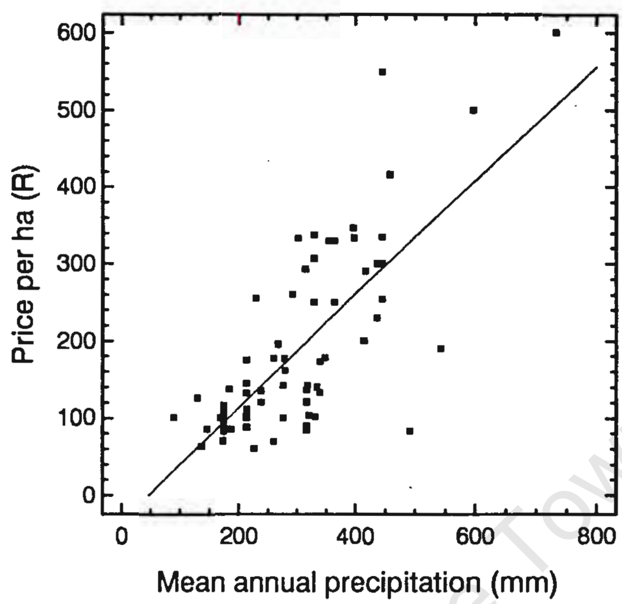

Figure 8.12. The relationship between the selling price of farms in the Karoo and rainfall.

croplands. The availability of ESCOM electricity and non-irrigated ploughed lands on the farm also influenced the fit of the regression line, but not to any significant extent.

The best value for money, for a protected area in the Karoo, is to buy as large a farm as possible, without irrigated croplands, drylands, or ESCOM electricity.

The cost to the local community and to the country in terms of agricultural products, if an area of farm land is taken out of production, is more difficult to calculate. The amount of money generated by ranching small domestic livestock in the Karoo is highly variable and dependent not only on local markets, but also on world markets. Average gross margins per ha per year for four breeds of domestic livestock commonly ranched in the Karoo are shown in **Figure 8.13**. The curves have been fitted using the regression equation given by van den Berg (1983) for the relationship between grazing capacity and rainfall. Angora goats generate most return at present. The graphs, however, must be interpreted with caution. The fitted curves are for livestock at the recommended Department of Agriculture carrying capacity, and many farmers actually stock above carrying capacity in arid areas in the Karoo. None of the livestock types shown in Figure 8.12 can be ranched across the entire Karoo because of aridity, unsuitable vegetation and other factors. Thus, Merino sheep (for fine wool) can be ranched in the Karoo only where the vegetation is in relatively good condition. Dorper sheep (for mutton) are less successful at higher rainfall and probably do best in arid areas. Angora goats (for mohair) are sensitive to extreme temperatures and also require taller vegetation (to browse) so they are ranched more in the southern and eastern Nama-Karoo than in the central, northern and western Nama-Karoo. Boer goats (for meat) are ranched in the northwestern Succulent Karoo and in parts of the eastern Nama-Karoo where there are shrubby *Acacia karroo* trees or the vegetation has been so severely overgrazed in the past that it will not support any other breed of livestock.

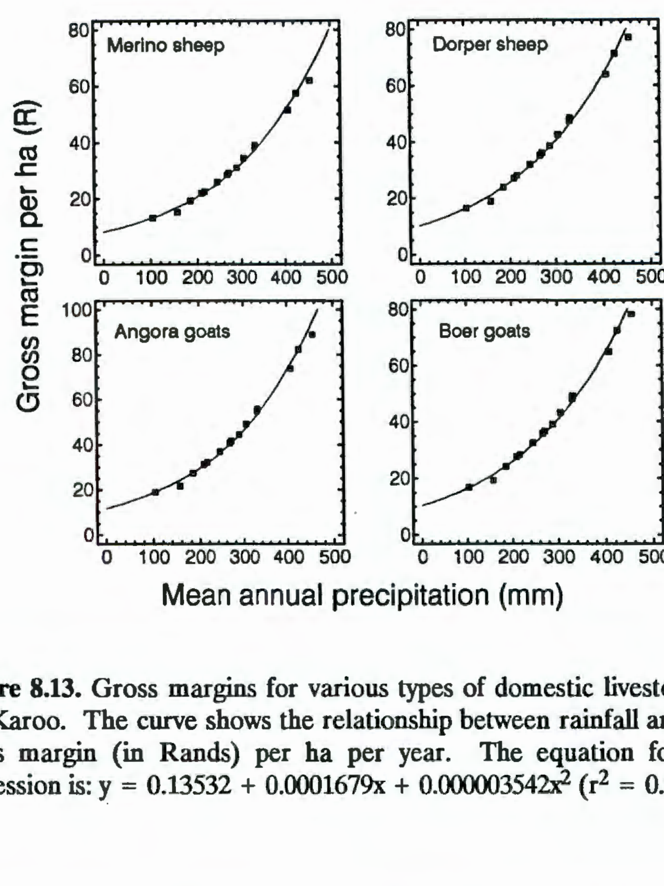

Figure 8.13. Gross margins for various types of domestic livestock in the Karoo. The curve shows the relationship between rainfall and the gross margin (in Rands) per ha per year. The equation for the regression is: $y = 0.13532 + 0.0001679x + 0.000003542x^2$ ($r^2 = 0.99$).

Gross margins calculated from the curves in Figure 8.12 suggest that ranching livestock, even in fairly arid parts of the Karoo, is profitable, provided that the farmer has incurred no major debts.

I then considered the effect of removing a sheep farm of 10 000 ha in the more arid parts of the Nama-Karoo from the production of domestic livestock. A farm of this size could conservatively keep about 1500 Dorper sheep, mainly ewes. Dorper ewes each produce about three lambs in two years. From the breeding stock, about 300 old ewes, and from the second last or third last lambing about 600 ram lambs would be culled every year. This gives a total production for the farm of 900 slaughter sheep annually, or 0.11% of the total number of sheep and goats slaughtered annually in South

Africa (comparative data for 1989/1990 only, taken from Anon (1991)), so the loss to the total meat production of the country is fairly insignificant. The loss in production in the example given above means, in effect, that for every ha taken out of livestock production, there will be a loss of 0.09 slaughter sheep to the annual mutton production of South Africa.

On the other hand, many farmers in the arid central Nama-Karoo receive government aid in the form of low interest loans, soil conservation and drought subsidies, which has sustained stock farming in unsuitable parts of the Karoo at a high cost to the South African tax-payer. About R65 million was paid out to 2 083 farmers from 1983 to 1987, and R41 million was paid out in drought relief from April to August 1993 (Vorster, 1994). These amounts probably far exceed the value of the livestock products generated by farms in the arid central Nama-Karoo.

The more significant effect of removing an area of 10 000 ha from livestock production would be on the local community. The average staff on a sheep farm of 10 000 ha in the southern Karoo is three shepherds, who, together with their families, live on the farm. They would receive meat, clothing and the opportunity to keep a few head of livestock of their own. These benefits would fall away with termination of employment. These displaced people would not be easily absorbed by other farms in the area, and would not be easily employed in villages in the area, because there is already considerable competition for employment in most Karoo villages (pers. obs).

In short, if a productive farm in the Karoo is taken out of livestock production and turned into a protected area, every effort should be made to ensure that the protected area continues to provide services and employment to the local community.

Ecotourism in the Karoo

Apart from the need for areas to protect a diversity of plants and animals in the Succulent and Nama-Karoo, there is a growing ecotourism industry in South Africa (Anon, 1993). Ecotourism is based on ecological resources, and it could be a means of generating wealth in a sustainable way from areas that are relatively undisturbed or uncontaminated (Ceballos-Lascurain, 1991; Cowling, 1993; Novellie, 1993). Cowling & Hilton-Taylor (1994) suggest that income from ecotourism will have to support conservation action in South Africa in the future, so ecotourism could be a vital part of any conservation initiative in the Karoo. A recent government White Paper (Anon, 1993) stresses that one of the national tourism objectives is "to ensure that the country's 'unique selling features' in tourism, i.e. its natural environment, fauna and flora are protected and developed rapidly to maximize their contribution to the economy, with due care being exercised to protect fragile ecological systems". The potential assets of ecotourism have now been recognized and recent government interest in the industry include the White Paper (Anon, 1993) on tourism in South Africa, and the R600 million made available by the Industrial Development Corporation (IDC) for investment in projects for the expansion of tourist facilities (Anon, 1993).

There is an important and lucrative ecotourist industry in the western and northwestern Succulent Karoo. It may be said that annual flowers in Namaqualand drive the economy, at least for some of the time, aptly summed up in a line from a song about Namaqualand "I'm as happy as a hotel, when the flowers bloom again" (David Kramer). Many thousands of tourists, both local and from other countries, visit the western and northwestern Succulent Karoo annually to see the white, yellow and orange "Namaqualand daisies" in full bloom. Namaqualand, and the Richtersveld of the northwestern Succulent Karoo, are two of the areas in the Karoo *sensu lato* that do have many attractions for the ecotourist and where, in Namaqualand at least, there is a thriving ecotourist industry. Although there is spectacular, rugged mountain scenery, a diversity of plants and animals, and charming, attractive villages in the central and southern Nama-Karoo, ecotourism is largely undeveloped in this general area.

More than 90% of foreign tourists come to South Africa to enjoy the scenery and the fauna and flora (Anon, 1993). South Africa offers many resources to the ecotourist. It is a relatively small country with exceptionally rich plant and animal species richness, beautiful scenery and a good transport infrastructure (Cowling, 1993). But the ecotourist industry is dependent to some extent on the unspoiled nature of the resource. Protected areas can offer the ecotourist the opportunity to enjoy wild places and interactions with wild species (Norton, 1987). Eroded, or heavily grazed, sparsely vegetated "desertified" rangelands do not fit the ecotourist ideal.

Cowling & Hilton-Taylor (1994) suggest that it is possible to estimate directly the value of environmental resources, including biodiversity. There is certainly a need to evaluate ecotourism in comparison with stock farming in the Karoo. For example, land in national parks in Kenya generates R112 per ha per year, as opposed to R3.60 it would raise if used for agriculture (Cowling, 1993). It is unlikely that the difference in income per hectare between ecotourism and stock farming in the Karoo would be anywhere near as great, but without the appropriate research and results this is unknown. However, land in national parks, or used for ecotourism, will only generate a high income if high tourist numbers are concentrated in a relatively small area, so ecotourism is probably not a viable alternative to stock farming throughout the Karoo. Furthermore, water use by large numbers of visitors to national parks or other protected areas in arid zones is high, and water supplies in the Karoo may not be constant enough to sustain large visitor numbers. After extended drought, for example, water supplies in the Mountain Zebra National Park and the Karoo National Park diminished to the point where the needs of the restcamps could not be met (Novellie, 1993).

There are further caveats in the development of ecotourist facilities in arid regions. There are two types of ecotourist; "specialists" and "generalists" (Duffus &

Dearden, 1990), classified mainly on the depth of their respective knowledge of wildlife. Specialist ecotourists require little in the way of interpretive facilities, prefer simple accommodation and have a low tolerance for crowds. Generalist ecotourists need interpretive services and comfortable accommodation. Novellie (1993) points out that only two national parks in South Africa generate significant revenue, Kruger National Park in mesic savanna in the Eastern Transvaal and Tsitsikama National Park on the Eastern Cape coast. Both parks attract generalist ecotourists. Visitor numbers to the Kalahari Gemsbok National Park, in the arid savanna, on the other hand, are low and the park does not generate large profits, and probably tends to attract specialists. For various reasons, large numbers of visitors are not attracted to national parks in the arid zone (Novellie, 1993). Ecotourist facilities in national parks or other protected areas in the arid zone should not be over-developed, but should instead have a limited staff and infrastructure, and should cater for the specialist ecotourist, rather than the generalist (Novellie, 1993).

Conclusions

Only two bird species, among the Karoo endemics, are high priorities for protection. The Red Lark is restricted to perennial desert grasslands on sandy plains and dunes, and the population appears to have been reduced by habitat destruction (Dean *et al.*, 1991). A protected area that included extensive areas of habitat for the Red Lark would also serve to protect several other endemic and rare species in the Nama-Karoo. The second priority species is Sclater's Lark, and both this species and the Red Lark could be protected in the same area, particularly if Sclater's Lark is more sedentary than other species classified as nomads. A third species, Cinnamonbreasted Warbler, should be considered a priority for protection in the Karoo. Although this species does occur in a few protected areas, it inhabits granite inselbergs that are essentially islands in a sea of unsuitable habitat. No information is available on the effects of grazing on Cinnamonbreasted Warbler habitat, but Hockey *et al.* (1989) suggest that this species moves away when vegetation cover increases. A study of the precise habitat requirements and population dynamics of the Cinnamonbreasted Warbler is urgently needed.

The nomadic species, particularly the granivorous larks and bunting, are also priorities for protection. It is the availability of habitat suitable for breeding in this group that is critical. Areas, or patches, in which the nomadic larks and bunting breed are high resource patches, where domestic livestock also concentrate. It is important, therefore, that some of the areas in which these patches occur are set aside as protected areas. Although some of the granivorous nomadic larks and the Larklike Bunting occur in large numbers and are widespread in their distribution in the Karoo, the present abundance of the birds does not ensure their continued survival.

Chapter 9

Synthesis

There are a number of key elements in the physical environment and vegetation of the Karoo that have major consequences for the avifauna, and for the protection of the avifauna. It is useful to construct a conceptual framework for the ecology of the avifauna of the Karoo, similar to that outlined for the ecology of arid Australia by Stafford Smith & Morton (1990). The framework is summarized below. The Succulent and Nama-Karoo have not been treated separately since all the key elements apply equally to both biomes. Some of the components of elements of the framework are hypothetical, for which there is currently no support. Data, or references, supporting other concepts in the framework have been presented in earlier chapters.

Key elements that frame the ecology of birds in the Karoo are:

The physical environment

1. Rainfall unpredictable, low and patchy (Chapter 2; Venter *et al.*, 1986).

2. Rainfall seasonality (Cowling *et al.* 1994) and amount, and soils structure the vegetation and consequently habitats for birds.

3. Topographically heterogeneous fertile landscape (Chapter 2; Visser, 1986; Ellis & Lambrechts, 1986).

Habitat features

4. Water (rainfall) and soil texture, rather than fertility of soils govern plant production (Noy-Meir, 1973; Fourie & Roberts, 1976; Rutherford, 1978, 1980 Werger, 1985; Venter, 1992).

5. Vegetation (habitats for birds) can increase in primary production and cover rapidly in response to rainfall (Werger, 1985; Hoffman *et al.*, 1990).

6. Patchy distribution of habitats (plant growth forms) within the landscape (Chapter 2; Werger, 1985; Hoffman & Cowling, 1987).

Consequences of the physical environment and habitat features for birds

7. Species richness of birds correlated with rainfall amount (Chapter 3).

8. Endemic species are associated with aridity (Clancey, 1994) and geological, or geomorphological features (Chapter 3).

9. Low production supports persistent (resident) low density consumers (Chapters 3, 5 and 6; Winterbottom, 1968a; Vernon, 1986).

10. Patchy high production encourages high density nomadic consumers (Chapters 4, 5 & 6; Maclean, 1970a, 1970b; Liversidge, 1980; Vernon, 1986).

11. Brief "windows" of primary production select for short breeding periods and small clutch sizes in nomadic species (Chapter 4).

12. Low production encourages group foraging in low density residents (and possibly co-operative breeding) in species with specialized diets.

Of all biomes in southern Africa, the Succulent and Nama-Karoo are probably the most complex in vegetation and animal distribution patterns. No biome other than the Succulent and Nama-Karoo in southern Africa has a similar range in rainfall seasonality, amount and patchiness. It is the arid southern, central and northern parts of the Nama-Karoo in which rainfall is most patchy in space and time (Chapter 2), and this has a marked influence on vegetation structure (Cowling *et al.*, 1994) and on the avian species assemblages found there (Chapters 3 and 4). It is in these parts of the Karoo that the avifauna differs most from adjacent biomes and it is here that protected areas are most needed (Chapter 8).

The Karoo *sensu lato* is rich in bird species around the edges, with a steady decrease in species richness towards the arid centre (Chapter 3). This is, however, accompanied by a shift in the way that birds use the environment and a concomitant increase in the number of nomadic species, with a trend towards high temporal variability in the density of individuals of resident species (Chapters 4, 5, 6). In a conservation context, this shifting mosaic of species assemblages and abundances in response to pulses in the primary and secondary production of the environment means that no single area, unless it is very large, will provide protection for all of the birds all of the time. Several protected areas, strategically placed in landscapes in which a high species richness and high numbers of nomadic birds have been recorded, and in which probabilities of suitable breeding habitat are high, are required for adequate protection. It is unlikely that the movements of nomadic birds are entirely random, and nomadic birds probably return to patches where they have successfully nested in the past. There is very little evidence for this, but repeated nesting by nomadic birds in the same locality has been observed, so the idea is not without some support. Repeated nesting by nomadic birds in certain areas has implications for the identification of potential protected sites; patches that are consistently used by nomadic birds for breeding should be identified as a first step in any conservation initiative that has as its goal the protection of nomadic species.

From what, though, are these birds being protected? Why are protected areas necessary in an arid landscape that many South Africans would consider a worthless desert? These issues can be addressed more easily if the question is turned around:

what are the consequences for the avifauna of the greater Karoo if protected areas are not established?

Are protected areas necessary for the protection of birds in the Karoo?

Ecological changes have taken place in the Karoo since the settlement, by European colonists, of the arid interior of South Africa. These changes relate chiefly to the extinction of the hunter-gatherer peoples (the Khoi-San), the removal of the large ungulates from the ecosystem, and the creation of "oases" around farmhouses and water-points in rangelands.

Although small herds of springbok still "trekked" through the southern Karoo until about 1900, by 1880 the herds of ungulates, together with their large predators, had largely been eliminated from the Karoo (Skead, 1980). Avian scavengers and large raptors lingered on in the Karoo for some time after the large ungulates had gone, but under the pressure of persecution and "problem animal control", they too became increasingly rare. Many species of vultures and eagles now occupy only a fraction of their former distributions (Boshoff *et al.*, 1983). The loss of these components of the ecosystem almost certainly caused cascades that ran through the system. What remains today in the Karoo is the surviving subset of what, by all (anecdotal) accounts, must have been a rich assemblage of species. There have also been some gains in bird species through the widespread planting of trees around farmhouses, and the creation of water-points, allowing commensal species and water-dependent species of birds to colonize parts of the arid Karoo.

It seems unlikely that livestock grazing in the Karoo can be sustained at present levels by the vegetation. The decrease in livestock biomass over the past 75 years (Dean & Macdonald, 1994) implies a loss in usable primary production, but does not imply a reduction in vegetation cover or a shift in vegetation type. I showed in Chapter 7 that birds nest successfully in plants that are toxic or distasteful to herbivorous mammals, so shifts in the ratio between unpalatable and palatable plants are not likely to affect birds to any great extent if this is the only change in the habitat. However, the available evidence (Chapter 7) suggests that heavy grazing by livestock and transitions of vegetation to new states (Milton *et al.*, 1994; Milton & Hoffman, 1994) does affect the composition of the bird species assemblages and the numbers of individual birds in Karoo rangelands. The effects of changes in rangeland vegetation on the biota as a whole are less clear, but it is likely that synergistic interactions between seeds, ants and birds as a result of shifts in palatable to unpalatable plants and a decrease in vegetation cover on heavily grazed areas will shape and reshape faunal assemblages. Preliminary results from other studies, including birds (Chapter 7), suggest these reshaped faunal assemblages will not be as species rich as they formerly were (Milton *et al.*, 1994; Dean *et al.*, in press b) and that there will be changes in the relative abundance of individuals of the species concerned. This is certainly true for cicadas (Homoptera: Cicadidae)

(Milton & Dean, 1992), ants (Hymenoptera: Formicidae) (Milton & Dean, 1993) and birds (Chapter 7).

What is essential for the continued existence of the nomadic bird species in the Karoo is the availability of high resource patches to provide breeding habitat. These patches would also provide high quality grazing for domestic livestock so there is likely to be increased grazing pressure on these patches by livestock at the time when the birds are breeding. Nomadic birds, and resident granivorous birds, tend to feed on the seeds of plants that are palatable to livestock (Chapter 4) and domestic livestock can substantially reduce the seed production of individual plants by herbivory (Crawley, 1983). There may be competitive interactions between livestock and birds indirectly for the same resource, as well as a general reduction in food available to the birds. Areas that are protected from grazing, or at the least, from sustained heavy grazing, would be important in providing breeding habitat for the nomads, and for this reason alone, refuge areas should be established. A reduction in the relative abundance of individuals of nomadic species is likely in the absence of refuges, or areas protected from domestic livestock. Assuming that stocking rates and grazing pressure in the Karoo continue at present levels, and without protected areas, an important part of the avian diversity in the Karoo may be lost.

For the rare, resident, Karoo endemic species, the future without protected areas may be equally uncertain. Although many of the Karoo endemic species are widespread and relatively abundant, for some species habitats are shrinking in area, and populations are becoming increasingly fragmented. All these species are adapted to an ecosystem in which there is patchiness in habitats, fluctuations in rainfall timing and amount and shifts in vegetation states. It is unlikely, though, that these birds are adapted, or pre-adapted to the present Karoo, where there have been changes in components of the ecosystem and perhaps changes in ecosystem processes. For example, the domestic livestock that now constantly graze Karoo rangelands probably do not simulate the intermediate disturbances caused by the dynamic, patch-selective grazing of the wild ungulates. Too little is known about the role of birds in ecosystem processes in the Karoo, and too little is known about the disruption of ecosystem processes by domestic livestock and the effects this may have on birds. For example, domestic livestock may severely disrupt decomposition cycles by reducing the cover of vegetation. This reduction in cover leads to increases in soil erosion and soil temperature, changes in the stability and species richness of plants, and can affect the numbers of insects and seeds on the soil surface (Chapter 7). For birds, this may mean less suitable nest sites (because of reduced cover and increased soil surface temperature), less food for the insectivores (because there are less insects with less cover; Dean & Milton (in press)), or more food at times for the granivores (because of changes in the stability of the plant assemblage, and increases in the number of annual plants) (Chapter 7).

Do the present protected areas in the Karoo adequately serve to protect the birds? Most of the bird species in the Succulent and Nama-Karoo are represented in statutory protected areas, but representation in larger protected areas (>10 km^2) is poor, particularly in the Succulent Karoo. Priority species (Karoo endemics, dryland and aquatic nomadic species, and larks) have not been frequently recorded from protected areas. This may reflect the fairly sparse data available on birds in protected areas, rather than a real absence of species.

The overlay maps that show species richness and the distribution of protected areas in the Karoo (Chapter 8) suggest that areas rich in species are protected at present. It is the species-poor, but Karoo endemic species-rich areas that lack protected areas, and it is to these parts of the Karoo that conservation initiatives should be directed.

The species that were selected as priorities for protection were chosen because they were (a) endemic to the Karoo, (b) nomadic species apparently not well represented in existing protected areas, and, (c) a group of species (the larks) that are particularly species-rich in the Karoo. If areas had been selected on species richness alone, some of the Karoo endemics (**Figure 9.1**), many of the southern African endemics (**Figure 9.2**) and some of the larks (**Figure 9.3**) would have been included, but areas rich in nomadic birds would not have been selected (Chapter 4: **Figure 4.4**). Furthermore, areas in which Red Lark, Cinnamonbreasted Warbler and Sclater's Lark are relatively abundant would not have been selected, because these species occur in generally (avian) species-poor areas in the northwestern Nama-Karoo and western Succulent Karoo. Doubts have been expressed of the value of the species concept, and therefore species number, as criteria for determining sites for protected areas (Bond, 1989). Avian species richness alone cannot be used to focus priorities for protected areas in the Karoo. Species-rich areas in the Karoo may simply include many species that are common and adequately protected in other biomes.

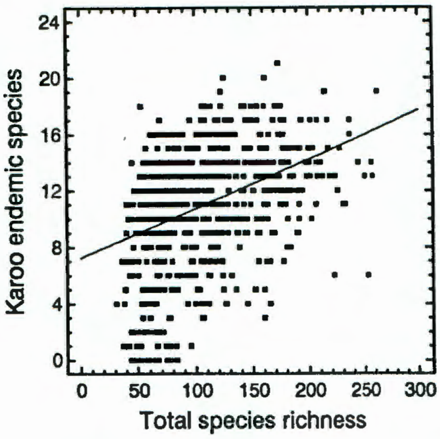

Figure 9.1. A regression of the number of Karoo endemic bird species against total species richness in quarter-degree squares ($r^2 = 0.15$, $y = 7.2 + 0.034x$, $p < 0.001$).

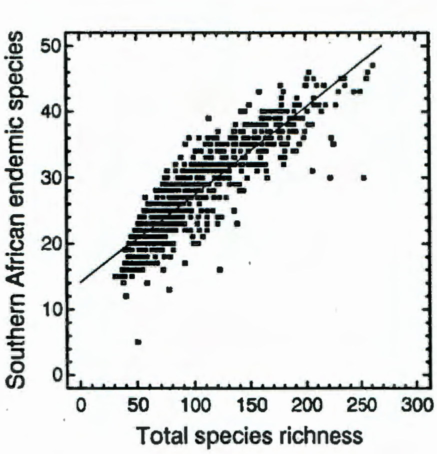

Figure 9.2. A regression of the number of southern African endemic bird species against total species richness in quarter-degree squares in the Karoo ($r^2 = 0.76$, $y = 14.12 + 0.13x$, $p < 0.001$).

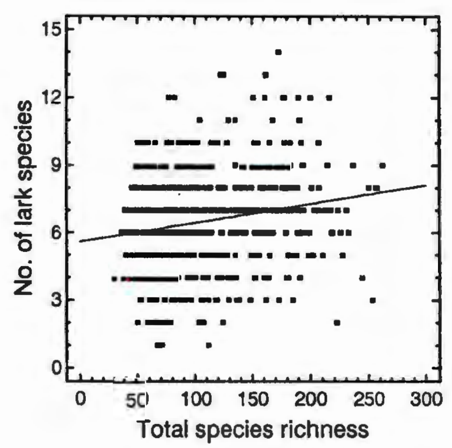

Figure 9.3. A regression of the number of lark species against total species richness in quarter-degree squares in the Karoo (r^2 = 0.03, y = 5.59 + 0.08x, p <0.001).

On the other hand, sites that are rich in Karoo endemics, southern African endemics and larks are also rich in other species. If the objectives are to protect avian diversity in the Karoo, the best method seems to be to protect sites rich in Karoo endemics, southern African endemics and larks, provided that such sites include priority species for protection. The best method, however, of protecting nomadic species richness is to protect sites rich in nomads, and not necessarily otherwise species-rich.

What areas in the Karoo should be protected

It is possible, using the SABAP database, to identify parts of the Succulent and Nama-Karoo that contain particular elements of the avifauna. Combining bird data with climatic data and vegetation distributional data provides a very useful first approximation of where protected areas should be situated. But these data are limited, both in scope and application, and at the coarse scale at which the data are mapped, can only provide a general picture of where protected sites should be situated. The coverage of the Karoo *sensu lato* by SABAP observers is patchy in time and in space, and this also places severe limitations on the usefulness of the database for more detailed analyses. Given that there is considerable patchiness in habitats at the local and the landscape level in the Karoo, bird distributional data should be mapped at least at a one-eighth degree (7.5' x 7.5') scale if not at a 1' x 1' scale.

The paucity of plant distributional data for the Karoo unfortunately made it impossible to evaluate the selected areas for the protection of endemic Karoo plants. No national database of locality records for reptiles exists, and the distribution of invertebrates in the Karoo is poorly known, and these data should, ideally, be incorporated into any selection process for protected areas in the Karoo.

There are two critical components of any proposal to protect parts of the landscape:

1. Where, and how large should protected areas be?
2. What difference will it make to the local economy, and to the country as a whole if the land is taken out of agricultural production?

I identified a set of quarter-degree squares in the Succulent and Nama-Karoo that could be further investigated for suitable potential protected sites. Sites to be protected should be identified in the field and surveyed at the landscape level. Such surveys should, ideally, be done as co-operative projects, and decisions based on the results of thorough field surveys that provide some measure of bird population sizes and dynamics, habitat use, plant species assemblages and condition of the vegetation. What is especially important is the identification of the landscape units to be protected. Complete watersheds may be important as target conservation areas in the arid Nama-Karoo, where drainage is often managed and diverted into bottomland agriculture. The life expectancy, or the production potential, of many of these bottomland croplands is often short-lived due to salinization and drought. The recovery of the vegetation to its original state on these old croplands is slow (Macdonald, 1989; Dean & Milton, in press).

Other targets for protected areas are the plains and inselbergs of the north-central and northern Nama-Karoo. Protected areas, incorporating granite and gneiss inselbergs and sandy and stony plains with sparse desert grasslands would include much of the avian diversity of the region, while not greatly affecting the local production of domestic livestock. In Chapter 2 I showed that this part of the Nama-Karoo has a low carrying capacity for domestic livestock, and a low dryland agriculture potential, while supporting a high species richness and abundance of nomadic birds (Chapter 4).

The effect of the removal of productive rangelands from livestock ranching might be significant if the area was large and particularly productive. Analyses of the economics of livestock ranching in the arid parts of the Nama-Karoo are confounded by government aid to farmers, and it is difficult to calculate the real cost of removing rangelands from livestock production. It is also difficult to calculate the loss in terms of goods and services to the local community if agricultural land is taken out of production. These effects should be considered when a protected area is planned, and as much as possible should be done to ensure the continued well-being of the local community.

There has been considerable debate on the size of protected areas (reviewed by Simberloff, 1988). Central to the debate is whether a single large, or several small reserves would preserve the same number of species. For the smaller organisms, this debate is probably irrelevant (Franklin, 1993). In the context of protected areas in the Karoo, where the density of birds is low and the primary and secondary production of habitats variable, large areas would intuitively appear to be more effective at preserving populations of certain species than small areas, simply because they contain more temporally asynchronous patches and more individual birds (Chapters 5 and 6). Large areas would also contain more of the elements with which the birds evolved, such as predators, and small digging mammals, that may be important in creating small-scale disturbances in which birds forage. Although some processes in the Karoo may have been disrupted by the virtual extinction of the large mammals in the region, protecting large areas may ensure that other processes are maintained. The Nama-Karoo, and the more arid parts of the Succulent Karoo, are two regions of southern Africa where it is still possible to acquire large tracts of land without large initial expenditure, and without a significant reduction in the local production of domestic livestock.

It must be accepted that for some species protected areas in the Karoo are never going to be large enough. For these species, and for many others, the area between protected areas, or the "unreserved matrix" (Franklin, 1993) will be critical. Many species of birds could survive, and indeed have survived, outside of protected areas in the Karoo. Although the unprotected matrix is almost entirely occupied by domestic livestock, and has been severely overgrazed in parts (Acocks, 1964; Leistner, 1979; Roux & Vorster, 1983; Werger, 1985; Dean *et al.*, 1991), it will always be important to the avifauna of the Succulent and Nama-Karoo ecosystems. Directed, long-term research on the interactions between domestic livestock and vegetation and the effects of herbivory on native animals, including birds, in rangelands of the unprotected matrix is essential. Little is known of ecosystem processes at the landscape level, or indeed at any level, in the Karoo. Comparative studies between protected areas and the rangelands of the unprotected matrix should also be done, if only to be able to put the management of protected areas on a sound basis. It would be an added bonus to be able to use knowledge of the ecosystem gained from research in protected areas to evaluate livestock management systems and to improve the secondary production of the Karoo, while at the same time protecting a rich and well-adapted avifauna.

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Appendix 1: List of bird species recorded in the Succulent and Nama-Karoo

A list of bird species recorded in quarter-degree squares in the Karoo. The frequency is the percentage and (number of squares) in which the species has been recorded out of a total of 163 squares in the Succulent Karoo and 513 squares in the Nama-Karoo.
Note: Although the Ostrich *Struthio camelus* has been recorded in 40.24% (272) of the quarter-degree squares in the Karoo, it can no longer be considered a wild bird in this region and is not included in the list. Similarly, the Feral Pigeon *Columba livia* has been recorded in 27.5% (186) squares in the Karoo, but has also been excluded from the list because there may be confusion between "domesticated" Feral Pigeons and "wild" Feral Pigeons.

(a): Species considered to be widespread in the Karoo and that have been included in the database used for all analyses.

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Great Crested Grebe *Podiceps cristatus*	12.3 (20)	4.5 (23)
Blacknecked Grebe *Podiceps nigricollis*	21.5 (35)	8.0 (41)
Dabchick *Tachybaptus ruficollis*	42.3 (69)	35.3 (181)
Whitebreasted Cormorant *Phalacrocorax carbo*	44.8 (73)	35.5 (182)
Reed Cormorant *Phalacrocorax africanus*	44.2 (72)	40.4 (207)
Darter *Anhinga melanogaster*	31.3 (51)	23.4 (120)
Grey Heron *Ardea cinerea*	57.7 (94)	54.2 (278)
Blackheaded Heron *Ardea melanocephala*	69.3 (113)	58.1 (298)
Goliath Heron *Ardea goliath*	6.1 (10)	10.1 (52)
Purple Heron *Ardea purpurea*	14.1 (23)	3.5 (18)
Great White Egret *Casmerodius albus*	8.6 (14)	5.1 (26)
Little Egret *Egretta garzetta*	31.9 (52)	17.2 (88)
Yellowbilled Egret *Egretta intermedia*	14.1 (23)	6.0 (31)
Cattle Egret *Bubulcus ibis*	45.4 (74)	39.0 (200)
Blackcrowned Night Heron *Nycticorax nycticorax*	19.0 (31)	10.3 (53)
Little Bittern *Ixobrychus minutus*	12.9 (21)	2.7 (14)
Hamerkop *Scopus umbretta*	49.7 (81)	40.9 (210)
White Stork *Ciconia ciconia*	20.2 (33)	26.7 (137)
Black Stork *Ciconia nigra*	27.6 (45)	27.3 (140)
Yellowbilled Stork *Mycteria ibis*	0.0 (0)	6.8 (35)
Sacred Ibis *Threskiornis aethiopicus*	45.4 (74)	47.0 (241)
Glossy Ibis *Plegadis falcinellus*	7.4 (12)	5.5 (28)
Hadeda Ibis *Bostrychia hagedash*	30.7 (50)	45.0 (231)
African Spoonbill *Platalea alba*	39.3 (64)	40.9 (210)
Greater Flamingo *Phoenicopterus ruber*	13.5 (22)	15.8 (81)
Lesser Flamingo *Phoeniconaias minor*	8.0 (13)	6.0 (31)
Whitefaced Duck *Dendrocygna viduata*	1.8 (3)	9.4 (48)
Egyptian Goose *Alopochen aegyptiacus*	79.8 (130)	78.9 (405)
South African Shelduck *Tadorna cana*	79.8 (130)	77.4 (397)
Yellowbilled Duck *Anas undulata*	54.0 (88)	54.6 (280)

Appendix 1(a) continued

Species	Frequency	
	Succulent Karoo	Nama-Karoo
African Black Duck *Anas sparsa*	41.1 (67)	32.2 (165)
Cape Teal *Anas capensis*	39.3 (64)	32.9 (169)
Redbilled Teal *Anas erythrorhyncha*	31.3 (51)	35.9 (184)
Cape Shoveller *Anas smithii*	29.4 (48)	23.8 (122)
Southern Pochard *Netta erythrophthalma*	20.2 (33)	12.9 (66)
Spurwinged Goose *Plectropterus gambensis*	33.1 (54)	34.1 (175)
Maccoa Duck *Oxyura maccoa*	17.2 (28)	5.3 (27)
Secretarybird *Sagittarius serpentarius*	22.7 (37)	44.1 (226)
Cape Vulture *Gyps coprotheres*	3.1 (5)	5.1 (26)
Whitebacked Vulture *Gyps africanus*	0.0 (0)	7.4 (38)
Yellowbilled Kite *Milvus migrans*	18.4 (30)	13.1 (67)
Blackshouldered Kite *Elanus caeruleus*	57.1 (93)	48.3 (248)
Black Eagle *Aquila verreauxii*	60.7 (99)	39.4 (202)
Tawny Eagle *Aquila rapax*	0.6 (1)	13.5 (69)
Booted Eagle *Hieraaetus pennatus*	54.6 (89)	24.8 (127)
Martial Eagle *Polemaetus bellicosus*	42.3 (69)	40.2 (206)
Blackbreasted Snake Eagle *Circaetus pectoralis*	25.8 (42)	16.0 (82)
African Fish Eagle *Haliaeetus vocifer*	26.4 (43)	20.7 (106)
Steppe Buzzard *Buteo buteo*	39.9 (65)	43.7 (224)
Jackal Buzzard *Buteo rufofuscus*	82.8 (135)	62.0 (318)
Redbreasted Sparrowhawk *Accipiter rufiventris*	14.1 (23)	5.7 (29)
African Goshawk *Accipiter tachiro*	8.0 (13)	2.3 (12)
Gabar Goshawk *Micronisus gabar*	9.2 (15)	15.2 (78)
Pale Chanting Goshawk *Melierax canorus*	93.3 (152)	95.3 (489)
African Marsh Harrier *Circus ranivorus*	11.0 (18)	5.3 (27)
Black Harrier *Circus maurus*	50.9 (83)	22.4 (115)
Gymnogene *Polyboroides typus*	26.4 (43)	10.5 (54)
Peregrine Falcon *Falco peregrinus*	11.0 (18)	2.9 (15)
Lanner Falcon *Falco biarmicus*	47.2 (77)	39.8 (204)
Rock Kestrel *Falco tinnunculus*	98.2 (160)	91.2 (468)
Greater Kestrel *Falco rupicoloides*	55.8 (91)	66.7 (342)
Lesser Kestrel *Falco naumanni*	18.4 (30)	32.0 (164)
Pygmy Falcon *Polihierax semitorquatus*	0.0 (0)	17.0 (87)
Greywing Francolin *Francolinus africanus*	42.3 (69)	22.4 (115)
Orange River Francolin *Francolinus levaillantoides*	0.0 (0)	7.6 (39)
Cape Francolin *Francolinus capensis*	53.4 (87)	7.2 (37)
Common Quail *Coturnix coturnix*	41.1 (67)	25.7 (132)
Helmeted Guineafowl *Numida meleagris*	43.6 (71)	49.9 (256)
Blue Crane *Anthropoides paradiseus*	14.1 (23)	31.6 (162)
Black Crake *Amauromis flavirostris*	12.9 (21)	2.5 (13)
Moorhen *Gallinula chloropus*	30.7 (50)	24.4 (125)
Redknobbed Coot *Fulica cristata*	47.2 (77)	48.5 (249)
Kori Bustard *Ardeotis kori*	13.5 (22)	35.7 (183)
Stanley's Bustard *Neotis denhami*	8.0 (13)	6.0 (31)
Ludwig's Bustard *Neotis ludwigii*	65.6 (107)	65.1 (334)
Blue Korhaan *Eupodotis caerulescens*	0.0 (0)	17.5 (90)
Karoo Korhaan *Eupodotis vigorsii*	50.9 (83)	75.4 (387)
Redcrested Korhaan *Eupodotis ruficrista*	0.0 (0)	7.2 (37)

Appendix 1(a) continued

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Black Korhaan *Eupodotis afra/afraoides*	55.2 (90)	70.0 (359)[1]
Ringed Plover *Charadrius hiaticula*	11.0 (18)	6.0 (31)
Chestnutbanded Plover *Charadrius pallidus*	4.9 (8)	3.3 (17)
Kittlitz's Plover *Charadrius pecuarius*	30.7 (50)	38.8 (199)
Threebanded Plover *Charadrius tricollaris*	79.8 (130)	79.9 (410)
Crowned Plover *Vanellus coronatus*	47.2 (77)	60.2 (309)
Blacksmith Plover *Vanellus armatus*	79.1 (129)	79.1 (406)
Common Sandpiper *Actitis hypoleucos*	33.7 (55)	19.7 (101)
Wood Sandpiper *Tringa glareola*	22.1 (36)	20.3 (104)
Marsh Sandpiper *Tringa stagnatilis*	16.6 (27)	15.0 (77)
Greenshank *Tringa nebularia*	45.4 (74)	41.7 (214)
Curlew Sandpiper *Calidris ferruginea*	21.5 (35)	16.8 (86)
Little Stint *Calidris minuta*	26.4 (43)	31.4 (161)
Sanderling *Calidris alba*	12.3 (20)	2.5 (13)
Ruff *Philomachus pugnax*	18.4 (30)	18.3 (94)
Ethiopian Snipe *Gallinago nigripennis*	16.0 (26)	5.8 (30)
Avocet *Recurvirostra avosetta*	51.5 (84)	44.4 (228)
Blackwinged Stilt *Himantopus himantopus*	48.5 (79)	52.0 (267)
Spotted Dikkop *Burhinus capensis*	50.9 (83)	52.0 (267)
Water Dikkop *Burhinus vermiculatus*	12.3 (20)	1.4 (7)
Burchell's Courser *Cursorius rufus*	9.8 (16)	19.5 (100)
Doublebanded Courser *Smutsornis africanus*	16.0 (26)	48.9 (251)
Greyheaded Gull *Larus cirrocephalus*	11.7 (19)	10.5 (54)
Whiskered Tern *Chlidonias hybridus*	7.4 (12)	5.7 (29)
Whitewinged Tern *Chlidonias leucopterus*	16.0 (26)	17.9 (92)
Namaqua Sandgrouse *Pterocles namaqua*	83.4 (136)	84.4 (433)
Burchell's Sandgrouse *Pterocles burchelli*	0.0 (0)	5.7 (29)
Rock Pigeon *Columba guinea*	96.3 (157)	88.7 (455)
Redeyed Dove *Streptopelia semitorquata*	45.4 (74)	47.0 (241)
Cape Turtle Dove *Streptopelia capicola*	92.0 (150)	97.5 (500)
Laughing Dove *Streptopelia senegalensis*	90.2 (147)	93.8 (481)
Namaqua Dove *Oena capensis*	86.5 (141)	96.7 (496)
Redchested Cuckoo *Cuculus solitarius*	9.2 (15)	4.9 (25)
Great Spotted Cuckoo *Clamator glandarius*	3.1 (5)	8.2 (42)
Jacobin Cuckoo *Clamator jacobinus*	3.1 (5)	8.4 (43)
Klaas's Cuckoo *Chrysococcyx klaas*	23.9 (39)	3.1 (16)
Diederik Cuckoo *Chrysococcyx caprius*	30.7 (50)	40.7 (209)
Barn Owl *Tyto alba*	18.4 (30)	18.3 (94)
Cape Eagle Owl *Bubo capensis*	12.9 (21)	6.6 (34)
Spotted Eagle Owl *Bubo africanus*	55.8 (91)	57.3 (294)
Fierynecked Nightjar *Caprimulgus pectoralis*	17.8 (29)	9.2 (47)
Rufouscheeked Nightjar *Caprimulgus rufigena*	9.8 (16)	24.2 (124)
Freckled Nightjar *Caprimulgus tristigma*	11.7 (19)	1.9 (10)
Black Swifts *Apus apus & A. barbatus*[2]	36.8 (60)	24.8 (127)
Bradfield's Swift *Apus bradfieldi*	6.1 (10)	3.3 (17)
Whiterumped Swift *Apus caffer*	52.1 (85)	51.1 (262)
Horus Swift *Apus horus*	5.5 (9)	7.4 (38)
Little Swift *Apus affinis*	71.2 (116)	76.6 (393)
Alpine Swift *Apus melba*	61.3 (100)	29.4 (151)

Appendix 1(a) continued

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Speckled Mousebird *Colius striatus*	33.7 (55)	24.2 (124)
Whitebacked Mousebird *Colius colius*	77.9 (127)	79.5 (408)
Redfaced Mousebird *Urocolius indicus*	58.3 (95)	63.9 (328)
Pied Kingfisher *Ceryle rudis*	28.2 (46)	24.0 (123)
Giant Kingfisher *Megaceryle maxima*	28.2 (46)	16.4 (84)
Malachite Kingfisher *Alcedo cristata*	31.3 (51)	20.1 (103)
Brownhooded Kingfisher *Halcyon albiventris*	14.7 (24)	13.6 (70)
European Bee-eater *Merops apiaster*	55.2 (90)	50.9 (261)
Swallowtailed Bee-eater *Merops hirundineus*	7.4 (12)	14.8 (76)
European Roller *Coracias garrulus*	3.1 (5)	6.2 (32)
Hoopoe *Upupa epops*	52.8 (86)	46.6 (239)
Redbilled Woodhoopoe *Phoeniculus purpureus*	0.6 (1)	5.7 (29)
Scimitarbilled Woodhoopoe *Rhinopomastus cyanomelas*	3.1 (5)	16.0 (82)
Pied Barbet *Tricholaema leucomelas*	73.0 (119)	85.4 (438)
Greater Honeyguide *Indicator indicator*	17.8 (29)	11.1 (57)
Lesser Honeyguide *Indicator minor*	9.8 (16)	11.1 (57)
Ground Woodpecker *Geocolaptes olivaceus*	47.2 (77)	15.6 (80)
Cardinal Woodpecker *Dendropicos fuscescens*	27.0 (44)	20.1 (103)
Melodious Lark *Mirafra cheniana*	0.0 (0)	4.9 (25)
Rufousnaped Lark *Mirafra africana*	0.0 (0)	6.6 (34)
Clapper Lark *Mirafra apiata*	44.8 (73)	48.1 (247)
Fawncoloured Lark *Mirafra africanoides*	0.0 (0)	28.3 (145)
Sabota Lark *Mirafra sabota*	10.4 (17)	56.3 (289)
Longbilled Lark *Certhilauda curvirostris*	73.6 (120)	76.6 (393)
Karoo Lark *Certhilauda albescens*	84.7 (138)	30.8 (158)
Red Lark *Certhilauda burra*	1.8 (3)	8.4 (43)
Spikeheeled Lark *Chersomanes albofasciata*	74.8 (122)	94.5 (485)
Redcapped Lark *Calandrella cinerea*	82.8 (135)	67.4 (346)
Pinkbilled Lark *Spizocorys conirostris*	0.0 (0)	13.8 (71)
Sclater's Lark *Spizocorys sclateri*	1.2 (2)	13.5 (69)
Stark's Lark *Eremalauda starki*	5.5 (9)	19.7 (101)
Thickbilled Lark *Galerida magnirostris*	89.6 (146)	65.9 (338)
Chestnutbacked Finchlark *Eremopterix leucotis*	0.0 (0)	4.9 (25)
Greybacked Finchlark *Eremopterix verticalis*	61.3 (100)	80.5 (413)
Blackeared Finchlark *Eremopterix australis*	18.4 (30)	50.5 (259)
European Swallow *Hirundo rustica*	72.4 (118)	87.3 (448)
Whitethroated Swallow *Hirundo albigularis*	46.6 (76)	49.5 (254)
Pearlbreasted Swallow *Hirundo dimidiata*	28.2 (46)	13.6 (70)
Redbreasted Swallow *Hirundo semirufa*	0.0 (0)	7.6 (39)
Greater Striped Swallow *Hirundo cucullata*	50.9 (83)	64.7 (332)
Lesser Striped Swallow *Hirundo abyssinica*	1.2 (2)	7.2 (37)
S. African Cliff Swallow *Hirundo spilodera*	0.6 (1)	30.0 (154)
Rock Martin *Hirundo fuligula*	98.2 (160)	88.7 (455)
House Martin *Delichon urbica*	12.3 (20)	10.1 (52)
Brownthroated Martin *Riparia paludicola*	68.7 (112)	54.2 (278)
Banded Martin *Riparia cincta*	8.6 (14)	3.3 (17)
Forktailed Drongo *Dicrurus adsimilis*	19.6 (32)	24.2 (124)
European Golden Oriole *Oriolus oriolus*	3.1 (5)	3.9 (20)

Appendix 1(a) continued

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Black Crow *Corvus capensis*	67.5 (110)	30.2 (155)
Pied Crow *Corvus albus*	89.6 (146)	63.0 (323)
Whitenecked Raven *Corvus albicollis*	44.8 (73)	29.8 (153)
Southern Grey Tit *Parus afer*	81.0 (132)	44.4 (228)
Ashy Tit *Parus cinerascens*	4.3 (7)	23.8 (122)
Cape Penduline Tit *Anthoscopus minutus*	56.4 (92)	41.9 (215)
Cape Bulbul *Pycnonotus capensis*	63.8 (104)	7.2 (37)
Redeyed Bulbul *Pycnonotus nigricans*	28.2 (46)	69.4 (356)
Sombre Bulbul *Andropadus importunus*	17.2 (28)	7.4 (38)
Olive Thrushes *Turdus olivaceus* & *T. smithi*[3]	57.7 (94)	51.3 (263)
Cape Rock Thrush *Monticola rupestris*	28.8 (47)	11.7 (60)
Sentinel Rock Thrush *Monticola explorator*	7.4 (12)	4.7 (24)
Shorttoed Rock Thrush *Monticola brevipes*	1.2 (2)	14.4 (74)
Mountain Chat *Oenanthe monticola*	89.6 (146)	87.1 (447)
Capped Wheatear *Oenanthe pileata*	63.2 (103)	54.6 (280)
Familiar Chat *Cercomela familiaris*	96.9 (158)	96.7 (496)
Tractrac Chat *Cercomela tractrac*	46.6 (76)	52.6 (270)
Sicklewinged Chat *Cercomela sinuata*	47.2 (77)	55.4 (284)
Karoo Chat *Cercomela schlegelii*	96.9 (158)	74.7 (383)
Anteating Chat *Myrmecocichla formicivora*	69.9 (114)	95.3 (489)
Stonechat *Saxicola torquata*	51.5 (84)	39.2 (201)
Cape Robin *Cossypha caffra*	65.6 (107)	53.6 (275)
Karoo Robin *Erythropygia coryphoeus*	95.1 (155)	86.2 (442)
Kalahari Robin *Erythropygia paena*	1.2 (2)	22.6 (116)
Titbabbler *Parisoma subcaeruleum*	59.5 (97)	74.7 (383)
Layard's Titbabbler *Parisoma layardi*	68.1 (111)	41.5 (213)
African Marsh Warbler *Acrocephalus baeticatus*	38.7 (63)	32.0 (164)
Cape Reed Warbler *Acrocephalus gracilirostris*	37.4 (61)	33.1 (170)
African Sedge Warbler *Bradypterus baboecala*	20.9 (34)	4.7 (24)
Willow Warbler *Phylloscopus trochilus*	12.9 (21)	16.0 (82)
Barthroated Apalis *Apalis thoracica*	28.2 (46)	13.1 (67)
Longbilled Crombec *Sylvietta rufescens*	74.2 (121)	61.8 (317)
Yellowbellied Eremomela *Eremomela icteropygialis*	51.5 (84)	85.2 (437)
Karoo Eremomela *Eremomela gregalis*	38.7 (63)	25.7 (132)
Cinnamonbrstd Warbler *Euryptila subcinnamomea*	17.2 (28)	7.6 (39)
Grassbird *Sphenoeacus afer*	17.2 (28)	2.3 (12)
Fantailed Cisticola *Cisticola juncidis*	29.4 (48)	26.1 (134)
Desert Cisticola *Cisticola aridulus*	0.0 (0)	31.6 (162)
Cloud Cisticola *Cisticola textrix*	9.2 (15)	12.3 (63)
Greybacked Cisticola *Cisticola subruficapillus*	92.6 (151)	69.0 (354)
Levaillant's Cisticola *Cisticola tinniens*	35.6 (58)	38.4 (197)
Neddicky *Cisticola fulvicapillus*	25.2 (41)	29.6 (152)
Blackchested Prinia *Prinia flavicans*	6.7 (11)	59.5 (305)
Spotted Prinia *Prinia maculosa*	97.5 (159)	64.3 (330)
Namaqua Warbler *Phragmacia substriata*	66.3 (108)	39.4 (202)
Rufouseared Warbler *Malcorus pectoralis*	83.4 (136)	95.1 (488)
Spotted Flycatcher *Muscicapa striata*	19.6 (32)	21.6 (111)
Dusky Flycatcher *Muscicapa adusta*	12.3 (20)	3.1 (16)

Appendix 1(a) continued

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Marico Flycatcher *Melaenornis mariquensis*	0.0 (0)	7.2 (37)
Chat Flycatcher *Melaenornis infuscatus*	50.9 (83)	90.1 (462)
Fiscal Flycatcher *Sigelus silens*	47.2 (77)	49.9 (256)
Cape Batis *Batis capensis*	20.9 (34)	6.0 (31)
Chinspot Batis *Batis molitor*	0.6 (1)	5.5 (28)
Pririt Batis *Batis pririt*	57.7 (94)	53.2 (273)
Fairy Flycatcher *Stenostira scita*	67.5 (110)	58.3 (299)
Paradise Flycatcher *Tersiphone viridis*	13.5 (22)	9.7 (50)
African Pied Wagtail *Motacilla aguimp*	8.6 (14)	9.9 (51)
Cape Wagtail *Motacilla capensis*	93.3 (152)	83.0 (426)
Grassveld Pipit *Anthus cinnamomeus*	58.3 (95)	68.2 (350)
Longbilled Pipit *Anthus similis*	34.4 (56)	27.3 (140)
Plainbacked Pipit *Anthus leucophrys*	11.0 (18)	14.6 (75)
Buffy Pipit *Anthus vaalensis*	0.0 (0)	7.0 (36)
Rock Pipit *Anthus crenatus*	8.6 (14)	21.4 (110)
Orangethroated Longclaw *Macronyx capensis*	11.0 (18)	14.4 (74)
Lesser Grey Shrike *Lanius minor*	0.6 (1)	16.4 (84)
Fiscal Shrike *Lanius collaris*	97.5 (159)	97.7 (501)
Redbacked Shrike *Lanius collurio*	2.5 (4)	20.9 (107)
Southern Boubou *Laniarius ferrugineus*	24.5 (40)	9.4 (48)
Crimsonbreasted Shrike *Laniarius atrococcineus*	0.0 (0)	6.8 (35)
Brubru *Nilaus afer*	2.5 (4)	10.9 (56)
Southern Tchagra *Tchagra tchagra*	17.2 (28)	9.4 (48)
Bokmakierie *Telophorus zeylonus*	99.4 (162)	87.9 (451)
European Starling *Sturnus vulgaris*	52.8 (86)	26.5 (136)
Pied Starling *Spreo bicolor*	73.0 (119)	64.3 (330)
Wattled Starling *Creatophora cinerea*	47.2 (77)	56.5 (290)
Glossy Starling *Lamprotornis nitens*	27.6 (45)	36.5 (187)
Redwinged Starling *Onychognathus morio*	39.9 (65)	28.8 (148)
Palewinged Starling *Onychognathus nabouroup*	77.9 (127)	49.9 (256)
Cape Sugarbird *Promerops cafer*	22.1 (36)	0.8 (4)
Malachite Sunbird *Nectarinia famosa*	86.5 (141)	36.6 (188)
Orangebreasted Sunbird *Nectarinia violacea*	21.5 (35)	0.2 (1)
Lesser D/collared Sunbird *Nectarinia chalybea*	89.6 (146)	31.6 (162)
Greater D/collared Sunbird *Nectarinia afra*	9.8 (16)	5.5 (28)
Dusky Sunbird *Nectarinia fusca*	68.7 (112)	68.8 (353)
Black Sunbird *Nectarinia amethystina*	4.3 (7)	5.7 (29)
Cape White-eye *Zosterops pallidus*	60.7 (99)	60.4 (310)
Whitebrowed Sparrowweaver *Plocepasser mahali*	1.2 (2)	40.9 (210)
Sociable Weaver *Philetarius socius*	2.5 (4)	31.2 (160)
House Sparrow *Passer domesticus*	82.8 (135)	92.4 (474)
Great Sparrow *Passer motitensis*	0.0 (0)	5.7 (29)
Cape Sparrow *Passer melanurus*	100.0 (163)	100.0 (513)
Greyheaded Sparrow *Passer diffusus*	12.3 (20)	42.7 (219)
Yellowthroated Sparrow *Petronia superciliaris*	1.2 (2)	5.7 (29)
Scalyfeathered Finch *Sporopipes squamifrons*	3.1 (5)	39.2 (201)
Cape Weaver *Ploceus capensis*	74.8 (122)	26.3 (135)
Masked Weaver *Ploceus velatus*	77.3 (126)	94.7 (486)

Appendix 1(a) continued

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Redbilled Quelea *Quelea quelea*	5.5 (9)	41.7 (214)
Red Bishop *Euplectes orix*	60.1 (98)	62.6 (321)
Golden Bishop *Euplectes afer*	0.6 (1)	10.9 (56)
Yellowrumped Widow *Euplectes capensis*	36.2 (59)	1.6 (8)
Longtailed Widow *Euplectes progne*	0.0 (0)	6.8 (35)
Redbilled Firefinch *Lagonostica senegala*	2.5 (4)	11.3 (58)
Common Waxbill *Estrilda astrild*	69.3 (113)	55.4 (284)
Swee Waxbill *Estrilda melanotis*	9.8 (16)	3.7 (19)
Quail Finch *Ortygospiza atricollis*	1.2 (2)	17.9 (92)
Redheaded Finch *Amadina erythrocephala*	3.1 (5)	49.7 (255)
Pintailed Whydah *Vidua macroura*	32.5 (53)	36.1 (185)
Yelloweyed Canary *Serinus mozambicus*	0.0 (0)	8.4 (43)
Blackthroated Canary *Serinus atrogularis*	16.6 (27)	47.0 (241)
Cape Canary *Serinus canicollis*	44.8 (73)	25.5 (131)
Cape Siskin *Pseudochloroptila totta*	20.9 (34)	0.8 (4)
Blackheaded Canary *Serinus alario*	89.6 (146)	68.4 (351)
Bully Canary *Serinus sulphuratus*	14.7 (24)	7.0 (36)
Yellow Canary *Serinus flaviventris*	95.1 (155)	91.0 (467)
Whitethroated Canary *Serinus albogularis*	99.4 (162)	85.0 (436)
Streakyheaded Canary *Serinus gularis*	27.0 (44)	10.3 (53)
Goldenbreasted Bunting *Emberiza flaviventris*	1.8 (3)	8.4 (43)
Cape Bunting *Emberiza capensis*	98.2 (160)	67.4 (346)
Rock Bunting *Emberiza tahapisi*	0.6 (1)	21.4 (110)
Larklike Bunting *Emberiza impetuani*	76.7 (125)	96.1 (493)

Notes: [1]*Eupodotis afra* and *E. afraoides* are now considered separate species (Crowe *et al.*, 1994).

[2]It is likely that there has been some confusion by observers between these two species. The frequency given is the highest total of either species seen in the two Karoo biomes.

[3]Atlas records do not distinguish between *T. olivaceus* and *T. smithi*, which has been considered an incipient species (Clancey, 1992) and is likely to be a full species (R.K. Brooke, pers. comm.).

Appendix 1(b): Species occurring in less than 25 quarter-degree squares in the Karoo, and considered to be restricted to particular habitat patches in the Karoo, or that occur in the Karoo only when environmental conditions are favourable for them.

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Squacco Heron *Ardeola ralloides*	1.2 (2)	1.2 (6)
Greenbacked Heron *Butorides striatus*	1.2 (2)	1.2 (6)
Abdim's Stork *Ciconia abdimii*	0.0 (0)	3.9 (20)
Marabou Stork *Leptoptilos crumeniferus*	0.6 (1)	0.8 (4)
Whitebacked Duck *Thalassornis leuconotus*	3.1 (5)	1.6 (8)
Hottentot Teal *Anas hottentota*	1.8 (3)	1.9 (10)
Lappetfaced Vulture *Torgos tracheliotus*	0.0 (0)	2.7 (14)
Crowned Eagle *Stephanoaetus coronatus*	0.0 (0)	1.2 (6)
Bateleur *Terathopius ecaudatus*	0.0 (0)	1.4 (7)
Forest Buzzard *Buteo trizonatus*	1.8 (3)	0.4 (2)
Little Sparrowhawk *Accipiter minullus*	2.5 (4)	1.4 (7)
Black Sparrowhawk *Accipiter melanoleucus*	1.2 (2)	1.4 (7)
Osprey *Pandion haliaetus*	2.5 (4)	1.2 (6)
Hobby Falcon *Falco subbuteo*	1.2 (2)	1.0 (5)
Rednecked Falcon *Falco chicquera*	0.0 (0)	2.3 (12)
Eastern Redfooted Kestrel *Falco amurensis*	0.0 (0)	2.5 (13)
Redwing Francolin *Francolinus levaillantii*	1.2 (2)	1.9 (10)
Rednecked Francolin *Francolinus afer*	3.1 (5)	1.9 (10)
Swainson's Francolin *Francolinus swainsonii*	0.0 (0)	3.9 (20)
Kurrichane Buttonquail *Turnix sylvatica*	0.0 (0)	2.5 (13)
Crowned Crane *Balearica regulorum*	0.0 (0)	1.4 (7)
African Rail *Rallus caerulescens*	6.7 (11)	1.0 (5)
Baillon's Crake *Porzana pusilla*	6.1 (10)	0.6 (3)
Redchested Flufftail *Sarothrura rufa*	6.1 (10)	0.0 (0)
Purple Gallinule *Porphyrio porphyrio*	7.4 (12)	1.2 (6)
Whitebellied Korhaan *Eupodotis cafra*	0.0 (0)	1.2 (6)
African Jacana *Actophilornis africanus*	5.5 (9)	1.8 (9)
Painted Snipe *Rostratula benghalensis*	2.5 (4)	1.8 (9)
Temminck's Courser *Cursorius temminckii*	0.6 (1)	2.5 (13)
Doublebanded Sandgrouse *Pterocles bicinctus*	1.2 (2)	0.8 (4)
Rameron Pigeon *Columba arquatrix*	8.6 (14)	1.9 (10)
Greenspotted Dove *Turtur chalcospilos*	0.0 (0)	3.5 (18)
Rosyfaced Lovebird *Agapornis roseicollis*	0.6 (1)	3.5 (18)
European Cuckoo *Cuculus canorus*	0.6 (1)	1.9 (10)
Black Cuckoo *Cuculus clamosus*	1.8 (3)	1.8 (9)
Burchell's Coucal *Centropus burchellii*	7.4 (12)	1.8 (9)
Marsh Owl *Asio capensis*	0.6 (1)	1.4 (7)
Whitefaced Owl *Otus leucotis*	0.0 (0)	1.4 (7)
Pearlspotted Owl *Glaucidium perlatum*	0.0 (0)	3.3 (17)
Giant Eagle Owl *Bubo lacteus*	0.0 (0)	2.3 (12)
European Nightjar *Caprimulgus europaeus*	1.8 (3)	3.9 (20)
Palm Swift *Cypsiurus parvus*	0.0 (0)	2.3 (12)
Halfcollared Kingfisher *Alcedo semitorquata*	3.7 (6)	1.4 (7)

Appendix 1(b) continued

Species	Frequency	
	Succulent Karoo	Nama-Karoo
Striped Kingfisher *Halcyon chelicuti*	0.6 (1)	1.0 (5)
Whitefronted Bee-eater *Merops bullockoides*	0.0 (0)	1.8 (9)
Lilacbreasted Roller *Coracias caudata*	0.0 (0)	3.5 (18)
Grey Hornbill *Tockus nasutus*	0.0 (0)	1.6 (8)
Southern Yellowbilled Hornbill *Tockus leucomelas*	0.0 (0)	3.1 (16)
Crowned Hornbill *Tockus alboterminatus*	0.0 (0)	2.7 (14)
Blackcollared Barbet *Lybius torquatus*	0.0 (0)	2.9 (15)
Redfronted Tinker Barbet *Pogoniulus pusillus*	0.0 (0)	3.9 (20)
Crested Barbet *Trachyphonus vaillantii*	0.0 (0)	4.1 (21)
Goldentailed Woodpecker *Campethera abingoni*	0.6 (1)	3.7 (19)
Knysna Woodpecker *Campethera notata*	1.2 (2)	1.8 (9)
Redthroated Wryneck *Jynx ruficollis*	0.0 (0)	2.5 (13)
Shortclawed Lark *Certhilauda chuana*	0.0 (0)	1.4 (7)
Sand Martin *Riparia riparia*	1.8 (3)	2.3 (12)
Black Cuckooshrike *Campephaga flava*	0.0 (0)	1.6 (8)
Blackheaded Oriole *Oriolus larvatus*	1.2 (2)	3.1 (16)
Southern Black Tit *Parus niger*	0.0 (0)	3.1 (16)
Blackeyed Bulbul *Pycnonotus barbatus*	0.0 (0)	2.3 (12)
Mocking Chat *Thamnolaea cinnamomeiventris*	0.0 (0)	3.3 (17)
Cape Rockjumper *Chaetops frenatus*	8.0 (13)	0.4 (2)
Whitebrowed Robin *Erythropygia leucophrys*	0.0 (0)	3.5 (18)
Garden Warbler *Sylvia borin*	0.0 (0)	1.2 (6)
Great Reed Warbler *Acrocephalus arundinaceus*	0.0 (0)	1.9 (10)
Victorin's Warbler *Bradypterus victorini*	8.0 (13)	0.2 (1)
Ayres's Cisticola *Cisticola ayresii*	0.0 (0)	1.8 (9)
Wailing Cisticola *Cisticola lais*	0.0 (0)	3.3 (17)
Tawnyflanked Prinia *Prinia subflava*	0.0 (0)	1.0 (5)
Yellow Wagtail *Motacilla flava*	0.6 (1)	1.0 (5)
Threestreaked Tchagra *Tchagra australis*	0.0 (0)	2.7 (14)
Olive Bush Shrike *Telophorus olivaceus*	3.1 (5)	1.9 (10)
Collared Sunbird *Anthreptes collaris*	0.6 (1)	1.0 (5)
Spectacled Weaver *Ploceus ocularis*	0.0 (0)	2.5 (13)
Melba Finch *Pytilia melba*	0.0 (0)	1.9 (10)
Bluebilled Firefinch *Lagonostica rubricata*	0.0 (0)	2.9 (15)
Violeteared Waxbill *Uraeginthus granatinus*	0.0 (0)	3.7 (19)
Blackcheeked Waxbill *Estrilda erythronotos*	0.0 (0)	4.1 (21)
Shafttailed Whydah *Vidua regia*	0.0(0)	2.9 (15)
Steelblue Widowfinch *Vidua chalybeata*	0.0 (0)	1.2 (6)
Protea Canary *Serinus leucopterus*	12.3 (20)	0.0 (0)

Appendix 1(c): Species that have been recorded in less than 5 quarter-degree squares in the Karoo *sensu lato.*

Species	Frequency
Black Egret *Egretta ardesiaca*	0.1 (1)
Saddlebilled Stork *Ephippiorhynchus senegalensis*	0.3 (2)
Steppe Eagle *Aquila nipalensis*	0.1 (1)
Wahlberg's Eagle *Aquila wahlbergi*	0.4 (3)
Longcrested Eagle *Lophaetus occipitalis*	0.1 (1)
Brown Snake Eagle *Circaetus cinereus*	0.4 (3)
Little Banded Goshawk *Accipiter badius*	0.1 (1)
Montagu's Harrier *Circus pygargus*	0.3 (2)
Pallid Harrier *Circus macrourus*	0.4 (3)
Natal Francolin *Francolinus natalensis*	0.4 (3)
Mongolian Plover *Charadrius mongolus*	0.3 (2)
Caspian Plover *Charadrius asiaticus*	0.6 (4)
Green Sandpiper *Tringa ochropus*	0.1 (1)
Blacktailed Godwit *Limosa limosa*	0.1 (1)
Grass Owl *Tyto capensis*	0.1 (1)
Bluecheeked Bee-eater *Merops persicus*	0.1 (1)
Little Bee-eater *Merops pusillus*	0.4 (3)
Monotonous Lark *Mirafra passerina*	0.1 (1)
Groundscraper Thrush *Turdus litsitsirupa*	0.6 (4)
Icterine Warbler *Hippolais icterina*	0.4 (3)
Olivetree Warbler *Hippolais olivetorum*	0.1 (1)
European Marsh Warbler *Acrocephalus palustris*	0.4 (3)
European Sedge Warbler *Acrocephalus schoenobaenus*	0.1 (1)
Rattling Cisticola *Cisticola chiniana*	0.1 (1)
Lazy Cisticola *Cisticola aberrans*	0.6 (4)
Indian Myna *Acridotheres tristris*	0.3 (2)
Burchell's Starling *Lamprotornis australis*	0.3 (2)
Marico Sunbird *Nectarinia mariquensis*	0.4 (3)
Blue Waxbill *Uraeginthus angolensis*	0.6 (4)
Paradise Whydah *Vidua paradisaea*	0.1 (1)

Appendix 1(d): Species that have been recorded only in quarter-degree squares that include coastal or estuarine habitats or in quarter-degree squares that include forest, grassland or arid savanna on the perimeter of the Karoo *sensu lato*.

Species	Frequency
White Pelican *Pelecanus onocrotalus*	0.9 (6)
Cape Cormorant *Phalacrocorax capensis*	0.6 (4)
Bank Cormorant *Phalacrocorax neglectus*	0.1 (1)
Crowned Cormorant *Phalacrocorax coronatus*	0.3 (2)
Dwarf Bittern *Ixobrychus sturmii*	0.1 (1)
Bald Ibis *Geronticus calvus*	0.1 (1)
Fulvous Duck *Dendrocygna bicolor*	0.1 (1)
Knobbilled Duck *Sarkidiornis melanotos*	0.3 (2)
Western Redfooted Kestrel *Falco vespertinus*	0.1 (1)
Wattled Crane *Bugeranus carunculatus*	0.1 (1)
African Crake *Crex egregia*	0.1 (1)
Buffspotted Flufftail *Sarothrura elegans*	0.1 (1)
African Finfoot *Podica senegalensis*	0.4 (3)
Whitefronted Plover *Charadrius marginatus*	3.1 (21)
Sand Plover *Charadrius leschenaultii*	0.4 (3)
Grey Plover *Pluvialis squatarola*	3.6 (24)
Blackwinged Plover *Vanellus melanopterus*	0.7 (5)
Turnstone *Arenaria interpres*	0.7 (5)
Terek Sandpiper *Xenus cinereus*	0.1 (1)
Redshank *Tringa totanus*	0.1 (1)
Knot *Calidris canutus*	0.1 (1)
Bartailed Godwit *Limosa lapponica*	1.2 (8)
Curlew *Numenius arquatus*	0.7 (5)
Whimbrel *Numenius phaeopus*	2.5 (17)
Rednecked Phalarope *Phalaropus lobatus*	0.1 (1)
Blackwinged Pratincole *Glareola nordmanni*	0.4 (3)
Kelp Gull *Larus dominicanus*	0.9 (6)
Lesser Blackbacked Gull *Larus fuscus*	0.1 (1)
Hartlaub's Gull *Larus hartlaubi*	2.8 (19)
Caspian Tern *Hydroprogne caspia*	1.6 (11)
Swift Tern *Sterna bergii*	0.1 (1)
Sandwich Tern *Sterna sandvicensis*	0.1 (1)
Common Tern *Sterna hirundo*	0.4 (3)
Arctic Tern *Sterna paradisaea*	0.4 (3)
Yellowthroated Sandgrouse *Pterocles gutturalis*	0.1 (1)
Tambourine Dove *Turtur tympanistria*	2.5 (17)
Cinnamon Dove *Aplopelia larvata*	0.3 (2)
Cape Parrot *Poicephalus robustus*	0.1 (1)
Knysna Lourie *Tauraco corythaix*	1.2 (8)
African Cuckoo *Cuculus gularis*	0.1 (1)
Emerald Cuckoo *Chrysococcyx cupreus*	0.3 (2)
Wood Owl *Strix woodfordii*	0.6 (4)
African Scops Owl *Otus senegalensis*	0.3 (2)
Narina Trogon *Apaloderma narina*	0.4 (3)
Purple Roller *Coracias naevia*	0.3 (2)
Scalythroated Honeyguide *Indicator variegatus*	0.1 (1)
Sharpbilled Honeyguide *Prodotiscus regulus*	0.3 (2)

Appendix 1(d) continued

Species	Frequency
Bearded Woodpecker *Thripias namaquus*	0.1 (1)
Olive Woodpecker *Mesopicos griseocephalus*	1.8 (12)
Black Sawwing Swallow *Psalidoprocne holomelas*	2.8 (19)
Grey Cuckooshrike *Coracina caesia*	1.2 (8)
Bush Blackcap *Lioptilus nigricapillus*	0.1 (1)
Terrestrial Bulbul *Phyllastrephus terrestris*	1.2 (8)
Buffstreaked Chat *Oenanthe bifasciata*	0.4 (3)
Chorister Robin *Cossypha dichroa*	0.3 (2)
Starred Robin *Pogonocichla stellata*	0.1 (1)
Brown Robin *Erythropygia signata*	0.3 (2)
Barratt's Warbler *Bradypterus barratti*	0.1 (1)
Knysna Warbler *Bradypterus sylvaticus*	0.3 (2)
Yellowthroated Warbler *Seicercus ruficapillus*	0.7 (5)
Yellowbreasted Apalis *Apalis flavida*	1.0 (7)
Bleating Warbler *Camaroptera brachyura*	1.2 (8)
Black Flycatcher *Melaenornis pammelaina*	0.7 (5)
Bluemantled Flycatcher *Trochocercus cyanomelas*	0.7 (5)
Longtailed Wagtail *Motacilla clara*	0.1 (1)
Puffback *Dryoscopus cubla*	1.3 (9)
Orangebreasted Bush Shrike *Telophorus sulfureopectus*	0.3 (2)
Greyheaded Bush Shrike *Malaconotus blanchoti*	0.6 (4)
Whitecrowned Shrike *Eurocephalus anguitimens*	0.1 (1)
Blackbellied Starling *Lamprotornis corruscus*	0.7 (5)
Redbilled Oxpecker *Buphagus erythrorhynchus*	0.1 (1)
Whitebellied Sunbird *Nectarinia talatala*	0.1 (1)
Grey Sunbird *Nectarinia veroxii*	0.6 (4)
Thickbilled Weaver *Amblyospiza albifrons*	0.4 (3)
Forest Weaver *Ploceus bicolor*	0.7 (5)
Spottedbacked Weaver *Ploceus cucullatus*	0.7 (5)
Yellow Weaver *Ploceus subaureus*	0.1 (1)
Redcollared Widow *Euplectes ardens*	0.4 (3)
Orangebreasted Waxbill *Sporaeginthus subflavus*	0.1 (1)
Bronze Mannikin *Spermestes cucullatus*	0.1 (1)
Black Widowfinch *Vidua funerea*	1.6 (11)
Forest Canary *Serinus scotops*	1.9 (13)

Appendix 2: List of Karoo bird species and their attributes

A list of species considered to be frequent to common and widespread in the Karoo and that has been used as the database for all analyses. Food categories are: aquatic = some, if not all food taken from water, regardless of whether animal or vegetable; mixed = mixed seeds and insects; remainder of the food categories self-explanatory. Status categories are: resident; P-migrant = Palaearctic migrant; Af-migrant = intra-African migrant; local nomad (or nomadic at landscape scale); nomad = nomadic at a regional scale. Most habitat categories are self-explanatory; wide = equally common in several habitats. Weight (mass) is given in grams.

Species	Food	Status	Habitat	Mass
Great Crested Grebe	aquatic	resident	aquatic	595
Blacknecked Grebe	aquatic	local nomad	aquatic	298
Dabchick	aquatic	resident	aquatic	147
Whitebreasted Cormorant	aquatic	resident	aquatic	1616
Reed Cormorant	aquatic	resident	aquatic	540
Darter	aquatic	resident	aquatic	1510
Grey Heron	aquatic	resident	aquatic	1500
Blackheaded Heron	raptor	resident	grassland	1135
Goliath Heron	aquatic	resident	aquatic	4320
Purple Heron	aquatic	resident	aquatic	920
Great White Egret	aquatic	resident	aquatic	1110
Little Egret	aquatic	resident	aquatic	450
Yellowbilled Egret	aquatic	resident	aquatic	500
Cattle Egret	insect	resident	grassland	365
Blackcrowned Night Heron	aquatic	resident	aquatic	535
Little Bittern	aquatic	resident	aquatic	100
Hamerkop	aquatic	resident	aquatic	425
White Stork	insect	local nomad	grassland	3500
Black Stork	aquatic	resident	aquatic	3000
Yellowbilled Stork	insect	Af-migrant	aquatic	1150
Sacred Ibis	aquatic	resident	aquatic	1498
Glossy Ibis	insect	resident	aquatic	1000
Hadeda Ibis	insect	resident	forest	1262
African Spoonbill	aquatic	resident	aquatic	1550
Greater Flamingo	aquatic	nomad	aquatic	2714
Lesser Flamingo	aquatic	nomad	aquatic	1721
Whitefaced Duck	insect	local nomad	aquatic	690
Egyptian Goose	aquatic	resident	aquatic	2110
South African Shelduck	aquatic	local nomad	aquatic	1250
Yellowbilled Duck	aquatic	resident	aquatic	900
African Black Duck	aquatic	resident	aquatic	900
Cape Teal	aquatic	resident	aquatic	400
Redbilled Teal	aquatic	resident	aquatic	570
Cape Shoveller	aquatic	resident	aquatic	642
Southern Pochard	aquatic	local nomad	aquatic	780
Spurwinged Goose	aquatic	resident	aquatic	6200

Appendix 2, continued.

Species	Food	Status	Habitat	Mass
Maccoa Duck	aquatic	resident	aquatic	687
Secretarybird	raptor	resident	savanna	4000
Cape Vulture	raptor	resident	grassland	8600
Whitebacked Vulture	raptor	resident	savanna	5400
Yellowbilled Kite	raptor	Af-migrant	savanna	805
Blackshouldered Kite	raptor	resident	savanna	251
Black Eagle	raptor	resident	Karoo	4076
Tawny Eagle	raptor	nomad	savanna	2352
Booted Eagle	raptor	P-migrant	Karoo	843
Martial Eagle	raptor	resident	savanna	4000
Blackbreasted Snake Eagle	raptor	local nomad	savanna	1502
African Fish Eagle	raptor	resident	aquatic	2820
Steppe Buzzard	raptor	P-migrant	wide	714
Jackal Buzzard	raptor	resident	grassland	1064
Redbreasted Sparrowhawk	raptor	resident	aquatic	191
African Goshawk	raptor	resident	forest	340
Gabar Goshawk	raptor	resident	savanna	154
Pale Chanting Goshawk	raptor	resident	Karoo	750
African Marsh Harrier	raptor	resident	aquatic	518
Black Harrier	raptor	local nomad	Karoo	600
Gymnogene	raptor	local nomad	forest	725
Peregrine Falcon	raptor	resident	savanna	650
Lanner Falcon	raptor	nomad	savanna	590
Rock Kestrel	raptor	resident	wide	200
Greater Kestrel	raptor	local nomad	Karoo	261
Lesser Kestrel	insect	P-migrant	grassland	134
Pygmy Falcon	insect	resident	savanna	60
Greywing Francolin	mixed	resident	Karoo	390
Orange River Francolin	mixed	resident	grassland	450
Cape Francolin	mixed	resident	Fynbos	767
Common Quail	mixed	Af-migrant	grassland	100
Helmeted Guineafowl	mixed	resident	savanna	1352
Blue Crane	mixed	resident	grassland	4650
Black Crake	aquatic	resident	aquatic	90
Moorhen	mixed	resident	aquatic	247
Redknobbed Coot	aquatic	resident	aquatic	737
Kori Bustard	mixed	resident	savanna	14500
Stanley's Bustard	mixed	local nomad	grassland	8000
Ludwig's Bustard	mixed	local nomad	Karoo	5000
Blue Korhaan	mixed	resident	grassland	1400
Karoo Korhaan	mixed	resident	Karoo	1350
Redcrested Korhaan	mixed	resident	savanna	680
Black Korhaan	mixed	resident	grassland	704
Ringed Plover	insect	P-migrant	aquatic	60
Chestnutbanded Plover	insect	local nomad	aquatic	35
Kittlitz's Plover	insect	resident	aquatic	42
Threebanded Plover	insect	local nomad	aquatic	34
Crowned Plover	insect	resident	grassland	167

Appendix 2, continued.

Species	Food	Status	Habitat	Mass
Blacksmith Plover	insect	resident	aquatic	158
Common Sandpiper	aquatic	P-migrant	aquatic	44
Wood Sandpiper	aquatic	P-migrant	aquatic	60
Marsh Sandpiper	aquatic	P-migrant	aquatic	75
Greenshank	aquatic	P-migrant	aquatic	220
Curlew Sandpiper	aquatic	P-migrant	aquatic	65
Little Stint	aquatic	P-migrant	aquatic	25
Sanderling	aquatic	P-migrant	aquatic	25
Ruff	seeds	P-migrant	aquatic	160
Ethiopian Snipe	aquatic	resident	aquatic	109
Avocet	aquatic	nomad	aquatic	318
Blackwinged Stilt	aquatic	nomad	aquatic	170
Spotted Dikkop	insect	resident	grassland	450
Water Dikkop	insect	resident	aquatic	300
Burchell's Courser	insect	local nomad	grassland	75
Doublebanded Courser	insect	local nomad	Karoo	90
Greyheaded Gull	mixed	local nomad	aquatic	280
Whiskered Tern	aquatic	nomad	aquatic	70
Whitewinged Tern	aquatic	P-migrant	aquatic	56
Namaqua Sandgrouse	seeds	nomad	Karoo	176
Burchell's Sandgrouse	seeds	nomad	savanna	170
Rock Pigeon	seeds	resident	wide	350
Redeyed Dove	seeds	resident	wide	250
Cape Turtle Dove	seeds	resident	wide	152
Laughing Dove	seeds	resident	wide	101
Namaqua Dove	seeds	local nomad	savanna	40
Redchested Cuckoo	insect	Af-migrant	forest	70
Great Spotted Cuckoo	insect	Af-migrant	savanna	90
Jacobin Cuckoo	insect	Af-migrant	savanna	80
Klaas Cuckoo	insect	resident	savanna	38
Diederik Cuckoo	insect	Af-migrant	savanna	34
Barn Owl	raptor	resident	savanna	334
Cape Eagle Owl	raptor	resident	Karoo	1115
Spotted Eagle Owl	raptor	resident	wide	696
Fierynecked Nightjar	insect	Af-migrant	wide	54
Rufouscheeked Nightjar	insect	Af-migrant	savanna	52
Freckled Nightjar	insect	resident	savanna	80
European Swift	insect	P-migrant	wide	43
Black Swift	insect	Af-migrant	wide	43
Bradfield's Swift	insect	resident	Karoo	48
Whiterumped Swift	insect	Af-migrant	wide	25
Horus Swift	insect	Af-migrant	wide	26
Little Swift	insect	local nomad	wide	26
Alpine Swift	insect	Af-migrant	wide	77
Speckled Mousebird	fruit	resident	forest	55
Whitebacked Mousebird	fruit	resident	Karoo	41
Redfaced Mousebird	fruit	resident	savanna	60
Pied Kingfisher	aquatic	resident	aquatic	81

Appendix 2, continued.

Species	Food	Status	Habitat	Mass
Giant Kingfisher	aquatic	resident	aquatic	355
Malachite Kingfisher	aquatic	resident	aquatic	18
Brownhooded Kingfisher	insect	resident	savanna	60
European Bee-eater	insect	Af-migrant	grassland	54
Swallowtailed Bee-eater	insect	local nomad	savanna	23
European Roller	insect	P-migrant	savanna	120
Hoopoe	insect	resident	wide	56
Redbilled Woodhoopoe	insect	resident	savanna	71
Scimitarbilled Woodhoopoe	insect	resident	savanna	31
Pied Barbet	fruit	resident	wide	32
Greater Honeyguide	insect	local nomad	savanna	46
Lesser Honeyguide	insect	local nomad	savanna	28
Ground Woodpecker	insect	resident	Fynbos	120
Cardinal Woodpecker	insect	resident	savanna	30
Melodious Lark	mixed	resident	grassland	20
Rufousnaped Lark	mixed	resident	savanna	42
Clapper Lark	mixed	resident	grassland	26
Fawncoloured Lark	mixed	resident	savanna	23
Sabota Lark	mixed	resident	savanna	25
Longbilled Lark	mixed	resident	Karoo	50
Karoo Lark	mixed	resident	Karoo	31
Red Lark	mixed	resident	Karoo	37
Spikeheeled Lark	mixed	resident	Karoo	27
Redcapped Lark	seeds	nomad	Karoo	26
Pinkbilled Lark	seeds	nomad	grassland	14
Sclater's Lark	mixed	nomad	Karoo	20
Stark's Lark	seeds	nomad	Karoo	19
Thickbilled Lark	seeds	resident	Karoo	44
Chestnutbacked Finchlark	seeds	nomad	savanna	14
Greybacked Finchlark	seeds	nomad	Karoo	17
Blackeared Finchlark	seeds	nomad	Karoo	15
European Swallow	insect	P-migrant	wide	18
Whitethroated Swallow	insect	Af-migrant	aquatic	22
Pearlbreasted Swallow	insect	Af-migrant	Karoo	12
Redbreasted Swallow	insect	Af-migrant	savanna	30
Greater Striped Swallow	insect	Af-migrant	Karoo	27
Lesser Striped Swallow	insect	Af-migrant	savanna	17
South African Cliff Swallow	insect	Af-migrant	grassland	21
Rock Martin	insect	Af-migrant	Karoo	23
House Martin	insect	P-migrant	wide	18
Brownthroated Martin	insect	Af-migrant	aquatic	13
Banded Martin	insect	Af-migrant	grassland	25
Forktailed Drongo	insect	resident	savanna	50
European Golden Oriole	mixed	P-migrant	savanna	64
Black Crow	mixed	resident	Karoo	500
Pied Crow	mixed	resident	savanna	567
Whitenecked Raven	mixed	resident	Karoo	820
Southern Grey Tit	insect	resident	Karoo	21

Appendix 2, continued.

Species	Food	Status	Habitat	Mass
Ashy Tit	insect	resident	savanna	20
Cape Penduline Tit	insect	resident	Karoo	8
Cape Bulbul	fruit	resident	Fynbos	39
Redeyed Bulbul	fruit	resident	Karoo	31
Sombre Bulbul	mixed	resident	forest	33
Olive Thrush	mixed	resident	forest	78
Cape Rock Thrush	insect	resident	Karoo	61
Sentinel Rock Thrush	insect	local nomad	Karoo	55
Shorttoed Rock Thrush	insect	resident	Karoo	55
Mountain Chat	insect	resident	Karoo	32
Capped Wheatear	insect	local nomad	Karoo	32
Familiar Chat	insect	resident	Karoo	22
Tractrac Chat	insect	resident	Karoo	22
Sicklewinged Chat	insect	resident	Karoo	20
Karoo Chat	mixed	resident	Karoo	30
Anteating Chat	insect	local nomad	Karoo	42
Stonechat	insect	resident	Fynbos	15
Cape Robin	insect	resident	forest	28
Karoo Robin	insect	resident	Karoo	20
Kalahari Robin	insect	resident	savanna	20
Titbabbler	mixed	resident	savanna	15
Layard's Titbabbler	mixed	resident	Karoo	15
African Marsh Warbler	insect	Af-migrant	aquatic	10
Cape Reed Warbler	insect	resident	aquatic	19
African Sedge Warbler	insect	resident	aquatic	14
Willow Warbler	insect	P-migrant	savanna	9
Barthroated Apalis	insect	resident	forest	11
Longbilled Crombec	insect	resident	savanna	12
Yellowbellied Eremomela	insect	resident	savanna	8
Karoo Eremomela	insect	resident	Karoo	10
Cinnamonbreasted Warbler	insect	resident	Karoo	10
Grassbird	insect	resident	grassland	30
Fantailed Cisticola	insect	resident	grassland	9
Desert Cisticola	insect	resident	grassland	9
Cloud Cisticola	insect	resident	grassland	10
Greybacked Cisticola	insect	resident	Karoo	11
Levaillant's Cisticola	insect	resident	aquatic	11
Neddicky	insect	resident	savanna	9
Blackchested Prinia	insect	resident	savanna	9
Spotted Prinia	insect	resident	Karoo	9
Namaqua Warbler	insect	resident	Karoo	11
Rufouseared Warbler	insect	resident	Karoo	10
Spotted Flycatcher	insect	resident	wide	15
Dusky Flycatcher	insect	resident	forest	12
Marico Flycatcher	insect	resident	savanna	24
Chat Flycatcher	insect	local nomad	Karoo	37
Fiscal Flycatcher	insect	resident	Karoo	26
Cape Batis	insect	resident	forest	12
Chinspot Batis	insect	resident	savanna	12

Appendix 2, continued.

Species	Food	Status	Habitat	Mass
Pririt Batis	insect	resident	Karoo	10
Fairy Flycatcher	insect	local nomad	Karoo	6
Paradise Flycatcher	insect	Af-migrant	forest	14
African Pied Wagtail	insect	resident	aquatic	27
Cape Wagtail	insect	resident	aquatic	21
Grassveld Pipit	insect	resident	grassland	25
Longbilled Pipit	insect	resident	grassland	23
Plainbacked Pipit	insect	resident	grassland	24
Buffy Pipit	insect	resident	grassland	28
Rock Pipit	insect	resident	grassland	23
Orangethroated Longclaw	insect	resident	grassland	44
Lesser Grey Shrike	insect	P-migrant	savanna	48
Fiscal Shrike	insect	resident	Karoo	41
Redbacked Shrike	insect	P-migrant	grassland	28
Southern Boubou	insect	resident	forest	50
Crimsonbreasted Shrike	insect	resident	savanna	48
Brubru	insect	resident	savanna	25
Southern Tchagra	insect	resident	Karoo	47
Bokmakierie	insect	resident	Karoo	70
European Starling	mixed	resident	wide	75
Pied Starling	mixed	resident	grassland	99
Wattled Starling	mixed	nomad	savanna	67
Glossy Starling	mixed	resident	savanna	83
Redwinged Starling	fruit	resident	Karoo	135
Palewinged Starling	fruit	resident	Karoo	100
Malachite Sunbird	nectar	local nomad	Fynbos	16
Lesser Doublecollared Sunbird	nectar	local nomad	Karoo	8
Greater Doublecollared Sunbird	nectar	local nomad	forest	12
Dusky Sunbird	nectar	local nomad	Karoo	8
Black Sunbird	nectar	local nomad	forest	12
Cape White-eye	fruit	resident	Karoo	11
Whitebrowed Sparrowweaver	mixed	resident	savanna	47
Sociable Weaver	insect	resident	savanna	27
House Sparrow	mixed	resident	wide	24
Great Sparrow	mixed	resident	savanna	31
Cape Sparrow	mixed	resident	wide	27
Greyheaded Sparrow	mixed	resident	savanna	24
Yellowthroated Sparrow	mixed	resident	savanna	27
Scalyfeathered Finch	seeds	resident	savanna	11
Cape Weaver	mixed	resident	Fynbos	43
Masked Weaver	mixed	resident	Karoo	26
Redbilled Quelea	seeds	local nomad	savanna	20
Red Bishop	seeds	resident	wide	22
Golden Bishop	seeds	resident	grassland	16
Yellowrumped Widow	seeds	resident	renoster	21
Longtailed Widow	seeds	resident	grassland	42
Redbilled Firefinch	seeds	resident	savanna	9
Common Waxbill	seeds	resident	grassland	9

Appendix 2, continued.

Species	Food	Status	Habitat	Mass
Swee Waxbill	seeds	resident	forest	7
Quail Finch	seeds	resident	grassland	11
Redheaded Finch	seeds	local nomad	savanna	23
Pintailed Whydah	seeds	resident	grassland	15
Yelloweyed Canary	seeds	local nomad	savanna	13
Blackthroated Canary	seeds	local nomad	Karoo	11
Cape Canary	seeds	resident	Fynbos	15
Cape Siskin	seeds	local nomad	Fynbos	12
Blackheaded Canary	seeds	nomad	Karoo	12
Bully Canary	seeds	local nomad	forest	29
Yellow Canary	seeds	local nomad	Karoo	17
Whitethroated Canary	seeds	local nomad	Karoo	27
Streakyheaded Canary	mixed	local nomad	savanna	22
Goldenbreasted Bunting	mixed	local nomad	savanna	20
Cape Bunting	seeds	local nomad	Karoo	21
Rock Bunting	seeds	local nomad	Karoo	15
Larklike Bunting	seeds	nomad	Karoo	15

Appendix 3: Bird species most frequently recorded in the Succulent and Nama-Karoo

A list of bird species recorded (a) most frequently in the Succulent Karoo, (b) most frequently in the Nama-Karoo, and (c) equally common in both biomes.

a. Succulent Karoo

Great Crested Grebe
Blacknecked Grebe
Dabchick
Whitebreasted Cormorant
Reed Cormorant
Darter
Grey Heron
Blackheaded Heron
Purple Heron
Little Egret
Yellowbilled Egret
Cattle Egret
Blkcrowned Night Heron
Little Bittern
Hamerkop
African Black Duck
Cape Teal
Cape Shoveller
Southern Pochard
Maccoa Duck
Yelobilled/Black Kite
Blackshouldered Kite
Black Eagle
Booted Eagle
Martial Eagle
Blkbreasted Snake Eagle
African Fish Eagle
Jackal Buzzard
Redbreasted Sparrowhawk
Pale Chanting Goshawk
African Marsh Harrier
Black Harrier
Gymnogene
Peregrine Falcon
Lanner Falcon
Rock Kestrel
Greywing Francolin
Cape Francolin
Common Quail
Black Crake
Redknobbed Coot
Moorhen
Ludwig's Bustard
Ringed Plover
Common Sandpiper
Wood Sandpiper
Greenshank
Curlew Sandpiper
Sanderling
Ethiopian Snipe
Avocet
Water Dikkop
Rock Pigeon
Klaas Cuckoo
Cape Eagle Owl
Fierynecked Nightjar
Freckled Nightjar
Whiterumped Swift
Alpine Swift
Speckled Mousebird
Pied Kingfisher
Giant Kingfisher
Malachite Kingfisher
Brownhooded Kingfisher
European Bee-eater
Hoopoe
Greater Honeyguide
Ground Woodpecker
Cardinal Woodpecker
Karoo Lark
Redcapped Lark
Thickbilled Lark
Pearlbreasted Swallow
Rock Martin
House Martin
Brownthroated Martin
Black Crow
Pied Crow
Whitenecked Raven
Southern Grey Tit
Cape Penduline Tit
Cape Bulbul
Sombre Bulbul
Olive Thrush
Cape Rock Thrush
Mountain Chat

Capped Wheatear
Karoo Chat
Stonechat
Cape Robin
Karoo Robin
Layard's Titbabbler
African Marsh Warbler
Cape Reed Warbler
African Sedge Warbler
Barthroated Apalis
Longbilled Crombec
Karoo Eremomela
Grassbird
Fantailed Cisticola
Greybacked Cisticola
Spotted Prinia
Namaqua Warbler
Dusky Flycatcher
Fiscal Flycatcher
Cape Batis
Pririt Batis
Fairy Flycatcher
Paradise Flycatcher
Cape Wagtail
Longbilled Pipit
Southern Boubou
Southern Tchagra
Bokmakierie
European Starling
Pied Starling
Redwinged Starling
Palewinged Starling
Cape Sugarbird
Malachite Sunbird
Orangebreasted Sunbird
Lesser D/collrd Sunbird
Cape Weaver
Red Bishop
Yellowrumped Widow
Common Waxbill
Cape Canary
Cape Siskin
Blackheaded Canary
Bully Canary
Yellow Canary
Whitethroated Canary
Protea Canary
Streakyheaded Canary
Cape Bunting

b. Nama-Karoo

Goliath Heron
White Stork
Hadeda Ibis
Greater Flamingo
Redbilled Teal
Secretarybird
Tawny Eagle
Steppe Buzzard
Gabar Goshawk
Greater Kestrel
Lesser Kestrel
Pygmy Falcon
Helmeted Guineafowl
Blue Crane
Kori Bustard
Blue Korhaan
Karoo Korhaan
Black Korhaan
Kittlitz's Plover
Crowned Plover
Little Stint
Blackwinged Stilt
Burchell's Courser
Doublebanded Courser
Cape Turtle Dove
Laughing Dove
Namaqua Dove
Diederik Cuckoo
Spotted Eagle Owl
Rufouscheeked Nightjar
Little Swift
Redfaced Mousebird
Swallowtailed Bee-eater
Scimitarbilled Woodhoopoe
Pied Barbet
Lesser Honeyguide
Clapper Lark
Fawncoloured Lark
Sabota Lark
Longbilled Lark
Spikeheeled Lark
Pinkbilled Lark
Sclater's Lark
Stark's Lark
Greybacked Finchlark
Blackeared Finchlark

European Swallow	Plainbacked Pipit
Whitethroated Swallow	Rock Pipit
Greater Striped Swallow	Orangethroated Longclaw
S. A. Cliff Swallow	Lesser Grey Shrike
Forktailed Drongo	Redbacked Shrike
Ashy Tit	Brubru
Redeyed Bulbul	Wattled Starling
Shorttoed Rock Thrush	Glossy Starling
Tractrac Chat	Whtbrowed Sparrowweaver
Sicklewinged Chat	Sociable Weaver
Anteating Chat	House Sparrow
Kalahari Robin	Greyheaded Sparrow
Titbabbler	Scalyfeathered Finch
Willow Warbler	Masked Weaver
Yellowbellied Eremomela	Redbilled Quelea
Desert Cisticola	Golden Bishop
Cloud Cisticola	Redbilled Firefinch
Levaillant's Cisticola	Quail Finch
Neddicky	Redheaded Finch
Blackchested Prinia	Pintailed Whydah
Rufouseared Warbler	Blackthroated Canary
Spotted Flycatcher	Rock Bunting
Chat Flycatcher	Larklike Bunting
Grassveld Pipit	

c. Equally common in both biomes	
Black Stork	Greyheaded Gull
Sacred Ibis	Whitewinged Tern
African Spoonbill	Namaqua Sandgrouse
Egyptian Goose	Redeyed Dove
South African Shelduck	Barn Owl
Yellowbilled Duck	European/Black Swifts
Spurwinged Goose	Whitebacked Mousebird
Threebanded Plover	Familiar Chat
Blacksmith Plover	Fiscal Shrike
Marsh Sandpiper	Dusky Sunbird
Ruff	Cape White-eye
Spotted Dikkop	Cape Sparrow

Appendix 4: Species, overall biomass, metabolised energy and estimated food intake for birds in karroid shrublands

Mean weights for each species are given in Appendix 2, and specific names are given in Appendix 1.

Tierberg, Prince Albert

Species	Biomass (g/km^2)	Density ($birds/km^2$)	Metab. energy ($kJ/day/km^2$)	Food intake ($g/day/km^2$)
South African Shelduck	75.00	0.06	1247.27	121.09
Pale Chanting Goshawk	60.00	0.08	890.31	54.95
Common Quail	8.00	0.08	235.50	16.82
Kori Bustard	740.00	0.12	6287.86	449.13
Ludwig's Bustard	1950.00	0.39	3114.01	222.42
Karoo Korhaan	2038.50	1.51	1312.26	93.73
Doublebanded Courser	26.10	0.29	219.68	12.20
Namaqua Sandgrouse	355.52	2.02	342.01	18.58
Rock Pigeon	28.00	0.08	538.38	29.25
Cape Turtle Dove	15.20	0.10	310.47	16.87
European Swift	44.72	1.04	134.92	7.49
Black Swift	5.59	0.13	134.92	7.49
Whiterumped Swift	2.75	0.11	94.33	5.24
Alpine Swift	13.86	0.18	198.19	11.01
Redfaced Mousebird	7.20	0.12	168.10	12.00
Longbilled Lark	168.50	3.37	149.05	10.64
Karoo Lark	43.09	1.39	108.72	7.76
Spikeheeled Lark	292.95	10.85	99.24	7.08
Redcapped Lark	2.34	0.09	96.80	5.26
Thickbilled Lark	68.64	1.56	136.99	7.44
Greybacked Finchlark	27.54	1.62	73.13	3.97
Blackeared Finchlark	12.30	0.82	67.33	3.65
European Swallow	34.38	1.91	75.94	4.21
Greater Striped Swallow	3.78	0.14	99.24	5.51
Rock Martin	4.83	0.21	89.28	4.95
Black Crow	290.00	0.58	681.27	48.66
Cape Penduline Tit	2.08	0.26	44.47	2.47
Tractrac Chat	48.84	2.22	86.70	4.81
Karoo Chat	497.10	16.57	106.39	7.59
Karoo Eremomela	6.10	0.61	51.52	2.86
Greybacked Cisticola	6.71	0.61	54.87	3.04
Rufouseared Warbler	63.30	6.33	51.52	2.86
Grassveld Pipit	3.25	0.13	94.33	5.24
Plainbacked Pipit	11.52	0.48	91.82	5.10
Fiscal Shrike	22.96	0.56	130.75	7.26
Bokmakierie	8.40	0.12	186.11	10.33
Wattled Starling	46.90	0.70	180.80	12.91
Redwinged Starling	126.90	0.94	287.09	20.50
Palewinged Starling	10.00	0.10	235.50	16.82
Malachite Sunbird	1.28	0.08	70.26	3.41

Tierberg, continued

Species	Biomass (g/km^2)	Density (birds/km^2)	Metab. energy (kJ/day/km^2)	Food intake (g/day/km^2)
Dusky Sunbird	0.48	0.06	44.47	2.15
Cape Sparrow	41.58	1.54	99.24	7.08
Masked Weaver	3.90	0.15	96.80	6.91
Blackheaded Canary	18.12	1.51	58.11	3.15
Yellow Canary	99.96	5.88	73.13	3.97
Whitethroated Canary	105.03	3.89	99.24	5.39
Cape Bunting	3.57	0.17	84.07	4.56
Larklike Bunting	13.20	0.88	67.33	3.65
Totals	8459.97		19199.75	1329.71

Melton Wold, Victoria West.

Species	Biomass (g/km^2)	Density (birds/km^2)	Metab. energy (kJ/day/km^2)	Food intake (g/day/km^2)
Jackal Buzzard	3936.00	3.70	4149.38	256.13
Pale Chanting Goshawk	922.00	1.23	1095.08	67.60
Karoo Korhaan	13338.00	9.88	12965.14	926.08
Burchell's Courser	370.00	4.94	962.20	53.46
Namaqua Sandgrouse	3261.00	18.53	6337.44	349.36
Namaqua Dove	395.00	9.88	1270.92	70.06
Little Swift	597.00	22.98	2224.50	123.58
Longbilled Lark	877.00	17.54	2614.27	186.73
Spikeheeled Lark	504.00	18.70	1855.84	132.56
Redcapped Lark	256.00	9.88	956.40	52.72
Pinkbilled Lark	17.00	1.23	79.13	4.36
Greybacked Finchlark	42.00	2.47	180.63	9.96
Blackeared Finchlark	915.00	61.03	4109.26	226.53
European Swallow	66.00	3.70	280.98	15.61
Whitethroated Swallow	43.00	1.97	170.79	9.49
Greater Striped Swallow	100.00	3.70	367.20	20.40
Rock Martin	45.00	1.23	109.81	6.10
Southern Grey Tit	78.00	3.70	311.08	17.28
Mountain Chat	561.00	17.54	1947.28	108.18
Capped Wheatear	79.00	2.47	274.22	15.23
Familiar Chat	81.00	3.70	320.78	17.82
Tractrac Chat	179.00	6.17	534.91	29.72
Sicklewinged Chat	148.00	7.41	603.25	33.51
Karoo Robin	374.00	18.70	1522.37	84.58
Karoo Eremomela	49.00	4.94	254.52	14.14
Spotted Prinia	67.00	7.41	356.14	19.79
Rufouseared Warbler	230.00	22.98	1184.00	65.78
Chat Flycatcher	878.00	23.72	2898.20	161.01
Fiscal Shrike	517.00	12.60	1647.43	91.52
Pied Starling	366.00	3.70	865.61	61.82
Cape Sparrow	1067.00	39.53	3923.08	280.22
Yellow Canary	479.00	28.17	2060.08	113.57

Melton Wold, Victoria West, continued.

Species	Biomass (g/km^2)	Density (birds/km^2)	Metab. energy (kJ/day/km^2)	Food intake (g/day/km^2)
Cape Bunting	26.00	1.23	103.41	5.70
Larklike Bunting	1320.00	87.97	5923.18	326.53
Totals	32183.00		64458.5	3957.13

Klaarstroom

Species	Biomass (g/km^2)	Density (birds/km^2)	Metab. energy (kJ/day/km^2)	Food intake (g/day/km^2)
Pale Chanting Goshawk	262.00	0.35	311.61	19.24
Rock Kestrel	24.00	0.12	44.65	2.76
Common Quail	12.00	0.12	28.26	2.01
Ludwig's Bustard	600.00	0.12	373.68	26.69
Karoo Korhaan	7762.00	5.75	7545.50	538.96
Spotted Dikkop	54.00	0.12	76.26	4.24
Doublebanded Courser	11.00	0.12	26.36	1.46
Namaqua Sandgrouse	991.00	5.63	1925.51	106.15
Rock Pigeon	710.00	2.03	1092.90	60.25
Cape Turtle Dove	436.00	2.87	891.04	49.12
Namaqua Dove	24.00	0.59	75.89	4.18
Black Swift	5.00	0.12	16.19	0.90
Little Swift	6.00	0.23	22.26	1.24
Whitebacked Mousebird	14.00	0.35	45.76	3.27
Redfaced Mousebird	143.00	2.39	401.77	28.70
European Bee-eater	6.00	0.12	18.82	1.05
Pied Barbet	15.00	0.47	52.18	3.73
Longbilled Lark	401.00	8.03	1196.84	85.48
Karoo Lark	111.00	3.59	390.30	27.87
Spikeheeled Lark	285.00	10.55	1047.01	74.78
Redcapped Lark	37.00	1.43	138.43	7.63
Thickbilled Lark	52.00	1.19	163.01	8.99
Greybacked Finchlark	32.00	1.91	139.68	7.70
European Swallow	34.00	1.91	145.05	8.06
Whitethroated Swallow	5.00	0.23	19.94	1.11
Greater Striped Swallow	6.00	0.23	22.83	1.27
Rock Martin	3.00	0.12	10.71	0.60
Black Crow	1555.00	3.11	2118.75	151.33
Southern Grey Tit	10.00	0.47	39.52	2.20
Cape Penduline Tit	11.00	1.43	63.59	3.53
Redeyed Bulbul	4.00	0.12	13.05	0.93
Familiar Chat	8.00	0.35	30.34	1.69
Tractrac Chat	34.00	1.55	134.38	7.47
Karoo Chat	684.00	22.79	2424.62	173.18
Cape Robin	3.00	0.12	12.20	0.68
Karoo Robin	26.00	1.31	106.65	5.92
Titbabbler	18.00	1.19	80.12	5.72
Layard's Titbabbler	2.00	0.12	8.08	0.57

Klaarstroom, continued

Species	Biomass (g/km^2)	Density ($birds/km^2$)	Metab. energy ($kJ/day/km^2$)	Food intake ($g/day/km^2$)
Longbilled Crombec	4.00	0.35	20.34	1.13
Yellowbellied Eremomel	8.00	0.95	42.24	2.35
Karoo Eremomela	106.00	10.60	546.14	30.34
Greybacked Cisticola	21.00	1.91	104.80	5.82
Spotted Prinia	1.00	0.12	5.77	0.32
Rufouseared Warbler	42.00	4.19	215.88	11.99
Chat Flycatcher	53.00	1.43	174.72	9.71
Pririt Batis	2.00	0.23	10.23	0.57
Fairy Flycatcher	4.00	0.71	26.11	1.45
Cape Wagtail	5.00	0.23	19.34	1.07
Grassveld Pipit	63.00	2.51	236.76	13.15
Fiscal Shrike	34.00	0.83	108.52	6.03
Malachite Sunbird	13.00	0.83	58.32	2.83
Lesser D-coll. Sunbird	11.00	1.19	55.93	2.71
Dusky Sunbird	3.00	0.35	15.56	0.76
Cape Sparrow	165.00	6.11	606.38	43.31
Scalyfeathered Finch	6.00	0.59	32.37	1.78
Blackheaded Canary	8.00	0.71	41.26	2.27
Yellow Canary	34.00	2.03	148.45	8.18
Whitethroated Canary	103.00	3.83	380.10	20.95
Cape Bunting	15.00	0.71	59.69	3.29
Larklike Bunting	18.00	1.19	80.12	4.42
Totals	15115.0		24242.8	1605.09

Appendix 5: Protected areas in the Karoo

Appendix 5(a): Statutory nature reserves and other protected areas in the Succulent and Nama-Karoo. SADF = South African Defence Force

Protected area	Size(ha)	Biome	Authority	Locality(QDS)
97 Ammunition Depot	6284	Nama-Karoo	SADF	3023DB
Aberdeen Nature Reserve	574	Nama-Karoo	Subsidized	3224AC
Akkerendam Nature Reserve	2301	Succ.-Karoo	Subsidized	3119BC, 3119BD
Anysberg Nature Reserve	34051	Succ.-Karoo	Cape Nature Conservation	3320DA
Appie van Heerden Nature Reserve	762	Nama-Karoo	Subsidized	3022CC, 3122AA
Augrabies Falls National Park	82415	Nama-Karoo	National Parks Board	2820AC, 2820AD, 2820CA, 2820CB
Bokkeveld Nature Reserve	10	Succ.-Karoo	Cape Nature Cons.	3119AC
Bosberg Nature Reserve	3521	Nama-Karoo	Subsidized	3225DA
Boshof Townlands Nature Reserve	685	Nama-Karoo	Local municipality	2825CA
Commando Drift Nature Reserve	5983	Nama-Karoo	Cape Nature Cons.	3225BB
Dassieshoek Nature Reserve	865	Succ.-Karoo	Subsidized	3319DD
De Aar Nature Reserve	51	Nama-Karoo	Subsidized	3023DB, 3024CA
Die Bos Nature Reserve	60	Nama-Karoo	Subsidized	2922DB
Doornkloof Nature Reserve	8765	Nama-Karoo	Cape Nature Cons.	3024BB, 3024BD, 3025AC
Dries Le Roux Nature Reserve	2575	Succ.-Karoo	Cape Prov. Admin.	3319BD, 3320AC
Eeufees Nature Reserve	11	Succ.-Karoo	Subsidized	3320CC
Gamkapoort Nature Reserve	8002	Succ.-Karoo	Cape Nature Cons.	3321BA, 3321BC, 3321BD
Genl de Wet training Area	16974	Nama-Karoo	SADF	2925BC
Goegap Nature Reserve	14864	Succ.-Karoo	Cape Nature Cons.	2917DB, 2918CA
Granstad Training Area	5970	Nama-Karoo	SADF	3326AD
Hendrik Verwoerd Dam Nature Reserve	11237	Nama-Karoo	O.F.S. Nature Cons.	3025CB, 3025DA, 3025DB, 3026CA

Appendix 5(a), continued

Protected area	Size(ha)	Biome	Authority	Locality(QDS)
Kalahari Gemsbok National Park	959103	Nama-Karoo	National Parks Board	2620AD
Kalkfontein Dam Nature Reserve	162	Nama-Karoo	O.F.S. Nature Cons.	2925AC, 2925AD, 2925CA, 2925CB
Karoo National Park	32792	Nama-Karoo	National Parks Board	3222AA-AD, 3222BA, 3222BC
Karoo Nature Reserve	14270	Nama-Karoo	Cape Nature Cons.	3224AB, 3224AD, 3224BA, 3224BC
Ladismith-Klein Karoo Nature Reserve	2766	Succ.-Karoo	Subsidized	3321CA
Marloth Nature Reserve	11269	Succ.-Karoo	Cape Nature Cons.	3320CB, 3320CC
Mountain Zebra National Park	6536	Nama-Karoo	National Parks Board	3225AB
Nababiep Nature Reserve	10984	Succ.-Karoo	Cape Prov. Admin.	2817CB
Nieuwoudtville Nature Reserve	66	Succ.-Karoo	Subsidized	3119AC
Oorlogskloof Nature Reserve	5070	Succ.-Karoo	Cape Nature Conservation	3119AC, 3119CA
Oudtshoorn Training Area	13393	Succ.-Karoo	SADF	3322CA
Oviston Nature Reserve	13000	Nama-Karoo	Cape Nature Conservation	3025DA-DD
Prieskakoppie Nature Reserve	32	Nama-Karoo	Subsidized	2922DB
Ramskop Nature Reserve	54	Succ.-Karoo	Subsidized	3218BB
Richtersveld National Park	162445	Succ.-Karoo	National Parks Board	2816BB, 2816BD, 2817AA-AD, 2817CA-CB
Riemvasmaak Training Area	70240	Nama-Karoo	SADF	2820AC, 2820AD
Rolfontein Nature Reserve	6938	Nama-Karoo	Cape Nature Conservation	2924DD, 3024BA-BB
Spitskop Nature Reserve	2740	Nama-Karoo	Subsidized	2821AC
Strydenburg Aalwynprag Nature	2	Nama-Karoo	Subsidized	2923DC
Tankwa Karoo National Park	27064	Succ.-Karoo	National Parks Board	3219BB-BD, 3220AA, 3220AC
The Mountain Nature Reserve	413	Nama-Karoo	Subsidized	3026CD
Thomas Baines Nature Reserve	1003	Nama-Karoo	Cape Nature Conservation	3326AD
Tierberg Nature Reserve	77	Nama-Karoo	Subsidized	2820DB, 2821CA
Touws River Training Area	14857	Succ.-Karoo	SADF	3319BD
Tussen-die-Riviere Game Farm	21000	Nama-Karoo	O.F.S. Nature Conservation	3026AC-AD, 3026CA-CB

Appendix 5(a), continued

Protected area	Size(ha)	Biome	Authority	Locality(QDS)
Van Rhynsdorp Training Area	15707	Succ.-Karoo	SADF	3118AD, 3118BC, 3118CB
Vastrap Training Area	49994	Nama-Karoo	SADF	2721CB, 2721DA
Victoria West Nature Reserve	428	Nama-Karoo	Subsidized	3123AC
Villiersdorp Nature Reserve	508	Succ.-Karoo	Subsidized	3319CD
Vrolijkheid Nature Reserve	2027	Succ.-Karoo	Cape Nature Cons.	3319DD
Wuras Dam Nature Reserve	262	Nama-Karoo	O.F.S. Nature Cons	2925DB
Zevenfontein Horse Stud Farm	5243	Nama-Karoo	SADF	3023DB

Appendix 5(b): Mountain catchment reserves and forest reserves on the edge of the Karoo.

Protected area	Size(ha)	Biome	Authority	Locality(QDS)
Baviaanskloof State Forest	68542	Succ.-Karoo	Cape Nature Conservation	3323AD, 3323BC-BD
Cederberg Mountain Catchment Area	73986	Succ.-Karoo	Cape Nature Conservation	3219AA, 3219AD
Cederberg Wilderness Area	64400	Succ.-Karoo	Cape Nature Conservation	3218BB
Cockscomb State Forest	69209	Nama-Karoo	Cape Nature Conservation	3324DB
Gamka Mountain Nature Reserve	9428	Succ.-Karoo	Cape Nature Conservation	3321DB
Groot Swartberg Mountain Catchment	10386	Succ.-Karoo	Cape Nature Conservation	3322BC
Klein Swartberg Mountain Catchment	17999	Succ.-Karoo	Cape Nature Conservation	3321AD, 3321BD
Koue Bokkeveld Mountain Catchment	96348	Succ.-Karoo	Cape Nature Conservation	3219CB
Langeberg West Mountain Catchment	58326	Succ.-Karoo	Cape Nature Conservation	3319DA, 3319DD
Langeberg West State Forest	3419	Succ.-Karoo	Cape Prov. Administration	3319DD
Montagu Mountain Nature Reserv	1200	Succ.-Karoo	Subsidized	3320CC
Riviersonderend Mountain Catchment	43037	Succ.-Karoo	Cape Nature Conservation	3319CD, 3319DC-DD
Rooiberg Mountain Catchment Area	12417	Succ.-Karoo	Cape Nature Conservation	3321CA
Rooiberg State Forest	12928	Succ.-Karoo	Cape Prov. Administration	3321CA
Swartberg East Mountain Catchment	17514	Succ.-Karoo	Cape Nature Conservation	3323AD
Swartberg East State Forest		Succ.-Karoo	Cape Nature Conservation	3323AD
Swartberg State Forest	109021	Succ.-Karoo	Cape Nature Conservation	3321BC-BD, 3322BC-BD, 3323AC-AD
Swellendam State Forest	721	Succ.-Karoo	Cape Nature Conservation	3320DC
Winterhoek State Forest	6754	Succ.-Karoo	Cape Prov. Administration	3219AD

Appendix 6: Bird species recorded in protected areas in the Succulent and Nama-Karoo

Two sets of data for each biome are presented here. The first column (All) gives the total number of protected areas, regardless of size, in which the species has been recorded. The second column ($>10\ km^2$) gives similar data for protected areas above 10 km^2.

	Number of protected areas in which the species recorded:			
	Succulent Karoo		Nama-Karoo	
Species	All	$>10\ km^2$	All	$>10\ km^2$
Great Crested Grebe	2	0	1	1
Blacknecked Grebe	2	0	0	0
Dabchick	6	2	8	4
Whitebreasted Cormorant	5	2	11	5
Reed Cormorant	7	2	10	5
Darter	6	3	10	5
Grey Heron	5	2	11	5
Blackheaded Heron	7	3	10	5
Goliath Heron	2	1	7	3
Purple Heron	2	1	1	0
Great White Egret	2	1	0	0
Little Egret	4	2	4	3
Yellowbilled Egret	3	1	0	0
Cattle Egret	9	3	9	4
Blackcrowned Night Heron	4	2	4	2
Little Bittern	3	1	3	2
Hamerkop	7	2	11	5
White Stork	3	2	9	5
Black Stork	5	2	9	3
Yellowbilled Stork	0	0	4	2
Sacred Ibis	6	3	8	4
Glossy Ibis	1	1	0	0
Hadeda Ibis	7	2	11	5
African Spoonbill	5	2	10	5
Greater Flamingo	0	0	3	2
Lesser Flamingo	0	0	1	1
Whitefaced Duck	0	0	0	0
Egyptian Goose	10	4	10	5
South African Shelduck	7	3	10	5
Yellowbilled Duck	8	2	10	5
African Black Duck	9	3	10	5
Cape Teal	3	2	5	3
Redbilled Teal	4	2	10	5
Cape Shoveller	1	0	4	1
Southern Pochard	3	1	7	2
Spurwinged Goose	5	3	10	5
Maccoa Duck	1	0	2	1

Appendix 6, continued

Species	Number of protected areas in which the species recorded:			
	Succulent Karoo		Nama-Karoo	
	All	> 10 km²	All	> 10 km²
Secretarybird	2	2	9	4
Cape Vulture	3	2	7	3
Whitebacked Vulture	0	0	2	0
Yellowbilled Kite	4	3	7	3
Blackshouldered Kite	10	4	10	5
Black Eagle	10	4	9	5
Tawny Eagle	1	1	4	1
Booted Eagle	8	3	7	3
Martial Eagle	6	4	10	5
Blackbreasted Snake Eagle	3	2	1	1
African Fish Eagle	6	3	10	5
Steppe Buzzard	6	2	8	3
Jackal Buzzard	9	4	9	4
Redbreasted Sparrowhawk	2	1	5	2
African Goshawk	2	1	4	1
Gabar Goshawk	2	1	2	1
Pale Chanting Goshawk	7	3	9	5
African Marsh Harrier	1	0	2	1
Black Harrier	8	4	4	1
Gymnogene	5	2	7	3
Peregrine Falcon	4	3	2	0
Lanner Falcon	8	4	6	3
Rock Kestrel	10	4	10	5
Greater Kestrel	3	2	7	3
Lesser Kestrel	2	1	6	2
Pygmy Falcon	0	0	1	1
Greywing Francolin	6	2	7	2
Orange River Francolin	0	0	2	2
Cape Francolin	9	3	1	1
Common Quail	6	3	9	4
Helmeted Guineafowl	8	3	11	5
Blue Crane	3	2	9	4
Black Crake	2	0	0	0
Moorhen	5	2	7	2
Redknobbed Coot	6	2	10	5
Kori Bustard	2	1	7	3
Stanley's Bustard	1	0	8	4
Ludwig's Bustard	6	3	5	3
Blue Korhaan	0	0	3	2
Karoo Korhaan	5	3	7	3
Redcrested Korhaan	0	0	0	0
Black Korhaan	3	1	6	3
Ringed Plover	1	1	1	0
Chestnutbanded Plover	0	0	0	0
Kittlitz's Plover	2	1	4	3
Threebanded Plover	7	2	10	5
Crowned Plover	5	3	9	4
Blacksmith Plover	7	2	10	5

Appendix 6, continued

Species	Succulent Karoo All	Succulent Karoo >10 km²	Nama-Karoo All	Nama-Karoo >10 km²
Common Sandpiper	4	1	5	2
Wood Sandpiper	1	0	2	1
Marsh Sandpiper	1	1	1	1
Greenshank	6	2	4	1
Curlew Sandpiper	1	0	1	1
Little Stint	4	2	0	0
Sanderling	0	0	0	0
Ruff	0	0	1	0
Ethiopian Snipe	1	0	3	2
Avocet	3	3	7	3
Blackwinged Stilt	5	3	8	4
Spotted Dikkop	9	4	9	4
Water Dikkop	2	0	4	2
Burchell's Courser	2	1	0	0
Doublebanded Courser	3	2	8	4
Greyheaded Gull	1	0	5	2
Whiskered Tern	0	0	2	0
Whitewinged Tern	1	0	1	0
Namaqua Sandgrouse	7	3	8	5
Burchell's Sandgrouse	0	0	0	0
Rock Pigeon	10	4	11	5
Redeyed Dove	8	3	9	3
Cape Turtle Dove	11	4	11	5
Laughing Dove	11	4	11	5
Namaqua Dove	7	3	9	5
Redchested Cuckoo	4	2	4	1
Great Spotted Cuckoo	1	0	3	1
Jacobin Cuckoo	2	1	5	2
Klaas Cuckoo	4	1	3	0
Diederik Cuckoo	5	1	11	5
Barn Owl	4	2	10	5
Cape Eagle Owl	4	3	5	2
Spotted Eagle Owl	10	4	9	4
Fierynecked Nightjar	7	4	4	2
Rufouscheeked Nightjar	3	2	8	5
Freckled Nightjar	2	1	1	1
European Swift	2	1	1	1
Black Swift	7	3	7	3
Bradfield's Swift	1	1	0	0
Whiterumped Swift	8	3	10	5
Horus Swift	0	0	3	1
Little Swift	9	3	7	4
Alpine Swift	10	4	7	3
Speckled Mousebird	8	2	9	5
Whitebacked Mousebird	8	3	9	5
Redfaced Mousebird	8	3	8	4
Pied Kingfisher	4	1	9	5
Giant Kingfisher	8	3	9	4

Number of protected areas in which the species recorded.

Appendix 6, continued

	Number of protected areas in which the species recorded:			
	Succulent Karoo		Nama-Karoo	
Species	All	>10 km^2	All	>10 km^2
Malachite Kingfisher	7	2	9	4
Brownhooded Kingfisher	5	2	6	2
European Bee-eater	7	2	7	3
Swallowtailed Bee-eater	1	1	1	1
European Roller	0	0	1	0
Hoopoe	9	4	11	5
Redbilled Woodhoopoe	0	0	4	0
Scimitarbilled Woodhoo	1	1	4	2
Pied Barbet	9	3	11	5
Greater Honeyguide	3	2	7	3
Lesser Honeyguide	3	1	6	3
Ground Woodpecker	11	4	7	3
Cardinal Woodpecker	6	3	8	3
Melodious Lark	0	0	0	0
Rufousnaped Lark	0	0	3	0
Clapper Lark	4	2	8	3
Fawncoloured Lark	0	0	0	0
Sabota Lark	0	0	3	3
Longbilled Lark	6	2	6	4
Karoo Lark	6	3	1	1
Red Lark	1	1	0	0
Spikeheeled Lark	2	2	9	5
Redcapped Lark	7	3	5	3
Pinkbilled Lark	0	0	0	0
Sclater's Lark	0	0	0	0
Stark's Lark	2	2	0	0
Thickbilled Lark	6	3	5	3
Chestnutbacked Finchlark	1	1	0	0
Greybacked Finchlark	3	2	8	4
Blackeared Finchlark	1	1	3	2
European Swallow	8	3	8	3
Whitethroated Swallow	7	1	9	4
Pearlbreasted Swallow	5	2	8	3
Redbreasted Swallow	0	0	0	0
Greater Striped Swallow	9	3	10	4
Lesser Striped Swallow	1	0	3	1
South African Cliff Swallow	0	0	1	1
Rock Martin	11	4	11	5
House Martin	6	2	7	3
Brownthroated Martin	9	2	9	5
Banded Martin	1	0	1	1
Forktailed Drongo	6	3	8	2
European Golden Oriole	1	0	0	0
Blackheaded Oriole	0	0	2	0
Black Crow	8	4	5	2
Pied Crow	5	3	9	4
Whitenecked Raven	7	3	10	4
Southern Grey Tit	7	3	9	5

Appendix 6, continued

Species	Number of protected areas in which the species recorded:			
	Succulent Karoo		Nama-Karoo	
	All	>10 km^2	All	>10 km^2
Ashy Tit	1	1	0	0
Cape Penduline Tit	7	3	5	3
Cape Bulbul	11	4	0	0
Redeyed Bulbul	4	3	9	5
Sombre Bulbul	4	1	5	1
Olive Thrush	9	4	11	5
Cape Rock Thrush	6	3	10	4
Sentinel Rock Thrush	1	1	3	2
Shorttoed Rock Thrush	1	1	0	0
Mountain Chat	8	3	10	5
Capped Wheatear	4	2	2	2
Familiar Chat	11	4	11	5
Tractrac Chat	3	2	2	2
Sicklewinged Chat	3	1	5	3
Karoo Chat	7	3	5	4
Anteating Chat	4	2	9	5
Stonechat	7	3	8	4
Cape Robin	9	3	11	5
Karoo Robin	10	3	9	5
Kalahari Robin	1	1	1	1
Titbabbler	6	1	10	5
Layard's Titbabbler	8	3	8	4
African Marsh Warbler	7	2	7	3
Cape Reed Warbler	4	1	7	3
African Sedge Warbler	8	3	1	0
Willow Warbler	1	1	3	1
Barthroated Apalis	8	2	6	2
Longbilled Crombec	9	3	8	4
Yellowbellied Eremomela	5	2	7	5
Karoo Eremomela	4	3	2	1
Cinnamonbreasted Warbler	4	2	2	2
Grassbird	5	2	1	0
Fantailed Cisticola	3	1	6	3
Desert Cisticola	0	0	3	2
Cloud Cisticola	0	0	2	1
Greybacked Cisticola	11	4	6	3
Levaillant's Cisticola	8	2	8	5
Neddicky	5	2	6	2
Blackchested Prinia	1	1	2	2
Spotted Prinia	11	4	9	3
Namaqua Warbler	6	3	5	3
Rufouseared Warbler	7	3	8	5
Spotted Flycatcher	2	1	3	2
Dusky Flycatcher	2	1	4	0
Marico Flycatcher	0	0	1	1
Chat Flycatcher	4	3	6	4
Fiscal Flycatcher	9	3	9	4
Cape Batis	7	2	3	1

Appendix 6, continued

Species	Number of protected areas in which the species recorded:			
	Succulent Karoo		Nama-Karoo	
	All	>10 km^2	All	>10 km^2
Chinspot Batis	0	0	5	1
Pririt Batis	4	2	6	3
Fairy Flycatcher	9	3	9	5
Paradise Flycatcher	3	1	6	2
African Pied Wagtail	1	1	5	2
Cape Wagtail	9	3	11	5
Grassveld Pipit	6	3	9	4
Longbilled Pipit	6	3	5	3
Plainbacked Pipit	4	1	3	1
Buffy Pipit	0	0	0	0
Rock Pipit	3	1	4	2
Orangethroated Longclaw	1	0	4	2
Lesser Grey Shrike	0	0	3	1
Fiscal Shrike	11	4	11	5
Redbacked Shrike	1	1	4	1
Southern Boubou	8	3	5	1
Crimsonbreasted Shrike	0	0	0	0
Brubru	1	1	1	1
Southern Tchagra	6	2	6	2
Bokmakierie	11	4	10	4
European Starling	7	3	2	1
Pied Starling	9	3	10	5
Wattled Starling	5	2	9	4
Glossy Starling	2	2	9	4
Redwinged Starling	7	2	8	4
Palewinged Starling	6	3	8	4
Malachite Sunbird	11	4	10	4
Lesser Doublecollared Sunbird	11	4	7	3
Greater Doublecollared Sunbird	3	2	4	1
Dusky Sunbird	5	3	7	3
Black Sunbird	1	1	5	1
Cape White-eye	9	3	11	5
Whitebrowed Sparrowweaver	0	0	6	3
Sociable Weaver	0	0	2	1
House Sparrow	7	4	6	3
Great Sparrow	1	1	1	1
Cape Sparrow	11	4	10	5
Greyheaded Sparrow	2	1	6	3
Yellowthroated Sparrow	0	0	6	2
Scalyfeathered Finch	0	0	6	2
Cape Weaver	9	4	7	4
Masked Weaver	8	3	10	5
Redbilled Quelea	1	1	4	2
Red Bishop	7	2	10	5
Golden Bishop	0	0	1	1
Yellowrumped Widow	7	2	2	1
Longtailed Widow	0	0	2	1
Redbilled Firefinch	1	0	3	2

Appendix 6, continued

Species	Number of protected areas in which the species recorded:			
	Succulent Karoo		Nama-Karoo	
	All	>10 km^2	All	>10 km^2
Common Waxbill	9	3	11	5
Swee Waxbill	5	1	5	2
Quail Finch	0	0	2	0
Redheaded Finch	0	0	7	3
Pintailed Whydah	8	3	10	4
Yelloweyed Canary	0	0	5	1
Blackthroated Canary	2	2	4	3
Cape Canary	8	2	7	3
Cape Siskin	6	2	0	0
Blackheaded Canary	6	3	9	5
Bully Canary	6	2	4	1
Yellow Canary	8	2	8	4
Whitethroated Canary	9	3	8	5
Streakyheaded Canary	5	1	6	2
Cape Bunting	11	4	8	4
Rock Bunting	0	0	4	2
Larklike Bunting	7	3	5	3

Appendix 7: Environmental and other information about the first-tier priority quarter-degree squares (see Table 8.5).

Quarter-degree square reference #2918BB. The mining town of Aggeneys is situated in the southwest corner of the square. Topographically an area of plains and inselbergs, with extensive red sand dunes in the Koa River valley. The square includes two of Acocks (1953) Veld Types, Namaqualand Broken Veld and False Desert Grassveld. Rangelands are generally in fair to good condition in the area, although some of the dunes in the Koa river valley have been totally denuded of vegetation (Dean *et al.*, 1991). There is some mining for non-ferrous metals in the area. Part of the quarter-degree square is owned by Goldfields, but most of the land in the square is privately-owned (du Plessis, 1992). Livestock in the area are Dorper and Nama sheep, and cattle.

Quarter-degree square reference #2918BD. South of Aggeneys. Topographically similar to 2918BB, but the inselbergs are smaller, the plains are more extensive and the dune field is broader. The vegetation in the square is Arid Karoo and False Desert Grassveld (Acocks, 1953) and the rangelands are in fair to good condition. Displays of annual flowers on the red sand dunes are spectacular at times. About 70 km^2 is owned by Black Mountain Mineral Development Company, subsidiary of Goldfields, and this part of the mine property is maintained as a protected area. The photograph in Figure 2.23 shows a view southwest across this protected area. The remainder of the land in the square appears to be privately-owned (du Plessis, 1992). Livestock in the area are Dorper and Nama sheep, and cattle.

Quarter-degree square reference #2920DC. Nearest town Brandvlei (about 60 km to the south). The topography is mostly flat, with extensive shallow ephemeral saline pans, all forming part of an endorheic drainage system. The square includes part of Verneukpan. The vegetation is Arid Karoo and False Desert Grassveld (Acocks, 1953) and the rangelands are in fair condition. The photograph in Figure 2.22 shows grassland on one of the better drained parts of the area. A common practice among farmers in the area is to rip and disc plough bare poorly drained areas to provide germination sites. This has the effect of allowing alien plants, such as *Atriplex lindleyi* and *Salsola kali* to establish in the furrows, and disrupts water movement into the pans. There is no protected area in the square at present, and all the land in the square is apparently privately-owned. Livestock in the area are Dorper sheep.

Quarter-degree square reference #2921AC. The town of Kenhardt is situated in the eastern part of the square. Topographically an area of plains and inselbergs, with clearly defined watercourses draining to the north. The vegetation was classified as Orange River Broken

Veld by Acocks (1953), but it also includes elements of the arid savanna, and large *Acacia erioloba* trees are common along the major drainage lines. The rangelands are in fair condition. There is a small "nature reserve" just west of Kenhardt, that includes a substantial population of *Aloe dichotoma* but is unremarkable for its avifauna. The "reserve" is not protected from domestic livestock and was being grazed by Dorper sheep, March 1994. Land in the square is apparently all privately-owned. Livestock in the area are Dorper sheep and cattle.

Quarter-degree square reference #3020AA. The town of Brandvlei is just east of the square. An area of plains and low, small hills, with extensive stony flats. The photograph in Figure 2.20 illustrates the area very well. Generally poorly drained. The vegetation is Arid Karoo and False Desert Grassveld (Acocks, 1953). The rangelands are in fair condition. As in 2920DC, many of the poorly drained bare areas have been ripped, with similar consequences, to provide germination sites. There is no protected area in the quarter-degree square, and all the land is apparently privately-owned. Livestock in the area are Dorper sheep and Angora goats.

Quarter-degree square reference #3020DB. Southeast of the town of Brandvlei. Topography rather more broken than areas further north, with less extensive plains and small hills and inselbergs. Red to yellow sand dunes (possibly relics of the Koa River valley system) occur in small isolated patches. Drainage is endorheic. The vegetation is Arid Karoo and False Desert Grassveld (Acocks, 1953). The photograph in Figure 2.21 shows similar rangeland vegetation. The rangelands are in fair condition. There is no protected area in the quarter-degree square, and all the land is apparently privately-owned. Livestock in the area are Dorper and Merino sheep.

Quarter-degree square reference #3022AC. East of the town of Vanwyksvlei. The topography is flat to undulating, with a few low hills. Drainage apparently endorheic. The vegetation is Arid Karoo and False Desert Grassveld (Acocks, 1953). The rangelands are in fair condition, but overgrazed in parts. There is no protected area in the quarter-degree square, and all land in the square appears to be privately-owned. Livestock in the area are most frequently Dorper sheep.

Quarter-degree square reference #3024AA. About 60 km north of De Aar, and northwest of Philipstown. Fairly broken topography, with high hills and wide valley bottoms. The vegetation is False Arid Karoo (Acocks, 1953) and the rangelands are in fair condition. The area is part of the Platberg Conservancy and is probably not in need of a formal protected area. Livestock in the area are mainly Merino sheep.

Quarter-degree square reference #3025BC. The town of Springfontein is situated on the eastern edge of the square. The square is also just north of the Gariep Dam (Hendrik Verwoerd Dam) on the Orange River. The topography is fairly flat, with low hills and ridges. The vegetation is False Upper Karoo (Acocks, 1953). The rangelands in this general area have been heavily grazed in the past (Shaw, 1875) and are regarded by Acocks (1953) to have been invaded by karroid shrubland. There is no protected area in the square, but the square is adjacent to protected areas administered by Northern Cape Nature Conservation and Orange Free State Nature Conservation. Livestock in the area are Merino sheep.

Quarter-degree square reference #3123BB. Just north of Richmond. Topographically very broken country, with high hills and a few wide valleys. The vegetation is False Upper Karoo (Acocks, 1953), and rangelands in the area are in fair condition. There is no protected area in the square, but the square is adjacent to the Platberg Conservancy, which lies just to the north. The livestock in the square are mainly Merino sheep. Land is apparently all privately-owned. The presence of a major powerline through the area (at present, two parallel lines, with the construction of a third line already at the planning stage (G. Fourie, ESCOM, pers. comm.) reduces the potential for a protected area.

Quarter-degree square reference #3125CB. South and east of Middelburg. Topography fairly flat with a large inselberg that rises to 1552 m (Doringberg) in the southern part of the square. The vegetation includes False Upper Karoo and False karroid Broken Veld, both vegetation types that Acocks (1953) considered to have been invaded by karroid shrublands. Rangelands in the area are in fair condition. There is no protected area in the square, and most of the square is apparently privately-owned. Livestock in the area are mainly Merino sheep, with some Angora goats in areas to the south.

Quarter-degree square reference #3221BB. South and east of Fraserburg. The topography is flat to undulating on the top of the plateau, with almost sheer cliffs on the edge of the escarpment. The vegetation includes Central Upper Karoo on the plateau and Mountain Renosterveld below the escarpment. Rangelands in the area are in fair condition. The photograph in Figure 2.16 shows topography and shrubland on top of the plateau, and Figure 2.25 shows the vegetation and topography below the escarpment. A protected area in this square is unlikely to protect more avian species richness than the Karoo National Park, which lies just to the east of the square. Livestock in the area are mostly Merino sheep.

Quarter-degree square reference #3222DA. South and east of Beaufort West. Topography flat, with very few rises in the ground. The area is poorly drained and much of the drainage is endorheic. The vegetation is classified as Central Lower Karoo (Acocks, 1953). Rangelands in the area have been heavily overgrazed in parts. Although the area is close to the Karoo National Park, and would not include any more avian species richness than the Karoo National Park, the poorly-drained shrubland plains of this area are not represented in any protected area. Livestock in the area are mostly Angora goats, with some Merino sheep and ostriches.

Quarter-degree square reference #3223AA. The square includes the village of Nelspoort. The topography is flat with distinctive isolated hills and ridges. Although Acocks (1953) considers the vegetation of the area to be Central Lower Karoo, desert perennial grasses are frequent on sandy soils. Rangelands are in fair condition. Livestock in the area are mainly Merino sheep. There is a Department of Agriculture (Western Cape) experimental farm in the square.

Quarter-degree square reference #3319BB. North and west of Touwsrivier, in the Ceres Karoo. Topography fairly flat, with low ridges. The vegetation is Succulent Karoo (Acocks, 1953). The photograph in Figure 2.15 was taken to the north of this area, and is a fairly representative illustration of the shrublands throughout the area. The shrublands have been very heavily grazed in the past. A protected area in this square is unlikely to protect more avian species richness than the recently established Tankwa Karoo National Park, which lies to north of this square. Livestock in the area are mainly Dorper sheep.