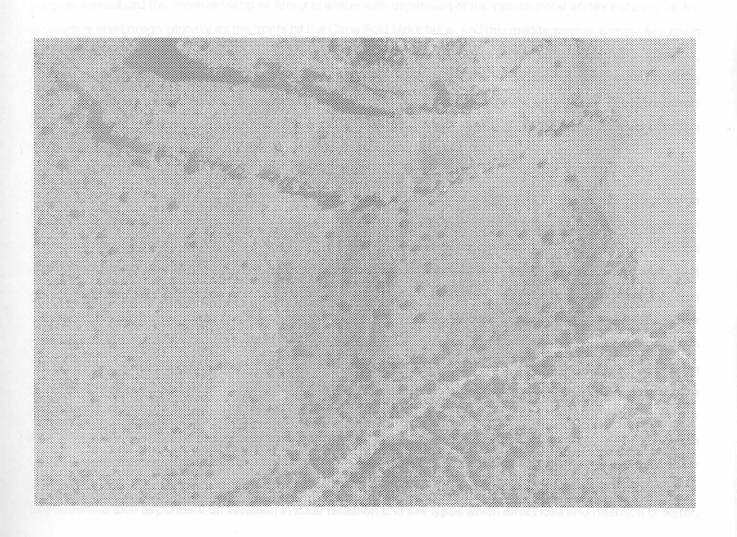
ENVIRONMENT AND THE REFUGE RESOURCE



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CHAPTER 2

STUDY ENVIRONMENT

Karoo

To the north and south of the equatorial belt, Africa has always been a drought-ridden continent (Kingdon 1990). The south-west regions of Africa, encompassing Namibia, half of Botswana and the Cape Province of South Africa, are especially starved of moisture because the Benguela current, which runs north along the west coast drawing water from Antarctica and from the ocean depths, is too cold for extensive evaporation. Cyclonic weather fronts from Antarctica bombard the south-west tip of Africa in winter with expansion of the circum-polar vortex but most of this moisture is shed orographically as the fronts hit the Cape Fold Mountains, and this mediterranean climate has given rise to the richest and smallest floristic kingdom in the world, the Fynbos (Hilton-Taylor & Le Roux 1989). Likewise, moist air emanating from the warm Indian ocean in the east is prevented from reaching the interior by the high peaks of the Drakensberg escarpment. Only rarely do the tropical, anticyclonic weather systems push far enough south to bring thunderstorms to the arid south-west in summer. This dry corner of Africa, the Namib-Karoo, has become a centre of endemism for many arid-adapted plants and animals (Kingdon 1990).

The name 'Karoo' derives from 'Karu', a Khoisan word translated as 'the place of great dryness'. Traditionally, Karoo referred to the arid interior of the Cape Province, an area of some 427000km² characterised by its eroded landscape of koppies (inselbergs) and flat-topped mountains and by its thin covering of small shrubs. Ecologists now use the word karoo to describe this characteristic dwarf shrubland as a veld (vegetation) type which extends to the west coast of the Cape (Namaqualand) and northward, encompassing most of southern Namibia, but narrowing as it becomes sandwiched by the truly arid Namib desert along the west and the moister arid savannah along the east, to disappear near the coast in southern Angola (Fig. 3). The total extent of karoo veld in southern Africa probably exceeds 700000km². Most areas supporting karoo veld receive less than 250mm rain per annum (Cowling 1986), and can be described as semi-arid or arid. However, annual rainfall varies along a gradient from less than 100mm in the western extremes to over 500mm in the eastern limits (Venter, Mocke & de Jager 1986). While the distinction between the Karoo and the Namib desert is fairly accepted, the borders between karoo veld and the moister arid savannah in the southern Kalahari, and the moister grasslands in the southern Orange Free State are changeable and still under debate (Acocks 1953; Werger 1986; Hoffman & Cowling 1987, 1990a). Classification of these regions as arid or semi-arid deserts is also dependent on variation in solar radiation and soil types which affect loss and retention of water.

Karoo veld covers 35% of South Africa but receives only 10% of the nation's rainfall. This area suffers drought (as defined as <60% mean annual rainfall) for 30-50% of the time, and in some areas droughts may last longer than three years (Roux & Opperman 1986). Aridity is probably the major factor which enables dwarf shrubs to dominate the grass component in karoo flora, but weak soils, herbivory and the absence of fires may also be involved. Dwarf shrubs or chamaephytes in karoo veld are either non-succulent (especially *Asteraceae* e.g.. *Pentzia incana*, *Eriocephalus ericoides*) or succulent (especially *Mesembryanthemaceae* e.g.. *Ruschia* spp.). These shrubs are usually thinly spread and rarely project more than 30cm above or below ground level (Hoffman & Cowling 1987). Although

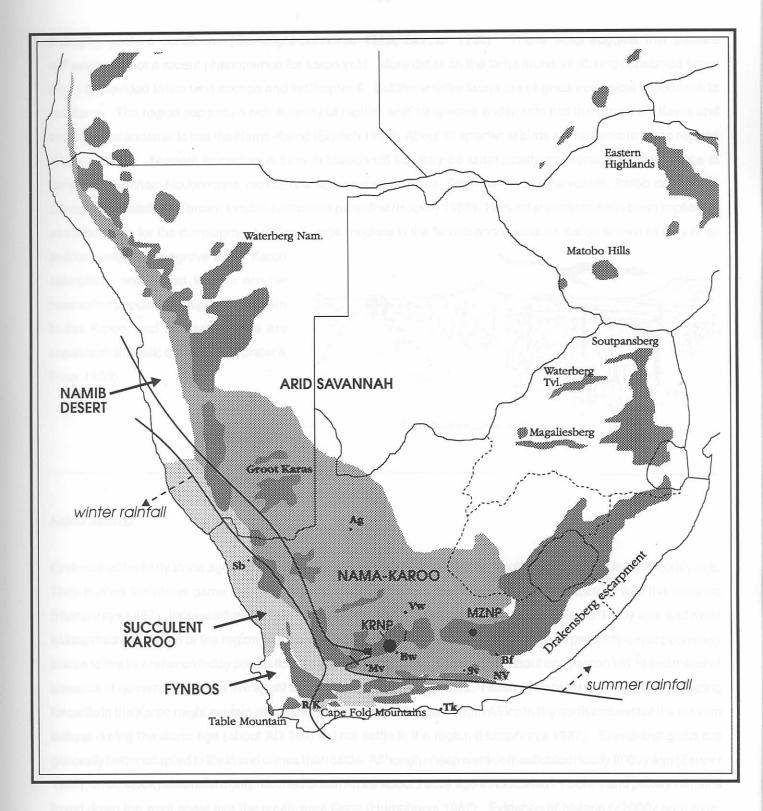


Figure 3. Distribution of mountains (dark grey), Nama-Karoo (grey) and Succulent Karoo (pale grey) in southern Africa (from Anon 1970; Cowling 1986; Kingdon 1990; and Lovegrove 1993). Summer rainfall regions are separated from winter rainfall regions by continuous lines (after Werger 1986). The belt in between these receives rain at any time of the year. From hashed lines representing provincial boundaries within South Africa (as at 1993), it is evident that karoo veld occupies most of the Cape Province and some of the southern Orange Free State. Mountain ranges referred to in this thesis are named in full. Place names are abbreviated. KEY: Sb Springbok (Namaqualand); Ag Augrabies Falls National Park; Vw Victoria West; Bw Beaufort West; Mv Merweville; Sv Steytlerville; Bf Bedford; Tk Tsitsikama; NV Noorsveld; RK Robertson Karoo; MZNP Mountain Zebra National Park; KRNP Karoo National Park. The KRNP lies in the Nuweveldberg which links with the Roggeveldberg to the west and with the Sneeu/Winterberg to the east. These contiguous ranges are separated by dark lines. The Sneeu/Winterberg link to the southern Drakensberg to the east of the MZNP. A dark rectangle denotes the study area of Boshoff & Palmer (1988) 80km west of the KRNP (see text).

changing pasture conditions (Conwright-Schreiner 1925; Skinner 1993). These treks suggest that pasture exhaustion is not a recent phenomenon for karoo veld. More detail on the large fauna inhabiting conserved karoo areas is provided in the next section and in Chapter 5. But the smaller fauna are of great ecological importance to the Karoo. The region supports a rich diversity of reptiles with 19 species endemic to just the Succulent Karoo and nine species endemic to just the Nama-Karoo (Branch 1988). About 19 species of birds are endemic to karoo regions (Huntley 1984). Nutrient re-cycling is slow in karoo veld but may be dramatically accelerated by the actions of harvester termites Hodotermes mossambicus, snouted termites Trinervitermes trinervoides, karoo caterpillars Loxostega frustalis and brown locusts Locustana pardaline (Hockey 1988). Harvester termites have been implicated as responsible for the development of rich floristic mounds in the Namib and Succulent Karoo known as fairy rings

and 'heuweltijes' (Lovegrove 1993). Karoo caterpillars and brown locusts are renowned for population irruptions after rain in the Karoo, and all four species are capable of dramatic defoliation (Vorster & Roux 1983).



Black harrier Circus maurus

Karoo farming

Evidence of the early stone age indicates that Karoo regions were peopled by 'hunter-gatherers' at least 200000y ago. They hunted the plains game but probably also relied on some staple food plants, and moved with the seasons (Humphreys 1987). Increased aridity may have caused some depopulation of the Cape Karoo 9000y ago, and more widespread population of the region probably only began 4000y ago. Karoo regions have probably never been easy places to live in, and even today population density in this part of the Cape is low (about one person km⁻²) and massive amounts of government funds are spent in drought aid to karoo farmers. Harsh climate for crops and poor grazing for cattle in the Karoo might explain why Bantu farmers who colonised South Africa to the north and east of the 400mm isohyet during the stone age (about AD 200) did not settle in the region (Humphreys 1987). Sheep and goats are generally better adapted to life in arid climes than cattle. Although sheep were domesticated nearly 9000y ago (Zeuner 1963), small stock pastoralism only reached South Africa about 2000y ago as indicated by bones and pottery remains found down the west coast into the south-west Cape (Humphreys 1987). Evidence of historic (<2000y ago) overgrazing has been found in one isolated locality (Sampson 1985), but extensive (sedentary) herding of small stock on karoo veld probably only began with the movements of the Europeans and Khoi-khoi from the south-west Cape in the late 1700's. Undoubtedly the single most important factor which enabled this exploitation of karoo veld was the ability of these farmers to tap into the extensive underground water systems which lie in sandstone joints and along dolerite dykes not far below most of the karoo surface, and thus to supply drinking water to their domestic animals in otherwise uninhabitable areas. Most boreholes in the Karoo are driven by regular winds and require only maintenance. Their water supply may vary from 1 lsec⁻¹ in the arid west to 4 lsec⁻¹ in the moister eastern regions (Hodgson 1986).

The plains game that roamed the Karoo were hunted by the European immigrants on an unprecedented scale for sport and to clear the way for the livestock. Quaggas were initially very numerous (Harris 1840), and probably largely endemic to karoo regions. But the hunting led to the total extermination of quaggas and also bluebuck *Hippotragus leucophaeus* (south of the Cape Fold Mountains), and devastation of most other game populations. Today, only springbok (96% farms) and to a lesser extent blesbok *Damaliscus dorcas phillipsi* (22% farms) are seen regularly on karoo farms, and these usually in small numbers (Jooste 1983). The larger predators were also killed off. Black-back jackals *Canis mesomelas* survived in most karoo areas, and in a massive campaign to control this predator and to enable more intensive livestock management, the entire Cape Karoo was fenced off into paddocks by the 1920's (Pringle & Pringle 1979), and this has been maintained at enormous expense (Siegfried *in litt.*). These fences prevented the movements of any surviving plains game. Fencing was completed at a later stage (mid 1960's) in Namibia (Lensing & Joubert 1976; Lensing 1979).

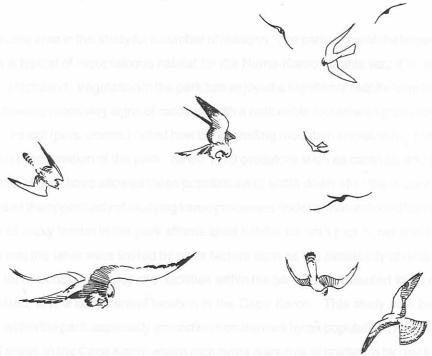
The breed of small livestock most favoured by the European farmers was the arid-adapted, wool-producing Merino sheep, and by 1820 substantial numbers of this animal could be found throughout the Cape Karoo (Van der Merwe 1938). Growth of the karoo flock was slowed by the Anglo-Boer war, but by 1933 it reached its zenith of 40,3 million woolled sheep. The long-term 'safe' carrying capacity of the Cape Karoo for small livestock has been estimated at 7 - 7,5m animals, and since the wool boom numbers have been reduced to just under 10 million sheep Ovis aries and goats Capra hircus (Roux et al. 1981). The Cape Karoo flock now comprises 4745363 woolled sheep, 3449110 mutton sheep, 959803 Angora goats and 354996 Boer goats (Department of Agriculture, Middelberg, in litt.). Most of these livestock are maintained under open-range conditions and are heavily reliant on the farmer for protection from disease and predators, for water and for feed during drought. Goats and meat-producing sheep are favoured in arid regions or in difficult terrain (thickets and rocky areas). Only 8% of the Karoo (the endangered riverine habitat) has been suitable for cultivation (Roux et al. 1981). Karoo livestock provide 36% of the wool, 48% of the mutton, 60% of the mohair and 60% of the goat meat produced in South Africa (one of the six largest wool-producing nations in the world). Karoo veld, on which the livestock rely, is thus an important national resource in South Africa. Through growth of the human population and a tradition of subdividing land between sons, farms in the Cape Karoo have become progressively smaller. There are now 8972 farms in the Cape Karoo, owned by 6200 farmers (Department of Agriculture, Middelberg, in litt.). The average karoo farmer thus manages about 4700ha and just over 1500 small livestock. These produce about 820 lambs p.a. during one or two distinct lambing seasons which are geared to maximise production (Roux et al. 1981). In Beaufort West most lambs (65%) are born in March. It has been calculated that karoo farms need to support 1200 small livestock to be economically viable, and many fall well below this target.

The once wide variety of nomadic herbivores has been replaced by intensively-stocked monocultures of small livestock with specialist feeding habits. Nearly 200y of this treatment has had a devastating effect on karoo soils and vegetation in most areas. Prolonged heavy grazing is considered to suppress shoot/root formation and flowering in karoo flora (Cowling 1986) which leads to depletion and thinning out of the vegetation, particularly those components which sheep find palatable (Vorster, Botha & Hobson 1983). Intense damage from grazing and trampling is found around water points on which sheep are highly dependent in the Karoo (Davies & Skinner 1986). Thinning of the already sparse vegetation layer has greatly accelerated rates of soil erosion (mainly sheet, gulley, splash and wind erosion). Experimental continuous heavy grazing for 25y caused depletion of the top 15cm of the orthic A horizon

in the top soil (Roux & Opperman 1986). Just removal of the top 1-5mm by wind erosion can kill seedlings (Roux 1960). It is estimated that rivers carry 32 million m³ of sediment from the Karoo each year (Midgley undated). Soil erosion has been described as the biggest environmental and agricultural problem in South Africa, and although 70% of Karoo farms have been planned to reduce erosion only a small minority of these farms implement the recommendations (Roux & Opperman 1986).

Where the dry compact B soil horizon is exposed by erosion, the more hardy brack grasses and less palatable shrubs take hold. Roux & Vorster (1983) contend that most of the Cape Karoo is in a third phase of desertification where unpalatable species are revegetating areas cleared of the palatable plants in a process of succession. Non-succulent chamaephytes are better suited for colonising bare ground and surviving droughts than grasses (unfortunately they afford less protection to the topsoil). Acocks (1953) was the first to document and predict the replacement of sweet grassveld by karoo shrubs in the eastern regions. He predicted that karoo veld was spreading eastward at a rate of 2-3km per annum and that it would encompass most of the Orange Free State by 2050. Hoffman & Cowling (1990a) have used historical photographs and vegetation analyses to largely refute these predictions. These authors (1987) argue that karoo shrubs appear not from a succession process but rather through 'exadapation' to drought conditions, and that the southern Orange Free State and the eastern Cape form a highly dynamic interface between grassveld and karoo veld. However these same authors have found positive evidence of desertification in the lower Sundays River Valley (Noorsveld) where areas of subtropical thicket are being ousted by karoo shrubs (Hoffman & Cowling 1990b), and there can be little doubt that heavy grazing has had a major influence on the vegetation within karoo regions. Besides soil planning, management measures taken to curb this degradation have been rotational grazing, stock reduction and diversification of stock with other livestock breeds and with game (Vorster et al. 1983; Davies 1985). Although conditions are much improved since the wool boom, vegetation changes in the Karoo are now very difficult or even impossible to reverse.

Human activities have led to a reduction in the quality of the vegetation and in the diversity of animals living in karoo regions. Besides destruction of the plains game and potential predators of livestock (details of the bounty system are provided in Chapter 11), farmers have also persecuted aardvarks Orycteropus afer for their habit of digging holes under jackal-proof fences and allegedly allowing predators access to flocks. Predator control operations have involved placing gin traps in such holes under fences and innumerable bat-eared foxes Otocyon megalotis. aardwolves Proteles cristatus and other potentially important insectivores have been killed in this way. Many farmers still place gin traps and strychnine bait in and around sheep carcasses to kill potential predators, but it has been estimated that these indiscriminate methods may kill 100 non-target animals for every jackal or caracal (Brown 1988a). Strychnine is still widely available to karoo farmers and it is estimated that only 15% is sold legitimately. Use of poison is almost certainly responsible for the disappearance of large scavenging raptors such as Cape vultures Gyps coprotheres, lappet-faced vultures Torgos tracheliotus, bateleurs Terathopius ecaudatus and most tawny eagles Aquila rapax from the Cape Karoo (Allan 1989), and from parts of Namibia (Brown 1988a, 1991). Another poison which has been used extensively in karoo regions (to control outbreaks of brown locusts Locustana pardaline) is benzene hexachloride (BHC). Vast quantities of this chemical were used in control operations in 1985/1986 costing approximately R48 million (Hockey 1988). Extremely high levels of BHC contamination were subsequently recorded in many insectivores (Erasmus pers. comm.). The net result of these destructive human activities in karoo regions has been the degradation and simplification of a once highly dynamic, diverse and somewhat vulnerable ecosystem. More simple ecosystems tend to be less stable (Simpson 1949). Removal or impedance of important components within the karoo system has been implicated in the aggravated irruptions of varied pest species which appear to be manifestations of this instability. Termite problems appeared to be aggravated on the farm Montana near Victoria West where heavy grazing and destruction of natural predators had occurred (pers. obs.). Destruction of vegetation resources by major outbreaks of karoo caterpillars *Loxostege frustalis*, has been linked to overgrazing and the spread of non-succulent chamaephytes (host plants, see Möhr 1982), and a reduction in natural predators may explain recent increase in the frequency of locust outbreaks (Hockey 1988). It is important that irruptions of rock hyrax should be viewed in this holistic perspective of change in karoo regions.



Lesser kestrels *Falco naumanni* catching brown locusts *Locustana pardaline* near Beaufort West (November 1989)

Karoo National Park

Despite the changes which are threatening the rich diversity of karoo biota only 1,2% of the Succulent Karoo and only 0,5% of the Nama-Karoo are currently protected within conserved areas (Hilton-Taylor & Le Roux 1989). Following a campaign by the South African Nature Foundation, the Karoo National Park (KRNP) was proclaimed in 1979 to protect an area of the Nama-Karoo. The park actually conserves a major buttress of the Nuweveld Mountains (Figs. 3 & 4) overlooking Beaufort West (32°21'S; 22°35'E). This mountain range forms the central, southern part of the African continental escarpment separating the Great Karoo from the Central Upper Karoo (Acocks 1953), and the buttress at Beaufort West also separates the Atlantic and Indian Ocean drainage systems. Mountains within the park rise to 920m above the plains and 1830m above sea level providing marked altitudinal zonation. Initially the park encompassed three farms: Stolshoek, Mountain View and Grootplaat. In 1983 another farm, Doringhoek, was included increasing the total extent of the conserved area to 330km²; and in 1989 (during this study) a fifth farm,

Sandrivier, was purchased to extend the park in a westerly direction. Inclusion of these farms within the park marked the removal of domestic livestock and cessation of predator control programmes. Certain indigenous wild ungulates have been re-introduced, but stocking rates only approach estimated carrying capacity on the plain 'Lammetjiesleegte' near Beaufort West. While the park embraces some of the most spectacular scenery to be found in the Karoo, the predominance of mountainous habitat is not strictly representative of karoo veld and there are plans afoot to expand the park further to the west to encompass more plains habitat. Some of the mountainous habitat in the east may be exchanged for this land and the area known as Grootplaat is currently under negotiation. All analyses in this study include Grootplaat and exclude Sandrivier as parts of the park (unless otherwise stated). Restcamps and tarmac roads have only recently (1988) been established in the park to provide public access.

The KRNP was chosen as the core area in this study for a number of reasons. The park is one of the largest conserved areas in the Cape Karoo and is typical of mountainous habitat for the Nama-Karoo. In this way it is representative of rocky habitats on most karoo farmland. Vegetation in the park has enjoyed a significant respite from heavy grazing by livestock and is currently showing promising signs of recovery with a noticeable increase in grass cover (Novellie & van Heerden pers. comm.). Fairall (pers. comm.) noted how bare, eroding mountain slopes in the park have been stabilised by grass cover since proclamation of the park. Since 1979 predators such as caracals and black eagles have been unmolested, and this should have allowed these populations to settle down after the disruptive influence of removals. So the park afforded the opportunity of studying karoo processes under as natural conditions as possible. Furthermore, the abundance of rocky terrain in the park affords ideal habitat for both rock hyrax and black eagles. and there was no suggestion that the latter were limited by other factors such as the availability of nest sites. There were other logistical reasons for this choice of study site: facilities within the park and in Beaufort West nearby; easy access to neighbouring farmland; and a fairly central location in the Cape Karoo. This study also benefited from previous research conducted within the park, especially groundwork on the rock hyrax population (Fairall 1991, in litt.). Attempts to find other 'control areas' in the Cape Karoo where rock hyrax were free of predation by black eagles were unsuccessful. Accurate determination of hyrax numbers is very labour-intensive (Chapter 4) so these efforts were confined to a core area within the park to be thorough. But livestock predation by black eagles was assessed from nest studies outside the park and from visits to farms over a wide area of the Cape Karoo (see Chapter 11).

A detailed map of the park and surrounding areas (separating mountain slopes from plateaus and plains) can be found in Appendix 1. This map also shows road access from Beaufort West and a 1km numbered grid which has been used by other researchers in the park. Two substantial dolerite sills are exposed in the KRNP as a lower and upper escarpment. The lower escarpment at 310m above the plains has cliffs of up to 55m high and has become highly convoluted due to river incision. The upper escarpment at 920m above the plains has cliffs of up to 120m high and faces predominantly south. The rock on these cliffs crumbles easily and is not well suited for climbing. These sills are major features in the park and separate the topography into five major habitats: bottom plains, lower slopes, middle plateau, upper slopes and upper plateau (Fig. 4). For a cross-section through the underlying geology see Figure 5. The dramatic relief of the park is shown by a TIN model created from 100' contour lines off 1:50000 topocadastral maps using ARCINFO (Fig. 6). These figures are derived from a geographical information system of the habitats within the park which is fully explained in the next chapter.

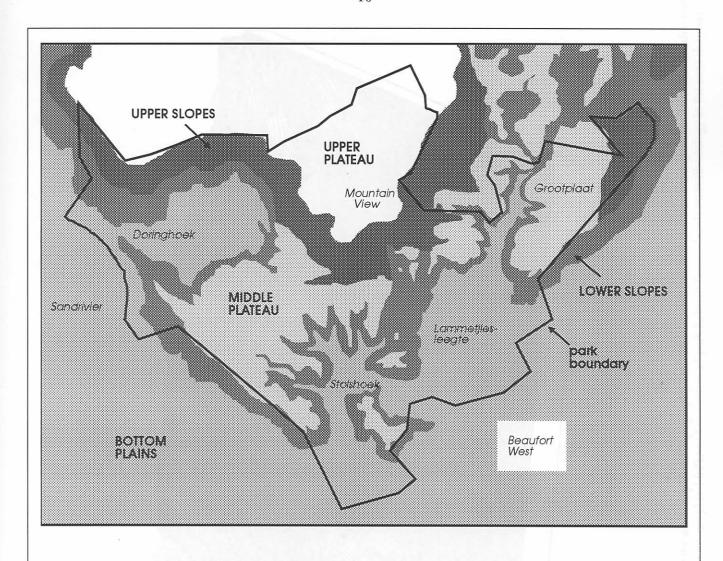


Figure 4. The Karoo National Park (KRNP) at Beaufort West and the major topographical habitats that it encompasses.

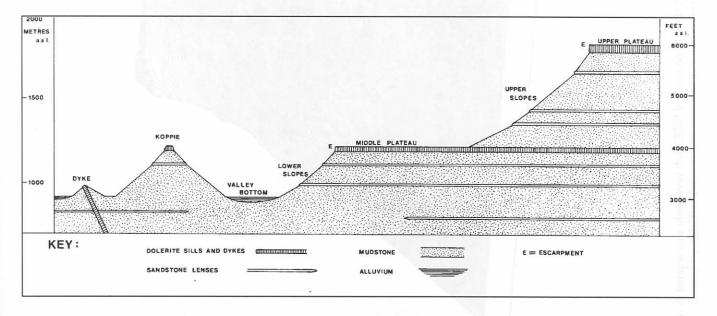


Figure 5. Cross-section through the Nuweveldberg in the KRNP (south to left; north to right) showing the underlying geology responsible for the topography.

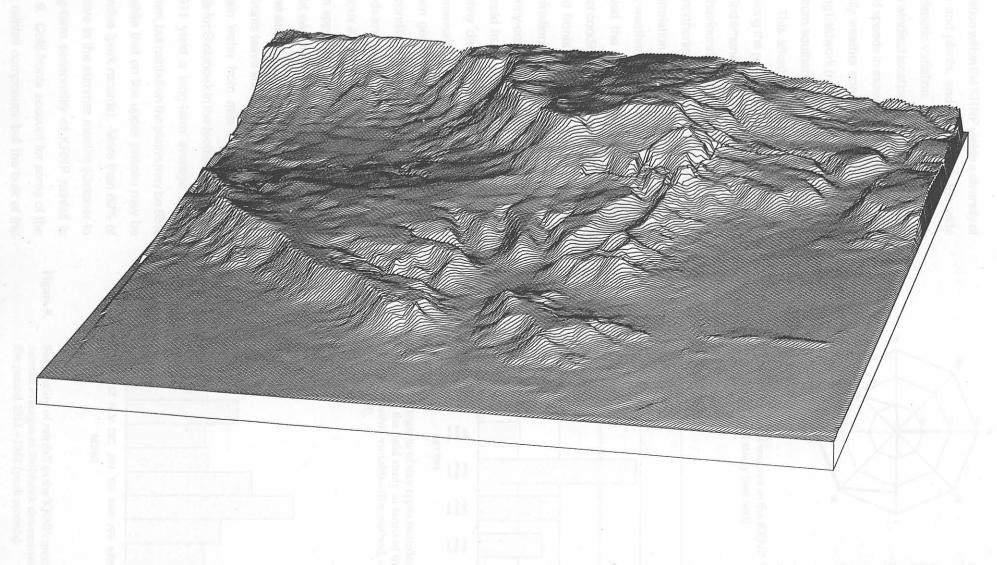


Fig. 6. A perspective view over the KRNP looking north-west clearly showing the eroded, plateau topography and the river incision into the lower escarpment. This 'TIN-model' was created by ARCINFO from 100' contour lines which were digitised for a geographical information system of park habitats (more details on methodology in the next chapter).

Altitudinal zonation within the KRNP yields a diversity of micro-habitats and plants, and encourages the wide and sudden climatic variation. Beaufort West is renowned as the windiest location in South Africa (Milford 1987) and wind speeds in excess of 170kph have been recorded. Daily weather conditions in the park were analysed during fieldwork (n=1250d) and revealed prevailing winds from southerly and south-easterly directions (Fig. 7). This affords ideal flying conditions for black eagles along the predominantly south-facing escarpments. Wind emanated mainly from the west or the east during behavioural observations (n=80d), with few southerlies or northerlies. Westerlies were significantly stronger. Correlation analyses were performed on important daily weather variables (full details in Chapter 8) and revealed the following: windy-sunny-warm (typical summer conditions) and windy/still-cloudy-cool (typical of cold fronts) were the most frequent daily weather combinations accounting for 65% days (see Fig. 8); still-sunny-cool days, which occur just after the passing of a cold front, were the least frequent day types; hot, sunny days were seldom windless; high atmospheric pressure was associated with cool, overcast days when gentle easterly winds brought high humidity; still conditions were much more prevalent in winter, but winds are generally strongest in the Karoo in September (Roux & Opperman 1986). Temperatures in the park can approach 45°C on the low-lying plains in summer, but can plummet to -15°C on the upper plateau with the arrival of a cold front in winter. Some of these cold fronts leave snow on the mountain tops. which also gain water from mist in the mornings. Rainfall records for Stolshoek in the foothills of the park kept since 1911 yield a long-term average annual rainfall of 270mm, but rainfall on the plains may be 85% of this value while that on the upper plateau may be 140% of this value (park records). More than 60% of these rains arrive in the summer months (October to March). Long-term seasonality of KRNP rainfall is shown in Fig. 9. Cold fronts account for some of the early summer rainfall component, but the bulk of the

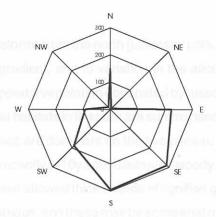


Figure 7. Prevailing wind sources in the KRNP during the field study (see text)

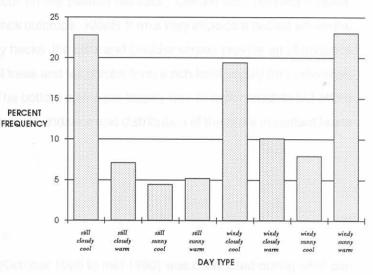


Figure 8. Frequency histogram of day types recorded in the KRNP during the field study in terms of three important weather variables (for method, see text and Chapter 8).

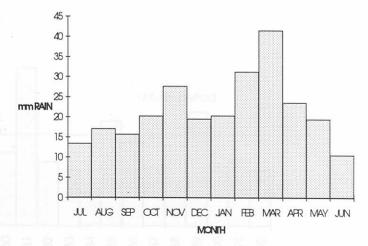


Figure 9. Seasonality of rainfall in the KRNP: monthly rainfall averages at Stolshoek determined for the period 1911 - 1982 (park records).

rain received is brought in late summer by anticyclonic tropical thunderstorms from the north (Lindesay pers. comm.). Vegetation cover in the park corresponds to the orographic rainfall gradient, and to variation in the alkaline soils (Webber 1989). High altitude conditions on the upper plateau have trapped a vegetation dominated by tussock grass and renosterbos. Full ecological descriptions of the major topographical habitats in the park are summarised in Table 1 to save lengthy description, and may be referred to for detail. Grasses are dominant on the two plateau habitats; on the sunny, northern aspects of the lower slopes; and where fire has recently (<10y ago) destroyed woody material. Good rainfall, low grazing pressure and the absence or rarity of fires have allowed thick swards of lignified grass and woody material to accumulate in some parts of the middle and upper plateaus, and these may be somewhat moribund. Riparian thickets comprising an overstory of subtropical trees and shrubs trace the courses of the episodic rivers. Rocky habitats are fully treated in the next chapter, but some details are given in Table 1. The majority of rocky habitats in the park are contained within the lower and upper slope macro-habitats (98% of screes; 84% linear outcrops), but substantial surface outcrops of the dolerite sills do occur on the plateau habitats. Certain flora (Grewia robusta, Hermannia burkei) are found in close association with rock outcrops. Kloofs form a very important habitat where the lower slopes and escarpment cliffs converge into valley necks: the cliffs and boulder screes provide an abundance of rock crevices; while a dense overstory of subtropical trees and tall shrubs form a rich food supply for herbivores. Kloofs may also provide important sources of water. The bottom plains are largely free of rocky habitats but afford good access to water courses and associated vegetation. Abundance and distribution of the more important fauna in the park are treated in Chapter 5.

The period of study

As mentioned earlier, the field research for this study (October 1986 to mid 1990) was conducted during what can be considered a period of recovery for karoo biota following a devastating drought in the early 1980's (Tyson 1983). KRNP rainfall data show that this drought was preceded by years of excellent rainfall prior to 1978 (Fig. 10), and this is in agreement with Tyson's (1986) 18y oscillation in the summer rainfall regions. The 3-4y rainfall pattern reported for Beaufort West is also apparent in these data. Stolshoek rainfall during the study period was just above the long-

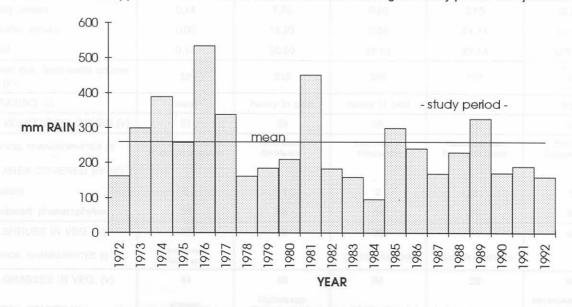


Figure 10. Annual rainfall (January to December) recorded at Stolshoek between 1972 and 1992.

TABLE 1 ECOLOGICAL PHYSIOGNOMY OF THE MAJOR TOPOGRAPHICAL HABITATS WITHIN THE KAROO NATIONAL PARK

Sources: i - image analyser; ii - De Graaf, Robinson, van der Walt, Bryden & van der Hoven (1979); iii - park records; iv - Webber (1989); v - line transect sampling (Chapter 5); vi - ARCINFO geographical information system of the park (see Chapter 3). Statistical comparisons of habitat parameters (line-transect data) are presented on p. 69.

| ATTRIBUTE (& source) | BOTTOM PLAINS | LOWER SLOPES | MIDDLE PLATEAU | UPPER SLOPES | UPPER PLATEAU |
|---|---------------------------------------|---|---------------------------|-------------------------------------|--|
| EXTENT km2 (i) | 117,1 | 80,3 | 62,3 | 42,1 | 33,8 |
| ALTITUDE m a.s.l. (ii) | 910 | | 1220 | | 1830 |
| RELATIVE CLIMATE (ii) | arid hot | intermediate | intermediate | wet cool | wet cold |
| MIST, FROST & SNOW (ii) | rare | rare | rare | occasional | occasional |
| ANNUAL RAINFALL mm (iii) | 220 | 260 | intermediate | >350 | 360 |
| SLOPE ANGLE (deg.) (i) | 0 | 19 | 0 | 24 | 0 |
| ASPECTS (i) | - | convoluted | _ | southerly | - |
| KLOOFS (i) | 0 | 10% area | o | 0 | 0 |
| SOILS (iv) | deep, light, sandy, loamy | shallow, stony (Swartland) | deep in places | shallow, stony | dark, moist |
| % AREA COVERED BY (v): | | | | | |
| bare ground | 90 | 1 | 13 | 0 | 20 |
| small, loose rocks | 10 | 55 | 70 | 56 | 54 |
| large, loose rocks | 0 | 28 | 5 | 39 | 13 |
| Mean dist. from outcrop m (v) | >1000 | 32 | 106 | 18 | 42 |
| DENSITY OF LINEAR ROCK OUTCROPS km/km2 (vi): | | | | | |
| dolerite escarpment | 0,00 | 1,70 | 0,24 | 0,96 | (0,24) |
| sandstone lenses | 0,34 | 2,98 | 0,09 | 2,53 | (0,09) |
| dolerite dykes | 0,06 | 0,23 | 0,05 | 0,23 | (0,05) |
| other | 0,02 | 0,09 | 0,01 | 0,00 | (0,01) |
| total | 0,42 | 5,00 | 0,39 | 3,73 | (0,39) |
| DENSITY OF 2D ROCK OUTCROPS ha/km2 (vi): | | | | | |
| surface outcrops | 0,00 | 0,04 | 27,63 | 0,03 | (27,63) |
| koppies | 0,00 | 0,52 | 0,35 | 0,00 | (0,35) |
| rocky screes | 0,14 | 7,75 | 0,60 | 2,65 | (0,60) |
| boulder screes | 0,00 | 18,29 | 0,04 | 24,44 | (0,04) |
| total | 0,14 | 26,60 | 28,62 | 27,14 | (28,62) |
| Mean dist. from water course m (v): | 58 | 313 | 395 | 157 | 189 |
| GRAZING (ii) | heavy | heavy in past | heavy in past | light | light |
| % VEGETATION COVER (v) | 31 | 53 | 65 | 70 | 78 |
| TYPICAL PHANEROPHYTES (ii) | Lycium oxycladum Rhigozum obavatum | Rhus lucida; Grewia spp. | Elytropappus rhinocerotis | Asparagus spp.; Hermannia burkei | E. rhinocerotis; Euryops annae |
| % AREA COVERED BY (v): | Day Ford | 10000 700 | | | |
| thickets | Parer 5 Calling | 1989; 11 to retur | 2 . | 8 | 5 |
| scattered phanerophytes | 30 | 86 | 84 | 70 | 30 |
| % SHRUBS IN VEG. (v): | 56 | 52 | 36 | 74 | 40 |
| TYPICAL CHAMAEPHYTES (ii) | Pentzia spp.; Felicia spp. | mikud- | Chrysocoma ciliata | (macchia vegetation) | |
| % GRASSES IN VEG. (v): | 44 | 48 | 64 | 26 | 60 |
| TYPICAL GRASSES (ii): | annuals; perrenials v. scarce | Digitaria spp. Themeda trianda (esp. northerly aspects) | Aristida diffusa | few | Merxmuellera distich (dominant tussock grass) |
| ALOES (ii): | Aloe claviflora | | A. broomii/ microstigma | A. striatula | The state of the s |

term average. After reasonably good rains in 1985 and 1986 which broke the drought, conditions were relatively dry again for two consecutive summers, but became wetter during 1989, culminating in a bumper season of early summer rainfall towards the end of 1989 (Fig. 11). Beaufort West rainfall in November 1989 was the highest ever recorded for that month. This was a good rainfall event for most of the Karoo. Lesser kestrels *Falco naumanni* and wattled starlings *Creatophora cinerea* gathered in their thousands around Beaufort West at this time to feed on the locust swarms. This event was not followed up by good rains the following summer, and very dry conditions prevailed at the end of the field study. A chronological plan of the research is presented in Fig. 12 for reference purposes.

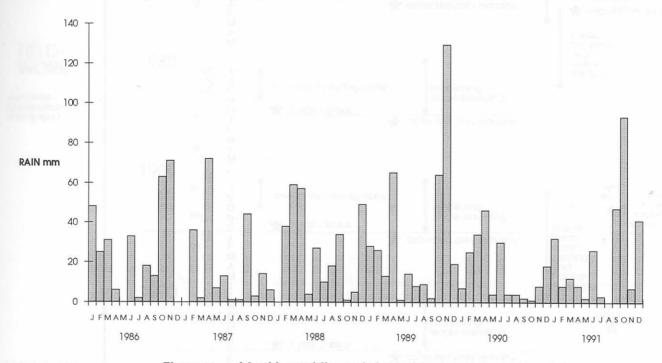


Figure 11. Monthly rainfall recorded at Stolshoek over the study period.

Previous, relevant research

Although black eagles had not been researched in the KRNP prior to this study, Fairall (1991, in litt.) and workers had done some important monitoring of the hyrax population. Counts at two colonies suggested a four-fold decline in numbers between 1981 and 1985 (Fig. 13). This was part of a more widespread population decline described earlier. The current study was thus carried out at a time when prey density was low and may have been well below the carrying capacity of the rocky environment for small herbivores. This has an important bearing on the study because numerous

field studies have indicated that predation pressure is generally greatest when prey are at low density (e.g. Pearson 1966, 1971; Fitzgerald 1977; Hansson 1984; Henttonen 1985; Newsome, Parer & Catling 1989; Sinclair, Olsen & Redhead 1990; Boutin 1992; Pech, Sinclair, Newsome & Catling 1992). Population data were also available for ungulates in the park (including small antelope) from annual helicopter censuses conducted by the National Parks Board since 1987

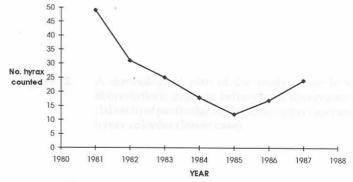
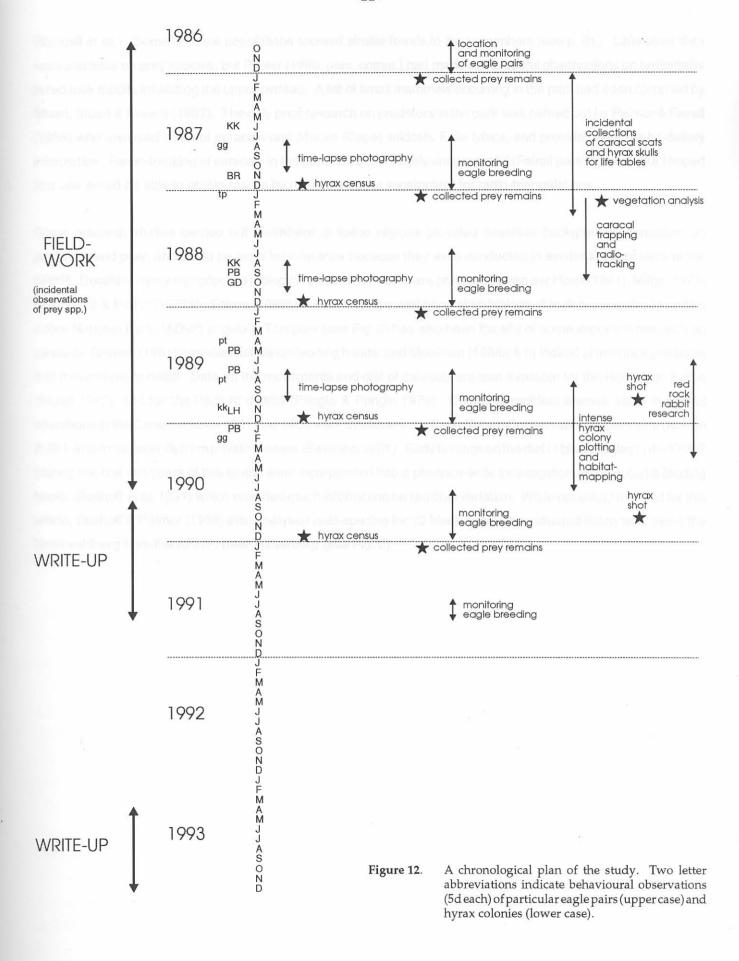


Figure 13. Number of hyrax counted at two colonies (combined) in the KRNP (prior to this study) by Fairall (in litt.)

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(Randall *in litt.*). Some of these populations showed similar trends to hyrax numbers (see p. 81). Little other data were available on prey species, but Pepler (1990; pers. comm.) had made some useful observations on territoriality in red rock rabbits inhabiting the upper plateau. A list of small mammals occurring in the park had been compiled by Stuart, Stuart & Braack (1987). The only prior research on predators in the park was carried out by Palmer & Fairall (1988) who analysed scats of caracals and African (Cape) wildcats *Felis lybica*, and provided very useful dietary information. Radio-tracking of caracals in the park had been largely unsuccessful (Fairall pers. comm.), but I hoped that one would be able to obtain results by using the upper escarpment for radio-triangulations.

Some research studies carried out elsewhere in karoo regions provided essential background information on predators and prey, and could be used for reference because they were conducted in similar environments to the KRNP. Details of hyrax reproductive biology in parts of the Karoo are provided by van der Horst (1941), Millar (1971) and Fourie & Perrin (1987a). Fourie (1983) looked at the general population biology of rock hyrax in the Mountain Zebra National Park (MZNP) in detail. This park (see Fig. 3) has also been the site of some important research on caracals: Grobler (1981) provided details on feeding habits; and Moolman (1986a & b) looked at livestock predation and movements in detail. Data on the movements and diet of caracals are also available for the Robertson Karoo (Stuart 1982), and for the Bedford district (Pringle & Pringle 1979). Details of problem animals killed in control operations in the Cape between 1931 and 1955 were available from Cape Nature Conservation Department (Norton *in litt.*), and more recently from private farmers (Swiegers *in litt.*). Early findings on the diet of black eagles in the KRNP (during the first two years of this study) were incorporated into a province-wide investigation of black eagle feeding habits (Boshoff *et al.* 1991) which provided much information on regional variation. While collecting material for this article, Boshoff & Palmer (1988) also analysed nest-spacing for 13 black eagle pairs situated 80km west along the Nuweveldberg from the KRNP, near Fraserberg (see Fig. 3).