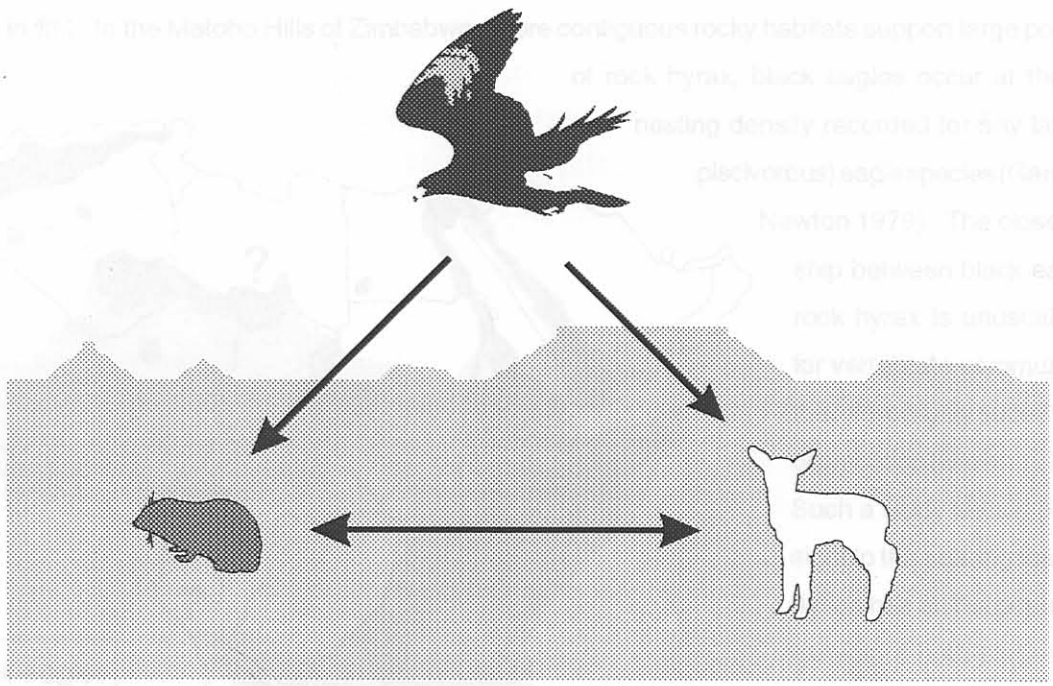
GENERAL INTRODUCTION

"'Whether or not vertebrate predators regulate their prey?' is currently debated among animal ecologists, as this question is important to issues of pest control, wildlife ecology and conservation of rare species."

(Korpimäki 1993)

"The preference for rock hyrax almost to the exclusion of other prey makes Verreaux's Eagle a very good subject for a close study of the predator-prey relationship. ..... It should be possible to ascertain the total range of a pair, the approximate number of hyrax in that range, and the effect of the eagles upon the hyrax population, with a degree of accuracy which would be elusive with most species of eagles."

(Leslie Brown 1970)



"The question of predation by various species of eagles on livestock, especially sheep, has been vigorously debated on several continents and has been a major concern in the management of both kinds of populations. An effective understanding of this often complex problem cannot be achieved in an atmosphere of bitterness and acrimony, and it is therefore essential that accurate information from research studies by disinterested parties be acquired wherever possible."

(Murphy 1976)

CHAPTER 1

INTRODUCTION AND GENERAL APPROACH

The mountains and koppies (inselbergs) of Africa can be inhospitable places to live. Small mammals inhabiting these areas are often exposed to extreme climatic variation and a wide array of predators. Furthermore, burrowing to escape these adversaries is not usually an option in the rugged, rocky terrain. Rock hyrax or 'dassies' (genus *Procavia* and *Heterohyrax*) solve these problems by taking refuge in rock crevices and interstices. They are well adapted to this lifestyle (Sale 1970a), and are often the most abundant small to medium-sized, mammalian herbivore encountered in the rocky parts of sub-Saharan Africa. The successful exploitation of these habitats by hyrax since perhaps the Oligocene (Sale 1970a), has permitted and possibly encouraged the evolution of a large avian predator, the black or 'Verreaux's' eagle *Aquila verreauxii*, which is reportedly highly prey-specific to rock hyrax (Brown 1952, 1970; Vernon 1965; Gargett 1977, 1990; Steyn 1982; Tarboton & Allan 1984). The current distribution of black eagles coincides with that of rock hyrax and mountains in most parts of Africa, but they are inexplicably absent from the Sahel (Fig. 1; Thiollay *in litt.*). In the Matobo Hills of Zimbabwe where contiguous rocky habitats support large populations of rock hyrax, black eagles occur at the highest nesting density recorded for any large (non-piscivorous) eagle species (Gargett 1975; Newton 1979). The close relationship between black eagles and rock hyrax is unusually simple for vertebrate communities and therefore highly suited to a study of predation (Brown 1970: p112). Such a study should provide insight to the bearing that this predation has on the population dynamics of both parties, as well as an indication of its evolutionary consequences in terms of form and behaviour. Yet, although both predator and prey have received considerable scientific attention separately (see Chapters 4 & 6 for more detail), their relationship to one another has not been looked at in any detail.

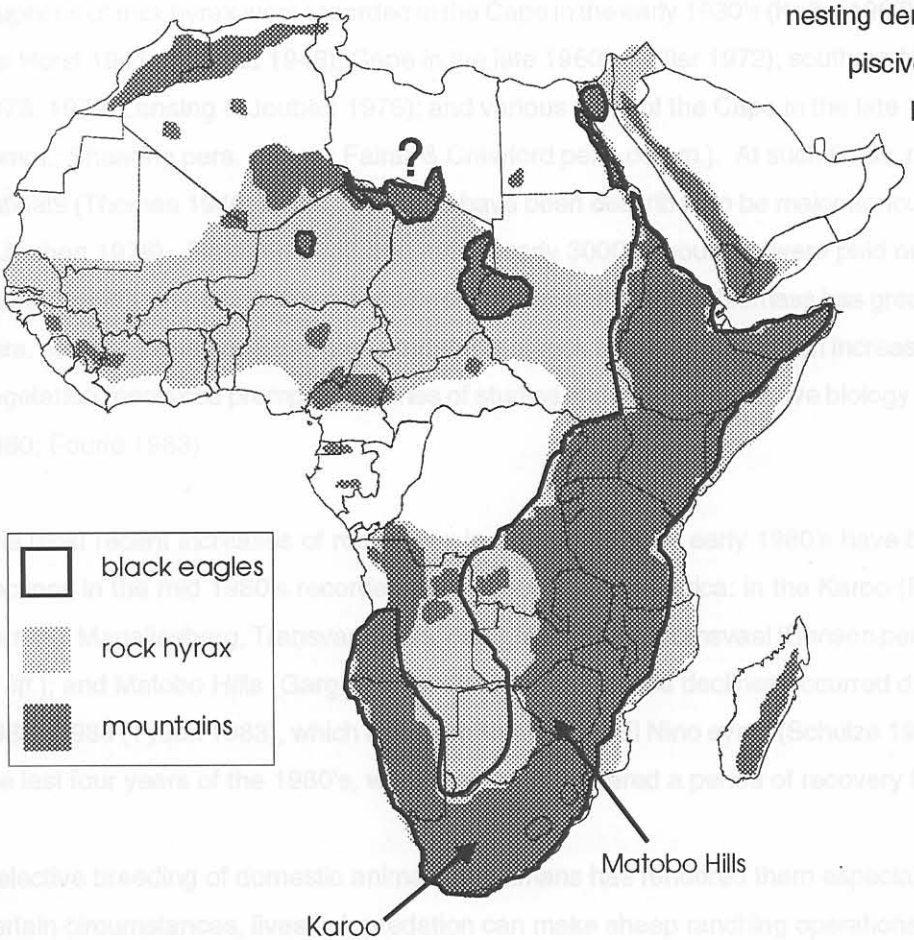


Figure 1. Distribution patterns of mountains (from Anon 1970), rock hyrax (after Bothma 1971; Kingdon 1971; Fourie 1983; Skinner & Smithers 1990) and black eagles (after Snow 1978 & Thiollay *in litt.*) in Africa.

In the Karoo of South Africa, relationships between rock hyrax (*Procavia capensis*) and their predators take on added significance because both are reputed to interfere with the farming of small livestock. Karoo veld or vegetation spans most of the interior of the Cape Province and extends into southern Namibia. It is maintained as a dwarf shrubland by the influence of a semi-arid climate. Annual rainfall is less than 250mm in most karoo regions (Cowling 1986). The extent of karoo veld in South Africa is 427000km^2, representing 23% of the nation's land area and 41% of the natural pasture (Roux, Vorster, Zeeman & Wentzel 1981; Vorster & Roux 1983). Since the advent of the European settlers, the principal land-use in the Karoo has been the open-range farming of small domestic livestock for the production of meat, wool and mohair. The Karoo currently supports a population of nearly ten million small livestock. Numbers have been reduced by 60% since the wool boom in the 1930's (Roux *et al.* 1981), but overgrazing continues to cause degradation of the vegetation resource (see Chapter 2). Livestock in the Karoo are not managed intensively and are at risk to any large predators in the region, particularly in the inaccessible, rocky areas. Koppies and flat-topped mountains comprise 15% of the eroded Karoo landscape (Roux *et al.*1981). Resistant 'caps' of sandstone or dolerite protect the underlying cones of soft mudstones, and provide ideal conditions for rock hyrax and their predators.

Normally hyrax graze and browse only in the rockiest habitats where sheep seldom venture, and competition for available forage on Namibian farmland has been described as negligible (Lensing 1979, 1982). However, major irruptions of rock hyrax were recorded in the Cape in the early 1930's (Kolbe 1967); Cape Midlands in the 1940's (van der Horst 1941; Thomas 1946); Cape in the late 1960's (Millar 1972); southern Namibia in the late 1960's (Lensing 1978, 1979; Lensing & Joubert 1976); and various parts of the Cape in the late 1970's / early 1980's (Wilmot pers. comm.; Shearing pers. comm.; Fairall & Crawford pers. comm.). At such times, rock hyrax may colonise non-rocky habitats (Thomas 1946; Kolbe 1967) and have been described to be major agricultural pests (Hanse 1962; Lensing & Joubert 1976). Between 1947 and 1957 nearly 300000 bounties were paid out for the destruction of rock hyrax (Norton *in litt.*). In certain areas it has been estimated that hyrax biomass has greatly exceeded that of sheep (Fairall pers. comm.). This observed high propensity of rock hyrax for population increase, and the threat that this posed to vegetation resources prompted a series of studies on hyrax reproductive biology in South Africa (Millar 1971; Steyn 1980; Fourie 1983).

The most recent increases of rock hyrax in the late 1970's / early 1980's have been followed by major population declines in the mid 1980's recorded throughout southern Africa: in the Karoo (Fairall 1991, *in litt*; Swiegers pers. comm;); Magaliesberg, Transvaal (pers. obs.); Waterberg, Transvaal (Benson pers. comm.); Drakensberg (Bowland *in litt.*); and Matobo Hills (Gargett & Banfield *in litt.*). These declines occurred during or after the 'great drought' of 1983 - 1984 (Tyson 1983), which has been linked to an El Nino event (Schulze 1983). The present field study spans the last four years of the 1980's, which can be considered a period of recovery for karoo biota.

Selective breeding of domestic animals by humans has rendered them especially vulnerable to predators. Under certain circumstances, livestock predation can make sheep ranching operations untenable (e.g. O'Gara, Brawley, Munoz & Henne 1983). Many karoo farmers believe that black eagles kill small livestock, especially juveniles. This belief is based mostly on hearsay accounts and traditional notions (pers. obs.). Brown (1975) argued that diet studies have largely exonerated the bird. But more recent investigations in the Cape Province have confirmed that domestic

lamb remains are indeed found in varying amounts at black eagle nest sites (Boshoff, Palmer, Avery, Davies & Jarvis 1991). However, nest-based diet studies do not give a good indication of the problem (Matchett & O'Gara 1987), and the real extent of livestock predation by black eagles in the Karoo has not been properly researched.

Despite this, persecution of eagles by farmers in the Karoo has been very intense. Five thousand bounties were paid out for the destruction of eagles in the Cape Province between 1930 and 1955 (Boshoff & Vernon 1980). This represents a kill rate of three eagles 10000km^{-2} y^{-1}, and may be underestimated. In the 1960's farmers in the Philipstown district claimed a kill rate of 20 eagles (mostly martial eagles *Polemaetos bellicosus*) 10000km^{-2} y^{-1}; while farmers in the Laingsburg district claimed a kill rate of 166 eagles (mostly black eagles) 10000km^{-2} y^{-1} (Siegfried 1963a). The wedge-tailed eagle *Aquila audax* in Australia was once described as the most heavily persecuted large raptor (Brown, L.H. 1976: p195). Over a 38y period in western Australia, approximately 18 wedge-tailed eagles were killed 10000km^{-2} y^{-1}, and it was thought that this may have caused population declines in unstable areas (Ridpath & Brooker 1986). Large eagles are long-lived and have a relatively low reproductive output, so it is very likely that such persecution by humans has contributed to the world-wide decline in these birds (Brown 1976; Newton 1979). The extremely high kill rate claimed for black eagles in Laingsburg is nearly twice the expected annual production of juveniles for the population in that district. Such areas would have acted as a sink for the Cape eagle population, and it seems likely that these levels of persecution would have caused population declines in large areas of the Cape and the Karoo in the past.

Naturalists have argued that the destruction of predators and the irruptions of rock hyrax are linked. Rock hyrax are natural prey for a variety of predators that have been killed in large numbers in control operations in the Karoo, especially caracals *Felis caracal* and black eagles. Caracals can be described as generalist predators: they take a wide variety of prey and are sufficiently powerful to pose a serious threat to adult sheep and goats (Pringle & Pringle 1980; Moolman 1986a, 1986b). A total of 26220 caracals were killed in the Cape Province between 1931 and 1943 (Moolman 1986a). Control operations continue in earnest but caracals remain the major 'problem animal' in this province (Stuart 1981). In the eastern Karoo, where black eagles may be nest-site limited, they are considered to be the major hyrax predator and their relationship to this prey has been fairly extensively researched and modelled mathematically (Grobler 1981; Fourie 1983; Swart, Perrin, Hearne & Fourie 1986). It is believed by some that the destruction of black eagles, caracals and other predators has led directly to the population irruptions of the fecund rock hyrax and consequent damage to the vegetation resources (Thomas 1946; Kolbe 1967; Rubidge in Kolbe 1983). The coincidence of major hyrax irruptions with the completion of jackal-proof fencing and the onset of effective predator control in both the Karoo in the early 1930's (Pringle & Pringle 1979; Rubidge in Kolbe 1983) and in Namibia in the late 1960's (Lensing & Joubert 1976) provides circumstantial evidence in favour of this hypothesis.

I became personally interested in this topic when I visited the farm Montana near Victoria West in the Karoo in 1984. Predator control had been very intense on this farm, with as many as 78 caracals killed in the previous six years. The farm appeared to be over-run with rock hyrax which were to be seen in large numbers, well away from rocky habitats and apparently very vulnerable. The farmer showed me thousands of hyrax skins from animals that he had shot but this apparently had not been sufficient to prevent a major irruption. By August 1984 the grazing resources had deteriorated to such an extent that the farmer was forced to move his livestock to a farm near Britstown. Subsequently

most of the hyrax disappeared (in synchrony with population declines elsewhere) and the farmer brought his livestock back to Montana six months later, after the veld had received rainfall.

A link between this irruption of rock hyrax and the intensive predator control campaign seemed obvious at the time. But traditional notions about 'the balance of nature' have been increasingly displaced by the observation of unpredictable or chaotic ecosystem behaviour (May 1989), and the long-lasting debate about whether predators actually 'control' their prey or not is far from resolved (see review in Chapter 12). Many ecologists still follow Errington's (1946, 1963) belief that predators merely remove a doomed surplus of their prey, and Siegfried (1963a) stated "In many cases, the value of eagles, as a means of combating and controlling the dassie (hyrax) plague has been accorded exaggerated importance". I felt that this issue would be worthy of detailed investigation. The relationships between rock hyrax, black eagles and domestic livestock in the Karoo are summarised in Figure 2:

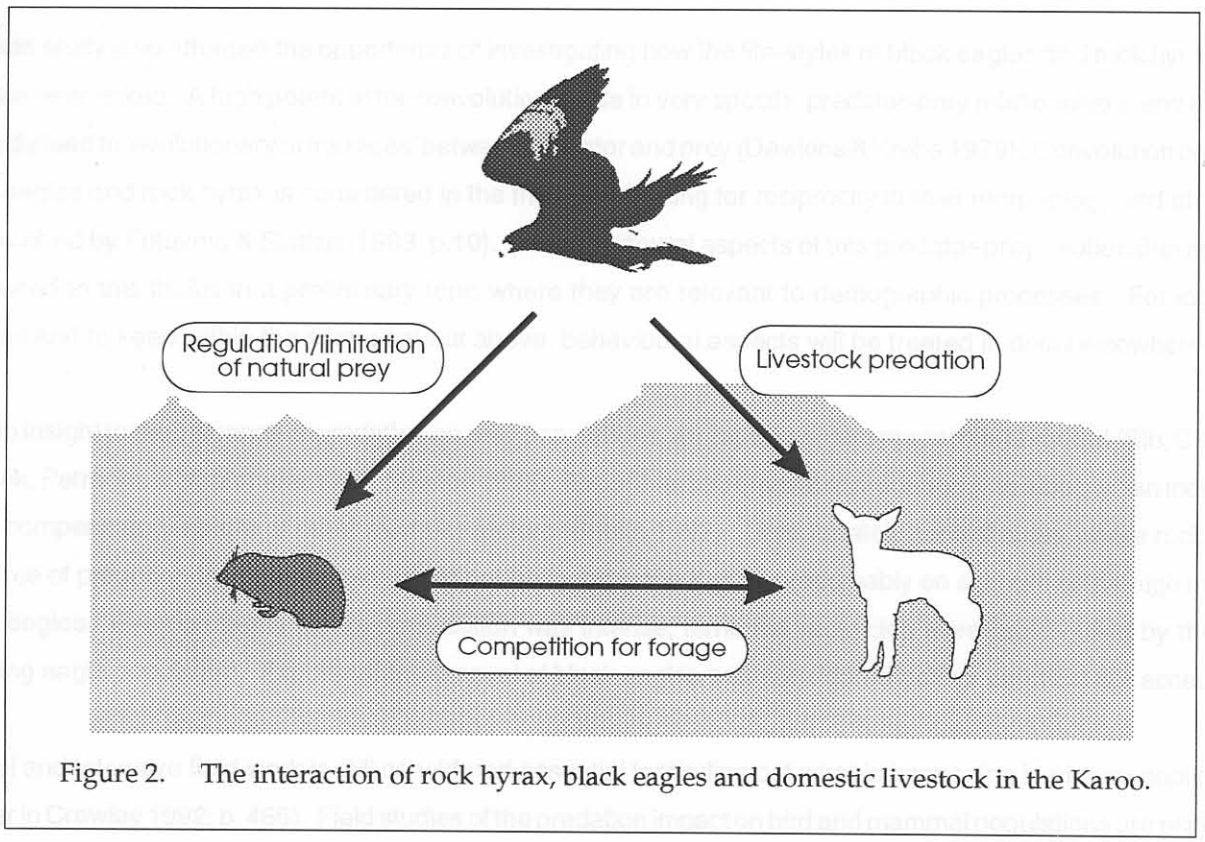


Figure 2. The interaction of rock hyrax, black eagles and domestic livestock in the Karoo.

By seeking an understanding of predator-prey relationships within this system, I attempt to resolve two principal controversies in this thesis:

1. **do predators such as black eagles limit or regulate rock hyrax populations in the Karoo?**
   (and, can it be inferred that hyrax irruptions were caused by predator control?)

2. **do eagles kill domestic livestock in the Karoo?**
   (if so, to what extent does this occur, under what circumstances, and how can it be avoided or minimised)

This study of a rather unique vertebrate predator-prey system was largely intended as an academic contribution in the field of population biology. Even if predation proved unimportant as a factor affecting hyrax population change, it was hoped that this study would still shed some light on other factors responsible for the obvious increase and decline phases that so characterise rock hyrax populations in the Karoo. By necessity, much of the attention in this thesis revolves around rock hyrax demographic processes. The entire scope of this thesis however, relates to the usefulness of this research in clarifying the ecological role of a controversial and potentially vulnerable predator on farmland, and I have endeavoured to address both the harmful and the beneficial influences of black eagles as thoroughly as possible. It is sincerely hoped that the findings herein will benefit farmers and conservationists alike, and help prevent the development of rifts between these parties which have plagued the contentious issue of livestock predation by large eagles in the past (Murphy 1976). Although the system under study is highly specific, the principles gained on relationships between eagles and their prey may find wider application.

The field study also afforded the opportunity of investigating how the life-styles of black eagles and rock hyrax have become inter-linked. A high potential for coevolution exists in very specific predator-prey relationships, and this can allegedly lead to 'evolutionary arms races' between predator and prey (Dawkins & Krebs 1979). Coevolution between black eagles and rock hyrax is considered in the thesis by looking for reciprocity in their morphology and ethology, as described by Futuyma & Slatkin (1983: p.10). But behavioural aspects of this predator-prey relationship are only introduced to this thesis in a preliminary form where they are relevant to demographic processes. For logistical reasons and to keep within the scope set out above, behavioural aspects will be treated in detail elsewhere.

To gain insight to the influence of predation on prey populations, an experimental approach is favoured (Sih, Crowley, McPeek, Petranka & Strohmeier 1985; Newton 1992). Experimental removal of predation may also give an indication of the compensatory nature of other mortality factors (Boutin 1992). Unfortunately control areas where rock hyrax were free of predation by black eagles, could not be found in the Karoo, presumably on account of the high mobility of the eagles. Even on farms where persecution was intense, territorial vacancies were rapidly filled by the non-breeding eagle population. Experimental removal of black eagles was considered neither practical nor acceptable.

Careful and intensive field work is still considered essential for finding out what is happening in natural populations (Endler in Crawley 1992: p. 486). Field studies of the predation impact on bird and mammal populations are especially needed (Sinclair 1989). So the approach adopted in this study was to intensively describe the black eagle - rock hyrax system over a five year field study under natural conditions in a conserved area of the Karoo where predators had not been persecuted for at least seven years (livestock predation by black eagles was researched concurrently on neighbouring farmland). Some previous monitoring of hyrax and caracals in the conserved area (Fairall 1991, *in litt.*; Palmer & Fairall 1988) provided background for the present study. Certain key elements were recognised as important components in the natural system:

1. refuge-dependent rock hyrax
2. a popular alternate prey species, Smith's red rock rabbit *Pronolagus rupestris*
3. permanent and patchy distribution of the refuge resource

which determines a fixed extent of safely-accessible vegetation for rock hyrax

4. periodic enrichment of this lower trophic level by seasonal and somewhat cyclical rainfall interspersed by severe drought
5. predation by 'specialist' black eagles
6. predation by 'generalist' caracals

It was felt that inferences on the demographic influence of black eagles on rock hyrax could not be drawn unless all interacting elements within the system were researched. So data were sought on all key elements to provide a comprehensive understanding, and to construct 'as good a model as possible' of the system. This population model of rock hyrax is run using climatic data for the last century to effectively extrapolate the period of investigation into the long term. Those factors which most influence rock hyrax population change are examined empirically during the short-term field study and theoretically using the long-term predictions of the model. Experimental removal or impedance of predators is simulated and examined by use of the model, and the resulting cost in terms of damage to grazing resources by hyrax surpluses is predicted. This approach of using models to conduct factor analyses and to test hypotheses generated from empirical field studies has been endorsed for the study of predator-prey interactions (Hansson 1988a).

The first half of this thesis provides the necessary background information on the study environment (Chapter 2), the refuge resource (Chapter 3), the prey base (Chapters 4 & 5), and the predator guild (Chapters 6 & 7). This involves much description and general biology. Field research on caracals was not as successful as hoped, but extensive reference could be made to the findings of other researchers in Chapter 7. The second half of the thesis deals with the interaction of predator and prey (beginning with some treatment of the impact of caracals on hyrax in Chapter 7). Feeding habits of black eagles are treated in three separate chapters: prey capture rate (Chapter 8); the selection of prey species (Chapter 9); and the selection of rock hyrax population classes (Chapter 10). Livestock predation by black eagles is addressed in Chapter 11. On account of the difficulty in finding any evidence of stock predation by black eagles, this chapter includes a worldwide literature review of livestock predation by eagles. The information provided in previous chapters is then collated and used in the model to assess the demographic influence of black eagle predation on rock hyrax in Chapter 12. Reciprocal behavioural and morphological traits of black eagles and rock hyrax are considered in the synthesis which includes an appraisal of this predator-prey system in comparison to others, and a costs/benefits analysis of black eagles on karoo farmland.

NOTE

the addresses of all persons cited 'pers. comm.' or *'in litt.'* in this thesis may be found in Appendix 11 on the last page.