CHAPTER 12

BLACK EAGLE PREDATION AS A FACTOR INFLUENCING ROCK HYRAX POPULATIONS

INTRODUCTION

To test the claim by naturalists that eradication of predators such as eagles led to irruptions of hyrax in the past (e.g. Thomas 1946; Kolbe 1967; Rubidge in Kolbe 1983), and to establish the ecological role of black eagles on karoo farmland, requires a comprehensive examination of the impact of eagle-predation on rock hyrax in relation to other factors that lead to loss or addition of individuals to the prey population. The influence of predators on their prey (and *vice versa*) has been a dominant theme in empirical and theoretical ecology (Berryman 1992), perhaps giving rise to more literature than any other ecological topic (Matson & Berryman 1992). The ability of predators to 'control' their prey has been especially questioned for vertebrate communities, with early researchers complaining that the debate was 'generating more heat than light' (Gabrielson in Craighead & Craighead 1956). Numerous field studies, experimentation, and recent modification of general predator-prey theory are now presenting a clearer picture for the role of predation, but disagreements still persist (for example compare Erlinge *et al.* 1984 with Kidd & Lewis 1987, or Ballard, Whitman & Reed 1990 with Boutin 1992).

Much empirical and theoretical research on predation and other factors affecting vertebrate prey populations has been directed at trying to understand cyclicity among certain far northern hemisphere prey populations. Best known are the 10y cycle for snowshoe hares and associated species in North America (Elton & Nicholson 1942; Keith, Todd, Brand, Adamick & Rusch 1977; Keith, Cary, Rongstad & Brittingham 1984), and the 4y cycle for microtines and associated species in northern Europe (Erlinge *et al.* 1983; Liberg 1984; Henttonen, Oksanen, Jortikka & Haukisalmi 1987; Hansson & Henttonen 1988; Korpimäki 1993). These cycles have provided a focal point for study of the factors that affect prey population dynamics and a brief account of this research will provide a useful framework for the discussions in this chapter. A multitude of explanations have been offered for the phenomenon of cycles (for reviews see: Bulmer 1974; Lidicker 1988; Akçakaya 1992). In the 1950's and 1960's abiotic and then intrinsic mechanisms of population regulation were the most popular explanations (e.g. Christian 1950; Chitty 1960), but intrinsic mechanisms could not explain cyclicity in non-microtines (Hansson 1984; Henttonen 1985; Korpimäki 1986; Korpimäki & Norrdahl 1989a), nor the synchrony and the regional variation in the amplitude of cycles (Hansson 1988b). Much information gathered from field studies has been published in the 1980's and it is now becoming accepted that predation and refuge play key roles in the pattern of cycles, while depletion of food supplies and possibly disease may be involved in initiating the decline from peak prey densities.

Early predator-prey theory evolved prior to this knowledge but also found focus on population cycles at times. Oscillations of predator and prey populations were a feature of the earliest predator-prey model derived by Lotka (1925) and then Volterra (1928, translated in Chapman 1931) from Verhulst's (1838) 'logistic' equation. But the

Lotka-Volterra equations worked on the chemical principle of mass action whereby the population responses were proportional to the product of their biomass densities. Consequently, the oscillations in this early model were neutrally stable and were highly dependent on initial conditions. This problem was passed on to subsequent predator-prey models, and a series of theoretical propositions (functions of predator interference, prey refuge etc.) were incorporated to confer stability (equilibria or stable limit cycles) on the basic model (e.g. Nicholson & Bailey 1935). Most of the early predator-prey models were based on laboratory studies and simulations of insect parasitoid interactions, so they were far removed from the biological data that were accumulating from a progression of field studies on vertebrate predator-prey interactions (Hansson 1988a; Akçakaya 1992).

While the theoretical study of predation was evolving, early field observations of vertebrate predator-prey systems were not shedding much light on the controversial role of predation. Wildlife biologists maintained that raptors exerted control over rodent pests (e.g. Craighead & Craighead 1956), but not over valued game species. Errington (1946, 1963) introduced the valuable concept of compensatory mortality, but he contended that nearly all prey killed by predators belonged to a 'doomed surplus' which would have died anyway, and concluded that predators have little effect on prey populations. This argument immersed wildlife biologists into "a morass of tortuous verbal logic, a morass from which they are only just now emerging and which would have been quickly and cleanly bridged by the mathematical theory" (Taylor 1984). The generalisation that predators consume a doomed surplus is still widely accepted by ecologists today. However, an increasing number of field studies and predator-removal experiments (e.g. Schnell 1968; Trautman, Frederickson & Carter 1973; Gassaway, Stephenson, Davis, Shepherd & Burris 1983; Sih *et al.* 1985; Angerbjörn 1989; Marcstrom, Engren, Cary & Keith 1989; Newsome *et al.* 1989; Newsome 1990) now show that predation can be a significant and additive mortality factor affecting certain vertebrate prey populations, and may have a particularly devastating impact in sudden relationships (e.g. island introductions) which have not had time to evolve (Elton 1927; Carlquist 1965; Pimm 1987; Ebenhard 1988; Woodroffe & Lawton 1990). It has become clear that the generalisation that predators do not control vertebrate prey is as inappropriate as the generalisation that they do.

Ecologists now use a more succinct terminology and ask whether predators limit or regulate their prey (Boutin 1992; Messier & Crete 1985; Korpimäki 1992). Limiting factors are any factors which affect population growth through increased production or loss of individuals; while regulating factors are limiting factors which behave in a density-dependent fashion (Kidd & Lewis 1987; Sinclair 1989; Messier 1991; Korpimäki 1992). A density-dependent factor may in turn be defined as "any component of the environment whose intensity is correlated with population density and whose action affects survival and reproduction" (Murray 1982). Any factor which is found to be mostly responsible for restraining a prey population is described as the principal limiting factor. But demographic factors do not have to suppress a prey population to be described as limiting. In contrast to predictions of the Lotka-Volterra model, field research on prey cycles has often revealed that predation pressure is not maximal at the peak in prey numbers but rather during the decline phase, and prolonged heavy predation is thought to extend the low phase of the prey cycle and thereby influence its periodicity (Pearson 1966, 1971; Fitzgerald 1977; Henttonen *et al.* 1987; Korpimäki *et al.* 1991). In this context, predation fits the definition of a limiting factor but it cannot be described as regulatory.

For predators to regulate prey populations around some equilibrium level requires that predation rate be maximal at peak prey densities and minimal at low prey densities (density-dependence). This has become an important criterion in recent predator-prey research (e.g. Erlinge 1987; Kidd & Lewis 1987; Erlinge *et al.* 1988; Sinclair 1989; Messier 1991; Boutin 1992; Korpimäki 1992). For predation to be truly regulatory it must also be largely additive, i.e. not matched by some other mortality factor when removed. Of special interest is whether predator-regulated prey equilibria are lower than food-regulated equilibria (Taylor 1984). For cyclic prey populations, predation has often been found to be density-dependent in a delayed fashion (Pearson 1966, 1971; Keith *et al.* 1977; Henttonen *et al.* 1987; Korpimäki *et al.* 1991). Many researchers have reported that food shortage is involved in initiating the decline of cyclic prey from peak densities (Kalela 1971; Tast & Kalela 1971; Henttonen & Järvinen 1981; Oksanen & Oksanen 1981; Laine & Henttonen 1983; Keith *et al.* 1984). Only a couple of studies have indicated that predation pressure may be responsible for actually initiating the declines (Henttonen *et al.* 1987; Trostel *et al.* 1987). But experimental provision of food has not prevented declines (see Akçakaya 1992) and most researchers are now in agreement that the delay or time-lag shown by specialist predators is a crucial element in the pattern of cycles. These time-lags have been attributed to slower rates of reproduction by the predator, and prey refuges such as snow for microtines or thickets for snowshoe hares.

With the resurgence of 'ratio-dependent' predator-prey theory, there has been a closer marriage of theoretical and empirical studies on predation and a clearer explanation of vertebrate population processes. Predator rate of increase and predation rate are now modelled on the ratio of prey to predators (*per capita* resources), rather than absolute prey density. Thus a simple element of interference and sharing between predators is inherent in these new models which are more stable as well as being more plausible for many biological systems. Ratio-dependent theory also solves some of the previous paradoxes of predator-prey models such as enrichment of the lower trophic level (Slobodkin 1992). Akçakaya (1992) used ratio-dependence theory to develop a simple model which adequately explains prey cycling as an interaction between predation and food resources in the presence of a refuge function. This model correctly predicted the periodicity of snowshoe hare cycling and the decline in cycle amplitude towards southern latitudes. This latter tendency is well-known and workers in southern Fennoscandia have now supplied evidence of density-dependent predation by generalist predators which can result in truncated prey peaks or the absence of cycles farther south (Erlinge 1987; Erlinge *et al.* 1988; Korpimäki & Norrdahl 1989b; Korpimäki & Norrdahl 1991; Korpimäki 1992). Greater efficiency of the southern predation response (at preventing major build-ups in prey populations) has been attributed to: reduced prey refuge; the rapid functional response of resident generalist predators subsisting on alternate prey; and the very rapid numeric response of mobile raptors (Korpimäki 1985a; Korpimäki 1992).

Studies of the influence of predation on cyclic prey have been pertinent to observations on non-cyclic but irruptive prey populations. In Australia and New Zealand populations of rabbits and house mice have exhibited 'apparent' cycles which have been characterised by destruction of food resources at peak prey densities and by high predation impact during the low phase (Gibb 1981; Newsome *et al.* 1989; Newsome 1990; Sinclair *et al.* 1990; Pech *et al.* 1992). But these outbreaks have not been regular and the build-up in numbers were attributed to periods of optimal conditions for prey growth, whilst the declines were associated with episodic droughts. For these reasons, this interaction has been best-described as 'environmentally-modulated predation' (Newsome *et al.* 1989). Situations where predation is extremely limiting or density-dependent (regulatory) at low prey densities but not at high prey densities have also been observed for large ungulate prey populations in North America (Crête, Taylor & Jordan 1981; Bergerud, Wyett & Snider 1983; Gassaway *et al.* 1983, 1992; Messier & Crête 1984, 1985; Messier 1987, 1989; Van Ballenberghe 1987; Ballard *et al.* 1990). In these circumstances, prey populations are regulated for extended periods by predators after they have been reduced to low density by some other factor. Certain predator removal experiments have demonstrated that predation can be extremely limiting in this way (e.g. Trautman *et al.* 1973; Gassaway *et al* 1983, 1992; Newsome *et al.* 1989; Newsome 1990; Pech *et al.* 1992; see Table 21.1 in Crawley 1992).

Environmentally-modulated predation might be anticipated for rock hyrax populations living in the 'boom and bust' karoo environment. Hyrax irruptions have been reported four times in South Africa and Namibia during the last century (details in Chapter 1: p. 2). There is no indication from these reports that the irruptions were occurring at regular intervals. After the major hyrax decline reported throughout southern Africa which preceded the present study, one might expect that predation impact, especially by specialist black eagles, would be greatest during current low prey densities, but rock hyrax populations have an important analogy to cyclic prey populations in the northern hemisphere - that of a refuge resource which is likely to confer protection at low densities. But unlike snow and microtines, rock crevices are permanent and afford protection to hyrax from nearly all predators. The presence of permanent, effective refuge and the periodic enrichment of hyrax food resources in the vicinity of the refuge habitat by sporadic rainfall events are two characteristics which combine to make this predator-prey system rather unique.

A number of rock hyrax population studies were initiated in response to the alleged agricultural importance of hyrax irruptions. With their readily discernible age classes and a distinct birth-pulse, rock hyrax populations in the Cape are well suited to population modelling. Swart *et al.* (1986) modelled the interaction between rock hyrax and caracals in the Mountain Zebra National Park, and incorporated some elements of ratio-dependence. Their model predicted that caracals merely tracked changes in hyrax density (rather than influencing these changes), and sensitivity analysis suggested that juvenile hyrax mortality had a greater influence on population change than predation (these factors were considered separate). Black eagle predation was set at a very high rate (@307 hyrax pair^{-1} y^{-1}) and not allowed to vary for simulations of their model. Fairall *et al.* (1986) constructed a simpler model of the growth of a small rock hyrax population in the Tsitsikama National Park and created equilibrium by means of an increasing death rate factor which was held to represent the limiting influence of shelter on the population. Estimates of carrying capacity were arbitrarily chosen for both models and hyrax mortality was assumed to vary as a simple function of density in relation to carrying capacity. Neither model incorporated a lower trophic level to include the very profound effects of rainfall (via enrichment of food supplies) and drought on hyrax population dynamics (see Chapter 4), but Fairall *et al.* (1986) did simulate population recovery after a catastrophic mortality event. The assumption that hyrax mortality is simply density-dependent and the lack of a lower trophic sub-model to cater for rainfall effects are thought to confer a high degree of artificial stability on both these models.

The prime aim of this chapter is to elucidate what effect black eagles have on hyrax demography. The possible influence of black eagles on hyrax morphology, lifestyle and behaviour is treated elsewhere. In the first part of this chapter all information presented in previous chapters of this thesis is collated in order to assess the immediate impact of black eagle predation on rock hyrax during the study period in terms of hyrax standing crop, recruitment and mortality. Comparisons are made with other similar studies of the impact of predation within vertebrate communities. To take these inferences further in the context of the highly changeable Karoo, a specific hyrax population model is evolved in the second part of the chapter. The model is based on accurate measurement of the refuge habitat, and incorporates periodic enrichment of the system through a lower trophic level to yield dynamic estimates of carrying capacity. Hyrax demographic processes are modelled on the ratio between population size and this variable carrying capacity and on rainfall effects, rather than simple density-dependence. The new notion of 'availability-dependent' predation is backed up with evidence from the field. Using long-term climatic data from the Karoo to effectively extend the study period, the model makes predictions which are compared with records of historic hyrax irruptions. The model is used to examine the influence of various aspects of black eagle predation and other factors on rock hyrax demographic processes, and so establish whether hyrax numbers are most influenced by their lower trophic interaction with food supplies or by predation. Consequences of predator control programmes for karoo farmers are forecasted by simulated removal/impedance of predators.

PART 1

THE IMMEDIATE INFLUENCE OF PREDATION BY BLACK EAGLES ON ROCK HYRAX DEMOGRAPHY DURING THE STUDY PERIOD

METHODS (part 1)

Keith (1974) provided the following guidelines for evaluating the relative importance of a factor that might affect populations: identify its immediate demographic effect(s), and compare its impact with other factors; describe its interaction with other factors in terms of additive, compensatory or modifying effects; and characterise its action in relation to population density. In this first part of the chapter analyses of hyrax demographic processes during the study period provide the foundation for evolution of a population model in the second part which characterises the long-term action of predation on hyrax population density in the Karoo.

Immediate demographic effect of predation by black eagles on rock hyrax

Field data for the study period on rock hyrax demography (Chapter 4), black eagle demography (Chapter 6), prey capture rate by black eagles (Chapter 8), and black eagle diet (Chapters 9 & 10), are provided earlier in this thesis. For methodology see relevant chapters. This part of the chapter is a collation and interpretation of all these data to derive the immediate impact of predation by black eagles on rock hyrax during the period of study in terms of hyrax standing crop, recruitment and mortality. A literature review (Dialog Information Services, Inc.) provided similar case studies of vertebrate predation for comparison.

Other factors

The impact of caracals and other generalist predators on different components of rock hyrax populations is assessed from data and literature on the demography and feeding habits of these predators treated in Chapter 7. Inferences on other mortality factors affecting the hyrax population under study (e.g. starvation and disease), and factors affecting recruitment to this population (e.g. conception rates and foetal resorption) are drawn from observations of hyrax population change, from data from the shot sample, and from the literature (see Chapter 4). Predation impact of black eagles on red rock rabbits (and other alternate prey) is derived from data on rabbit demography (see Chapter 5), to enable comparison with black eagle impact on their main prey. Impact of black eagles on domestic livestock was treated in Chapter 11.

Interactive effects of demographic factors

Predation is more likely to remove a random sample of both sick and healthy individuals from a prey population in the case of raptors which rely mainly on surprise tactics in their hunting, than in the case of raptors which actively outfly their prey (Rudebeck 1950, 1951; Kenward 1978a). Black eagles definitely fall into the former category (Chapter 6), but it also seems probable that rock hyrax which are severely food-stressed are more likely to be captured by eagles because they may have to forage farther from shelter (see later). To address the question of whether prey taken by a predator 'would have died anyway' (doomed surplus), is very difficult in the absence of experimental manipulation (Boutin 1992). Black eagles could not be removed in the present study, and the degree of 'compensation' in rock hyrax predation by black eagles could only be explored in a largely speculative way (however, incidental observations of hyrax population change on a farm where all predators except black eagles were actively removed did provide some valuable insights). The age structure of hyrax captured by black eagles in the present field study (Chapter 10) coupled with the amount of age-specific mortality attributable to eagles, did provide some clues as to how many of the rock hyrax captured might have died anyway from old age. But the field study did not provide an indication of how many of the rock hyrax captured by black eagles were dying from starvation or disease. The only literature accessed on compensatory predation by eagles pertained to predation on domestic livestock. But heavy predation of dying lambs by eagles is not very relevant to the black eagle - rock hyrax system, because there is usually an abundance of sickly lambs and because juvenile domestic livestock are close to the maximum size limit of prey taken by eagles. Literature on rock hyrax predation by caracals was accessed to indicate the impact of this predator where black eagles were limited by nest-site availability and vegetation density (details in Chapter 7). The effects of compensatory mortality of hyrax in the absence of predation by black eagles, are further explored in the second part of this chapter when simulating removal of the eagles from the hyrax population model.

RESULTS AND DISCUSSION (part 1)

The impact of predation by black eagles in relation to hyrax standing crop

Estimates for the number of rock hyrax (in three age classes) alive at the start of each year, dying in the course of the year, and captured by black eagles in the average lower escarpment eagle territory, are presented in Table 42. These data are taken from previous chapters in this thesis (see methods). For the three years when all parameters were comprehensively researched (1988 - 1990), the number of hyrax removed by black eagles from an eagle territory in an average year (117) was equivalent to 11% of the average standing crop of hyrax (1062) at the start of the year, just after the birth pulse. The relative influence of this predation rate on population density depends on the turnover of the hyrax population in terms of annual recruitment and mortality.

TABLE 42

ANNUAL ESTIMATES OF PREY AVAILABILITY AND PREY CAPTURED IN AN AVERAGE EAGLE TERRITORY DURING THE STUDY PERIOD

Estimates of hyrax availability, composition and mortality were derived from December counts at colonies in conjunction with group plotting (Chapter 4). Red rock rabbit population estimates were based on midden densities and animal to midden ratios (Chapter 5). The toll taken by eagles of these two prey was derived from information on eagle feeding habits presented in Chapters 8, 9 & 10.

YEAR	1986	1987	1988	1989	1990	1991
hyrax composition:						
JUVENILES AT START		(510)	428	351	431	199
IMMATURES AT START		(262)	208	144	144	262
ADULTS AT START		(673)	588	405	451	461
TOTAL AT START		(1445)	1224	899	1025	904
hyrax mortality:						
JUVENILES DYING		(302)	284	207	169	
IMMATURES DYING		(97)	114	40	43	
ADULTS DYING		(250)	277	58	91	
TOTAL DYING		(649)	675	305	303	
impact of predation:						
HYRAX KILLED BY EAGLES	(118)	122	136	98	(118)	
% STANDING CROP REMOVED		(8,4)	11,1	10,9	(11,5)	
% EQUIVALENT IN RECRUITMENT		(24)	32	28	(27)	
% MORTALITY ATTRIBUTABLE TO EAGLES		(19)	20	32	(39)	
other prey:						
RED ROCK RABBITS AT START					441	
RED ROCK RABBITS KILLED BY EAGLES	(35)	24	33	49	(35)	

Vertebrate predators normally remove about 15% of vertebrate prey populations. This figure is derived as the average impact for 50 similar investigations of such systems accessed from the literature, but some of these studies refer to predator communities rather than individual species (Table 43). Predation impact is evidently highly variable in vertebrate communities (s.d.=14%; Table 43), and it has to be borne in mind that predation studies are probably less likely to be carried out where predation impact is suspected to be minimal. The studies in Table 43 (consult table for reference numbers) suggest that predation impact is usually high for prey species which can show rapid population turnover, for instance small mammals (e.g. 1, 5, 8, 11, 55, 56) and fish (52). But there was no clear relationship with prey body size. In fact moose (7) and wildebeest (9) were amongst the most heavily preyed upon species. Even carnivores suffered extremely heavy predation in one study (2), but this case could be attributed to cyclicity of a predominant prey species in keeping with the alternative prey hypothesis (Hagen 1952; Lack 1954). Predation impact on cyclic prey is known to be relatively light during the irruptive phase (50), but can be extremely heavy during the decline phase (1). Predation impact by the same predators on the same prey species can vary dramatically with predator-prey ratios on a regional basis (25 vs. 41), and also in relation to the social status of the prey animals (19 vs. 42). Impact also appears to vary with prey vulnerability, for instance raptor communities in North America remove a greater component of mammalian prey populations (4, 11, 13) than avian prey populations (24, 32). Less vulnerable prey species suffer considerably less predation from predators which are concentrating their efforts on more available prey species in the area (5 vs. 43 & 49). Black eagle predation impact on rock hyrax might be expected to be relatively high on the basis that this is a highly specialised predator concentrating on a prey which can be extremely vulnerable. Predation impact is often greatest when specialist predators pursue their prey at low density (e.g. Pearson 1966, 1971; Fitzgerald 1977; Hansson 1984; Henttonen 1985; Henttonen *et al.* 1987; Korpimäki *et al.* 1991). Also rock hyrax are renowned for their propensity for population increase (Millar 1971; Fourie 1983). It was surprising therefore that the impact recorded in this study was lower than the average recorded for vertebrate systems as represented in Table 43.

The impact of predation by black eagles on other prey species

Red rock rabbit midden densities assessed by transect sampling and the accumulation rate of faeces on certain middens indicated that the average lower escarpment eagle territory accommodated approximately 440 red rock rabbits early in 1990 (see Chapter 5). It is estimated that black eagles annually removed an average of 35 rabbits per eagle territory (Table 42). This would imply a predation rate of 8% of the rabbit standing crop. However, incidental observations indicated wide variation in rabbit numbers over the study period (Chapter 5) with a seven-fold increase in sightings between 1987 and 1989. Time-lapse data on rabbit predation in the second half of 1989 provided the closest data on prey capture rate for comparison with the population estimate derived early in 1990, and suggests that predation impact may have been as high as 11% of the standing crop at that time.

Lower predation impact on hyrax than expected, and substantial reliance on red rock rabbits and other alternate prey (Table 34, p. 195) are suggestive that black eagles were hard pressed to catch rock hyrax during the study period. This is supported by the low rate of prey capture observed in the present study (Chapter 8) in comparison with work in the Matobo Hills (Gargett 1990). A likely explanation for this is that after their major population decline in the early 1980's, the rock hyrax in the KRNP were now well protected within the safe confines of their refuge habitat (for predation impact of black eagles on domestic livestock see Chapter 11).

TABLE 43

PREDATION IMPACT STUDIES OF VERTEBRATE PREDATORS UPON VERTEBRATE PREY - IN TERMS OF THE PORTION OF STANDING CROP REMOVED OVER VARYING TIME PERIODS

(numbers in the first column are used for reference from the text)

Ref. no.	SOURCE	PREDATOR	PREY	PORTION OF STANDING CROP REMOVED	TIME PERIOD
1	Pearson (1966): decline phase	various	California vole	25 - 88%	(decline)
2	Korpimaki & Norrdahl (1989a)	mainly raptors	mustelids	20 - 80%	1 y
3	Edminster (1939)	various	ruffed grouse	40%	1 y
4	Craighead & Craighead (1956)	raptors	rabbits	33 - 47%	fall & winter
5	Luttich et al. (1970)	red-tailed hawk	Richardson's ground squirrel	32 - 44%	summer
6	Linden & Wickman (1983)	Goshawk	Hazel Grouse	36%	1 y
7	Gassaway et al. (1992)	various	moose	31%	1 y
8	Fitzgerald (1977)	ermine	vole	6 - 54%	1 y
9	White (unpubl.)	lion	wildebeest	28%	1 y
10	Keith et al. (1977)	various	snowshoe hare	12 - 43%	1 y
11	Craighead & Craighead (1956)	raptors	meadow mouse	22 - 26%	fall & winter
12	Gassaway et al. (1983)	wolves	moose	13 - 34%	winter
13	Craighead & Craighead (1956)	raptors	white-footed mice	22 - 24%	fall & winter
14	Kenward (1978b)	goshawks	pheasants	20%	winter
15	Messier & Crete (1985): low hunting	wolves	moose	19,3%	1 y
16	Whitfield (1985)	raptors	ringed plovers	19%	winter
17	Whitfield (1985)	raptors	redshanks	16 - 20%	winter
18	Fuller & Keith (1980)	wolves	moose	15%	1 y
19	Jenkins et al. (1964)	various	non-territorial red grouse	14%	10 mth
20	Perrins & Geer (1980)	sparrowhawk	adult tits	14%	summer
21	Goransson (1975)	goshawks	pheasants	10 - 15%	winter
22	Mills (unpubl.)	lion	zebra	12%	1 y
23	Craighead & Craighead (1956)	raptors	game birds	5 - 18%	fall & winter
24	present study	black eagle	rock hyrax	11%	1 y
25	Kruuk (1972a): Ngorogoro	hyenas	adult wildebeest	11%	1 y
26	Fourie (1983): estimated	caracal	rock hyrax	11%	1 y
27	Van Dobben (1952)	cormorants	eels & pike-perch	10%	breed season
28	Banfield (1947): outbreak	short-eared owls	voles	10%	1 y
29	Kruuk (1972a): Ngorogoro	hyenas	zebra	9%	1 y
30	Messier & Crete (1985): heavy hunting	wolves	moose	6 - 11%	1 y
31	Korpimaki (1981)	Tengmalm's owl	small mammals	1 - 15%	1 y
32	Craighead & Craighead (1956)	raptors	small birds	4 - 11%	fall & winter
33	Picozzi (1978)	Hen Harrier	Red Grouse	7,4%	1 y
34	Ballard et al. (1987): exploited wolves	wolves	moose	4 - 6%	1 y
35	Whitfield (1985)	raptors	turnstones	4 - 5%	winter
36	Craighead & Craighead (1956)	raptors	fox squirrel	4 - 5%	fall & winter
37	Nellis et al. (1972)	lynx	snowshoe hare	2 - 6%	winter
38	Nellis et al. (1972)	lynx	ruffed grouse	1 - 6%	winter
39	Messier & Crete (1985): heavy hunting	bears	moose	1,5 - 5%	1 y
40	Kruuk (1972a): Serengeti	hyenas	gazelles	1,1 - 3,5%	1 y
41	Kruuk (1972a): Serengeti	hyenas	adult wildebeest	1,6 - 2,6%	1 y
42	Jenkins et al. (1964)	various	territorial red grouse	2%	10 mth
43	Luttich et al. (1970)	red-tailed hawk	ruffed grouse	1,5 - 2,4%	summer
44	Kruuk (1972a): Ngorogoro	hyenas	gazelles	1,8%	1 y
45	Nellis et al. (1972)	lynx	red squirrel	1 - 2%	winter
46	Whitfield (1985)	raptors	knots	0,5 - 1,5%	winter
47	Blanco & Hiraldo (1991)	red kites	rabbits	1,2%	breed season
48	Kruuk (1972a): Serengeti	hyenas	zebra	0,8 - 1,0%	1 y
49	Luttich et al. (1970)	red-tailed hawk	snowshoe hare	0,7 - 1,2%	summer
50	Chitty (1938): outbreak	short-eared owls	field voles	0,05%	1 y
51	Calaby (1951)	little eagle	rabbits	2,4%	10 w
52	Whoriskey & Fitzgerald (1985)	Avian	Stikkleback	30%	2 mth
53	Southern & Lowe (1982)	Tawny Owl	Bank vole	25%	2 mth
54	Tinbergen (1946)	sparrowhawks	sparrows	8%	1 mth
55	Erlinge et al. (1983)	various	field vole	12 - 60%	1 mth
56	Erlinge et al. (1983)	various	wood mice	10 - 30%	1 mth
57	Raptor Group (1982)	raptors	voles	0,2%	1 d

The impact of predation by black eagles in relation to hyrax mortality

For the years 1988 through to 1990, the number of hyrax dying annually in a lower escarpment eagle territory averaged 428. Predation by black eagles could account for 27,4% of the hyrax that were dying (=117). More than half of the total mortalities were juvenile hyrax, and smaller, generalist predators may have been more involved in these deaths (Chapter 7). The average amount of mortality in vertebrate predator-prey systems that could be attributed to predators was 52% for 20 studies accessed from the literature (Table 44 - consult this table for reference numbers cited in the text), but again this was highly variable (s.d.=26%). Predators were the most important cause of death in studies of large ungulates (57, 58, 61, 62) and in studies of declining, cyclic prey (59, 60). Predators accounted for much greater portions of prey mortality when conditions were good (57) than when conditions were bad (70). Very high losses of hyrax to factors other than eagles in the dry year of 1988 were partly responsible for the relatively low portion of mortality attributable to predation by eagles in the present study. In 1988 eagles accounted for only 20% of hyrax deaths in their territories, but this figure rose to 32% and 39% in 1989 and 1990 respectively, following good rains in 1989. In the two latter years, predation by eagles accounted for most of the adult hyrax dying in their territories (Fig. 95, p. 216). The role of predation by eagles in age-specific mortality was considered in detail in Chapter 10, but it is important to note that other predators are probably more involved in the removal of juvenile hyrax. Black eagles however, exert a high rate of predation on old hyrax, which normally comprise about 16% of hyrax captured (Chapter 10). In the absence of eagles, a component of these would probably die from old age. The degree of such compensatory mortality is likely to vary with circumstance because eagles are more likely to kill surplus elements of hyrax populations such as males and old animals (which may die from other causes) from large vulnerable populations (Chapter 10). Predation is more likely to remove healthy and contributing individuals from a small prey population (additive mortality) where the predator to prey ratio is high (Chapter 10; Kruuk 1972a).

The impact of predation by black eagles in relation to hyrax recruitment

Prey vulnerability can vary markedly with life cycle, and the eggs or young of animals may be exposed to a much wider array of predators than the adults. Naive behaviour and small size of juveniles can render them especially vulnerable to predation (Chapter 10). Seventeen studies of predation impact on juvenile elements in prey populations are summarised in Table 45 - these yield an average impact of just over one third of young being removed by predators. Predation evidently has a very dramatic impact on recruitment in certain small mammal (78, 79, 82) and ungulate (80, 81) prey populations. While black eagles accounted for a small proportion of the juvenile hyrax that were dying (Chapter 10), it is enlightening to equate total numbers removed by the eagles with total numbers added each year.

The estimated annual toll of rock hyrax removed from a lower escarpment territory by black eagles for the years 1988 to 1990 (117) was equivalent to 29% of the mean number of juveniles produced at each birth pulse preceding these three years (average no. juveniles = 403; this figure is reduced to 352 if the birth pulse at the end of 1990 is included). Annual recruitment for this period was thus 6% lower than annual mortality and the hyrax population showed an

TABLE 44
PREDATION IMPACT STUDIES OF VERTEBRATE PREDATORS UPON VERTEBRATE PREY - IN TERMS OF THE PROPORTION OF PREY MORTALITY ACCOUNTED FOR BY PREDATORS

(numbers in the first column are referred to from the text)

Ref. no.	SOURCE	PREDATOR	PREY	% MORTALITY ACCOUNTED FOR	TIME PERIOD
58	Mills (unpubl.)	lion	wildebeest	93%	wet years
59	Filonov (1989)	various	roe deer	91%	1 y
60	Trostel et al. (1987)	various	snowshoe hare	85,1%	1 y
61	Keith et al. (1984)	various	snowshoe hare	80 - 90%	1 y
62	Gassaway et al. (1992)	various	moose	80,5%	1 y
63	Jedrzejewski et al. (1992)	mainly wolves	red deer	80%	1 y
64	Filonov (1989)	various	red deer	65%	1 y
65	Smeenk in Brown (1976)	eagles	dik diks	40 - 60%	1 y
66	Eng & Guilliam (1962)	goshawk	ruffed grouse	50%	winter
67	Keith et al. (1977)	various	snowshoe hare	22 - 71%	1 y
68	Luttich et al. (1970)	red-tailed hawk	adult Richardson's ground squirrels	38 - 53%	summer
69	Nelson & Mech (1981)	wolves	deer	45%	1 y
70	Luttich et al. (1970)	red-tailed hawk	juvenile Richardson's ground squirrels	37 - 44%	summer
71	Mills (unpubl.)	lion	wildebeest	38%	dry years
72	Nellis et al. (1972)	Canadian lynx	Snowshoe hare	37%	winter
73	Tinbergen (1946)	sparrowhawk	small birds	25 - 50%	season
74	Hauge & Keith (1981)	wolves	moose calves	29%	1 y
75	Southern (1954)	owls	rodents	25%	1 y
76	Nellis et al. (1972)	lynx	snowshoe hare	8 - 37%	1 y
77	Dumke & Pils (1973)	raptors	pheasant	20%	1 y
78	Jedrzejewski et al. (1992)	mainly wolves	wild boar	13%	1 y

TABLE 45
PREDATION IMPACT STUDIES OF VERTEBRATE PREDATORS UPON VERTEBRATE PREY - IN TERMS OF THE PROPORTION OF JUVENILE ELEMENTS REMOVED BY PREDATORS

(numbers in the first column are referred to from the text)

Ref. no.	SOURCE	PREDATOR	PREY	PORTION REMOVED	TIME PERIOD
79	Erlinge et al. (1983)	various	field vole production	97%	1 y
80	Wood (1980)	various	rabbit juveniles	up to 90%	1 y
81	Nelson & Mech (1981)	wolves	deer fawns	71%	fall - winter
82	White (unpubl.)	lion	wildebeest recruitment	71%	1 y
83	Myers & Schneider (1964)	various	rabbit juveniles	70%	1 y
84	various in Boutin (1992)	bears	moose calves	34 - 52%	1 y
85	Scott & Klimstra (1955)	red fox	bobwhite quail nests	41,3%	1 y
86	Maclean et al. (1974)	weasel	lemming nests	35%	winter
87	Murie (1992)	badgers	Columbian ground squirrels juveniles	25%	1 y
88	Hauge & Keith (1981)	wolves	moose calves	21%	1 y
89	Dunn (1977)	weasel	tit nests	21 % (up to 51%)	1 y
90	Jarvinen (1985)	mustelids	passerine nests in holes	20%	1 y
91	Perrins & Geer (1980)	sparrowhawk	great tit recruitment	18 - 34%	1 y
92	Perrins & Geer (1980)	sparrowhawk	blue tit recruitment	18 - 27%	1 y
93	various in Boutin (1992)	wolves	moose calves	1 - 18%	1 y
94	Sherman (1981)	badgers	Belding's ground squirrel juveniles	8%	1 y
95	Liberg (1984)	Domestic cat	Common rabbit production	4%	1 y
96	Lloyd (1976)	raptors	pheasant poults	0,25%	1 y

overall decline of 26% between November 1987 and November 1990 (some of this decline must be attributed to the extremely poor recruitment at the end of 1990). The highest annual toll taken by black eagles in the present study (136 per territory in 1988) was equivalent to 68% of the smallest hyrax birth pulse (199 per territory in 1990). Annual predation rates of hyrax by black eagles recorded for the Matobo Hills by Gargett (1990), are much greater than the minimum hyrax birth-pulse recorded for an average eagle territory in the present study. Predation by black eagles evidently has the capacity to be a major restraining influence on hyrax population growth. By slowing the rate of increase of the hyrax population, predation by black eagles can be described as a limiting factor (Sinclair 1989; Messier 1991; Boutin 1992; Korpimäki 1992). Without modelling, it is difficult to predict the precise influence of such a restraint on population density, but in the event-driven karoo situation any factor which slows hyrax population growth during enrichment should help alleviate destruction of food resources in subsequent droughts. The field data indicates that, unlike sympatric generalist predators, specialist black eagles continue to exert such an influence (albeit reduced) even when small hyrax populations are well protected within their refuge habitat.

The impact of predation by generalist predators on rock hyrax during the study period

Caracals in the KRNP probably outnumber black eagles by a factor of three under normal circumstances, and may consume more than six times as much food (Chapter 7). Yet scat analyses did not indicate that caracals were an important predator of rock hyrax in the early part of the present field study. It is likely that some hyrax were being captured by caracals during the study period, but this remained undetected by the methods employed. Hyrax have comprised a significant portion of caracal diet previously in the KRNP and in other areas, and it is calculated that caracals have the potential to remove approximately 400 hyrax annually from an eagle territory under more usual conditions of hyrax availability (see Chapter 7). The functional and numeric response of caracals should enable this predator to have a much greater impact on surplus rock hyrax than black eagles, when the hyrax population exceeds the carrying capacity of its refuge habitat. Other predators of large hyrax which may have an impact on populations elsewhere in Africa were not sufficiently abundant in the KRNP to have a significant influence on hyrax demography. For more detail on the potential impact of caracals on rock hyrax see Chapter 7.

In an average year during the study period, about 220 (55%) of the 403 juvenile hyrax born in an eagle territory died in their first year. This juvenile mortality has been shown to be highly variable (Chapter 4) and of great importance to hyrax population dynamics (Fourie 1983; Swart *et al.* 1986). Black eagles showed a low preference rating for juveniles in their diet, presumably because of low profitability of such small prey items (Chapter 10). Caracals are larger predators and may exhibit similar prey choice but this has not yet been investigated. In addition to caracals and black eagles, juvenile hyrax are exposed to a wide array of smaller, generalist predators such as Cape wildcats, various raptors and Cape cobras. The impact of the latter on the rock hyrax study population was not comprehensively researched in the present study, but it is roughly estimated that all predators in the KRNP have the potential to account for 40% of the juvenile mortality (Chapter 7). Such an impact may have an important bearing on rock hyrax population change. Predation and juvenile mortality cannot be divorced as separate demographic factors. Observations on the farm Montana, near Victoria West (140km north-east of the KRNP) suggest that removal of generalist predators may lead to very rapid hyrax population growth. In 1984, an irruption of hyrax on this farm forced the landowner to move his livestock elsewhere. Shortly afterwards most of the hyrax disappeared in synchrony with a widespread decline during the drought. I revisited the farm in 1990 and learned that the hyrax population had already nearly recovered to the population level experienced prior to the major decline (J.H. Swiegers pers. comm.). Unfortunately this farm was not monitored as a control because black eagles were resident and not persecuted. A second pair of eagles had colonised the farm in the interim. Carnivores however (caracals, Cape wildcats, black-backed jackals, Cape fox), had been heavily persecuted (details in Chapter 11: p. 230-231), and this was considered to be the major difference between the farm Montana and the study area in the KRNP where the hyrax population had shown no obvious recovery between 1986 and 1990. Prolonged suppression of prey populations at low density by a healthy complement of predators has been demonstrated elsewhere (Gibb 1981; Gassaway *et al.* 1983, 1992; Van Ballenberghe 1987; Newsome *et al.* 1989; Ballard *et al.* 1990; Newsome 1990; Sinclair *et al.* 1990; Pech *et al.* 1992). Heavy predation of juveniles in a prolific prey species may be necessary for this effect.

The influence of non-predatory mortality on the hyrax population

Considerable numbers of hyrax in the study area were evidently dying of causes other than predation by eagles during 1988. Other predators may have been involved in these removals but analyses of scats collected mainly in 1987 did not implicate caracals. It seems likely that many of the hyrax were dying of drought-related causes such as starvation and disease. But very little evidence of such non-predatory mortality could be found, possibly because dying hyrax were either removed by scavengers or they died concealed in crevices. With heavy predation on old hyrax by black eagles and possibly caracals, it is unlikely that a significant number of hyrax reach their full life-expectancy and die of old age. Dental attrition from age eight years onwards can be expected to affect body condition deleteriously and render these animals more vulnerable to predators.

One adult hyrax was observed on the upper escarpment in 1989 which showed behaviour that may have been symptomatic of rabies (salivation, poor vision and coordination, and no fear of humans). A farmer in the area reported many such cases when hyrax were at high population density in the mid 1970's (D. Shearing pers. comm.). Rock hyrax are 'close-contact' social animals, and would be very susceptible to a disease epidemic, especially when high densities of animals are stressed by drought. The spread of disease through hyrax populations may be significantly hampered however, by removal of sickly individuals by predators. Hyrax populations have been known to be affected by outbreaks of bubonic plague (Kingdon 1971) and sarcoptic mange (Hoeck 1982); and an acid-fast bacillus which causes pulmonary tuberculosis was isolated from lungs of hyrax collected in the New Bethesda region (Wagner, Buchanan, Bokkenheuser & Leviseur 1958; Wagner & Bokkenheuser 1961). This raises the speculation that the major population declines observed in the early 1980's may have been caused by disease. However, researchers were censusing hyrax at the time of the decline in the KRNP and did not observe any diseased individuals (N. Fairall pers. comm.). It does seem likely that disease might be involved in hyrax population declines, but it is probably encouraged by other circumstances such as high densities and drought. Major declines of springbok in 1984 on a farm at Victoria West (140km north east of the KRNP) were attributed to a lack of fermentable carbohydrate in the vegetation (Davies 1985), and it is considered most likely that the synchronous hyrax decline was also associated with such food stress.

At high densities, agonistic encounters between hyrax may also lead to deaths. Wounds inflicted by fighting amongst males can become heavily infested with ixodid ticks, and these animals sometimes die of secondary bacterial infection (Fourie 1983). Incidence of major fractures amongst hyrax skeletal material collected beneath eagle nests suggests that some hyrax may also die as a result of falls and other accidents. Heavy parasite burdens are suspected to cause some hyrax mortalities but this has not yet been confirmed by haematological study of wild animals (Fourie 1983). Hyrax parasite burdens become heavier during periods of good rains (Fourie 1983) - major population increases of hyrax recorded at such times (Chapter 4) do not indicate that heavier parasite loads cause any significant mortality amongst hyrax. Juvenile hyrax appear to be the most susceptible to non-predatory mortality. Fourie (1983) ascribes high mortality of juveniles to heavy parasite burdens; low fat reserves; low thermolability; greater susceptibility to disease; and a reluctance to forage away from natal colonies. These characteristics should indeed render juveniles less adept at coping with food stress during drought, but juveniles were observed to accompany adults on group foraging bouts away from colonies in the present study (Chapter 4).

The influence of variable recruitment on the hyrax population

The rate of addition of individuals to the hyrax study population between 1987 and 1990, in terms of mean litter size and pregnancy rate, was very similar to that recorded in other studies of rock hyrax populations in the Karoo (see Chapter 4). It was calculated that in a lower escarpment eagle territory recruitment over the entire study period averaged 352 juveniles per birth pulse (these comprised about 35% of the post birth pulse population). But this recruitment showed considerable annual variation in keeping with other studies (Millar 1971). Three principal factors are involved in this variability: ovulation rates; the incidence of precocious puberty in females; and the incidence of pre-natal mortality (Millar 1971; Fourie 1983). Millar (1971) showed that in good conditions ovulation rates can be considerably higher, and up to 33% of 4-5mth old female hyrax may conceive. These observations were offered as an explanation for the sudden population increases attributed to rock hyrax in the Cape. In less favourable conditions precocious puberty of females is negligible (Fourie 1983) or absent (Steyn 1980), and low ovulation rates result in small litter sizes (Millar 1971; Fourie 1983). Conception rates (in April) are probably most influenced by the amount of preceding summer rainfall (see Chapter 4). After conception in April some of the embryos or foetuses may be aborted or resorbed. Millar (1971) found foetal loss in up to 24% of litters in dry karoo areas (up to 10% foetuses lost), while Fourie (1983) noted heavier foetal loss among older females. Comparisons of reproductive data gathered from females shot in October with the estimated number of births in November were highly suggestive of late pre-natal mortality in 1990 (pages 52 & 62): the number of juveniles counted in December 1989 were only 1% less than predicted from the reproductive data (assuming no neo-natal mortality); whereas the number of juveniles counted in December 1990 were 64% less than expected. Fourie (1983) observed a significant correlation between the extent of pre-natal loss and rainfall during the gestation period (April - November). November rains explained 84% of the variation in hyrax recruitment in the present study (p. 49). Such rains are presumably important to the onset of lactation. But in keeping with Fourie (1983), strongest correlations were obtained between recruitment and rainfall over the entire gestation period from April to November (Figure 105).

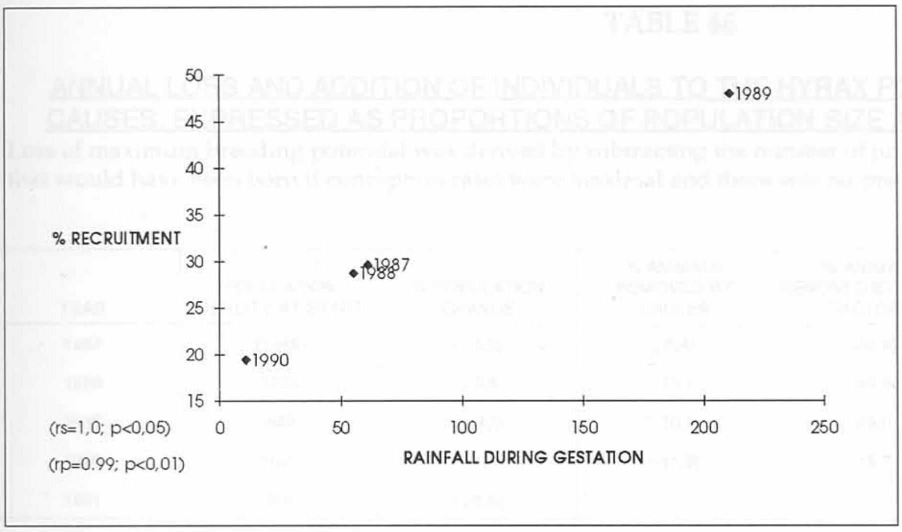

Figure 105. The relationship between hyrax recruitment (no. juveniles at a particular birth pulse compared with total population size at the start of the preceding year) and the amount of rain falling during the gestation period.

So the addition of individuals to rock hyrax populations varies dramatically with conception rates (influenced by preceding summer rains) and pre-natal mortality (influenced by rains during gestation). Alternating periods of enrichment and drought, so characteristic of the Karoo, are certain to lead to a changeable recruitment and a highly variable population structure. Population growth can be expected when favourable conditions lead to large birth pulses which may exceed the immediate capacity of local predation. The number of juveniles produced and the number of these which survive their first year are important factors involved in rock hyrax population change, because of their great variability and because of the magnitude of the juvenile population component.

Inter-annual variation of demographic factors affecting the hyrax population during the study period

Accurate hyrax census data were only obtained for the four birth pulses between November 1987 and November 1990, but inferences could be made on hyrax population size at the end of 1986 from incidental observations of decline. Some data were gathered in November 1991 but were not reliable. This yielded only 5 data points and four interims for most inter-annual comparisons of demographic factors affecting the hyrax population during the study period. Despite this small sample size, such comparisons may provide a valuable insight to the factors which were most involved in hyrax population change. This can be considered as a simple key-factor analysis (Varley & Gradwell 1960). Estimates of population change in each year of study, mortality to eagles, mortality to other factors, and recruitment, all expressed as a percentage of the population density at the start of respective years are given in Table 46. Trends emerging from correlation analyses performed on these data are given in Table 47. Only two relationships emerged as statistically significant for the appropriate Spearman's rank correlation test. Pearson's correlation coefficients as listed are not suited for testing the significance of relationships on such limited data, but they do give a more appropriate indication of the relative strength of co-relationships. Correlations between demographic factors and population change can be used to suggest which factors are limiting, and limiting factors can be considered regulatory if they are shown to be density-dependent (see earlier). For comparison of recruitment with mortality factors in this way, recruitment should be considered as loss of maximum breeding potential (Clutton-Brock, Major & Guinness 1985; Messier 1991). Loss of breeding potential was derived as the difference between the number of juvenile hyrax born and the number that would have been born if conception rates were maximal and pre-natal mortalities minimal.

TABLE 46

ANNUAL LOSS AND ADDITION OF INDIVIDUALS TO THE HYRAX POPULATION DUE TO VARIOUS CAUSES, EXPRESSED AS PROPORTIONS OF POPULATION SIZE AT THE START OF EACH YEAR

Loss of maximum breeding potential was derived by subtracting the number of juveniles born from the maximum number that would have been born if conception rates were maximal and there was no pre-natal mortality (see text)

YEAR	POPULATION DENSITY AT START	% POPULATION CHANGE	% ANIMALS REMOVED BY EAGLES	% ANIMALS REMOVED BY OTHER FACTORS	% ADDITIONS AT THE END OF THE YEAR	% LOSS OF MAXIMUM BREEDING POTENTIAL
1987	(1445)	(-15,3)	(-8,4)	(-36,5)	(+29,6)	(-63,4)
1988	1224	-26,6	-11,1	-44,1	+28,7	-56,5
1989	899	+14,0	-10,9	-23,0	+47,9	-50,7
1990	1025	-11,8	(-11,5)	-19,7	+19,4	-81,3
1991	904	(-26,6)				

TABLE 47

KEY-FACTORS ANALYSIS PERFORMED ON THE INTER-ANNUAL VARIATION OF CERTAIN FACTORS INVOLVED WITH HYRAX DEMOGRAPHY

Demographic values used in this analysis were expressed as proportions of population size at the start of the year(most are listed in Table 46). See Table 46 and text for an explanation of the loss in breeding potential. Spearman's rank correlation is the only appropriate test for the significance of relationships based on such limited data sets (n=4 intervals), but Pearson's correlation coefficients are also presented because these give a better indication of the amplitude of the correlation.

VARIABLES		Pearson's correlation	Spearman's correlation
population growth	total mortality	r=-0,72; p=0,27	n.s.
population growth	non-eagle mortality	r=-0,71; p=0,29	n.s.
population growth	loss of breeding potential	r=-0,33; p=0,68	n.s.
population growth	black eagle predation	r=-0,12; p=0,88	n.s.
population growth	population density	r=-0,70; p=0,30	n.s.
population density	black eagle predation	r=-0,80; p=0,21	n.s.
population density	non-eagle mortality	r=0,73; p=0,27	n.s.
population density	loss of breeding potential	r=0,05; p=0,95	n.s.
loss of breeding potential	preceding summer rain	r=0,97; p=0,03	n.s.
loss of breeding potential	total annual rain	r=-0,84; p=0,16	r=1,0; p<0,05
loss of breeding potential	gestation rain	r=-0,78; p=0,22	n.s.
recruitment	gestation rain	r=0,99; p<0,01	r=1,0; p<0,05
recruitment	total annual rain	r=0,90; p=0,10	n.s.
non-eagle mortality	preceding summer rain	r=-0,63; p=0,30	n.s.

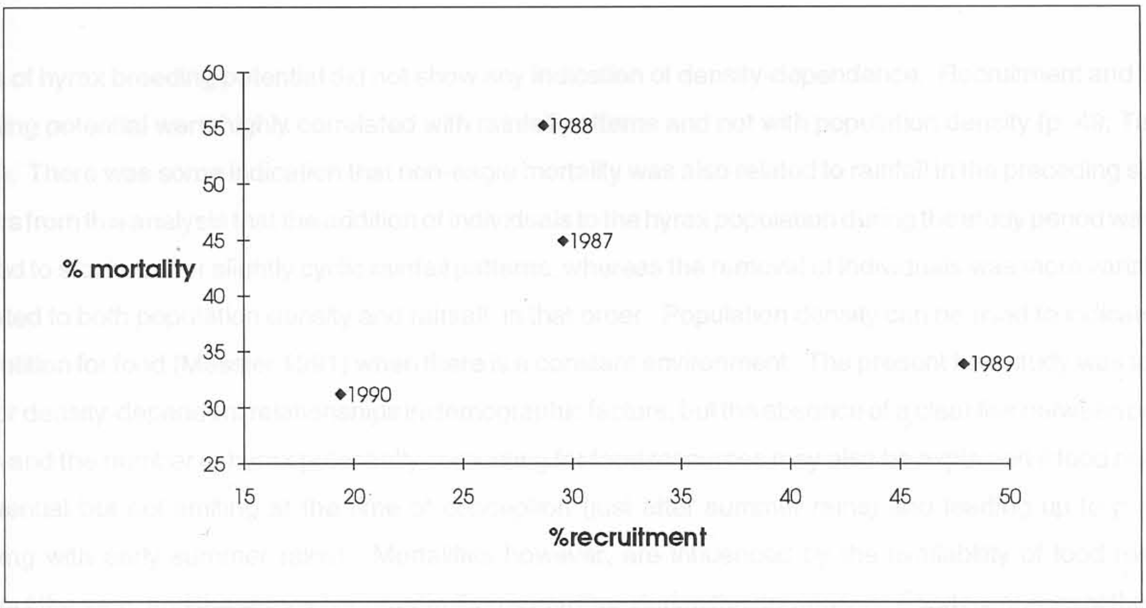

Figure 106. Annual plots of mortality and recruitment affecting the hyrax population for the four years of intensive field study. Mortality is calculated as the proportion of the starting population that dies in the following year. Recruitment is calculated as the proportion of the starting population that is added at the end of the year.

Hyrax population change during the study period showed stronger correlations with total mortality and non-eagle mortality than with the loss of breeding potential (Table 47). If recruitment is plotted against mortality for the four years of intensive study (Figure 106), it is relevant to note that the year of greatest population growth (1989) experienced minimal mortality and maximal recruitment, whereas the year of greatest decline (1988) experienced maximal mortality but recruitment was not below average. Numbers removed from the hyrax population during the study period showed more variation than numbers added, and population changes correlated more with the former than the latter (Table 47). Population change in rock hyrax is clearly the combined product of variable mortality and variable recruitment. Although birth pulses did vary dramatically during the study, these were not more responsible for the observed population changes than variation in mortality. There was an overall decline in hyrax numbers during this study - a different result from this analysis may have resulted had the study been conducted during a growth phase for the hyrax population. The involvement of variable additions and variable removals in hyrax population change through alternating growth and decline phases is explored by modelling in the second part of this chapter.

There was no suggestion of any statistical trend linking population growth with predation rate by black eagles. A slight trend between population growth and population density (Table 47) suggested some density-dependent factor/s may have been operating. Non-eagle mortality was the main factor which might have behaved in this manner during the study period. Predation rate by black eagles was apparently negatively correlated with density, but this trend could be entirely attributed to 1987 data when population density was not accurately determined. Black eagles actually captured more hyrax in 1988 (Chapter 8) when the prey population was larger than in subsequent years, but predation rate was remarkably consistent at 11% for the three years when the relevant parameters were well known.

The loss of hyrax breeding potential did not show any indication of density-dependence. Recruitment and the loss of breeding potential were highly correlated with rainfall patterns and not with population density (p. 49; Table 47; Fig. 106). There was some indication that non-eagle mortality was also related to rainfall in the preceding summer. It appears from this analysis that the addition of individuals to the hyrax population during the study period was highly correlated to stochastic or slightly cyclic rainfall patterns, whereas the removal of individuals was more variable and was related to both population density and rainfall, in that order. Population density can be used to indicate levels of competition for food (Messier 1991) when there is a constant environment. The present field study was too short to look for density-dependent relationships in demographic factors, but the absence of a clear link between breeding success and the number of hyrax potentially competing for food resources may also be explained if food resources are influential but not limiting at the time of conception (just after summer rains) and leading up to parturition (coinciding with early summer rains). Mortalities however, are influenced by the availability of food resources throughout the year, and these may become limiting some time during the dry season. Food resources at this critical period would presumably determine the carrying capacity in the vicinity of the refuge habitat to support hyrax. When numbers exceed this carrying capacity they should be more vulnerable to predation, and if predators are not able to remove the surplus, more susceptible to starvation also.

It is more sensible to expect mortality and predation of rock hyrax to vary with this excess or surplus, rather than as a simple function of density. Large populations of hyrax may be comfortably supported by ample food resources within their refuge habitat after good rains. It is clear that much of the variation in rock hyrax population density in the arid Karoo can be attributed to the short- or long-term influence of rainfall on the vegetation resources. Good rains maximise population growth by leading to both increased recruitment and reduced mortality. Droughts have the opposite effect, especially at high population density. Alternating wet and dry periods have the effect of destabilising hyrax numbers in the Karoo.

Predation by black eagles had the effect of limiting hyrax population growth but did not behave in a density-dependent manner during the present field study. Although black eagles are potentially capable of much higher prey capture rates than observed during the present study, territorial behaviour is strong in this species (Chapter 6) and limits the response that this predator might show to changes in prey density. However Gargett has recently (1992 unpubl.) provided evidence of surprisingly dramatic change in the number of territories maintained by black eagles in the Matobo Hills. If hyrax predation by black eagles is not density-dependent over the long-term, then current theory on predator-prey relationships would hold that such predation could not be regulatory (Kidd & Lewis 1987; Sinclair 1989; Messier 1991; Boutin 1992; Korpimäki 1992). But in the context of the highly variable, 'event-driven' karoo environment, any demographic factor which acts as a consistent 'hand-brake' on population growth may help prevent imbalance arising between prolific species such as hyrax and their changeable food resources. In the absence of experimental manipulation, the exact influence of such a factor can best be explored by population modelling.

PART 2

THEORETICAL PREDICTIONS ON THE LONG-TERM ACTION OF PREDATION BY BLACK EAGLES ON ROCK HYRAX POPULATION DENSITY IN THE KAROO

METHODS (part 2)

FORMULATION OF THE HYRAX POPULATION MODEL -

Population composition and age-specific rates of mortality and fecundity

A system dynamics model (Forrester 1968) was formulated for the hyrax population using the 13 annual age classes as recognised by Fourie (1983). Modelling the population to the resolution of these age classes was favoured over simpler versions because processes could then be based on sound biological data, and because recruitment can be expected to vary as the mature female component in the population structure varies. Initial composition of these age classes for males and females was derived from a spreadsheet model (MICROSOFT EXCEL version 4.0) which satisfied most observations of the hyrax population during the period of study (see Chapter 10: Fig. 92, p. 214; Table 36, p. 213), and which was stable over time. On account of the dramatic influence of rainfall on hyrax population structure (Chapters 4 & 10), such stability is strictly only representative of a population in an homogenous environment. However, this structure provided a useful point of departure for further modelling because it represented mediocre conditions when the hyrax population was neither increasing nor declining.

Minima and maxima rates of age-specific mortality and fecundity (pregnancy and litter size) were then needed in order to simulate population change under best conditions (small populations, well protected in the refuge habitat, after good rains) and worst conditions (large populations in an overcrowded refuge habitat during drought). These were derived from the present study (Chapter 4) and from other similar investigations (Millar 1971; Fourie 1983; Fairall *et al.* 1986). Some of the age-specific parameters had to be manipulated in the spreadsheet model in order to yield overall results on adult/immature mortality etc. which conformed to counts at colonies which were cruder (in terms of age classes), but were considered to be more reliable than the life table calculations performed on limited samples. The values used are given in Appendix 6. All further modelling was performed using TURBO PASCAL version 7.0 (Borland International Inc.). A complete print-out of the population model referred to in this chapter is supplied in Appendix 10.

Carrying capacity in a standard year

Actual age-specific rates of mortality and fecundity used by the model in a given year were derived (see next section) from the ratio of P:K, where P equals hyrax population size within a black eagle territory after the birth pulse; and K equals the number of hyrax that can comfortably be accommodated by food resources within the 'safe feeding area' as determined by rocky habitat in the territory. Behavioural observations and vegetation zones (Chapter 4: p. 56-57) indicated that hyrax foraged up to 15m from rocks in the KRNP, so the total 'safe feeding areas' in four neighbouring black eagle territories were determined by 'buffering' all rock outcrops on the geographical information system (ARCINFO) by a radius of 15m. Safe feeding area averaged 538ha (s.d.=24ha) and was the least variable habitat parameter across four eagle territories (but solid rock outcrops occupied 33% of this, leaving only 358ha available for normal plant growth). The carrying capacity of this area for rock hyrax in a standard year was calculated using mean group size for rock hyrax (=16,2: p. 46) and the average area over which individual groups ranged (derived as 4,8ha from Fig. 28, p. 53, for a group of 16,2 hyrax). Not all of the safe feeding area would be suitable for hyrax, but some flexibility in group size is also to be expected. It was concluded that the safe feeding area in an average eagle territory could comfortably accommodate 112 hyrax groups or 1816 individuals under conditions of average rainfall and food supplies (indicating that hyrax densities during the study period were at nearly 60% of this saturation density). Hereon, normal conditions refer to years of average rainfall and average plant production.

Interpolating mortality and fecundity on P:K ratio

A fundamental assumption of the model is that hyrax mortality is raised and fecundity is lowered when P exceeds K, whereas the reverse situation engages when P is lower than K. Actual values for age-specific mortality and fecundity were chosen in a given year by linear interpolation (between average and extreme values) based on the discrepancy between P and K. Detailed field data are not yet available on this relationship so a simple linear function was assumed. The discrepancy between P and K necessary to invoke the maximal or minimal rates of mortality and fecundity presented in Appendix 6 is explored later in the modelling - a factor of 3,5 was chosen for standard runs of the model. This is also based to some degree on field data: very heavy mortality and lowered fecundity resulted in a four-fold decline in the hyrax population in the KRNP during the early 1980's (Fairall 1991, *in litt.*), and it was assumed that the hyrax must have exceeded the carrying capacity of their habitat by about four times in order to invoke this decline. So predation is handled in a ratio-dependent manner in the present model, but the predation response is (unconventionally) dependent on the ratio between hyrax and their food resources rather than the ratio between predators and prey. Modelling mortality and fecundity in this way accounts for the way in which food-stress, crowding (and disease transmission), and vulnerability to predation can be expected to vary. It also accommodates for compensatory effects in recruitment resulting from heavy predation. Data in the first part of this chapter suggested that the addition of individuals to the hyrax population was primarily related to rainfall patterns and not population density. This may be because the study was carried out during relatively low hyrax population densities. Nevertheless, accommodation is made in the population model to compare recruitment modelled on rainfall with recruitment modelled on P:K ratio. That hyrax mortality should be high when P far exceeds K seems intuitive, but this fundamental assumption of the model is also based on a few lines of field evidence with regard to predation.

During the present study, black eagle predation and other mortalities of hyrax were highest in the dry year of 1988 and lowest in the wet years of 1989 and 1990 (Chapters 4 & 8). There was also limited indication that hyrax remained closer to shelter in good conditions (Chapter 4) and that the delivery rate of rock hyrax prey to black eagle nests declined shortly after good rains (Chapter 8). In the Matobo Hills, black eagle breeding success improved from wet years to dry years and declined from dry years to wet years for 23 of the 27 years monitored (see Fig. 107: data given in Gargett 1990, referred to by Allan 1988). The four years when this pattern was not evident occurred after the major hyrax decline in the early 1980's (V. Gargett *in litt.*; R. Barry pers. comm.). Breeding success in raptors is normally related to prey availability (Newton 1979). Bounty records for the Cape Province show that more rock hyrax were destroyed (probably shot) during the dry year of 1949 than in the preceding wet years, suggesting that hyrax mortality due to human predation also increases during drought (P. Norton *in litt.*; see Fig. 108) . Many farmers report that hyrax emerge from rocky outcrops and range farther to feed as conditions become drier (pers. rec.). The fore-going rationale is similar to that proposed by Jones (1979) in a simple model of prey populations (pertaining to vertebrates) where different components of the population are exposed to different rates of predation.

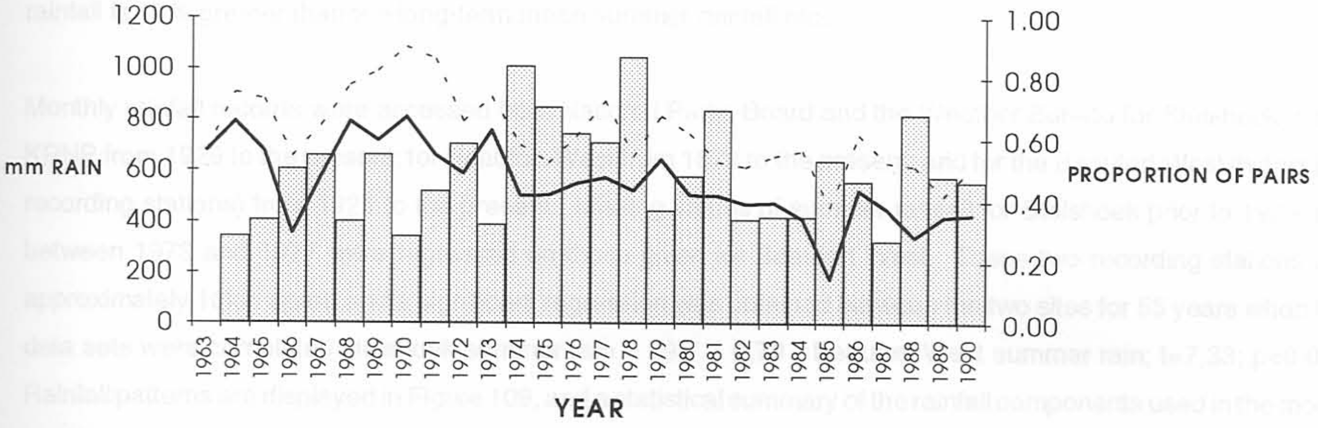

Figure 107. Summer rainfall patterns in the Matobo Hills, Zimbabwe, and concordant change in the effort and success of black eagle breeding attempts monitored by Gargett (1990: Tables 1 & 34) & Banfield (*in litt.*). For most of Gargett's study, eagle breeding success improved as rainfall declined and dropped off as rainfall improved (see text). This is thought to reflect changes in hyrax vulnerability and the data are shown here to support rationale adopted in the present hyrax model.

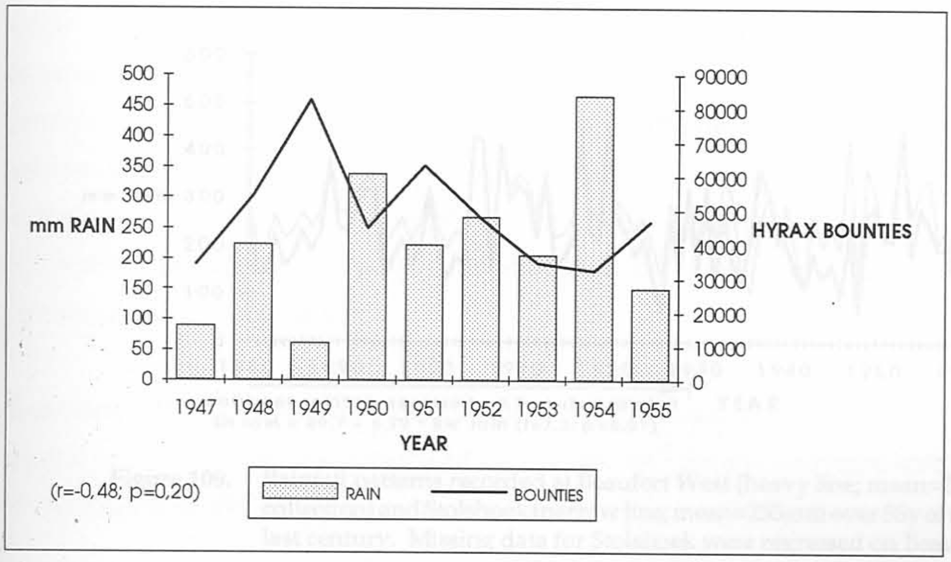

Fig. 108. Bounties paid out for the destruction of hyrax in the Cape Province between 1947 and 1955, and rainfall patterns over the same period (from data records of CDNEC - Norton *in litt.*). Beaufort West hyrax bounties reflected a similar trend.

A dynamic measure of carrying capacity

Hyrax population processes were also modelled on the relationship of P to K in previous theoretical investigations (Fairall *et al.* 1986; Swart *et al.* 1986), but K was not based on measurement of rocky habitat in those studies. The present model departs further from these studies by introducing the concept of a dynamic value for K which can take into account the effects of enrichment of the lower trophic level: while the safe feeding area in an eagle territory is a relatively permanent feature determined by the distribution of rocks, the number of hyrax that it can safely support will be greater than standard K in years of good rainfall, and less than standard K during drought. Departure of K from standard K in years of varying rainfall should primarily relate to variation in plant production (hyrax food supply). Extensive analyses of the relationship between rainfall and plant production in arid and semi-arid range-lands by Le Houérou, Bingham & Skerbek (1988) have revealed that variability (measured as the coefficient of variation: $\sigma / \bar{x}$) in plant production on these lands is 1,5 times greater than variability in rainfall. Thus, if the standard deviation of annual rainfall is 10% larger than the mean value, then the standard deviation of annual plant production will be 15% larger than its respective mean. In this model it is assumed that K will be 15% greater than standard K when summer rainfall is 10% greater than the long-term mean summer rainfall etc..

Monthly rainfall records were accessed from National Parks Board and the Weather Bureau for Stolshoek in the KRNP from 1929 to the present; for Beaufort West from 1879 to the present; and for the Beaufort West district (32 recording stations) from 1921 to the present. Missing values of summer rainfall for Stolshoek prior to 1929 and between 1973 and 1977 were regressed on those given for Beaufort West. These two recording stations are approximately 10km apart, and a significant regression was obtained between the two sites for 55 years when the data sets were complete (Stolshoek summer rain = 89,7 + 0,79 * Beaufort West summer rain; t=7,33; p<0,01). Rainfall patterns are displayed in Figure 109, and a statistical summary of the rainfall components used in the model is given in Appendix 7. For most runs of the model, Beaufort West rainfall data are used because of the long history of raw data collection.

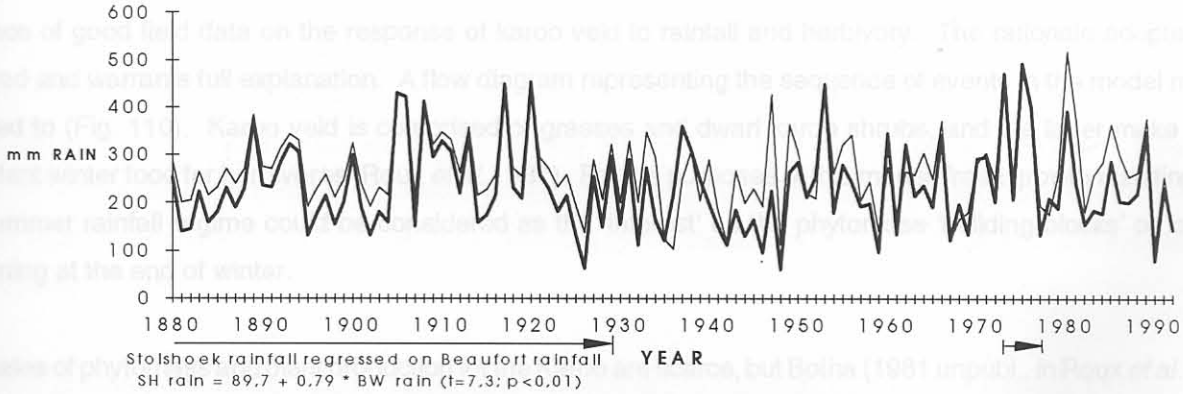

Figure 109. Rainfall patterns recorded at Beaufort West (heavy line; mean=212mm over 55y of raw data collection) and Stolshoek (narrow line; mean=255mm over 55y of raw data collection) over the last century. Missing data for Stolshoek were regressed on Beaufort West data as shown.

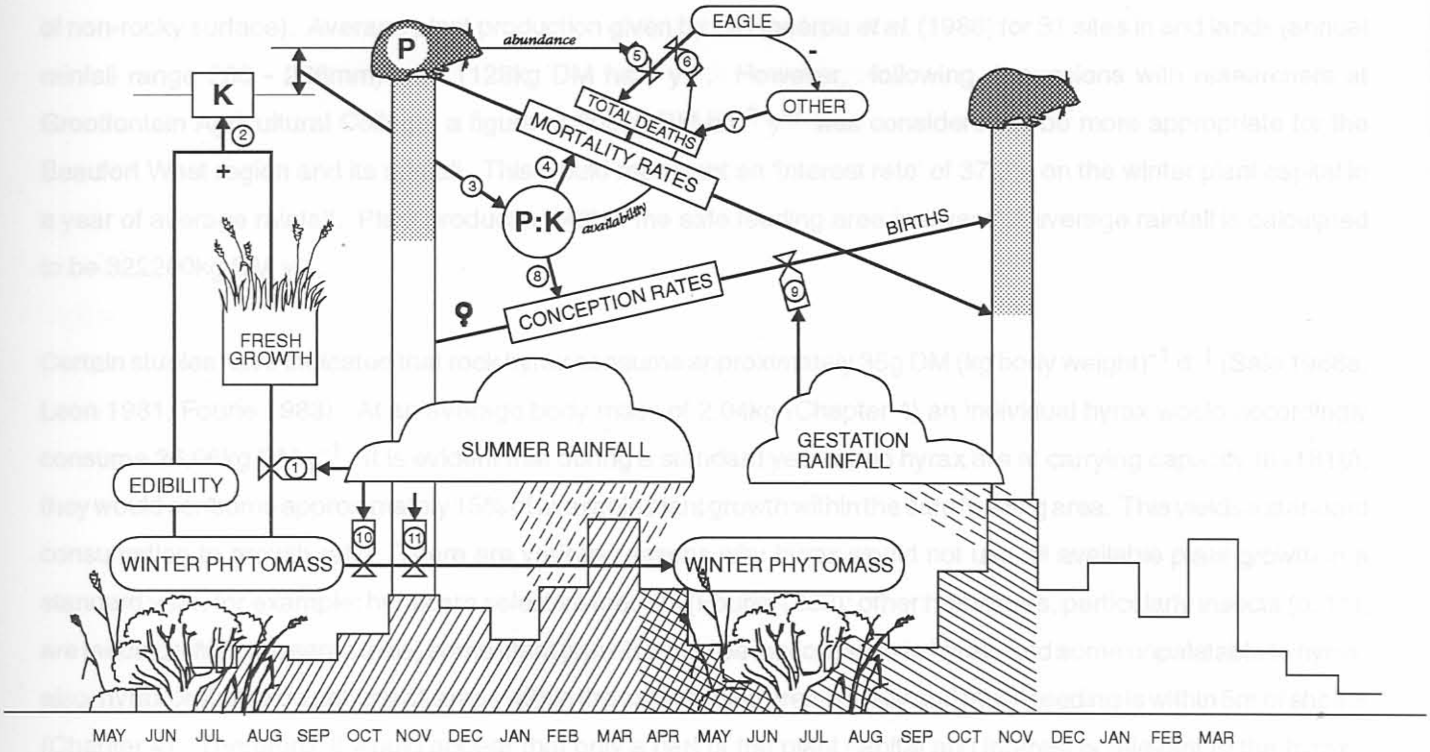

Figure 110. Schematic flow-diagram of the hyrax population model. The various steps at each iteration of the model (from one year to the next) are numbered for refering from the text. Shaded histograms at the base of the diagram represent the different rainfall components used by the model. Tall columns represent the hyrax population (P) within a standard eagle territory at each birth-pulse (juvenile component shaded). K is the carrying capacity of food supplies in the vicinity of the refuge habitat. See text for full explanation.

Lower trophic interaction between vegetation, rainfall and hyrax

Annual estimates of K derived in this way were very erratic and were an instantaneous reflection of rainfall. They did not take into account the cumulative effects of good or bad years on karoo veld. It was considered that phytomass should improve after good rains and decay slowly during drought; while significant depletion of the phytomass may occur during years of very high consumption by hyrax. Modelling this lower trophic interaction was difficult in the absence of good field data on the response of karoo veld to rainfall and herbivory. The rationale adopted was involved and warrants full explanation. A flow diagram representing the sequence of events in the model may be referred to (Fig. 110). Karoo veld is comprised of grasses and dwarf karoo shrubs, and the latter make up an important winter food for herbivores (Roux *et al.* 1981). For the purposes of this model, fresh growth resulting from the summer rainfall regime could be considered as the 'interest' on the phytomass 'building blocks' or 'capital' remaining at the end of winter.

Estimates of phytomass and plant production for the Karoo are scarce, but Botha (1981 unpubl., in Roux *et al.* 1981) gave a figure of 2415kg dry matter (DM) phytomass ha^{-1} for well managed karoo veld in winter. This would yield an estimate of 864570kg DM for winter plant capital within the safe feeding area in an average eagle territory (358ha of non-rocky surface). Average plant production given by Le Houérou *et al.* (1988) for 31 sites in arid lands (annual rainfall range 200 - 266mm) was 1128kg DM ha^{-1} y^{-1}. However, following discussions with researchers at Grootfontein Agricultural College, a figure of 900kg DM ha^{-1} y^{-1} was considered to be more appropriate for the Beaufort West region and its rainfall. This would represent an 'interest rate' of 37,3% on the winter plant capital in a year of average rainfall. Plant production within the safe feeding area in a year of average rainfall is calculated to be 322200kg DM y^{-1}.

Certain studies have indicated that rock hyrax consume approximately 35g DM (kg body weight)$^{-1}$ d^{-1} (Sale 1966a; Leon 1981; Fourie 1983). At an average body mass of 2,04kg (Chapter 4) an individual hyrax would accordingly consume 26,06kg DM y^{-1}. It is evident that during a standard year when hyrax are at carrying capacity (n=1816), they would consume approximately 15% of available plant growth within the safe feeding area. This yields a standard consumption to growth ratio. There are various reasons why hyrax would not use all available plant growth in a standard year, for example: hyrax are selective feeders (Fourie 1983); other herbivores, particularly insects (p. 11), are feeding within the same area; some plant growth would be inaccessible to hyrax; and some unpalatable to hyrax; also, hyrax probably do not use all areas within the safe feeding area equally and much feeding is within 5m of shelter (Chapter 4). Therefore, it would appear that only a part of the plant capital and interest is relevant to the hyrax.

On the assumption that plant capital would be depleted when consumption to growth ratio was greater than the standard ratio, and that capital would accumulate when consumption to growth ratio was lower than the standard ratio, annual change in plant capital was initially modelled on departure from the standard ratio. Allowances had to be incorporated in this sub-routine for the magnitude of the hyrax consumption, as well as the consumption to growth ratio. This 'ratio-dependent' approach has found favour in the emulation of enrichment of lower trophic levels (Slobodkin 1992), but the approach assumes that hyrax consumption and rainfall have an equal and opposing influence on phytomass, and problems arose in the lower trophic model when the removal of predators was artificially simulated. Plants grow in response to rainfall not the absence of herbivory. Removal of plant matter by herbivory is probably far more effective than the decay of phytomass during drought. So it was considered that rainfall would be more involved in the accumulation of phytomass, while consumption by hyrax would be more involved in its depletion.

In order to accommodate this, it became necessary to separate the capital modification into two steps (elements 10 & 11 in Fig. 110). The first step was to modify capital (phytomass) in response to rainfall. A rainfall 'modifier' was derived which would cause capital to accumulate by 25-30% in the very wettest years, and to decay by 5-6% in the very driest years. In any year, the rainfall modifier was selected as a value between 0,94 and 1,30 by linear interpolation based on the difference between rainfall in that year and minimum and maximum long-term rainfall values. Again, a simple linear function had to be assumed here in the absence of detailed field data on the response of karoo veld to rainfall.

The second step represented capital modification in response to herbivory by hyrax. Modelling this interaction proved difficult because the estimates of phytomass consumed by hyrax were minute in comparison to estimates of total phytomass in the safe feeding area. From the estimate that hyrax at standard K (1816) removed only 15%

of fresh growth in the safe feeding area under conditions of average plant growth, it was assumed that only 15% of the total capital was relevant to the hyrax - the remainder being largely inedible, unpalatable or fed on by other animals. It was decided to reduce winter capital to 15% of its total value and use this in all calculations of the model so that absolute values of growth and consumption could be compared. So in a year of average rainfall the fresh growth on this reduced capital should equal the consumption of 1816 hyrax. In years when consumption was less than fresh growth, it was assumed that hyrax could obtain all their food requirements from the fresh growth, and capital subsequently remained unchanged. In years when consumption was greater than fresh growth, the exact deficit was removed from the (reduced) capital, minus some portion which could be obtained from the less palatable or less accessible phytomass and growth. The latter component was described as the unpalatable buffer, and this was set as 10% of the hyrax food needs that were not met by fresh growth.

Trial runs of the model using this arrangement for capital modification resulted in rates of phytomass change which were in keeping with observations on the decline and recovery periods for karoo biota during major events such as the 1983-84 drought (e.g. see Fig. 59, p. 132), and with the contentions of range managers. Winter capital could totally recover or totally deteriorate between its minimum and maximum limits over about four or five years, in extreme circumstances. For phytomass to show such annual variation in the absence of any stabilising functions in the lower trophic model necessitated upper and lower constraints. Vegetation analyses within and outside the main feeding area of a hyrax colony revealed that edible phytomass was 30% greater beyond the 15m zone (Chapter 4). These analyses were carried out during the dry summer of 1988, and it is estimated that phytomass may have improved by another 30% during wetter conditions. Accordingly, phytomass was generally constrained by 30% above and below the mean value in the model. These constraints are justified on the basis that karoo veld does not change from being a dwarf shrubland even after excellent rains, and that woody, inedible phytomass would always persist even in years of very heavy grazing by hyrax.

In any year, fresh growth on this changing capital was determined in accordance with summer rainfall (e.g. 15% more growth than the usual interest rate, if rainfall was 10% greater than the mean; element 1 in Fig. 110). Total hyrax food resources in a given year were calculated as fresh growth plus the edible component (set at 10% - element 2 in Fig. 110) of the winter capital. Food resources in a standard year can accommodate 1816 hyrax. So the number of hyrax that can be accommodated in a given year was derived by comparing food resources in the given year with standard food resources. This dynamic estimate of K was thus sensitive both to the immediate effects of rainfall, and to the long-term effects of enrichment, or drought and heavy grazing. The annual change in K for a standard run of the model is shown in Figure 111 along with the earlier version of K which was based solely on annual rainfall and fresh growth on a fixed winter capital. The highly erratic behaviour of the latter has been replaced by a more gradual accumulation or depletion of carrying capacity which is considered more realistic for the Karoo. Modelling carrying capacity in this way, it is implicitly assumed that food supply around rocky habitat is limiting, rather than the availability of rock crevices for overnight shelter. In Chapter 4 it was estimated that the mean number of rock crevices per eagle territory (n=4) was 44350 (s.d.=6152). Further rationale to justify this assumption is presented later.

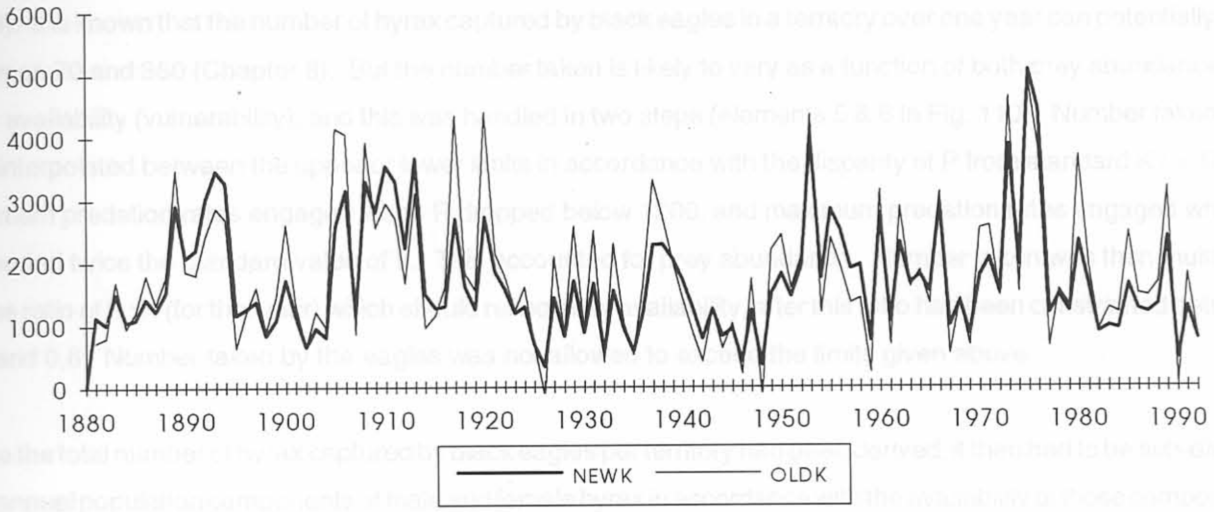

Figure 111. Change in two versions of carrying capacity (number of hyrax that can be supported in a standard eagle territory) predicted by a standard run of the model (from 1880 to 1992). One version (OLDK) is based simply on annual rainfall; the other (NEWK) incorporates the influence of cummulative changes in phytomass resulting from good or bad years (see text for full details).

Pre-natal mortality

The mortality and fecundity rates for hyrax were interpolated in accordance with the departure of P from K as mentioned earlier (elements 3, 4 & 8 in Fig. 110), but an additional factor was incorporated to represent pre-natal mortality (foetal-resorption) in very dry years (which could not be related to the previous summer rainfall season). Extensive pre-natal mortality was inferred for the very dry period at the end of 1990 (Chapter 4). Pre-natal mortality has also been recorded by Fourie (1983) and Millar (1971). In keeping with the findings of Fourie (1983), correlation analyses in the first part of this chapter revealed that rainfall during the entire gestation period (rather than rain falling late in the gestation period) was most closely related to variation in births, so this component of the rainfall (April - November) was used to modify pre-natal loss (element 9 in Fig. 110). Missing rainfall data for Stolshoek were regressed on Beaufort West data using the following equation: Stolshoek rainfall during gestation = 36,3 + 1,03 * Beaufort West rainfall during gestation ($t=9,2$; $p<0,01$). Foetal resorption was allowed to vary between 2% and 20% (mean = 11%), and this was interpolated on the difference of rainfall during gestation from the long-term mean for this parameter. A similar interpolation was used as an option to explore the potential influence of sex-biased recruitment in response to rainfall (as suggested in Chapters 4 & 10).

Removals by black eagles

Black eagles can be considered specialist predators of rock hyrax and pursue this prey even at low density (Chapters 8 & 9). It is known that the number of hyrax captured by black eagles in a territory over one year can potentially vary between 70 and 350 (Chapter 8). But the number taken is likely to vary as a function of both prey abundance and prey availability (vulnerability), and this was handled in two steps (elements 5 & 6 in Fig. 110). Number taken was first interpolated between the upper or lower limits in accordance with the disparity of P from standard K (= 1816). Minimum predation rates engaged when P dropped below 1200, and maximum predation rates engaged when P exceeded twice the standard value of K. This accounted for prey abundance. Number taken was then multiplied by the ratio of P : K (for that year) which should reflect prey availability, after this ratio had been constrained between 1,4 and 0,6. Number taken by the eagles was not allowed to exceed the limits given above.

Once the total number of hyrax captured by black eagles per territory had been derived, it then had to be sub-divided into annual population components of male and female hyrax in accordance with the availability of those components in the prey population, and with the preference shown by black eagles for those components. Preference ratings for the various population components were calculated in Chapter 10 (Fig. 93, p. 216), and are given in Appendix 8. Because preference ratings had been derived from field data as percent use of respective components among eagle prey divided by percent availability amongst the prey population, it followed that by multiplying the number of hyrax in each component of the population being modelled by its respective preference rating an artificial population was derived which should reflect the composition of the sample of hyrax that would be taken by the eagles. This artificial population was then proportionally reduced to conform to the number of hyrax that the model predicted the eagles would capture in that particular year. To compare selective with non-selective predation by black eagles, all preference ratings were set to unity.

For standard runs of the model with predators present all mortality could be embraced in one operation, but for the investigation of the influence of age-selective predation, and for the simulated removal of the eagles, it was necessary to separate hyrax captured by black eagles from hyrax dying from other factors (element 7 in Fig. 110). Simply replacing animals that would have died due to eagle predation back into the population to emulate predator-removal did not prove to be a realistic option. As the hyrax population outgrew its carrying capacity in the absence of eagle predation, the model predicted a maximum eagle kill (350 p.a.) - when this inflated 'kill' was returned to the population as survivors at each iteration, the net result was that fewer hyrax were dying from non-eagle mortalities than in a standard run of the model and the simulated removal was grossly exaggerating the influence of the eagles.

To emulate predator removal more realistically, mortality due to eagles and mortality due to other factors had to be modelled separately. Fortunately age-specific mortality to eagles and age-specific mortality to all causes (inclusive mortality) were both known for varying conditions, so age-specific mortality rates due to factors other than eagles could be calculated at each iteration by subtraction during a standard run of the model. Mean, minimum and maximum age-specific mortality rates to factors other than eagles derived in this way are presented in Appendix 9. Test runs of the model (with mortality modelled in two steps) were then conducted to ensure that 'non-eagle' mortality was behaving in the same fashion whether eagles were present or not. In consistent standard runs of the model, 'non-violent' mortalities (total deaths minus black eagle and caracal kills) were estimated to kill 25,7% of hyrax when total deaths were modelled inclusively, and 25,8% of hyrax when eagle and non-eagle mortalities were modelled separately. The similarity in hyrax population change for standard runs of the model using both inclusive and separated mortality models is shown in Figure 112a. The highly exaggerated effect of eagle removal in the old earlier version is evident in Figure 112b. Separated mortality rates are used for all runs of the model unless otherwise stated.

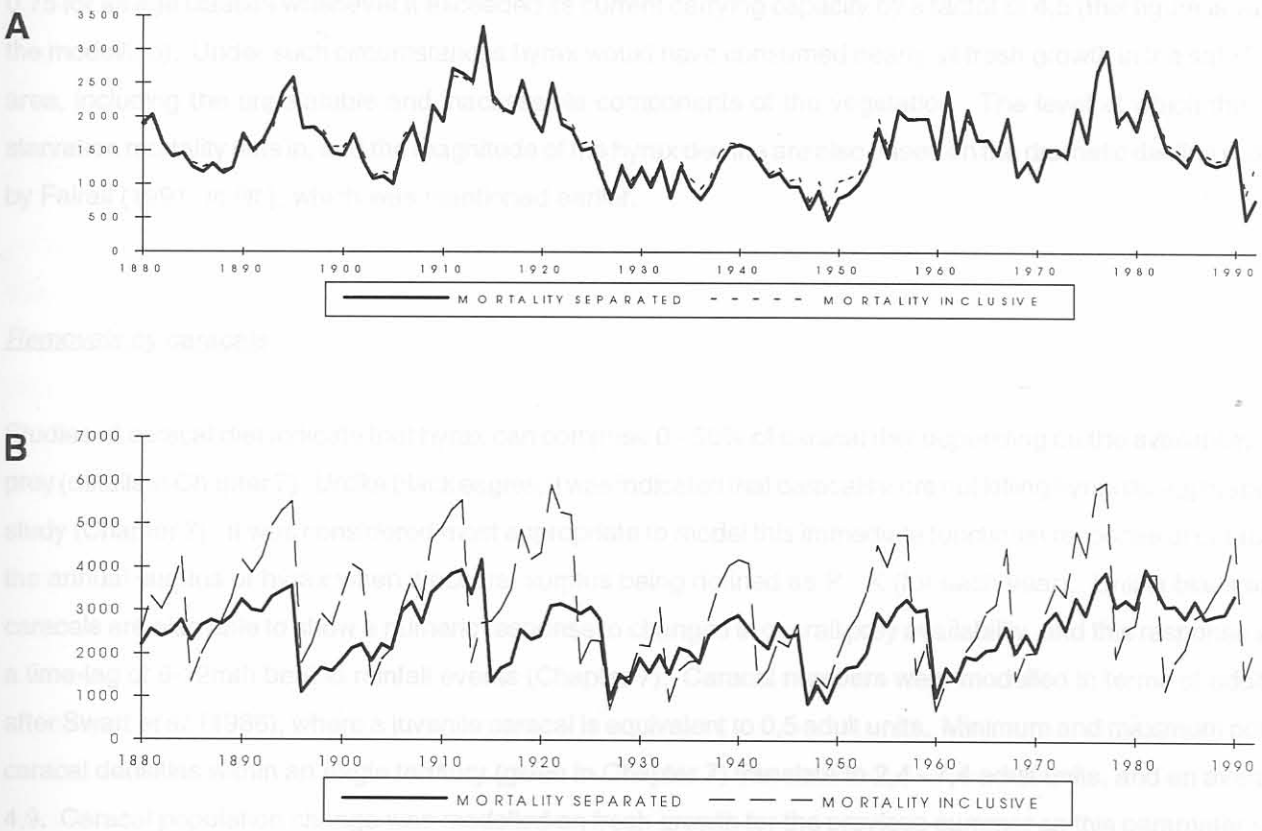

Figure 112. Predicted change in hyrax density (per eagle territory) using two model versions with full complement of predation (A) and with eagles removed (B). Mortalities due to eagles were modelled separately from mortalities due to other causes in the updated version. This predicts a very similar pattern of hyrax population change to the old version (inclusive mortality) when predators are present (A) but the old version led to gross exaggeration of the influence of removing eagles (B). See text for a full explanation of why the mortality factors had to be modelled separately.

Compensatory mortality

It is still not appropriate to assume that all of the potential hyrax prey of black eagles would survive had they not been killed by eagles. A certain component of the potential prey animals would have died anyway. This compensatory mortality was handled in two ways. First, it was assumed that 10% of hyrax captured by black eagles would have died anyway due to old age, accidents and other inevitable causes, irrespective of the prevailing environmental conditions. Old hyrax are highly preferred by the eagles and comprised 16% of all hyrax captured during the study period (Chapter 10). Compensatory mortality due to starvation and disease was treated separately because these factors probably only come into play when the hyrax population interacts destructively with vegetation resources. The worst-case figures of inclusive mortality given in Appendix 6 were derived mostly from data gathered during the present study when the hyrax population did not decline dramatically. Therefore these mortality rates would be unlikely to result in a dramatic decline if the hyrax food resources were to collapse. It was important that the same conditions for this starvation and disease mortality should prevail whether predators were removed or not. For the purposes of the model it was assumed that the hyrax population would experience a very heavy mortality rate of 0,75 for all age classes whenever it exceeded its current carrying capacity by a factor of 4,5 (this figure is varied in the modelling). Under such circumstances hyrax would have consumed nearly all fresh growth in the safe feeding area, including the unpalatable and inaccessible components of the vegetation. The level at which this heavy starvation mortality sets in, and the magnitude of the hyrax decline are also based on the dramatic decline observed by Fairall (1991, *in litt.*), which was mentioned earlier.

Removals by caracals

Studies of caracal diet indicate that hyrax can comprise 0 - 50% of caracal diet depending on the availability of this prey (details in Chapter 7). Unlike black eagles, it was indicated that caracals were not killing hyrax during the present study (Chapter 7). It was considered most appropriate to model this immediate functional response of caracals on the annual surplus of hyrax when it occurs, surplus being defined as P - K (for each year). Unlike black eagles, caracals are also able to show a numeric response to changes in overall prey availability, and this response shows a time-lag of 6-12mth behind rainfall events (Chapter 7). Caracal numbers were modelled in terms of adult units after Swart *et al.* (1986), where a juvenile caracal is equivalent to 0,5 adult units. Minimum and maximum potential caracal densities within an eagle territory (given in Chapter 7) translate to 2,4 - 7,4 adult units, and an average of 4,9. Caracal population change was modelled on fresh growth for the previous summer as this parameter should provide a good measure of environmental enrichment, and is also used to model hyrax population change (the latter being an important potential prey of caracals). The increase or decline of caracal numbers was not allowed to exceed 30% per annum (Chapter 7) and was derived by a direct linear interpolation on fresh growth, in relation to minimum and maximum values. Numbers were not allowed to exceed the density constraints given above.

Hyrax surplus was divided by the number of caracals to give a measure of availability per predator, after 75% of the number captured by black eagles had been subtracted from the total surplus. Black eagles were given this advantage because they are highly specialised predators of rock hyrax and able to hunt this prey even at low availability - this predation is likely to detract somewhat from the surplus available to the more generalist caracals. It is unlikely that caracals would remove every remaining surplus hyrax but they probably capture a small number of hyrax even when these are well protected (despite the fact that this was not detected by methods employed in the present study). The minimum proportion of hyrax in caracal diet was set at 2% for all years. In years when there was a surplus of hyrax, the proportion of caracal diet made up by this prey was modelled on surplus per caracal. The maximum number of hyrax that may be captured by a single adult caracal is estimated to be 206 p.a. It was assumed that hyrax would comprise a maximum portion of caracal diet (50%) when surplus per caracal exceeded 250.

The number of hyrax captured per adult caracal was calculated as: the total food requirement of an adult caracal (463 kg p.a. - see Chapter 7) multiplied by the portion of caracal diet in that year that would be comprised of hyrax, and divided by the amount of food available on an average hyrax (1,122kg - see Chapter 8). This value was then multiplied by the number of adult caracal units per eagle territory in that year to yield the total number of hyrax captured by caracals. In the absence of data on age-specific predation by caracals it was assumed that caracals captured the various components of the hyrax population in direct relation to their availability (after Swart *et al* 1986).

Predator impedance

Hyrax predation by caracals has not been studied in as much detail as that by black eagles. For most purposes of this model the number of hyrax captured by caracals was estimated but not used in the modelling processes - it was assumed that predation by caracals comprised part of the non-eagle mortality. Predation by caracals could not be separated from remaining mortality factors in the same fashion as black eagle predation because of the poor data, and also because caracal predation was modelled in a very different way (on surpluses). However, it was desirable to know how the model would behave to impedance of both black eagles and caracals in varying degrees of predator persecution. This is termed the predator impedance factor and is considered more appropriate for the karoo situation because caracals are actually more likely to be persecuted than black eagles and neither predators have been totally eradicated. A factor which impedes predators to varying degrees can also be considered on the same continuum as compensatory mortality, which is still a largely unknown element in this system. To run the model on 10% predator impedance, the number of hyrax dying in any given year was computed as: (90% of the potential black eagle kill) + (all non-eagle mortality - 10% of the potential caracal kill). Non-eagle mortality is protected from the effects of inflating eagle kills as described above. Any exaggerations due to inflation of the potential caracal kills impinging on remaining mortality factors could be checked by studying the behaviour of non-predatory mortality with and without impedance. When both predators were impeded by 50%, the portion of hyrax dying non-violently did drop slightly to 24,6%.

Estimating the cost of hyrax vegetation impact to karoo farmers

Lensing (1982) calculated that rock hyrax on Namibian farmland in the Karas Mountains do not have a dramatic detrimental effect on farm revenue (less than 1% gross revenue) because livestock do not make extensive use of the rocky habitats favoured by hyrax, and because hyrax use much vegetation which is unavailable to livestock. So any reduction of phytomass by hyrax in the vicinity of rocky habitat is probably not of great financial significance to karoo farmers. Consumption of karoo veld by hyrax can be expected to impinge on the forage resources of domestic livestock when hyrax exceed the immediate carrying capacity of phytomass in the vicinity of rocky habitats and are forced to meet their forage requirements by moving farther from the rocks to feed. The surplus of rock hyrax in such years can effectively be measured as P - K.

Food consumption by hyrax is given as 35g DM/kg body weight/day (see earlier). Thus an adult hyrax weighing 3,2kg can be expected to consume 112g food per day. This measure will of course depend on the energy content of the feed. Adult Merino sheep on arid rangelands consume about 1,2kg of vegetation (DM) per day (Davies 1985; Short 1985). An adult Merino needs to consume 10,7 times as much food as an adult rock hyrax. Hyrax may need to consume greater quantities of bulk karoo veld than indicated, but they are selective feeders (Fourie 1983) and it is likely that they would choose smaller quantities of energy-rich food from the veld, so the estimate of daily food consumption may not be far wrong.

Kleiber (1975) noted that energy demand was directly related to metabolic weight (body mass^{0,75}). Metabolic mass of an adult rock hyrax weighing 3,2kg is calculated as 2,4 kg, and that of an average rock hyrax weighing 2,04kg (Chapter 4) as 1,71kg. Metabolic mass of an adult Merino sheep weighing 45kg (Davies 1985; R. Wilmot pers. comm.; D. Conroy pers. comm.) is calculated as 17,4kg. This indicates that an adult Merino sheep needs to metabolise 7,3 times as much food energy as an adult rock hyrax and 10,2 times as much food energy as an average rock hyrax.

One adult Merino sheep is evidently equivalent to 7,3 - 10,7 rock hyrax in terms of energy and food requirements. For economic calculations at the end of this chapter it is assumed that one adult unit in the domestic sheep population is equivalent to ten units in the hyrax population. A monetary value can be ascribed to grazing requirements given the current (1993) letting rates for karoo veld of approximately R30 per head (small stock) per annum (R. Wilmot pers. comm.; D. Conroy pers. comm.).

RESULTS AND DISCUSSION (SECTION 2)

PREDICTIONS OF THE MODEL -

Standard run with predators present

The predicted changes in hyrax numbers, winter phytomass and fresh growth for an average eagle territory near Beaufort West between 1880 and 1992 are shown in Figure 113 for a standard run of the model with predators present. Peaks in hyrax numbers correspond to periods of good growth on undepleted winter phytomass. While declines correspond with drought as expected. Minimum time taken for phytomass to change between upper and lower constraints is about six years, but slightly smaller yet dramatic changes in phytomass take place within a few years, which is considered to be appropriate for karoo veld. Predicted values of P are plotted against the changing estimates of K in Figure 114. Although hyrax numbers do not change as erratically as K, it is clear that under normal circumstances the hyrax population can comfortably track the less sudden but more dramatic changes in carrying capacity brought about through accumulation or depletion of the phytomass. Close tracking of K by P under normal conditions prevents the occurrence of large surpluses of hyrax. Nevertheless, it is estimated that the annual surplus of hyrax in a black eagle territory near Beaufort West averages 466 (with the full complement of predators).

The peaks in hyrax numbers predicted by the model do not correspond to reports in the literature of hyrax irruptions in southern Africa (mainly the Karoo). These irruptions are denoted by asterixes in Figure 113. The reported irruptions all correspond rather to periods of low rainfall and drought following three to seven years after enrichment. It appears from the model that these irruptions were not population explosions at all, but more likely to be major decline phases where large increases in hyrax numbers due to enrichment subsequently experience serious imbalance with food supplies during drought. Under such conditions it is to be expected that food resources in the vicinity of rocky shelter would be depleted and that the hyrax would be forced further from the rocks to feed. At the

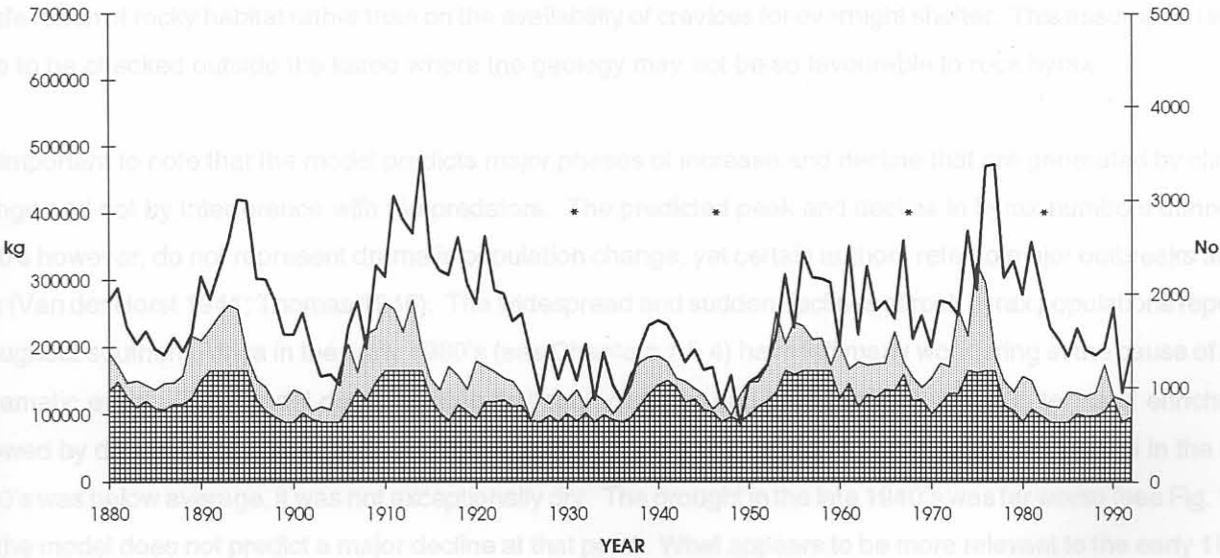

Figure 113. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a standard run of the model with the full complement of predation, using Beaufort West rainfall data. Asterixes denote timing of hyrax irruptions reported in the literature. Phytomass values are expressed as kg dry matter in the 'safe feeding area'.

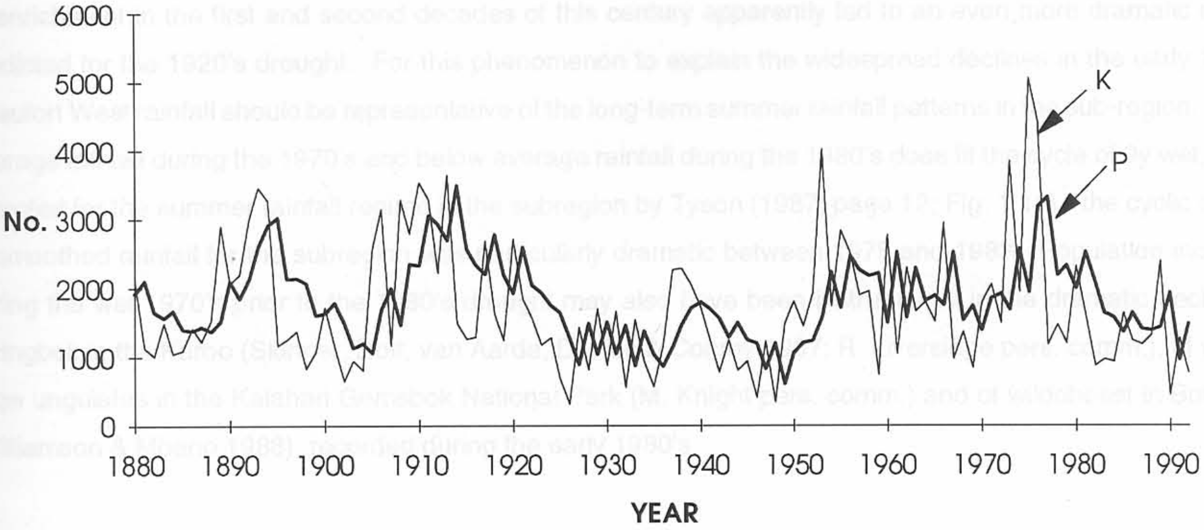

Figure 114. Changes in the carrying capacity of food supplies in the 'safe feeding area' of a standard eagle territory for hyrax (K) and concordant changes in hyrax population density (P) predicted by a standard run of the model with the full complement of predation, using Beaufort West rainfall data.

same time there would be increased pressure to disperse to find more favourable conditions. This would explain colonisation of sub-optimal habitats such as dykes and ditches by hyrax during the said irruptions (Thomas 1946). The irruptions reported in the literature may have been symptomatic of rock hyrax habitat shift and may even have involved mass dispersal more reminiscent of lemming (*Lemmus* spp.) populations (Pitelka 1973; Thompson 1955). The population 'explosions' probably refer to phases when these animals are actually in decline but becoming much more apparent as they are forced from their refuge environment. This hypothesis is in keeping with the observations of increased availability of rock hyrax to black eagles and humans during drought (see methods). Coincidence of reported irruptions with drought suggests that forage in the vicinity of rocks is limiting at high density rather than crevices (for overnight shelter). Rock crevices must have been in sufficient supply to accommodate major population increases during periods of enrichment. Detailed study of rocky habitats (Chapter 3) certainly did not indicate that suitable crevices were in short supply. Therefore it appears justified to model carrying capacity on food supplies in safe reach of rocky habitat rather than on the availability of crevices for overnight shelter. This assumption would have to be checked outside the karoo where the geology may not be so favourable to rock hyrax.

It is important to note that the model predicts major phases of increase and decline that are generated by climatic change and not by interference with the predators. The predicted peak and decline in hyrax numbers during the 1940's however, do not represent dramatic population change, yet certain authors refer to major outbreaks at this time (Van der Horst 1941; Thomas 1946). The widespread and sudden declines of rock hyrax populations reported throughout southern Africa in the early 1980's (see Chapters 1 & 4) have left many wondering at the cause of such a dramatic event. This model demonstrates that such declines can be explained simply in terms of enrichment followed by drought, with no additional involvement of disease or predator eradication. While rainfall in the early 1980's was below average, it was not exceptionally dry. The drought in the late 1940's was far worse (see Fig. 109), yet the model does not predict a major decline at that point. What appears to be more relevant to the early 1980's decline is the pronounced build up in hyrax numbers during the wet 1970's which can mostly be attributed to two major birth pulses in the very wet summers at the end of 1976 and 1977. Major increases in hyrax numbers due to enrichment in the first and second decades of this century apparently led to an even more dramatic decline predicted for the 1920's drought. For this phenomenon to explain the widespread declines in the early 1980's, Beaufort West rainfall should be representative of the long-term summer rainfall patterns in the sub-region. Above average rainfall during the 1970's and below average rainfall during the 1980's does fit the cycle of 9y wet, 9y dry detected for the summer rainfall regime in the subregion by Tyson (1987; page 12; Fig. 1.11) - the cyclic change in smoothed rainfall for the subregion was particularly dramatic between 1975 and 1983. Population increases during the wet 1970's prior to the 1980's drought may also have been instrumental in the dramatic declines of springbok in the Karoo (Skinner, Dott, van Aarde, Davies & Conroy 1987; R. Liversidge pers. comm.), of various large ungulates in the Kalahari Gemsbok National Park (M. Knight pers. comm.) and of wildebeest in Botswana (Williamson & Mbano 1988), recorded during the early 1980's.

Linking conception rates to rainfall patterns

A different pattern emerges for a standard run of the model if conception rates are interpolated (linearly) on summer rainfall rather than P:K ratio (Fig. 115). As expected, the hyrax population is less influenced by the immediate erratic behaviour of K, but still follows gradual accumulation or depletion of phytomass in a smoother, more fluid fashion. There appears to be more of a 'wave action' in hyrax numbers when conception is modelled on rainfall only, with two major peaks separated by about 60y. Increase in the major peaks can be attributed to large birth pulses at high population density when conception is only affected by rainfall. Disparity between the two versions is somewhat reduced if phytomass constraints are tighter when conception is modelled on rainfall only, leading to a reduction in major peaks and an increase in minor peaks. Modelling conception on rainfall only may be appropriate for the study period when population density was relatively low, but the absence of a crowding effect on reproduction (well demonstrated in other animals) is considered unrealistic. Elements from both versions are probably involved in the real situation, but for this study conception is modelled on P:K ratio for all standard runs of the model unless otherwise stated.

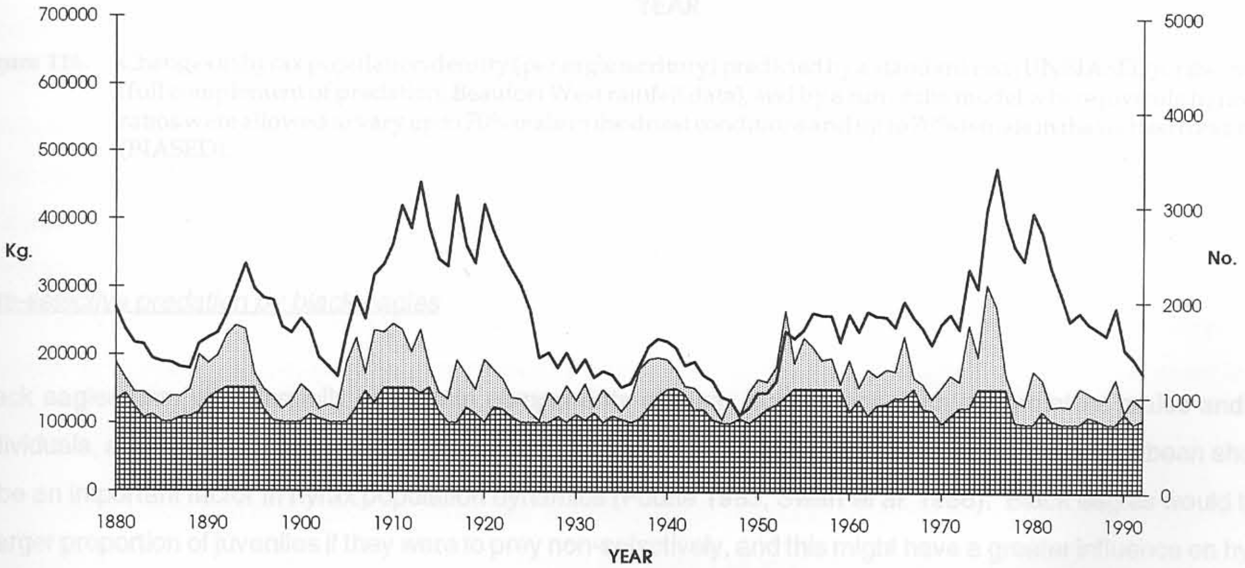

Figure 115. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a standard run of the model with the full complement of predation (using Beaufort West rainfall data), but in this case with hyrax conception rates modelled on preceding summer rainfall rather than P:K ratio.

The potential influence of a bias in recruitment of the sexes

The influence of certain demographic processes on hyrax numbers can be investigated with standard runs of the model with predators present. In Chapters 4 & 10 it was indicated from three lines of field evidence that more male hyrax are recruited in dry years and more females in wet years. It is conceivable that such bias might have a destabilising influence on hyrax population density because greater production of males and impaired production of females in dry conditions should impair the ability of the population to grow, whereas the converse would hold for wet conditions. However this was not indicated when juvenile sex ratios in the model were allowed to vary up to 70% male in the years of least rainfall during the gestation period, and up to 70% female in the years of most rainfall during the gestation period. This run of the model is compared with a standard run in Figure 116. There was no significant difference in the variation of population density (F=1,07; p=0,37), in the mean population size (z=0,30; p=0,38), or in the distribution of values of population density (Smirnov test: T=0,08; p>0,20) for these two runs of the model. It is concluded that any rainfall-related bias in recruitment of the sexes would not have a significant effect on rock hyrax population change.

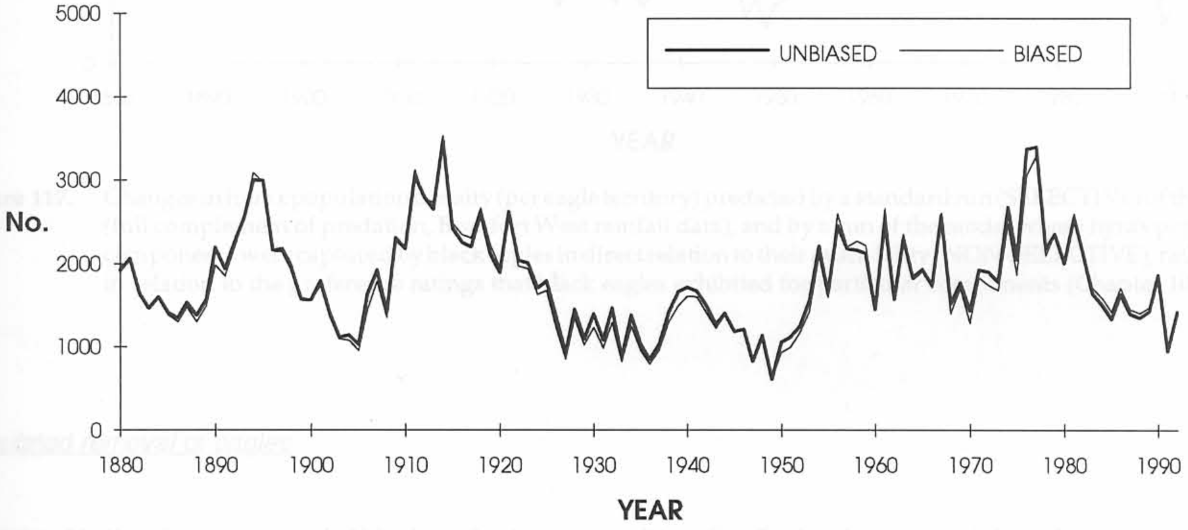

Figure 116. Changes in hyrax population density (per eagle territory) predicted by a standard run (UNBIASED) of the model (full complement of predation, Beaufort West rainfall data), and by a run of the model where juvenile hyrax sex ratios were allowed to vary up to 70% male in the driest conditions and up to 70% female in the wettest conditions (BIASED).

Age-selective predation by black eagles

Black eagles prey preferentially on certain components of hyrax populations such as immature males and old individuals, and show low preference or avoidance for juveniles (Chapter 10). Juvenile mortality has been shown to be an important factor in hyrax population dynamics (Fourie 1983; Swart *et al.* 1986). Black eagles would take a larger proportion of juveniles if they were to prey non-selectively, and this might have a greater influence on hyrax population change. To test for any differences in hyrax demography due to age-selective or non-selective predation by black eagles, eagles were assumed to take hyrax individuals in direct proportion to their availability in one run of the model and this was compared with a standard run where hyrax were captured in relation to both availability and preference rating (Figure 117). No significant differences were detected in the variation of population density (F=1,04; p=0,44), in the mean population size (z=0,27; p=0,39), or in the distribution of values of population density (Smirnov test: T=0,07; p>0,20) between the results. The pattern of age-specific predation by black eagles on rock hyrax is evidently not of great significance to hyrax population change. However, it should be noted that due to the dynamic nature of the model, any short-term effects of such factors may be compensated for in the long-term by changes in mortality or recruitment.

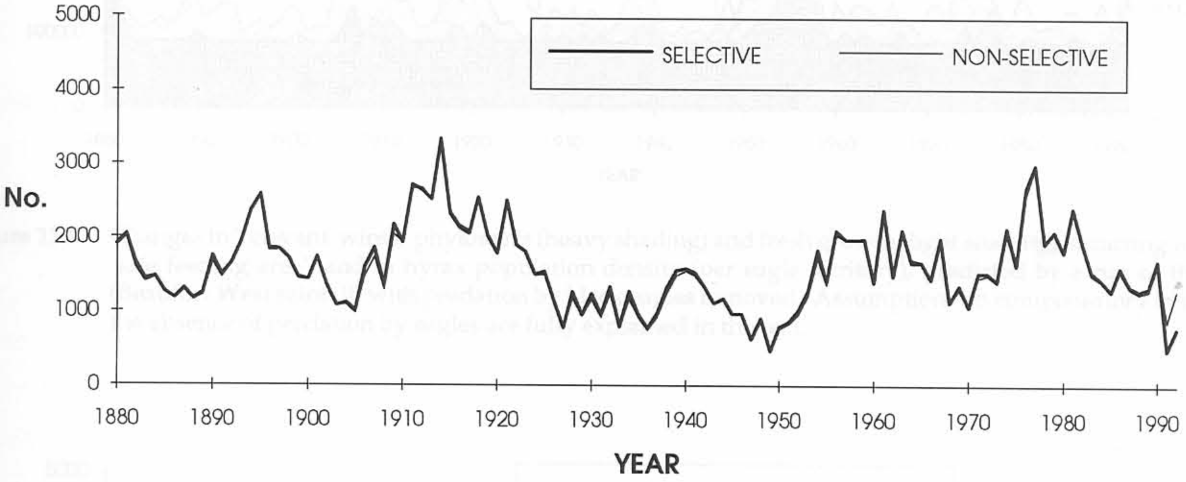

Figure 117. Changes in hyrax population density (per eagle territory) predicted by a standard run (SELECTIVE) of the model (full complement of predation, Beaufort West rainfall data), and by a run of the model where hyrax population components were captured by black eagles in direct relation to their availability (NON-SELECTIVE), rather than in relation to the preference ratings that black eagles exhibited for particular components (Chapter 10).

Simulated removal of eagles

In contrast to the above, removal of black eagles has a very dramatic effect on hyrax population change as predicted by the model (Figs. 118 & 119). In this removal simulation it was assumed that 10% of the potential black eagle kill would have died anyway from inevitable factors (as justified in the methods section). A far more rapid rate of growth of the hyrax population is predicted in the absence of eagles and consequently the population density regularly rises to a level where it is estimated that food resources can no longer support the population and major compensatory mortality due to starvation and disease set in. The population reaches this critical limit (4,5*K) seven times in the last century for runs of the model when eagles are removed, and not once for runs of the model when eagles are present. One such crash in the absence of eagles coincides with the 1983 drought following enrichment in the 1970's.

The model predicts that in the absence of eagles hyrax numbers are sufficient to depress phytomass in the vicinity of their refuge habitat by about 17%. This is apparent in Figure 118, and only in very wet periods is the phytomass able to increase from its lower constraint. Accordingly, carrying capacity set by edible phytomass and fresh growth on total phytomass is also reduced by a similar proportion. Despite this, mean hyrax numbers are predicted to be

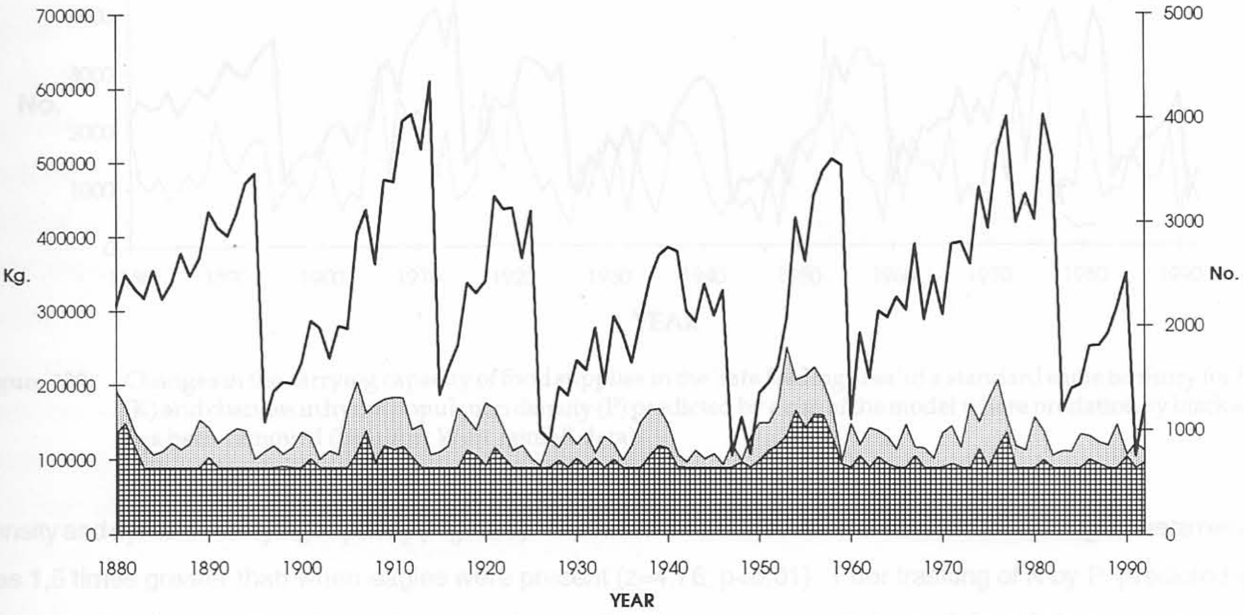

Figure 118. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model (Beaufort West rainfall) with predation by black eagles removed. Assumptions on compensatory mortality in the absence of predation by eagles are fully explained in the text.

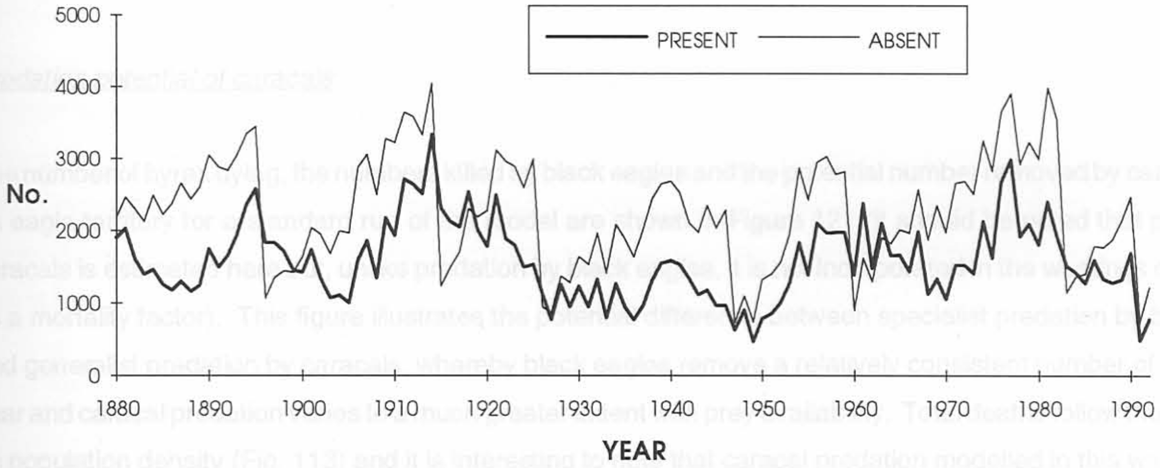

Figure 119. Hyrax population change predicted by the model (Beaufort West rainfall) with predation by black eagles PRESENT and ABSENT.

32% higher in runs of the model when eagles are removed. In comparison with a standard run of the model (eagles present; see Fig 119), this difference is statistically highly significant (z=5,90; p<0,01). The same comparison also revealed highly significant statistical differences in the variability of population density (F=2,08; p<0,01) and in the distribution of population density values (Smirnov test: T=0,34; p<0,01). Variability in population density when eagles were removed, as measured by the coefficient of variation (s.d./mean), was 6% larger than variability with eagles present. Much of this can of course be attributed to the predicted crashes. It would appear that diminished removals from the hyrax population in the absence of black eagles prevents close tracking between population

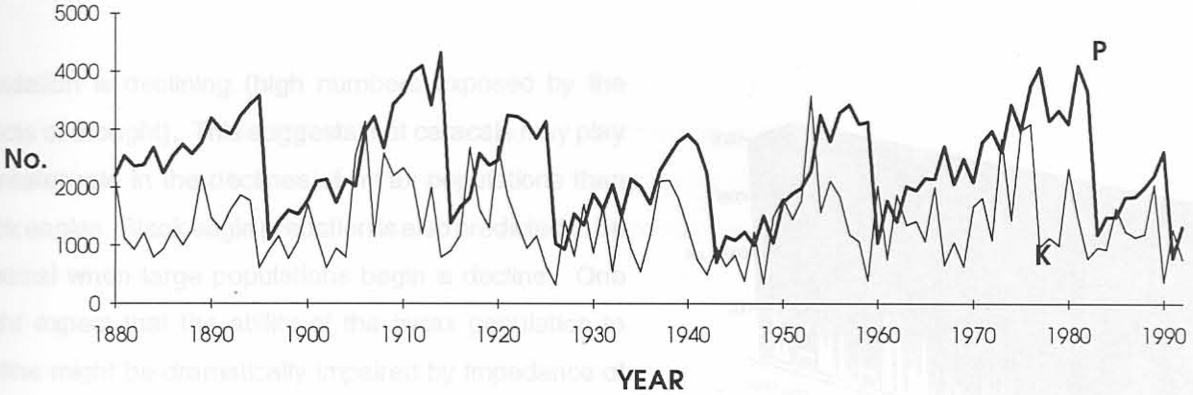

Figure 120. Changes in the carrying capacity of food supplies in the 'safe feeding area' of a standard eagle territory for hyrax (K) and changes in hyrax population density (P) predicted by a run of the model where predation by black eagles has been removed (Beaufort West rainfall data).

density and dynamic carrying capacity (Fig. 120). The mean annual deviation of P from K when eagles were removed was 1,5 times greater than when eagles were present (z=4,76; p<0,01). Poor tracking of K by P, predicted in the absence of eagles, results in larger hyrax surpluses. If eagles are removed, the model predicts an average annual surplus of 1088 hyrax. Accurate prediction of hyrax surpluses depends mostly on correct estimation of standard carrying capacity and correct handling of compensatory mortality in the absence of eagles. These matters are treated further under sensitivity analysis. In theory then, removal of black eagles should have a dramatic effect upon hyrax population change. Certain predator removal experiments have provided empirical evidence demonstrating such a dramatic effect upon other prey populations (see p. 256).

Predation potential of caracals

The number of hyrax dying, the numbers killed by black eagles and the potential number removed by caracals within an eagle territory for a standard run of the model are shown in Figure 121 (it should be noted that predation by caracals is estimated here but, unlike predation by black eagles, it is not incorporated in the workings of the model as a mortality factor). This figure illustrates the potential difference between specialist predation by black eagles and generalist predation by caracals, whereby black eagles remove a relatively consistent number of hyrax every year and caracal predation varies to a much greater extent with prey availability. Total deaths follow the same trend as population density (Fig. 113) and it is interesting to note that caracal predation modelled in this way is minimal while the population increases (population well protected during periods of enrichment), and maximal while the

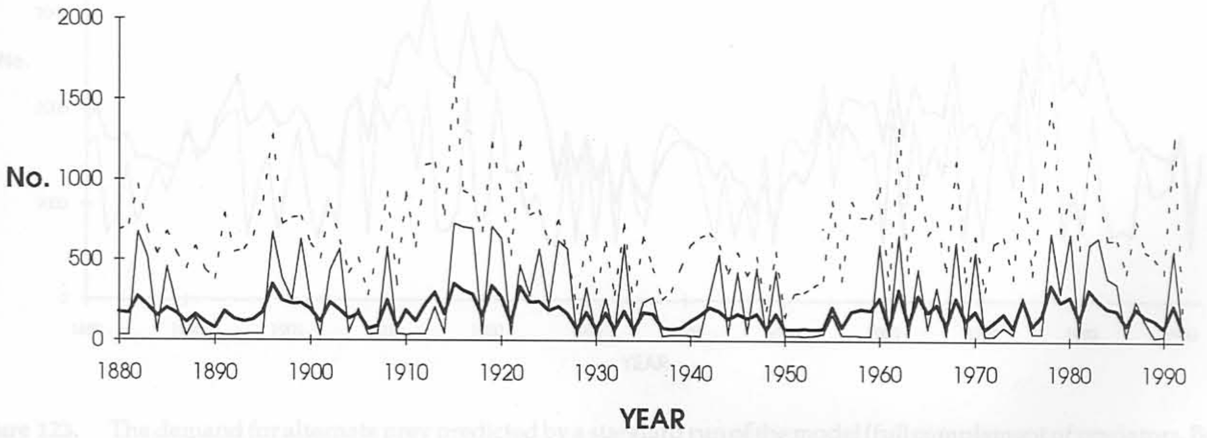

Figure 121. Total number of hyrax dying (broken line), hyrax kill by eagles (heavy line) and potential hyrax kill by caracals (faint line) as predicted by a standard run of the model (full complement of predation, Beaufort West rainfall).

population is declining (high numbers exposed by the effects of drought). This suggests that caracals may play a greater role in the declines of hyrax populations than black eagles. Black eagle predation is also predicted to be maximal when large populations begin a decline. One might expect that the ability of the hyrax population to decline might be dramatically impaired by impedance of these predators. On account of their greater consumption rates, numeric and functional responses, caracals have a much greater potential for removing hyrax surpluses (Fig. 122) than black eagles. Although caracals did not reach their maximum potential population density in a standard run of the model, the range in the number of hyrax that they removed was three times that of black eagles. Had caracals realised their full predation potential, this difference would have been nearly five-fold.

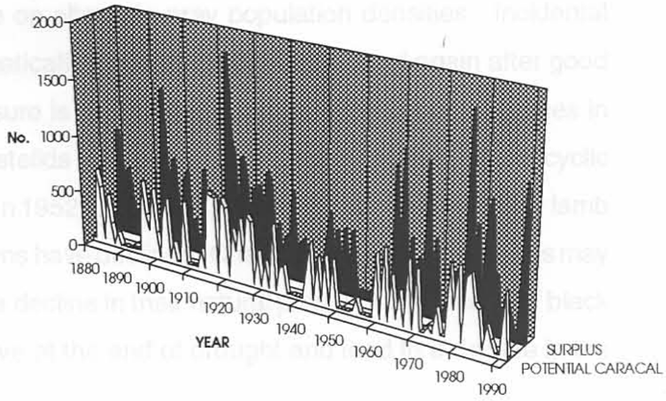

Figure 122. Annual surplus (P-K) of hyrax (dark shaddow), and potential hyrax kill by caracals (white peaks) as predicted by a standard run of the model (full complement of predation, Beaufort West rainfall data).

The demand for alternate prey

By calculating the total number of prey captured by both predator species, and then removing from this the number of hyrax captured, it is possible to predict the demand for alternate prey. This is plotted against hyrax numbers in Figure 123 for a standard run of the model. In keeping with the prediction that predation of rock hyrax by black eagles and caracals is maximal during decline phases, the demand for alternate prey is evidently maximal during the increase phase of the hyrax population when hyrax are less available. On a shorter time-scale, demand for alternate prey is high in wet years and low in dry years. Time-lapse photography indicated that non-hyrax prey of black eagles

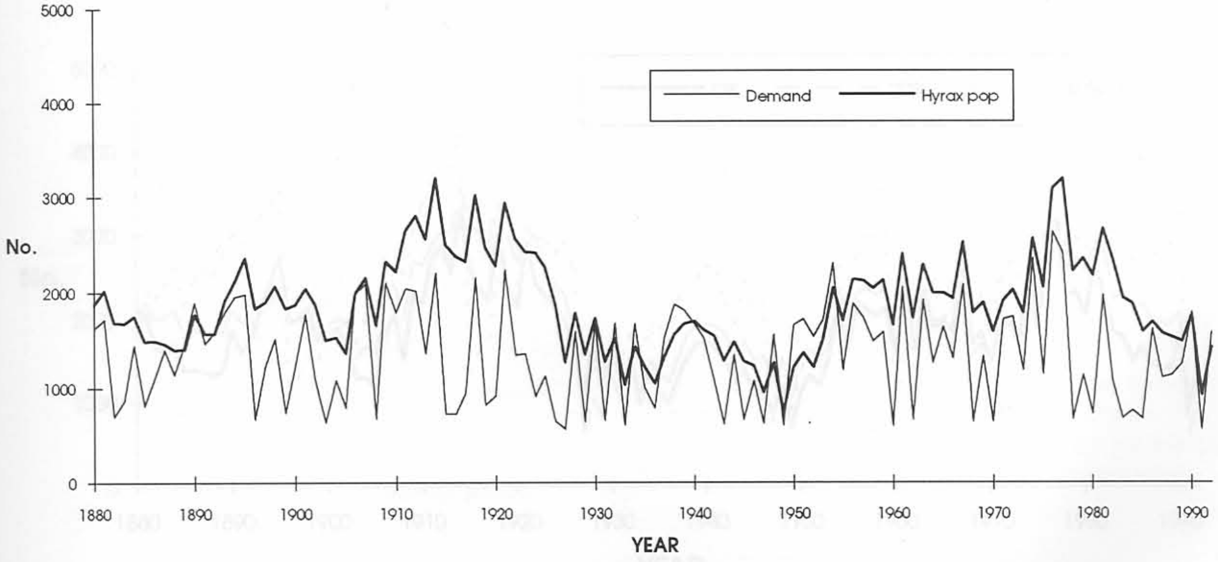

Figure 123. The demand for alternate prey predicted by a standard run of the model (full complement of predators, Beaufort West rainfall data) as total prey captured by black eagles and caracals minus hyrax prey captured by black eagles and caracals. Predicted changes in hyrax population density is shown for reference (heavy line).

featured least in eagle diet in the dry year of 1988, and most in 1989 when good rains arrived (Chapter 9: Fig. 83, p. 198). This variable predation may have had an influence on alternate prey population densities. Incidental observations of red rock rabbits in the KRNP increased dramatically through 1988 and declined again after good rains at the end of 1989 (Chapter 5). Heavy predation pressure is held responsible for synchronous declines in alternate prey species such as game birds and even mustelids (Korpimäki & Norrdahl 1989c) when cyclic populations of small mammals or snowshoe hares crash (Hagen 1952; Lack 1954). Farmers complain of heavy lamb losses to predators during drought when natural prey populations have declined (Chapter 11). For caracals this may be so, especially when high densities of caracals experience a decline in their natural prey, but in the case of black eagles stock predation is most likely to occur when rains arrive at the end of drought and lead to a decline in the availability of already reduced hyrax populations.

Impeding both predators

Total removal of black eagles is an unrealistic scenario for the Karoo where caracals are more likely to be persecuted by farmers, and where persecution seldom leads to total eradication of either. Impedance of both predators (see methods) is much more realistic and can be modified to investigate the influence of different levels of persecution. This type of analysis is also less demanding with respect to the largely unknown element of compensatory mortality and permits incorporation of the effect of caracals into the workings of the model for the first time.

Changes in hyrax population density for 0% 20% and 40% impedance of both predators are shown in Figure 124. A similar pattern of hyrax population change to that for removal of the eagles (Fig. 118) is achieved by a 40% impedance of both predators. Diminished removals from the hyrax population with progressive impedance of predators is manifest as a more rapid rate of increase during enrichment and impaired decline during drought. At higher levels of impedance, sporadic crashes caused by great discrepancy between P and K can even lead to population increases at times when otherwise the population would be declining. The predicted increase in hyrax

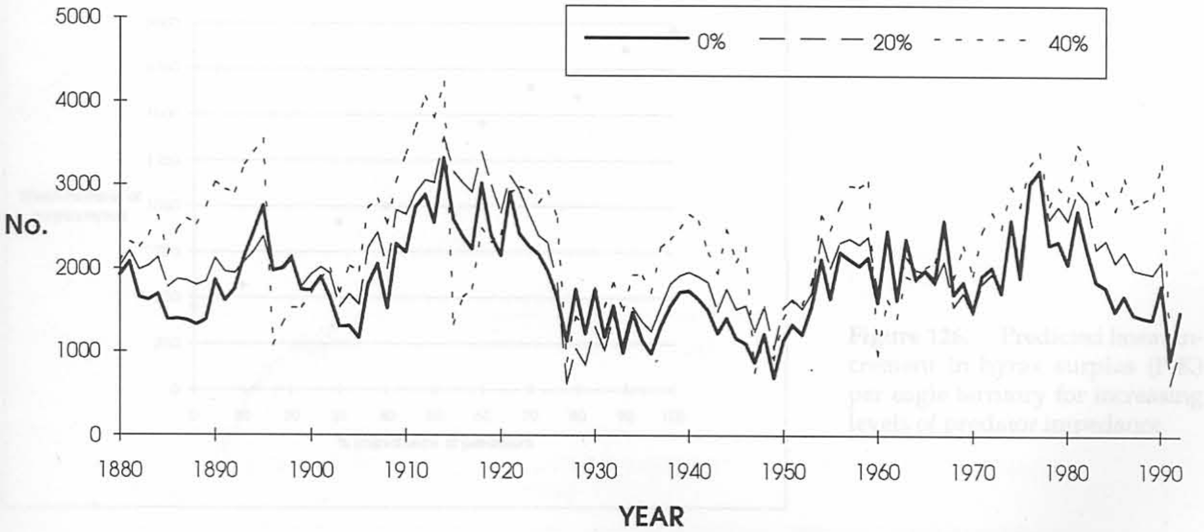

Figure 124. Predicted changes in hyrax population density for different runs of the model (Beaufort West rainfall data) with varying levels of predator 'impedance' - see text for method.

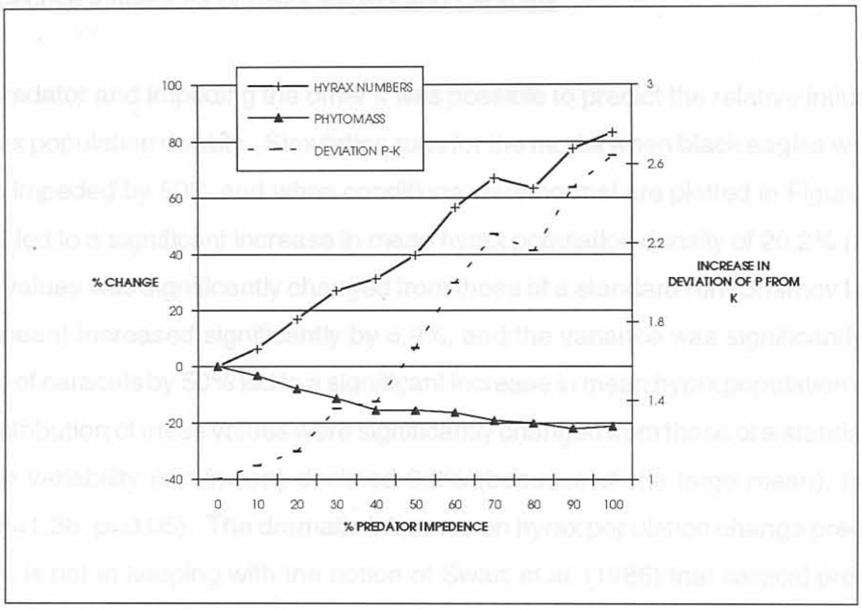

Figure 125. Predicted increment of average hyrax population density and population variability (as measured by the difference of P from K), and decrement of average winter phytomass, for increasing levels of predator impedance.

population density, deviation of P from K, and the reduction in phytomass for increasing levels of predator impedance are plotted in Figure 125. Here deviation of P from K illustrates changes in the variability of population density. Variance in population density becomes significantly different from that in a standard run of the model when predators are impeded by 30% ($F=1,73$; $p<0,01$). The mean hyrax population density and the distribution of these values become significantly different from those for a standard run of the model when predators are impeded by only 10% ($z=-3,77$; $p<0,01$; Smirnov test: $T=0,30$; $p<0,01$). Phytomass is not much reduced beyond 40% impedance on account of lower constraints on this parameter. The relative increase of mean hyrax population density is a linear function with predator impedance leading to a linear increase in hyrax surpluses (Fig. 126).

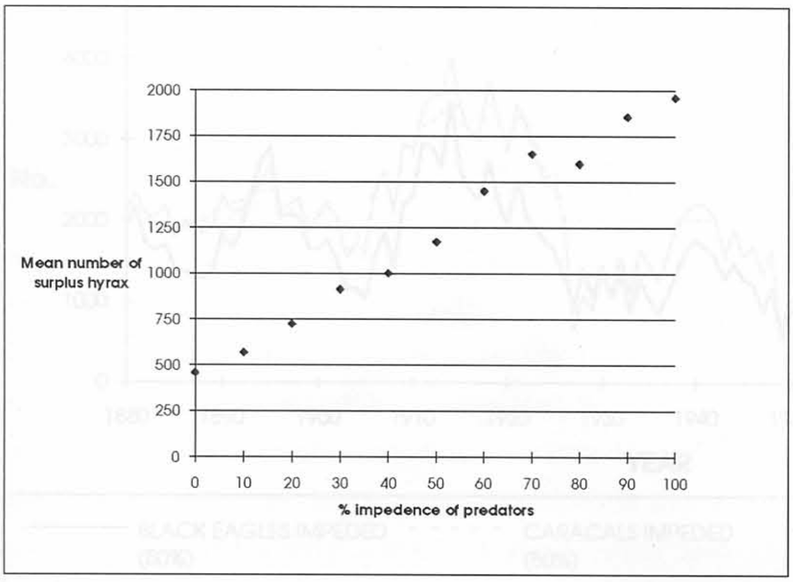

Figure 126. Predicted linear increment in hyrax surplus (P-K) per eagle territory for increasing levels of predator impedance.

Contrasting the respective influences of black eagles and caracals

By controlling one predator and impeding the other it was possible to predict the relative influence of black eagles and caracals on hyrax population density. Simulation runs for the model when black eagles were impeded by 50%, when caracals were impeded by 50% and when conditions were normal are plotted in Figure 127. Impedance of black eagles by 50% led to a significant increase in mean hyrax population density of 20,2% (z=-4,13; p<0,01); the distribution of these values was significantly changed from those of a standard run (Smirnov test: T=0,30; p<0,01); the variability (s.d./mean) increased significantly by 6,9%, and the variance was significantly increased (F=1,65; p<0,01). Impedance of caracals by 50% led to a significant increase in mean hyrax population density of 21,1% (z=-4,58; p<0,01); the distribution of these values were significantly changed from those of a standard run (Smirnov test: T=0,35; p<0,01); the variability (s.d./mean) declined 3,8% (because of the large mean), but variance was still significantly larger (F=1,36; p=0,05). The dramatic influence on hyrax population change predicted when caracals are impeded by 50% is not in keeping with the notion of Swart *et al.* (1986) that caracal predation merely tracks changes in hyrax density. More noticeable increase in the variability of hyrax population density under black eagle impedance rather than caracal impedance could be attributed to the additional hyrax population crash predicted in 1960.

There was some suggestion then that impedance of black eagles had more influence on hyrax population change than impedance of caracals, especially at peak prey densities (Fig. 127). This was contrary to expectations based on the greater potential of caracals to remove hyrax surpluses, and indicates the importance of a demographic factor which consistently removes a number of the hyrax population. Significant differences in mean population density, in the distribution of density values, and in the variances of population density between black eagle impedance and caracal impedance could not be demonstrated statistically. However predation by black eagles was free to compensate for changes in prey density when caracals were impeded whereas the reverse situation was not true and this may have influenced the result. Also, caracal predation of hyrax is not yet based on accurate data.

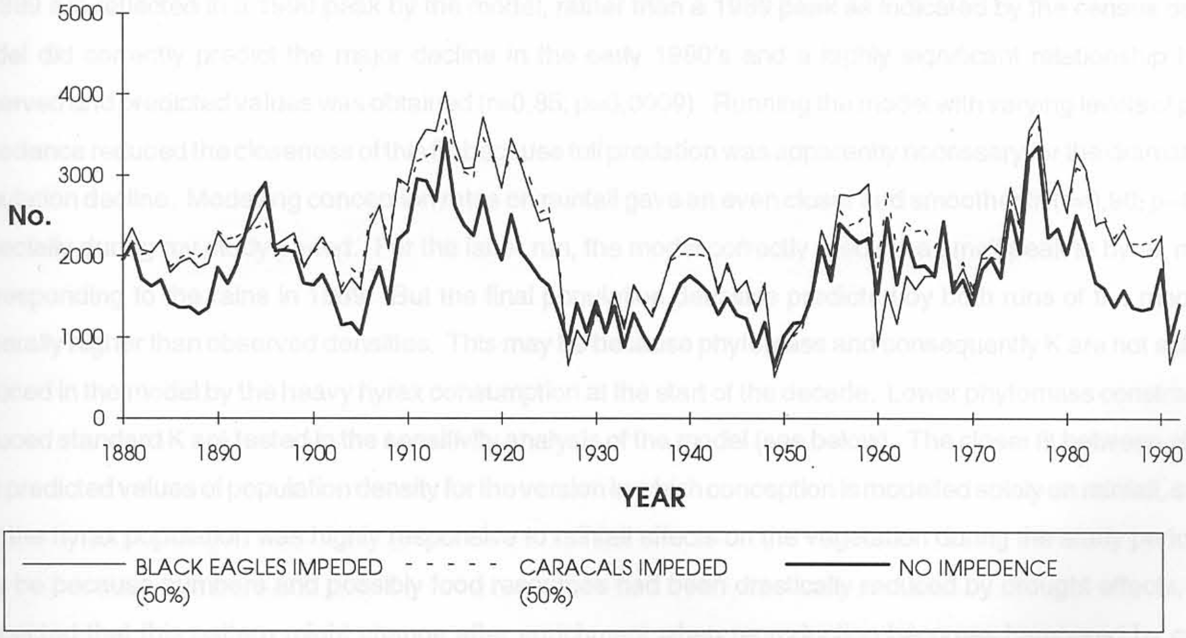

Figure 127. The predicted departure of hyrax population change from a standard run of the model (NO IMPEDANCE, Beaufort West rainfall) when black eagles are impeded by 50% and when caracals are impeded by 50%.

ASSESSMENT OF THE MODEL -

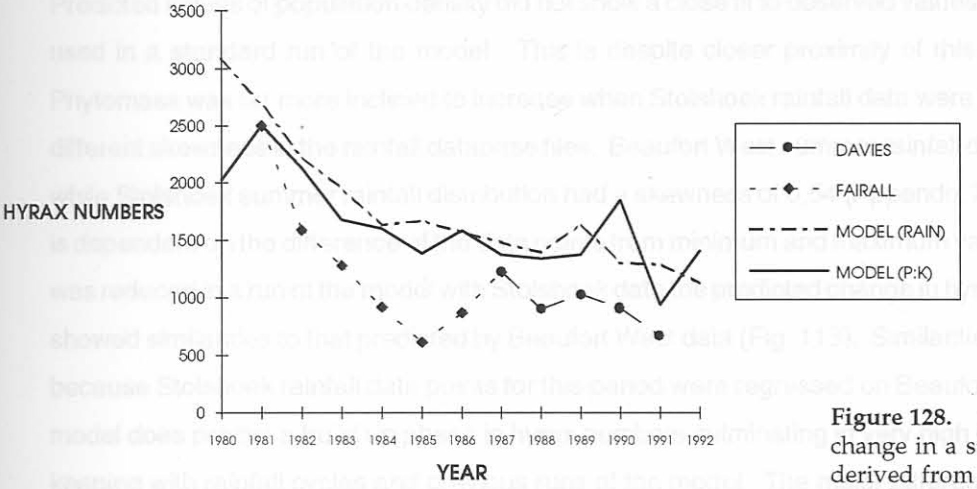

Figure 128. Observations of hyrax population change in a standard eagle territory in the KRNP derived from counts at colonies by Fairall (in litt.) and Davies (the present study), in comparison with predictions of hyrax population change after a full standard run of the model with hyrax conception based both on rainfall and on P:K ratio.

Fit to hyrax census data

In Figure 128 estimates of hyrax population density per average eagle territory in the KRNP are plotted against predicted values for population density from 1980 through until 1992. Estimates of population density (per eagle territory) were extrapolated from data on group size gathered from counts at 16 colonies conducted during the present study (1987 - 1991), and from counts at two of these colonies conducted by Fairall (*in litt.*) for the preceding period from 1981 until 1987. Predicted values are derived from running the model on the entire rainfall database (1880 - 1992) with conception rates modelled on P:K ratio (standard run) and on rainfall. Although predicted values derived from a standard run did not closely match estimates of population density during my study period (good rains in 1989 are reflected in a 1990 peak by the model, rather than a 1989 peak as indicated by the census data), the model did correctly predict the major decline in the early 1980's and a highly significant relationship between observed and predicted values was obtained (r=0,85; p=0,0009). Running the model with varying levels of predator impedance reduced the closeness of this fit, because full predation was apparently necessary for the dramatic hyrax population decline. Modelling conception rates on rainfall gave an even closer and smoother fit (r=0,90; p=0,0002), especially during my study period. For the latter run, the model correctly predicts a small peak in hyrax numbers corresponding to the rains in 1989. But the final population densities predicted by both runs of the model were generally higher than observed densities. This may be because phytomass and consequently K are not sufficiently reduced in the model by the heavy hyrax consumption at the start of the decade. Lower phytomass constraints and reduced standard K are tested in the sensitivity analysis of the model (see below). The closer fit between observed and predicted values of population density for the version in which conception is modelled solely on rainfall, suggests that the hyrax population was highly responsive to rainfall effects on the vegetation during the study period. This may be because numbers and possibly food resources had been drastically reduced by drought effects, but it is suspected that this pattern might change after enrichment when reproduction becomes hampered by crowding effects at high population density.

Different rainfall regimes

Predicted values of population density did not show a close fit to observed values when Stolshoek rainfall data were used in a standard run of the model. This is despite closer proximity of this collection site to the study area. Phytomass was far more inclined to increase when Stolshoek rainfall data were used. This may have been due to different skewness in the rainfall database files. Beaufort West summer rainfall distribution had a skewness of 0,84 while Stolshoek summer rainfall distribution had a skewness of 0,54 (Appendix 7). Phytomass response to rainfall is dependent on the difference of the data points from minimum and maximum values. When phytomass sensitivity was reduced in a run of the model with Stolshoek data the predicted change in hyrax population density (Figure 129) showed similarities to that predicted by Beaufort West data (Fig. 113). Similarities prior to 1929 are to be expected because Stolshoek rainfall data points for this period were regressed on Beaufort West rainfall. But this run of the model does predict a build up phase in hyrax numbers culminating in very high population density in the 1970's in keeping with rainfall cycles and previous runs of the model. The major difference when Stolshoek data are used is that the model does not predict a major decline in hyrax numbers in the early 1980's. This can be attributed to the unexpected finding that Stolshoek rainfall in the early 1980's was not markedly below average. All summer rainfall for this period was average or above average except for summer rainfall at the end of 1982 which was 30% lower than normal. It is not clear why Stolshoek data did not indicate drought in the early 1980's which was reported to be widespread (Tyson 1983, 1986). Perhaps the location of this collection site in the foothills of the Nuweveldberg mountains experienced more consistent amounts of orographic rain.

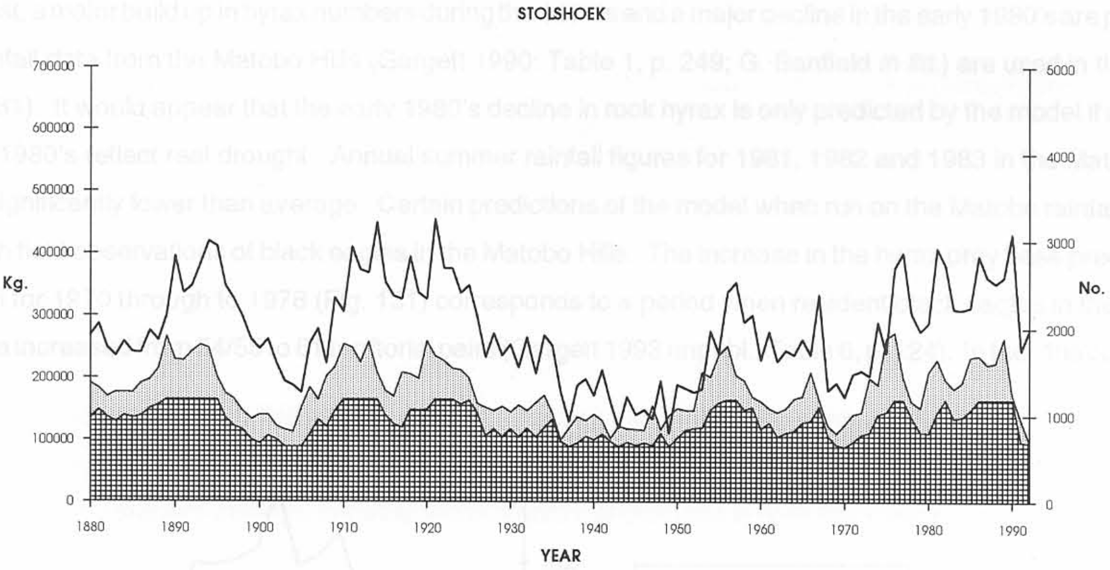

Figure 129. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model using rainfall data recorded for Stolshoek.

It was more surprising to discover that rainfall for the Beaufort West district (32 sites) was also average to above average for the same period except for summer rain at the end of 1982 (30% lower than normal). This might also be due to the proximity of the continental escarpment. In keeping with predictions using Beaufort West rainfall, a run of the model using district rainfall data (Figure 130) revealed hyrax declines corresponding to droughts in the

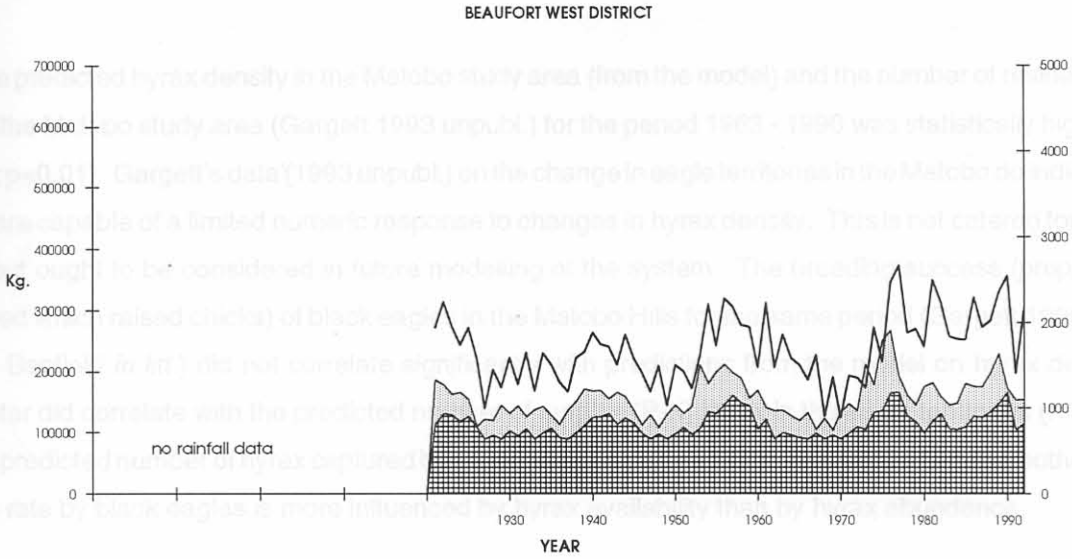

Figure 130. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model using the average of rainfall data recorded for 32 stations in the Beaufort West District.

early 1930's and the late 1940's, and a build up phase which began in the 1950's and culminated in very high densities in the 1970's. But again no major decline is predicted for the early 1980's and this can also be attributed to the apparent absence of drought in the rainfall database for that period.

By contrast, a major build up in hyrax numbers during the 1970's and a major decline in the early 1980's are predicted when rainfall data from the Matobo Hills (Gargett 1990: Table 1, p. 249; G. Banfield *in litt.*) are used in the model (Figure 131). It would appear that the early 1980's decline in rock hyrax is only predicted by the model if rainfall in the early 1980's reflect real drought. Annual summer rainfall figures for 1981, 1982 and 1983 in the Matobo Hills were all significantly lower than average. Certain predictions of the model when run on the Matobo rainfall pattern tallied with field observations of black eagles in the Matobo Hills. The increase in the hyrax prey base predicted by the model for 1970 through to 1978 (Fig. 131) corresponds to a period when resident black eagles in the Matobo study area increased from 54/55 to 61 territorial pairs (Gargett 1993 unpubl.: Table 6, p. 124). In fact, the correlation

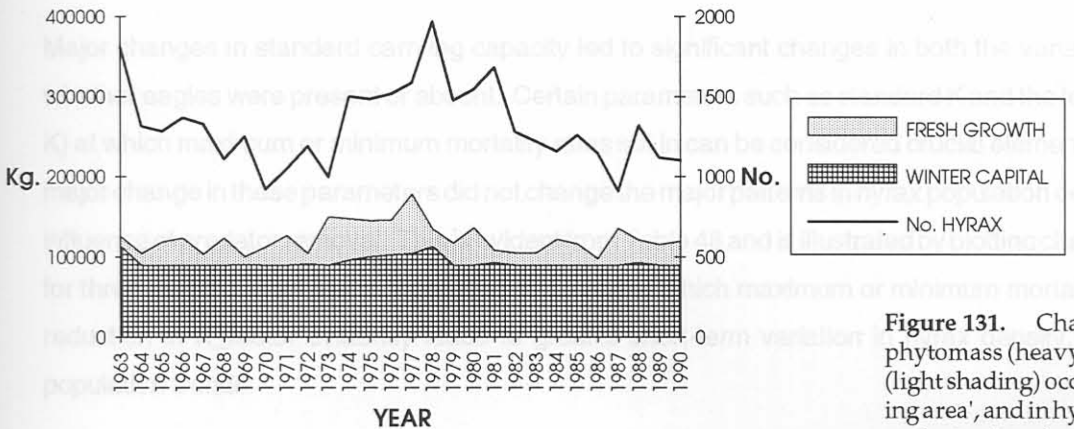

Figure 131. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model using rainfall data for the Matobo Hills.

between predicted hyrax density in the Matobo study area (from the model) and the number of resident black eagle pairs in the Matobo study area (Gargett 1993 unpubl.) for the period 1963 - 1990 was statistically highly significant (r=0,53; p<0,01). Gargett's data (1993 unpubl.) on the change in eagle territories in the Matobo do indicate that black eagles are capable of a limited numeric response to changes in hyrax density. This is not catered for in the current model but ought to be considered in future modelling of the system. The breeding success (proportion of pairs monitored which raised chicks) of black eagles in the Matobo Hills for the same period (Gargett 1990: Table 34, p. 259; G. Banfield *in litt.*) did not correlate significantly with predictions from the model on hyrax density, but this parameter did correlate with the predicted number of surplus (P-K) hyrax in the eagle territories (r=0,46; p=0,01), and the predicted number of hyrax captured by the eagles (r=0,42; p<0,05). This supports the hypothesis that hyrax capture rate by black eagles is more influenced by hyrax availability than by hyrax abundance.

Sensitivity analysis

The main purpose of this model was to examine predation as a demographic factor affecting rock hyrax population change. The model predicts a very dramatic effect on the variance and size of hyrax populations when eagles are removed or predators are impeded. To test how robust this prediction is, the effect of removing eagles was examined for multiple runs of the model when individual parameters used in the workings of the model were varied dramatically. Parameters were increased or decreased by at least 50% where possible. But sometimes this was inappropriate (e.g. the heavy compensatory mortality rates due to starvation and disease set at 0,75), and was reduced to avoid extinction. In some cases, parameters such as standard carrying capacity could not be varied sensibly without covariance of another parameter (winter capital in this case).

To test the general robustness of the model, differences between the results of these runs and appropriate standard runs of the model (eagles present or absent) were assessed using three statistical tests: the F-test to detect differences in variation of population density; the normal test to detect differences in mean population density; and the Smirnov test to detect differences in the distribution of population density values. The results of these tests and examinations are presented in Table 48, and the conditions of parameter manipulation are described therein.

Major changes in standard carrying capacity led to significant changes in both the variation and density of hyrax whether eagles were present or absent. Certain parameters such as standard K and the levels (difference of P from K) at which maximum or minimum mortality rates set in can be considered crucial elements in the model. But even major change in these parameters did not change the major patterns in hyrax population density and in the predicted influence of predator removal. This is evident from Table 48 and is illustrated by plotting change in population density for three very different levels (known as K_factor) at which maximum or minimum mortality set in (Figure 132). A reduction in K_factor evidently leads to greater short-term variation in hyrax density, but the same long-term population trends.

TABLE 48

THE RESULTS OF A SENSITIVITY ANALYSIS PERFORMED ON THE MAIN PREDICTIONS OF THE HYRAX POPULATION MODEL

The principal effects of removing eagles (depletion of winter phytomass; overall increase in hyrax numbers; overall increase in the variability of hyrax population density; overall increase in the departure of P from K; and overall increase in hyrax surpluses) are listed for major perturbations of the important variables used in the population model. These perturbations are described under CONDITIONS. Predictions on hyrax population change for each perturbation were compared statistically to test for departure from patterns of hyrax population change predicted by the model under standard conditions. In each case, this was carried out for runs of the model with the full complement of predation and for runs of the model with eagles removed. Three statistical tests were used: the F-test to detect differences in variation; the Normal-Test to detect differences in mean population density; and the Smirnov-Test to detect differences in the distribution pattern of predicted hyrax densities. Asterixes denote where a statistically significant difference was obtained (two asterixes indicate P<0,01). The number of 'crashes' (when P > 4,5*K, and heavy compensatory mortality occurs) are also listed for each perturbation with and without eagles.

	PRINCIPAL EFFECTS OF REMOVING EAGLES					Comparisons with appropriate standard runs of the model							
						EAGLES PRESENT				EAGLES ABSENT			
CONDITIONS	% REDUCTION OF PHYTOMASS	% INCREASE IN HYRAX NUMBERS	% INCREASE IN VARIABILITY (coefficient of variation)	INCREASED DEVIATION OF P FROM K	ADDITIONAL HYRAX SURPLUS	F-TEST	NORMAL TEST	SMIRNOV TEST	NO. CRASHES	NO. CRASHES	F-TEST	NORMAL TEST	SMIRNOV TEST
STANDARD RUN		+32	+6	1.53	622				0	7			
starting population halved		+28	+7	1.40	560				0	7			
starting population doubled		+28	+10	1.34	517				0	8			
initial phytomass down 30%		+32	+9	1.46	586				0	7			
initial phytomass up 30%		+30	+11	1.48	601				0	7			
edibility of winter phytomass doubled	-18	+38	+10	1.98	787				0	6		*	
edibility of winter phytomass halved	-19	+28	+7	1.27	521	*			3	10	*		
phytomass constraints 50% wider	-35	+7	-18	1.19	412	**			1	7	**	**	**
phytomass constraints 50% narrower	-8	+46	+25	1.66	757				0	7		**	*
levels for maximum mortality raised 43%	-17	+53	+13	2.04	1004				0	7		**	*
levels for maximum mortality lowered 43%	-14	+14	+4	1.06	248	*			2	10		**	**
phytomass 50% more sensitive to rain/herbivory	-15	+36	+21	1.48	628				0	7			
phytomass 50% less sensitive to rain/herbivory	-9	+51	+6	1.73	668	**	**	**	1	7			
standard carrying capacity up 50%	-14	+16	+4	1.29	599	**	**	**	3	7	**	**	**
standard carrying capacity down 17%	-25	+50	-12	1.35	617		**	**	0	7	*	**	**
mortality rate during crash up 13%	-12	+27	+32	1.47	513				0	7			
mortality rate during crash down 13%	-17	+38	-1	1.61	698				0	9			
growth rate down by one third (phytomass up 50%)	-24	+27	+33	1.74	773		**	**	0	6	*	**	
growth rate up by one third (phytomass down 25%)	-11	+36	+11	1.40	535		*		1	9			
variability of pre-natal mortality doubled	-16	+33	+16	1.54	612				0	8			
variability of pre-natal mortality halved	-19	+37	+4	1.47	673				0	5			

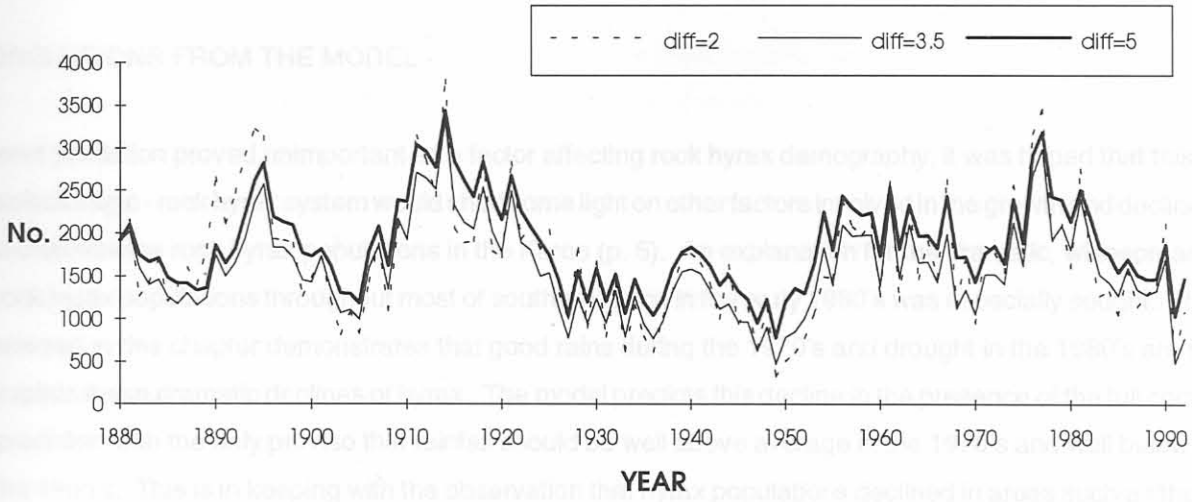

Figure 132. Predicted changes in hyrax population density for three variations of K_factor (the difference of P from K which invokes maximal or minimal values of mortality and fecundity) in the model (Beaufort West rainfall).

Parameter changes associated with increased variation in hyrax numbers were: an increase in standard K; a decrease in the edibility of winter capital (K primarily determined by erratic fresh growth); wider constraints on winter phytomass; and a lowering of the levels at which maximum or minimum mortality/conception rates set in. Increased variability in dynamic carrying capacity leads to increased variability of hyrax numbers as would be expected. Parameter changes identified as responsible for decline in mean population density were: lowering standard K; lowering winter capital and raising interest rates; and reduced sensitivity of phytomass to rainfall and herbivory. Widening the constraints on winter capital (allowing further depletion of phytomass by heavy hyrax consumption) did not lead to significant change in mean population density when compared with a standard run of the model with predators present. Discrepancy between observed and predicted hyrax densities during the study period might be explained by exaggeration of standard K in the model. But reducing standard K did not lead to a closer fit. Standard K in this model is based on accurate measurement of hyrax density in relation to the refuge environment, and there is no obvious reason why this should be over-estimated. As yet the discrepancy between the levels of observed and predicted values for population density during the study period remain unexplained.

Despite large perturbations of parameters in this analysis, the predicted effects of eagle removal on hyrax population density were remarkably consistent. Minor variation in the number of crashes (times when P exceeded K by 4,5) occurred, but the number of crashes was always much greater when eagles were removed. Inefficient tracking of K by P in the absence of eagles was represented by greater departure of P from K in all runs of the model. Consequently, an increase in hyrax surplus was predicted when eagles were removed for all parameter perturbations. This (average) increase varied between roughly 250 and 1000 hyrax per territory, but most perturbations indicated a similar increase to that under standard conditions (622 hyrax). Changing the P:K ratio level at which maximum/minimum mortality/conception rates set in had most bearing on the surplus of hyrax because this directly controlled the ability of P to track K. Hyrax surpluses in the absence of eagles were also affected (reduced) by widening of the constraints on phytomass. This results from further suppression of the phytomass and consequent reductions in hyrax densities in the absence of eagles. But both of these parameters that affect hyrax surpluses were based on inferences drawn from the observation of karoo biota and are not likely to be too far from real values. The sensitivity analysis indicates that impaired tracking of K by P in the absence of eagles (or impedance of predators) is robust for a wide range of parameter variation.

CONCLUSIONS FROM THE MODEL -

Even if predation proved unimportant as a factor affecting rock hyrax demography, it was hoped that this study of the black eagle - rock hyrax system would shed some light on other factors involved in the growth and decline phases that characterise rock hyrax populations in the Karoo (p. 5). An explanation for the dramatic, widespread decline in rock hyrax populations throughout most of southern Africa in the early 1980's was especially sought. The model presented in this chapter demonstrates that good rains during the 1970's and drought in the 1980's are sufficient to explain these dramatic declines of hyrax. The model predicts this decline in the presence of the full complement of predation with the only proviso that rainfall should be well above average in the 1970's and well below average in the 1980's. This is in keeping with the observation that hyrax populations declined in areas such as the Matobo Hills, where no predator control was in practice. Detailed analyses of rainfall patterns in the summer rainfall region over most of southern Africa have indeed revealed a particularly dramatic change from good rains in the 1970's to drought in the 1980's, and this change was also reflected in the population composition of hyrax captured by black eagles during the two decades.

A very simple lower trophic interaction in the model predicts that the food supplies and thus the carrying capacity for hyrax within the safe feeding area around rocky habitats shows phases of increase and decline due to the influences of rainfall and herbivory. These are closely followed by the hyrax population for a standard run of the model with predators present. Irruptions reported for hyrax populations in the Cape and Namibia correspond to decline phases in the model when shrinking food resources presumably forced the hyrax to become much more obvious (and vulnerable). This coincidence lends some support to the basic pattern of population change predicted by the model which remained robust despite dramatic parameter perturbation. Further supporting evidence for the basic model comes from fieldwork in the Matobo Hills where the predicted increase in hyrax during the 1970's and decline in the 1980's was mirrored by observed changes in the number of resident black eagle pairs, and from the KRNP where the predicted decline of hyrax in the early 1980's showed a strong correlation with hyrax counts at colonies. From very simple rainfall data, the model makes robust predictions about hyrax population change which concur with field observations.

So changes in food supplies and the number of hyrax that these can safely accommodate within the refuge environment can be considered to be the ultimate cause for the observed patterns of population change in a standard run of the model. The question remains as to whether the population changes are effected (proximate causes) primarily through the lower trophic interaction (e.g. through variation in numbers added to the population, and in numbers dying due to starvation), or primarily through the upper trophic interaction (through variation in numbers killed by predators), or by a combination of these effects. This can be explored either by key-factor analysis of population processes during a standard run of the model with predators present, or by simulating the removal of predation.

For a standard run of the model, mortality acting in the upper trophic level was calculated for each year as the number of hyrax killed by black eagles, plus the potential number of hyrax killed by caracals, plus 20% of the number of juveniles dying (the latter was taken to represent juvenile predation by small, generalist predators). Mortality acting through the lower trophic level was calculated as the loss in breeding potential (described earlier) plus all remaining (non-violent) mortalities which are probably mostly caused by starvation, disease and possibly fighting. In a standard run of the model, population growth showed a significant negative correlation with mortality from above (r=-0,80; p<0,01), and an insignificant correlation with mortality from below (r=-0,14), suggesting that deaths due to predators can explain 64% of population change while losses due to the lower trophic level can explain only 2% of the change (conception rates were modelled on P:K ratio in these standard runs of the model, and not on stochastic rainfall patterns). Whether the population increases or declines is a function of both recruitment and mortality, but the results of this key factor analysis corroborate those of the field study which indicated that annual additions to the hyrax population are less varied and less involved in population change than annual removals by predators. But during the increase phase in hyrax numbers through the 1970's, population growth showed a stronger correlation with losses due to the lower trophic level (r=-0,64) while the relationship with predation remained unchanged. Variability in births appears to be partly involved in population change during growth phases. On the basis of these findings, I do not agree with the conclusion of other researches on karoo hyrax populations (Fourie 1983; Swart *et al.* 1986) that juvenile mortality is more involved than predation in hyrax population change, especially since the two cannot be separated.

It is important to note that rainfall influences both lower trophic losses and predation in opposite ways through food supply. This influence is destabilising to hyrax populations because good rains lead to increased recruitment and increased protection from predators, while drought leads to diminished recruitment and aggravated predation. This is supported by various lines of field evidence supplied in this thesis. Climate-induced destabilisation might be expected to have a far more dramatic influence on rock hyrax populations if these populations were not protected by a highly effective refuge resource when below the carrying capacity of this resource, and if these populations were not susceptible to very effective predation when above the carrying capacity of the refuge resource. The refuge resource of rock hyrax differs from most other forms of refuge in that it is effective against nearly all predators, and although food supplies in the vicinity of shelter may vary, the amount of rock crevices is not altered by climate or herbivory. Effectiveness of the hyrax refuge in this case probably prevents predation by specialist predators from destabilising the prey population, as it is known to do in other circumstances. The state of balance that exists between the food requirements of the hyrax population and the food supplies around the refuge habitat is apparently reflected in the distance that hyrax must venture from their rocks to feed, and thus in their vulnerability to predation. Some other prey populations may enjoy extra protection from predators when vegetation cover improves after rainfall, but most prey populations can be expected to become more available to predators as they become more abundant. The effectiveness of the refuge resource used by rock hyrax and the profound influence of enrichment on hyrax vulnerability are two key elements which appear to make this system rather unique amongst predator-prey relationships, and thus the present model must be regarded as specific.

The handling of hyrax capture rate by black eagles and especially by caracals in this model can best be described as 'availability-dependent'. The number of hyrax caught annually, as predicted by the model, was dependent on hyrax population density for both black eagles (r=0,77; p<0,01) and caracals (r=0,43; p<0,01) over a standard run of the model (112 years). However, there was no indication during a standard run of the model that predation rate (i.e. the proportion of the hyrax population removed) by black eagles or caracals behaved in a density-dependent fashion, and this is more relevant to rock hyrax population change. Current demographic theory contends that if predation rate is not density-dependent then the predators cannot regulate the prey population (see earlier). Korpimäki (1993) reviewed definitions of population regulation and concluded from the disparity among these that it is a vague ecological concept: regulation has been strictly defined as 'the stabilisation of population density by density-dependent feedback mechanisms' (Solomon 1976; Kuno 1987), or 'the process whereby a population returns to equilibrium' (Nicholson 1933; Murdoch 1970; Sinclair 1989; Boutin 1992), and more leniently as 'long-term persistence and fluctuations within limits' (Mountford 1988; Hanski 1990; Messier 1991). I would argue that both key factor analysis (above) and simulated removal of predation (below) indicate that predation in this model does regulate hyrax populations in the lenient sense of the term - not around a simple equilibrium point, but around the number of hyrax that can be safely accommodated within the refuge habitat, and this number fluctuates primarily due to the stochastic influence of rainfall patterns. Large populations of hyrax may be safely accommodated within the refuge habitat during enrichment, while small hyrax populations may be exposed to predation during drought. Thus any long-term density-dependent trends in predation are obscured by short-term variation in the number of protected prey. This example illustrates that while density-dependent predation may still provide good evidence for regulation of prey by predators, the absence of density-dependence does not necessarily prove the contrary as is widely contended. Regulatory influence of predators may be less obvious in predator-prey systems which are complicated by variability in the number of protected prey. So variability in the number of red grouse protected by heather, in the number of voles protected by snow, or in the number of snowshoe hares protected by thickets ought to be considered before it is concluded that these prey are not regulated by predators on the grounds that predation was not clearly density-dependent. But safe and unsafe habitats are not likely to be more clearly defined than in the present system

Most of the above conclusions refer to predictions of the model when predators are present. Dramatic differences in hyrax population change when the model is used to simulate predator removal or impedance certainly corroborate the above indications that predation serves an important role in hyrax population change. Comparison of the patterns of population change with and without predators indicates that predation restricts departure of population density from the dynamic carrying capacity of the refuge habitat during enrichment, and especially assists its return during drought. The model indicates that the predation potential of black eagles and caracals has the capacity to remove the surpluses (P-K) of hyrax, even at high population densities assuming that these predation factors are realistically handled. Significant correlations between the breeding success of black eagles in the Matobo Hills and predictions from the model of the hyrax surpluses available to these eagles and the number of hyrax captured by these eagles, indicate that this is so. Predation of hyrax in the model is based on sound, biological field data for both black eagles and caracals. The dramatic influence of removing or impeding predation on hyrax population change indicates that variable hyrax birth rates and variable non-violent mortality rates as indicated during the present field study and from other lines of field evidence (and as handled under current assumptions of compensatory mortality) are evidently incapable at maintaining a close relationship between hyrax population density and changeable food supplies within the refuge habitat. This is despite the fact that both these parameters were modelled on P:K ratio thus affording opportunity for density-dependent effects.

By impairing the ability of the hyrax population to track the dynamic carrying capacity of the refuge habitat, it is predicted that predator removal or impedance gives rise to major peaks and crashes in hyrax populations, and to large surpluses of hyrax which will be forced to meet their forage requirements outside of the refuge habitat. On the basis that one adult sheep requires the same amount of food as 10 hyrax, it is estimated that the additional hyrax surpluses in the absence of black eagles would cost the average karoo farmer in mountainous terrain R3732 per annum (see methods). Low variability in the extra hyrax surplus predicted on removal of eagles for a wide range of dramatic parameter perturbations in the model (Table 48) indicates that this predicted cost is robust. Impedance of both eagles and caracals may be more appropriate for the karoo situation - just a 30% impedance of these predators may cost the farmer over R2700 in terms of grazing resources lost to increased hyrax surpluses. This extra cost may increase to nearly R7200 if predators are impeded by 70%, but high levels of predator impedance may be unrealistic for the simple assumptions on compensatory mortality in this model. These simulations did not involve impedance of small, generalist predators which may be responsible for a significant component of juvenile mortality. There was also no allowance in the model for colonisation of new habitats by hyrax in the absence of predators.

Unfortunately there are no good field data available to compare with these predictions, but it is likely that predator control was involved in major hyrax population increases reported in the Cape in the 1940's and on the farm Montana in the 1980's - these would not have been predicted by a standard run of the model with predators present. The validity of the predictions on the influence of predator removals rests mostly on the assumptions regarding compensatory mortality in this model. Undoubtedly these are a simplification of a complex phenomenon, but the object of the model was to capture the essence of this predator-prey system and the assumptions on the number of potential hyrax prey that would have died anyway due to old-age, starvation and disease were based on the limited field data available. Most support for the predictions is drawn from the sensitivity analysis performed on the model which demonstrated that increases in hyrax population density, variability and surpluses in the absence or impedance of predators all remained robust despite dramatic perturbation of even the most important parameters in the model.

The indications from the model presented in this chapter are that hyrax numbers change ultimately in response to changes in food supply within their refuge habitat, and that predation is essential for close tracking of these changes, although variable birth rates may also be involved during periods of enrichment and population growth. In this system, predation exerts an important regulating influence on a potentially unstable situation involving highly changeable food resources and a herbivore with a great propensity for population increase. Effectiveness of both refuge and predation contribute to population stability in rock hyrax, while alternating periods of enrichment and drought, and impedance of predation destabilise hyrax numbers. More information from field studies is still needed for the following aspects of this predator-prey system: the lower trophic interaction between rainfall, herbivory and karoo vegetation; the involvement of small, generalist predators in juvenile hyrax mortality; age-selective predation of rock hyrax by caracals; and, most important, the behaviour of non-violent mortality and compensatory mortality where predators are removed or impeded.