CHAPTER 13

SYNTHESIS AND CONCLUSION

Much of the work covered in this thesis was collated and analysed in the previous chapter. The prime aim of this chapter is to answer the questions set out in the introduction which specifically pertain to the effect of black eagle predation on rock hyrax demography and the effect of black eagle predation on livestock in the Karoo. But before I do this I think it is necessary to briefly describe and contrast this predator-prey system with other systems, and the period of the present field study with others. Although only partly relevant to the demographic influence of black eagles on rock hyrax, I would also like to use this opportunity to draw conclusions on how black eagles may have influenced the 'lifestyle' of rock hyrax and *vice versa*.

The system under investigation

Despite a four-fold decline in hyrax numbers prior to the present study, rock hyrax were still the most important herbivores in the mountainous habitats of the KRNP. They are probably the most important competitors to domestic livestock for the veld resource in these habitats which occupy 15% of the Karoo. But the distribution of rock hyrax is clearly limited by that of their refuge resource. The fixed distribution of rocky habitats in the Karoo imposes a very real measure of 'K' or carrying capacity on this landscape for rock hyrax. Rock hyrax are extremely vulnerable to predators outside their refuge environment and may even be captured by humans on foot when found out in the open. Within their refuge environment, hyrax are extremely dextrous in their escape from predators, and rock crevices afford an effective refuge for hyrax from nearly all their predators (except possibly snakes). This refuge resource is unusual in comparison with other forms of refuge in predator-prey systems (e.g. snow and vegetation) because of its permanence and because of the high degree of protection it affords to an otherwise very vulnerable prey.

Although the degree of protection conferred upon the hyrax population is thus very clearly defined by rocks, evidence suggests that this parameter in the system is still variable. Hyrax must fulfil their food requirements by grazing or browsing vegetation growing outside the rock crevices. In the present study hyrax ventured farthest from shelter when they were foraging, and this was when eagles launched most of their hunting flights, made more of their strikes at prey and delivered more prey to nests. It appears that after enrichment of the system through rainfall, hyrax can achieve their food requirements at shorter distances from their crevices. After especially good rains, flushes of verdant green vegetation grow upon the nitrate-rich soils at the entrances to well-used rock crevices. During drought however, hyrax must forage further from the rocks and therefore they become more vulnerable to predators.

This deduction seems intuitive but it is also based on a few lines of field evidence: a negative correlation was established between the average distance moved from shelter by hyrax on 27 observation days at colonies and rainfall over the preceding 40d (although this correlation was not quite significant when one outlying observation was removed); time-lapse photography indicated that significantly more hyrax were delivered to black eagle nests in the dry year of 1988, and they comprised a larger portion of black eagle diet in the same year; the delivery rate of hyrax to black eagle nests apparently increased during dry spells and declined one to two weeks after rainfall events in

1987 and 1988 (but this could not be demonstrated statistically); bounty records also suggested a tendency that more hyrax were killed in dry years and fewer in wet years; these observations concur with the notion held by many karoo farmers that hyrax move far from their rocky shelters when stressed by drought (I actually observed this on the farm Montana in 1984); black eagle breeding success improved as conditions became dry, and declined as conditions became wet for all years that they were monitored in the Matobo Hills by Gargett (1990) prior to the early 1980's hyrax decline; eagle breeding success was also maximal in the present study during the dry year of 1988 (raptor breeding success is usually associated with food availability).

So while the area of safely-accessible vegetation around rocky habitats is fixed, the number of hyrax that this food resource can support appears to vary with rainfall. Greater protection afforded to hyrax after enrichment probably depends on the size of the rainfall event and the state of balance or imbalance between hyrax and their food resources. The phenomenon can be thought of as protection for a variable number of hyrax, but of course all hyrax will be influenced by the state of their food resources in the vicinity of shelter. Although increased vegetation cover after rains might confer some extra protection to prey in other systems, increases in prey abundance after enrichment are generally associated with increases in prey availability, and this is often reflected in correlations between rainfall and the reproductive rate of predators. Improved breeding success by black eagles during dry years rather than wet years is rather anomalous, especially for water-limited African environments, and suggests that variation in prey vulnerability may have more influence within this system than variation in prey abundance (at least on a year to year basis). So the black eagle-rock hyrax predator-prey system is characterised by a 'permanent' refuge resource which affords effective protection to a clearly-defined number of otherwise highly vulnerable prey, and this number varies in response to the influence of enrichment by rainfall. In the summer rainfall region of southern Africa, especially the Karoo, this rainfall is stochastic but shows some indication of long- and short-term cyclicity.

By reducing mortality rates affecting all hyrax age classes, and by encouraging very large birth-pulses, good rainfall events can have a very dramatic effect on rock hyrax population size and structure in the Karoo. The size of the birth pulses are most influenced by variation in conception rates, in precocious puberty of females and in pre-natal mortality. Each of these parameters is influenced by body condition, which depends on food, which in turn is affected by rainfall. Rainfall leading up to the birth-pulse explained nearly all the variation in hyrax recruitment in the present field study. But it is anticipated that crowding effects would have an influence on recruitment at higher hyrax densities. Heavy pre-natal mortality (possibly by abortion or resorption of foetuses) was suggested in the present study during very dry conditions in 1990, and has been noted in other studies of hyrax reproduction. Lactation might be impossible if the water content of the vegetation is very low, and termination of foetuses before birth would relieve female hyrax of this heavy burden. A sex-bias towards more male hyrax recruited in dry conditions was suggested by the frequency distribution of birth dates of male and female hyrax in both the large sample captured by eagles and the small sample collected by shooting (significantly so). Foetal sex ratio in the small shot sample did not differ significantly from parity but did lean heavily towards females (1,6 per male) in the wet year of 1989. It is not yet clear whether such a rainfall-related bias in recruitment of the sexes occurs before or after birth, nor how it might come about. If further research does not demonstrate a rainfall-related bias in foetal sex ratio, then the phenomenon is most likely explained by rainfall-related variation in predation risk operating on young dispersing male hyrax (during wet conditions most hyrax are well protected from predators and dispersers will be especially vulnerable). However, modelling did not indicate that this phenomenon would have a significant demographic effect.

So rainfall greatly influences the number of hyrax added to the population annually, and possibly the sex ratio of the first age class. The number of juveniles produced each birth-pulse 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. As a result of rainfall effects, rock hyrax population structure is highly dynamic in the Karoo, and correlations were apparent between the age distributions of hyrax captured by black eagles and preceding rainfall patterns for the present study and for various other regions in the Cape Province sampled at different times. Variation in the size of adult hyrax skulls from prey remain collections also correlated with rainfall patterns both geographically and temporally, and not with vegetation type or temperature as has previously been suggested.

Overnight shelters must be in sufficient supply to accommodate the population increases of hyrax that are observed following good rains. Habitat mapping indicated that the average eagle territory in the KRNP contained over 44000 rock crevices available for use by the resident hyrax (about 63 groups). Hyrax population declines during drought suggest that safely-accessible food supplies in the vicinity of the refuge habitat set the local carrying capacity for hyrax, and not crevices for overnight shelter (which do not decline during drought). Hyrax groups were evenly spread through adequate rocky habitats in the KRNP but were often located close to riparian thickets and tended to cluster in kloofs where both food and shelter abounded. The fragmented and eroding rock outcrops of the Karoo appear to afford a surplus of rock crevices which can accommodate relatively high densities of rock hyrax. Foraging ranges of hyrax groups in the KRNP followed the distribution of rock outcrops, screes and riparian thickets, and within these ranges it appeared that suitable overnighting shelters were not in short supply. Suitable overnighting crevices may be more limiting in environments where the geology is not as suited to rock hyrax, but observations of hyrax in the Mackinder Valley in Kenya also indicated that the location of groups was more closely related to high quality food than high quality shelter (Sale 1965). For the Karoo at least, it appears justified to model hyrax demography on the amount of safely-accessible food around rocky habitat, rather than measures of overnight shelter.

As mentioned, hyrax in the KRNP as well as many other populations throughout southern Africa showed a significant decline in numbers during the early 1980's prior to the present study. The hyrax population in the KRNP declined further during the first years of field study. Detailed measurement of the refuge habitat and the frequency and foraging ranges of hyrax groups, indicated that hyrax were at 60% of their 'saturation level'. Hyrax were not using any temporary shelters for overnighting in the present study, as has been observed under high density conditions. Density estimates of hyrax in the present study were indeed much lower than those elsewhere in the Karoo and in Africa. It is indicated that the present study was carried out during conditions of unusually low hyrax abundance. Having declined by a factor of four, the hyrax population subsequently experienced several years of average rainfall and presumably average plant growth. One would expect the study population to be well protected within the confines of its refuge resource, and various lines of evidence did indicate a very low level of hyrax availability to resident predators:

Caracals used all habitats in the KRNP and probably occurred at a density intermediate between that recorded in the eastern Karoo and that in the south-west Cape (as indicated by trapping success rates). Despite this, caracals did not appear to be catching hyrax at all during the field study and instead, like true generalist predators, were relying on alternate prey notably wild and domestic bovids. Black eagles were laying relatively small clutches and were breeding later than usual, except on farmland where they were making use of domestic lambs born and dying just prior to the eagle breeding season. Observations of foraging eagles indicated that they were putting more effort into hunting methods which were seldom observed in other studies. Success of strikes at prey and food provisioning rates at nests were much lower than has been observed elsewhere. Food provisioning rates did not vary with food need nor the hunting abilities of both parents suggesting a prevailing low level of foraging success. Provisioning rates by breeding eagles actually fell below the minimum food requirements estimated by metabolic predictions. Some eaglets had to survive nine days without food, and some eaglets probably died for reasons associated with low provisioning rates. Reduced food wastage through consumption of hyrax pelts and opening of hyrax crania occurred more frequently in situations where eagles were thought to be more food-stressed. It was estimated that black eagles removed 11% of the standing crop of hyrax annually, and this is lower than the average indicated by the literature for vertebrate predator-prey systems. Adult and old hyrax were seldom dying of any causes other than predation by black eagles except during the dry year of 1988. Black eagles were making use of the full range of prey species available, and may even have been removing 11% of the standing crop of a cryptic, nocturnal lagomorph, Smith's red rock rabbit. This prey species was evenly distributed throughout the mountainous habitats of the KRNP and comprised a convenient alternate prey for many eagle pairs. Pairs which took a large proportion of lagomorphs in their diet were able to achieve higher provisioning rates at nests. Unlike the predation of rock hyrax, variation in the predation of red rock rabbits closely reflected dramatic changes in the abundance of rabbits. These changes corresponded to rainfall patterns, but may also have been influenced by shifts in predation pressure caused by variation in the vulnerability of the dominant prey (in keeping with the alternate prey hypothesis). Over the entire field study, most lines of evidence indicated that hyrax were well protected within the confines of their refuge environment and relatively unavailable to resident predators. This should be borne in mind when interpreting the results of the present field study.

Black eagles occur at a high density in the KRNP, second only to the population in the Matobo Hills. The spacing of eagle nests along the upper escarpment in the park is the closest recorded along any linear mountain range so far. The high density of eagles can be attributed to the suitability of rocky habitats in the area which usually support relatively high densities of rock hyrax, and which afford the eagles with many tall cliffs for breeding. So the KRNP can be considered prime habitat for black eagles, and the population is probably limited by food rather than nest sites. The extent of eagle territories in the area was very closely related to the extent of prime hyrax habitat. Black eagles devoted slightly more time to defending their territories than to foraging, and the maintenance of territories is obviously essential for successful breeding. Black eagle territories have previously been considered very stable over time, and the possibility was considered in this thesis that eagles might use the distribution of rocky habitat as a cue for long-term indication of hyrax numbers. But rocks are of no use to the eagles when there are insufficient prey, and recent rather dramatic change in eagle territories in the Matobo Hills suggests that food is still the prime determinant of black eagle territory size where nest sites are not limiting. Despite low abundance and availability of hyrax during the present study, many eagles were still managing to raise chicks and the overall breeding success was not dissimilar to that recorded for the Matobo Hills population over a long period. Apart from the indications of low prey availability, the study population of eagles is not considered atypical for the species in good hyrax habitat, but black eagles elsewhere in the Karoo maybe more limited by the availability of nests sites.

There were consistent, detectable trends in the composition of black eagle diet from place to place and from time to time that were apparently related to hyrax:eagle ratios. Eagles in situations associated with a low hyrax:eagle ratio took many alternate prey and a small hyrax prey component in their diet amongst which females and juvenile hyrax were prevalent. Eagles in situations associated with a high hyrax:eagle ratio took few alternate prey and a large hyrax prey component in which males and old hyrax were prevalent. Eagles with many hyrax available to them can apparently fulfil their needs by preying on surplus elements of the hyrax population, whereas eagles with few hyrax available are forced to take more alternate prey and to prey upon healthy breeding stock amongst the hyrax population and more easily-captured but less profitable juveniles. A large portion of surplus prey elements such as males and old individuals in predator diet has been associated with high prey:predator ratios for hyenas preying on wildebeest in the Serengeti (Kruuk 1970, 1972a) and with inefficient predation upon ungulate prey populations during the Oligocene - more healthy young adult ungulates fell prey to the efficient predators of the Eocene (Bakker 1983). For black eagles this variation can apparently come about in one of three ways: certain pairs may inhabit mountain ranges where hyrax densities are low and hyrax:eagle ratios are low despite large hunting ranges (e.g. mountains in the Fynbos biome); certain pairs may experience low hyrax:eagle ratios after a significant decline in hyrax abundance; and certain pairs may experience an effective low hyrax:eagle ratio when good rains lead to reduced availability of hyrax. Variation in eagle diet between the 1970's and the 1980's in two regions of the Cape may have been caused by changes in both hyrax abundance and availability. In the present study black eagles nesting on the upper escarpment showed symptoms of low hyrax:eagle ratio which were probably related to both topography and changes in hyrax abundance. Consequently upper escarpment pairs did not breed as successfully as lower escarpment pairs (despite higher failure rates of the accessible lower escarpment nests), and suffered more territorial intrusions. The only advantages enjoyed by upper escarpment pairs were better flying and hunting conditions. Black eagles which occupy small territories in high density hyrax habitat (e.g. Matobo Hills; upper escarpment) are probably more susceptible to instabilities in the hyrax prey base, and this might explain recent, quite dramatic territory changes among black eagles in the Matobo Hills following a hyrax decline (Gargett 1993 unpubl.).

Links between the lifestyles of black eagles and rock hyrax

Despite relatively low prey:predator ratios inferred during the present study, rock hyrax still comprised the principal food of black eagles as indicated by a variety of methods. So, unlike the generalist caracals, black eagles were behaving as specialist predators of rock hyrax by pursuing their preferred prey at low density and low availability. There was no indication that black eagles 'switched' to other prey in response to changes in their abundance (but it is unlikely that suitable alternate prey were in sufficient supply within eagle territories to invoke such responses). Specialist predation on rock hyrax by black eagles was also apparent when comparing black eagle diet with that of martial eagles resident in the area. Rock hyrax have dominated black eagle prey in nearly every study of black eagle diet. Comparison of methodology in the present study indicated that this dominance is significantly exaggerated in most studies where collections of prey remains are analysed, and small lagomorph prey are consistently under-estimated by this technique. Nevertheless, a heavy reliance on rock hyrax is indicated for black eagles wherever they occur in Africa.

Specialist predation by black eagles exerts hard selection upon adult hyrax. During the present study, it was estimated that approximately three out of four deaths of adult and old rock hyrax were caused by black eagles. In the presence of such strong selective pressure operating on reproductively-active adult hyrax, morphological or behavioural adaptations that enable hyrax to evade predation by eagles should accumulate in the population. Bakker (1983) estimated that only one death per 100 - 1000 in each generation (5y) was necessary to cause the observed evolution of cursorial limbs among mesonychid predators and their prey over a 15 million year period. Bakker maintained that this very weak overall level of selection (by standards of animal breeders) would not be swamped by random genetic events because the rate of selection was not gradual and short periods of heavy selection are likely to have occurred in between long periods of stasis. Some authors have suggested that coevolution between predators and prey should result in prey populations that are highly productive and, consequently, a high ratio of consumers to producers (Allen 1976). Others have argued the exact opposite (Ives & Dobson 1987). There are many factors involved in the crop of rock hyrax removed by black eagles and in the overall ratio of hyrax to eagles as already described. These parameters are also subject to limitations characteristic of populations of warm-blooded vertebrates, so I do not think they give any indication of the likelihood that coevolution has arisen in this system. Previous coevolution between black eagles and rock hyrax can be considered likely because of the heavy reliance of black eagles on this prey for food (indicated by all studies) and thus for successful breeding; and because of the hard selection exerted upon reproductively active rock hyrax by black eagles as evidenced in the present study. It is possible that both species may have been extant for the last 25 million years. Coevolution would be inevitable if these conditions of the predator-prey relationship had been operating over such a period. However, it should be noted that while black eagles appear to rely on hyrax throughout their range, rock hyrax must face other threats besides black eagles, especially as juveniles, especially at high densities, and especially in regions where black eagles may be nest-site limited or absent.

Coevolution requires specificity and reciprocity, and is usually taken to mean 'that a trait of one species has evolved in response to a trait of another species, which trait itself has evolved in response to the trait in the first' (Futuyma & Slatkin 1983: p. 1). In the following section the possible occurrence of coevolution between black eagles and rock hyrax is considered by comparing their functional morphology and ethology. As Futuyma & Slatkin (1983: p. 10) state: "Careful analysis of unusual or unique characters of each of two interacting species can show these features are one species' adaptations to the other species. This evidence is indirect and often not conclusive but may be the only kind available".

Identifying morphological features that may have resulted from coevolution in this system is difficult because many of the adaptations that assist black eagles to catch rock hyrax, or that assist rock hyrax to evade black eagles can also be considered as adaptations to the rocky, mountainous habitats in which they live. The stout build, low centre of gravity, thermal lability and rubber-like soles of rock hyrax are some of the numerous adaptations that enable this species to successfully exploit rocky environments (Sale 1970a). The high aspect-ratio wing 'design' of black eagles enables them to make good use of the slope lift over mountains. These morphological features can disadvantage the animals outside of their natural habitat - hyrax are especially vulnerable to predators away from rocky shelter, and black eagles do not soar as efficiently as other eagle species on thermals over plains. These pressures are likely to have reinforced their mountain lifestyles.

Certain morphological features of rock hyrax provide advantages against all predators, such as their cryptic coloration. Sale (1970a) argued that the dorsal spot of *Procavia capensis* is not strikingly coloured because these animals inhabit areas of low predation pressure where a visual alarm signal is not needed. As the present study indicates, there is very strong predation pressure affecting *P. capensis*, perhaps even more so than in East Africa and especially West Africa where black eagles are absent. I believe that the auditory alarm signals employed by *P. capensis* are far more effective than any visual signals, and that the dorsal spot is used to signal intention to conspecifics (pers. obs.). I think Sale's argument should be inverted - that *P. capensis* has a cryptic dorsal spot because of **high** predation pressure. The only morphological feature of rock hyrax that might be attributed to the evolutionary influence of an avian predator is the adjustable umbulacrum of the iris - it has been suggested (Millar 1971) that this structure might enable rock hyrax to detect eagles making strikes with the sun behind them (a behaviour that was observed in the present study). The absence of such a structure in eyes of *Procavia* spp. from West Africa where black eagles are absent, would be strong supporting evidence for this hypothesis.

Black eagles in the present study fed mainly on immature and adult rock hyrax. Full-grown hyrax are formidable prey. Despite the fact that golden eagles hold most of the records for largest prey killed by eagles (Table 26 - this may be because golden eagles have received most attention), mean prey size killed by black eagles in the present study was more than twice that recorded in two golden eagle studies. I suggest that the large foot dimensions of black eagles, which are considerably larger than any other *Aquila* spp. (including the golden eagle which is 14% larger than the black eagle by mass), have been selected for the hunting of large hyrax prey. Male black eagles have particularly large feet (almost as large as female feet) for their body size, and I suggest that this is due to the fact that pairs of black eagles hunt cooperatively for the same large hyrax prey.

Predation may also have an influence on the breeding biology of rock hyrax and black eagles. High predation pressure (from all predators) may explain why rock hyrax show a distinct birth pulse in an unpredictable climate. Black eagle nestlings fledged immediately prior to the modal hyrax parturition date, affording the young eaglets an abundance of available prey. Similar timing of fledging has been observed for other raptor species (Olsen & Georges 1993). But there is also some indication that black eagle nesting seasons throughout the continent may be timed to coincide with high hyrax availability during the dry season (see Moreau 1950).

Moving on to behaviour, the risk of predation to a hyrax living in an average black eagle territory in the KRNP was 0,03% day^{-1}. This is comparable to the risks incurred during racing car driving for humans. Rock hyrax showed two principal behavioural lifestyle characteristics which minimise these risks: 98% of the population lived in groups; and the entire population lived in a refuge environment. Both these characteristics have other advantages besides reducing predation risk, but tolerance of sexually-quiescent adult male hyrax within harem groups (suggested in the present study and confirmed in other studies) indicates that maintenance of adequate group size might be more important than strict social organisation. Disappearance and coalescence of small hyrax groups in 1988 indicates that these small groups may have suffered very high predation pressure through lower vigilance. Large groups benefit from increased vigilance, and rock hyrax posted obvious sentinels (mainly old females) when group-foraging to give early warnings of predator attacks. Dispersing hyrax (mainly immature males) are known to reduce the risks of predation by moving through non-rocky terrain at night, but may find themselves in risky situations during the day.

Immature males and old females were the most highly preferred hyrax prey of black eagles in the present study. Young dispersing male hyrax probably become vulnerable to eagles when moving away from familiar terrain without the group benefits of vigilance and sentinels. Sentinels probably run the risk of eagle attack when hurrying to catch up with foraging groups. Perhaps on account of low hyrax availability, black eagles preferred to first sight their prey from a perch or a high altitude flight and then plan their approach which usually involved some use of cover to maximise the element of surprise and delay early warnings by their intended prey. This technique differed from that described in the Matobo Hills (Gargett 1990) where black eagles appeared to fly more randomly around rock outcrops and surprise hyrax in passing, apparently without previously sighting their prey and planning their approach.

Black eagles can detect rock hyrax from at least two kilometres distance and make hidden approaches to their prey at speeds which are 4-10 times faster than the maximum escape speed of rock hyrax. It cannot be said that there is much 'adaptive gap' between this predator and its prey. The early warning system employed by foraging hyrax requires immediate access to refuge in the presence of such highly mobile predators. Hyrax spent 96% of their time within 5m of a bolt hole and did not forage farther than 15m from their rocks - this was reflected in a distinct vegetation zone around well-used outcrops. It is suggested that the apparent cut-off point at 15m from shelter is the product of a trade-off between foraging return and risk of predation. Eagles and other predators evidently exert a strong behavioural as well as numeric influence on hyrax populations. In a fast glide, black eagles travel at four times the maximum speed of hyrax, so the reluctance of hyrax to venture beyond 15m suggests that in the topography of the KRNP black eagles are probably able to conceal most attacks until about 60m from their intended prey. By similar reasoning, relaxed behaviour of hyrax when they are within 5m of shelter suggests that eagles find it difficult to remain undetected until within 20m of their intended prey. These safe and unsafe zones probably depend on topography and eagle:hyrax ratios (likelihood of attacks). Hyrax effectively minimise time spent away from their rocks by conducting casual feeding in the immediate vicinity of rock outcrops and by making extremely efficient use of their time on group foraging bouts while they access better quality vegetation: for one to two hours on most days hyrax groups engaged in intense bouts of feeding, usually in riparian thicket, sometimes 500m from their colony rocks; foraging groups were highly mobile through the network of linear outcrops, screes, and thickets, and appeared to actively harvest or garden different parts of riparian thicket on consecutive days.

Many raptors attacking prey, such as eagles attacking lagomorphs, miss on their first strike and often only secure their prey on a second or third attempt. For a prey species which spends 96% of its time within 5m of a bolt-hole, the chances of a second strike are minimal. I suggest that the prevalence of tandem behaviour in black eagles has arisen through the advantages of cooperative hunting as a means of capturing elusive rock hyrax. Tandem attacks at prey were nearly twice as successful as solo attacks (although this difference was not statistically significant), and the eagles probably only experience a limited number of attack opportunities each day. Black eagles spent 80% of their hunting time together and in close contact. Tandem hunting by black eagles fulfilled most of the requirements for true cooperative hunting, and the division of labour employed by eagle pairs during an attack could be related to the dimorphic capabilities of the sexes.

Certain links could be established between the foraging behaviour of hyrax and eagles. Coincidence of black eagle and rock hyrax daily foraging rhythms on an overall, seasonal basis suggests that eagles are mostly able to predict hyrax availability in time and adjust their own activity accordingly. This is probably because hyrax face certain daily limitations on how they use their time, such as the need to spend the mornings sunning during winter, and the need to avoid midday heat in summer. However, hyrax were apparently able to avoid high risk periods in the short-term and did not venture on group foraging bouts on windy days when eagles were more active (and delivered significantly more prey to their nests).

Rock hyrax populations in the Karoo show obvious population fluctuations related to rainfall. But hyrax can be very obvious animals and habitat shift and dispersion during drought may have been perceived as the population 'explosions' reported in the literature. Even during the 'dramatic' decline in the early 1980's hyrax numbers in the KRNP only varied by a factor of four. Hyrax populations on Serengeti koppies, monitored for 17 years by Hoeck (1989) did not show more than a four-fold variation in numbers (only two-fold for *Procavia*). More typical eagle prey such as lagomorphs show far greater variation in numbers than this. Even red rock rabbits during the present study showed a ten-fold variation, and that was not noticed by most observers in the KRNP. It is quite common for lagomorphs to show a 30-fold variation in numbers (Caro & FitzGibbon 1992). Rabbits in Australia and smaller raptor prey elsewhere can show even greater population variation than this e.g. vole numbers can vary by a factor of 100 (Korpimäki 1986; Norrdahl 1990), and lemming numbers can vary by a factor of 1000 (Maclean *et al.* 1974). The low variability of hyrax numbers makes this a very unusual prey for raptors. Lagomorph numbers vary far more than hyrax numbers because lagomorphs have a greater potential for population increase and they are rarely limited or protected by a permanent refuge resource. Unlike vulnerable hyrax, lagomorphs may sometimes escape the local predation capacity.

Relatively stable and high densities of rock hyrax have permitted black eagles to become highly prey-specific and to nest at unusually high densities for such a large eagle species. Because they nest relatively close together, black eagles have evolved spacing behaviour based on visual cues. They are highly conspicuous birds, especially in their undulation display. Most mountainous habitat in Africa appears to be saturated with black eagle breeding territories. Black eagles are long-lived, so the chances of juvenile eagles surviving to adulthood and establishing themselves in these breeding territories are very small. Simmons (1988, 1991) argues that this selection operating against young black eagles has led to conservative reproductive behaviour, involving obligate siblicide, which tends to produce high quality and competitive offspring. I would like to add to this argument the influence of a stable hyrax prey base which can be expected to encourage stable black eagle territories. Breeding opportunities for immature black eagles are probably more hard to come by than breeding opportunities for other immature *Aquila* eagles in environments where prey bases are much more variable and where harsh climates may cause eagle mortalities. So many facets of black eagle lifestyle can be related to a high degree of stability which is resonant in this predator-prey system, and which is created primarily by the fixed extent and the effectiveness of the rocky refuges used by hyrax.

Do black eagles limit rock hyrax populations in the Karoo?

Unlike the evolutionary influence of black eagles upon rock hyrax, their demographic influence could be directly measured in this study. The field study indicated that the number of hyrax removed from the prey population annually was equivalent to nearly one third of the numbers added annually. Many of the hyrax removed by black eagles belonged to age classes (e.g. adults) which suffered low mortality to factors other than eagles, so only a minority of these unfortunate individuals were likely to have died in a given year if they had not been captured. This was especially the case for hyrax captured in upper escarpment eagle territories where prey:predator ratio was low and the eagles were preying extensively upon apparently healthy breeding stock. It is concluded that during the present study much predation of rock hyrax by black eagles comprised additive rather than compensatory mortality. By removing a significant number of hyrax from the population which were otherwise unlikely to have died, it can be said that black eagles did have a limiting influence on their prey during the field study. This is easy to state given the broad definition of a limiting factor as any factor which affects population growth through increased production or loss of individuals (p. 254), and the conclusion that black eagles can limit rock hyrax actually tells us little about their long-term influence on hyrax population density in the Karoo. This is best explored by key-factors analyses and modelling.

Were hyrax 'irruptions' in southern Africa caused by the removal of predators?

First, the field evidence does not suggest that rock hyrax populations can usually be described as irruptive or epidemic. Many reports that hyrax populations reached 'plague' proportions in the past were probably over-stated. The rock hyrax population in the KRNP at the start of the 1980's was described as such and there were eye-witness accounts of 'hillsides teeming with dassies', yet counts in the park indicated that the population subsequently only declined by a factor of four (Fairall 1991; *in litt.*) to the low levels observed in the present study. This represents an extremely low level of population variation when compared with populations of other medium-sized eagle prey such as lagomorphs. Rock hyrax are very obvious diurnal animals, and I think it is likely that habitat shift (moving far from rocky outcrops to feed) and dispersal (to colonise sub-optimal refuge habitat) made them even more obvious at times when the populations were stressed, giving rise to the perception of sudden population 'explosions' or plagues. Reports of these phenomena actually coincided with predictions from the hyrax population model of major decline phases, as would be anticipated, when large hyrax populations were stressed by drought. So I think much of the perception of hyrax population irruptions was actually caused by a greater noticeability of the animals due to behaviour change, and this is in keeping with the many lines of evidence listed earlier which indicated that hyrax become more available to their predators in dry years when vegetation deteriorates. Population 'eruptions' (moving out) is probably a more fitting term for these situations than population irruptions (moving in).

All-said, there is little doubt that hyrax populations throughout southern Africa were at a peak at the end of the 1970's and many showed a subsequent decline to maybe a quarter of their former numbers during the 1980's. The observation that this dramatic population change occurred in the Matobo Hills where predators were not persecuted, concurs with the observation that the same order of change is predicted by the hyrax population model in the presence of the full complement of predation. In fact, a very different order of change is predicted in the absence of predators, because predation is apparently an important facilitator for the decline phase. It is clear that hyrax populations rise and fall fairly dramatically without any interference by predator removals, and it is inferred that the apparent 1980's hyrax population eruption was not caused by predator removals.

So what are the 'eruptions', and the increase and decline phases that characterise rock hyrax populations caused by? A relatively simple, but specific population model for rock hyrax predicts that these phases can be adequately explained simply in terms of rainfall patterns and concordant change in the food supplies available to hyrax in the vicinity of rocky habitat. In this model it is assumed that hyrax mortality (including predation) and recruitment rates, both based on field data, are determined by the state of balance between the hyrax population and food supplies in the vicinity of rocky habitat. The predation response is thus modelled not on the ratio of prey to predators but on the ratio between prey and their own food resources. The food supplies, in turn, are modelled on the relationship between plant production and rainfall which has been observed for arid and semi-arid rangelands. When it is assumed that the base for plant growth is fixed from year to year, the model predicts erratic change in food supplies and hyrax numbers. But when plant production is modelled as the rainfall-determined interest (annual fresh growth) on a capital (winter phytomass) that is allowed to increase in years of good rains and light herbivory, and to decline in years of drought and heavy herbivory (within realistic limits), then the model predicts more gradual increase and decline phases for the hyrax population, the most recent of which showed strong agreement with field observations from both the KRNP and the Matobo Hills. Three previous declines (when phytomass was suppressed to its lower limit) were predicted at times when hyrax eruptions were reported in the literature. These predictions of the model were robust for a wide range of dramatic parameter perturbations.

The increase phases of the hyrax population occur when good rains and improved food supplies lead to both reduced mortality and increased recruitment. Reduced mortality at such times can be attributed to better protection from predators and reduced competition for food supplies which can be expected to lead to improved body condition and less fighting. If conditions are optimal then major birth pulses are likely resulting in extremely large populations. It appears that this build-up phase in the hyrax population may pass unnoticed by human observers, presumably because the animals can obtain all their food requirements in the vicinity of their rocky habitat. If such large hyrax populations enter a period of drought, then shrinking food supplies in the vicinity of the rocky habitat can be expected to cause a decline through reduced recruitment and aggravated mortality (for reasons opposite to those listed above). In this way alternating periods of enrichment and drought (which characterise the Karoo) have the effect of destabilising hyrax numbers. Such climate-induced destabilisation might be expected to have a far more dramatic influence on hyrax populations if these populations were not protected so effectively by a refuge resource when below the carrying capacity of this resource (set by food supplies in the vicinity of rocky habitat), and if these populations were not susceptible to such efficient predation when above the carrying capacity. In this context, predation of rock hyrax differs from what has been described as 'environmentally-modulated predation' for Australian situations where prey species such as rabbits can escape the local predation capacity when conditions for population growth are optimal. Climate-induced destabilisation of hyrax populations can be expected to be greater in regions where climate is more variable and less predictable. It is relevant to note that major hyrax eruptions have only been recorded in the arid summer-rainfall areas of the Karoo and southern Namibia where rainfall is more stochastic and droughts are more severe.

The model predicts that major enrichment followed by major drought are both necessary to cause a dramatic hyrax decline, as observed in the early 1980's. Simultaneous dramatic declines of other ungulates suggest that elements in the lower trophic model (although simplistic and based on minimal field evidence) may find wider application for vegetation-herbivore interactions. Large hyrax populations may suffer heavy predation and decline when conditions are dry for a year, but the major eruptions were only reported after three to seven years of drought following enrichment. This suggests that total pasture exhaustion is necessary for dramatic alteration of hyrax behaviour and the invasion of new habitat. The reported eruptions also showed some coincidence with the timing of 'treks' by springbok in the arid zone (see Skinner 1993). These treks also involve dramatic behaviour change and have been linked to pasture deterioration.

It is likely that all the reported eruptions were caused by such pasture exhaustion, except possibly for the 1940's eruption. Only minor increase and decline phases are predicted for this period by the model whether based on Beaufort West, Stolshoek or district rainfall, and this is not in keeping with Thomas' (1946) observations that hyrax in the Cape midlands had recently increased enormously in numbers and had overflowed from the rocky habitats onto the plains. Construction of jackal-proof fences had been completed and destruction of predators had been very intense over the preceding 10 - 15 years, so it would appear that the 'magnitude' of this reported eruption may owe more to predator removals than to climate. The severe drought at that time may have forced the hyrax to invade new habitat, but predators were probably insufficient to remove these surplus animals. It is possible that a similar scenario was involved in the hyrax eruption reported for Namibia in the late 1960's. The unexpected recovery of hyrax on the farm Montana where caracals and secondary predators were heavily persecuted also indicates that interference with predators may alter the natural pattern of hyrax population change. To conclude, increase and decline phases in hyrax populations are naturally caused by changes in their food supplies in the vicinity of rocky habitats, and may result in major eruptions when large hyrax populations experience extended drought and pasture exhaustion. This pattern may be altered, and eruptions may be 'aggravated' by the removal of predators.

Do black eagles regulate hyrax populations in the Karoo?

A potentially unstable situation exists when a prey species with a very high propensity for population increase experiences a changeable food supply. In Australia for instance, this type of situation has led to massive irruptions of rabbits. If hyrax numbers follow changes in their food supplies in the vicinity of rocky habitat, it is important to know whether the change in hyrax numbers is brought about through the upper trophic level (mortality due to predators) or through the lower trophic level (loss of breeding potential and starvation), i.e. what are the proximate factors causing population change? Key factors analysis performed on population change during the short field study indicated stronger correlations with predation than with lower trophic factors. Although birth pulses varied greatly in the field study they were more related to rainfall patterns and they only affect the first age class, whereas predation affects all 12 age classes. The implication was that losses through the upper trophic level were more varied and more involved in hyrax population change than losses through the lower trophic level. However this result was likely to be influenced by conditions during the short field study. To escape these limitations, key factor analysis was conducted on a full run of the population model (over 112 years), in which the limits of demographic factors had been set in accordance with a variety of field studies. This analysis indicated that upper trophic losses could explain most population change and lower trophic losses a negligible amount. Despite the magnitude of variable hyrax birth pulses, this demographic factor appears to have more influence on hyrax population structure than on population size. The only time lower trophic losses appeared to be partly involved in population change was during periods of enrichment when large birth pulses facilitated growth. Predators appear to be essential for facilitating population declines when food supplies shrink. This tallies with observations on cyclic prey, where predators appear to be more involved with the decline phase than with the increase phase. One implication of this is that predator removal experiments conducted during enrichment are likely to yield very different results from predator removal experiments conducted during drought.

With the full complement of predators, the model predicts that hyrax populations are able to closely track changes in the carrying capacity of their refuge resource set by food supplies. Indications of the key factor analyses that predation is mostly involved in this close tracking were supported by simulating predator removals. Simulated removal of eagles or relatively low impedance of both eagles and caracals resulted in increased hyrax population density and large surpluses which regularly invoked heavy compensatory mortality when the population greatly exceeded the carrying capacity. A similar increase in the frequency of brown locust 'outbreaks' in the Karoo has also been attributed to the removal of natural predators (Hockey 1988). A much more significant increase in hyrax numbers was predicted for the 1940's with removal of eagles or >30% impedance of both major predators. The increased propensity for hyrax population growth under these simulations was so great that the model predicted increase phases when the population would naturally be declining. The predicted chain of events in the absence of eagles was robust for a wide range of dramatic parameter perturbations. Losses through the lower trophic level (variable birth rates and non-violent mortality rates) were based on field data and modelled on the ratio of hyrax food need to hyrax food supply, but they were evidently not sufficiently variable to ensure close tracking of food supplies by the hyrax population. Whereas the local predation response, also based on extensive field research, had the capacity to annually remove hyrax surpluses as they arose (even at high densities).

The black eagle - rock hyrax system shows some similarities to other predator-prey systems. Like other prey populations, hyrax populations rise and fall intermittently and predators play a key role during rapid decline phases. But these phases are not regular as for cyclic prey - they correspond to periods of enrichment and drought like the environmentally-modulated systems of Australia. But unlike the Australian systems, hyrax populations do not under natural conditions escape the capacity of the local predation response, and they enjoy effective protection from predators when their food requirements can be met within their refuge environment. Consequently the order of magnitude variation in hyrax numbers is far lower than that recorded in other cyclic or environmentally-modulated systems. Enhanced stability of rock hyrax populations in comparison to other prey can be attributed to three main factors: a fixed area of refuge habitat; the effectiveness of this refuge against nearly all hyrax predators; and high vulnerability of hyrax to numerous and efficient predators outside of their refuge environment. Rock hyrax are also unusual when compared with other prey because they become less available, despite increased abundance during enrichment, and more available despite decreased abundance during drought. The black eagle - rock hyrax system may be described as a 'refuge-mediated' predator-prey system which can be destabilised to a limited degree by climate.

Predators clearly ensure close tracking of food supplies within rocky habitat by hyrax populations. They do this by efficient removal of surplus animals. Does this mean that the predators are regulating hyrax numbers? No density-dependence could be found for the predation response in the field study or in a standard run of the model. In accordance with current demographic theory it would appear that this predation does not fulfil the strict definition of a regulating factor as: 'the process whereby a population returns to equilibrium'. But hyrax populations are unusual in that large populations may be protected from predators in wet years while small populations may be exposed to predators in dry years. This annual variation in the number of protected prey is likely to have hidden any density-dependence in the predation response. Population regulation has been defined in a more lenient sense as 'long-term persistence and fluctuations within limits'. I believe that the predators of rock hyrax, by efficient removal of surplus animals, do regulate hyrax populations in this sense of the term, between long-term limits that are defined by minimum and maximum food supplies within the well-defined patches of refuge habitat.

As to the question of whether black eagles, specifically, regulate hyrax populations in the Karoo, this would appear unlikely. In the model, predation by black eagles was free to compensate when caracals were impeded by 50%, yet the predation response of the eagles did not have sufficient capacity to prevent departure of the hyrax population from its carrying capacity. Black eagles (two pairs) on the farm Montana were apparently unable to prevent a hyrax population increase which was attributed to destruction of caracals and secondary predators of hyrax. Yet simulated removal of eagles in the hyrax population model did have a very dramatic effect on hyrax population change (this effect might be somewhat reduced in real situations where caracals may compensate). I would conclude that black eagles are not the sole agent responsible for regulation of hyrax populations, but that black eagles, caracals and the secondary predators of juvenile hyrax are all essential ingredients for an efficient predation response which can regulate hyrax populations about the changing carrying capacity of the refuge environment. Rather than reaching an equilibrium with their prey, these predators have the effect of maintaining an equilibrium in the lower trophic level within the refuge environment.

Most specialist predators have a destabilising influence on their prey due to time-lags in their numeric responses, and by pursuing their prey at low density. Black eagles were indeed catching hyrax despite very low prey availability, but at an apparently reduced rate. Destabilisation of rock hyrax populations by specialist black eagles (in the generation of regular cycles) is prevented by limitations on any numeric response by black eagles, and by the high degree of protection afforded to hyrax populations when their food need can easily be met by food supplies within the refuge environment. The model did not indicate much difference between the demographic influence of specialist predation by black eagles and generalist predation by caracals upon the hyrax population. It was anticipated that more consistent predation by eagles might have more influence during enrichment, while caracals would have a greater capacity for removing large surpluses in drought. However, interactive effects were probably not properly handled in the model to draw any conclusions on this matter. Field evidence suggests that the emphasis of age-specific predation upon hyrax by black eagles might change with prey:predator ratio, but the model did not indicate that this would be of great demographic significance.

The system under investigation is unusual as a refuge-mediated predator-prey system for the reasons given above, and the hyrax population model evolved in this thesis must be viewed as specific to this situation. Nevertheless the results of this investigation may find some application in other systems. The lower trophic interaction is simulated in the model in a very simple fashion based on changeable 'plant capital and interest', yet the predictions agree with field data and may be used to explain synchronous declines in ungulate populations in the early 1980's. Much still needs to be learned about the effects of rainfall on vegetation - herbivore interactions in the Karoo, and knowledge gained through modelling should prove to be of economic value to the farming community. I suggested earlier that many lifestyle characteristics of black eagles could be attributed to the relative stability of their prey base. More could be learned about the consequences of the order of magnitude variation in prey bases on raptor lifestyles. With regard to investigations of predator-prey systems which involve refuge, it should be borne in mind that there are likely to be other systems where predators regulate vulnerable prey between limits set by the extent of discrete refuge habitats, but where stochastic change in the degree of protection offered to prey may over-ride statistical detection of any density-dependent responses by the predators.

I have attempted to cover the key elements of this predator-prey system as comprehensively as possible, but more research is still warranted on the following aspects: interactive effects of rainfall, vegetation and herbivory in the lower trophic level; the influence of rainfall on the birth and survival rates of juvenile male and female hyrax; observations of hyrax foraging behaviour during experimental manipulation of predation risk and/or foraging return; comparative morphology and behaviour of rock hyrax inhabiting regions of Africa where black eagles are absent; numbers of hyrax captured by caracals under conditions of normal or high prey availability, and the emphasis of this predation on different hyrax population classes; the involvement of secondary predators in the extensive mortality of juvenile hyrax; and the compensatory behaviour of non-violent hyrax mortality on farms where predators are still controlled. A short-term indication of this compensatory mortality might be gleaned by comparing the bone marrow fat content of fresh hyrax carcasses collected beneath eagle feeding sites with that of hyrax from a randomly shot sample. This might reveal how many hyrax captured by eagles were already likely to die of other causes, but it should be remembered that compensatory non-violent mortality is likely to increase along with hyrax population density in the absence of predators. Other related research fields which would provide useful data would be feeding energetics of captive black eagles on a hyrax diet; post-mortem examinations of fresh lamb carcasses brought to black eagle nests, and an extensive survey by necropsy of factors causing deaths of domestic lambs on karoo farmland. Captive trials on the effectiveness of lithium chloride as a taste-aversion agent to discourage lamb-killing eagles are planned.

Do black eagles kill domestic livestock in the Karoo, and if so what steps can be taken to prevent this?

Feeding studies indicate that two black eagle pairs on an average karoo farm in mountainous terrain are likely to consume 6 - 13 domestic lambs annually. Utilisation of this food resource was indicated by earlier nesting by eagles on farmland. It is not known whether such lambs were dead, dying to other causes or healthy when the eagles 'collected' them. But it is probable that 145 lambs die on the average karoo farm annually (mostly just after birth), and that black eagles, like golden eagles, scavenge most of the lambs that they bring to their nests. No reliable conclusions can be drawn from these data but an overall worst-case scenario of 2 - 5 lambs killed annually per farm by black eagles is suggested for mountainous karoo terrain.

Reliable and extensive field necropsy surveys of lamb mortalities under open-range conditions around the world indicate that 20% of lambs born are likely to die before weaning, and that predators are the prime cause of death for about 1,7% of lambs born under semi-arid, open-range conditions. Only limited surveys have been conducted in South Africa which indicate lower rates of predation than elsewhere. But black eagles were not implicated in nearly 600 carcass examinations, all of which were conducted in black eagle habitat. Black eagles were exonerated on two out of three carcass inspection surveys conducted on Cape farms in response to farmers complaining of major losses to eagles. It is concluded that lamb-killing by eagles does occur in the karoo but very rarely. Most eagles appear to prefer natural prey, possibly because they became 'wedded' to such prey as nestlings. Being specialist predators of hyrax, black eagles may have a well-developed 'specific search image' for this prey, and unlike other *Aquila* eagles, they are highly territorial and are not recorded to aggregate at lambing paddocks. These reasons are offered to explain why lamb-killing by eagles in mountainous parts of the Karoo occurs less frequently than might otherwise be expected.

Of the 820 lambs born on the average karoo farm each year, 145 are likely to die. Using the very extensive and comparable Australian data (which actually indicated higher predation rates than the South African surveys), it is calculated that (all) predators are likely to be the prime cause of 13,6 of these deaths and eagles are likely to be the prime cause of only 0,32 lamb deaths on the average karoo farm annually. This gives a reliable indication of the overall scale of the problem but some farmers are likely to suffer more losses than others. Problem situations involving eagles can be dealt with by more intensive flock management during the vulnerable lambing period. This can involve the use of shepherds or scarecrows; removal of all carcasses from the lambing area; and conducting lambing away from areas of eagle activity, especially when breeding pairs have young nestlings which may adopt a lamb-eating habit. Taste-aversion using lithium chloride may prove a useful deterrent in the future, but persistent lamb-killers should be trapped and sent to zoos or falconers to prevent further spread of the trait.

The role of black eagles on karoo farmland

The net influence of black eagles on human commercial activities in the Karoo can best be judged by comparing the cost of their predation on domestic lambs with the benefits of their predation on rock hyrax, a potential competitor for the veld resource. The current market value of weaned lambs is R74, so the overall cost of lamb predation by black eagles to the average karoo farmer in mountainous terrain, as indicated by extensive and reliable studies of lamb mortality and the relative involvement of predators, is R24. This cost is equivalent to 0,05% of proceeds from lamb sales on the average farm, and would comprise a much smaller equivalent to gross farm income. It is concluded that lamb predation by black eagles in the Karoo is of negligible financial importance overall.

Assessing the financial benefits of black eagles to karoo farmers in terms of alleviation of competition between hyrax and domestic livestock for grazing is more difficult. But an indication of this can be obtained by looking at the increase in numbers that is predicted by the hyrax population model in the absence of predation by eagles. Lensing (1982) has argued that competition between livestock and hyrax on Namibian farms is negligible because livestock rarely venture into the rocky habitats used by hyrax. However, the food requirements of surplus hyrax (defined in the model as the excess of population density over carrying capacity of food supplies within the refuge environment) must be met outside of the vicinity of rocky habitat. On the basis that 10 hyrax consume as much food as an adult Merino sheep and current letting rates of R30 per head per year, the additional hyrax surpluses predicted in the absence of eagles (about 622 extra hyrax per eagle territory annually) are likely to cost the average karoo farmer in mountainous terrain (two eagle territories) in the order of R3700 each year. Most farmers control caracals rather than eagles and seldom eradicate either, so impedance of the predation response is a more realistic interpretation, and it is estimated that just a 30% impedance of both caracals and eagles will create additional hyrax surpluses which will consume R2700 worth of grazing annually.

Black eagles are very important members of a guild of predators which are essential for restricting hyrax to their refuge environment and for removing any surpluses. The predicted cost of hyrax surpluses when black eagles are removed from karoo farmland exceeds the estimated overall cost of lamb-killing by black eagles by a factor of 150. Even the cost of the worst-case scenario of five lambs killed by eagles per karoo farm, that is indicated by unreliable prey remains data, is still ten times less than the estimated saving that can be attributed to black eagles through prevention of hyrax surpluses. Eagles would need to kill up to 50 lambs per farm annually before the total removal of eagles would make any financial sense. However, more intensive management of flocks during the crucial lambing period, using practical techniques, should enable karoo farmers to reap the benefits of having black eagles on their farms without incurring any significant costs in terms of lambs lost. The financial benefits of black eagles to karoo farmers greatly outweigh the negligible overall costs, and management can minimise any costs arising in very rare problem situations involving eagles. So I conclude that, in financial terms, black eagles are clearly compatible with the open-range farming of small livestock in the Karoo.

To prevent the development of rifts between farmers and conservationists, it is important that conservation officers do not deny that eagles may kill lambs, and that they take an active interest when farmers report problem situations. From experience gained in the present study, carcass examinations conducted in such 'problem situations' provide real data which usually exonerate eagles and educate both farmer and conservation officer as to the real causes of lamb mortalities, thereby affording ideal opportunities for constructive interaction between two parties who can, otherwise, easily become diametrically-opposed in the absence of reliable information concerning the problem.

Black eagles are evidently extremely efficient at catching rock hyrax so it is likely that they out-compete many other predators for this dominant prey in areas where they are not nest-site limited. Less compatible predators may be attracted by abundant hyrax on farms where eagles have been removed. Caracals are not as obviously compatible with small-stock farming operations as black eagles because certain individuals may cause extensive damage to livestock. But the present investigation indicates that the highly variable capacity of caracals to remove hyrax may have just as much demographic influence in the prevention of hyrax surpluses as specialist predation by black eagles. Where problems occur with caracals it is recommended that farmers adopt the management principles suggested by Stuart (1981a) whereby individuals rather than species are controlled. Gin traps and strychnine are indiscriminate and inhumane methods of control and do untold damage by removing innocent predators, many of which may be important as primary or secondary predators of pest species such as hyrax. These methods should be abandoned forthwith and replaced by toxic collars, cage traps and other selective methods which allow for the effective and humane removal of those individuals responsible for killing livestock.

Not all the benefits of eagles to farmers can be assessed in financial terms. Eagles are likely to play an important role in preventing the spread of diseases by removing animals whose sickly and aberrant behaviour triggers the predation response. The spread of rabies by small carnivores (e.g. mongooses) may be significantly curtailed by large raptors. This is one way in which eagles act as agents of natural selection and remove unfit individuals, thereby maintaining healthy stock in their prey populations.

It is especially hard to place a value on the aesthetic pleasure that people derive from watching wildlife, especially spectacular and evocative species such as large eagles. Many populations of these large, slow-breeding birds are vulnerable to the effects of people and development, and have declined worldwide. It is likely that with growing human populations in the third world more wilderness areas will lose out to development and eagle populations will decline further through loss of suitable habitat. With the growing popularity of ecotourism, farmers with large eagles on their properties may find that they have a valuable and marketable commodity. A good chance of seeing large eagles is already a 'draw-card' for game lodges and guest houses in South Africa.

But large eagles have probably inhabited southern Africa and the Karoo for 10000 times longer than human beings, and it is a sad view to believe that such wildlife must demonstrate a positive economic value to ensure its survival. Where farmers are still uneducated as to the role played by large eagles in the environment, it may be necessary to stress the financial advantages of conserving such obviously beneficial species as black eagles, as indicated above. But what of species such as martial eagles which do not demonstrate such an easily-identifiable positive role? Progressively more farmers are demonstrating that they certainly do have an aesthetic appreciation of, and enjoy, the wildlife on their farms. In some areas this has almost grown into a competition among peers to boast such flagship species as eagles on their land. I suggest that future education campaigns pay progressively more attention to instilling this aesthetic appreciation of wildlife among landowners and encouraging the conservation of species which do not necessarily demonstrate a noticeable positive role, rather than simply stressing the financial advantages of mutually-beneficial species.

Many of the current ecological problems in the Karoo, such as degradation of the vegetation resource and irruptions of pest species, can be associated with simplification of this ecosystem by human activities. By replacing the diverse plains game with monocultures of livestock, and by eradicating many carnivores, scavengers and even beneficial insectivores, some key players in a once-diverse system have been taken out. With its stochastic, water-limited climate the Karoo could not have been described as truly stable before the advent of farming, but these arid systems are especially sensitive to interference, and simplification tends to reduce the stability of ecosystems. Just tolerance of compatible predators such as large eagles is one simple and easy management step that karoo farmers can take to restore the ecology on their farm to something of its former diversity and stability.

SUMMARY

Grazing resources in the Karoo and in Namibia have been damaged in the past by 'irruptions' of rock hyrax which have been attributed by some naturalists to predator eradication. But many ecologists have maintained that predators do not limit or regulate their prey in vertebrate communities. The highly specific predator-prey relationship between black eagles and rock hyrax is ideally suited to an investigation of predation. A study of this system was initiated to assess the impact of black eagles on their prey (including domestic livestock) in terms of numbers and population dynamics, and so resolve the predation debate with regard to this system and establish the role of this predator on karoo farmland. The study also afforded the opportunity of investigating how the 'lifestyles' of black eagles and rock hyrax have become inter-linked. Certain key elements were identified in this predator-prey system including an important alternate prey species and an important competing predator species. During a five year field study, all elements were researched as comprehensively as possible to construct 'as good a model as possible' of the system which is used in conjunction with the results of the field study to address key questions regarding the demographic influence of black eagles on rock hyrax.

The study was conducted in the semi-arid interior of the Cape Province known as the Karoo, an extensive dwarf shrubland which is prone to a stochastic climate and droughts, but which supports an important small livestock industry. Livestock predation by black eagles was investigated on farmland throughout the central Karoo, but the Karoo National Park (KRNP) at Beaufort West was chosen for the detailed study of the demographic influence of black eagles on rock hyrax. This site was representative of mountainous regions in the Karoo and contained natural populations of predators which had not been persecuted for seven years prior to the present study. Rocky habitats in the park comprised prime habitat for both rock hyrax and black eagles and there was no indication that the eagles were limited by nest sites. The summer rainfall regime experienced in the Karoo is somewhat cyclic: excellent rains in the late 1970's were followed by major drought in the early 1980's, and previous researchers in the KRNP recorded a fourfold decline in hyrax prior to the present study. Rainfall during the study period was average, so this could be regarded as a period of recovery for karoo biota.

It was established early on in the study that refuge played a key role in this predator-prey system. All rock outcrops (n=3365) in the central part of the park (140km^2 - encompassing more than four eagle territories) were classified and described in detail, and then mapped onto a geographical information system (GIS) of the study area to allow detailed measurements. Mudstones form the bulk of karoo bedrock but are not sufficiently resistant to form outcrops. The characteristic koppies and plateaus of the Karoo are created by resistant sandstone lenses and intrusions of dolerite. Two major dolerite sills are exposed as an upper and lower escarpment in the KRNP, and divide the park into five major topographical habitats: upper plateau, upper slopes, middle plateau, lower slopes and bottom plains. Continuous lineal outcrops (dolerite escarpment and lineal sandstone outcrops on slopes) occupied 3% of the mapped area. Discontinuous screes and dolerite knolls were scattered over a further 14% of the area. Most rock outcrops were exposed on the mountain slopes (84% of lineal outcrops, 98% of screes). Highest densities of apparently suitable crevices (for hyrax) were recorded in lineal sandstone outcrops and where dolerite escarpment had weathered into pillars.

The rock hyrax prey base in the KRNP was studied by annual intensive counts at colony outcrops and by plotting all hyrax groups within the mapped area. Population estimates (end 1989) were 1025 for an average eagle territory and 13335 for the park. Density (69 per km^2 in mountainous terrain) was much lower than recorded elsewhere. Over 98% of hyrax in the KRNP occurred in groups and all overnighted in rock outcrops which had been rated at least adequate for colonies (none in temporary shelter). Larger groups occurred closer together in the large, crevice-rich igneous escarpment outcrops, especially where these converged into kloofs with boulder screes and dense vegetation. Groups were often located close to riparian thicket. The distribution suggested that 'safely-accessible food' was most important, and that within group ranges suitable overnight shelter was not limiting. Most groups occurred on slopes (where most rocks were) and there was some

favouring of east-facing aspects which receive early-morning sun. Despite these trends groups were fairly regularly distributed through adequate habitat. Despite some habitat-related variation, most harem groups approached an average of 16,4 members. Disappearance/coalescence of small groups and the tolerance of sexually-quiescent males within harems suggested that maintenance of adequate group size was important. Predation risk is considered the main reason why hyrax spent 96% of their time within 5m of shelter and never ventured further than 15m from a bolt hole. Distinct vegetation zones around well-used outcrops conformed to this pattern. Hyrax posted sentinels and used screes and thickets to access quality vegetation on intense group-feeding bouts and made extremely efficient use of this time away from their shelters by harvesting different parts of their range on consecutive days. These trips were not made on windy days. Dispersal through non-rocky terrain occurred at night. Predation pressure may also explain why hyrax in the unpredictable Karoo show a distinct birth-pulse (modal parturition date 12 Nov). Composition of the hyrax population was determined from the three age classes recognisable during counts immediately after the birth-pulse, and from life-table analyses of skulls collected in the field. Variable mortality and especially recruitment rates related to rainfall and caused a significant population decline in the dry year of 1988. There were indications of late pre-natal mortality in very dry conditions, and that sex ratio of the first age class varied with rainfall. Hyrax population structure is evidently highly dynamic in response to the stochastic rainfall of the Karoo.

Transect sampling of the major habitats in the KRNP revealed that middens of Smith's red rock rabbits occurred at densities of 400 - 500 km^{-2} in mountainous terrain. Studies of faecal accumulation rate on middens indicated a ratio of one animal to about 15 middens. An overall density of 30 rabbits km^{-2} was inferred with an estimate of 6652 for the KRNP in 1989, and 441 for the average (lower escarpment) eagle territory. But incidental sightings of rabbits suggested a ten-fold increase in numbers by 1989 from a 'low' in 1987. Other potential prey populations also showed 'troughs' in numbers in 1987 or 1988 which were probably drought-related. Red rock rabbits did not occur on the non-rocky bottom plains, but were relatively homogeneously distributed through the mountainous habitats - so they occurred at one third the density of rock hyrax on mountain slopes, but double their density on the rocky plateaus. Some variation in midden density indicated that loose rocks strewn over gentle slopes were preferred, while grassy, northerly aspects were avoided (possibly for thermoregulatory reasons). Sitings of middens indicated that some access to rock crevices is a prerequisite for the ranges of individual rabbits - these may serve as bolt-holes for adults or nest sites for young. Defence of these discrete, limited resources is offered as an explanation for territorial behaviour in this species.

Twenty two pairs of black eagles were located in the study area (13 nested in the park). This density (4,14 pairs per 100km^2) is higher than all estimates from other mountain ranges except the Matobo Hills. Eagle pairs nested significantly closer together along the upper escarpment (mean 2,7km) than along the lower escarpment (mean 4,6km), and the former represents the closest nest-spacing yet recorded for any linear mountain feature. Floaters (> 40% immatures) probably occurred at a ratio of one per 15 resident pairs. The continental escarpment ranges in the Karoo are likely to accommodate over 600 pairs, and the entire mountain ranges in the Cape over 2000 pairs. The habits of black eagles preserve them from most forms of human persecution which have eradicated large scavenging raptors from the Karoo. Black eagle pairs in the KRNP occupied inter-locking territories with no unused space. Overlap between pairs was minimal (<10%) especially for foraging behaviour. Average territory size was 24km^2. Three pairs each defended 52km of lineal rock outcrops, a fourth 60km. But the safe feeding area for hyrax around rock outcrops was the habitat parameter which showed least variation across territories. An hypothesis that eagles might use rocky habitats as a structural cue for stable territories despite fluctuating hyrax numbers is not supported by recent observations of territory vacation in the Matobo Hills. Territories also contained relatively consistent amounts of food (mean 63 hyrax groups) and an abundance of prey refuge (mean > 44000 crevices). Nearly all nests were located in core areas of territories, but radio-carbon dating of material from one tall nest (3,8m) did not supply evidence that nests (and thus perhaps the core areas) were very ancient. Nests were preferentially sited on tall sheer dolerite cliffs facing south. Relatively late breeding (except on farmland) and small clutch size were suggestive of low food availability, but overall breeding effort (61% pairs) and success (46% pairs) was not dissimilar to that recorded elsewhere. Most nest failure occurred on accessible lower escarpment cliffs at the small chick stage, and could be attributed to predation by mongooses twice. Pairs suffering high failure rate tended to have more alternate nest sites. Large lower escarpment territories probably contained more prey for despite high failure rate, these pairs made more breeding effort and raised more chicks than upper escarpment pairs.

Black eagles spent 24% of their daytime flying, and allocated slightly more of this flying time to territorial defence than to foraging. Eagle flight paths recorded during 40d of watching resident pairs were analysed by GIS. An average flight speed of 47kph (range 10-125kph) was calculated from 693 flights covering 2747km and spanning 58h. The timing of hunting flights and strikes at prey showed seasonal change which matched the changing foraging rhythms of hyrax. Eagle foraging behaviour was state-dependent and weather-dependent. Eagles flew more on windy days. Hunting eagles flew mostly over slopes which were close to their nests, afforded good hyrax habitat and good lift for prevailing wind sources. They preferred to first sight their prey from a perch or high altitude flight and then make a hidden approach. Only 8% of strikes at prey resulted in kills. Strikes from perches were twice as successful as strikes from flights, and tandem strikes were twice as successful as solo strikes, but these improvements were not statistically significant. Eagle pairs spent 85% of their flight time together. When hunting in pairs, black eagles fulfilled most of the characteristics of cooperative hunting, and their division of labour could usually be related to the dimorphic capabilities of the sexes.

Radio-tracking of four caracals in the KRNP was unsuccessful, but trapping success experienced during the capture of these animals suggested intermediate density (4,8 adult units per 24km^2 eagle territory) between that recorded in the south-west Cape (2,4 adult units per 24km^2) and that recorded in the eastern Karoo (7,4 adult units per 24km^2), and this would concur with intermediate rainfall. Caracals are likely to outnumber black eagles by a factor of three in the KRNP, and metabolic predictions suggest that they might consume nearly six times as much food. Unlike black eagles, the flexible social organisation of caracals allows them to show a significant numeric response to changes in prey availability. The density estimates from elsewhere in the Cape provide likely upper and lower limits to this response. Long-term trapping records of caracals on farms suggest that numbers may increase by up to 22% p.a., and decrease by up to 34% p.a. in conjunction with major rainfall events (after a time-lag of 6-12 months). Hyrax can comprise over 50% of caracal food in the Karoo, but no hyrax remains were found in 100 caracal scats analysed in the present study. As generalist predators, caracals were relying on other prey, notably wild and domestic bovids. Secondary predators occur in sufficient numbers in the KRNP (@ six per 24km^2) to pose a significant additional threat to juvenile hyrax.

Feeding trials and metabolic predictions indicated that an average black eagle needs to consume between 1500 and 1700 KJd^{-1} food energy for maintenance in captivity. Approximately 500g of hyrax would fulfil this requirement allowing for 40% wasted and 75% metabolised. It is likely that wild nestlings can get by on slightly less food than this (overall), but that wild adults may need up to 25% more. Field observations and time-lapse photography at nests indicated that eagle pairs were catching 0,43 prey/d when not breeding and 0,57 prey/d when provisioning young. Eagles had to catch an additional prey item every five to six days when provisioning young but this requirement varied with nestling age. These prey capture rates were much lower than those recorded in similar studies of black and other large eagles. But mean prey mass was much larger (2565g) such that rates of biomass captured (446kg/y) and consumed (284kg/y) by breeding pairs were not markedly dissimilar from other studies. Observed rates of food consumption were still lower than the predicted minimum requirements (especially when breeding), and eagle pairs with a large lagomorph component in their diet were able to achieve higher provisioning rates, so low hyrax availability is inferred. Prey capture rate did not vary with nestling food requirement nor the hunting abilities of the pair. High rates of hyrax deliveries to nests coincided with periods of drought and with the time of day when hyrax were likely to be foraging.

Rock hyrax comprised 88% of 3823 prey items identified from remains collected beneath black eagle eyries in the study area. In comparison with other studies of black eagle diet by the same method, this is average to high and does comply with the popular belief that black eagles are highly prey-specific. However, comparison with time-lapse photography and other methods indicated that rock hyrax remains are significantly over-represented in collections of prey remains, and small lagomorphs are extremely under-represented. The most likely composition of black eagle diet was interpolated from various methods: hyrax comprised 67% (range 46-83% for different pairs from reliable data), lagomorphs 25%, bovids 4% and carnivores 2% by frequency. Most prey items (97%) fell in the size range 500-4000g. Juveniles predominated among bovid prey, and eagles generally avoided this category presumably because of risk of injury. Domestic lambs comprised 1,2% of prey remains, and up to 3,4% of prey deliveries to nests on farmland. It is not known how many of these were scavenged, but carrion might fulfil 4-11% of eagle food needs. Upper escarpment eagle pairs, despite smaller territories, took more alternate prey (especially birds and reptiles) than lower escarpment pairs. The composition of prey in black eagle diet was very similar to the composition of prey available (except for avoidance of bovids), so are black eagles truly prey-specific? Many lines of evidence indicated that hyrax were well-protected within their refuge environment during the field study, and this low availability was reflected in the absence or low frequency of hyrax in the diet of two large generalist predators in the area. Also, there was no evidence of a switch response in black eagle diet to increased abundance of red rock rabbits. It is concluded that black eagles were behaving as specialist predators by pursuing their favoured prey despite low availability.

The age and sex of hyrax maxillae belonging to 3359 hyrax eaten by black eagles in the KRNP and 2259 hyrax eaten by black eagles elsewhere in the Cape were determined from patterns of tooth eruption and tooth wear. Composition of population classes among KRNP prey were compared with composition of the prey population. Eagles showed avoidance for the very abundant first age class, presumably because juveniles are of low profitability (1/16 of adult mass at birth). Eagles showed positive preference for immature hyrax (1-2y olds) which comprised the most frequent age class captured. Eagles caught significantly more immature males than females, and this heavy predation was partly responsible for the observed skew in the adult prey population towards females. Dispersal is more obligatory for immature males, and these animals presumably become more vulnerable to eagle attack when they enter unfamiliar terrain without the advantages of group vigilance and sentinels. Adult hyrax are presumably more experienced at evading eagles and did not occur more frequently among eagle prey than expected. But eagles exerted hard selection on adult and old hyrax, and could account for three out of every four deaths among these age classes. Old hyrax (8-13y) fell prey to eagles more frequently than expected, presumably because of deteriorating flight response, and the eagles were able to remove one third of these hyrax annually. More old female hyrax were available to the eagles than old males, but they were still captured significantly more frequently than expected. This may be because females are more inclined to adopt high-risk sentinel behaviour, and other factors may be more involved in the deaths of males. So the overall pattern of age-selective predation of hyrax by black eagles could be explained in terms of vulnerability rather than 'prudent predation'. This pattern showed great geographical and temporal variation which correlated significantly with respective rainfall patterns prior to the collections - testament to the dynamic nature of hyrax population structure and to the validity of the methods used for age-determination. The size of adult hyrax captured (as indicated by maxillae) also correlated with rainfall patterns. Lower escarpment eagles preyed more heavily on surplus elements in their hyrax prey base, such as males and old hyrax. Upper escarpment eagles captured relatively more unprofitable juveniles and healthy breeding stock such as adult females (along with more alternate prey). Upper escarpment eagles were thought to be suffering low hyrax:eagle ratios, and this was also suggested by reduced wastage (more hyrax crania opened). These symptoms of low hyrax:eagle ratio were also evident in eagle diet from low hyrax density mountain ranges (e.g. Fynbos), and in eagle diet when hyrax were at low abundance and reduced availability (E. Cape & Fynbos during early 1970's).

Early nesting by black eagles on farmland suggested that these pairs were utilising food resources unavailable in the KRNP. Nest-based studies of feeding habits indicated that black eagles were consuming 6-13 domestic lambs annually on the average karoo farm in mountainous terrain (= two eagle territories). These studies did not indicate whether these lambs were healthy, dying or dead when 'collected' by the eagles. About 20% of lambs die before weaning, which would leave about 145 carcasses available to eagles per karoo farm. It seems likely that black eagles, like golden eagles, scavenge most of the lambs brought to nests. Surveys of lamb mortality by field necropsy in lambing areas yield the most reliable and comprehensive indication of livestock predation. Extensive surveys of Merino mortalities under open-range conditions in Australia (very comparable to the Karoo) indicate that predators are the prime cause of death for 1,7% of lambs born, and worldwide surveys indicate that eagles may be responsible for 2,4% of predator kills. Limited mortality surveys in South Africa (in black eagle habitat) indicate lower losses to predators and no involvement of eagles. In the absence of good karoo data, the Australian data indicate that the overall cost of livestock predation by eagles to karoo farmers is likely to be 0,32 lambs or R24 - i.e. negligible. Direct observations suggested that most eagles in the Karoo prefer natural prey, to which they may have become 'wedded' as nestlings. Unlike other large eagles, black and martial eagles are not recorded to congregate in lambing areas. Nevertheless there is proof that black eagles have killed lambs in the Karoo and it is likely that such problems would be concentrated on a minority of farms. It is suggested that affected farmers manage their flocks more intensively during lambing by the use of shepherds/scarecrows, by removal of carcasses and by conducting lambing away from areas of eagle activity. Flock management is far more effective than predator management (e.g. eagle translocation), but taste-aversion may prove useful in the future, and persistent offenders should be removed (to zoos/falconers) to prevent spread of a lamb-killing trait.

Rock hyrax were at low density and low availability during the present field study. During the years of accurate data collection, black eagles removed an average of 11% (117) of the hyrax standing crop (1062) per territory per annum. They also removed 8% of the red rock rabbit standing crop (11% in 1989). The hyrax toll taken by the eagles could account for 27% of hyrax mortality and was equivalent to 29% of annual hyrax recruitment. Key-factor analysis indicated that hyrax population change during the study period was more related to losses through the upper trophic level (predators) than to losses through the lower trophic level (loss of breeding potential and non-violent mortality). The study was presumably too short to confirm any density-dependence of demographic factors, but mortality was more closely related to density than recruitment. Presumably reproduction would only be hampered by crowding effects at high density. Despite changes in hyrax density, eagles consistently removed 11% of the population. Many hyrax killed by eagles were from age classes with high survivorship, so it is likely that much of this mortality was additive, and therefore it can be stated that the eagles exerted a limiting influence on hyrax population growth during the field study. Fluctuating food supplies and a hyrax population with high propensity for increase is a potentially unstable situation - any factor which acts as a consistent 'handbrake' on population growth should help prevent imbalances developing between the population and food supplies.

Data from the present study and other field research were collated to develop a detailed and specific hyrax population model which simulated hyrax demography in response to long-term climatic data for the Karoo. The model departs from previous hyrax modelling attempts in precise measurement of the refuge environment and its carrying capacity (set by food), and by allowing this carrying capacity to vary in a simple lower trophic sub-routine which accommodated herbivory and the profound effects of rainfall (enrichment). Population processes are dependent in the model on the ratio of the hyrax population (P) to this dynamic carrying capacity (K), such that small hyrax populations after good rains experienced minimum mortality and maximum recruitment, whilst large populations during drought experienced the opposite. The model shows that natural predation enables hyrax populations to closely track climate-induced changes in their food supplies within the confines of their refuge environment. Irruptions of hyrax reported in the literature corresponded to predicted decline phases - these hyrax probably became more noticeable because of habitat shift and dispersal in response to pasture exhaustion within the refuge environment. The puzzling widespread decline of hyrax in the early 1980's can be explained in simple terms of enrichment followed by severe drought. Predictions of this decline for different rainfall regimes showed strong correlations with field observations of hyrax in the KRNP and black eagles in the Matobo Hills. Climate-induced irruptions are more likely to occur in arid regions with stochastic rainfall. So irruptions were primarily caused by pasture exhaustion, but predator eradication is likely to have greatly aggravated the irruption reported in the 1940's. Key factor analyses and simulated removal or impedance of predators demonstrated that the variable predation response had the capacity to remove hyrax surpluses as they arose (even at high density). Although modelled on P:K ratio, variable recruitment and non-violent mortality in the absence or impedance of natural predation were insufficient to prevent rapid departure of P from K which resulted in large hyrax surpluses and regular population crashes when heavy compensatory mortality was predicted due to grave imbalance with food resources. These predictions were robust for a wide range of dramatic parameter perturbations. Annual variation in the number of protected hyrax obscured density-dependence in the predation response, but it can be stated that predators still regulate hyrax populations in the lenient sense of the term by confining them to refuge patches and by ensuring persistent fluctuation within limits set by minimum and maximum food supplies within the refuge patches. Pasture exhaustion during severe drought may occasionally force large surpluses of hyrax from their refuge patches but the natural complement of predators has the capacity to remove these animals. Separate impedance of black eagles and caracals in the model did not indicate any obvious difference in the demographic influence of these very different predators, but it was clear that the full complement of predation was required for regulating the hyrax population and this was confirmed by field indications of hyrax population change on a farm where all predators except black eagles were persecuted. Hyrax populations differ from cyclic prey populations because increase and decline phases are irregular and climate-induced, but unlike the environmentally-modulated predator-prey systems described in Australia, hyrax populations do not naturally escape the local predation capacity. The unique character of the black eagle - rock hyrax system can be attributed to the influence of a permanent and highly effective refuge habitat, and to the destabilising phenomenon of reduced prey availability despite increasing abundance during enrichment.

Black eagles were reliant on rock hyrax as their principal food in this and other studies in Africa, and exerted very hard selection on adult and old hyrax, so it was not surprising that a comparison of the functional morphology and ethology of rock hyrax and black eagles revealed traits that appeared to have evolved reciprocally between the species. Both show obvious adaptations to their habitat as well as to each other, and such adaptations have probably reinforced their mountain lifestyles. To avoid predation, hyrax minimised their time away from shelter (especially on windy days when eagles were more active) and made use of an early-warning system when foraging in groups. In response: eagles timed their hunts to coincide with hyrax foraging rhythms; they hunted cooperatively to allow double strikes at elusive prey and to capture prey which took refuge in vegetation; and they made maximum use of cover and adverse light conditions to conceal attacks. A special light-shielding structure has evolved in the eyes of rock hyrax which may facilitate detection of attacking eagles, while disproportionately large feet are likely to be an adaptation of black eagles for capturing hyrax which are twice as large as normal *Aquila* prey. Many aspects of black eagle lifestyle, such as their striking territorial behaviour and their conservative reproductive behaviour, can be linked to the unusual degree of stability of the hyrax prey base which can be attributed to the permanent and patchy distribution of a very effective refuge resource.

Black eagles have been known to kill domestic lambs, but it happens so rarely that the overall cost to karoo farmers is negligible. When farmers complain of problems with eagles, these situations can be investigated by examining carcasses in the lambing areas to reveal real causes of lamb mortality - this approach is far more constructive than denial of the problem which can often lead to rifts between farmers and conservationists. If eagles are implicated then management practices can be recommended which should minimise or prevent losses. But it is likely that the examinations will exonerate eagles of blame, and they will have afforded an opportunity for education. The present study indicates that financial benefits of black eagles on farmland, in terms of grazing saved from hyrax surpluses, may outweigh overall costs by a factor of 150. Financial advantages of conserving such obviously beneficial species can be stressed in education campaigns, but these campaigns should not neglect species which have less obvious financial or ecological benefits. Tolerance of compatible predators such as large eagles is one simple and easy step that karoo farmers can take to restore the ecology on karoo farmland to something of its former diversity and stability.

OPSOMMING

Weiding in die Karoo en Namibië is in die verlede beskadig deur "uitbrake" van klipdassies wat, volgens sommige natuurkenners, deur die uitroei van roofdiere veroorsaak is. Daarenteen is baie ekoloë van mening dat, binne vertebraat-gemeenskappe, roofdiere nie hul prooigetalle beheer nie. Die spesifieke roofdier-prooi verhouding tussen dassies en witkruisarende is 'n ideale onderwerp vir so 'n studie. So 'n ondersoek is onderneem met die oog daarop om die invloed van arende op hul prooi (insluitende vee) se getalle en bevolkingstruktuur te bepaal. Op hierdie wyse kan die reguleringsvraagstuk vir hierdie stelsel opgelos word, en die rol van arende binne die Karoo-omgewing te bepaal word. Die studie bied ook die geleentheid om te bepaal hoe die biologie van die roofdier en prooi wedersyds beïnvloed word. Alternatiewe prooi vir die arende en addisionele predasie deur ander roofdiere blyk belangrike fasette van die stelsel te wees. Die resultate van vyf jaar se veldwerk, waartydens alle aspekte van die stelsel so intensief moontlik ondersoek is, word gebruik om 'n model saam te stel wat die belangrike vrae rakende die invloed van witkruisarende op die demografie van dassies aanspreek.

Die studie is gedoen in die half-droeë Karoo van die sentrale Kaapprovinsie, 'n uitgebreide bossieveld wat aan 'n wisselende klimaat en aan droogtes onderhewig is, maar wat 'n belangrike kleinveebedryf huisves. Predasie van arende op kleinvee is ondersoek op plase dwarsdeur die sentrale Karoo, maar 'n diepgaande studie van die demografiese invloed van arende op dassiebevolkings is in die Karoo Nasionale park (KRNP) te Beaufort-Wes onderneem. Hierdie nasionale park verteenwoordigend die bergagtige Karoo wat beskik oor natuurlike bevolkings roofdiere wat gedurende die voorafgaande sewe jaar nie gejag is nie. Klipperige habitat het goeie woonplek verskaf aan beide dassies en arende en daar was geen aanduiding dat die getal arende beperk is deur 'n gebrek aan nesmaakplek nie. Die somer-reënval in die gebied is deels siklies: hoë reënval gedurende die laat 1970's is gevolg deur ernstige droogtes gedurende die vroeë 1980's. Vorige navorsing het getoon dat dassiegetalle in die KRNP viervoudig verminder het gedurende hierdie tydperk. Vir die duur van die studie was die reënval gemiddeld gewees en gedurende hierdie tydperk het die Karoo se diere- en plantelewe waarskynlik herstel van die droogte.

Dit het gou duidelik geword dat skuiling 'n sleutelrol in die roofdier-prooistelsel inneem. Alle klipkoppies (n=3365) in die sentrale deel van die KRNP (140 km^2 - wat meer as vier arend-territoria insluit), is in besonderhede beskryf en geklassifiseer. Die klipkoppies is deur middel van 'n geografiese inligtingstelsel (GIS) gekarteer sodat noukeurioge metings gedoen kon word. Sedimentêre gesteentes vorm die grootste deel van die Karoo se grondlaag, maar is nie hard genoeg om klipkoppies te vorm nie. Die kenmerkende koppies van die Karoo word deur formasies van sandsteen en doleriet gevorm. Twee groot doleriet-vlakke vorm 'n hoë en lae platorant in die KRNP, en veroorsaak dat die park in vyf topografiese habitatte verdeel kan word: boonste plato, hoë hellings, middel-plato, lae hellings en vlakte. Aaneenlopende, liniêre koppies, bestaande uit doleriet dagsome en sandsteen koppies op hellings, beslaan 3% van die gekarteerde oppervlak. 'n Verdere 14% van die oppervlak word beslaan deur verspreide bergpuin en dolerietbultjies. Die meeste klipkoppies is teen die berghellings geleë (84% van die liniêre koppies, 98% van die bergpuin). Die hoogste digtheid van geskikte skeure vir dassies is in liniêre sandsteenkoppies gevind, sowel as in die verweerde rotspilare van die doleriet-platorand.

Die dassie-prooibevolking in die KRNP is jaarliks intensief by hul koppies getel en gekarteer. Bevolkingskattings (einde 1989) was 1025 vir 'n gemiddelde arend-territorium en 13335 vir die hele park. Die dassie-digtheid (69 km^{-2} in bergagtige gebied) was baie laer as wat blyk uit opnames wat elders gedoen is. Meer as 98% van die dassies in die park het in groepe voorgekom en almal het oornag in klipkoppies wat geklassifiseer is as permanente dassie-skuilplek. Groter groepe is in die skeur-ryke stollingsgesteentes van die platorant gevind, veral in die omgewing van klowe met bergpuin en digte bos. Dassiegroepe is dikwels naby bos langs spruite gevind. Hul verspreiding het aangetoon dat voedsel naby toeganklike skuiling, 'n beperkende faktor is maar dat skuiling waarin oornag word, nie 'n beperkende faktor is nie. Die meeste groepe het teen glooiings voorgekom (waar die meeste klipskuiling was). Daar was tekens van 'n voorkeur vir oos-liggende hellings waarop die oggendson skyn. Afgesien hiervan is groepe redelik eweredig versprei in geskikte habitat. Die haremgroepe het 'n gemiddelde grootte van 16,4 dassies gehad, met habitat-afhanklike variasie. Die verdwyning of samesmelting van klein groepies en die verdraagsaamheid teenoor nie-telende mannetjies binne haremgroepe het getoon dat die instandhouding van 'n voldoende groepgrootte belangrik was. Predasie word beskou as die hoofoorsaak daarvoor dat dassies 96% van hul tyd binne 5 m van skuiling bestee en nooit verder as 15 m daarvandaan wegbeweeg nie. Hierdie gedrag is bevestig deur kenmerkende plantegroei-sones rondom goedbewoonde koppies. Dassies het 'brandwagte' en gebruik bergpuin en digte bos om by hoë-gehalte voedsel uit te kom gedurende intense groepvoedingsaktiwiteit. Hulle maak van verskillende dele van hul woongebied gebruik gedurende opeenvolgende dae. Gedurende winderige dae het sulke gedrag nie voorgekom nie. Verstrooiing oor nie-klipperige habitat het snags plaasgevind. Predasie mag ook die oorsaak wees dat dassies in die onvoorspelbare Karoo 'n duidelike geboorte-puls, toon (modus 12 Nov.). Die samestelling van die dassiebevolking is bepaal deur tellings van drie waarneembare ouderdomsklasse onmiddelik na die geboorte-puls sowel as deur die saamstel van lewenstabelle van skedels wat in die veld gevind is. Variasie in geboortes en sterftes het verband gehou met reënval. Dit het veroorsaak dat 'n betekenisvolle afname in getalle plaasgevind het gedurende die droë 1988. Daar was aanduidings dat voorgeboortelike sterftes gedurende droë toestande plaasgevind het en dat die geslagsverhouding van pasgebore dassies deur reënval beinvloed is. Die dassie-bevolkingstruktuur is hoogs veranderlik weens die onvoorspelbare reënval van die Karoo.

Transek-monstering van die belangrike habitatte in die park het getoon dat mishopies van Smith se klipkonyne voorgekom het teen 400-500 km^{-2} in die bergagtige gebied. Die ophoping van mishope het aangetoon dat een konyn ongeveer 15 mishopies veroorsaak. 'n Digtheid van 30 konyne km^{-2} is hieruit afgelei, met 'n skatting van 6652 vir die park gedurende 1989 en 441 konyne in 'n gemiddelde arend-territorium langs die lae platorand. Onbeplande waarnemings het egter gedui op 'n tienvoudige toename in die aantal konyne vanaf 1987 to 1989. Ander potensiële prooispesies het gedurende 1987 en 1988 bevolkingslaagtepunte getoon, waarskynlik weens die droogte. Klipkonyne het nie op die nie-klipperige vlaktes voorgekom nie, maar was relatief eweredig versprei langs die bergagtige habitat - teen 'n derde van die dassie-digtheid teen die hellings maar teen dubbeld die dassie-digtheid op die plato-gebiede. Variasie in die digtheid van konynmishopies het getoon dat gebiede met los rotse langs vlak hellings verkies word, terwyl grasserige, noordliggende glooiings vermy is, moontlik weens effekte t.o.v. termoregulering. Die plasing van mishopies het aangedui dat toegang tot rotsskeure 'n vereiste is vir individuele konyne - moontlik as skuiling of as teelplekke. Die territoriale gedrag van die konyne kan moontlik verklaar word deur die verdediging van hierdie verspreide, beperkte hulpbronne.

Twee-en-twintig pare witkruis-arende het die studiegebied bewoon, waarvan 13 binne die park gebroei het. Uitgesonder vir die Matobo heuwels is hierdie digtheid (4,14 pare km^{-2}) hoër as vir enige ander berggebiede. Arendpare het nader aan mekaar nesgemaak teen die hoë platorand (2,7 km; die hoogste witkruis-arend digtheid in enige liniêre bergreeks) as teen die lae platorand (4,6 km). Rondswerwende arende (>40% onvolwassenes) kom waarkynlik voor teen 'n verhouding van een dier per vyftien broeipare. Die kontinentale platorand van die Karoo huisves waarskynlik meer as 600 pare, en die berge van die Kaapprovinsie meer as 2000 pare. Witkruisarende se gewoontes beskerm hulle teen die vorms van menslike vervolging waaraan ander aasvretende roofvoels in die Karoo blootgestel is. Territoria van witkruisarende in die park was gemiddeld 24 km^2 groot, het nie oorvleuel nie en het ook geen onbenutte oppervlak gelaat nie. Oorvleueling tussen territoria was minimaal (<10%), veral tydens jag-gedrag. Drie pare het 52 km platorand verdedig en 'n vierde paar het 60 km verdedig. Die hipotese dat arende die teenwoordigheid van klipkoppies, en nie dassie-digtheid nie, gebruik as maatstaf vir territoriumgrootte, is strydig met onlangse waarnemings in die Matobo heuwels waar arende hul territoria verlaat het. Territoria in die KRNP het relatiewe konstante getalle dassies (gemiddeld 63 dassie groepe) en prooi-skuiling (>44000 klipskeure) bevat. Amper alle neste was binne die kerngebiede van territoria, maar radiokoolstofbepalings van 'n 3,8m-hoë nes het getoon dat die neste en moontlik kerngebiede nie baie oud is nie. Neste is meesal gebou op hoë, suidliggende kranse. Laat broeigedrag (behalwe op plase) en klein broeisels hou moontlik verband met lae voedselbeskikbaarheid. Die algehele broeitempo (61% pare) en broeisukses (46% pare) het egter nie verskil van dié vir arende in ander gebiede nie. Broeimislukkings het hoofsaaklik in die vroeë kuikenstadium op toeganklike kranse op die lae platorand plaasgevind. By twee geleenthede is dit aan predasie deur muishonde toegeskryf. Arende wat baie broeimislukkings gehad het, het meer neste gehad. Groot territoria langs die lae platorand het meer dassies bevat en het, ondanks 'n laer broeisukses, meer broeipogings en meer kuikens gelewer.

Arende het bedags 24% van die tyd gevlieg. Daar is effens meer tyd aan territoriale verdediging bestee as aan jag. Die vlugroetes van broeipare vir 40 waarnemingsdae is d.m.v. 'n GIS gekarteer. 'n Gemiddelde vlugspoed van 47 kmh^{-1} (10-125 kmh^{-1}) is bereken uit 693 vlugte wat 2747 km en 58 h beslaan. Die voorkoms van jagvlugte en aanvalle het seisoenaal gewissel en het saamgeval met veranderinge in die voedingsaktiwiteit van dassies. Jag deur arende was toestand- en weerafhanklik. Arende het meer gedurende winderige dae gevlieg en het geneig om naby hul neste te vlieg oor hellings wat goeie dassie-habitat en gunstige lugstrome gehad het. Hulle het geneig om hul prooi eers van 'n hoë sitplek of vanuit 'n hoë vlug waar te neem en om dan 'n verskuilde aanval te loods. Slegs 8% van die aanvalle was suksesvol. Aanvalle vanaf sitplekke was tweemaal so suksesvol as die vanuit 'n vlug, en aanvalle deur 'n paar was tweemaal so suksesvol as die deur 'n enkele arend. Hierdie verskille was egter nie statisties betekenisvol nie. Arend-pare het 85% van hul vlugtyd saam gevlieg. Terwyl hulle in pare gejag het, is die meeste van die kenmerke van ko-operatiewe jag waargeneem. Hul werksverdeling het gewoonlik met die dimorfisme tussen geslagte verband gehou.

Radio-opsporing van vier rooikatte in die KRNP was onsuksesvol. Uit die sukses tydens die vangs van hierdie roofdiere het dit geblyk dat hulle teen 'n gemiddelde digtheid voorkom, wat waarskynlik verband hou met die gemiddelde reënval van die KRNP vergeleke met ander plekke waar rooikatte bestudeer is (suid-wes Kaap: 2,4 volwassenes per 24 km^2; oostelike Karoo: 7,4 volwassenes per 24 km^2). Binne die park is rooikatte waarskynlik drie maal so volop as witkruisarende, terwyl voorspellings met betrekking tot metaboliese tempo toon dat hulle byna ses keer soveel voedsel benodig. Anders as by arende veroorsaak die sosiale gedrag van rooikatte dat hulle getalle kan vermeerder as dassies volop word. Die digtheidskattings vir ander dele van die Kaapprovinsie dui moontlik op die onderste en boonste grense t.o.v. die wisseling in rooikatgetalle. Langtermyn-vangste van rooikatte op plase toon dat hulle getalle kan toeneem met sowat 22% en kan afneem met sowat 34% as reaksie op reënval, met 'n tydvertraging van 6-12 maande. Dassies kan meer as 50% van rooikatte se voedsel uitmaak, maar geen dassiereste is gevind in 100 ketels wat in hierdie studie ontleed is nie: as ongespesialiseerde roofdiere het die rooikatte hoofsaaklik mak en wilde hoefdiere gevang. Sekondêre roofdiere kom in digthede (ses per 24 km^2) voor wat 'n betekenisvolle bedreiging vir jong rooikatte kan inhou.

Voedingseksperimente en metaboliese voorspellings toon dat 'n gemiddelde witkruisarend 1500-1700 kJd^{-1} voedingsenergie in gevangenskap benodig, waarvan ongeveer 75% gemetaboliseer word. Indien 40% van die voedsel verlore gaan, voldoen sowat 500g dassie per dag aan hierdie metaboliese behoefte. Terwyl kuikens in die natuur waarskynlik met effens minder voedsel kan oorleef, het wilde volwassenes moontlik tot 25% meer kos nodig. Veldwaarnemings en robot-fotografie by neste het getoon dat volwasse arendpare 0,43 prooi/dag vang buite die broeiseisoen en 0,57 prooi/dag terwyl hulle kuikens het. Arende moes dus elke vyf tot ses dae 'n addisionele prooi-item vang terwyl hulle kuikens voer, maar hierdie syfer het gewissel na gelang van die ouderdom van die kuikens. Hierdie prooivang-tempo is aansienlik laer as dié tydens ander studies van witkruis- en ander groot arende. Die gemiddelde massa van prooidiere in die park (2565g) was egter sodanig groter dat die arende se totale prooivangste (446 kgy^{-1}) en totale voedselinname (284 kgy^{-1}) vergelykbaar was met dié van die ander studies. Die waargenome voedselinname was egter steeds laer as die voorspelde minima, veral tydens die broeityd. Arende wat baie haas-agtige diere gevang het, het groter voedseliname-tempos gehad. Dit is waarskynlik toe te skryf aan 'n gebrek aan genoeg dassies as prooi. Die vangstempo van arende het nie gewissel na gelang van broei-aktiwiteite of die jagvermoeëns van die paar nie. Tydens droogtes en gedurende daardie geddeltes van die dag wanneer dassies voed het die arende baie prooidiere na hul neste gebring.

Dassies het 88% uitgemaak van 3823 voedselreste wat onder arendneste in die studiegebied versamel is. Vergeleke met ander studies van die dieët van witkruis-arende waarvan dieselfde metodes gebruik gemaak is, is hierdie verhouding nie baie hoog nie. Dit weerlê dit die siening dat witkruisarende hoogs spesifiek in hul keuse van prooi is. Robot-fotografie en ander metodes het egter getoon dat dassiereste oorverteenwoordig is in die prooi-reste en dat klein haasagtiges baie sterk onderverteenwoordig is. Die mees waarskynlike witkruisarend-dieëtsamestelling is verkry deur die samevoeging van resultate van verskeie waarnemingsmetodes: dassies het 67% van die dieët uitgemaak (46-83% vir arendpare met betroubare data), terwyl haasagtiges 25%, hoefdiere 4% en roofdiere 2% van die prooigetalle uitgemaak het. Van die prooi het 97% in die grootte-klas 500-4000 g geval. Die hoefdier-prooi-items was hoofsaaklik onvolwasse diere en die arende het hierdie diere waarskynlik vermy weens die gevaar van beserings. Skaaplammers het 1,2% van die prooireste en 3,4% van die prooi by neste op plase uitgemaak. Dit is onbekend hoeveel van hierdie prooi geaas is, maar aas vorm waarskynlik 4-11% van die arende se voedselinname. Arende langs die hoë platorand het, desondanks kleiner territoria, meer alternatiewe prooi-items (hoofsaaklik voëls en reptiele) bekom as arende langs die lae platorand. Behalwe vir hoefdiere wat vermy is, was die prooisamestelling van witkruisarende soortgelyk aan die beskikbaarheid van prooi. Is witkruisarende dus prooi-spesifiek? Dassies was tydens my studie beskerm in hulle skuilings, en hulle lae beskikbaarheid is weerspieel deur die feit dat twee groot, nie-gespesialiseerde roofdierspesies in die park geen dassies in hul dieët gehad het nie. Daar was ook nie tekens van 'n verandering in die dieëtsamestelling van arende tydens die toename in getalle van klipkonyne nie. Daar kan dus afgelei word dat witkruisarende spesialisroofdiere is wat dassies vang ten spyte van hierdie prooi se relatiewe lae beskikbaarheid.

Die erupsie en slytasie van die tande in 3359 dassie-maksillae uit arend-prooi in die KRNP en nog 2259 maksillae elders uit die Kaapprovinsie is gebruik om die geslags- en ouderdomsamestelling van dassie-prooi te bepaal, en dit is met die geslags- en ouderdomsamestelling van die bevolking in die park vergelyk. Baie jong dassies is deur die arende vermy, waarskynlik weens lae voedselwaarde (1/16 van die volwasse massa). Arende het een-tot-twee-jaar-oue dassies verkies wat die grootste enkele ouderdomsklas van die bevolking uitgemaak het. Hulle het betekenisvol meer onvolwasse mannetjie-dassies as wyfies gevang: dit het 'n ongelyke geslagsverhouding onder volwasse dassies tot gevolg gehad. Verstrooiing van onvolwasse mannetjie-dassies kom dikwels voor en hierdie diere is waarskynlik kwesbaar wanneer hulle in vreemde gebiede beweeg sonder die voordele van "brandwagte". Volwasse dassies is vermoedelik beter in staat om arende te ontduik, en hul voorkoms in prooireste weerspieël die bevolkingsamestelling. Arende was egter vir drie uit elke vier mortaliteite onder volwasse en ou dassies verantwoordelik. Ou dassies (8-13 jaar oud) is meer dikwels as verwag deur arende gevang, waarskynlik omdat hulle nie so vinnig kon vlug nie. Die arende het jaarliks sowat 'n derde van hierdie diere gevang. Alhoewel meer ou wyfie dassies beskikbaar was as prooi, vergeleke met ou mannetjies, is daar disproportioneel-baie ou wyfies gevang, waarskynlik omdat wyfie-dassies die "brandwagte" is, terwyl ander faktore bydra tot die dood van mannetjies. Die hoofneigings in prooivoorkoms tussen dassies word dus verklaar deur die kwesbaarheid van verskilende geslags/ouderdomsgroepe en nie deur die aktiewe voorkeur deur arende nie. Hierdie patrone is onderhewig aan groot wisselings met tyd en tussen geografiese gebiede. Dit het gekorreleer met reënval - 'n bewys van die dinamiese dassie-bevolkingstruktuur en die geldigheid van die ouderdomsbepalingstegnieke. Die grootte van volwasse dassies, soos geskat deur maksilla-grootte, het ook gekorreleer met reënval. Arende langs die lae platorand het meer "oortollige" dassies, bv. jong mannetjies en ou wyfies, gevang. Arende langs die hoë platorand het meer "moeilike" prooi gevang, bv. onvolwasse dassies en gesonde teeldiere, bv. volwasse wyfies, asook ander prooispesies. Arende langs die hoë platorand is klaarblyklik blootgestel aan 'n lae dassie:arend verhouding, soos blyk uit die feit dat daar minder dassie-reste oorbly en dat meer dassie-skedels deur die arende oopgeskeur word. 'n Soortgelyke tendens is ook bespeur by data uit ander berggebiede waar daar relatief min dassies is, bv. Fynbos, en tydens tye wanneer dassies in lae getalle voorgekom het, bv. in die oos-Kaap en in die Fynbos gedurende die vroeë 1970's.

Vroeë nesmaak deur arende op plase wys dat hierdie roofvoëls voedselbronne benut het wat ontoeganklik is in die KRNP. Waarnemings by neste toon dat sowat twee arendpare op 'n gemiddelde veeplaas in bergterrein jaarliks 6-13 skaaplammers vreet. Dit is nie bekend of hierdie lammers gesond, sterwend of dood was toe hulle deur die arende gevang is nie. Ongeveer 20% van die lammers vrek voor speen-ouderdom, wat sowat 145 lammers/jaar laat wat deur arende op 'n Karoo-plaas geaas kan word. Witkruisarende aas waarskynlik meeste van die lammers wat na neste gebring word, soos blyk uit ander studies op groot arende, bv. die goue arend. Betroubare ontledings van lam-mortaliteit deur predasie kan net gedoen word deur die lykskouing van lammers in die veld tydens lamtyd. Wye opnames van vrektes onder Merino in Australië (baie vergelykbaar met die Karoo) toon dat predasie die oorsaak van dood is by 1,7% van die lammers. Wêreldwye opnames toon verder dat arende verantwoordelik is vir 2,4% van alle predasie. Beperkte opnames in witkruisarend-habitat in Suid-Afrika toon laer verliese weens predasie, waarvan niks aan arende toegeskryf kan word nie. By gebrek aan goeie Suid-Afrikaanse data, wys die Australiese data dat die gemiddelde verlies op 'n Karoo-plaas ongeveer 0,32 lammers per jaar of R24 is - 'n minimale verlies. Waarnemings toon dat die meeste arende in die Karoo natuurlike prooi verkies, waaraan hul as kuikens gewoond raak. In teenstelling met sommige ander groot arendspesies, vergader witkruisarende en breëkoparende nie in gebiede waar skape lam nie. Daar is egter bewyse dat sommige witkruisarende wel lammers vang, en sulke probleme is waarskynlik beperk tot 'n klein getal veeplase. Verliese kan beperk word deur meer intensiewe plaasbestuur: die gebruik van skaapwagters tydens lamtyd, verwydering van karkasse en die lam van skape in kampe waar arende nie jag nie. Die bestuur van vee is goedkoper as die bestuur van roofdiere, bv. die vervoer van arende. Afweer weens slegte smaak mag in die toekoms nuttig wees, maar indiwiduele arende met volgehoue predasie op kleinvee behoort verwyder te word na dieretuine of falkeniere om te verhoed dat hierdie gedrag deur ander arende aangeleer word.

Dassies het tydens my studie 'n lae digtheid en 'n lae beskikbaarheid gehad. Tydens die jare van akkurate dataversameling is gemiddeld 11% (117) van die 1062 dassies per arend-territorium gevang. Die arende het ook 8% van die klipkonyngetalle gevang (11% gedurende 1989). Die predasie deur arende verteenwoordig 27% van die dassie-mortaliteit en vergestalt 29% van die jaarlikse dassie-geboortes. Kernfaktorontleding het getoon dat verandering in die dassiegetalle verbind kon word met predasie, en nie soseer met voedseltekorte of ander effekte t.o.v die lae trofiese vlak nie. Die duur van my studie was waarskylik te kort om digtheidsafhanklike demografiese effekte te toon, maar mortaliteit was meer verwant aan dassie-digtheid as met hul geboortetempo. Voortplanting word vermoedelik weens oorbevolking versteur deur hoë dassie-digthede. Afgesien van wisselings in die dassie-getalle het die arende jaarliks 'n konstante 11% van die dassies gevang. Baie dassies wat gevang is, was uit ouderdomsklasse met 'n hoë oorlewing en het daarom 'n additiewe effek gehad. Arende het dus tydens hierdie studie 'n remmende effek op bevolkingsgroei gehad. Wisselende plantevoedselbeskikbaarheid en 'n dassiebevolking met 'n hoë potensiaal vir toename skep 'n onstabiele toestand: enige faktor met 'n volgehoue remmende effek op bevolkingsgroei speel dus 'n rol om wanbalanse tussen die dassies en hul voedsel te verminder.

Data uit my studie asook uit ander veldstudies is versamel om 'n gedetaileerde en spesifieke bevolkingsmodel saam te stel wat die dassies se demografie gesimuleer het na aanleiding van langtermyn-klimatologiese data vir die Karoo. Hierdie model wyk af van vorige modelle vir dassies deurdat dit die akkurate meting van skuiling en dassie-drakrag van die veld in ag neem, en deurdat dit die verhoging van drakrag weens die jaarlikse reënval en die verlaging van drakrag weens dassie-beweiding in ag neem. Bevolkingsverskynsels in die model word bepaal deur die verhouding van aantal dassies (P) tot dinamiese drakrag (K), sodat 'n klein dassiebevolking na goeie reën 'n minimum-hoeveelheid mortaliteit en 'n maksimum voortplantingstempo getoon het. Groot dassie-bevolkings het tydens droogtes die teenoorgestelde ondervind. Die model wys dat predasie veroorsaak dat dassie-getalle die hele tyd na aan die veld se drakrag is. Die drakrag word op sy beurt weer bepaal word deur reënval-bepaalde nuwe plantegroei binne die 'veilige' area naby dassie-skuilings. Gedokumenteerde bevolkings-'ontploffings' van dassies in die verlede het elke keer saamgeval met voorspelde afnames in dassiegetalle: hierdie dassies het waarskynlik meer opsigtelik geword deur bewegings en verstrooiing weens 'n afnemende voedselbeskikbaarheid en drakrag binne die 'veilige' gebiede vir dassies. Die raaiselagtige afname in dassiegetalle tydens die vroeë 1980's kan toegeskryf word aan goeie groei van plante, gevolg deur 'n knellende droogte. Voorspellings uit die model t.o.v. hierdie bevolkings-afname onder verskillende reënval-toestande het sterk gekorreleer met veld-tellings van dassies in die KRNP, asook in die Matobo heuwels. Reënval-aangedrewe dassie-'uitbrake' is meer waarskynlik in in droeë gebiede met ‘n wisselende reënval. ‘Uitbrake’ word volgens die model hoofsaaklik veroorsaak deur oorbeweiding van die habitat, maar die uitroei van roofdiere het waarskynlik grootliks bygedra tot die dassie-‘uitbraak’ gedurende die 1940’s. Kernfaktoronteding en die gesimuleerde verwydering van roofdiere in die model, sowel as kompensatoriese predasie, toon dat roofdiere maklik enige ‘surplus’-dassies verwyder, selfs teen hoë dassie-digthede. In die afwesigheid van predasie was mortaliteit weens voedseltekort en die samehangende afname in vrugbaarheid nie genoeg om in tye van hoë dassiegetalle en ‘n lae drakrag gereelde ‘uitbrake’ en, daarna, drastiese afnames in dassiegetalle te verhoed nie. Hierdie voorspellings was konsekwent vir ‘n wye reeks van drastiese parameter-veranderings binne die model. Jaarlikse wisseling in die aantal dassies in die ‘beskermde’ gebiede het ‘n digtheidsafhanklike roofdier-prooi interaksie versluier. Die roofdiere het egter steeds prooigetalle beheer in die swak sin deurdat die dassies tot areas met skuiling beperk word en deurdat dassiegetallewisseling bepaal word deur die wisseling van die hoeveelheid voedsel naby skuilings. Uitputting van voedselbronne tydens ernstige droogtes kan groot dassie-emigrasies van ‘surplus’-dassies tot gevolg hê, maar die normale getal roofdiere is in staat om hierdie dassies te verwyder. Verwydering van die effekte van arende alleen of rooikatte alleen in die model, het nie groot verskille in die demografie van die dassies veroorsaak nie, maar die teenwoordigheid van beide roofdiere was nodig om die volle beperkende effek op dassie-bevolkings te veroorsaak. Hierdie gevolgtrekking is versterk deur waarnemings op dassies op ‘n plaas waar alle roofdiere behalwe witkruisarende uitgeroei is. Dassiebevolkings verskil van die sikliese bevolkings wat elders bestudeer is deurdat die bevolkingsgetalle ongereeld verander onder die invloed van die onvoorspelbare reënval van die Karoo. In teenstelling met die klimaat-beheerde roofdier-prooi stelsels in Australië ontsnap dassies amper nooit die effek van predasie nie. Die unieke eienskap van die witkruisarend-dassie stelsel is toe te skryf aan die effekte van permanente en doeltreffende skuilings, asook aan die buitengewone situsie dat die effektiewe dassie-beskikbaarheid vir roofdiere baie laag is ondanks relatiewe hoë dassiegetalle na reënval.

Hierdie studie, sowel as ander studies elders in Afrika, toon dat witkruisarende hoofsaaklik prooi op klipdassies en dat sterk predasie op volwasse en ou dassies plaasvind. Daarom is dit nie verbasend dat die morfologie asook die gedrag van beide dassies en arende, kenmerke van onderlinge aanpassing toon nie. Beide spesies toon opsigtelike aanpassings t.o.v. hulle omgewing sowel as t.o.v. mekaar. Hiedie aanpassings het waarskynlik hul afhanklikheid van hul berg-habitat versterk. Dassies bestee so min as moontlik tyd weg van hul skuiling om sodoende predasie te vermy, veral op winderige dae wanneer arende baie aktief is. Hulle maak ook gebruik van ‘brandwagte’ terwyl hulle groepsgewys voed. Arende, daarenteen, jag tydens tye van die dag wanneer dassies weg van skuiling voed. Hulle jag paarsgewys om dubbele aanvalle op hul ontduikende prooi moontlik te maak en om prooi te vang wat in ruigtes skuil. Hulle maak ook gebruik van verskuilde aanvalsmetodes. ‘n Spesiale ligskerm in die oë van dassies mag help dat dassies aanvallende arende makliker kan raaksien. Abnormale groot pote van witkruisarende is waarskynlik ‘n aanpassing om prooi te vang wat dubbeld so groot is as die prooi van ander vergelykbare arende. Baie aspekte van die arende se lewens-styl, bv. hul duidelike territorialiteit en hul konserwatiewe broeigedrag, hou verband met die ongewone stabiliteit van die dassiegetalle, wat op sy beurt weer verklaar word deur die permanente skuilings en die nabygeleë weidingsareas van dassies. Witkruisarende vang soms lammers, maar dit gebeur so selde dat die skade vir die gemiddelde veeboer in die Karoo minimaal is. Indien boere kla oor probleme betreffende arende, kan hierdie gevalle indiwidueel ondersoek word deur die karkasse van lammers te ontleed vir die ware oorsaak van dood: hierdie benadering is baie meer positief as die ontkenning van die probleem wat dikwels ‘n verwydering tussen boere en bewarings-georiënteerdes veroorsaak. Indien arende wel skade aanrig kan bestuurstegnieke aanbeveel word wat die skade sal minimeer of uitskakel. Daar bestaan egter ‘n grrot moontlikheid dat die indiwiduele arende onskuldig is en dat hulle deur menslike betrokkenheid ‘n opvoedingsgeleentheid aan iemand gebied het. Hierdie studie toon dat die finansiële voordele van arende op ‘n plaas in terme van die beskerming van weiding hul nadele kan oorskadu met ‘n faktor van 150. Die finansiële voordeel van die bewaring van so ‘n voordelige diersoort moet beklemtoon word tydens opvoedingsprojekte, maar hierdie projekte moet nie diersoorte wat minder opsigtelike finansiële en ekologiese voordele inhou, oor die hoof sien nie. Verdraagsaamheid t.o.v. aanpasbare groot roofdiere soos arende is ‘n eenvoudige en maklike maatreël wat boere in die Karoo kan tref om die ekologie van die Karoo tot sy vorige kompleksiteit en stabiliteit te herstel.