

The Influence of Predation by Black Eagles *Aquila verreauxii* on Rock Hyrax Numbers in the Arid Karoo

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INTRODUCTION

Black Eagles *Aquila verreauxii* occupy a controversial position on karoo farmland: whether they harm the sheep farmer by preying on livestock; and/or whether they benefit the farmer by limiting their principal prey, rock hyrax *Procavia capensis* which can compete with domestic sheep for available forage. Under normal conditions there may be 1.2 million hyrax living in the rocky habitats of the karoo biome with an appetite equivalent to 7% that of the entire sheep flock for the region. Hyrax numbers vary noticeably in the Karoo and there have been several reported irruptions of the species during the twentieth century when farmers have experienced significant harm to the veld resource at times when they need it most for their sheep. It was a visit to a farm where hyrax had irrupted in 1984 that prompted a five year doctoral field study on this predator-prey system (Davies 1994: referred to herein as the field study). The extent and cost of livestock predation by Black Eagles as revealed by the study were reported elsewhere (Davies in press.) The present paper presents the influence of Black Eagles on rock hyrax numbers and thus the benefits that these birds may offer to farmers. Many of the inferences presented herein are drawn from a novel and high-resolution hyrax population model.

KEY ELEMENTS IN THE SYSTEM

Rock hyrax are excellent subjects for population modelling. They are easily classified by sex and into annual age classes from the dentition of maxillary remains. They have a high propensity for population increase and reproduce in a synchronised annual birth-pulse, the size of which is usually predictable from rainfall events during the gestation period. There is much reference work available from research studies on hyrax reproduction (including some modelling, e.g. Fourie 1983, Swart *et al.* 1986). Rock hyrax occur in discrete and countable groups. They are well adapted to life in rocky habitats (Sale 1970). At night they allow their body temperature to drop to conserve energy. This obliges them to sunbathe every morning, providing an opportunity for counting.

The adaptations that equip hyrax for life in rocky habitats enable them to evade nearly all predators when they are within this refuge but the same adaptations render them highly vulnerable to an efficient guild of predators when they are away from their rocks. Refuge in this predator-prey system is unusual in that it is highly effective and it is permanent. This can be expected to confer stability on

the system. Hyrax feed close to their rocks and were not observed further than 15m from shelter in the field study. These feeding patterns result in a distinct vegetation zone around rock outcrops which are highly visible from the air. Previous hyrax models have not included measurement of refuge.

While the safe feeding zone determined by rock outcrops is fixed, the number of hyrax that it supports varies with rainfall. In the semi-arid Karoo rainfall is highly stochastic. Alternating periods of enrichment and drought can be expected to destabilise the system in the manner observed for environmentally-modulated predation systems in Australia. Enrichment through the lower trophic level has an obvious and profound effect on hyrax population processes (not accommodated in previous hyrax models).

Livestock rarely venture into rocky habitats in the Karoo (Lensing 1982) so we assess the cost of hyrax to the sheep farmer as the surplus of hyrax whose food requirement is not met within their safe feeding zone. The food requirements of ten hyrax are equivalent to that of one sheep and this grazing is valued at \$8.70 per annum.

Paradoxically the breeding performance of Black Eagles shows an inverse relationship with rainfall (Allan 1988). Hyrax become more available to eagles when they are forced to move further from their refuges to find food during drought. This mismatch of prey availability and prey abundance appears to be a unique attribute of the system. All diet studies using prey remains collected beneath eyries have indicated that Black Eagles are obligate predators of rock hyrax. However time-lapse cameras positioned at eagle nests during the field study revealed that Black Eagles captured significant numbers of red rock rabbits *Pronolagus rupestris*, not indicated by the prey remains. A population study of the rabbits indicated that this predation related merely to changes in the availability of alternate prey, not changes in hunting emphasis by the eagles. Black Eagles behaved as specialist predators in the present study by pursuing their preferred hyrax prey despite low abundance and low availability. Predation of hyrax by Black Eagle pairs varied between 70 and 180 per annum (per pair) and has been estimated to exceed 350 elsewhere (Gargett 1972, 1990). The assumption of a constant annual kill by Black Eagles in previous hyrax models is unrealistic.

Caracals are the other major predator of rock hyrax in the Karoo, but they are generalist predators and scat analyses conducted in the field study revealed that they were subsisting on alternative prey. Diet studies show that the hyrax component can vary between 2-50% of caracal prey. This instantaneous 'functional response' is known to greatly empower the influence of generalist predators in regulating their prey. Caracals are also able to show a numerical response. Farm trapping records indicate that numbers can change by up to 30% per annum, usually following a six month time-lag after rainfall events. Caracals probably occur at a density of 4.9 adult units per eagle territory in the study area (it is estimated that they consume six times as much food as the resident eagles). Studies elsewhere in the Karoo indicate that this density might vary between 2.4 and 7.4 adult units per eagle territory (Stuart 1982; Moolman 1986a & b).

STUDY AREA AND APPROACH

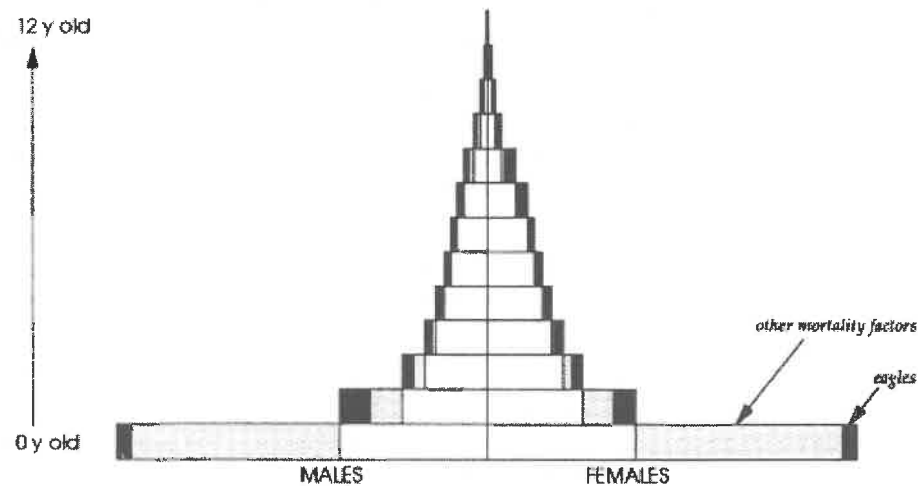
All key elements were comprehensively evaluated in a five year field study. The results were combined with other research findings and with long-term rainfall data in a population model designed to escape the limitations of the field study and forecast hyrax population change in the long-term. The field study was conducted in the Karoo National Park where predators had not been persecuted for seven years. Counts at hyrax colonies indicated a fourfold decline in hyrax numbers in the park immediately prior to the present study (Fairall 1991). Synchronous declines in hyrax populations were reported throughout southern Africa and an explanation of this was sought. Twenty-two pairs of eagles were located in the vicinity of the park. Overlap between neighbouring territories was minimal (<10%). All hyrax refuge habitats spanning four complete territories and parts of two others (149km²) were classified and mapped out. Density of hyrax was not found to be predictable in these refuge habitats so a population estimate was obtained by plotting all groups (n=303) and determining mean group size (16.2). The average eagle territory was found to accommodate 63 groups and 1062 hyrax. Variation in hyrax numbers and the extent of refuge habitats across eagle territories was very low.

We assumed that territories were stable and used the territory (24km²) as the unit area for all measures in the model. Direct observations of hyrax groups indicated that the safe feeding area (358ha) in an average territory should be able to accommodate 112 groups. This indicated a carrying capacity of 1816 hyrax per territory in a standard year and that the refuge habitat was currently 60% saturated.

IMMEDIATE ACTION OF PREDATION

All field data were collated in a spreadsheet model (Microsoft Excel) to represent what was happening to the hyrax population over the study period (Figure 1). Black Eagles removed 11% of the hyrax standing crop from their territories in an average year. This amount was equivalent to 29% of the numbers added to the hyrax population annually. Clearly Black Eagles were not important mortality factors for juvenile hyrax but they took a greater toll of immature hyrax and they could account for most of the mortality of adult age classes. Many of the hyrax captured by eagles were from age classes with good survival expectancy rates. For some adult hyrax age classes Black Eagles were responsible for three quarters of all deaths. By removing an amount of rock hyrax equivalent to almost a third of the annual recruitment to the population, Black Eagles qualify as one of the limiting factors affecting hyrax population change. By removing breeding adults Black Eagles have a greater inhibitory influence on hyrax population growth than a predator which removes surplus elements such as young or old individuals. The emphasis of this predation on adult hyrax age classes (which are otherwise unlikely to die) also suggests that these losses would not readily be compensated by other, non-violent, mortality factors in the absence of eagles. For this predation to be regulatory, current theory demands that it should be density-dependent. There was no evidence of this during the field study, but losses to the population did explain more of the variation in population change than additions which proved to be highly correlated with rainfall. The spreadsheet model represents an annual snapshot of the population but it gives a hypothetical structure that represents a hyrax population in a constant environment. In reality, hyrax population structure responds in a highly dynamic fashion to variation in mortality and especially the birth pulse. The model provides a convenient point of departure for how the hyrax population behaves under average conditions.

Figure 1. A diagrammatic summary of age- and sex-specific predation by Black Eagles in relation to the availability and the annual mortality of the hyrax population classes. This summary was derived by computer simulation of a stable hyrax population which best represents the population under study.



LOWER TROPHIC INTERACTION

Various field observations confirm that hyrax suffer heavier predation during drought and lighter predation after rain. We assume that hyrax populations experience lowest mortality and show greatest recruitment when small populations (relative to the carrying capacity of the safe feeding zone) benefit from good rains, and we assume the reverse when large populations are stressed by drought (i.e. processes modelled on P:K). The refuge habitat accommodates 1816 hyrax under average conditions but the same vegetation would support more hyrax in good years and fewer during drought. Variation in plant production on arid range-lands is generally one and a half times greater than the variation in rainfall (Le Houérou *et al* 1988). We therefore assume that the refuge habitat will support 15% more hyrax than average when there is 10% more rainfall than usual. Estimates of 'K' derived in this way did not reflect cumulative effects of several years of drought or several years of good rain. To accommodate these effects, we separated the vegetation resource into winter phytomass which can be thought of in a simple financial analogy as the capital, and fresh summer growth which can be thought of as the interest on that capital. We allowed capital to appreciate by up to 30% per annum in years of good rains and depreciate or decay by up to 6% per annum during drought. In a second step we allowed herbivory by hyrax to accelerate the depreciation when hyrax appetite outweighed the available fresh growth. We constrained the capital between likely limits derived from veld studies.

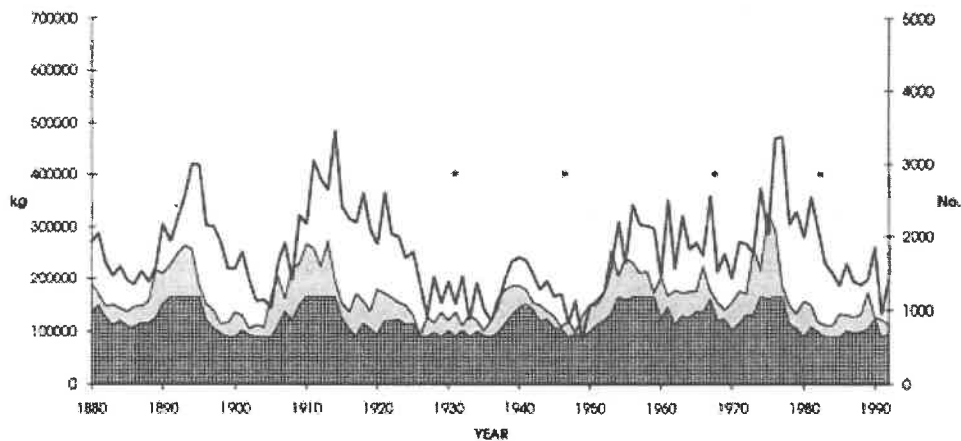
UPPER TROPHIC INTERACTION

Mortality and conception rates were set in accordance with P:K ratio. Prenatal mortality was allowed to claim 2-20% of foetuses in accordance with rainfall during gestation. Eagle kill was modelled both on hyrax abundance (P) and availability (P:K). Caracal functional response was modelled on hyrax surplus (P-K) and the numerical response on fresh growth (an indicator of enrichment which included a time-lag of six months). Compensatory mortality of hyrax for simulations of eagle removal was handled in two ways: first it was assumed that 10% of the eagle kill would have died anyway (old animals made up 16% of eagle prey); second we invoked a starvation mortality of 0.75 affecting all age classes whenever hyrax appetite exceeded the food supplies by a factor of 4.5 or more. This was based on observations of population declines. This starvation mortality factor was latent in the model whether eagles were removed or not. For most runs of the model the caracal kill was estimated but treated as part of non-eagle mortality.

STANDARD RUN OF THE MODEL UNDER NATURAL CONDITIONS (PREDATORS PRESENT)

In a standard run of the model (Figure 2), it was evident that veld condition could totally recover or totally deteriorate over four or five years. We felt that this was realistic for karoo biota and it tallied with the contentions of range managers. The model predicted phases of increase and decline for the hyrax population reflecting underlying changes in its food supplies. Modelling conception on previous summer rainfall rather than P:K ratio did not alter this pattern significantly. Historic reports of hyrax irruptions corresponded to drought and predicted decline phases. The 1946 irruption coincided with numerous springbok treks which are generally associated with pasture exhaustion (Skinner 1993). It seems likely that these were not 'population explosions' but rather perceptions of increase created by dispersal of hyrax out of the safe feeding zone. A most important feature was that the model correctly predicted the observed hyrax population decline during the early 1980's ($r=0.9$; $p<0.001$). This decline was predicted for a variety of regions in southern Africa wherever enrichment during the 1970's was followed by drought during the 1980's. Predator interference was not a requirement and this complies with field observations of declines in conserved areas. Using Matobo Hills rainfall data, the model predicted change in hyrax density which correlated significantly ($r=0.5$; $p<0.01$) with the limited numerical response of the Black Eagles observed by Gargett (1993). The breeding performance of these eagles correlated significantly ($r=0.5$; $p<0.01$) with predicted hyrax surplus.

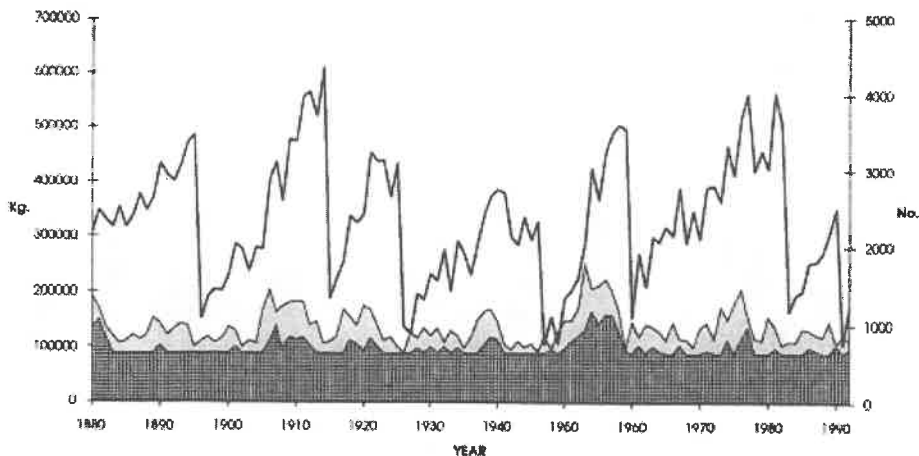
Figure 2. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a standard run of the model with the full complement of predation, using Beaufort West rainfall data. Asterixes denote timing of hyrax irruptions reported in the literature. Phytomass values are expressed as kg dry matter in the 'safe feeding area'.



SIMULATED REMOVAL OF BLACK EAGLES

In the absence of Black Eagles the model predicts rapid increase in hyrax numbers and impaired decline (Figure 3). There is a 17% depression in the phytomass and so carrying capacity is set lower. Despite this, hyrax density is 32% greater in this simulation, and regularly attains levels where gross imbalance occurs between hyrax and their food supplies, resulting in heavy starvation mortality. It is important to remember that the recruitment rate of the hyrax population and non-eagle mortality rate

Figure 3. Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model (Beaufort West rainfall) with predation by Black Eagles removed. Assumptions on compensatory mortality in the absence of predation by eagles are explained in the text.



are still accorded opportunity for density-dependent feedback in this simulation. Juvenile mortality is relatively unaffected by the removal of eagles, so the rapid increase in the population can be ascribed primarily to enhanced survivorship of adult hyrax (and their subsequent contribution to reproduction) in the absence of eagles.

HYRAX SURPLUSES WITH AND WITHOUT EAGLE PREDATION

Under natural conditions hyrax numbers appear to be able to comfortably track the dramatic changes in the carrying capacity of their refuge environment (Figure 4a). By removing predation we impair this ability of hyrax numbers to track changes in carrying capacity. Average departure of density from carrying capacity was 50% greater in simulations after eagle removal. This results in a far greater surplus of hyrax not supported within the safe feeding zone (Figure 4b). The amount of grazing consumed by the additional hyrax surplus in the absence of Black Eagle predation on the average karoo farm (two territories) is valued at US\$ 1080. This benefit of having eagles on the farm outweighs the cost of occasional lamb predation by the eagles by a factor of 155 times.

Figure 4a. Changes in the carrying capacity of food supplies in the 'safe feeding area' of a standard eagle territory for hyrax, K, and concordant changes in hyrax population density, P, (visible black area represents surplus) predicted by a standard run of the model with the full complement of predation, using Beaufort West rainfall data.

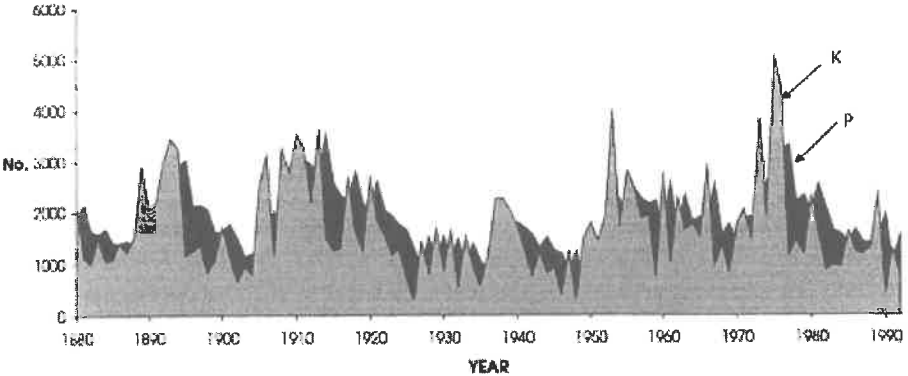
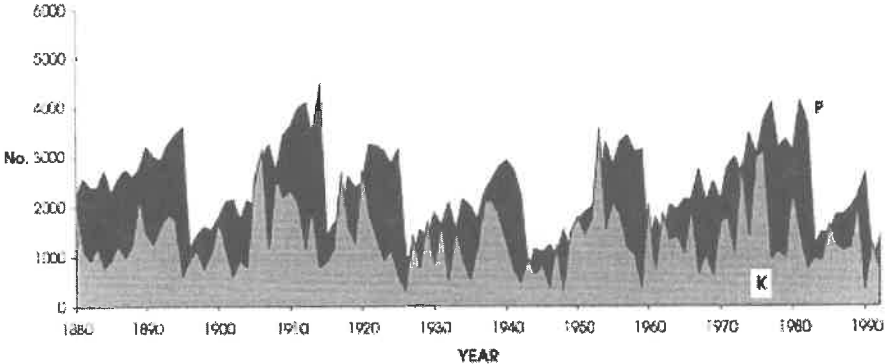


Figure 4b. Changes in the carrying capacity of food supplies in the 'safe feeding area' of a standard eagle territory for hyrax, K, and changes in hyrax population density, P, (visible black area represents surplus) predicted by a run of the model where predation by Black Eagles has been removed (Beaufort West rainfall data).



RESPECTIVE ROLES OF THE PREDATORS

During increase phases of the hyrax population (when K exceeded P) specialist predation by Black Eagles (as modelled here) greatly exceeded predation by caracals and so acted as more of a brake on the hyrax population. Predation by caracals was minimal at these times and the concordant demand for alternate prey (by both predators) was maximal. But caracals removed many more hyrax during the decline phases and exhibited a far greater capacity than Black Eagles for removing surpluses in excess of the carrying capacity. The range in hyrax numbers removed by caracals was three times greater than that taken by Black Eagles. Compensation by caracals (not incorporated into the model) is likely to lessen the effect of removing eagles, but most karoo farmers persecute caracals before eagles and just a 10% impedance (=removal) of both predators (i.e. 10% of both predicted kills survive) resulted in a significant predicted increase in hyrax density. Hyrax surplus increased as a linear function of predator impedance such that a 40% impedance of both predators resulted in a similar cost to the farmer as did total removal of the eagles.

SENSITIVITY ANALYSIS AND CONCLUSION

The model predicts that removing or impeding predators has a profound effect upon hyrax population change, but how robust is this prediction? We tested this robustness by running the model with and without eagles while varying the most important parameters dramatically. For each perturbation the model returned the same prediction, that hyrax density and its variability increase significantly when predators are interfered with. So why is predation such an essential ingredient for close tracking of changing food supplies by the hyrax population? For a standard run of the model we measured losses through the upper trophic level (predation) and losses through the lower trophic (loss of full breeding potential plus non-violent mortality). Losses in the lower trophic level explained only 2% of the predicted change in hyrax numbers whereas losses to predators could explain as much as 64%. Losses through the lower trophic level, although much larger than losses to predators, were less variable and appeared instrumental to population change only during periods of enrichment such as the 1970's when they explained 41% of the change. Predators prove to be essential facilitators of the decline phase. An important bearing of this is that the results of field studies will be highly dependent on whether the study is conducted during an increase or decline phase. Losses through the lower trophic level exert a profound influence on hyrax population structure but they primarily affect only the first age class. Perhaps the build-up in hyrax numbers during the 1970's (and subsequent crash) was amplified by the lack of effective density-dependent feedback in this component. It is easy to see that hyrax numbers in the arid Karoo could be as unstable as rabbit numbers in Australia were it not for the effective and permanent refuge resource, and the stability induced by this refuge facilitates the highly effective co-existence of the specialist Black Eagles and generalist caracals. The model demonstrates that these predators have the capacity to remove surplus hyrax not supported by the refuge habitat even after extraordinary birth-pulses. Stochastic climate-induced variation in the number of protected prey obscures any direct relationship between this predation and hyrax density. We offer this as an example of how predation can still regulate prey numbers between limits without showing density-dependence (where density is measured as animals per unit area).

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REFERENCES

- ALLAN, D.G. 1988. Breeding success, nest spacing and territory size of Black Eagles in the Magaliesberg, South Africa. *Gabar* 3: 76-81.
- DAVIES, R.A.G. 1994. Black eagle *Aquila verreauxii* predation on rock hyrax *Procavia capensis* and other prey in the Karoo. Ph.D. thesis, University of Pretoria.

- DAVIES, R.A.G. (extended abstract in press). The extent, cost and control of livestock predation by eagles with a case study on Black Eagles *Aquila verreauxii* in the Karoo. 'Solving Raptor-Human Conflicts' symposium, Canterbury, Sept. 1993. *J. Raptor Res.* 33.
- FAIRALL, N. 1991. Factors affecting the dynamics of hyrax populations. *Proc. XXth Congr. Int. Union Game Biol.*, (Gödöllő, Hungary), part 1: 372-377.
- FOURIE, L.J. 1983. The population dynamics of the rock hyrax *Procavia capensis* (Pallas, 1766) in the Mountain Zebra National Park. Ph.D. thesis, Rhodes University, Grahamstown.
- GARGETT, V. 1972. Observations at a Black Eagle's nest in the Matopos, Rhodesia. *Ostrich* 43: 77-108.
- GARGETT, V. 1990. *The Black Eagle, a Study*. Acorn Books, Johannesburg. 279pp.
- GARGETT, V. 1993. Territory boundaries and occupancy and related behaviours of Black Eagles (*Aquila verreauxii*) in the Matobo Hills. Report to Department of National Parks and Wildlife Management, Zimbabwe, January 1993, (unpubl. mimeograph), 142pp.
- LE HOUÉROU, H.N., R.L. BINGHAM, & W. SKERBEK 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *J. Arid Environ.* 15: 1-18.
- LENSING, J.E. 1982. Feeding strategy of the rock hyrax and its relation to the rock hyrax problem in southern South West Africa. *Madoqua* 13: 177-196.
- MOOLMAN, L.C. 1986a. Aspekte van die ekologie en gedrag van die rooikat *Felis caracal*, Schreber, 1776 in die Bergkwagga Nasionale Park en op die omliggende plase. M.Sc. thesis, University of Pretoria.
- MOOLMAN, L.C. 1986b. Aspekte van die ekologie en gedrag van die rooikat *Felis caracal* (Schreber 1776) in die Bergkwagga Nasionale Park en op die omliggende plase. *Pelea* 5: 8-21.
- SALE, J.B. 1970. Unusual external adaptations in the rock hyrax. *Zool. Afr.* 5: 101-113.
- SKINNER, J.D. 1993. Springbok (*Antidorcas marsupialis*) treks. *Trans. Roy. Soc. S. Afr.* 48: 291-305.
- STUART, C.T. 1982. Aspects of the biology of the caracal (*Felis caracal* Schreber, 1766) in the Cape Province, South Africa. M.Sc. thesis, University of Natal, Pietermaritzburg.
- SWART, J., M.R. PERRIN, J.W. HEARNE & L.J. FOURIE 1986. Mathematical model of the interaction between rock hyrax and caracal lynx, based on demographic data from populations in the Mountain Zebra National Park, South Africa. *S. Afr. J. Sci.* 82: 289-294.

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