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Eagles as indicators of ecosystem health: Is the distribution of Martial Eagle nests in the Karoo, South Africa, influenced by variations in land-use and rangeland quality?

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Abstract

We examined the relationship between the distribution of Martial Eagles *Polemaetus bellicosus* (and other large eagle species) breeding on electricity transmission pylons in the central and southwestern Karoo, South Africa, and the general environmental health of commercially managed farmland in that region. Eighty-three eagle territories were located along 1400 km of surveyed pylon line. The influence of habitat quality on eagle distributions was assessed in terms of (i) patterns of dispersion and spacing between territories, (ii) macro-scale differences between the habitat composition of eagle territories and an equivalent array of random plots, and (iii) micro-scale differences in habitat quality assessed at points within and outside of eagle territories. Territories were generally irregularly distributed along the pylon line ($p < 0.025$). At the landscape scale, Martial Eagles significantly favoured habitats with lower and/or less predictable winter rainfall and lower primary productivity, while Tawny Eagles *Aquila rapax* preferred habitats with higher and/or more predictable summer rainfall and higher primary productivity. All eagles avoided areas of highest primary productivity and were absent from cultivated areas. On a local scale, habitat qualities within eagle territories were generally not significantly different to those recorded outside territories. However, eagle densities in areas stocked with indigenous game were significantly higher than in areas

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supporting only domestic stock (nearest neighbour distances, 7 km vs. 12 km, $p = 0.025$). This study shows that (i) large eagle distributions in the Karoo are significantly influenced by both macro- and micro-scale variation in habitat quality, and by the nature of land management, and (ii) that the Martial Eagle is potentially suitable as an indicator of ecosystem quality and functionality in the Karoo.

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1. Introduction

General ignorance of the fundamental influences of anthropogenic land transformation on ecosystem functioning stands as an obstacle to the successful conservation of African biodiversity (Macdonald, 1989). Depleted populations of animal taxa outside of formally protected areas are an obvious manifestation of these influences, and yet the factors limiting these populations are often little studied. For example, many large African raptor species occur at very low densities outside of conservation areas (Liversidge, 1984, 1994; Aumann, 1997; Herremans and Herremans-Tonnoeyr, 2000). The incipient effects of habitat degradation on these eagle and vulture populations have been widely acknowledged (Brandl et al., 1985; Virani and Watson, 1998; Herremans and Herremans-Tonnoeyr, 2000) but remain poorly understood.

The Martial Eagle *Polemaetus bellicosus* is a large, Pan-African eagle species that is threatened across its range (Brown et al., 1982; del Hoyo et al., 1994). The South African population probably comprises less than 600 breeding pairs, mostly confined to conservation areas in the Lowveld and Kalahari regions (Barnes, 2000). The rarity of the Martial Eagle outside of extensive protected areas may be the result of widespread persecution of the species on privately owned land because of its reputation as a predator of domestic livestock (Brown, 1991; Boshoff, 1993; Herholdt and Kemp, 1997). However, the relative importance of agriculture and ranching in degrading habitat (and depleting food resources) for Martial Eagles inhabiting non-conserved land has not yet been investigated.

The present study examines the relationship between the breeding distributions of large eagles (particularly Martial Eagle, but including Black Eagle *Aquila verreauxi* and Tawny Eagle *A. rapax*) in the central and southwestern Karoo, South Africa, and the general environmental health of commercially managed farmland in this region. Historical information suggests that the Tawny Eagle, in particular, has decreased in numbers and receded in distribution in the western Karoo in the last century (Boshoff et al., 1983), and there are indications that Martial Eagles may also have declined somewhat (Boshoff, 1997). The Karoo is a poorly conserved biome (Low and Rebelo, 1996), and does not present the stark contrasts in large eagle densities that occur typically across game reserve boundaries in the savannas further north in Africa (e.g. Tarboton and Allan, 1984; Aumann, 1997; Krüger et al., 2002). However, given that livestock grazing pressure in the Karoo is generally high, with

an attendant loss of primary production (Dean and Macdonald, 1994), there is likely to be considerable variation in the quality of the natural environment (depending on the management policies applied by each private landowner—Brandl et al. (1985), Joubert and Ryan (1999)) that may be reflected in the distribution of eagle pairs. Hypothetically, eagle densities in the Karoo are depressed on poorly managed farms (with compromised ecological integrity—Milton et al. (1994)), and healthy or inflated on well-managed properties.

This hypothesis is examined here in terms of the distribution of large eagle nests in pylon structures along electricity transmission lines in the Karoo in relation to measures of habitat quality at both landscape (macro-) and local (micro-) scale. Eagle nests in electricity pylons are relatively easy to locate and monitor (Boshoff, 1993), allowing the study to cover a large area of Karoo ranchland, and include information for a meaningful sample of nests across this area.

Specifically, the study addresses the following key questions: (i) Are eagle territories regularly or irregularly dispersed along the surveyed transmission pylon lines (as an initial index of environmental sensitivity)?; (ii) Does habitat composition of eagle territories, in terms of a range of digitally mapped biotic and abiotic variables, differ significantly from the composition of a comparable sample of random plots?; and (iii) Are micro-scale measures of habitat quality within eagle territories significantly different from those outside of eagle territories?

2. Methods

2.1. Study area

The study was conducted in the central and southwestern Karoo region of South Africa, including the entire south-central portion of the Nama Karoo Biome, the eastern half of the Succulent Karoo Biome, and the northern fringes of the Fynbos Biome (Fig. 1).

The two Karoo biomes share some plant and animal species but are generally regarded by botanists as clearly distinct (Dean, 1995). Rainfall in the Karoo has some regional pattern and predictability (e.g. predominantly summer or winter rainfall, increasing from west to east), although it occurs erratically at any given location (Desmet and Cowling, 1999). The region generally features some degree of topographic relief. Soil depth varies with topography (Milton and Dean, 1996), but soils are mostly lime-rich and weakly developed (Low and Rebelo, 1996).

Urbanization and agriculture are minimal in the Karoo. Most of the region is used for ranching, mainly of small domestic livestock (sheep and goats), but also of indigenous stock such as Ostrich *Struthio camelus* (Dean, 1995) and small to medium-sized antelope species such as Springbok *Antidorcas marsupialis* and Gemsbok *Oryx gazella*. Ranching can be commensurate with conservation, but recommended stocking rates are frequently exceeded and much of the region is chronically overgrazed (Roux and Van der Vyver, 1988; Macdonald, 1989).

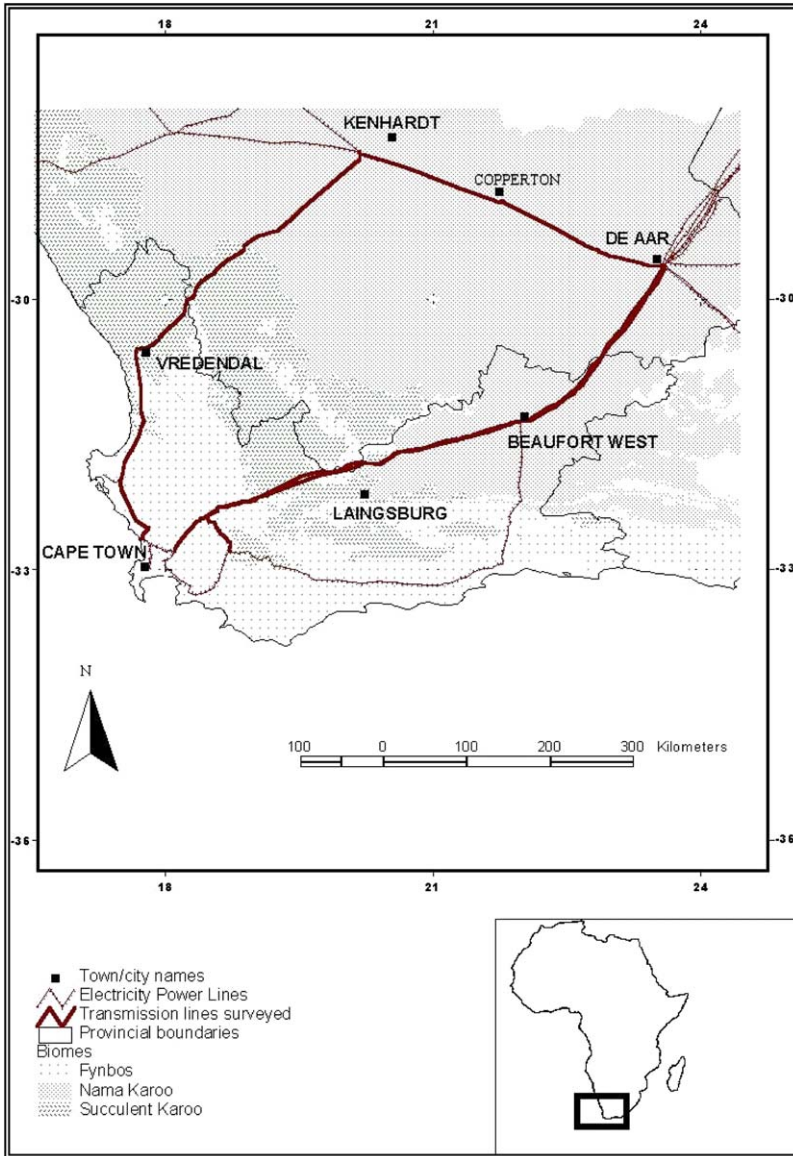


Fig. 1. The location of the study area in the Western and Northern Cape Provinces, South Africa, showing the lay-out of the surveyed electricity transmission pylon lines in relation to biome type.

The vegetation of the Nama Karoo is dominated by grassy, dwarf shrubland. Grasses tend to be more common on sandy soils, and less abundant on clay-based soils. Under conditions of overgrazing, many shrubs proliferate (e.g. Threethorn *Rhigozum trichotomum*, Bitterbos *Chrysocoma ciliata*), and many grasses and other palatable species are lost. Rainfall in the Nama Karoo varies from 100 to

520 mm year⁻¹, absolute temperatures range from -5 °C (winter minimum) to 43 °C (summer maximum) (Milton and Dean, 1990), and altitude ranges from 500 to 2000 m above sea level (a.s.l.), with most of the biome falling between 1000 and 1400 m a.s.l.. Less than 1% of the Nama Karoo is formally conserved (Low and Rebelo, 1996).

Much of the vegetation of the Succulent Karoo has taxonomic affinities with the shrublands of the Cape Floral Kingdom. It is dominated by dwarf, succulent shrubs, of which the Vygies (*Mesembryanthemaceae*) and Stonecrops (*Crassulaceae*) are particularly important (Low and Rebelo, 1996). Rainfall varies between 20 and 290 mm year⁻¹ and falls mostly in winter. The temperature range is similar to that of the adjacent Nama Karoo and, during summer, temperatures in excess of 40 °C are common. Most of the biome covers a flat to gently undulating plain, with some hilly and 'broken' rangeland. The altitude is mostly below 800 m a.s.l., but in the east it may reach up to 1500 m a.s.l.. Just over 2% of the area of the Succulent Karoo Biome is formally conserved (Cowling et al., 2003).

The Fynbos Biome comprises the highly diverse and unique Fynbos and Renosterveld vegetation groups (Low and Rebelo, 1996). Renosterveld used to support herds of large ungulates but these are now mostly extinct in the region outside of conservation areas (Low and Rebelo, 1996). In contrast, Fynbos is much richer in plant species and holds most of the biome's endemic amphibians, birds and mammals. Soils (and hence plants) in the Fynbos Biome are nutrient-poor, and the region generally cannot sustain the densities of game or domestic stock that are characteristic of the Karoo (Low and Rebelo, 1996).

2.2. Eagle surveys

A sample section of about 1400 km of 400 kV electricity transmission pylon line, extending from Koeberg in the southwest, to Kenhardt in the north and De Aar in the east (Fig. 1), was surveyed by helicopter in early July 2002. The exact location of all large eagle nests observed was recorded using a Global Positioning System and coupled with information on observed eagle breeding activity. Ground surveys that followed the initial aerial survey were carried out between July and October–November 2002, primarily to collect eagle habitat and diet information, but also to confirm inactive nests and assess progress at active nests. About 640 km of Eskom servitude (tracks that run under all transmission lines to allow access for maintenance activities) were driven during these ground surveys, and about half of the eagle territories included in the total surveyed population were re-visited and examined more closely.

Pairs of large eagles often build more than one nest structure, and alternate between nests in successive breeding attempts. (e.g. Martial Eagle territories may contain up to seven nests—Steyn (1982)). In this study, where multiple nest structures were located in short sections of pylon line these were considered to be alternate nests within a single eagle territory. Note that, in some instances, nests of two separate pairs located close together may have erroneously been allocated to a single territory, resulting in an underestimation of the total number of eagle

territories in the study population. Once identified, eagle territories were classified either as active (a nest with obvious signs of occupation and breeding, containing fresh nest lining, an egg or a nestling) or inactive (possibly occupied by a pair of eagles, but no definite signs of breeding were recorded). Once plotted in a GIS (using ArcView software), the spatial extent of each eagle territory was demarcated by a circle centred on either the active nest or the centre point on the line between alternate nests in inactive territories. The radius of the circle was set at 6 km, determined as approximately half the overall average inter-nest distance recorded for Martial, Black and Tawny Eagles in southern Africa (Tarboton and Allan, 1984; Gargett, 1990; Herholdt et al., 1996), and deemed to adequately simulate the average territory size occupied by pairs of these species in the region.

The pattern of spacing between eagle territories was examined as an indication of the degree of sensitivity to extrinsic, environmental variables, with regular or even spacing reflecting a lack of sensitivity (with eagle distributions determined primarily by intrinsic social factors), irregular or uneven spacing reflecting a measure of sensitivity (perhaps to local or micro-scale variation in habitat quality), and clumped spacing reflecting pronounced sensitivity (to landscape or macro-scale variation in habitat quality). To test the null hypothesis that territories along the transmission lines were randomly or irregularly spaced, a randomization analysis was performed using 500 iterations. The standard deviation was used as the statistic to measure the pattern of dispersion of eagle territories. The observed standard deviation (around the mean distance between the centre points of adjacent territories) was compared with the empirical frequency distribution of standard deviations derived from the randomizations. The p -value was derived from the standard deviation of the number of observations, that is less than or equal to the standard deviation of the randomization divided by the number of iterations. Using a two-tail test with $\alpha = 0.05$, it was expected that, if $0.025 < p < 0.975$ accept the H_0 ; if $p < 0.025$, eagle distribution is uniform and if $p > 0.975$, eagle distribution is clustered or clumped (Zar, 1996).

2.3. Eagles and habitats at the macro-scale

Eagle habitat preferences at the landscape or macro-scale were examined by comparing habitat composition (in terms of the percentage area covered by each habitat category) within eagle territories with habitat composition within an equivalent array of random plots with the same shape and surface area.

ArcView GIS analysis was aided by extensions and scripts downloaded from ESRI (www.esri.com). Six broad-scale habitat variables, that describe general biotic and abiotic attributes of both the natural and modified environment, were selected according to the availability and relevance to this analysis. These were vegetation type (Department of Environmental Affairs and Tourism, Cape Town), landscape morphology (Fairbanks et al., 2000), soils (surface soil characteristics and topsoil textures, Institute of Soil, Climate and Water, Pretoria), primary productivity (Rutherford (1978, 1980); Department of Agricultural Engineering, University of Natal, Pietermaritzburg), land-cover (ARC/CSIR, Pretoria, Thompson, 1999) and

rainfall (Department of Agricultural Engineering, University of Natal, Pietermaritzburg). These GIS coverages were overlaid on eagle territory distributions and the distributions of random or selected random plots using the Albers Equal-Area Conic projection.

Randomization tests (Manly, 1991; Zar, 1996) were used to test the null hypothesis that the habitat composition of eagle territories did not differ from random. An ArcView extension '*Random Point Generator v. 1.1*' was used to generate 500 random points along the transmission pylon line. Each point was expanded to a circle with a 6 km radius to simulate an eagle territory, with the resulting complement of random plots representing all possible random rearrangements of eagle territories along the line. The habitat composition of all the eagle territories and of each random plot, in terms of the proportion of the total surface area occupied by each habitat parameter, was calculated for each of the different GIS coverages used. The mean habitat composition of a random sample of random plots (N = the number of eagle territories, all plots were available for selection more than once) was then calculated and compared with the mean habitat composition of eagle territories, and counters for upper and lower tail were updated according to:

Left tail counter

+ 1 if random proportion \leq observed proportion,

Right tail counter

+ 1 if random proportion \geq observed proportion.

This process was repeated for 500 samples of random plots and, ultimately, each habitat parameter was scored plus (+) or minus (–) according to the calculated probability that the observed proportion either exceeded or was less than the average random proportion.

Note that the soil coverage used in the overlay analysis did not completely cover the entire study site, leaving part of study area with two Martial Eagle nests uncovered. Therefore these two nests were excluded from the analysis.

2.4. Eagles and habitats at the micro-scale

All stretches of servitude driven during ground surveys served as transects through the landscape. Every 5 km travelled along the transmission lines, and at every eagle nest visited, a simple assessment of habitat quality was conducted. This included the calculation of a 'Rangeland Health Index' (RHI), based on criteria developed by Milton et al. (1998), as a measure of the level of impact on the environment of grazing and disturbance. Parameters contributing to the RHI were:

1. *Forage value*: What percentage (scored 1–5) of the vegetation was palatable to livestock, and what proportion poisonous or unpalatable?
2. *Grazing intensity*: How severely (scored 1–5) were the canopies of palatable plants browsed?

- 3. *Disturbance indicators*: How prevalent (scored 1–5) were alien, annual or mat-forming plants?
- 4. *Soil and habitat health*: How prevalent (scored 1–5) were positive (mulch, animal diggings, fertile patches, shade plants, living crust) vs. negative (rills, pedestals, terraces, mineral crust, exposed roots) signs of soil and habitat health? How well covered and bound was the topsoil by vegetation (the percentage of vegetation cover was estimated along a 50 × 4 m foot transect extended perpendicular to the servitude through a representative patch of habitat)?

The final RHI value was calculated as the sum of the four scores ($a + b + c + d$), and used to categorize rangeland condition as either excellent (score 18–20), good (score 13–17), intermediate (score 8–12) and poor (score <8).

The degree to which eagle distributions were influenced by local or micro-scale variation in habitat quality was determined by comparing RHI and percentage vegetation cover values measured at nests or at least within the plotted areas of each eagle territory, with those that were measured away from nests and outside eagle territories. Non-parametric Mann-Witney *U* tests were used to statistically evaluate these comparisons.

The type of livestock visibly present in the general area was also recorded in the course of each habitat assessment. Stock types were summarized into two groups: domestic stock (sheep, goats, cattle) and mixed stock (game or game and domestic stock). Each eagle territory in which habitat assessments were conducted was assigned to the appropriate stock type. In cases where more than one assessment was conducted in a single territory and stock types varied between assessments, the most inclusive type (mixed stock) was assigned. The ratio of active:inactive territories and the density of eagle pairs (in terms of nearest neighbour distance (NND)) was then examined relative to stock type.

3. Results

A total of 117 large eagle nests (94 Martial Eagle nests, 14 Tawny Eagle nests and nine Black Eagle nests) (Table 1) were plotted, coupled with basic information on the structure, placement and usage of each nest (Fig. 2). From these, 83 eagle territories

Table 1
Numbers of active and inactive large eagle nests and territories recorded along electricity pylon lines in the central and southwestern Karoo, South Africa

Species	No. nests	No. territories	No. active territories	No. inactive territories
Martial Eagle	94	62	34	28
Black Eagle	9	8	6	2
Tawny Eagle	14	13	8	5
Total	117	83	48	35

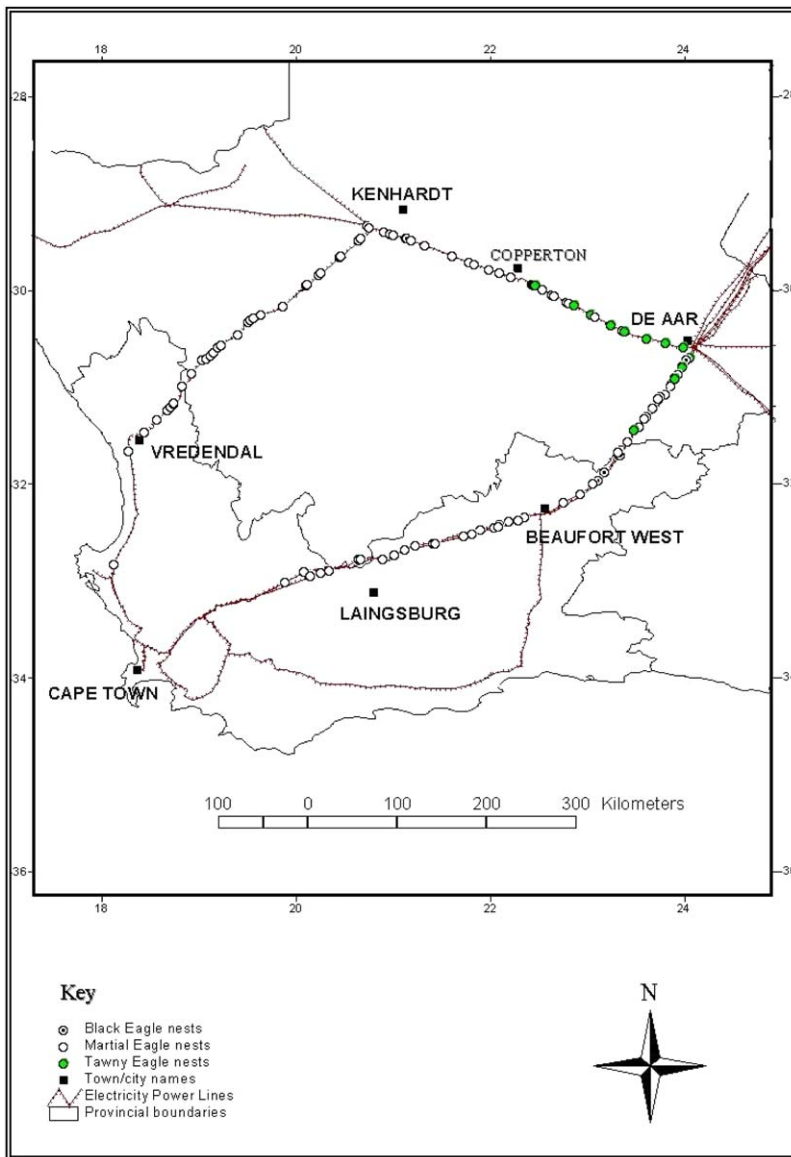


Fig. 2. Distribution of large eagle nests along electricity transmission pylon lines in the central and southwestern Karoo, South Africa.

were identified. Fifty-six (67%) contained a single nest structure, 21 (25%) contained two nests, five (6%) contained three nests, and one territory contained four nests. Sixty-four territories (77% of the total) were located within the Nama Karoo Biome (at an average linear density of 7.2 territories 100 km⁻¹ of transmission pylon

line), 15 (18%) were located in the Succulent Karoo (6.2 territories 100 km^{-1} of line), and four (5%) were located in the Fynbos Biome (2.2 territories per 100 km of line).

All subsequent analyses were conducted using data for all eagle territories together, and Martial and Tawny Eagle territories separately. The sample of Black Eagle nests obtained was considered too small to yield biologically meaningful results.

3.1. Spacing of eagle territories

All eagle territories were spaced irregularly (or randomly) along the pylon lines (Table 2), except active Tawny Eagle territories that were restricted to (or clustered within) a stretch of only 280 km (20%) of the total sample distance (Fig. 2, Table 2), and were regularly (or non-randomly) spaced within this restricted range (Table 2).

3.2. Broad-scale assessment of habitat composition

3.2.1. Vegetation types

The Bushmanland and Nama Karoo variants were the most widely occurring vegetation types in eagle territories (Fig. 3). In terms of the entire sample, Central Lower Nama Karoo was significantly less prevalent in eagle territories than in random plots (rejected, $p = 0.022$), and Upper Nama Karoo was significantly more prevalent in eagle territories than in random plots (selected, $p = 0.024$) (Fig. 3). Martial Eagles selected Bushmanland Nama Karoo ($p = 0.016$), while Upland Succulent Karoo was characteristic of (or 'selected' in) inactive Martial Eagle territories ($p < 0.001$). Tawny Eagles selected Eastern Mixed Nama Karoo ($p = 0.018$) and Upper Nama Karoo ($p < 0.001$). All other vegetation types were used randomly.

Table 2

Mean distances (± 1 standard deviation) between eagle territories along the sampled length of pylon line, with results of randomization tests to determine patterns of dispersion or spacing between territories

	No. territories	Mean distance (km)	p	Spacing
All eagle territories	83	17.4 \pm 0.0	0.166	Irregular
All active eagle territories	48	48.3 \pm 3.3	0.096	Irregular
All inactive eagle territories	35	37.7 \pm 1.1	0.070	Irregular
All Martial Eagle territories	62	31.2 \pm 1.1	0.124	Irregular
Active Martial Eagle territories	34	52.0 \pm 4.4	0.068	Irregular
Inactive Martial Eagle territories	28	51.3 \pm 6.6	0.056	Irregular
All Tawny Eagle territories	13	47.6 \pm 6.6	0.026 ^a	Regular
Active Tawny Eagle territories	8	80.3 \pm 7.7	0.016 ^a	Regular

^aStatistically significant values are marked.

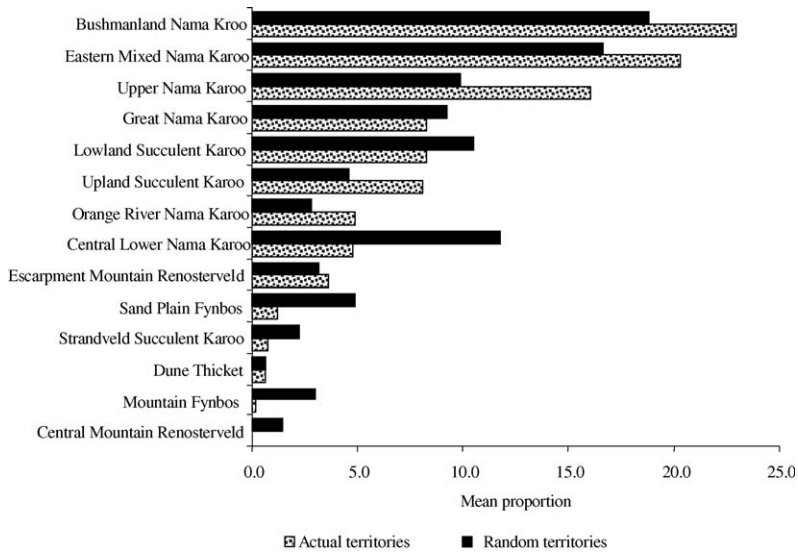


Fig. 3. Mean proportions of different vegetation types present in eagle territories vs. random plots along electricity transmission pylon lines in the central and southwestern Karoo, South Africa.

3.2.2. Landscape morphology

Generally, eagle territories were distributed randomly relative to landscape morphology although, for the entire sample, moderately undulating plains were rejected ($p = 0.014$), Martial Eagles selected slightly irregular plains ($p = 0.018$), Tawny Eagles rejected plains ($p = 0.022$) and selected slightly irregular plains ($p = 0.014$), and active Tawny Eagles selected lowlands and hills ($p = 0.020$).

3.2.3. Surface soil characteristics

All eagle territories combined, all active territories, and all active Martial Eagle and Tawny Eagle territories were distributed randomly relative to the distribution of surface soil characteristics, while rocky substrates ($p = 0.004$) and coarse desert pavements ($p = 0.004$) were characteristic of inactive eagle territories, and inactive Martial Eagle territories, respectively.

3.2.4. Topsoil textural characteristics

All eagle territories were randomly distributed relative to the distribution of topsoil textural characteristics.

3.2.5. Primary productivity

Generally, eagle territories were non-randomly distributed relative to the distribution of primary productivity (Fig. 4). Martial Eagles and Tawny Eagles showed a marked difference in selection/rejection patterns of more productive vs. less productive habitats: Martial Eagles selected less productive habitats ($p < 0.001$) and rejected more productive habitats, while Tawny Eagles selected moderately

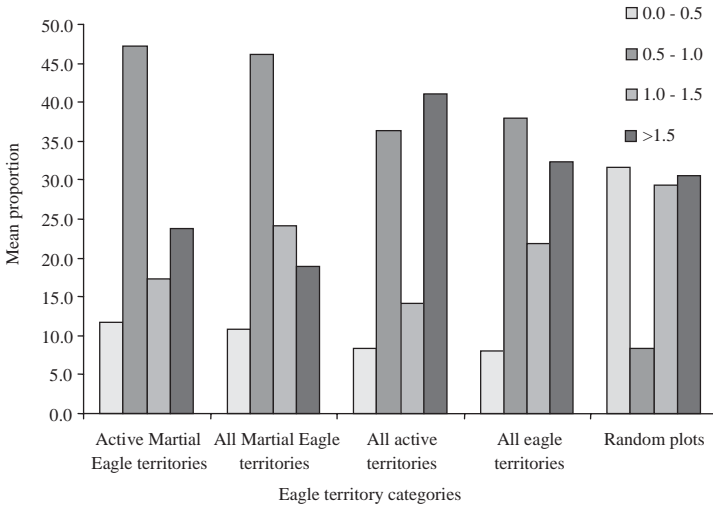


Fig. 4. Mean proportions of different levels of primary productivity (tonnes/hectare) present in eagle territories vs. random plots along electricity transmission pylon lines in the central and southwestern Karoo, South Africa.

productive habitats ($p < 0.001$). Interestingly, all eagles combined, avoided areas with highest primary productivity ($p < 0.001$).

3.2.6. Land cover

All eagles and all Martial Eagles, rejected cultivated land classes ($p < 0.001$, $p = 0.008$) and selected shrubland and low Fynbos ($p < 0.001$, $p = 0.002$), while Tawny Eagle territories were randomly distributed relative to the distribution of land cover classes.

3.2.7. Mean annual rainfall

Again, Martial Eagles and Tawny Eagles showed a marked difference in selection/rejection patterns of higher vs. lower rainfall areas: Martial Eagles selected lower rainfall habitats ($p = 0.006$) and rejected higher rainfall areas, while Tawny Eagles selected higher rainfall habitats ($p = 0.010$) and rejected lower rainfall areas ($p = 0.022$).

3.3. Micro-scale assessment of habitat quality

Eight sections of the transmission pylon line were surveyed on the ground. A total of 116 habitat assessments, with associated RHI and percentage vegetation cover values, were completed at points along the pylon lines. Of this total, 87 assessments were conducted at eagle nests or within plotted eagle territories, and 29 were conducted at points outside of plotted eagle territories.

Most (76%) RHI values measured fell into the intermediate category, with 6% scored as poor, 18% scored as good and 0% scored as excellent. In all cases, mean RHI and percentage vegetation cover figures within eagle territories were not significantly different to those measured outside eagle territories (Table 3).

Generally, there were no significant differences in RHI and percentage vegetation cover values between all active and inactive eagle territories (RHI: active territories 10.7 ± 2.1 vs. inactive territories 10.7 ± 1.6 , $Z = 0.131$, $p = 0.896$; percentage cover: active territories 32.8 ± 15.8 vs. inactive territories 37.7 ± 15.5 , $Z = -1.881$, $p = 0.060$) and in RHI values between active and inactive Martial Eagle territories (active territories 11.1 ± 2.0 vs. inactive territories 10.7 ± 1.6 , $Z = 0.861$, $p = 0.389$), but percentage vegetation cover was significantly lower in active Martial Eagle territories than in inactive Martial Eagle territories (active territories 32.9 ± 16.0 vs. inactive territories 38.6 ± 15.8 , $Z = -1.990$, $p = 0.047$).

Habitat assessments were conducted within 54 (65%) of the eagle territories plotted. In terms of the stock observed and recorded in these assessments, 63% of eagle territories were located on ranchland dominated by domestic stock, and 37% were located on farms with a mixture of domestic stock and game (Table 4).

Overall, the proportion of eagle pairs actively breeding in areas stocked with game (mixed stock) (80%) tended to be higher than in exclusively sheep or goat farming areas (about 71%) although this difference was not statistically significant ($\chi^2 = 0.659$, $p = 0.19$, Table 4). However, the density of eagle pairs (in terms of the distance between nearest neighbouring territories) was significantly higher in game or mixed farming areas than in areas with domestic stock only (Fig. 5).

Table 3

Statistical comparison (Mann-Witney U test) of mean Rangeland Health Index and percentage vegetation cover values measured within vs outside of eagle territories

	No. habitat assessments	Rangeland health index	p	% Cover	p
All eagle territories	86	10.7	0.849	34.2	0.846
Active eagle territories	62	10.7	0.737	32.7	0.783
Inactive eagle territories	24	10.5	0.858	37.7	0.228
All Martial Eagle territories	78	10.9	0.462	34.7	0.726
Active Martial Eagle territories	55	11.1	0.316	32.8	0.756
Inactive Martial Eagle territories	23	10.6	0.978	38.6	0.163
All Tawny Eagle territories	19	9.7	0.164	36.0	0.527
Active Tawny Eagle territories	17	9.5	0.092	32.9	0.946
Areas outside eagle territories	29	10.5	—	32.5	—

Table 4
Number of eagle territories in areas with domestic and/or mixed stock

	Domestic stock	Mixed stock	Unknown	Total
All eagle territories	34	20	29	83
Active eagle territories	24	16	8	48
Inactive eagle territories	10	4	21	35
All Martial Eagle territories	29	11	22	62
Active Martial Eagle territories	21	8	5	34
Inactive Martial Eagle territories	8	3	17	28
All Tawny Eagle territories	3	3	7	13
Active Tawny Eagle territories	2	3	3	8

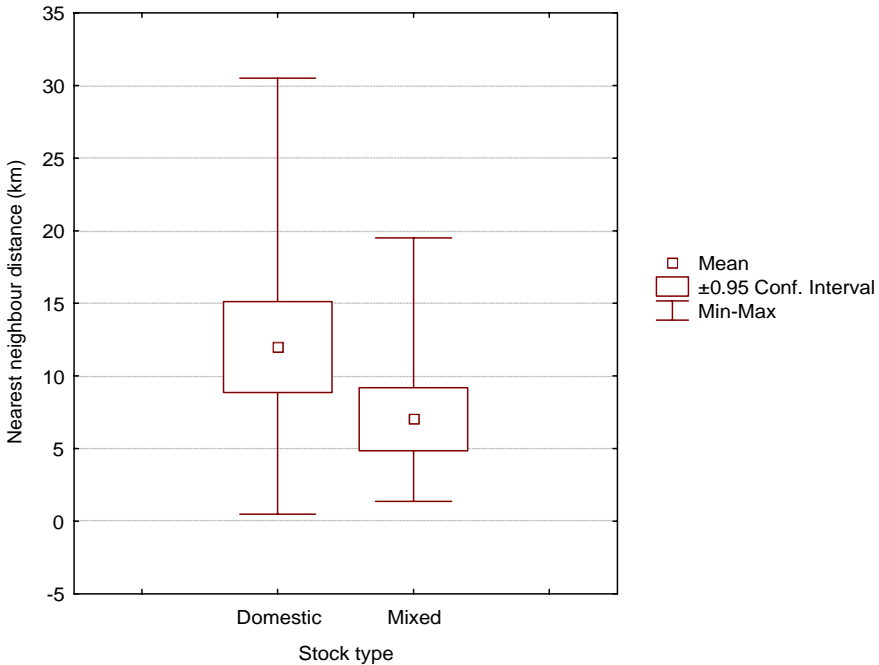


Fig. 5. Comparison of nearest neighbour distances (NND) between large eagle territories in areas predominated by domestic livestock vs. areas with both domestic stock and game (mixed stock) (mean NND in domestic livestock areas = 12.0 ± 9.1 km ($n = 34$ territories), mean NND in mixed livestock areas = 7.0 ± 4.8 km ($n = 20$ territories, $t = 2.3$, $df. = 54$, $p = 0.025$).

4. Discussion

4.1. Nest spacing and sensitivity to habitat variation

Over 60 Martial Eagle territories were located and monitored in this study, constituting more than 10% of the estimated South African population of this species

(Barnes, 2000). This emphasizes the importance of the Karoo in the conservation of Martial Eagles nationally (and globally), and the significance of fully understanding the relationship between the welfare of eagle populations and the management practices and attitudes of private landowners in this poorly conserved environment.

The irregular distribution of eagle territories along transmission pylon lines in the Karoo (Table 2) probably suggests sensitivity to relatively fine-scale measures of habitat quality. Because we were unable to thoroughly survey areas around the pylon lines for eagle nests not placed in pylons, it remains possible that sections of pylon line devoid of nests were actually occupied by eagles nesting on nearby trees or other suitable structures. However, we considered this unlikely given that (i) the large pylon structures appear to constitute optimal nesting sites, and any eagles occupying areas close to pylon lines were likely to have been drawn into using the pylons in the decades since their construction, and (ii) we knew of a number of nests on trees or smaller structures, but none were located close to transmission lines.

Martial Eagles were found along the entire length of surveyed line (Fig. 2), but the spacing between territories and active nests varied subtly and unpredictably along the pylon line. This could indicate that the density of eagle pairs is affected by localized variation in the availability of essential resources—either nest sites or food (Newton, 1979). We suspect that, although nest site availability was not quantified during this study, the number and quality of pylon structures and alternative/natural nest sites available to eagle pairs along the sampled section of pylon line is more or less uniform. Hence, spatial differences in the quality of the eagle prey base are more strongly implicated in affecting the distribution of territories, and either staple prey taxa (hares, small antelope, viverrids—Boshoff et al. (1990)) are patchily distributed or they are more or less susceptible to eagle predation in different habitats with different cover conditions. Alternatively, eagle populations may be impacted by farm-to-farm variation in the intensity of persecution by landowners. However, this may be more likely to affect the distribution of active vs. inactive territories (rather than all territories collectively), with inactive (and possibly unoccupied) territories resulting from conflict between formerly active eagle pairs and eagle-unfriendly farmers (e.g. Brown, 1991).

4.2. Eagle distributions and habitats at the landscape scale

The various GIS coverages used in this aspect of the study were considered to be representative of a cross-section of essential biotic and abiotic parameters that might affect the quality of eagle habitat, and hence the distribution of eagle territories. Most of the variables used are not in any way reflective of the effects of land management, largely because no such data were available. However, assessment of the sensitivity of large eagles to natural, landscape-scale biogeography is essential to understanding superimposed sensitivity to habitat modification (Thompson and McGarigal, 2002).

At some level, eagles were non-randomly distributed relative to the entire suite of habitat variables used. Interpretation of these data is confounded by a general lack of discernible pattern but some meaningful results have emerged.

Martial Eagles apparently favoured habitats with lower and/or less predictable winter rainfall (e.g. Bushmanland Nama Karoo, Upland Succulent Karoo, [Low and Rebelo, 1996](#)) and lower primary productivity ([Fig. 4](#)), while Tawny Eagles (on the basis of a relatively small sample size) preferred habitats with higher and/or more predictable summer rainfall (e.g. Eastern Mixed Nama Karoo, Upper Nama Karoo), and higher primary productivity. All eagles avoided areas of highest primary productivity. In terms of human impacts, eagles selected both poorly conserved/heavily grazed habitats (e.g. Upper Nama Karoo, Bushmanland Nama Karoo, Eastern Mixed Nama Karoo), and well conserved/lightly grazed habitats (e.g. Upland Succulent Karoo) ([Low and Rebelo, 1996](#)), but were conspicuously absent from cultivated areas.

These results only partly concur with previous studies of African eagle distributions (mostly conducted in tropical savannas), that have clearly shown (i) that large eagles occur at markedly lower densities outside of protected areas ([Gargett, 1977](#); [Tarboton and Allan, 1984](#); [Liversidge, 1994](#); [Aumann, 1997](#); [Herremans and Herremans-Tonnoeyr, 2000](#)) and (ii) that within a given environment, large eagles (including Martial Eagles) favour areas of higher productivity and higher rainfall ([Hustler and Howells, 1989, 1990](#); [Wichmann et al., 2003](#)). These differences, and particularly the persistence of Martial Eagles in drier, less productive environments, can probably best be explained in terms of the relatively homogeneous nature of Karoo shrublands, and the relatively unpredictable rainfall regime that sustains them. In such areas, while primary productivity and rainfall in combination may directly and positively influence the abundance of large eagle prey ([Nel, 1983](#); [Kerley, 1992](#)), they may also affect vegetation cover (and hence the accessibility of key prey taxa—e.g. [Gargett, 1977](#)) more profoundly than in more mesic habitats. These effects, in turn, are either dampened or exaggerated by grazing pressure ([Todd and Hoffman, 1999](#); [Landsberg et al., 2002](#)), and the complex, dynamic and ongoing interaction of these multiple factors probably ultimately controls foraging conditions for Karoo eagles. The coarse scale of the mapping used in this study, and the simplicity of the analyses conducted, were not suited to detecting such subtle and complex relationships ([Thompson and McGarigal, 2002](#)), and these warrant further investigation.

4.3. *Eagles and rangeland quality*

The lack of any obvious correlation between the distribution of large eagle territories and the condition of rangeland surveyed in this study suggests that eagles are generally insensitive to the quality of land management in the Karoo. However, this result should be qualified in terms of the degree of variation observed in the RHI and percentage vegetation cover figures obtained. While some extremes were recorded, the majority of assessments yielded intermediate values, and reflected the predominantly poor or indifferent condition of the areas evaluated. Once again, this relative homogeneity of the Karoo environment, even at the micro-scale, could mask responsiveness in the eagle population to rangeland health, and require that variation in habitat quality be more accurately assessed. This could entail more

extensive sampling or refinement of the assessment procedure to include parameters more directly pertinent to eagles and eagle resources. For example, the significant correlation between Martial Eagle breeding activity and the extent of vegetative cover suggests that the dynamics between prey abundance and the availability of protective cover might be a fruitful avenue for further, more detailed investigation.

The strong positive relationship between the density of eagle territories and the presence or absence of game on rangeland in the Karoo (Fig. 5) mirrors more extreme contrasts in both eagle and game densities observed across conservation area boundaries in Afrotropical savannas (Liversidge, 1984, 1994; Tarboton and Allan, 1984; Brandl et al., 1985; Aumann, 1997), and is perhaps the most significant finding of this study. Although game-dominated farms did not obviously feature better quality rangeland than those with domestic stock only, herds of indigenous antelope evidently interact with the Karoo environment in a subtly different way, that is beneficial (or less detrimental) to large eagle populations, even at excessive stocking rates. Hence stock type may be more significant in affecting the general health of commercially managed Karoo rangeland, and indirectly the density and performance of local eagle populations, than stocking rates or grazing regimes per se.

4.4. Persecution vs. habitat loss?

Depletion of large eagle populations in rangeland has been attributed mainly to high levels of persecution in many studies (e.g. Davies, 1999; Pedrini and Sergio, 2001). The Martial Eagle is widely regarded as a small-stock predator in the Karoo, and may be the most severely persecuted raptor in the region (Boshoff and Vernon, 1980). Consequently, the detrimental effects of inflated rates of adult mortality cannot be discounted as an important factor limiting the distribution and success of breeding pairs. For example, relatively healthy eagle populations in areas stocked with game may simply reflect the fact that game farmers are less inclined to attribute stock losses to eagles (Anderson, 2000), so eagles may be less heavily persecuted in game farming areas. Further, quantitative studies on the relationship between eagle densities in the Karoo and levels of direct persecution by farmers are urgently required.

However, the process of rangeland modification and degradation (primarily by overgrazing) must impact on eagle populations, at least indirectly by affecting the distribution, abundance and accessibility of prey. Grazing by domestic livestock is shaping landscapes in many regions of the world (Settele et al., 1998). In South Africa, rangelands have been consistently overstocked since at least the 1930s (Downing, 1978; Biggs and Scholes, 2002). In semi-arid rangelands, this situation is associated with accelerated rates of soil erosion and reductions in faunal biomass as a consequence of desertification, impaired productivity and the competitive effects of domestic livestock (Osem et al., 2002). Various studies on Karoo rangeland management have shown that overgrazing, and over-selective grazing, by domestic stock, result in the loss of plant cover and diversity, and reduced secondary production (Bosch, 1989; Milton et al., 1994; Dean et al., 1995; Eccard et al., 2000).

This study has clearly shown that, even in the relatively homogeneous conditions that prevail in the Karoo, eagle distributions are subtly but significantly influenced by both macro- and micro-scale variation in habitat type and quality, and that mismanagement of Karoo rangeland can impact on the welfare of eagle populations.

4.5. Eagles as indicators of habitat health

As widespread, conspicuous and mobile organisms, birds often serve as valuable and sensitive indicators of environmental change (Furness et al., 1993; Carrete et al., 2002), and measures of the distribution and abundance of key raptor species have been used previously as functional indices of habitat health (Robinson and Wilcove, 1989). We propose that the Martial Eagle is potentially suitable as such an indicator of ecosystem functioning in the Karoo. It is a large and obvious species, widely distributed and relatively easy to monitor, particularly where pairs breed on electricity pylons. As a predator of small to medium-sized mammals and large birds and reptiles, the Martial Eagle operates at the apex of the local food pyramid, and is well placed to detect and respond to imbalances at subordinate producer and consumer levels (Watson, 1991; Wichmann et al., 2003). Evidence presented here suggests that the species may indeed be sensitive to such imbalances.

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