Does bush encroachment impact foraging success of the critically endangered Namibian population of the Cape Vulture *Gyps coprotheres*?

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Abstract

The Namibian population of the Cape Vulture *Gyps coprotheres* has declined from around 300 birds in 1969 to a current low of 11 birds. Secondary poisoning is most likely the primary factor responsible for this decrease, but bush encroachment has also been implicated in contributing to the collapse of this population. I tested the impact of increased tree density on the foraging success of the Cape Vulture in the Waterberg region by two methods: 1) measuring the time taken for birds to locate carcasses experimentally placed in differing levels of tree density and 2) using PTT/GPS satellite data to find carcasses previously scavenged by Cape Vultures and measuring tree density at these sites.

Vultures located experimental carcasses more quickly in low density bush than in high density bush. Moreover, as tree density increased, the likelihood of detection decreased, to the point where food was never found by vultures in tree density greater than 2600 trees/ha. A total of 24 carcasses (at which vultures had fed 1-7 months prior to the study period) were located using the historic satellite data derived from three adult male Cape Vultures. The majority of carcasses (79%) were of game animals of which Greater Kudu *Tragelaphus strepsiceros* were the most common prey item (54.2% of all carcasses) followed by Eland *Tragelaphus oryx* (8.3%) and Oryx *Oryx gazella* (8.3%). The remainder were of domestic cattle *Bos taurus* (16.7%), and domestic horse *Equus caballus* (4.2%), with two carcasses unidentified. The majority of carcasses (83%) were located in either completely open habitat or low bush density (less than 1000 trees/ha), while two (8.3%) were in dense bush (>2000 trees/ha). Six carcasses (25%) were located along fencelines. Both results suggested that increasing tree density negatively impacts vulture foraging success. However, livestock and game densities appear to be adequate for vulture populations in north-central Namibia which may negate this impact. What is still necessary to determine is a more accurate assessment of carcass availability by developing a finer scale map of vegetation density of this region than is currently available.

Key words: Bush encroachment, Cape Vulture, population decline, satellite telemetry

Introduction

The southern African endemic Cape Vulture *Gyps coprotheres* is classified globally "Vulnerable" (BirdLife International, 2004) with an estimated 10 000 birds (Piper, 2004). Its main distribution centres on two breeding colonies in two distinct regions: one being in Lesotho, the former Transkei and western KwaZulu-Natal, the other in North West and Limpopo Provinces, southern Zimbabwe and eastern Botswana (Mundy et al., 1997). There are two outlying populations remaining: one in the Western Cape Province and the other in north-central Namibia based around the Waterberg Plateau Park (Mundy et al., 1997). Within Namibia, its national conservation status is "Critically Endangered" (Simmons and Brown, 2007) resulting from a decrease in the Waterberg population from an estimated 300 birds in 1969 to only 11 in the wild in 2006 (Brown, 1985; M. Diekmann, unpubl. data). This dramatic decline of almost 97% is not recent; the population had been reduced to *c*. 10 birds by 1985, then somewhat recovered with a supplementary feeding scheme in the ensuing years to *c*. 25 adult birds by 1991, but has subsequently stagnated (Brown, 1985; Simmons and Brown, 2007). Other Cape Vulture colonies in South Africa have also experienced population declines (Piper, 2004).

The Namibian Cape Vulture population is primarily threatened by direct and indirect poisoning, and habitat unsuitability resulting from bush encroachment (Brown, 1985; Bridgeford, 2001). Other threats that have impacted on southern African vulture populations include improvements in animal husbandry that have resulted in decreased food availability, land use change, drowning in farm reservoirs, human disturbance at breeding colonies, harvesting for use in traditional medicine and collisions with power lines (Brown, 1985; Anderson et al., 1999; Benson, 2000; Borello and Borello, 2002; Hengari et al., 2004; Piper, 2004). Climatic change has also been suggested as a possible threat, stressing the more northerly colonies or birds at north-facing colonies (Simmons and Jenkins, 2007).

Indirect poisoning by the laying of baits targeting mammalian predators has been a serious issue since the early 1900s in South Africa and for an unknown duration in Namibia (Mundy et al., 1992). The discovery of poisoned vultures and eagles is a direct and obvious mortality factor in Namibia (Brown, 1991a; Simmons, 1995) but what is less obvious is if this is the sole cause of the decline in the population.

The impact of bush encroachment

Bush encroachment is the conversion of grassland and woodland savannas to dense, *Acacia*-dominated thornveld with minimal grass cover (Barnard, 1998; Muntifering et al., 2006). Factors considered responsible are altered fire regimes and the fencing of stock and overstocking resulting in increased grazing pressure (Ward, 2005). It has accelerated since 1950 in many parts of southern Africa due to altered disturbance regimes (Ward, 2005). Bush encroachment is particularly a problem on communal lands in southern Africa, however in north-central Namibia it is a much bigger concern on commercial farmland (Mendelsohn, 2006). Climate change from increased CO_2 levels may also facilitate the increase of C_3-dominated vegetation types, thereby also favouring woody plant bush encroachment (Midgley et al., 2005).

The impact of bush encroachment on vultures is largely unknown (Smit, 2004) but it may have two effects on foraging Cape Vultures. First, it might reduce the visibility of carcasses in dense bush to the point where a carcass is not seen by vultures or is not accessible. Second, bush encroachment may have an indirect effect by causing a reduction in livestock stocking rates or a change in land use (Smit, 2004) which in turn may affect scavenger bird populations (Dean, 2004). In recent years stocking rates in north-central Namibia have decreased from one large stock unit per 5 hectares to one per 15 hectares (Bester, 1996). It is evident from the movements of satellite-tracked birds that their preferred foraging habitat is commercial farmland, and that they rarely go into the communal areas or even the vast protected area of Etosha National Park (Fig. 1 and Mendelsohn et al., 2005). Studies of vulture sightings in central and northern Botswana have shown that most vulture species peak in abundance at the interface between protected and grazing land, suggesting they exploit the best of both worlds (Herremans and Herremans-Tonnoeyr, 2000). They achieve this by benefiting from the security of breeding and roosting inside conservation areas and then feeding on livestock outside of these areas, similar to what has been observed in Israel with Griffon Vultures *Gyps fulvus* (Bahat, 1995). The Cape Vulture was not observed in the Botswana study, however, as it is likely to be somewhat restricted by the proximity of cliffs for suitable nesting sites, as found in south and eastern Botswana (Borello and Borello, 2002).

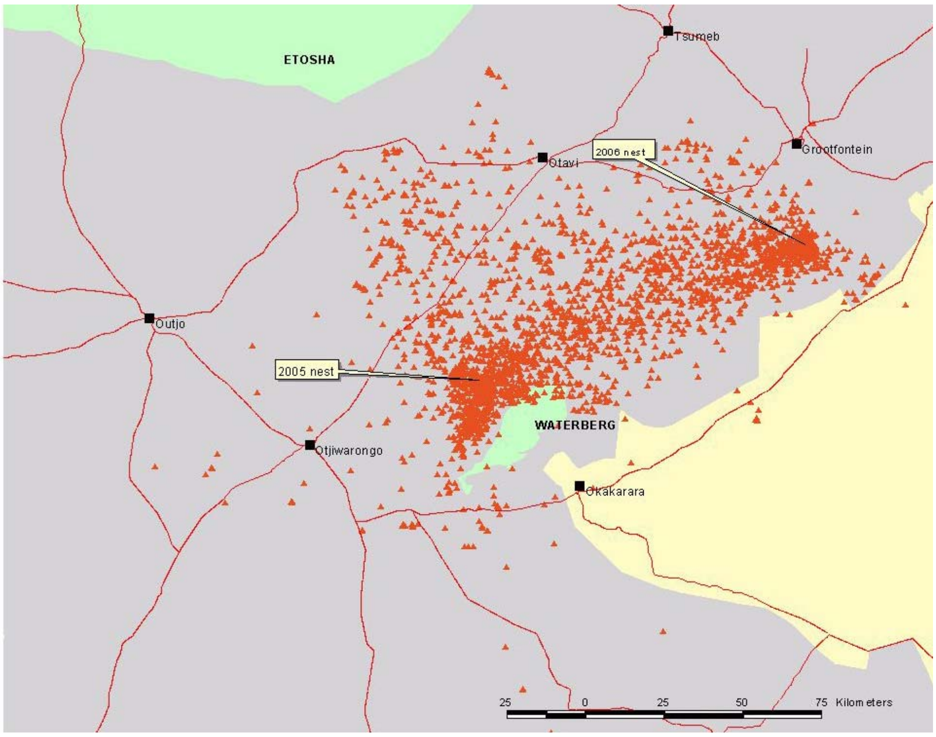

Figure 1. Positions (10786 data points) recorded from an adult male Cape Vulture (CV4) between November 2004 and December 2006 (J. Mendelsohn, unpubl.). Grey areas correspond to commercial farmland, beige areas are communal land and green areas are the protected areas of Etosha National Park and Waterberg Plateau Park.

Bush encroachment is also considered to hamper the hunting success of the cheetah *Acinonyx jubatus* (Muntifering et al., 2006). Because the cheetah is a common carnivore in this district anything that reduces their success may indirectly reduce the number of carcasses available to vultures. However, this is likely to be negligible because it has been suggested that carcasses from predator kills only contribute around 5% of the food intake of vultures of the Serengeti; the vast majority of carcasses are attributed to disease and natural mortality (Houston, 1974a).

Visibility of the carcass plays a significant role in carcass detection because it has been shown that olfaction plays no role in carcass detection in Old World vultures (Houston, 1974b; Mundy et al., 1992). Visibility within 100m of a carcass has been shown to be positively correlated to the probability of vulture presence at carcasses in the Caucasus (Gavashelishvili and McGrady, 2006). Therefore, the high vegetation density in bush encroached areas may negatively affect the ability of vultures to locate carcasses. It has also been suggested that ground level visibility in farmlands surrounding the Waterberg Plateau Park has decreased from around 85% in the 1940s to less than 10% in many places (Brown, 1985). The "patchiness" and unpredictability of carcasses in the landscape means that vultures make use of a "foraging network", in that soaring vultures will not only search the ground for carcasses but will also monitor the movements of other soaring vultures (Mundy et al., 1992). If one bird descends, this causes a ripple effect that indirectly communicates the detection of a carcass; Houston (1974b) suggested that vultures can be drawn in from at least 35km away. Thus if bush encroachment reduces the visibility and hence detection of carcasses it should impact on vulture populations as a whole.

Cape Vultures are cliff-nesters and prefer open habitat such as grassland and open woodland savanna (Brown, 1985). Cape Vultures have a high wing loading (112 N/m^2) which favours fast cross-country soaring (Pennycuick, 1972) and are assumed to be less able to reach carcasses that are visible but within closed woodland habitat. Even if they are able to land their ability to take off with a full crop may be compromised relative to the lighter species (and main competitors the African White-backed Vulture *Gyps africanus*), thereby making carcasses potentially less available to Cape Vultures in encroached habitat. The most common vulture in Namibia by far is the tree-nesting and smaller African White-backed Vulture, with a wing loading of 76 N/m^2 (Pennycuick, 1972; Bridgeford, 2004). This species has probably evolved in more wooded savanna and can most likely tolerate a greater degree of bush encroachment, which could partly explain why the population is not in the same predicament as the Cape Vulture in Namibia (Brown, 1985).

Several conservation measures have already been instigated to mitigate the threats to the Namibian Cape Vulture population. Since 1985 a supplementary feeding scheme by the weekly provision of carcasses at the Waterberg has been undertaken, whilst another "vulture restaurant" run by the Rare and Endangered Species Trust (REST), a local NGO, has regularly supplied offal from the local abattoir since 2002 (Brown and Jones, 1989; Diekmann et al., 2004). The latter restaurant regularly attracts in excess of 500 vultures at a feed, of which a maximum of five adult and two immature Cape Vultures have been observed on any one day (pers. obs). These restaurants have multiple purposes, chiefly to supply a "clean" source of food and hence reduce the vultures to exposure to potentially poisoned carcasses elsewhere and to aid in the reestablishment of vulture colonies (Verdoorn, 1997). Another conservation initiative is the translocation of rescued, rehabilitated and captive bred vultures from South African colonies (M. Diekmann, pers. comm..). Success of these translocation programs is greatly influenced by the quality of habitat that the birds are released into (Cade, 2000).

The main aim of this study is to experimentally determine what effect the high level of bush encroachment around the Waterberg Plateau Park has on the foraging efficiency of Cape and African White-backed Vultures. Because the latter species dominates the vulture populations here I have used the African White-backed Vulture as a proxy for the foraging decisions of the Cape Vulture. Because it has a lighter wing loading it is also a liberal estimate for the decisions that the heavier Cape Vulture might make under different levels of bush below it. I simultaneously assessed the foraging decisions made by three Cape Vultures fitted with satellite transmitters in relation to vegetation density in the seven months prior to my experiments. In this study I have focused on three questions: 1) Is bush encroached habitat suitable foraging habitat for the Cape Vulture? 2) What is the natural foraging behaviour of Cape Vultures, as determined from satellite telemetry analysis? 3) What is the contribution of vulture restaurants to the dietary requirements of the Cape Vulture? My main hypothesis to be tested can be stated as: The time taken to locate carcasses by Cape and African White-backed Vultures will increase significantly with increasing tree density and a threshold will be reached at which carcasses become unavailable.

Methods

Study Area

This study was centred on the Otjiwarongo district (19°30'S to 21°S and 16°E to18°E) and surrounding districts of north-central Namibia (Figure 2). The region lies within the thornveld biome and is dominated by *Acacia* and *Dichrostachys* bush species (Mendelsohn, 2002). The topography is generally flat and elevation is *c* 1500 m above sea level (Mendelsohn, 2002). The region is semi-arid and lies between the 400-450 mm annual rainfall isopleths (Meik et al., 2002) and is characterised by summer rainfall. Commercial cattle and game farming is the predominant land use type in this region (Doughton and Diekmann, 2006). The Waterberg Plateau Park is a state-protected sandstone plateau with a 150 km long escarpment that has historically provided Cape Vultures with suitable cliff sites for nesting (Simmons, 2002).

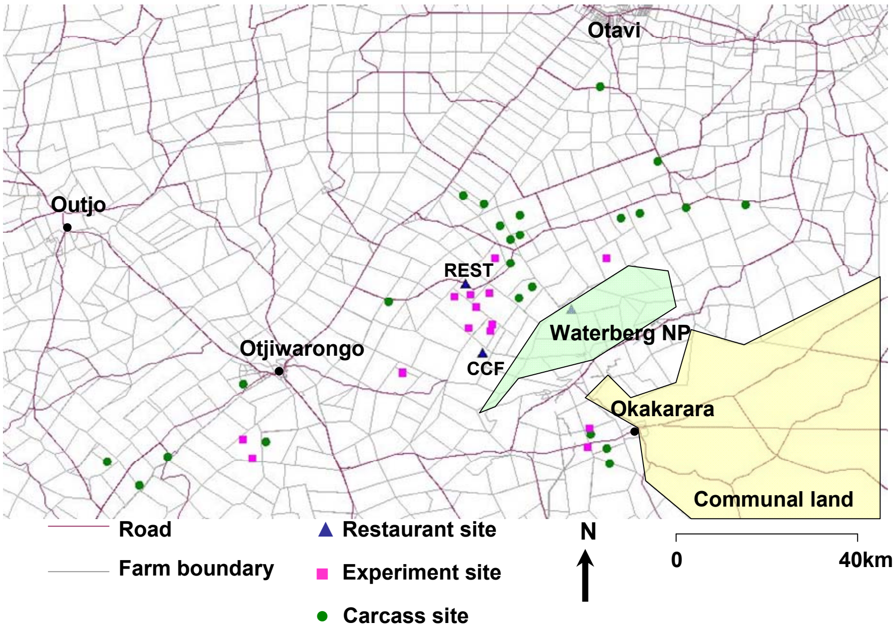

Figure 2. Map of study area encompassing the Otjiwarongo district in north-central Namibia, depicting vulture restaurants, naturally occurring carcasses and experiment sites. White areas with grey borders are commercial farms, the green area corresponds to the Waterberg Plateau Park and the beige area is communal land.

Carcass placement in habitats of differing tree density: experimental protocol

A series of experiments were performed to determine the impact of bush encroachment on the Cape Vulture's ability to locate carcasses. Animal carcasses of different species (goat, donkey and eland) or offal from the local abattoir were placed in varying levels of tree density. Vultures have been fed with offal at the REST vulture restaurant since 2002, thus have become accustomed to eating this food type. To avoid vultures associating my vehicle with food provision, offal was either placed out the night before or at sunrise on the morning of the experiment, and weighed approximately 400–500 kg. Birds were then observed from just after sunrise with 10x42 binoculars at hides that varied from 35–160 m away from the food (median

75m). Species of vultures present were observed and their abundance counted. Tree density was determined by counting the number of trees in four different height categories (<1 m, 1–2 m, 2–4 m and >4 m) in a circular plot of 6 m radius centred on the carcass (Muntifering et al., 2006). Experiments were truncated and frequently paired: if birds had not found the food within 24 (four times), 48 (twice) or 96 hours (once) in dense habitat the food was moved to an open patch nearby and the same protocol followed.

Statistical analysis was performed using an extension to the Mayfield method that allows explanatory variables to be modelled in this context (Underhill, submitted). In this approach, the time taken to find a carcass was modelled as an exponential distribution; a logarithmic link function was used to incorporate the explanatory variables into the parameter of the exponential distribution. The RSURVIVAL procedure within the Genstat 8.1 software program (Genstat Committee, 2005) was used to construct the models and to test explanatory variables for significance. Within this procedure it is possible to handle truncated experiments in which the carcass had not been located by the time of termination of the observations. The RUNSTEST procedure in Genstat 8.1 was used to perform the Wald-Wolfowitz runs test (Conover, 1971) to test for randomness of the effect of explanatory variables on the detection of carcasses by vultures. Factorial ANOVA, Wilcoxon matched pairs tests and Spearman rank order correlations were run in Statistica version 7 (StatSoft Inc., 2004).

Foraging site analysis

Six Cape Vultures have been fitted with PTT (platform transmitter terminal) satellite transponders since 2004, enabling studies of their movement patterns (Diekmann et al., 2004). Observations have been made of their foraging ranges, flight speed, foraging height and times and roosting sites (Mendelsohn et al., 2005). One of these birds was an immature bird fitted in February 2005 which had ranged widely through six countries, thereby making it unsuitable for the current analysis. Another two birds (an immature and adult) were translocated and released in October 2005 and August 2006 respectively and also excluded from the analysis for two reasons: they were based near the REST restaurant, hence did not forage regularly over the surrounding country and their co-ordinates were only downloaded every two hours. The three remaining birds (subsequently known as CV3, CV4 and CV5) were all adult males;

two were captured and fitted in November 2004 and the other in January 2005 (Diekmann et al., 2004). GPS co-ordinates (accurate to 10–15 m), height, speed and bearing were downloaded hourly between 0400 and 1900 h and stored on the ARGOS system (Mendelsohn et al., 2005).

Potential foraging sites were determined by analysing the hourly positions given by the satellite data for points where the birds were stationary (speed 0–5 km/hr) but not at their preferred roosting sites. The GPS points and the surrounding area within a 100m radius were then examined in the field for evidence of a carcass. The carcass species, age and sex (if possible), land use type (e.g. cattle or game farm), tree density and presence of vulture feathers were recorded. Tree density was determined as described in the experimental protocol. The minimum distance a Cape Vulture travelled from the previous night's roost site before reaching a carcass was determined by measuring the direct distance between hourly co-ordinates in Arcview v.3.3 GIS (geographic information system) software package (ESRI Inc., Redlands, CA, USA). Minimum convex polygons (MCP) to estimate home ranges were calculated using the Animal Movement extension (Hooge et al., 1999).

The satellite data from the three Cape Vultures was also analysed to determine the possible contribution of supplementary feeding to this Cape Vulture population by recording the number of visits to the three main restaurants in the study area: REST, Cheetah Conservation Foundation (CCF) and the Waterberg Park restaurants.

Results

Carcass experiments

Of the 21 experiments two were excluded due to a REST restaurant feed on the same day biasing the results. Of the remaining 19 experiments vultures did not locate the food during the observation time allotted on seven occasions. As an example, the Eland *Tragelaphus oryx* carcass in dense bush (3300 trees/ha) that had not been found within four days was then moved to a completely open area and subsequently located by vultures within two hours. On only one occasion did vultures locate food after the first 24 hours of an experiment.

There were significantly shorter location times for carcasses placed in low tree density than in high tree density (t = 5.17 P< 0.001). As tree density increased, the likelihood of detection decreased, to the point where food was never found by vultures in tree density greater than 2600 trees/ha (Figure 3). Distance from the REST vulture restaurant (Figure 4) and the number of days since the last REST feed (Figure 5) were not found to influence whether food was located by vultures. (Distance: t = 1.42 P = 0.17, Last feed: t = 0.4 P = 0.69). Wald-Wolfowitz runs tests were performed to determine whether the explanatory variables influenced the detection of carcasses by vultures; only tree density was found to have a non-random effect (Tree density: runs= 6 P<0.05; Distance from REST: runs= 9 P = 0.55; Last feed: runs= 8 P = 0.25).

When food was located, the average time taken to locate it was 4.9 h (SD 7.2 range 0.67 to 25 h). Tree height has not been taken into account but is also likely to have influenced visibility; when the same analysis was performed with a weighting factor for taller trees it marginally improved the statistical significance. As most experiments were paired (i.e. two within the same general location) and African White-backed Vulture breeding colonies were scattered throughout the study area the distance from the nearest colony was not controlled for.

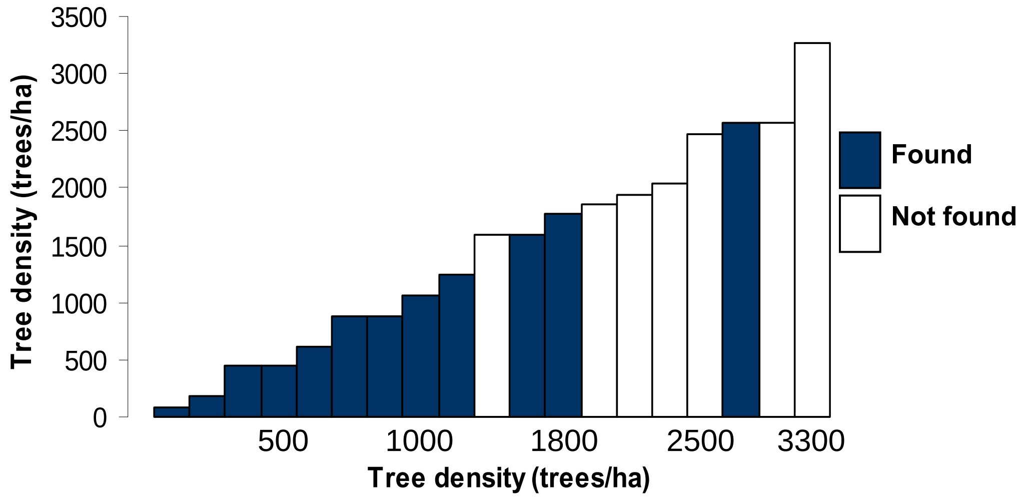

Figure 3. Tree densities of successful (solid bars) and unsuccessful (open bars) experiments in which vultures located carcasses in the Otjiwarongo district of Namibia. The experiments are ordered by increasing tree density. No. of runs present is 6; therefore reject the null hypothesis that tree density does not affect whether the carcass is located by vultures or not.

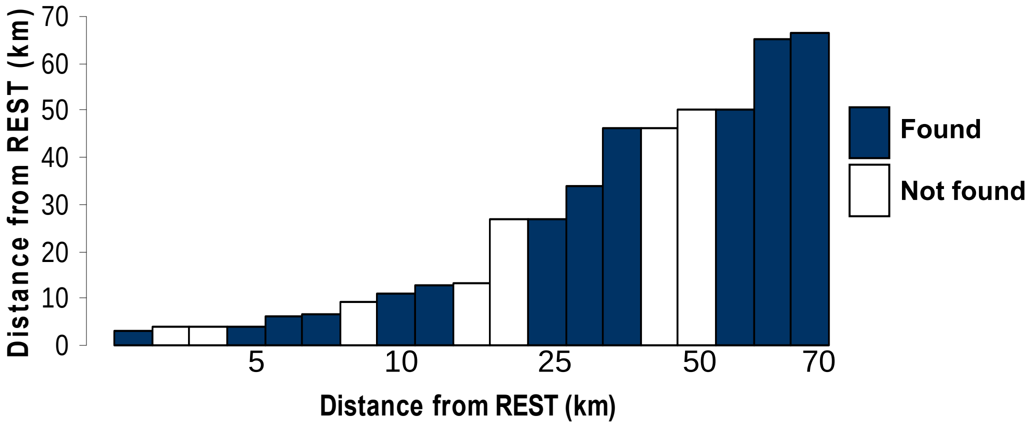

Figure 4. Distance from REST of successful (solid bars) and unsuccessful (open bars) experiments in which vultures located carcasses in the Otjiwarongo district of Namibia. The experiments are ordered by increasing distance from REST. 9 runs; accept the null hypothesis that whether the carcass is found or not is independent of the distance from REST.

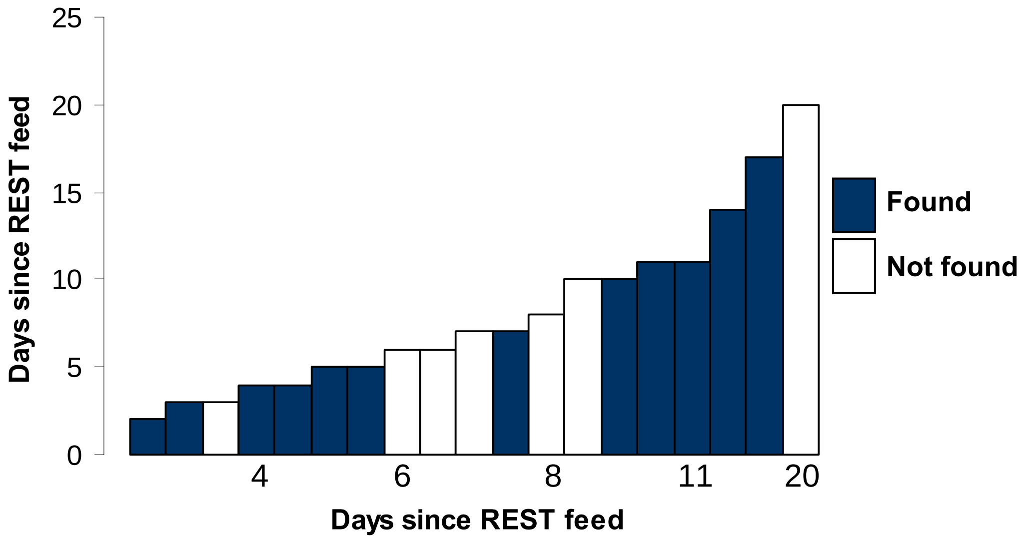

Figure 5. The number of days since the last REST feed for successful (solid bars) and unsuccessful (open bars) experiments in which vultures located carcasses in the Otjiwarongo district of Namibia. The experiments are ordered by increasing number of days since the last REST feed. 8 runs; accept the null hypothesis that whether the carcass is found or not is independent of the days since the last REST feed.

Cape Vultures were only present at five of the experiments (mean number of Cape Vultures 0.82 ± 1.08) making any interpretations about their ability to land and take off in areas of dense bush difficult. Tree density was not a significant factor in determining the presence or absence of Cape Vultures at located experiments (runs= 7 P = 0.65).

Of the 14 experiments in which food was located by scavengers, vultures (usually African White-backed Vultures but in one case a Lappet-faced Vulture *Torgos tracheliotus*) were the first to find it in 50% and the first to eat in 36.8% of these experiments. *Milvus* kites were the next most successful in locating food first (four times, 29%), black-backed jackals *Canis mesomelas* twice (14%) and a tawny eagle *Aquila rapax* once (7%). On two occasions *Milvus* kites directly preceded the appearance of vultures. The five number summary (minimum, lower quartile, median, upper quartile, maximum) for the numbers of vultures at experiments where the food was located was 98, 313, 340, 361, 368, indicating that in 50% of experiments the number of vultures present ranged between 313 and 361. African White-backed Vulture totals at these experiments were significantly greater than numbers at the Waterberg feeding station during the 1980s (Wilcoxon Matched Pairs Test $Z = 2.93$, $P < 0.005$). There was no significant correlation between tree density and total numbers of vultures of all species at located carcasses (Spearman's $R = 0.45$ $P = 0.16$).

Foraging site analysis

A total of 24 carcasses were located by retrospective analysis of the PTT satellite data: nine from CV3 data, five from CV4 and 10 from CV5. Carcasses up to seven months old were detected (median four months) and were generally found in the veld; even if a farmer knew of the carcass it had not been removed. Table 1 provides a summary of the foraging site characteristics of the located carcasses. The majority of carcasses (83%) were located in either completely open habitat (such as a waterhole or at a farmer's vulture feeding station) or low tree density (<1000 trees/ha), with two (8.3%) found in dense bush (>2000 trees/ha). Average tree density at all carcasses was 788 trees/ha while the highest tree density a carcass was located in was 2650 trees/ha, comparable to the findings of the experimental component. Fences appeared to contribute to ungulate mortality because three of the carcasses were animals which had had their hooves caught in fence wire. Fencelines make up only about 1.3% of the area on a commercial farm (assuming a 5m cleared area on each side), however in this study they contributed 25% of the located carcasses, a significant overrepresentation ($\chi^2 = 4.58$, df= 1, $P < 0.05$).

The majority of carcasses (79%) were of game animals of which Greater Kudu *Tragelaphus strepsiceros* were the most common prey item (54.2% of all carcasses). whilst two were unable to be identified (either a kudu or Eland visible from the air and either a kudu or cow from remnant bones); a summary of carcass characteristics is presented in Table 1. This use of wild game animals differs significantly ($\chi^2 = 74.38$ df = 1 P <0.01) from the pellet analysis conducted in the Potberg Cape Vulture colony in South Africa which found the majority of carcasses (96.1%) utilised were of domestic livestock (Robertson and Boshoff, 1986). All Namibian carcasses were located on land used for commercial enterprise.

Table 1. Summary of carcass species, habitat type and type of land use enterprise that carcasses were located in as determined from the satellite data analysis of potential foraging sites.

Species	No of carcasses	%	**Habitat**	No of carcasses	%	**Enterprise**	No of carcasses	%
Kudu	13	54.2	Fencelines	6	25.0	Mixed	9	37.5
Cattle	4	16.7	Open	6	25.0	Cattle only	7	29.2
Eland	2	8.3	Low bush density	10	41.7	Game only	6	25.0
Oryx	2	8.3	High bush density	2	8.3	Empty	2	8.3
Horse	1	4.2						
Unknown	2	8.3						
Total	24	100		24	100		24	100

Distances flown by birds from the previous night's roost position on known days where they located a carcass averaged a minimum 68.8 ± 29.9 km (range 22.4 to 185.7 km) assuming direct flight (Table 2). Due to their varied nesting and favoured roosting positions and different home range sizes, the mean distance travelled per bird differed significantly (Factorial ANOVA: $F_{2,21} = 4.02$ P <0.05). Time spent foraging was determined by dividing the hourly positions indicating flight by the total number of positions downloaded per bird.

Table 2.Summary of flight characteristics of three Cape Vultures determined from PTT satellite data analysis over the period November 2004 to December 2006.

	Bird				
	CV3	**CV4**	**CV5**	Mean	SD
MCP* (km^2)	11532	26004	22105	19880	7488
Mean distance to carcass (km)	45.7	102.6	58.2	68.8	29.9
Distance from 2006 nest to REST (km)	38.7**	120.2	23.9	60.9	51.9
Mean flight speed (km/hr)	55.1	60.4	62.3	59.2	3.7
No of daily hours spent foraging	4.0	2.3	2.4	2.9	1.0

* Minimum Convex Polygon estimate of foraging range
** average figure from three roosting sites because this bird did not breed in 2006.

There is a slight bias present as positions downloaded per bird varied; CV3 and CV5 had 11% and 7% respectively more flying points than stationary points downloaded thereby slightly inflating the number of hours spent foraging daily, whereas CV4 had a consistent number of points. It is likely that the lower number of daily foraging hours recorded by CV4 and CV5 were due to these birds spending more time on nesting duties such as incubation and brooding.

Impact of supplementary feeding

An analysis was performed on all satellite data available from the three adult Cape Vultures to determine the possible contribution of supplementary feeding to their overall diet. Out of a possible 2199 analysis days the three vultures visited the REST restaurant a total of 119 times, of which 62 (52%) were confirmed as feeding visits, with other restaurant visits listed in Table 3.

Table 3. Total numbers of visits to REST, Cheetah Conservation Fund (CCF) and the Waterberg restaurants by satellite-tagged Cape Vultures during the study period, and their likely contribution to Cape Vulture dietary requirements.

	Restaurant visits						
Bird	**REST**	**CCF**	**Waterberg**	Total	Total days of analysis	Expected no. of foraging days	%contribution to diet
CV3	41	13	31	85	749	250	34.0
CV4	31	15	12	58	749	250	23.2
CV5	47	7	18	72	701	234	30.8
Total	119	35	61	215	2199	733	29.4

It was not possible to verify all restaurant visits as corresponding to days when food was put out as restaurant records were not always kept. Cape Vultures have been found to require food approximately every third day (or about 500 g of meat per day) during the non-breeding season (Komen, 1992a), necessitating about 122 foraging trips annually if birds feed to repletion at each feed. If the total number of visits to restaurants is divided by the expected number of foraging trips during the study period, these visits represent an average contribution of 29% of their dietary requirements being met by these restaurants (Table 3). Breeding season requirements necessitate around 50% more foraging trips per parent vulture, reducing the possible contribution of supplementary feeding to around 20% (Komen and Brown, 1993).

Discussion

Impact of tree density on foraging success

My main experimental results showed that birds took longer to find carcasses placed in dense bush and those in the densest bush were sometimes never found. This was corroborated by retrospective analysis of foraging sites from the satellite data, in which the maximum tree density any scavenged carcass was recorded in was 2650 trees/ha. Because tree density frequently exceeds this, it would appear that bush encroachment hampers the foraging success of vultures in the Waterberg area as suggested by Brown (1985). This is primarily by reducing the visibility of carcasses to soaring scavengers. However, vultures can make use of low-flying scavengers such as the Bateleur *Terathopius ecaudatus* and *Milvus* kites and diurnal mammalian scavengers such as the jackal, in the indirect detection of carcasses (Mundy et al., 1992). Griffon Vultures have been found to be highly dependent on crows to assist in the location of carcasses in extensive grazing systems in Spain (Camina, 2004). Following other scavengers may help circumvent the problem of high vegetation density, as long as these scavengers' own visibility is not also compromised and the Cape Vulture's predation risk is not increased in areas where they may have difficulty extracting themselves once they have eaten. Anecdotally, Namibian farmers say that vultures frequently do not find carcasses in thick bush; unfortunately the proportion of carcasses not found by vultures in the veld could not be quantified.

Due to the paucity of Cape Vultures and the sites selected for these experiments I was unable to directly gauge the possible impact of vegetation density on the ability of Cape Vultures to reach a carcass and to successfully take off with a full crop. To test the ability of Cape Vultures to take off in dense bush was hampered by the fact most suitable hides for these experiments were located around waterholes, thereby providing a clear area for the birds to take off and land, even if the food itself was in a patch of dense bush. However, from the satellite telemetry foraging analysis the location of a Brahman bull carcass in heavily bush encroached habitat (2650 trees/ha) showed that a Cape Vulture had reached the carcass and managed to take off again despite the nearest clearing being only around 10m long. In fact the bird came back to within 1.2 km of the carcass the following day and then revisited the carcass four days later, the only time any of the Cape Vultures showed such revisiting behaviour during this analysis. This is unlikely behaviour if the bird had not been successful at feeding. However, one cannot assume that the bird fed or even that it took off with a full crop because vultures are known to regurgitate their meal if it impedes their ability to take off or they are under threat (Mundy et al., 1992). It is also unknown how far a bird will walk from a carcass in dense bush to find a suitable clearing for take-off. It is also possible that they may fly up into a tree and then be able to take off from there with the aid of a strong wind. Another unknown factor that needs to be considered is the effect of leaf cover and the seasonal variation of this. It is likely that during the dry season visibility of carcasses is facilitated by minimal leaf cover and ground cover because carcasses would stand out more against the bare ground.

Prey type and potential contributors to mortality

From the carcass data derived from the foraging site analysis vultures of the Waterberg rely more on game than domestic livestock for food, in contrast with the global tendency of vulture populations to become increasingly reliant on domestic livestock as a major food source (Robertson and Boshoff, 1986; Mundy et al., 1992; Shobrak, 1999; Yosef and Bahat, 2000; Camina, 2004). In the comparison of prey species of the Waterberg Cape Vulture colony to the Western Cape colony it is likely that higher numbers of game in north-central Namibia compared to the Western Cape Province of South Africa are responsible for this discrepancy rather than different food preferences between the two colonies.

The disproportionate numbers of kudu carcasses may be as a result of a recent outbreak of rabies in Namibia to which the Greater Kudu appear particularly susceptible (Swanepoel et al., 1993). A previous outbreak in the early 1980s caused the deaths of 30-50 000 kudu in Namibia over a five year period; a major contributing factor was thought to be the abnormally high kudu population densities (Marker et al., 1996). Kudu are considered the most common free-ranging large ungulate in this region of Namibia (Marker et al., 1996). Conversely, high numbers of kudu as prey species could indicate that bush encroachment has benefited browsing species and hence has increased prey density.

Fence lines appeared to contribute to foraging success in two ways: first by contributing to ungulate mortality and second, by being mostly cleared of vegetation and thus providing excellent visibility. Thus while vulture foraging efficiency may have decreased with increasing bush encroachment, fence lines appear to inadvertently play a role in enhancing foraging return.

Satellite data analysis

Carcasses were located on average 37 m (SD 35 range 0–100 m) from the GPS co-ordinate provided by the satellite position. Because Cape Vultures are dominant over the more numerous African White-backed Vultures at carcasses (Brown and Jones, 1989), can take as little as five minutes to fill their crop (Mundy et al., 1992) and will usually move away from the carcass thereafter (pers. obs), the carcass was not always found at the point where the vulture had been recorded. In three situations a carcass was not found within a 100 m radius of the GPS co-ordinate, twice the points were unreachable due to dense bush and in another three locations only waterholes were found. Therefore carcasses were found in 80% of the examined sites. A potential bias is that carcasses in dense bush were more difficult to access and locate, hence may be slightly underrepresented in the analysis.

It is possible for birds to feed at a carcass and move off within an hour and hence this point will not be identified from hourly satellite data as a potential foraging site. Some evidence comes from a comparison of known ring-identified Cape Vulture REST restaurant visits and the corresponding satellite data. Missing data points may also confound the analysis, as only 74% of a total 17585 potential flying points (mainly between 8am and 4pm) were downloaded from the satellite transmitters. The data quality from each bird varied substantially as the number of data points downloaded ranged from 52% (CV3) to 87% (CV4) of the possible totals. This means that hourly PTT data alone cannot be used for a comprehensive study of potential foraging sites.

Foraging ranges of Cape Vultures

The average home ranges of the three adult Cape Vultures corresponded to a foraging radius of approximately 80 km from their nest or roost site. However, CV4 has an elliptical home range with this bird moving over 200 km along its long axis in a south-westerly direction but only 20 km in the opposite direction in the 16 months since it has been nesting at its present site. This suggests that this bird has a definite preferred foraging area or that there is possibly an environmental factor such as the prevailing wind direction in effect. The majority (over 90%) of its foraging trips were in the direction of the three restaurants, suggesting that supplementary feeding serves as a focus of attraction for this Cape Vulture, or that these restaurants just happen to be situated in a productive foraging area for this vulture. The other two birds CV3 and CV5 nested or roosted within 40 km of the main restaurant REST, therefore this pattern is not as apparent. Rüppell's Vultures *Gyps rueppelli* in the Serengeti regularly fly up to 150 km from the nest site to concentrations of food which are mainly herds of migratory ungulates (Houston, 1974b). A distance of 110 km has been suggested as an average foraging radius for the same species (Pennycuick, 1972), which is 38% further than the 80 km findings of this study.

A radio-tracking study combined with farmer surveys conducted in the Western Cape suggested a foraging range for the Cape Vulture of 1940 km^2 (Robertson and Boshoff 1986) and from resighting data in the Drakensberg an estimated range of 9200 km^2 (Brown and Piper, 1988). However, it is difficult to draw any conclusions about the possible quality of the foraging habitats of each colony due to the different methods used to gather this data. Estimates of food availability in other South African Cape Vulture colonies have used a 100 km radius to calculate potential foraging areas and food availability (Komen, 1992b). This is equivalent to a foraging area of 31 400 km^2, slightly larger than those observed in this study.

The average number of hours spent foraging per day (2.9 h) in this study was similar to the 3.7 h calculated by Robertson and Boshoff (1986) for the Potberg colony in the Western Cape. Brown (1988) found that Cape Vultures on the Drakensberg escarpment were away from the colony for about 7 hours per day, however it is unknown how much of that time was spent actively foraging; it is possible that birds may have been roosting elsewhere for a portion of that time.

Potential food availability for vultures of the Waterberg

Many South African Cape Vulture colonies are thought to be limited by food availability, particularly due to land cover and land use change, decreased stocking rates and improved livestock husbandry (Vernon, 1999; Benson, 2000). A survey of ungulate mortality rates in the 1980s revealed that there was approximately 530 000 kg of carrion (livestock and game) left in the veld annually for vultures in an area of 20 000 km^2 (C.J. Brown, unpubl. data), which corresponds to the average home range of the adult Cape Vultures in this analysis. This figure takes into account what farmers might remove for consumption or bury (about 25%) and the edible amount available on a carcass to *Gyps* vultures (about 65%) (Mundy et al., 1983). African White-backed Vultures are thought to require around 400 g of meat per day (Houston 1976; Mundy et al., 1992) and if it is estimated that each breeding pair of African White-backed Vultures has slightly lower requirements than Cape Vultures of 1.1 kg of meat per day and there are approximately 1000 breeding pairs (assuming 25% immature proportion among the local population of 2730 – see appendix 1) then the population as a whole requires around 510 000 kg per year, which would be satisfied if about 95% of the carrion is available.

What is not known, however, is the percentage of carcasses that are *not* available due to bush encroachment. It is unlikely that vultures find all possible carcasses (Robertson and Boshoff, 1986; Vogeley, 1998). Richardson (1980) estimated that 70% of accessible carcasses in the extensive livestock farming areas of the Transvaal were located by Cape Vultures. As there is no fine-scale map of vegetation density of the study area available it is necessary to approximate areas of bush encroachment. It is estimated from surveys conducted by Marker et al. (1996) that around 39% of the habitat of central and north-central Namibia is grassland or sparse bush, 38% medium bush and 23% thick bush. If it is estimated that vultures find 80% of carcasses in open habitat, 50% in medium bush and only 10% in thick bush then this leaves only 53% of the habitat available to vultures, assuming carcasses are distributed evenly throughout the habitat types. This estimate does not take into account carcasses that vultures may find through indirect means such as other scavengers. If the habitat categories used by Marker et al. (1996) had quantified tree densities a better estimate of the proportion of available carcasses could be made from the carcass experiments performed in this study. Given these figures, only 280 000 kg of carrion would be available, or 55% of the vulture population's requirements would be met. It is more likely that this population of vultures forages over a larger area, for example 40 000 km^2; this area would then supply adequate carrion. This analysis also ignores the seasonal availability of carcasses as there is usually a bottleneck period of rapid nestling growth when more food is necessary (Robertson and Boshoff, 1986). Interpretation of this figure should also be exercised with caution as it compares prey numbers of the 1980s to estimated vulture numbers of 2006.

A further limitation of this approach is the likely underestimation of game numbers and mortality. Wildlife as an economic asset is increasing in importance in Namibia, as evidenced by the conversion of many commercial cattle-only farms into mixed enterprises that take advantage of wildlife-based tourism (Richardson, 1998). This has led to an apparent increase of 80% in animal numbers and biomass on commercial land between 1972 and 1992 (Barnes and de Jager, 1996). As a consequence, approximately 80% of Namibia's free-ranging ungulates are found on these commercial farms (Yaron et al., 1994), making it unsurprising that all carcasses fed on by Cape Vultures in this study were located on commercial farmland. However, a potential bias is that no carcasses were sought by me on communal or protected land, owing to the difficulty of access and the paucity of potential foraging sites as determined by the satellite data analysis.

A worsening of bush encroachment is likely to lead to a further reduction in cattle stocking rates, although what is difficult to know is if there is a corresponding reduction in wild game densities, which are probably more important to Cape Vultures in this population (Table 1). In a comparison of wildlife populations of an abandoned ranch to a neighbouring wildlife reserve in Tanzania there was a ten times higher biomass of wild browsers and grazers present in the wildlife reserve compared to the heavily bush-encroached former cattle grazing areas, despite there being three years of opportunity for immigration (Treydte et al., 2005).

Impact of supplementary feeding

Vulture restaurants around the Waterberg have been shown to contribute up to 29% of the non-breeding dietary requirements of Cape Vultures, similar to the estimate of Brown and Jones (1989) of 40% if the birds were to feed at the Waterberg restaurant weekly. These figures are based on the assumption that these Cape Vultures were successful at filling their crops at these sites. This assumption is based on the observations at the REST and Waterberg vulture restaurants where adult Cape Vultures were seen to leave with full crops 86% and 88% of the time respectively (Brown and Jones, 1989; REST, unpubl. data). On the remaining occasions Cape Vultures left with crops two-thirds full. The Waterberg data includes immature birds which may bring down this average as they may arrive at a carcass later and are not always as successful at competing with the more numerous African White-backed Vultures (Richardson, 1984; Mundy et al., 1992). In Botswana Cape Vultures were always found to leave carcasses with a full crop even though they constituted less than 8% of the vultures present at a carcass (Vogeley, 1998).

This contribution does not include possible visits to local farmer's vulture feeding stations, where dead livestock and the remnants of carcasses from hunting activities are provided. These feeding stations are relatively common on commercial farms in this region of Namibia primarily due to the farmer education and vulture awareness campaigns run by REST. However, the actual amount of consumable material would not be considered substantial and is irregularly provided.

It is unclear as to how much supplementary feeding and other conservation initiatives may have contributed to the status of the African White-backed Vulture population in the Waterberg area. If it is purely judged on the amount of food provided, (around 60 tonnes) this would correspond to around 10% of the population's requirements. However, the restaurants may benefit the colony in other ways. Vulture restaurants have been shown to make significant a contribution to the foraging and breeding success of several vulture species and colonies (Terrasse, 1985; Piper et al., 1999; Vlachos et al., 1999; Grubac, 2005). Their operation has also been shown to decrease home ranges of Indian White-backed Vultures, thereby decreasing the colonies exposure to poisons which has led to a decreased mortality rate due to diclofenac toxicity (Gilbert et al., in press). At least one Cape Vulture preferentially forages in the direction of REST; if it is presumed that farmer education has resulted in less poison put out in farms at a closer radius to REST then those further away, then a similar effect may be being seen in Namibia. Without comparing foraging ranges between periods when the restaurants are operational and when they are not, this can only be surmised.

Population trends of *Gyps* species in north-central Namibia

African White-backed Vultures were on average five times more numerous at these experimental feeds compared to the Waterberg vulture restaurant throughout the 1980s. This suggests an increased population of this species, but it may also arise from an aversion of these vultures to the habitat on the Waterberg plateau, greater human or predator disturbance at this restaurant or that there was simply more food available (about double the weight was available at the experimental feeds compared to Waterberg carcasses). The number of birds that arrive at a carcass is considered dependent on the number of birds that happen to be in a "foraging network" on any particular day and the size of the carcass (Houston, 1974b; Richardson, 1984; Mundy et al., 1992). There is no consensus on the status of African White-backed Vultures in Namibia: it has been suggested that their numbers are stable (Simmons and Bridgeford, 1997; Anderson, 2004), possibly increasing (Simmons and Brown, 2007) or possibly in decline (Doughton and Diekmann, 2006). From REST restaurant attendance data of vultures fitted with patagial tags, capture-mark-resighting analysis revealed an estimated local population of 2730 African White-backed Vultures in the Waterberg area alone (see Appendix 1).

What remains unclear is why the Namibian population of the Cape Vulture has declined so dramatically compared to the African White-backed Vulture population because the latter are considered just as susceptible to poison, if not more so (Mundy et al., 1992). It may be due to a higher initial population of African White-backed Vultures that have better withstood the anthropogenic threats or that the area is indeed acting as a sink for this species as well. The Cape Vulture colony at the Waterberg is the most northerly recorded breeding site for the species and hence on the edge of this species range, the nearest breeding colony being around 1000 km away in Botswana (Brown, 1985). Being a small and localised population with a slow breeding rate it has suffered population declines and range contractions similar to the Bearded Vulture *Gypaetus barbatus* in southern Africa (Brown, 1991b). Cape Vulture colonies are also known to be abandoned if the number of breeding pairs decreases below a certain threshold, a consequence of the Allee effect (Mundy et al. 1992). The translocation and release of twelve Cape Vultures in 2005 from South Africa and two in 2006 has also suffered from this, as only four of the birds (29%) have been frequently resighted around the Waterberg since. Two of these birds were captive-reared and released as sub-adults and are still reliant on the REST restaurant to varying degrees. It is possible that as there is no active colony on the Waterberg cliffs at present (only one bird confirmed roosting) the area does not exert any significant attraction to adult or immature Cape Vultures (Simmons, 2002). Conspecific attraction particularly on cliffs with good breeding success has been shown to be effective in attracting Griffon Vultures in France (Terrasse et al., 2004). Thus immigration does not seem to have helped redress the population decline, despite two adult South African-marked Cape Vultures being sighted near the Waterberg (M. Diekmann, pers. comm.).

The possibility of hybridisation as a mechanism decreasing Cape Vulture populations

An unusual observation that has arisen from the satellite data is that several Cape Vultures have been found to nest and roost in trees (Mendelsohn et al., 2005). This nesting behaviour is considered highly atypical for a cliff-dwelling species (Mundy et al., 1992), although it has also been documented in Rüppell's Vulture in West Africa (Rondeau et al., 2006). This has led to speculation of hybridisation occurring between at least one and up to three adult male Cape Vultures and female African White-backed Vultures; a novel threat that appears unique to this colony (M. Diekmann, pers. comm.). A sex bias among the adults in this tiny population is the most likely cause and would also contribute to the stagnation of the colonies population growth because any successful reproduction would not contribute to the population and effective breeding gene pool.

It is likely that a combination of these factors combined with ongoing exposure to poisons have influenced why the Cape Vulture population has not recovered despite conservation efforts.

Conclusions and Recommendations

It would appear that increased tree density reduces foraging success of African White-backed and Cape Vultures at the fine scale. At present the vultures of the Waterberg appear to be gaining their daily requirements through a combination of the high density of game in the region, mortalities along fence lines and the REST, CCF and Waterberg feeding stations. It would appear to require a much larger and more homogenous increase of tree density to significantly reduce the amount of carcasses available to the vultures of the Waterberg, due to the high prey densities of this region. An attempt at interpolation from known tree densities from experimental and located carcass GPS points to create a map of tree density of the study area was ineffective due to a small sample size, spatial unevenness and a bias towards lower tree densities at these points. Further research is necessary to accurately quantify vegetation densities by developing a finer scale map of vegetation density of this region than is currently available. The next step to accurately assess carcass availability to the Cape Vulture is to extrapolate from tree densities that permit successful and unsuccessful foraging which have been determined from this study, thus creating a habitat suitability map for the Cape Vulture of the Waterberg once vegetation densities have been quantified. A greater sample size of Cape Vultures fitted with satellite telemetry would also permit the generation of habitat selection models (Carrete and Donazar, 2005).

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Appendix 1. Capture-mark-resighting analysis of African White-backed Vulture population of the Waterberg.

$$\text{Est. Pop.} = \frac{\text{(mean total WbV count)*(original number tagged=58)}}{\text{(mean tag count)}}$$

Date	13/10/06	21/10/06	1/11/06	3/11/06	4/11/06	18/11/06	Mean	Est Pop
Tag count	19	18	6	24	19	8	15.67	2730
Total WbV count	522	819	352	864	1323	544	737.3	