Factors affecting diet, habitat selection and breeding success of the African Crowned Eagle *Stephanoaetus coronatus* in a fragmented landscape

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This study aimed to identify variables that affect habitat selection and nesting success of the African Crowned Eagle *Stephanoaetus coronatus*, the largest forest raptor, in north-eastern South Africa. A preference for nesting in the Northern Mistbelt Forest vegetation type was established and 82% of all nests were located in indigenous trees. Nest abandonment was less common when distances to the nearest neighbour were greater. The diet of this species was investigated by examination of prey remains beneath nests and verified by comparison with museum specimens. In total, 156 remains were found, representing a minimum of 75 prey individuals. The diet of African Crowned Eagles constituted almost entirely mammals (99%), which were predominantly antelopes (61%) and monkeys (25%). It was also found that the proportion of primates in the diet correlates with latitude: populations in equatorial latitudes have a higher proportion of primates in their diets, whereas further south antelopes are a much more common diet component.

Introduction

Large avian and mammalian carnivores are thought to be more vulnerable to local extinction in fragmented habitats due to their low numbers, relatively large ranges and direct anthropogenic persecution (Noss et al. 1996; Thiollay 2006). Larger body-sized species demand larger home ranges (Cardillo et al. 2005), which brings individuals belonging to larger species living in fragmented habitats into greater contact with humans. Human-induced population declines may be as a result of direct mortality of adults or as a reduction in breeding success. Breeding success can potentially be influenced by many factors, such as prey availability, population density, habitat quality and meteorological conditions, and additionally by many anthropogenic factors, such as habitat destruction and afforestation with exotic timber (Allan et al. 1997). Exotic timber plantations cover an increasingly large area of South Africa where their effects on nesting bird species are largely unknown (Allan et al. 1997; Malan and Robinson 2001). The use of exotic tree species in forestry plantations may enhance breeding success for tree-nesting raptors, by providing suitable trees for nesting (Malan and Robinson 2001), but may also reduce success via a reduction in biodiversity, i.e. food availability (Johns 1993). The effect of afforestation on the breeding success of the African Crowned Eagle *Stephanoaetus coronatus* is currently unknown.

The African Crowned Eagle is the largest eagle throughout most of its range in sub-Saharan Africa. It has declined in parts of Southern Africa where it is listed as Near Threatened (Barnes 2000) or Vulnerable (Swaziland; Monadjem et al 2003; Monadjem and Rasmussen 2008). However, this species is likely facing persecution over much of its range (Thomsett 2011). For example, it is specifically targeted by hunters in the Ebo forest, Cameroon (Whytock and Morgan 2010a, 2010b) and appears in fetish markets in West Africa (Nikolaus 2001).

The diet of the African Crowned Eagle has been shown to consist primarily of medium-sized mammals, particularly primates, smaller antelope and rock hyraxes, with a range of birds and reptiles preyed upon much less frequently (Brown 1976; Daneel 1979; Jarvis et al. 1980; Tarboton and Allan 1984; Skorupa 1989; Struhsaker and Leakey 1990; Boshoff et al. 1994; Mitani et al. 2001; Shultz 2002; Shultz and Thomsett 2007). There is, however, considerable variation in diet, with some studies reporting a predominance of primates (mainly the family Cercopithecidae; Skorupa 1989; Mitani et al. 2001) and others reporting a predominance of small antelopes (Brown 1966), hyraxes (Jarvis et al. 1980) or both (Boshoff et al. 1994). In the Taï National Park (Ivory Coast), the African Crowned Eagle has been identified as the most prevalent and important predator of mammals (Shultz 2002), where McGraw et al. (2006) found a preference for small duikers and carnivores despite the majority of prey being primates.

In this study, we (1) identify the habitat requirements of the African Crowned Eagle in a fragmented landscape

consisting of mosaics of vegetation and land-use types in north-eastern South Africa, (2) identify the dietary composition of this poorly known population, and (3) relate diet and habitat to breeding success. Our initial hypothesis is that breeding success will be negatively correlated with increasing fragmentation and neighbour distances. As our estimate of dietary composition is different from that of some prior studies, we also (4) collate diet information across studies and find a relationship between prey diversity and the geographical latitude of populations.

Methods

Study population

This study was conducted in the Nelspruit area (Mpumalanga province, South Africa; between 25°01′ and 25°51′ S, and 30°24′ and 30°32′ E) from November 2008 to April 2009, covering a single breeding season for the pairs that attempted to breed that year. Nelspruit is at an altitude of 670 m with mean maximum temperatures in midsummer (December–February) averaging 29 °C and 23 °C in mid-winter (June–July). Rainfall peaks in December and January (South African Weather Service 2009). The study area consisted of a variety of habitats including deciduous forest, savanna, forest–woodland mosaic and exotic plantations. A previous study estimated 105 breeding pairs to occur in the former 'Transvaal' province, which included this study area (Tarboton and Allan 1984). Permission was granted by the relevant authority to undertake field studies at each location listed and we can confirm that the field studies did not involve any endangered or protected species.

Nest location data

African Crowned Eagle nests are typically situated in the forks of large trees, often in remote locations (Brown 1966; Steyn 1982). Nests used in this study ($n = 30$) were located by local landowners or by searching on foot through areas with previous sightings of African Crowned Eagles. A number of nests in this sample had been previously monitored by two of the authors and pairs were found to be breeding biennially (GRB and DJS pers. obs.). Each nest found was classified as 'active' (incubating adult or chick present), 'post-active' (nest not containing egg or chick but territory still occupied) or 'abandoned' (nest and territory not used in either the current or the previous breeding season). Following the recommendations of Postupalsky (1973), we visited each active nest at least six times during the study to monitor nesting success and the behaviour of adult and juvenile eagles. Active nests were deemed successful if a chick fledged from the nest.

For each nest, we recorded the species of tree it was located in, the height of the tree and the height of the nest above the ground (measured using a clinometer). The location and altitude was recorded using a Global Positioning System (GPS) reading taken directly underneath the nest. The distance to the nearest neighbouring nest was calculated using Geographic Information System (GIS) software (ArcView 3.2, Environmental Systems Research Institute, Redlands, CA, USA); the relatively uniform inter-nest distances suggest that few (if any) nests within our study area were overlooked. We categorised the land use

and vegetation type surrounding the nest patch (100 m radius around nest) following Mucina and Rutherford (2006). The minimum distance from the nest to the edge of the nest patch was calculated using GIS to give the shortest distance between the nest and a different land use and vegetation type. Nesting site preferences were explored by comparing the observed number of nests within areas of each vegetation and land-use type with the numbers expected according to their proportional areas, after removing types that did not contain any nests ('barren rock', 'degraded', 'mines', 'pasture', 'grassland', 'urban' and 'wetland'). We explored geographical and dietary influences on the probability of nest abandonment in separate analyses due to only having dietary information on 15 of the nests but geographical records for all nests.

Prey collection and identification

The 15 nests used for the dietary analysis comprised 11 that were currently active, three that had adults present in the territory but were not breeding (but had been active in the previous season) and one in an abandoned territory. Prey remains were collected from below nests. Those at which birds were breeding were visited between four and 12 times, whereas post-active (birds attending to juvenile bird that fledged from the previous season) and abandoned nests were visited just once. In each initial collection, prey remains were gathered by hand from underneath the nest tree up to a radius of 10 m. The collection of prey remains from active nests was carried out by stretching 6 m² (3 m × 2 m) of black shade netting directly beneath the nests in order to catch any items falling from them. Netting was hung about 1 m above the ground using guy ropes to nearby trees, thus deterring scavengers such as bush pigs *Potamochoerus larvatus* and black-backed jackals *Canis mesomelas* from eating fallen prey remains (DJS pers. obs.). The nets were erected in November at the start of the study and were taken down in April when any chicks had fledged. Searching the ground surrounding the netting was continued on subsequent visits and ranged from three to eight visits per nest.

Prey items were identified from skin, hair, hoof and bone fragments. To prevent multiple counting, only bones that were dissimilar in appearance and decay and that were also the same type of bone (e.g. left femur) were recorded as deriving from different individual prey items.

To assist in prey identification, representative samples of each major bone were studied from the small mammal collection of the Ditsong National Museum of Natural History (formerly the Transvaal Museum), Pretoria, South Africa. The bones of all likely prey species were photographed and compared with the samples collected in this study. Skull fragments were identified to species level, whilst most other bones were identified to the family level. We were unable to identify the age or sex of the prey remains. We categorised the prey at each of the 15 nests as: predominantly (>50%) primate, predominantly antelope or no predominant prey type.

Inter-population dietary comparisons

We collated information on the type and number of prey items consumed by African Crowned Eagles from seven studies in eight populations across four different countries

(Uganda, Kenya, Ivory Coast and South Africa) in Southern, East and West Africa (Brown 1966; Jarvis et al. 1980; Tarboton and Allan 1984; Skorupa 1989; Struhsaker and Leakey 1989; Boshoff et al. 1994; Shultz 2002).

For each population, Simpson's diversity index (SDI; Krebs 1999) was calculated as a descriptor of prey diversity. A single linkage hierarchical cluster analysis (Krebs 1999) based on the prey similarities was conducted and a dendrogram constructed as an illustration of the relative similarity of the diets of the different populations. We also explored the potential relationship between prey diversity and the geographical latitude of study populations. As the importance of primates in the diet of African Crowned Eagles appears to vary widely (Skorupa 1989; Brown et al. 1982), we explored the relationship between the latitude of each study population and the proportion of primates in the diet.

Data analysis

We used logistic analysis (in GenStat version 11, VSN International, Hemel Hempstead, UK) to explore factors affecting the probability of a nest being abandoned. A binary response was defined as 1 if a nest was in an occupied territory (active and post-active nests) and 0 if it was abandoned, with the binomial denominator set as 1 (Crawley 1993, 2002; Wilson and Hardy 2002). Multiple explanatory variables that were highly mutually correlated were not included in the initial model to avoid interpretational problems due to collinearity (Grafen and Hails 2002; Quinn and Keough 2002). Spearman's rank correlation was used to identify correlations between variables, leading to the exclusion of patch edge distance, which was correlated with land patch area ($r_s = 0.766$, $P < 0.001$). Initially, main effects and those first-order interactions that could be included without aliasing were fitted. None of the interaction terms were significant so we present the results deriving from the analysis of an initial model containing main effects only.

We also performed a logistic analysis on those nests that were active during our study season. A binary response for nesting success was defined as 1 for a pair that raised a chick to fledging and 0 for a pair that failed in a nesting attempt. Again, only one of each set of highly mutually correlated explanatory variables was included.

Post-hoc power analyses (Quinn and Keough 2002) were used to estimate the relative power of the statistical tests used, using the G*Power statistical program version 3.1 (University of Kiel, 2008), to ascertain whether our tests could detect a low or medium influence of the variables. We chose not to include the analysis of a large influence because if a test could not detect a small difference then it would certainly not detect a large influence.

The potential relationship between prey diversity and the geographical latitude of study populations was evaluated using a Spearman's rank correlation test (Zar 1984) and latitudinal variation in the proportion of primates in the diet was explored using logistic regression of grouped binary data corrected for over-dispersion, using an empirically estimated scale parameter, due to the greatly varying total prey numbers reported in each study (Crawley 1993; Wilson and Hardy 2002).

Results

Nesting sites and habitat

We located a total of 30 African Crowned Eagle nests; however, two were not included in the analyses concerning site and habitat due to the fact that they were separated from the other nests by a large, unsearched area. Of the remaining 28 nests, six (21.4%) were in exotic trees (five *Eucalyptus grandis* and one *Pinus patula*), 22 (78.6%) were in indigenous trees, and one was in an unidentified tree. Indigenous nest tree species (with number of nests located) included *Breonadia salicina* (7), *Anthocleista grandiflora* (3), *Cussonia spicata* (3), *Prunus africana* (3), *Harpephyllum caffrum* (1), *Podocarpus falcatus* (1), *Balanites maughamii* (1), *Celtis africana* (1), *Faidherbia albida* (1) and *Ficus sycomorus* (1). Fourteen (50%) of the nests were found in plantations of exotic trees, but usually within patches of indigenous forest present within the plantation boundaries rather than in exotic trees themselves.

Nests were disproportionately distributed across vegetation types (Kolmogorov–Smirnov test, $D = 0.4615$, $P < 0.05$; Figure 1). Although the sample size ($n = 28$) was too small for formal utilisation-availability analysis (Byers and Steinhorst 1984), the data suggest that Northern Mistbelt Forest is the favoured type for nesting as this vegetation type contained a disproportionately high number of African Crowned Eagle nests (Figure 1). Nests were also disproportionately distributed across land-use types (Kolmogorov–Smirnov test, $D = 0.667$, $P < 0.05$; Figure 2).
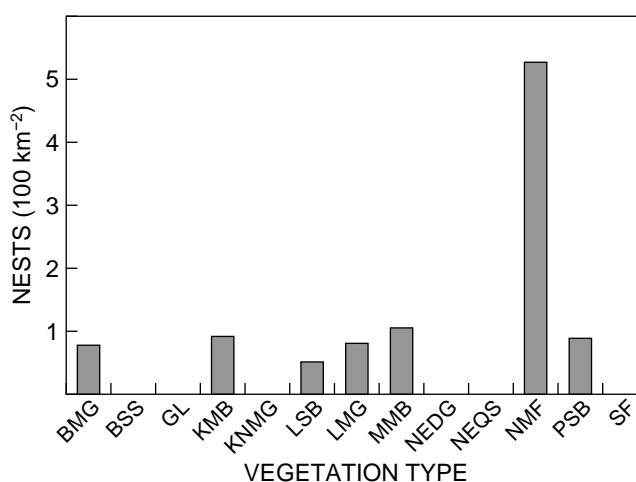

Figure 1: Number of African Crowned Eagle nests in each vegetation type within the study area. Vegetation types are: BMG = Barberton Montane Grassland, BSS = Barberton Serpentine Sourveld, KMB = Kaalrug Mountain Bushveld, LSB = Legogote Sour Bushveld, LMG = Lydenberg Montane Grassland, GL = Granite Lowveld, MMB = Malelane Mountain Bushveld, PSB = Pretoriuskop Sour Bushveld, NEDG = Northern Escarpment Dolomite Grassland, NEQS = Northern Escarpment Quartzite Grassland, NMF = Northern Mistbelt Forest, SF = Scarp Forest. These vegetation types represent three biomes: NEDG and NEQS are 'Grassland', NMF and SF are 'Afrotemperate, Subtropical and Azonal Forests' and the remainder are 'Savanna'. Vegetation types and biomes are according to Mucina and Rutherford (2006)

Nest status

Of the 28 nests used in this analysis, eight had been abandoned with no breeding attempt having been made over the previous two breeding seasons (GRB and DJS pers. obs.). At six sites the nest was post-active with the parents feeding a fledged offspring from the previous breeding season within the territory. The remaining 14 active nests had parents attempting to rear a chick that had hatched during the study season; this does not differ significantly from the null expectation of equality for a biennially (i.e. once every 24 months) breeding species (two-tailed binomial test, $P = 0.115$).

For geographical variables, the probability of nest abandonment decreased with increasing distance from the nearest neighbour nesting site (Table 1) but was uninfluenced by land-use type, patch area, vegetation type, or the exotic or indigenous nature of the nesting tree (Table 1). Prey composition (whether the diet was predominantly primate, antelope or without a predominant prey type) had no significant (~~$P = 0.063$~~) influence on the probability of nest abandonment ($G = 0.74$, df $= 1$, $P = 0.478$).

Active nest success

None of the pairs that bred during our study year had been active the previous year, leading to the conclusion that the pairs in the study population were biennial breeders. Analysis of nesting success, using the subset of 14 active and post-active nests, identified no significant influences of the variables explored. One explanation for this is that small sample size ($n = 14$) greatly increased the probability of type II error. Indeed, *post-hoc* power tests revealed that the power of our analyses were lower ($n = 14$, effect size $= 0.15$ [medium], $P = 0.18$; and effect size $= 0.02$ [low], $P = 0.07$) than 0.8, which is specified as a minimum level for confidence of not having committed a type II error (Smith et al. 2011). We also tested the abandonment analysis (nest usage, $n = 28$) and the results were similar (effect size $= 0.15$ [medium], $P = 0.39$; and effect size $= 0.02$ [low], $P = 0.09$). As above, the influence of diet was only marginally non-significant, again suggesting
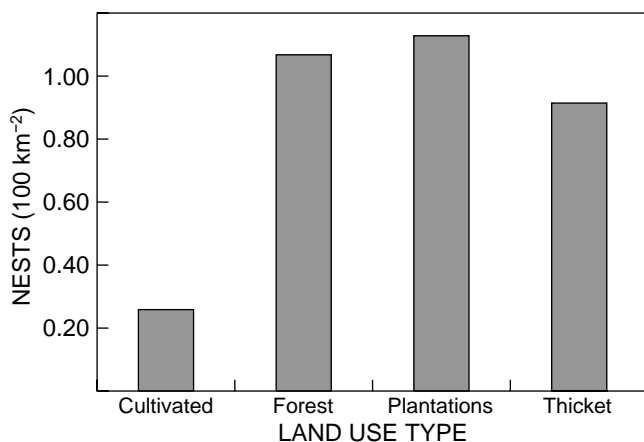

Figure 2: Number of African Crowned Eagle nests in each land-use type within the study area. There were no nests in any of the following seven land-use types: 'barren rock', 'degraded', 'mines', 'pasture', 'grassland', 'urban' and 'wetland'

that in the future a more detailed data set may reveal an underlying ecological effect.

Prey remains at nests

A minimum of 75 individuals were recognised from the 156 identifiable prey items (Table 2). Only one prey individual belonged to a non-mammalian species (a monitor lizard) making the mammalian component 98.7% of the individuals identified in the diet. The main prey type was small antelope, of which red and grey duikers made up the bulk (52%) of the remains. This was followed by monkeys and other prey remains comprised a diverse group of small carnivores, rodents and hyraxes (Table 2).

During the study we made two direct observations of prey being brought to a nest. These were at the same nest and the prey was a vervet monkey in both instances. Anecdotal evidence from local landowners further indicated predation of a klipspringer *Oreotragus oreotragus*, a bushbuck *Tragelaphus scriptus* and a rock hyrax *Procavia capensis*. These observations were, however, not included in the formal analysis for methodological consistency and to avoid double-counting of prey.

Dietary analysis across Africa

Across Africa, the African Crowned Eagle preys upon a wide variety of taxa but the most common are from the mammalian families Cercopithecidae, Herpestidae, Procaviidae and Bovidae. The Cercopithecidae was the most common prey family across all studies (38.4%), with the Bovidae second (29.8%) and the Procaviidae third (13.4%). Prey compositional data (Figure 3) indicate that the study from the Ivory Coast (Shultz 2002) and the two studies from Uganda (Skorupa 1989; Struhsaker and Leakey 1990) are similar in that primates (Cercopithecidae) predominate in the diet. In contrast, studies conducted in South Africa (Jarvis et al. 1980; Tarboton and Allan 1984; Boshoff et al. 1994) all observed that primates were less preyed upon than the Bovidae, Herpestidae and Procaviidae. The cluster analysis, taking the entire range of all prey species into account (Figure 4), indicated that the two most closely similar dietary studies were from the Kibale Forest, Uganda (Skorupa 1989; Struhsaker and Leakey 1990) and the populations within South Africa were generally similar to each other. The study from Kenya (Brown 1966) was more similar to the studies conducted further south, both having a high proportion of antelope in the diet. The diet of African Crowned Eagles in the Ivory

Table 1: Geographical influences on the probability of nest abandonment. Results are from logistic analysis

Explanatory variable	df	Deviance explained G	P
Nearest neighbour distance	1	4.09	0.043
Land use category	3	0.94	0.419
Altitude	1	0.63	0.429
Land patch area	1	0.05	0.815
Exotic tree	1	1.18	0.278
Vegetation type	7	1.35	0.220
Residual	13		
Total	27		

Coast (Shultz 2002) was the most dissimilar to all other populations due to a large range of prey species consumed at low frequency, and with a predominance of predation on primates. Indices of prey diversity (SDI) ranged between 0.23 and 0.69, with the lowest prey diversity observed in Ugandan populations and the highest in South African populations (Figure 3). The suggested relationship between prey diversity and geographical latitude was, however, marginally non-significant ($r_s = -0.601$, df = 6, $P = 0.081$). In terms of the proportion of primates in a population's diet, there was a highly significant increase with increasing latitude, south to north (logistic regression corrected for overdispersion: $F_{(1,7)} = 91.31$, $P < 0.001$, deviance explained = 97.06%).

Discussion

In our study, 20 of the nests (78.6%) were in indigenous trees, corroborating the work of Malan and Shultz (2002) and Tarboton and Allan (1984) who showed similarly high proportions of nests in indigenous trees (71% and 81%, respectively). It has been shown that the critical factor for nest selection by the African Crowned Eagle is access to the nest (Malan and Shultz 2002), suggesting that tree

Table 2: African Crowned Eagle diet in north-eastern South Africa. Vertebrate prey species were identified from remains located beneath 15 nests. Mammal taxonomy follows Skinner and Chimimba (2005)

Family and species	Vernacular name	n	Proportion of total (%)
Bovidae			
Cephalophus natalensis	Red duiker	40	25.6
Sylvicapra grimmia	Grey duiker	23	14.7
Tragelaphus scriptus	Bushbuck	11	7.1
Oreotragus oreotragus	Klipspringer	3	1.9
Unidentified		30	19.2
Subtotal		107	68.5
Cercopithecidae			
Chlorocebus aethiops	Vervet monkey	33	21.2
Unidentified		4	2.6
Subtotal		37	23.8
Procaviidae			
Procavia capensis	Rock hyrax	1	0.6
Herpestidae			
Galerella sanguinea	Slender mongoose	1	0.6
Mongos mongo	Banded mongoose	1	0.6
Subtotal		2	1.2
Viverridae			
Genetta sp.	Genet	3	1.9
Felidae			
Felis domesticus	Domestic cat	1	0.6
Thryonomidae			
Thryonomys swinderianus	Cane rat	1	0.6
Hystricidae			
Hystrix africaeaustralis	Porcupine	1	0.6
Varanidae			
Varanus sp.	Monitor lizard	1	0.6
Total		156	

structure is more important than tree species *per se*. This would explain the large variation in tree species utilised as nesting sites across the species range (Tarboton and Allan 1984; Malan and Shultz 2002; this study). The birds showed a marked preference for nesting in Northern Mistbelt Forest despite the highly limited distribution of this vegetation zone, a result foreshadowed by Tarboton and Allan (1984).

Contrary to our expectations, nest abandonment decreased with increasing neighbour distance. We hypothesise that the reason for decreasing abandonment with increasing isolation could be that where African Crowned Eagles are present at higher densities, they are more likely to abandon nests due to the intraspecific competition. Simmons (1993) discusses this in a population of Wahlberg's Eagles in Africa, finding that pairs in high densities of conspecifics produced half as many young annually as those in low densities. However, Simmons (1993) found that supplementary feeding of nonbreeding pairs did not induce a breeding attempt and that adaptive constraint caused the decrease in reproduction. The finding that abandonment probability is unrelated to land-use types concurs with that of Allan et al. (1997) but contrasts with Barnes (2000) who suggested that plantations are the main factor responsible for the population decline of the African Crowned Eagle in South Africa, perhaps as a result of reduced foraging efficiency due to the absence of their prey base in such plantations. Note, however, that in our study, most of the pairs categorised (by GIS) as nesting within a plantation had in fact located their nests within patches of indigenous forest surrounded by plantation. Hence, despite the fact that the plantation land-use type had the highest density of nests (Figure 2), the eagles were not actually using the plantation itself for nesting.

The analysis of factors affecting the breeding success of the active nests did not produce any significant results due to small sample size ($n = 14$; *post-hoc* power analyses showed that the statistical tests were not powerful enough given the sample sizes). Hence, we suggest that more research is needed to investigate these relationships further. In particular, we note that the non-significant trend that suggests the proportion of primates in the diet affects nesting success may be biologically meaningful.

The nesting success of African Crowned Eagles in our study during the 2009 breeding season was relatively high at 71%. Of 14 pairs that attempted breeding, 10 successfully reared a chick to fledging. The fecundity of African Crowned Eagles in our study was therefore 0.36 fledged offspring pair⁻¹ annum⁻¹, which included pairs that did not breed (Postupalsky 1973). This compares closely with 0.39 and 0.44 fledged offspring pair⁻¹ annum⁻¹ reported by Brown et al. (1977) and Brown (1966), respectively. These rates are lower than other eagle species, for example, 1.1 offspring pair⁻¹ annum⁻¹ in an American population of Golden Eagles (Beecham and Kochert 1975), 0.59 offspring pair⁻¹ annum⁻¹ from a Zimbabwean population of the African Hawk Eagle (Hustler and Howells 1988), and 0.36–1.24 offspring pair⁻¹ annum⁻¹ in a European population of Bonelli's Eagles (Real and Mañosa 1997). Furthermore, López-López et al. (2007) found a rate of 1.39 offspring pair⁻¹ annum⁻¹ of Bonelli's Eagles in eastern Spain. The higher fledging rates in the other species are probably due
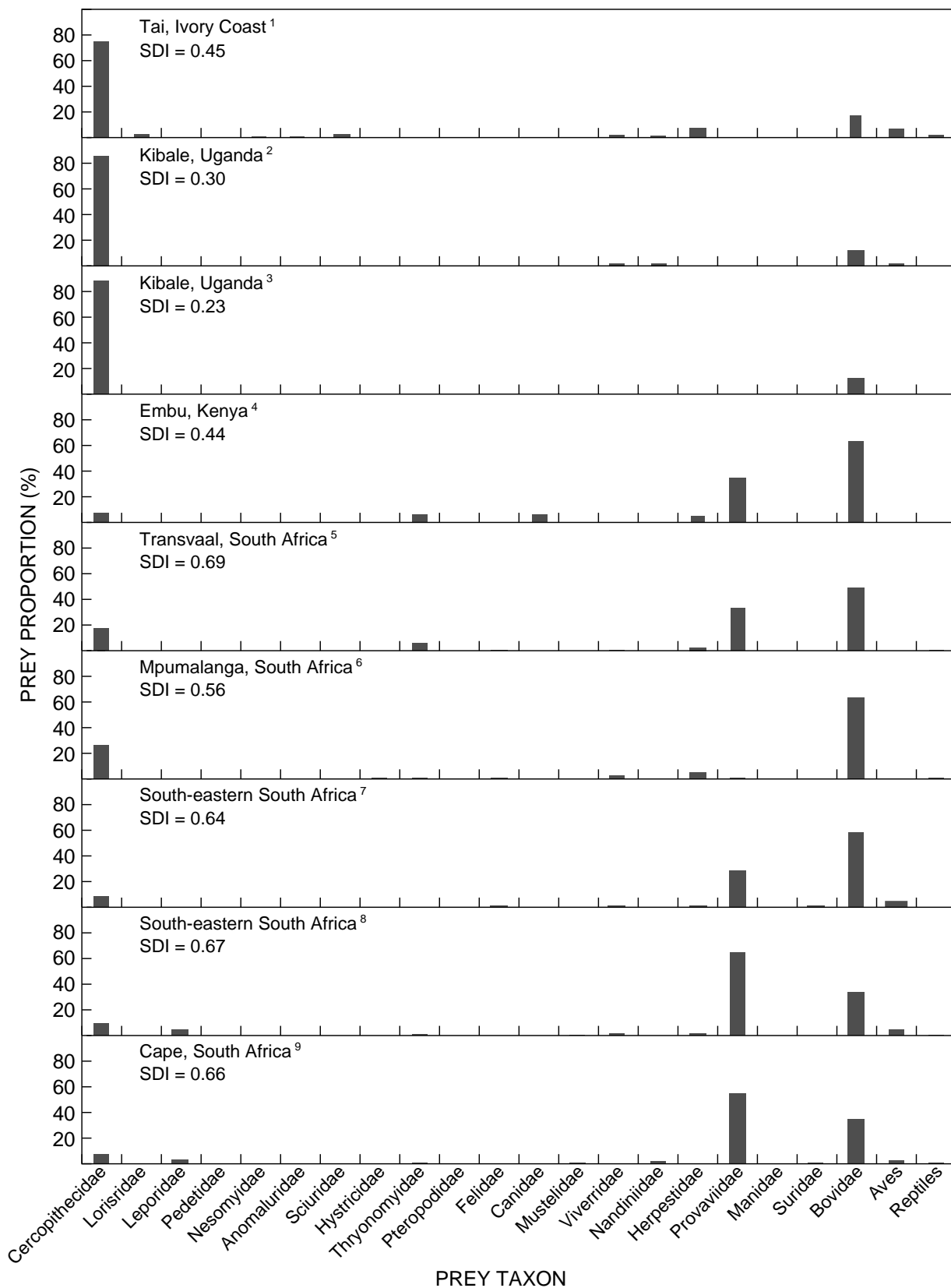
Figure 3: Percentages of prey families in the diet of African Crowned Eagles in nine different populations studied across Africa. Studies are arranged in order of decreasing latitude. SDI = Species diversity index. Data sources: [1] Shultz (2002), [2] Struhsaker and Leakey (1990), [3] Skorupa (1989), [4] Brown (1966), [5] Tarboton and Allan (1984), [6] this study, [7] Boshoff et al. (1994) [forest], [8] Boshoff et al. (1994) [savanna], [9] Jarvis et al. (1980)
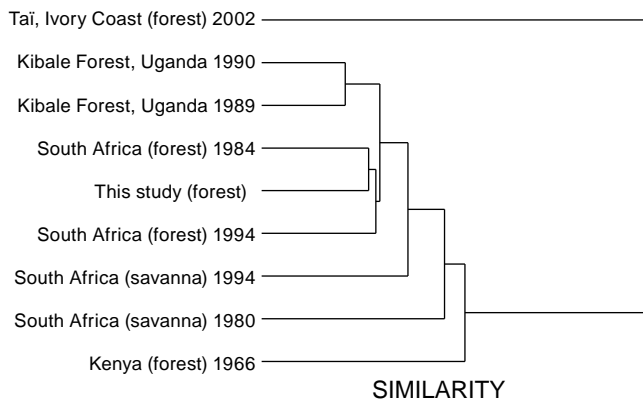
Figure 4: Dendrogram derived from hierarchical cluster analysis to show similarities in African Crowned Eagle diet composition across populations and the primary habitat in which the study was carried out

to the fact that these species breed annually, whereas the African Crowned Eagle breeds biennially in the Nelspruit area (GRB and DJS unpublished data).

There is much debate over whether the African Crowned Eagle is an annual or biennial (raising one chick every 24 months) breeder (see Malan 2005 for a discussion). It is thought that biennial breeding is due to a relatively extended period of high dependency of the young (Shultz and Thomsett 2007), which would fit with observations of pairs that are unsuccessful in one year attempting to breed again the following year (Tarboton and Allan 1984; Thomsett 2011; DJS pers. obs.). However, there are reports of annual breeding in marginal or savanna habitats (Malan 2005) where annual breeding cycles tend to range between 90 and 120 d. For biennially breeding pairs, estimates of the period between nest building and independence of fledged offspring range from 460 d (Skorupa 1989) to 22 months (c. 660 d) (Brown 1976).

We did not find any avian prey remains and just a single reptile, which is not surprising given that the African Crowned Eagle is known to be predominantly a predator of mammals (Brown 1976; Tarboton and Allan 1984). It should be noted that inferring diet from bone collection below the nest is not without controversy and Jarvis et al. (1980) and Rosenberg and Cooper (1990) have argued that it can only serve as a guide. Such prey analyses can be biased, as small bones tend to be completely digested (Brown et al. 1982; McGraw et al. 2006), but may give a good approximation of dietary composition (Boshoff et al. 1994).

The finding that the antelopes were the most common prey in this study corroborates the work of Tarboton and Allan (1984) who reported 43% of prey items consisted of antelope (91% of these being juveniles). Of those antelopes identified to species level, Tarboton and Allan (1984) recognised red duiker *Cephalophus natalensis*, grey duiker *Sylvicapra grimmia* and bushbuck *Tragelaphus scriptus* as the three main species in their study; these are the same species identified in our study. Furthermore, the statement by Brown et al. (1982) that monkeys are a minor dietary component outside of forests is supported by our study. However, prey remains at three of our nests consisted

primarily of primates, even though these nests were in savanna and not forest. This could suggest a preference by some pairs for primate prey.

The lack of rock hyraxes *Procavia capensis* in the prey analysis is noteworthy, particularly since Jarvis et al. (1980) and Boshoff et al. (1994) showed that populations of African Crowned Eagles in South Africa preyed mainly on hyraxes; however, a recent study based on a single nest showed a preponderance of bovids and primates (Symes and Antonites 2014). Tarboton and Allan's (1984) study, carried out in the same general area as ours, found hyraxes to comprise a total of 29% of the African Crowned Eagle diet, and at one particular nest comprised 67% of prey remains. We suggest that the lack of rock hyrax remains at our studied nests was due to a large population decline of hyrax in our area, which is supported by anecdotal evidence (GRB and DJS pers. obs.). Rock hyraxes are prone to such population fluctuations, which are mainly driven by disease (Prinsloo and Robinson 1992; Chiweshe 2002).

Habitat type could be associated with a preferred prey category, for example forest-based eagles could be expected to prey on more primates (Struhsaker and Leakey 1990; Mitani et al. 2001). However, Boshoff et al. (1994) found that wild antelopes were the main prey taxon for African Crowned Eagles inhabiting both forest and savanna habitats in South Africa. The data would indicate that African Crowned Eagles are not a 'monkey specialist' and that Brown et al. (1982) were correct in concluding that monkeys were a less important dietary component outside of rainforests. African Crowned Eagles breeding in Southern and East African forests face different habitat constraints to those in tropical rainforests of Central and West Africa; birds breeding in rainforest usually do so in large, continuous tracts of forest and therefore are restricted to that habitat. Forests in Southern and East Africa tend to be smaller patches allowing the birds to move into surrounding savanna habitat. This may affect their diets.

Predominantly, the high diversity (high SDI) diets were found in the South African savanna biome (Jarvis et al. 1980; Tarboton and Allan 1984; Boshoff et al. 1994), compared with the low diversity of diets in the rainforest biome (Skorupa 1989; Shultz 2002). This is despite the fact that the African Crowned Eagle may feed on the same number of prey families (13) in Ivory Coast (Shultz 2002) as in South Africa (Boshoff et al. 1994), i.e. prey species richness may be the same. Hence, diets of these eagles in the forest biomes of Ivory Coast and Uganda are less diverse (as a result of the preponderance of one or two prey types at the expense of the others) than those in South Africa, even though the birds may prey upon a similarly wide range of species. A suggestion for further work from this heuristic analysis would be to obtain dietary data from studies conducted on populations between 5° and 20° S, where there is currently a large gap in our knowledge.

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