

**RESEARCH ARTICLE** 

# Using web-sourced photography to explore the diet of a declining African raptor, the Martial Eagle (*Polemaetus bellicosus*)

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# ABSTRACT

Understanding a species' diet can be critical for effective conservation. While several traditional methods for assessing raptor diet exist, many pose inherit biases and often require extensive fieldwork that can limit sample sizes and the geographic scope of studies. This is especially true for species that nest at low densities (e.g., large eagles). Recently, several studies have demonstrated the value of web-sourced photographs in tackling ecological and evolutionary questions. Specialized software (e.g., MORPHIC) has been developed to systematically extract Google Images for this purpose. We used this approach to explore the diet of Martial Eagles (Polemaetus bellicosus). A shortage of prey is one of the proposed hypotheses for recent population declines across their range. Of the 4,872 photographs selected by MORPHIC, 254 were usable (5%). Birds, mammals, and reptiles each contributed similarly to overall identified prey. Helmeted Guineafowl (Numida meleagris) were the most important bird prey identified (12% of overall prey). The 4 most important mammalian prey species were Thompson's gazelle (Eudorcas thomsonii; 5%), impala (Aepyceros melampus; 4%), common duiker (Sylvicapra grimmia; 4%), and banded mongoose (Mungos mungo; 4%). Reptile prey was dominated by monitor lizards (Varanus spp.; 21%). Prey class proportions differed significantly by regions with mammalian prey being more common in eastern Africa and reptile prev being more common in southern Africa. Within South Africa, reptile prev proportion was greater in the east than in the west. These corroborate existing prey composition studies. Prey composition differed between age classes, with adult eagles preying on more birds than non-adults. There was no significant difference in the average estimated prey weight by eagle age or feeding position (ground, perched, or flying). Our results suggest that this approach may offer a useful method to explore the diet for raptor species that are well photographed across their range, at minimal cost and research effort.

Keywords: Google images, MORPHIC, Polemaetus bellicosus, prey composition, raptor diet, threatened species

# Utilisation de la photographie Web pour explorer le régime alimentaire d'un oiseau de proie africain en déclin

# RÉSUMÉ

Comprendre le régime alimentaire d'une espèce peut s'avérer essentiel pour assurer une conservation efficace. Bien qu'il existe plusieurs méthodes traditionnelles pour évaluer le régime alimentaire des oiseaux de proie, bon nombre causent des biais inhérents et nécessitent souvent un travail de terrain considérable qui peut limiter les tailles d'échantillons et la portée géographique des études. Cela est particulièrement vrai pour les espèces qui nichent en faibles densités (p. ex., grands aigles). Plusieurs études ont récemment démontré la valeur des photographies Web pour aborder des questions sur l'écologie et l'évolution. Des logiciels spécialisés (p. ex., MORPHIC) ont été développés pour extraire systématiquement des images Google à cette fin. Nous avons utilisé cette approche pour explorer le régime alimentaire de Polemaetus bellicosus. La pénurie de proies est l'une des hypothèses avancées pour expliquer les récents déclins de populations à travers son aire de répartition. Parmi les 4 872 photographies sélectionnées par MORPHIC, 254 étaient utilisables (5 %). Les oiseaux, les mammifères et les reptiles ont chacun contribué de façon similaire à l'ensemble des proies identifiées. Numida meleagris étaient la principale proie identifiée parmi les oiseaux (12 % de toutes les proies). Les quatre principales espèces mammaliennes de proies étaient Eudorcas thomsonii (5 %), Aepyceros melampus (4 %), Sylvicapra grimmia (4%) et Mungos mungo (4%). Chez les reptiles, Varanus spp. (21%) dominait les proies. Les proportions des classes de proies différaient significativement entre les régions, les proies mammaliennes étant plus communes dans l'est de l'Afrique et les proies reptiliennes étant plus communes dans le sud de l'Afrique. En Afrique du Sud, la proportion de proies reptiliennes était plus élevée dans l'est que dans l'ouest. Ceci corrobore les études existantes sur la composition des proies. La composition des proies différait entre les classes d'âge, les aigles adultes capturant davantage d'oiseaux que les non-adultes. Il n'y avait pas de différences significatives dans le poids moyen estimé des proies par âge de l'aigle

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ou par position d'alimentation (au sol, perché ou en vol). Nos résultats suggèrent que cette approche peut fournir une méthode utile pour explorer le régime alimentaire des espèces d'oiseaux de proie qui sont souvent photographiés à travers leur aire de répartition, pour un coût et des efforts de recherche minimaux.

*Mots-clés:* composition des proies, espèce menacée, images Google, MORPHIC, *Polemaetus bellicosus*, régime alimentaire d'un oiseau de proie

# INTRODUCTION

Food abundance can regulate populations (Newton 1998). Understanding the composition of a species' diet is therefore important to many aspects of ecological study including habitat use, foraging energetics, and demographic rates (Redpath et al. 2001). Understanding a species' diet can also help guide conservation strategies aimed at addressing declining populations (Margalida et al. 2009). These data may also help reveal sources of human–wildlife conflict (Moleón et al. 2011), responses to land-use change (Amar et al. 2004, Buij et al. 2013), and differential productivity at the landscape level (Sumasgutner et al. 2014, Murgatroyd et al. 2016).

Various approaches have been used to determine the diet of raptors including the use of prey remains found at nest sites (Murgatroyd et al. 2016, Suri et al. 2017), pellets (Tome 2009), hide watches (Amar et al. 2004), cameras at nests (McPherson et al. 2016, Murgatroyd et al. 2016), and stable isotopes (Resano-Mayor et al. 2014). While the combination of these methods has provided insights into avian diet, they are not without limitations and biases (Lewis et al. 2004). For example, in pellet analyses, avian prey is often underrepresented, whereas mammalian prey is relatively overrepresented (Redpath et al. 2001). Furthermore, these approaches tend to be focused on nest sites, which may limit their ability to explore the diet of nonbreeding birds (e.g., sub-adults) or diet outside the breeding season. Additionally, many of these methods are highly intensive and require researchers to visit nest sites, which are often in remote locations and require multiple visitations within a season. This can limit both sample size, especially for species that nest at low densities (e.g., large eagles), and the geographical scope of any such study, unless multiple similar studies are undertaken across the species' range (Terraube and Arroyo 2011, Murgatroyd et al. 2016, Resano-Mayor et al. 2016).

Gaglio et al. (2017) suggest the use of photographs as a potential noninvasive approach to describing avian diet composition. However, this has yet to be done with images sourced online. Several recent studies have demonstrated the value of web-sourced photographs in tackling a variety of ecological and evolutionary questions. For example, Leighton et al. (2016) showed that Google Images could be used, in a relatively unbiased way, to describe the spatial distribution of animal phenotypes for a variety of taxa. They also developed a web application called MORPHIC (https://morphs.io), which simplifies the extraction of information from Google Image searches. This approach has since been adapted to a variety of novel ecological applications, such as using Google Image–sourced photographs to determine pollinator preference (Bahlai and Landis 2016) and to estimate the breeding phenology of fish species (Atsumi and Koizumi 2017). Web-sourced video footage has even been used to reveal subtleties in shrike behavior (*Lanius* spp.; Dylewski et al. 2017). Given the success of these studies in using web-sourced information to produce reliable, relatively unbiased results, Google Images has considerable potential for dietary studies of raptors and other bird species, as suggested by Leighton et al. (2016).

Here we apply this approach to a declining raptor species, the Martial Eagle (Polemaetus bellicosus), the largest species of eagle in Africa. The Martial Eagle has recently been up-listed to "Vulnerable" on the IUCN's Red List of Threatened Species (BirdLife International 2017) due to declines throughout its range (Thiollay 2006, Amar and Cloete 2017). One proposed hypothesis for this observed decline is a reduction in prey availability (Thiollay 2007, Amar and Cloete 2017). There is, however, little quantitative data available that describes Martial Eagle diet across most of its range. Previous research suggests that prey species are typically between 1 and 5 kg, with a variety of small to medium-sized mammals, large birds, and reptiles being most frequently recorded (BirdLife International 2017). To our knowledge, there are only 3 published studies on the diet of this species. Two of those studies examined diet from prey remains at nest sites in the former Cape Province in southwestern South Africa (Boshoff and Palmer 1980, Boshoff et al. 1990) while the third examined diet from prey remains around nests in the former Transvaal Province in northeastern South Africa (Tarboton and Allan 1984). These studies identified contrasting trends in the relative importance of primary prey classes, with a higher proportion of mammals found in the west and more reptiles in the northeastern regions. However, nest sites can be difficult to locate because Martial Eagles nest in trees, have home ranges >100 km<sup>2</sup> (van Eeden et al. 2017), and nest at very low densities, with the highest recorded density being only 1 pair per 140 km<sup>2</sup> (Tarboton and Allan 1984). Thus, understanding most aspects of their ecology, especially their diet, remains logistically challenging, leaving these raptors gravely understudied (Virani and Watson 1998).

In this study, we used the MORPHIC web application (Leighton et al. 2016) to search Google Images for photographs of Martial Eagles with prey. Using these data, we describe Martial Eagle diet, exploring country, regional, and age-related differences in prey composition. Additionally, we investigate prey weight selection based on prey class, eagle feeding position, and eagle age.

# **METHODS**

#### **Data Collection from Photographic Images**

During October-December 2016, information on individual Martial Eagles and their prey was collated from online Google Image photographs using the MORPHIC application (Leighton et al. 2016). MORPHIC automatically removes duplicate images through a perpetual hashing algorithm (Niu and Jiao 2008) and avoids possible biases based on location of the browser through Google's Hummingbird relevance algorithm (Chauntelle and Yazdanifard 2014). Additionally, relevant photographs were reverse image searched using either TinEye Reverse Image Search (https://tineye.com) or Google Search by Image (https://images.google.com). These web pages were manually examined to ensure that multiple photos of the same predation event were removed and to help identify the original source of the image. Unique search queries, including both the common and scientific name of the species, as well as variations on eagle diet (e.g., feeding or prey) were used in the searches (Table 1). "Photographs" were specified in the search to filter out nonrelevant images (e.g., paintings, videos, and graphic interchange format files) and the resulting photographs were visually examined by researchers.

Photographs were classified as usable if they contained a wild Martial Eagle and its prey. The locations of these predation events were determined via the associated webpage or, when that information was unavailable, were confirmed through email correspondence with the original photographer. If additional relevant photographs and locations were provided by the photographer, they were included in the data collation process. The following data were

**TABLE 1.** Unique search parameters used to source photographs

 from Google Images through the MORPHIC search platform.

Search number	Unique search phrasing		
1	Martial + Eagle		
2	Martial + Eagle + Eating		
3	Martial + Eagle + Prey		
4	Martial + Eagle + Diet		
5	Martial + Eagle + Food		
6	Martial + Eagle + Feeding Polemaetus + bellicosus Polemaetus + bellicosus + Eating		
7			
8			
9	Polemaetus + bellicosus + Prey		
10	Polemaetus + bellicosus + Diet		
11	Polemaetus + bellicosus + Food		
12	Polemaetus + bellicosus + Feeding		

collected for each usable photograph: (1) geolocation of image or country-level location where no further locational data were available; (2) eagle age (i.e. adult or non-adult [juvenile and sub-adult birds]) based on plumage; (3) eagle feeding position (i.e. ground, perched, flying); and (4) identification of prey to the lowest possible taxonomic level.

To determine whether the broad dietary differences previously identified from prey remains were also identified through photographs, South African photographs were classified along the 25°E longitude and compared to the existing studies within western and eastern South Africa (Boshoff and Palmer 1980, Tarboton and Allan 1984, Boshoff et al. 1990).

# **Prey Weight**

Martial Eagle prey weight was estimated using the average weight provided by Chittenden and Upfold (2007) for birds, Smithers (1996) for mammals, and Alexander and Marais (2007) and Ciliberti et al. (2011) for reptiles. Where the literature was vague on estimated prey weights, specialists were consulted. In cases where the prey item was visibly immature, one-quarter of the published adult prey weight was used. Prey weight was then compared by prey class (bird, mammal, reptile), eagle position (flying, ground, perched) and between eagle ages (adult or non-adult).

# **Statistical Analysis**

All statistical analyses were run using R statistical software (R Core Team 2017). Differences in prey composition by region (southern Africa, eastern Africa), country (Namibia, Botswana, South Africa, Kenya, Tanzania) and areas within South Africa (west, east) were assessed by fitting a multinomial model using the MULTINOM function in the NNET package (Venables and Ripley 2002). Difference in prey composition by eagle age was explored using age class fitted as an explanatory variable, after controlling for country, to eliminate potential effects of country on diet composition and for the unequal sample size of different ages among countries. Overall significance of factors was determined using type III ANOVAs implemented using the CAR package (Fox and Weisberg 2011) and the relative effect of each prey class plotted using the EFFECTS package (Fox and Hong 2009). Tukey post-hoc analyses were then carried out using the LSMEANS package (Lenth 2016) to test for pairwise differences in the proportion of prey classes by region, country, and area. The same analyses were carried out to determine the effect of eagle age (adult, non-adult) on relative prey class proportion, while controlling for country-level variation in sampling.

A generalized linear model (GLM) framework and the LSMEANS package were then used to compare Martial Eagle prey weight (as the response variable) by prey class (bird, mammal, reptile) and position (ground, perched, flying). Prey weight differences by eagle age (adult, non-adult) were also explored. In this last analysis, we also fitted "prey type" as an additional explanatory variable in the analysis, to control for any potential differences in prey composition by eagle age.

# RESULTS

Of the 4,872 photographs extracted by 12 unique search terms submitted to MORPHIC (Table 1), 254 were usable (5%) and featured individual Martial Eagles with their prey (Supplemental Material Appendix 1). These photos, taken between 1998 and 2016, were used in subsequent analyses.

### **Overall Prey Composition**

Of the total 254 photographs, 239 prey items could be identified to class (94%) and a further 209 to genus or species level (82%). Birds, mammals, and reptiles each made up approximately one-third of the overall identified prey items (Table 2). Bird prey comprised 15 identified species, half of which were galliforms. Helmeted Guineafowl (Numida meleagris) were the most important bird prey identified forming 12% of the overall identified prey. Mammalian prey were more diverse, with a total of 23 species recorded. The 4 most important mammalian prey items were Thompson's gazelle (Eudorcas thomsonii), impala (Aepyceros melampus), common duiker (Sylvicapra grimmia), and banded mongoose (Mungos mungo), which together made up 17% of overall identified prey. Reptile prey was dominated by monitor lizards (Varanus species), which comprised 21% of overall prey.

### **Geographical Comparisons**

Images were obtained from 8 countries (Figure 1). There was considerable variation in sample size between countries (South Africa = 85; Kenya = 79; Namibia = 26; Botswana = 25; Tanzania = 23). Three countries were omitted from all analyses due to their small sample sizes (Zambia = 8; Zimbabwe = 5; Uganda = 4). We retrieved 136 photos from southern Africa (i.e. Namibia, Botswana, west and east South Africa) and 92 photographs from eastern Africa (i.e. Kenya and Tanzania), but no images from western Africa (Figure 1). There was a significant difference in prey composition by region ( $\chi^2$  = 23.33, df = 2 and 228, P < 0.001), with more reptile prey in southern Africa compared to eastern Africa (35% vs. 10%) and more mammal prey in eastern Africa compared to southern Africa (53% vs. 28%). In both regions there was a similar proportion of bird prey ( $\sim 37\%$ ).

There was a significant difference in prey composition by country ( $\chi^2$  = 43.9, df = 8 and 218, *P* < 0.001). This was primarily driven by Namibia having over double the percentage of bird prey than South Africa (75% vs. 26%), Kenya having nearly double the percentage of mammal prey than Botswana (31% vs. 58%) and South Africa (31% vs. 58%), and South Africa having substantially more reptile prey (43%) than either Kenya (7%) or Namibia (7%).

Within South Africa, a greater number of photographs were found from the east (n = 70) than the west (n = 15). There was a significant difference in prey composition within South Africa ( $\chi^2 = 7.65$ , df = 2 and 82, P < 0.05), where eastern South Africa had an almost 4 times higher percentage of reptile prey (50%) than western South Africa (13%).

### Age Comparison

After controlling for differences in diet between countries (Figure 1), there was a significant difference in prey composition by eagle age ( $\chi^2 = 6.29$ , df = 2 and 218, P < 0.05). Adult eagles had double the percentage of bird prey than non-adult eagles (20% vs. 42%), whereas mammal (36% vs. 49%) and reptile (24% vs. 31%) prey composition was similar between age classes.

### Weight of Prey by Class, Feeding Position, and Age

Mean (SE) prey weight for identified items was 3.1 (0.2) kg. Prey weight differed significantly by prey class (F = 23.32, df = 2 and 209, P < 0.001), with reptile prey being significantly heavier than bird (P < 0.001) and mammal (P < 0.01) prey, and mammal prey being significantly heavier than bird prey (P < 0.001; Figure 2A). Prey weight did not differ significantly by feeding position (F = 1.93, df = 2 and 206, P = 0.148; Figure 2B) nor by eagle age (F = 0.011, df = 2 and 205, P = 0.832), this latter result remained nonsignificant even after controlling for prey class, which was known to vary by age (F = 0.004, df = 2 and 205, P = 0.947; Figure 2C).

# DISCUSSION

Our study is the first to describe Martial Eagle diet across a large proportion of its range. The logistical challenges and financial barriers of working at this scale has rendered such a study impossible previously (Boshoff and Palmer 1980). Our analysis revealed that Martial Eagles prey on birds, mammals, and reptiles in similar proportions. However, these proportions differ substantially between regions and countries. In eastern Africa, their diet is predominantly mammalian, whereas in southern Africa reptile species feature more prominently. These distributions are further explained by the larger proportion of mammal prey in Kenya than Botswana and South Africa, and the larger proportion of reptile prey in South Africa than Kenya (Figure 1). This underlying geographic variation in dietary composition provides an additional layer of complexity to the prey availability hypothesis proposed to explain the declines of this species in many parts of its range (Thiollay 2006, Amar and Cloete 2017).

**TABLE 2.** Martial Eagle prey composition across all sites and overall dietary proportion by class, order, common name, scientific name, number of photographs from MORPHIC search, and mass assigned for prey weight analyses. Units in parentheses after class, order, and common name denote the proportional contribution (%) to overall Martial Eagle diet. Parentheses in "Total" denotes the number of immature prey recorded; in "Mass," this denotes the immature weight assigned (kg).

Helmeted Guineafowl (12) Spurfowl species (3) Vulturine Guineafowl (2) Crested Francolin (<1) Egyptian Goose (5) Spur-winged Goose (<1)* White Stork (2) Abdim's Stork (<1) Common Ostrich (1)* Cattle Egret (1) Hadeda Ibis (<1) Common Greenshank (<1) Spotted Thick-knee (<1) Esser Flamingo (<1) Kori Bustard (<1) Thompson's gazelle (5)* Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Numida meleagris Pternistis or Scleroptila spp. Acryllium vulturinum Dendroperdix sephaena Alopochen aegyptiaca Plectropterus gambensis Ciconia ciconia Ciconia abdimii Struthio camelus Bubulcus ibis Bostrychia hagedash Tringa nebularia Burhinus capensis Phoeniconaias minor Ardeotis kori Eudorcas thomsonii Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	30 7 (1) 4 1 3 (1) 5 1 (3) 2 1 1 1 1 1 1 2 (13) (11) 9 (2)	$\begin{array}{c} 1.80\\ 0.5\ (0.13)\\ 2.00\\ 0.50\\ 3.50\\ (1.75)\\ 4.00\\ 1.60\\ (4.50)\\ 0.50\\ 1.50\\ 0.25\\ 0.60\\ 2.00\\ 8.00\\ \end{array}$
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Common Greenshank (<1) Spotted Thick-knee (<1) s (<1) Lesser Flamingo (<1) Kori Bustard (<1) Thompson's gazelle (5)* Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Tringa nebularia Burhinus capensis Phoeniconaias minor Ardeotis kori Eudorcas thomsonii Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	1 1 1 12 (13) (11) 9 (2)	0.25 0.60 2.00 8.00 (2.50) (5.00) 5.30
Spotted Thick-knee (<1) s (<1) Lesser Flamingo (<1) Kori Bustard (<1) Thompson's gazelle (5)* Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Burhinus capensis Phoeniconaias minor Ardeotis kori Eudorcas thomsonii Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	1 1 12 (13) (11) 9 (2)	0.60 2.00 8.00 (2.50) (5.00) 5.30
s (<1) Lesser Flamingo (<1) Kori Bustard (<1) Thompson's gazelle (5)* Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Phoeniconaias minor Ardeotis kori Eudorcas thomsonii Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	1 12 (13) (11) 9 (2)	2.00 8.00 (2.50) (5.00) 5.30
Kori Bustard (<1) Thompson's gazelle (5)* Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Ardeotis kori Eudorcas thomsonii Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	1 (13) (11) 9 (2)	8.00 (2.50) (5.00) 5.30
Thompson's gazelle (5)* Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Eudorcas thomsonii Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	12 (13) (11) 9 (2)	(2.50) (5.00) 5.30
Thompson's gazelle (5)* Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Eudorcas thomsonii Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	(13) (11) 9 (2)	(2.50) (5.00) 5.30
Impala (4)* Common duiker (4) Bushbuck (1)* Steenbok (1)	Aepyceros melampus Sylvicapra grimmia Tragelaphus scriptus	(11) 9 (2)	(5.00) 5.30
Common duiker (4) Bushbuck (1)* Steenbok (1)	Sylvicapra grimmia Tragelaphus scriptus	(2)	5.30
Steenbok (1)	Tragelaphus scriptus	(2)	
SLEENDOK(I)		2	(2.50)
Common worthog (1)*	Raphicerus campestris	(2)	5.50
Springbok $(<1)$ *	Antidorcas marsupialis	(2)	(1.30)
Banded mongoose (4)	Munaos munao	10(1)	2.50
Common dwarf mongoose (2)	Heloaale parvula	4	0.40
Meerkat (1)	Suricata suricatta	3	1.00
Large grey mongoose (1)	Herpestes ichneumon	2	4.00
Large spotted genet (1)	Genetta tigrina	2	3.20
Slender mongoose (<1)	Herpestes sanguinea	1	0.80
White-tailed mongoose (<1)	Ichneumia albicauda	1	5.20
Bat-eared fox (<1)	Otocyon megalotis	1	5.00
Caracal (<1)*	Caracal caracal	(1)	(2.50)
African lion (<1)*	Panthera leo	(1)	(2.50)
Springhare (1)	Pedetes capensis	3	3.80
Striped ground squirrel (1)	Xerus erythropus	2	1.00
Acacia rat (<1)	Thallomys paedulcus	1	0.10
Vervet monkey (2)	Chiorocebus pygerythrus	4 (3)	8.00 (2.00)
Chacma baboon $(<1)^n$	Papio ursinus Lopus savatilis	(1)	(2.50)
Scrub hare (1)	Lepus saxatilis	2 4	4.50
Monitor lizard (21)	Varanus sop	53	4 00
	Python sebae	1	12 00
African rock python $(<1)$	Crocodylus niloticus	(2)	(2.50)
African rock python (<1) Nile crocodile (1)*		16	()
African rock python (<1) Nile crocodile (1)*		15	
	Acacia rat (<1) Vervet monkey (2) Chacma baboon (<1)* Scrub hare (1) Monitor lizard (21) African rock python (<1) Nile crocodile (1)*	Acacia rat (<1)Thallomys paedulcusVervet monkey (2)Chlorocebus pygerythrusChacma baboon (<1)*	Acacia rat (<1)Thallomys paedulcus1Vervet monkey (2)Chlorocebus pygerythrus4 (3)Chacma baboon (<1)*

Results obtained here cannot be interpreted as Martial Eagle prey selection since we only have data on prey consumption, and not prey availability (Sih and Christensen 2001). It is evident, however, that there is a spatial component to Martial Eagle diet, which may be reflective of different prey abundances between regions. It is noteworthy that monitor lizards (*Varanus* species), which form the bulk of the reptile prey class, do not occur widely in Namibia or western South

Africa (Alexander and Marais 2007). It could also be reflective of landscape differences between regions, with certain prey classes being more detectable or easier to catch in certain environments (Amar and Redpath 2005, Ontiveros et al. 2005). Another possibility for the variation in prey composition is that declines in specific prey classes or species in certain areas could be forcing Martial Eagles to shift their diets accordingly (Moleón et al. 2009).



**FIGURE 1.** Martial Eagle (*Polemaetus bellicosus*) prey class proportions across eastern and southern Africa (dark gray). Countries with insufficient data (light gray) were removed from our analyses. Relative proportion of each prey class: bird (blue), mammal (green), reptile (red), and unidentified photographs (yellow) are indicated per country. Pie chart size is proportional to sampling size per country (Kenya sample size = 79). Bar plots indicate prey composition by region and eagle age, with the significance of the comparison marked above (\*\*\*P < 0.001, \*P < 0.05).

Within South Africa, reptile prey proportion was greater in the east than the west, with more mammal prey in the west than the east. This finding was reassuring from a methodological perspective, as it closely matches the only other formal comparisons of diet for this species, which also showed the same pattern of increasing reptile prey in the east vs. the west of South Africa, using prey remains collected under nest sites (Boshoff and Palmer 1980, Tarboton and Allan 1984, Boshoff et al. 1990). Furthermore, our prey composition also closely matches that of a recent study assessing Martial Eagle diet based on GPS-based kill clusters in the Maasai Mara region of Kenya (Hatfield 2018), with very similar proportions of mammal (53 vs. 49%), bird (46 vs. 37%), and reptile prey (5 vs. 10%) found using the 2 approaches for this country.

Our results suggest that adult Martial Eagles consume a greater proportion of birds than do non-adults. Similar patterns have been observed in other raptor species. For



**FIGURE 2.** Martial Eagle (*Polemaetus bellicosus*) prey weight (kg) by prey class (**A**), eagle feeding position (**B**), and eagle age (**C**). Shown are the mean weights (kg) per category and the associated standard error as well as the sample sizes for each category on the top right of each box, with the significance of the comparison marked above (\*\*\**P* < 0.001, \*\**P* < 0.01).

example, Rutz et al. (2006) found that the proportion of agile bird prey increased as male Northern Goshawks (Accipiter gentilis) aged. They attributed this pattern to an improvement in hunting skills with age. A similar explanation is highly plausible for non-adult Martial Eagles having a lower proportion of birds in their diet, relative to the less agile reptiles and mammals. One of the greatest advantages of the method applied in this study was our ability to explore the diet of both adult and non-adult Martial Eagles. Examining the diets of nonbreeding raptors has proven difficult in the past because non-adult raptors or nonbreeders tend to range widely (Ferrer 1993, Grant and McGrady 1999, García-Ripollés et al. 2011, Krüger et al. 2014). In addition, nonbreeding birds do not tend to have a central location (e.g., nest site) from which diet data can be collected. Our method overcomes these limitations, providing a novel tool for obtaining dietary information for nonbreeders in a species currently lacking such information. Our results also suggest that a difference in dietary composition between age classes may indicate a need to develop conservation strategies that take into consideration or target specific age cohorts (Real and Manosa 1997).

The significant weight differences between all 3 prey classes indicate that Martial Eagles relying largely on reptilian prey obtain more biomass per successful hunting event. Birds, on the other hand, are on average the smallest of prey classes, suggesting that Martial Eagles relying mainly on birds likely require more successful hunting events to meet their dietary needs. This may be offset by the fact that bird meat carries a higher calorific content than mammal and reptile meat (Nagy et al. 1999). With regard to relative position, there was no difference in prey weight. This suggests that there is no weight-dependent detection bias through online imagery. Martial Eagles are as likely to perch or fly with heavier items as they are to feed on the ground. A fair number of eagles were photographed in flight, even with heavy prey (e.g., monitor lizards and a large rock python), which could suggest a high risk of kleptoparasitism when consuming prey in situ, forcing these Martial Eagles to consume prey in locations where they are less likely to be robbed. This presents a potential tradeoff of costs and benefits when targeting different sized prey items.

Our study shows that web-sourced images as identified through the MORPHIC web application (Leighton et al. 2016) can provide an effective means of investigating diet without undertaking intensive fieldwork. It can be used to explore diet outside of the breeding season and can overcome certain biases associated with the use of prey remains for similar surveys. This method does, however, present certain biases. For example, there is a geographic bias toward areas that are frequently visited by photographers (e.g., Protected Areas), which is evident in the lack of photos available from western Africa. In addition, the analyses presented here have not controlled for geographic variation in Martial Eagle population density, which can influence the likelihood of an individual eagle being photographed. However, such data are largely unavailable, particularly at the resolution required for this study. Furthermore, studies using web-sourced images are reliant on which photos people choose to publish, as well as where they choose to upload these images. Most importantly for ornithology, MORPHIC will find photographs on personal websites and a variety of social networking and photography platforms, but not at eBird/Macaulay Library (https://www. macaulaylibrary.org/) or iNaturalist (https://www.inaturalist. org). For Martial Eagles, most photographers upload their photos to multiple sites, but we recommend that eBird/ Macaulay and iNaturalist be screened separately. Given the relative rarity of witnessing a Martial Eagle feeding event, we feel that photographers are likely to share these photos, regardless of prey species rarity and photographic conditions. This is supported by the wide range in quality of photographs obtained. Another potential bias is that smaller prey species are consumed more quickly and are therefore less likely to be seen being consumed. However, we did find many photographs of smaller prey species, such as striped ground squirrel (Xenus erythopus) and acacia rat (Thallomys paedulcus), suggesting that these small prey items are detectable through our methods, but may still be underrepresented.

Although only a relatively small proportion of photographs retrieved from Google Images by MORPHIC were usable, a sufficiently large sample size was obtained to adequately describe Martial Eagle diet in 5 countries across eastern and southern Africa. While this method is not completely void of bias, it is reassuring that the findings from this method match the broad differences identified from nest site remains between the east and west of South Africa (Boshoff and Palmer 1980, Tarboton and Allan 1984, Boshoff et al. 1990), as well as the kill cluster remains of southern Kenya (Hatfield 2018). Given that Martial Eagle population declines have been documented (Thiollay 2006, Amar and Cloete 2017), it is important to obtain these baseline dietary data. As date stamps were provided in this study, future investigations will be able to update and explore any changes in diet for this species across different regions using websourced photographs. Furthermore, this approach is likely to be viable for many other bird species (e.g., other raptors) and other predators (e.g., big cats), and we would encourage researchers to explore this approach for their study species.

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**Author contributions**: V.N., E.W., and A.A. conceived the study and designed the experimental protocols with input from L.S. and B.K. Data were collected by V.N., L.S., E.W., and B.K. Analyses were conducted by V.N., L.S., and A.A. All authors discussed and interpreted the data. V.N., L.S., and A.A. wrote the manuscript with input from all co-authors.

### LITERATURE CITED

- Alexander, G., and J. Marais (2007). A Guide to the Reptiles of Southern Africa. Struik Publishers, Cape Town, South Africa.
- Amar, A., and D. Cloete (2017). Quantifying the decline of the Martial Eagle *Polemaetus bellicosus* in South Africa. Bird Conservation International. doi:10.1017/S0959270917000314
- Amar, A., and S. M. Redpath (2005). Habitat use by Hen Harriers *Circus cyaneus* on Orkney: Implications of land-use change for this declining population. Ibis 11:37–47.
- Amar, A., B. Arroyo, S. Redpath, and S. Thirgood (2004). Habitat predicts losses of Red Grouse to individual Hen Harriers. Journal of Applied Ecology 41:305–314.
- Atsumi, K., and I. Koizumi (2017). Web image search revealed large-scale variations in breeding season and nuptial coloration in a mutually ornamented fish, *Tribolodon hakonensis*. Ecological Research 32:567–578.

- Bahlai, C. A., and D. A. Landis (2016). Predicting plant attractiveness to pollinators with passive crowdsourcing. Royal Society Open Science 3:150677.
- BirdLife International (2017). *Polemaetus bellicosus* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2017: e.T22696116A112494400. http://dx.doi.org/10.2305/IUCN.UK.2017-1.RLTS.T22696116A112494400.en
- Boshoff, A. F., and N. G. Palmer (1980). Macro-analysis of prey remains from Martial Eagle nests in the Cape Province. Ostrich 51:7–13.
- Boshoff, A. F., N. G. Palmer, and G. Avery (1990). Regional variation in the diet of Martial Eagles in the Cape Province, South Africa. South African Journal of Wildlife Research 20:57–68.
- Buij, R., B. M. Croes, G. Gort, and J. Komdeur (2013). The role of breeding range, diet, mobility and body size in associations of raptor communities and land-use in a West African savanna. Biological Conservation 166:231–246.
- Chauntelle, O. Y. L., and R. Yazdanifard (2014). How Google's new algorithm, Hummingbird, promotes content and inbound marketing. American Journal of Industrial and Business Management 4:51–57.
- Chittenden, H., and G. Upfold (2007). Roberts Bird Guide. Jacana, Cape Town, South Africa.
- Ciliberti, A., P. Berny, M.-L. Delignette-Muller, and V. de Buffrénil (2011). The Nile monitor (*Varanus niloticus*; Squamata: Varanidae) as a sentinel species for lead and cadmium contamination in sub-Saharan wetlands. Science of the Total Environment 409:4735–4745.
- Dylewski, Ł., P. Mikula, P. Tryjanowski, F. Morelli, and R. Yosef (2017). Social media and scientific research are complementary—YouTube and shrikes as a case study. Die Naturwissenschaften 104:48.
- Ferrer, M. (1993). Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. Ibis 135:132–138.
- Fox, J., and J. Hong (2009). Effect displays in R for multinomial and proportional-odds logit models: Extensions to the effects package. Journal of Statistical Software 32:1–24.
- Fox, J., and S. Weisberg (2011). An R Companion to Applied Regression. Sage, Thousand Oaks, CA, USA.
- Gaglio, D., T. R. Cook, M. Connan, P. G. Ryan, and R. B. Sherley (2017). Dietary studies in birds: Testing a non-invasive method using digital photography in seabirds. Methods in Ecology and Evolution 8:214–222.
- García-Ripollés, C., P. López-López, and V. Urios (2011). Ranging behaviour of non-breeding Eurasian Griffon Vultures *Gyps fulvus*: A GPS-telemetry study. Acta Ornithologica 46:127–134.
- Grant, J. R., and M. J. McGrady (1999). Dispersal of Golden Eagles Aquila chrysaetos in Scotland. Ringing & Migration 19:169–174.
- Hatfield, R. S. (2018). Diet and space use of the Martial Eagle (*Palemaetus bellicosus*) in the Maasai Mara region of Kenya. M.S. thesis, University of Kentucky, Lexington, KY, USA. https:// uknowledge.uky.edu/forestry\_etds/44
- Krüger, S., T. Reid, and A. Amar (2014). Differential range use between age classes of Southern African Bearded Vultures *Gypaetus barbatus*. PLOS One 9:e114920.
- Leighton, G. R. M., P. S. Hugo, A. Roulin, and A. Amar (2016). Just Google it: Assessing the use of Google Images to describe geographical variation in visible traits of organisms. Methods in Ecology and Evolution 7:1060–1070.
- Lenth, R. V. (2016). Least-squares means: The R package Ismeans. Journal of Statistical Software 69:1–33.

- Lewis, S. B., A. R. Falter, and K. Titus (2004). A comparison of 3 methods for assessing raptor diet during the breeding season. Wildlife Society Bulletin 32:373–385.
- Margalida, A., J. Bertran, and R. Heredia (2009). Diet and food preferences of the endangered Bearded Vulture *Gypaetus barbatus*: A basis for their conservation. Ibis 151:235–243.
- McPherson, S. C., M. Brown, and C. T. Downs (2016). Diet of the Crowned Eagle (*Stephanoaetus coronatus*) in an urban landscape: Potential for human–wildlife conflict? Urban Ecosystems 19:383–396.
- Moleón, M., J. A. Sánchez-Zapata, J. M. Gil-Sánchez, J. M. Barea-Azcón, E. Ballesteros-Duperón, and E. Virgós (2011). Laying the foundations for a human–predator conflict solution: Assessing the impact of Bonelli's Eagle on rabbits and partridges. PLOS One 6:e22851.
- Moleón, M., J. A. Sánchez-Zapata, J. Real, J. A. García-Charton, J. M. Gil-Sánchez, L. Palma, J. Bautista, and P. Bayle (2009). Large-scale spatio-temporal shifts in the diet of a predator mediated by an emerging infectious disease of its main prey. Journal of Biogeography 36:1502–1515.
- Murgatroyd, M., G. Avery, L. G. Underhill, and A. Amar (2016). Adaptability of a specialist predator: The effects of land use on diet diversification and breeding performance of Verreaux's Eagles. Journal of Avian Biology 47:834–845.
- Nagy, K. A., I. A. Girard, and T. K. Brown (1999). Energetics of free-ranging mammals, reptiles and birds. Annual Review of Nutrition 19:247–277.
- Newton, I. (1998). Population Limitation in Birds. Academic Press, San Diego, CA, USA.
- Niu, X., and Y. Jiao (2008). An overview of perceptual hashing. Acta Electronica Sinica 36:1405–1411.
- Ontiveros, D., J. M. Pleguezuelos, and J. Caro (2005). Prey density, prey detectability and food habits: The case of Bonelli's Eagle and the conservation measures. Biological Conservation 123:19–25.
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Real, J., and S. Manosa (1997). Demography and conservation of western European Bonelli's Eagle *Hieraaetus fasciatus* populations. Biological Conservation 79:59–66.
- Redpath, S. M., R. Clarke, M. Madders, and S. J. Thirgood (2001). Assessing raptor diet: Comparing pellets, prey remains, and observational data at Hen Harrier nests. Condor 103:184–188.
- Resano-Mayor, J., A. Hernández-Matías, J. Real, F. Parés, R. Inger, and S. Bearhop (2014). Comparing pellet and stable isotope

analyses of nestling Bonelli's Eagle *Aquila fasciata* diet. Ibis 156:176–188.

- Resano-Mayor, J., J. Real, M. Moleón, J. A. Sánchez-Zapata, L. Palma, and A. Hernández-Matías (2016). Diet–demography relationships in a long-lived predator: From territories to populations. Oikos 125:262–270.
- Rutz, C., M. J. Whittingham, and I. Newton (2006). Age-dependent diet choice in an avian top predator. Proceedings of the Royal Society B 273:579–586.
- Sih, A., and B. Christensen (2001). Optimal diet theory: When does it work, and when and why does it fail? Animal Behaviour 61:379–390.
- Smithers, R. H. (1996). Smithers' Mammals of Southern Africa: A Field Guide. Southern Book Publishers, Rivonia, South Africa.
- Sumasgutner, P., E. Nemeth, G. Tebb, H. W. Krenn, and A. Gamauf (2014). Hard times in the city – Attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. Frontiers in Zoology 11:48.
- Suri, J., P. Sumasgutner, É. Hellard, A. Koeslag, and A. Amar (2017). Stability in prey abundance may buffer Black Sparrowhawks *Accipiter melanoleucus* from health impacts of urbanization. Ibis 159:38–54.
- Tarboton, W. R., and D. G. Allan (1984). The status and conservation of birds of prey in the Transvaal. Transvaal Museum Monographs 3:49–53.
- Terraube, J., and B. Arroyo (2011). Factors influencing diet variation in a generalist predator across its range distribution. Biodiversity and Conservation 20:2111–2131.
- Thiollay, J-M. (2006). The decline of raptors in West Africa: Long-term assessment and the role of protected areas. Ibis 148:240–254.
- Thiollay, J.-M. (2007). Raptor population decline in West Africa. Ostrich 78:405–413.
- Tome, D. (2009). Changes in the diet of Long-eared Owl *Asio otus*: Seasonal patterns of dependence on vole abundance. Ardeola 56:49–56.
- Van Eeden, R., D. P. Whitfield, A. Botha, and A. Amar (2017). Ranging behaviour and habitat preferences of the Martial Eagle: Implications for the conservation of a declining apex predator. PLOS One 12:e0173956.
- Venables, W. N., and B. D. Ripley (2002). Modern Applied Statistics with S. Springer, New York, NY, USA.
- Virani, M., and R. T. Watson (1998). Raptors in the East African and Western Indian Ocean islands: State of ecological knowledge and conservation status. Journal of Raptor Research 32:28–39.