Is the Black Harrier Circus maurus a specialist predator? Assessing the diet of a threatened raptor species endemic to Southern Africa

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Abstract

Studying the diet of wild animals is central for understanding their flexibility in food requirements. The Black Harrier *Circus maurus* is an endangered raptor in South Africa and Namibia. To date, information about the diet of the species is insufficient for a comprehensive understanding of their ecology. We studied the diet composition of breeding Black Harriers using ca. 1000 pellets (> 1700 identified prey) collected at nest sites in two geographical regions (coastal vs. interior-mountain) over 10 breeding seasons (2006-2015). We quantified the importance of small mammals in Black Harrier diet (64.4 % and 78.2 % of prey and consumed biomass, respectively), with the Four Striped Mouse *Rhabdomys pumilio* being a main trophic resource. We also reveal the importance of birds and reptiles as alternative prey, particularly in inland regions, and show inter-annual variations in diet in both regions. Our study confirms that this species can be considered a small mammal specialist. Specialist predators are more vulnerable than generalist ones and diet specialisation has been linked with a poorer conservation status in other species. Our results thus have implications for the conservation of this species in southern Africa. These are highlighted for the long-term sustainability of this threatened endemic species.

INTRODUCTION

Understanding the feeding habits of animals and assessing food resources use is at the core of ecological research (Martinez del Rio et al. 2009). Food supply is often the main factor affecting population densities of many bird species, including raptors (Newton 1979). The study of diet provides basic background information to understand food requirements, which is a crucial step in understanding any species' ecology (Arroyo 1997).

Specialist species use a narrow range of resources and preferentially feed on a given food type regardless of its abundance (see Pyke et al. 1977; Stephens et al. 2007), while generalists feed on a broader range of food types, varying opportunistically in response to changes in availability (Terraube and Arroyo 2011; Nadjafzadeh et al. 2016). However, there is often a continuum from specialization to generalization within and between species (Partridge and Green 1985; Woo et al. 2008). Typically, specialists are more efficient than generalists when foraging for their favoured prey, which is possibly associated with better adaptations or search images (MacArthur and Pianka 1966; Dukas and Kamil 2001; Terraube et al. 2010, 2014). However, the foraging success of specialists may be much lower than that of generalists when they target alternative prey (Terraube et al. 2010). In this context, a broader diet in specialist species may indicate a general decrease in the abundance or availability of the primary prey (Steenhof and Kochert 1988) that forces individuals to feed on alternatives and may be associated with a lower reproductive success (Korpimäki 1992; Bolnick et al. 2003; Arroyo & Garcia 2006; but see Whitfield et al. 2009 and Murgatroyd et al. 2016 for contradictory results).

The Black Harrier *Circus maurus* is an endemic ground-nesting raptor of southern Africa. The population of this medium-sized bird has been estimated at less than 1000 breeding individuals, and the species is listed as endangered in both South Africa and Namibia (Simmons et al. 2015; Taylor et al. 2015), which holds the totality of its breeding range. Black Harriers breed in natural vegetation in both coastal and interior-mountain regions of south western South Africa (Curtis et al. 2004; Curtis 2005, Garcia-Heras et al. 2016). The species has been tentatively described as a small mammal specialist (Van der Merwe 1981; Steyn 1982), although quantitative information on its diet is scarce and inconclusive. A previous study based on a relatively small sample size over three years (2000-2002) suggested that the diet may vary with geographical location: individuals breeding along the coast appeared to feed primarily on small mammals, while those breeding in interior or mountainous areas had a more diverse diet, including more birds (Curtis et al. 2004). Nonetheless, detailed information about the diet of this endangered species, and annual or regional variations, is overall lacking.

The aim of this paper is to describe the diet composition of this scarce and endangered species, to evaluate the numerical and biomass importance of the different categories of prey, and to examine potential regional or inter-annual variations in the diet. For this, we used a large data set of pellets (ca. 1000; 1760 identified prey) collected at active Black Harrier nests in South Africa during 2006-2015 across the breeding range.

MATERIALS AND METHODS

Study sites

This paper presents diet information collected over 10 years (2006-2015 breeding seasons) in two Provinces of south western South Africa. Geographically this spans the coast of the Western Cape Province (33°42'S - 18°27'; 33°08'S- 18°05'E), and inland in the Northern Cape Province in the Nieuwoudtville area (31°19'S; 19°05'E). Nests were located in and around National Parks (South African National Parks – SANParks properties), Provincial Protected Reserves (Cape Nature), or on private lands, spanning two main biomes, the Succulent Karoo and Fynbos (see Mucina and Rutherford 2006; Manning 2007; Garcia-Heras et al. 2016 for details on vegetation types). Depending on its geographical location (i.e. a combination of altitude, distance to the coast and biome), each nest was classified in two main regions, as either coastal or interior-mountain (hereafter called "inland"). This classification was initiated by Curtis et al. (2004) to explore regional differences in lay dates and productivity in Black Harriers, and it was also used and detailed by Garcia-Heras et al. (2016). Environmental conditions between the two regions (e.g. climate conditions, availability of prey) are also known to be different (see Mucina and Rutherford 2006; Manning 2007, Curtis et al. 2004). Coastal nests were defined as those within 15 km from the coast and with a maximal altitude of 100 mASL, and those nests located further than 15 km from the coast and with an altitude higher than 100 mASL were considered as inland (see Garcia-Heras et al. 2016 for more details). Black Harrier nests in inland regions were mostly within the Karoo biome, whereas those along the coast were within the Fynbos biome (see Garcia-Heras et al. 2016).

Pellet collection and analyses

The diet was assessed through analysis of regurgitated pellets containing prey remains such as bones, scales, feathers or hairs. Pellet analysis is a widely accepted technique for diet studies in raptors, including harrier (*Circus*) species (Errington 1930; Simmons et al. 1991; Arroyo et al. 1997;

Redpath et al. 2001). Some biases are inherent in analysing pellets, and sometimes other methods or a combination of methods are preferred depending on diet composition (Simmons et al. 1991; Redpath et al. 2001). However, since these biases are likely to be similar among areas and times of year, they allow within-species comparisons.

Active breeding nests and perch sites (e.g. posts or dead bushes known to be used by a specific breeding pair) were regularly checked for pellets. Pellet collection was extended over the Black Harrier breeding season: August-December in the coastal regions and September-December in the inland regions (Garcia-Heras et al. 2016). A total of 954 pellets were collected from 119 breeding sites (660 pellets from 83 breeding sites in coastal regions, and 294 pellets from 36 in the inland regions). Sample sizes varied between regions and years (Table 1).

After collection, pellets were air-dried and then transferred to individually labelled sealed plastic bags until analysis. We identified prey to the lowest taxon level possible (i.e. to species level) using the comparative osteology collections of the Iziko South African Museum, in Cape Town, South Africa. We determined the minimum number of individuals per taxon in each pellet based on: 1) for small mammals, the highest number of left or right mandibles, or left or right maxillaries, number of incisors and skulls; 2) for birds, upper and lower bills, left or right tarsus or other items that indicates presence; 3) for reptiles, left and right mandibles, maxillaries, or limbs that indicates presence. Reptiles were divided into two size categories (large and medium-small) based on the size of the largest skin scales within a pellet (i.e. <1mm for medium-small and >1mm for large). A relatively small number of insect remains (n = 75) were present in some pellets, in the form of very small pieces of body parts (e.g. mandibles, legs, elytra). However, we suspect that these came from the stomach contents of the birds and/or reptiles also present in those pellets. Black Harriers have rarely been described feeding on insects (Van der Merwe 1981; Steyn 1982; *authors personal observations*). Therefore, as insects are probably rarely voluntarily ingested by Black Harriers, and represented an insignificant amount of biomass, they were not considered in diet analyses.

For pellets containing fur only, hair imprints were conducted to identify small mammal species or group species, where possible. The microstructure of hairs (i.e. specific cuticular scale patterns on the surface of the hair; Ryder 1973) is a useful tool for identifying mammals, and has been widely used to assess carnivore diets (Bothma and Le Riche 1994; Breuer 2005) and the diets of scavenger raptors such as vultures (Donázar et al. 2010). A thin coat of clear nail varnish was applied to a clean microscope slide, and left to dry for about 5-10 seconds. Then, ten randomly selected hair from the same pellet were placed on the nail polish and left to set over for 24 hours. The hairs were then removed with tweezers, being careful to not damage the imprints. Each hair shape was then analysed with a light microscope at 10x and 40x magnification, and compared to those illustrated in

Keogh (1975). This technique was applied to 105 pellets and resulted in the identification of 174 specimens to species or small mammal groups.

Overall, 1760 prey items we identified at the group or species level, 1685 without counting the insects.

Biomass estimation

To assess the importance of prey categories in diets that includes very diverse prey in relation to size, it is important to estimate their relative contribution in terms of biomass (Arroyo 1997). We therefore present the dietary results as both the percentage of identified prey and their estimated biomass. For prey identified to species level, we used the average weight described for the species in Stuart & Stuart (1988) as an estimate of biomass. For broader prey categories, we used an estimated average weight (Table 2). For the assignment of biomass for "unidentified birds", we took into account that the identified birds consumed in inland regions included a higher proportion of Galliformes (particularly Common Quail *Coturnix coturnix*) than in coastal regions, where Passeriformes were more frequently consumed (see results, Table 2). We calculated what would be the average weight of an unidentified bird from the coast or from the inland regions taking into account the relative proportion of identified Passeriformes and Galliformes in each region. Hence, an "unidentified bird" found in the coastal region was attributed a weight of 45 g (since most identified birds here were Passeriformes), while "unidentified birds" from the inland regions were attributed a weight of 69 g (since most of the birds identifiend in inland pellets were Galliformes) (see Table 2).

Statistical analyses

We used R 3.2.3 (the R Foundation for statistical computing, 2015) for statistical analyses. Differences in diet composition (relative proportions of small mammals, birds and reptiles) between regions (coastal vs. inland) were investigated using Chi-square tests. Similarly, inter-annual variations in diet composition in a given region were also tested using Chi-square tests. For this latter test, we used only information from years for which we had a minimum of 25 identified prey. Thus, analyses for the coastal region excluded the years 2006 (n = 18) and 2011 (n = 9). Similarly, analyses for the inland regions were only conducted for the years 2009, 2011, 2013 and 2014, because sample size was too small for 2006 (n = 14) and 2008 (n = 20), and because no pellets were collected in 2007, 2010, 2012 and 2015 (see Table 1). Coefficients of Variation were calculated as 100 $\times$ Standard deviation/mean, and diet diversity was calculated using the Shannon Diversity Index (H') as H'= -

ΣPi log Pi, where Pi=Xi/X, and Xi = number of prey items taken from class i; X = total number of prey items.

RESULTS

Diet composition

Black Harriers preyed upon three main prey types: small mammals (64.4 % of 1685 identified prey, excluding insects), birds (19.2 %) and reptiles (16.3 %) (Table 2).

Among the identified small mammals, Black Harriers fed primarily on the Four Striped Mouse *Rhabdomys pumilio* (hereafter *R. pumilio*) (72.5 % of 487 identified small mammals), whereas the second main group was formed by Otomyinae (*Myotomys unisulcatus* and/or *Myotomys irroratus*), and *Micaleamys namaquensis (*25.3 % of the identified small mammals; Table 2). Black Harriers also fed to a lesser degree (< 3.0 %) on Musk Shrews (*Crocidura cyanea*), Forest Shrews (*Myosorex varius*), and Elephant Shrews (Elephantulus sp.), Grant's Golden Moles (*Eremitalpa granti*) and Cape Dune Mole Rats (*Bathyergus suillus*) (Table 2). However, more than half (55.2 %) of small mammal prey remained unidentified, because neither teeth nor jaws were found in the pellets, or because the shape of some hair imprints did not allow identification (Table 2). Overall, small mammals represented the main prey (78.2 % of consumed biomass).

Among birds, Passeriformes were the most common prey (73.5 % of 147 identified birds), followed by Galliforms (25.2 %; mainly Common Quails *Coturnix coturnix).* The remainder 1.3 % were identified as Columbiformes (Table 2). In some cases, bones and feathers were too damaged to allow identification to species level, and 176 (54.5%) birds remained as "unidentified". Information from identified prey showed that, in the inland regions, Black Harriers fed on Galliformes and Passeriformes in equal proportions, whereas in the coastal regions, they fed predominantly on Passeriformes (Table 2). Overall, birds represented the second main prey in terms of contributed biomass (16.6 %) (Table 2).

Among reptiles, pellet analyses showed that Black Harriers mostly consumed prey of small-medium size (58.8 %), but larger prey were also common (41.1%). We believe all of the reptiles to be lizards (i.e. Cape Skinks, authors', unpublished information).

Diet variation

Diet composition of Black Harriers differed significantly between regions (Chi square tests, X^2 = 28.52, df= 2, p< 0.0001). Small mammals were more prevalent in the diet in coastal than in inland regions, both numerically (67.8 % vs. 57.2 %, respectively) and in percentage of biomass (Table 2), whereas contribution of birds was higher in inland regions, where contribution in biomass was almost three times higher than in coastal areas (28.9 % vs 10.8 %. Respectively, Table 2). The consumption of reptiles was equivalent in both regions, both numerically (16.5 % vs. 16.3 % for coastal and inland respectively) and in terms of biomass (Table 2).

We also found significant inter-annual variation in diet composition within both coastal (X^2 = 28.11, df= 14, p = 0.014) and inland regions (X^2 = 34.82, df= 6, p< 0.0001) (Figure 1). Considering the Coefficients of Variation, the proportion of small mammals and reptiles was more variable among years in inland (CV = 24.6 and 68.4%, respectively) than in coastal regions (CV% = 14.4 and 50.8%, respectively), while an opposite pattern was found for the proportion of birds, with higher variability among years in the coastal region (CV = 40.4%) than in inland regions (CV = 25.6%). Shannon Diversity Index in coastal regions varied among years between 0.24 and 0.44, while in inland regions it ranged between 0.35 and 0.47, being on average higher in the latter than in the former (0.41 vs. 0.33 respectively).

DISCUSSION

Our study highlights the importance of small mammals in the diet of breeding Black Harriers, which represented about 65% of the total identified prey and 78% of consumed biomass. This confirms that this endemic and endangered raptor specialises in small mammals, as suggested in a previous study (Curtis et al. 2004). As with other South African raptor species (e.g. African Marsh Harrier *Circus ranivorus*, Simmons et al. 1991), our study also highlights the particular importance of the Four Striped Mouse *R. pumilio* in the Black Harrier's diet. This species is a common and locally abundant omnivorous rodent, described as resilient to fluctuations in environmental conditions and/or food availability, which probably explains its widespread distribution and capacity to inhabit very different biomes within South Africa (De Graaff 1981). Its diurnal habits and high seasonal productivity (Perrin 1980) may also explain its importance in Black Harrier diet, through a temporal overlap in activity patterns of both prey and predator (see activity diurnal patterns in Simmons 2000).

Species with a specialist narrow diet are frequently associated with a worse conservation status (Ferrer and Negro 2004; Huang 2013). In these species, changes in the abundance of the primary prey lead to strong declines in reproductive success (Newton 1998; Resano-Mayor et al. 2014). Some studies have also highlighted that the degree of dietary specialisation is often related with the species' distributional range, and that specialists show smaller distribution ranges than generalists (Boyes and Perrin 2009). Specialists are also likely to be less adaptable and more vulnerable to rapidly changing environmental conditions compared to generalists (Devictor et al. 2008). Thus, the dietary dependence of Black Harriers on small mammals, and more particularly on *R. pumilio,* may contribute to its scarcity and vulnerable status, which may further exacerbate in a context of global change.

The western region of South Africa has been intensively modified over the last century, with the anthropogenic conversion of the Fynbos and particularly Renosterveld vegetation losing over 90% of its former area to agriculture or urbanization (Curtis et al. 2004). This has reduced and fragmented the breeding habitats of several species, including Black Harriers by > 90% in the most productive regions of the Overberg. Furthermore, there has been a shift in rainfall and temperature patterns in South Africa over the past 50 years, and most notably in the Cape Floral Kingdom and Succulent Karoo (Midgley et al. 2002; Simmons et al. 2004). Here temperatures are predicted to become warmer and winter-rainfall more scarce, with longer and more frequent droughts (Midgley et al. 2002; Hockey et al. 2011; Cunningham et al. 2015). Given that several studies have described the importance of rainfall for the reproduction of several small mammals, including the Four Striped Mouse (Taylor and Green 1976; Jackson and Bernard 2006), these two phenomena combined could consequently lead to a reduction in the abundance and/or availability of the primary prey of specialist predators species like the Black Harrier, forcing them to switch to alternative prey. This in turn may lead to decreased foraging success and breeding outputs, as evident in other predatory species (e.g. Korpimäki 1992; Arroyo and Garcia 2006; Terraube et al. 2012).

However, some specialist species may show behavioural flexibility. For example, Verreaux´s Eagles *Aquila verreauxii* are considered to be highly specialised on hyrax species (Davies 1994, Davies and Allan 1997), but a recent study showed that individuals breeding in agricultural landscapes had the capacity to adapt positively to their changing environment (via the incorporation of energetically profitable and highly available prey to a broader diet) without negative effects in breeding performance (Murgatroyd et al. 2016). Within and between harrier species, there is a very wide range of diet patterns. Some species (essentially from the European continent) are generalist with broad diets, but may show specialist diets in certain contexts, like the Montagu's Harrier *Circus pygargus* (Schipper 1973; Terraube & Arroyo 2011; Limiñana et al., 2012), the Hen Harrier *Circus cyaenus* (Schipper 1973; Redpath et al. 2002; Millon et al. 2002; Garcia and Arroyo 2005), and the European Marsh Harrier *Circus aeruginosus* (Schipper 1973; Gonzalez-Lopez 1991). On the other hand, some species appear to be specialised on small mammals, for example the Pallid Harrier *Circus* *macrourus* (Terraube et al. 2010), the Northern Harrier *Circus cyaenus hudsonius* (Hamerstrom 1986; Barnard et al. 1987), or the Black Harrier (as shown in the present study), but the degree of diet flexibility in the absence of small mammals varies among species.

It seems therefore essential to carefully assess the factors that define dietary strategies and affect diet variation (e.g. prey abundance, availability and profitability) in this species, as well as their ecological consequences, particularly in the context of rapid and long-term environmental change. Further studies will also have to assess the long-term broader implications that diet specialisation coupled with climate change and habitat fragmentation may play on the population dynamic of this threatened endemic specialist predator.

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Table 1: Sample sizes (number of pellets analysed, their corresponding number of contributed prey items (in brackets), and the corresponding number of nests [in square braquets]), for the Black Harrier diet analysis according to year and region (coastal and inland). Fresh pellets were collected at or near Black Harrier active nests during each breeding season (July-December).

Years	Coastal Pellets (prey item) - [number of nests]	Inland Pellets (prey item) - [number of nests]	Total Pellets (prey item)
2006	8 (18)-[2]	7 (16)-[6]	15 (34)
2007	24 (46)-[3]	-	24 (46)
2008	27 (41)-[6]	-	27 (41)
2009	29 (58)-[7]	24 (54)-[5]	53 (112)
2010	69 (116)-[15]	-	69 (116)
2011	5 (9)-[2]	16 (35)-[4]	21 (44)
2012	96 (163)-[15]	-	96 (163)
2013	98 (162)-[14]	100 (214)-[13]	198 (376)
2014	186 (347)-[15]	147 (244)-[10]	333 (591)
2015	118 (237)-[12]	-	118 (237)
Total	660 (1197)-[91]	294 (563)-[38]	954 (1760)

Table 2: Prey categories and species identified in Black Harrier pellets (n= 954) according to regions (coastal and interior-mountain), collected during the 2006-2015 breeding seasons. A weight (in g) is also given for each prey category as an estimate of biomass of a prey unit: this is the average weight described for the species, or when prey could only be identified at a genus or family level, an estimated weight ($^{\psi}$) was used (see materiel and methods).

	Prey weight (g)	**Coastal** N prey (% Biomass*)	**Inland** N prey (% Biomass*)
Small mammals			
Bathyergus suillus	750	1 (1.08)	-
Crocidura cyanea	9	1 (0.01)	-
Elephantulus sp.	46	1 (0.07)	4 (0.56)
Eremitalpa granti	23	2 (0.07)	-
Micaelamys namaquensis	50	-	1 (0.15)
Myosorex varius	14	2 (0.04)	
Myotomys unisulcatus	125	3 (0.54)	8 (3.04)
Rhabdomys pumilio	50	255 (18.40)	98 (14.92)
Otomyinae$^{\psi}$	150	95 (20.56)	16 (7.31)
Unidentified$^{\psi}$	72	416 (43.21)	182 (39.90)
Total small mammals		**776 (83.98)**	**309 (65.88)**
Birds			
Alaudidae galerida	45	1 (0.06)	-
Coturnix coturnix	95	4 (0.55)	33 (9.54)
Crithagra flaviventris	18	1 (0.03)	-
Estrilda astrild	9	1 (0.01)	-
Ploceus capensis	44	1 (0.06)	-
Ploceus velatus	34	2 (0.10)	3 (0.31)
Pycnonotus capensis	39	3 (0.17)	-
Streptopelia senegalensis	81	1 (0.12)	1 (0.25)
Alaudidae$^{\psi}$	45	2 (0.13)	1 (0.14)
Coliidae$^{\psi}$	51	2 (0.15)	-
Fringillidae$^{\psi}$	20	4 (0.12)	-
Ploceidae$^{\psi}$	40	1 (0.06)	2 (0.24)
Pycnonotidae$^{\psi}$	40	3 (0.17)	-
Sylviidae$^{\psi}$	20	1 (0.03)	-
Passeriforme (medium size)$^{\psi}$	40	36 (2.08)	16 (1.95)
Passeriforme (small size)$^{\psi}$	20	16 (0.46)	12 (0.73)
Unidentified	45 and 69$^{\phi}$	101 (6.56)	75 (15.76)
Total birds		**180 (10.85)**	**143 (28.92)**

Table 2- continued

	Prey weight (g)	Coastal N prey (% Biomass*)	Inland N prey (% Biomass*)
Reptiles			
Large Lizard[ψ]	25	75 (2.71)	39 (2.97)
Medium/small Lizard[ψ]	15	114 (2.47)	49 (2.24)
Total reptiles		**189 (5.17)**	**88 (5.21)**
Insects			
Locust		22	14
Coleoptera		1	-
Mantidae		1	1
Orthopterea		2	-
Scarabidae		21	8
Unidentified		5	-
Total insects		**52**	**23**
Total prey		**1197**	**563**

*values calculated excluding insects.

[ϕ]for coastal and inland regions, respectively (see methods)