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Regional and temporal variation in diet and provisioning rates suggest weather limits prey availability for an endangered raptor

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Understanding variation in food requirements of wild animals is of central importance in population ecology and conservation, as it helps to identify where and when food may be limiting. Studies on diet variation or prey provisioning rates may give useful insights when direct information on prey availability is lacking. We assess spatial and temporal variation in the diet of an endangered predator, the Black Harrier *Circus maurus*. This raptor is endemic to southern Africa and specializes on small mammals but also feeds on birds and reptiles as alternative prey. Using data on 1679 prey identified in 953 pellets collected in inland and coastal regions from 2006 to 2015, we show that diet composition changed little throughout the breeding season in the coastal region, whereas there was a marked seasonal decline in the occurrence of small mammal prey in the inland region, with a concomitant increase in alternative prey. The proportion of small mammals in the diet declined with increasing maximum temperature, the latter being highest at the inland region late in the breeding season. Using camera recordings at nests in 2014, we further analysed daily patterns of prey provisioning to nestlings. A marked reduction in small mammal provisioning rates occurred during the middle of the day in the hotter inland region but not in the cooler coastal region. Reduced availability of the primary prey, small mammals, in hotter conditions, through a reduction in activity or overall abundance, could explain these patterns. Finally, we show a positive relationship between winter rainfall and interannual differences in the proportion of small mammals in the diet of Black Harriers breeding in the coastal region, suggesting relationships between diet and prey abundance that are mediated through rainfall. We discuss the need to consider spatial variation in food availability in conservation strategies.

Keywords: Black Harrier, *Circus maurus*, climate-mediated, conservation, food requirements, prey provisioning, seasonal decline, specialist predator.

Food supply is a primary natural limiting factor affecting birds, influencing all aspects of their annual cycle (Newton 1998), and is mainly related to food availability, which is determined by both the abundance and accessibility of food resources (Preston 1990). In the case of predators that feed on moving prey, factors such as habitat or weather may reduce accessibility by modifying prey behaviour or capture probability (Elkins 1983, Schlaich *et al.* 2015). This may create situations of food limitation despite high prey abundance (Robinson *et al.* 2016).

Quantifying and measuring the availability of prey in the environment remains a difficult and challenging task for many species (Rosenberg & Cooper 1990, Smith & Rotenberry 1990). Studies of diet variation may nevertheless give relevant and useful insights into these factors when direct information on prey availability is lacking (e.g.

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Amar *et al.* 2003, Terraube *et al.* 2011, Cartwright *et al.* 2014), particularly for specialist predators. Unlike generalists, specialist predators use a narrow range of resources, feeding primarily on one food resource when it is accessible (Pyke *et al.* 1977, Stephens *et al.* 2007). Changes in diet composition (reflected in a higher proportion of alternative prey in the diet) in these species arise primarily if the availability of the primary prey decreases (Newton 1998, Arroyo & García 2006). In the absence of prey abundance data, an indirect way to evaluate food availability in the environment may be to assess foraging yields (the number of individual prey animals caught per unit time of hunting, e.g. Simmons 2000, Terraube *et al.* 2011) or prey provisioning rates at nests by direct observations (Amar *et al.* 2003, Leckie *et al.* 2008) or using automated cameras at nests (Zárybnická *et al.* 2012, Schroeder *et al.* 2013, Robinson *et al.* 2016).

For specialist species of conservation concern, it is necessary to identify the conditions under which food becomes limiting. Specialist species are known to be less efficient when hunting alternative prey (Terraube *et al.* 2011). In this context, a reduction in the availability of primary prey in the environment may contribute to reducing an individual's breeding performance, and potentially has implications for the entire population (Newton 1979, 1998).

The ground-nesting Black Harrier *Circus maurus* is a scarce raptor endemic to southern Africa. Its population size has been estimated at fewer than 1000 breeding individuals and the species is currently considered Endangered in South Africa, Namibia and Lesotho, which corresponds to its whole distribution range (Simmons *et al.* 2015, Taylor *et al.* 2015). This medium-sized raptor breeds in indigenous vegetation in both coastal and inland areas of south-western South Africa, essentially within the Fynbos and the Karoo Biomes (Curtis *et al.* 2004, Curtis 2005, García-Heras *et al.* 2016). The species has recently been shown to be a small mammal specialist, with the Four-striped Mouse *Rhabdomys pumilio* being the main prey, although it also consumes alternative prey such as birds or reptiles (García-Heras *et al.* 2017, see also Van der Merwe 1981, Steyn 1982). Regional differences have also been found in its diet, with a greater consumption of birds inland than along the coast (García-Heras *et al.* 2017), but the potential reasons for such differences have yet to

be assessed. No quantitative data exist on the availability of the range of prey taken by this species over the landscape it occupies. Rainfall is considered to be a determinant factor of primary productivity in the most arid regions of South Africa (Schulze 1997, Lepage & Lloyd 2004, Rymer *et al.* 2013), and several studies have found that winter rainfall promotes the reproduction of small mammals, including the Four-striped Mouse (Taylor & Green 1976, Jackson & Bernard 2006). In this context, higher winter rainfall would be expected to result in a greater abundance of small mammals. On the other hand, high temperatures are also known to induce a reduction in the activity of South African small mammals such as the Four-striped Mouse (Nater *et al.* 2016). Therefore, high temperatures, such as those occurring at midday as the breeding season extends into summer, would be expected to result in a lower accessibility of small mammals.

In this paper, our aim was to investigate the spatial and temporal variation in the diet of breeding Black Harriers in South Africa. Using a large dataset of 1679 identified prey from 953 pellets collected at active nests during 2006–2015, we looked at temporal and regional variation in diet and investigated diet variation according to winter rainfall and maximum temperatures. We predicted that the occurrence of small mammals in the Black Harrier diet should increase with winter rainfall and decrease with increasing temperatures. We also assessed regional differences in provisioning rates as an indirect way of evaluating differences in prey availability.

METHODS

Study sites

Fieldwork was conducted in South Africa, along the coast of the Western Cape Province (from 33.700°S, 18.45°E to 33.133°S, 18.083°E) and inland in the Northern Cape Province in the Nieuwoudtville area (31.316°S, 19.083°E). Nests were located in and around National Parks (South African National Parks –SANParks properties), Provincial Protected Reserves (Cape Nature) or on private lands. We classified each nest as being either coastal or inland, depending on location and altitude: coastal nests were defined as those within 15 km of the coast and with a maximal altitude of 100 m asl, and those located further than 15 km from the

coast and with an altitude higher than 100 m asl were considered as inland (see García-Heras *et al.* 2016 for more details). Inland Black Harrier nests were mostly within the Karoo biome, whereas those along the coast were mostly within the Fynbos biome (see Mucina & Rutherford 2006, Manning 2007, García-Heras *et al.* 2016 for details on vegetation types).

Pellet collection and prey identification

Black Harrier diet was assessed through the analyses of pellets collected at active nests and nearby perching sites, such as posts or dead bushes known to be used by a particular breeding pair. Pellet collection occurred between July and December in the coastal region and between September and December in the inland region (García-Heras *et al.* 2017), covering both the incubation and the nestling periods of Black Harriers nesting in both areas during the study years. Each pellet was attributed to a region (coastal or inland) and a month of collection (i.e. the month when the pellet was collected in the field). For simplicity, we henceforth refer to months of collection as 'month'.

A total of 953 pellets were collected during the 2006–2015 breeding seasons from the two study regions ($n = 659$ and 294 for coastal and inland, respectively) at 111 active nests (79 coastal and 32 inland). We excluded from the analysis two pellets found in July (one in 2006 and one in 2011, totalling six identified prey) because they could not be confirmed to correspond to breeding birds. In the coastal region, pellets were collected in all study years, whereas in the inland region they were collected only in 2006, 2008, 2009, 2011, 2013 and 2014. Overall, the total number of identified prey was 1685, and we analysed 1679 after excluding those from pellets found in July.

Pellet contents (i.e. remains such as bones, scales, feathers or hairs) were analysed following the methods described in García-Heras *et al.* (2017). Briefly, prey were identified to the lowest possible taxon level (to species level when possible, or broader categories such as 'small mammals', 'passerines', 'galliformes' or 'reptiles' if not), and the minimum number of individuals per taxon for each pellet was determined. This was based on the highest number of mandibles, incisors, skulls, bills or limbs, where they occurred, and assuming only one individual was involved when only fur, feathers or scales were found. However, for a subsample of pellets with fur only ($n = 105$), hair imprint analysis allowed us to assess whether more than one small mammal species was present (García-Heras *et al.* 2017).

For prey identified to species levels, we took the average weight described for the species in Stuart and Stuart (2015). For broader prey categories (e.g. 'unidentified small mammals' or 'unidentified birds'), we used an estimated average weight, based on that of identified prey of the same taxonomic level (García-Heras *et al.* 2017). For analyses, we classified all identified prey into one of three categories: small mammals, birds or reptiles.

Provisioning rates

To determine provisioning rates, we set cameras (Ltl Acorn-6210M, 32GB SD card) at 18 active nests (11 coastal, seven inland) during the 2014 breeding season. Cameras were set 100–150 cm from the edge of the nest during the nestling period, when chicks were 7–41 days old, and were camouflaged and covered with vegetation to avoid disturbing the breeding birds and attracting potential nest predators. On average, each nest was monitored for 10 days throughout the nestling period, but not necessarily continuously (due to SD memory card or camera battery limitations). In the coastal region, 10 nests were monitored between 28 August and 27 October, except for one pair that started breeding later and for which recordings were made from 12 November to 3 December. Inland, all seven nests were monitored between 6 and 31 October. Cameras were either set to shoot an image every 5 s or to record a 60-s video sequence (with a time lapse of 1 s between two consecutive videos), and were active from sunrise until sunset (e.g. 06:00–19:59 h). With camera footage we were able to reconstruct prey provisioning rate for a total of 1488.3 h (82.7 ± 35.9 h per nest, range 15.5–142.1 h). We analysed videos and photos to identify when prey was delivered, and categorized each prey as a small mammal, bird, reptile or unidentified prey item. We used these data to compare average provisioning rates and their diurnal patterns between the study regions. We could not use these data to assess seasonal declines in provisioning rates, because cameras were not active for long enough, particularly inland. For those nests for which we had both pellets and cameras, data on diet identified with both methods correlated with each other

when the proportion of unidentified prey identified from cameras was low (see details in Appendix S1). When the proportion of unidentified prey was high, the camera data became less reliable. We therefore chose not to lump prey identified in cameras with those in pellets for analyses of diet variation for the one year (2014) when both methods were used, and to use only pellet data, as this rendered more comparable data across study years.

Regarding weather conditions, 2014 was average in terms of winter rainfall as compared with other study years; maximum temperatures were high in both coastal and inland regions, but within the observed range (see Table S1).

Rainfall and maximum temperature

Winter rainfall (June–September) is known to affect the onset of small mammal reproduction as well as their subsequent abundance (Rymer *et al.* 2013, Nater *et al.* 2016). Monthly rainfall data (mm) from seven weather stations located near study nests in the Western and Northern Cape Provinces were obtained for the periods 2006–2015 (South African Weather Services 2015 http://www.weathersa.co.za). We calculated total rainfall between June and September for each weather station and each year. We linked diet data from a given breeding site to the winter rainfall data from the nearest weather station.

Additionally, high temperatures during the middle of the day are known to reduce the activity of small mammals (Nater *et al.* 2016), thus reducing their availability as prey for Black Harriers. Monthly average daily maximum temperature data (°C) from the seven weather stations for each of the study years were also obtained, and linked to diet data from a given breeding site and collection month (nearest weather station). The distance between sampled nests and weather stations averaged 29 km $\pm$ 22 (sd).

Statistical analyses

We used R 3.2.3 (R Core Team 2015) for all statistical analyses.

Regional and seasonal variations in diet

We aimed to test the effects of month (seasonal variation), region, winter rainfall and maximum temperature on the occurrence of the different major prey groups (small mammals, birds and reptiles) in Black Harrier diet. However, some of these variables are intercorrelated, and could thus be collinear. Therefore, we first assessed whether winter rainfall differed between years and regions, and whether maximum temperatures differed between years, regions and months. For this, we used generalized linear mixed models (GLMMs), in which each response variable (winter rainfall and maximum temperature) was fitted as a normal distribution (package lme4, function lmer and log function; Bates *et al.* 2012). In the model for winter rainfall, year (a 10-level factor) and region (a 2-level factor: coastal vs. inland) were fitted as explanatory variables, whereas in the model for maximum temperature, year, region, month (a continuous variable ranging from 8 August to 12 December) and the region-by-month interaction were fitted as explanatory variables. In both models, the weather station was included as a random term to account for the non-independence of weather data from the same station. These analyses showed that maximum temperature was collinear with both region and month (see Results).

We analysed variation in the occurrence of the different prey groups in the diet using GLMMs. For this, our sample unit was each identified prey. We constructed three response variables (occurrence of small mammals, birds or reptiles) by attributing 1 to prey corresponding to a particular group, and 0 when it corresponded to any other prey group (e.g. occurrence of small mammals would be scored 1 for all small mammal prey, then 0 for both birds and reptiles). Response variables were fitted using a binomial distribution (package lme4, function glmer and a logit link function; Bates *et al.* 2012). We included year (a 10-level factor) and pellet ID as random terms, the former to account for potential between-year variation in diet for reasons not taken into account in our analyses (and because we were interested in describing overall patterns for any given year, rather than testing for between-year variation here), and the latter (pellet ID) to take into account potential lack of independence of data arising from the same pellet. Given that maximum temperature was collinear with both region and month (see above, and Results), we could not include those three variables in the same model. Thus, we first fitted models with month, region, their interaction and winter rainfall as explanatory variables, and separate ones with maximum

temperature instead of month and region. This was done to check whether differences in temperature could explain the observed seasonal and regional patterns.

Although 'month' corresponded to the month when pellets were collected, an exception was made for pellets collected at inland nests in 2014. That year, only two visits to the inland study site were conducted: one at the beginning and one at the end of October. For this year, and to incorporate temporal variability, we attributed pellets collected in the first visit ($n = 62$) to September as the month of collection. All nests found during the first visit (i.e. early October) were either still at the incubation stage or had young nestlings approximately 2–5 days old, and we could then reasonably assume that most pellets collected then were indicative of the adult diet during the month prior to collection. Additionally, 21 pellets collected in the first days of January 2008, 2009 and 2013 were attributed to the previous December as the month of collection, given that birds were no longer present at the time of collection and we assumed that the pellets represented diet during the previous month.

A stepwise backward procedure was performed for model selection (with the function drop1), where likelihood ratio chi-square tests (LRTs) on the residual sum of squares of models with and without interactions or individual variables were used for model selection (Zuur *et al.* 2009).

Interannual variation in diet with weather
To assess whether diet composition was associated with winter rainfall, we used Pearson correlations between winter rainfall and the overall proportion of each prey type in the diet for each study year. These analyses were conducted using only data from the coastal region, where potential sampling bias (arising from the month of collection) across years was not an issue because no seasonal variation in diet was found there (see Results). We excluded data from 2011 because only three prey were identified that year. For the inland region, we could not conduct a similar analysis because sampling in each year occurred in different months, complicating annual estimates of diet in a region where seasonal differences were apparent.

Regional variation in daily provisioning rates
To test for differences in daily provisioning rates between regions, we fitted the number of prey delivered at each monitored nest ($n = 18$ nests) during a given hour as the response variables (total prey items, small mammals, birds, reptiles and unidentified prey items) using GLMMs (Poisson distribution, package lme4, function glmer and log link function; Bates *et al.* 2012), and the log of duration of the recording time fitted as an offset. Recording time was set at 60 min if the camera had been active for the whole hour, but less if it had been inactive for part of that time. Hours with recording time < 30 min were excluded from analyses ($n = 78$). We included nest identity as a random term to account for the lack of independence of data coming for the same nest. We categorized recording hours (06:00–19:59 h) in three categories (daytime periods) as follows: morning (06:00–10:59 h), midday (11:00–15:59 h) and evening (16:00–19:59 h). Daytime period (a 3-level factor), region and their interaction were included as explanatory variables.

A stepwise backward procedure was performed for model selection as described above. All data are presented as means ± 1 se.

RESULTS

Temporal and spatial variation in weather

Winter rainfall varied significantly between years ($\chi^2_9 = 56.5$, $P < 0.0001$) but did not differ between regions ($\chi^2_1 = 0.15$, $P = 0.69$). Maximum temperature increased significantly with month ($\chi^2_1 = 174.5$, $P < 0.0001$, slope: $+1.85 \pm 0.15$), varied significantly among years ($\chi^2_9 = 31.5$, $P < 0.0002$) and differed between regions ($\chi^2_1 = 8.2$, $P = 0.004$; least squares (LS)-means: 23.0 ± 0.94 and 26.7 ± 0.90 for coastal and inland regions, respectively). The interaction month-by-region was not significant ($\chi^2_1 = 0.01$, $P = 0.91$). These results indicated that maximum temperature covaried with region and month.

Regional and seasonal variation in diet

Dietary variation throughout the breeding season differed between regions. Inland, a clear decline in the occurrence of small mammals was observed as the breeding season progressed (September–December; Fig. 1b), being replaced mostly by birds and some reptiles (lizards). The relative proportion of bird numbers and biomass in the diet
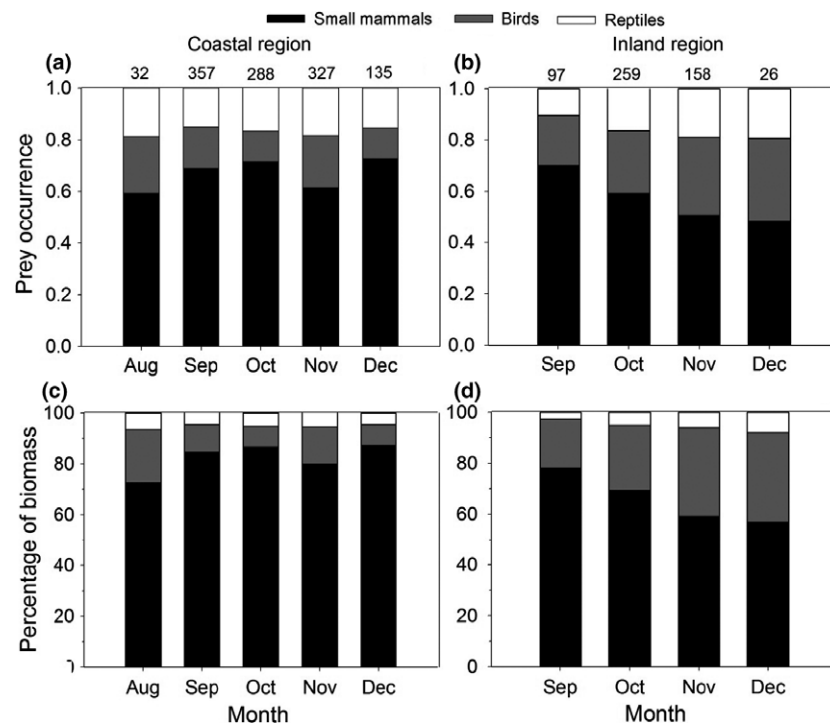
Figure 1. Monthly variation in the proportion of small mammals (black bars), birds (grey dark bars) and reptiles (white bars) in the diet of breeding Black Harriers. (a and c) Occurrence and the percentage of biomass in the coastal region, respectively. (b and d) Occurrence and the percentage of biomass in the inland region, respectively. For coastal regions, proportion of prey was calculated for 2006–2010 and 2012–2015, whereas for inland regions this was only available for the years 2006, 2008, 2009, 2011, 2013 and 2014. Sample sizes (number of identified prey) are indicated above bars, and excluded the prey identified in July ($n = 1679$ total identified prey).

doubled between September and December, when it reached 40% of the total biomass provisioned (Fig. 1b and 1d). In contrast, at coastal nests, diet composition was stable throughout the breeding months (August–December), with a clear predominance of small mammals representing 70–85% of the monthly biomass intake (Fig. 1a and 1c).

These differences in diet were further confirmed by GLMMs, which showed a significant region-by-month interaction explaining the occurrence of small mammals in the diet (Table 1, Fig. 2). The interaction reflected a strong negative relationship between the occurrence of small mammals and month in the inland region (slope: -0.40 ± 0.14) that was almost non-existent along the coast (slope: -0.006 ± 0.06; Fig. 2). When removing the interaction region-by-month from the model, small mammal occurrence in diet differed significantly between regions ($\chi^2_1 = 17.31$, $P < 0.0001$) and was significantly greater in the coastal (LS-means: 0.68 ± 0.09) than in the inland region (LS-means: 0.19 ± 0.13). No effect of winter

rainfall was found on the within-year occurrence of small mammals after taking regional and seasonal factors into account ($\chi^2_1 = 0.03$, $P = 0.87$).

The occurrence of birds in the diet also varied significantly between regions (Table 1), being greater inland (LS-means $\pm$ se: -0.81 ± 0.16) than along the coast (LS-means: -1.60 ± 0.13), but it did not vary with month ($\chi^2_1 = 0.002$, $P = 0.96$). Additionally, after taking regional variation into account, the occurrence of birds in the diet tended to increase with winter rainfall (Table 1, slope: 0.13 ± 0.07).

Seasonal variation in the occurrence of reptiles in the diet also tended to differ between study regions (marginally significant interaction of region-by-month; Table 1), with a seasonal increase in the inland region (slope: 0.33 ± 0.17) and no apparent trend in the coastal region (slope: 0.03 ± 0.07). When removing the interaction region-by-month from the model, the occurrence of reptiles was not significantly different between regions ($\chi^2_1 = 0.02$, $P = 0.90$). Winter rainfall did

Table 1. Results of generalized linear mixed models (GLMMs) of variation in the occurrence of small mammals, birds and reptiles in the Black Harrier diet.

Dependent variables	Explanatory variables	df	χ^2	P
Small mammal occurrence	Month × Region	1	7.69	0.006
Bird occurrence	Region	1	28.83	< 0.0001
	Rainfall	1	3.12	0.08
Reptile occurrence	Month × Region	1	3.50	0.06

df, degrees of freedom. Initial models included region (coastal or inland), month (August–December) and their interaction as explanatory variables. The table shows the best models (the results of comparing models with and without those variables) after stepwise backward selection. When the best model included a significant interaction, individual effects were also maintained. Year (2006–2015) and pellet ID were included as a random effect in all models.
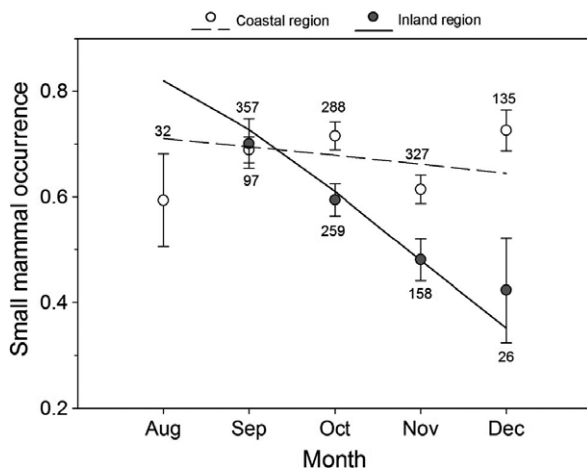
Figure 2. Monthly variation in the occurrence of small mammals in the diet of Black Harriers breeding in coastal (white circles/dashed line) and in inland (dark grey circles/solid line) regions. Lines represent modelled data from the GLMM results. Raw data (circles) are also shown. Sample sizes (number of identified prey) are indicated above/below the error bars.

not explain reptile occurrence in Black Harrier diet ($\chi^2_1 = 0.41$, $P = 0.52$).

When considering maximum temperature instead of region and month, we found that the occurrence of small mammals significantly declined with increasing temperature ($\chi^2_1 = 11.31$, $P = 0.0007$, slope: -0.18 ± 0.05), suggesting that the seasonal regional differences in diet could be linked to differences in maximum temperature. Accordingly, the occurrence of birds and reptiles increased

with maximum temperature ($\chi^2_1 = 5.9$, $P = 0.01$, slope: 0.16 ± 0.06 and $\chi^2_1 = 3.19$, $P = 0.07$, slope: 0.12 ± 0.06, respectively).

Interannual variation in diet with weather

In the coastal region, interannual variation in diet appeared to be correlated with winter rainfall. The average proportion of small mammals in the diet increased with the amount of winter rainfall (Pearson correlation, $r = 0.83$, $P = 0.005$), varying from 46% for years with little rain, up to 83% for wetter years. Conversely, the proportion of birds and reptiles decreased with increasing winter rainfall ($r = -0.85$, $P = 0.004$ and $r = -0.65$, $P = 0.06$, respectively; Fig. 3). The occurrence of birds in the diet varied from 31% during years with little rain, down to 1% during wetter years, and reptile occurrence varied from 23% for years with little rain, to < 1% for wetter years. The annual proportion of each prey type was not significantly related to the yearly average maximum temperature during the breeding months (all $P > 0.2$).

Provisioning rates

Variation in overall provisioning rates, i.e. total items delivered to the nest per hour, was best explained by a significant interaction between region and daytime period (Table 2), indicating that diurnal patterns of provisioning differed significantly between regions. At coastal nests, provisioning rate was similar during mornings (0.81 ± 0.04 prey/h) and midday (0.85 ± 0.04), and decreased slightly during evenings (0.65 ± 0.04). At inland nests, a marked drop in provisioning rates occurred during midday (0.42 ± 0.03) compared with mornings (0.59 ± 0.04) and evenings (0.64 ± 0.06; Fig. 4a). On removing the region-by-daytime period interaction, the provisioning rates significantly differed between regions ($\chi^2_1 = 13.73$, $P = 0.0002$) and were on average 46% greater in the coastal (0.78 ± 0.02 prey/h) than inland region (0.53 ± 0.02 prey/h).

Similar patterns were found when we examined provisioning rates of small mammal prey, for which a significant interaction between regions and daytime period was also found (Table 2). At coastal nests, small mammals were delivered at a similar rate during morning (0.48 ± 0.03) and midday (0.55 ± 0.03), but at a lower rate during
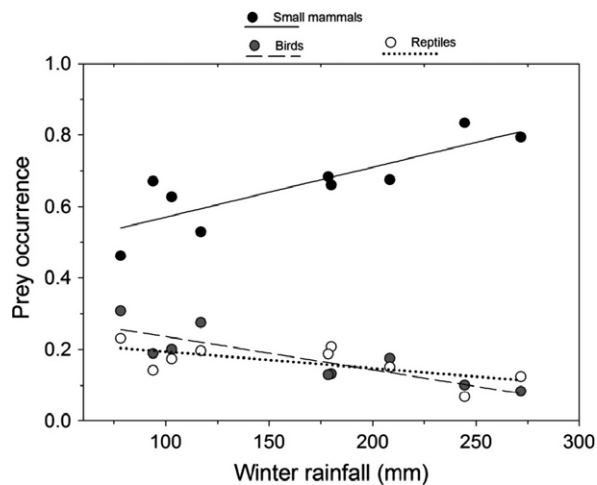
Figure 3. Relationships between winter rainfall (sum of rainfall June–September, in mm) and the yearly occurrence of small mammals (black circles/solid line), birds (dark grey circles/dashed line) and reptiles (white circles/dotted line) in the diet of Black Harriers breeding in the coastal region. Data from the years 2006–2010 and 2012–2015 were analysed.

Table 2. Results of generalized linear mixed models (GLMMs) of differences between daytime periods and regions in prey provisioning rates to nestlings (all prey items, small mammals, birds, reptiles and unidentified items).

Dependent variables	Explanatory variables	df	χ^2	P
Prey provisioning rate	Region × Daytime period	2	11.74	0.003
Small mammal provisioning rate	Region × Daytime period	2	12.67	0.002
Bird provisioning rate	Region × Daytime period	2	5.66	0.06
Reptile provisioning rate	Daytime period	2	7.99	0.02
Unidentified prey provisioning rate	Region	1	5.22	0.02

df, degrees of freedom. Initial models included region (coastal vs. inland), daytime period (morning, midday, evening) and their interaction. The table shows the best models (the results of comparing models with and without those variables) after stepwise backward selection. When the best model included a significant interaction, individual effects were also maintained. Nest identity was included as a random effect in all models.

evening (0.38 ± 0.02). At inland nests, a marked drop in small mammal provisioning rate was observed at midday (0.21 ± 0.02), relative to morning (0.33 ± 0.02) and evening (0.37 ± 0.03); Fig. 4b). Overall, the small mammal provisioning rate was 63% greater in the coastal than

inland region (0.49 ± 0.01 and 0.30 ± 0.01, respectively).

Provisioning rates of birds also varied between regions and diurnally (Table 2). Birds were delivered at a lower rate during evenings (0.030 ± 0.002) than during mornings (0.043 ± 0.002) or midday (0.052 ± 0.002) in the coastal region, whereas in the inland region, birds were delivered at a lower rate during midday (0.061 ± 0.004) but at a similar rate during mornings (0.13 ± 0.01) and evenings (0.10 ± 0.01; Fig. 4c).

Provisioning rates of reptiles only varied diurnally, without regional differences (Table 2): reptiles were delivered about three times more often during morning (0.070 ± 0.003), or midday (0.067 ± 0.003), than evening (0.026 ± 0.001; Fig. 4d).

Provisioning rates of non-identified items varied only between regions (Table 2), being more frequent along the coast (0.170 ± 0.005) than inland (0.100 ± 0.005). No diurnal patterns were found (Fig. 4e).

DISCUSSION

Diet composition of Black Harriers differed between the two study regions, with a greater proportion (and contributed biomass) of small mammals apparent in coastal regions than inland, where birds and reptiles were relatively more frequent in the diet. Overall differences between regions arose through seasonal changes in diet: early in the season (September), diet was similar in both regions, but inland it gradually shifted to fewer mammals with an increasing representation of birds and reptiles.

A possible explanation for this seasonal shift in diet could be that inland breeders have more opportunities for hunting birds later in the season. Inland nests were often surrounded by a mosaic of natural vegetation, pastures and occasionally wheat fields, which may increase the availability of alternative food resources such as reptiles or grassland birds such as Common Quail *Coturnix coturnix* (Ogada 2009, Murgatroyd *et al.* 2016). However, on inspection of provisioning rates, we found that, overall, the frequency of birds or reptiles delivered to inland nests was lower compared with coastal ones, suggesting a constraint rather than an adaptive or opportunistic shift. In other words, the observed seasonal dietary shift in the inland region probably arose from a general decrease in the
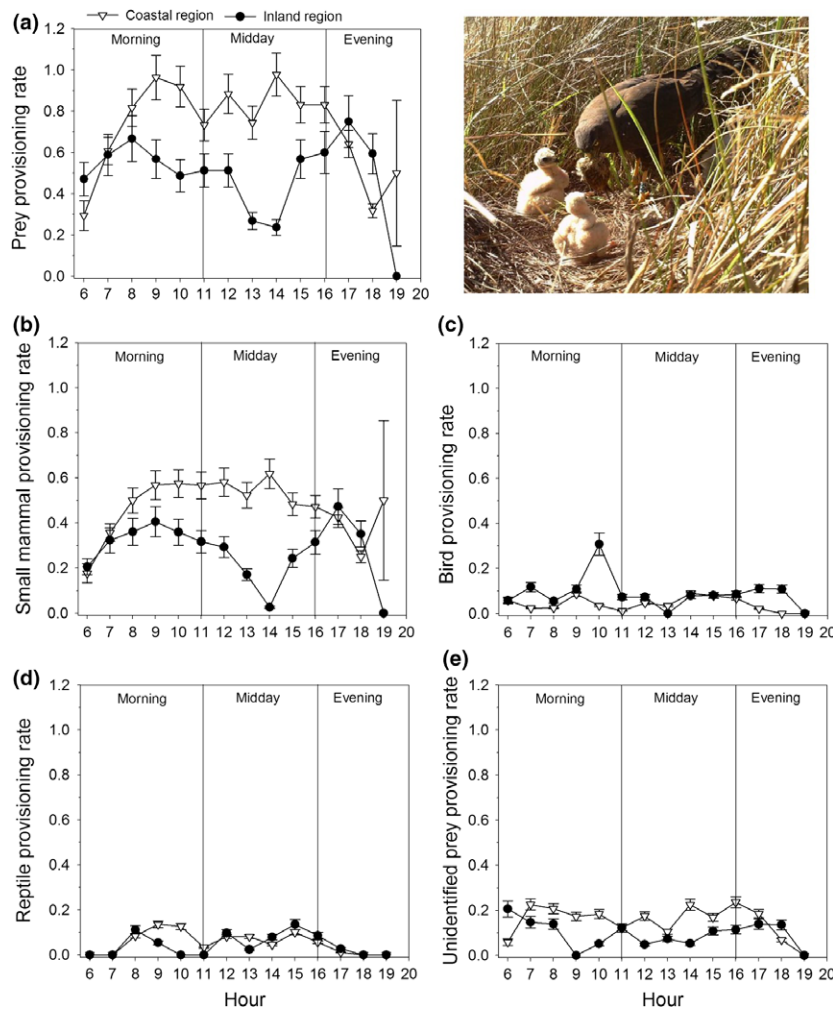
Figure 4. Daytime variation in average (±se) provisioning rates (prey deliveries per hour) at Black Harrier nests (*n* = 18) according to region (coastal in white triangles; inland in black dots). Provisioning rates/h of all prey (a), small mammals (b), birds (c), reptiles (d) and non-identified prey (e). Vertical lines separate the three analysed daytime periods (morning, midday and evening).

availability (i.e. abundance and/or accessibility) of the Black Harrier primary prey (small mammals) in that region later in the breeding season.

Prey provisioning rate analyses showed that provisioning rates of small mammals were reduced during the middle of the day at inland nests, whereas alternative prey such as birds and reptiles remained accessible and available throughout the day. This suggests that the reduced availability of the primary prey may be explained at least partly by temperature-mediated accessibility. Some studies have demonstrated that the Four-striped Mouse shows behavioural flexibility in response to daily temperature fluctuations in the succulent Karoo biome. In this region, the temperatures at midday can exceed 40 °C during summer days (i.e. the latter half of the Black Harrier breeding season), explaining why the peak of activity for the Four-striped Mouse at that time occurs at dusk and dawn (Perrin 1981, Haim *et al*. 1998, Schradin & Pillay 2004, Nater *et al*. 2016). The seasonal decline in the occurrence of small mammals in the Black Harrier diet may thus arise because they become less accessible to foraging Black Harriers during the increasingly hotter midday periods. Accordingly, our models using the monthly average of maximum temperatures revealed that the occurrence of small mammals in the Black Harrier's diet decreased significantly with increasing temperatures. Higher temperatures may also be

indicative of poorer environmental conditions and a concomitant reduction of small mammal reproduction and their overall abundance. Indeed, the breeding season of the Four-striped Mouse is shorter (3 months) in the succulent Karoo biome, where most inland Black Harrier nests are located, than in the Fynbos biome (6 months), where coastal nests are located, essentially due to the milder Mediterranean climate there (Mucina & Rutherford 2006).

Overall, our results support the idea that higher temperatures reduce small mammal availability (either accessibility through diurnal rhythms, abundance through reduced mouse reproduction, or both). It is also possible that regional differences in prey availability and diet depend on factors other than temperature, such as habitat, which may modulate the effect of temperature on small mammal behaviour (Meynard et al. 2012), but this would need to be examined in further studies. We cannot discount the additional, but not mutually exclusive, possibility that high temperatures are detrimental to the Harriers themselves, causing them to reduce hunting effort at midday, particularly at inland sites. This is supported by the observation that breeding birds seek shade at midday, nest on south-facing slopes and return to their nests to shade their young in full midday sun (R. E. Simmons pers. obs.).

We found no association between winter rainfall and small mammal occurrence in the diet after accounting for seasonal and regional differences for all nests. This may arise because the seasonal variation in diet of inland breeders is mostly influenced by temperature (influencing small mammal availability, as explained above) and winter rainfall did not differ between regions during the study years.

However, interannual comparisons for the coastal breeding sites alone revealed a positive association between the amount of winter rainfall and small mammal occurrence in the diet the same year, suggesting that, at least in this region, winter rainfall positively influences the abundance of Four-striped Mice. Some studies have also shown that the Four-striped Mouse abundance also varies with winter rainfall (June–August) in the succulent Karoo biome, where rain promotes the development of small succulent plants, which provide essential food for initiating reproduction, in turn increasing mouse abundance (Schradin & Pillay 2004, Jackson & Bernard 2006, Rymer et al. 2013). So it is possible that rainfall also influences

the overall annual proportion of mice for inland Harriers in this habitat. Winter rainfall probably interacts with temperature in explaining small mammal availability to inland Harriers, but our limited number of sample years for inland nests prevented us from further investigating interannual variation in diet there and its relation to both rainfall and temperature, although this should be addressed in future studies.

We also found that winter rainfall tended to be positively associated with the occurrence of birds in the diet. This suggests that, as alternative prey, birds are more frequently taken (in relation to reptiles) when winter rainfall has been greater, and therefore that winter rainfall may also have a positive influence on local bird abundance. This is corroborated by studies that show that the presence of the frequently taken Common Quail in the succulent Karoo biome is greater following high winter rainfall (Taylor 2005; R. E. Simmons & F. Van der Merwe pers. obs.). Thus, our results overall suggest that winter rainfall positively influences the abundance of both small mammals and birds in both regions, but that small mammals are preferred by Black Harriers when available, and that their availability is also influenced by temperature, which further shapes diet composition.

Among specialist predators, when there is a decline in the availability of the primary prey species in the environment, this is generally mirrored by a decline in reproductive success (Ferrer & Negro 2004, Resano-Mayor et al. 2014). Seasonal declines in breeding performance could thus also be associated with a deterioration of food conditions in the environment, such as certain prey types becoming less abundant or less accessible later in the breeding season (e.g. Bechard 1982, Widen 1994, Ontiveros et al. 2004). In the Black Harrier, an overall seasonal decline of all breeding parameters was found, but these declines were more pronounced for clutch size and productivity in the inland than coastal region (García-Heras et al. 2016). We suggest therefore that the steeper seasonal decline in reproductive output observed inland is likely to be associated with an overall decline in the availability of small mammals throughout the season there. A similar pattern has been found in Mauritius Kestrels Falco punctuates (Cartwright et al. 2014). In that species, the seasonal decline in breeding success was stronger for those territories that contained a higher proportion of agricultural land, and this was partly explained

by a lower availability of native Geckos *Phelsuma* spp., the preferred prey, late in the season in agricultural land (Cartwright *et al.* 2014).

In the case of Black Harriers, however, neither clutch size nor productivity were, on average, significantly different between regions, indicating that differences between regions early and late in the season balanced each other out (García-Heras *et al.* 2016). To explore this hypothesis, future studies of Black Harriers should investigate the link between diet, prey availability and breeding performance at the individual level, and how this varies in space and time.

Conclusions and conservation implications

This study provides evidence of a spatial and temporal (diurnal, seasonal and interannual) variation in dietary composition in an African specialist raptor, which is probably caused by variations in the availability of the primary prey (small mammals), mediated through rainfall and temperature. The seasonal decline in the occurrence of small mammals in the diet of inland Black Harriers coincides with a steeper decline in breeding performance there (García-Heras *et al.* 2016), suggesting that the lower prey availability in the inland region later in the season is probably limiting reproduction there. This concurs with the observation that breeding events were spread over a shorter period in the inland region (García-Heras *et al.* 2016). Conditions for successful breeding, in terms of food availability, mediated through weather and climate, may therefore frequently not be met outside the coastal region. This may provide a limit for the breeding range, which in turn could explain the scarcity of this species. Furthermore, differences in breeding suitability between regions may be exacerbated with climate change, as western regions of the country are expected to become warmer and rainfall more scarce, with longer and more frequent droughts (Simmons *et al.* 2004, Hockey *et al.* 2011, Cunningham *et al.* 2015). This may further limit the breeding suitability of the inland region for Black Harriers if prey availability is limited both by rainfall (inter-annually) and by temperature (diurnal accessibility). Additionally, this part of South Africa, particularly the Renosterveld with richer soils on the southern coast, has been intensively modified and fragmented by agriculture over the last century (Curtis *et al.* 2004). This has reduced the breeding and hunting habitats of several species, including the Black Harrier. Given our results, it would be particularly important to reverse such fragmentation in coastal regions where environmental conditions are more favourable for breeding Black Harriers. Conservation measures have already prioritized the protection of Fynbos vegetation, through the creation of national parks and private reserves. However, a strengthening of the law, reinforcing the protection and conservation of these natural habitats, with the strict prohibition of further habitat destruction, would help to avoid further fragmentation of natural habitats. This would then ensure that coastal regions act as source areas for the sustainability of the global Black Harrier population, and ultimately ensure the sustainable conservation of the species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Assessing diet composition using two methods: pellet analyses and image footage analyses.

Figure S1. Relation between the proportion of (a) small mammal numbers and (b) small mammal biomass derived from image footages and in pellets.

Figure S2. Relation between the proportion of (a) birds numbers and (b) bird biomass derived from image footages and in pellets.

Figure S3. Relation between the proportion of (a) reptile numbers and (b) reptile biomass derived from image footages and in pellets.

Table S1. Average maximum temperature and rainfall per year (2006–2015) and for each region (coastal and inland).