**Regional and temporal variations in diet and provisioning rates suggest weather limits
prey availability for an endangered avian predator.**

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15 **Summary**

16 Understanding variations in food requirements of wild animals is of central importance in
17 population ecology and conservation, as this helps identify where and when food may be
18 limiting. Studies on diet variation or prey provisioning rates may give useful insights when
19 direct information on prey availability is lacking. We report here on spatial-temporal
20 variations in the diet of an endangered predator, the Black Harrier *Circus maurus*. This raptor
21 endemic to southern Africa specializes on small mammals, but also feeds on birds and
22 reptiles as alternative prey. Using 1,679 prey identified in ca. 1000 pellets collected in inland
23 and coastal regions during 2006-2015, we show that diet composition hardly changes
24 throughout the breeding season in the coastal region. By contrast, we show a marked seasonal
25 decline in the occurrence of small mammal prey in the inland region, with a concomitant
26 increase of alternative prey. Proportion of small mammals in the diet declined with increasing
27 maximum temperatures, the latter being highest inland late in the breeding season. Using
28 camera recordings at nests in 2014, we further analysed daily patterns of prey provisioning to
29 nestlings. We show that a marked reduction in small mammal (but not other prey)
30 provisioning rates occurred during midday in the hotter inland region, but not in the cooler
31 coastal region. Reduced availability of the primary prey, i.e. small mammals, in hotter
32 temperatures, through a reduction of activity or overall abundance, could explain these
33 patterns. Finally, we also show a positive relationship between winter rainfall and inter-
34 annual differences in the proportion of small mammals in the diet of harriers breeding in the
35 coastal region, suggesting relationships between diet and prey abundance mediated through
36 rainfall. We discuss the need to consider spatial variations in food availability for
37 conservation strategies.

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39 **Keywords:**

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

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45 Introduction

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

52 However, quantifying and measuring the availability of prey in the environment
53 remains a difficult and challenging task for many species (Rosenberg & Cooper 1990, Smith
54 & Rotenberry 1990). Studies on diet variation may nevertheless give relevant and useful
55 insights on these factors when direct information on prey availability is lacking (e.g. Amar *et*
56 *al.* 2003, Terraube *et al.* 2011, Cartwright *et al.* 2014), particularly for specialist predators.

57 Unlike generalists, specialist predators use a narrow range of resources, feeding primarily on
58 one food resource when accessible (see Pyke *et al.* 1977, Stephens *et al.* 2007). Changes in
59 diet composition (i.e. a higher proportion of alternative prey in the diet) in these species arise
60 primarily if the availability of the primary prey decreases (Newton 1998, Arroyo & García
61 2006). Additionally, in the absence of prey abundance data, an indirect way to evaluate food
62 availability in the environment may be to assess foraging yields (i.e. number of individual
63 caught per unit time of hunting, e.g. Simmons 2000, Terraube *et al.* 2011) or prey
64 provisioning rates at nests via direct observations (Amar *et al.* 2003, Leckie *et al.* 2008) or
65 using automated camera recording at nests (Zárybnická *et al.* 2012, Schroeder *et al.* 2013,
66 Robinson *et al.* 2016).

67 For specialist species of conservation concern, it is paramount to identify under which
68 conditions food is limiting. Specialist species are indeed known to be less efficient while
69 hunting alternative prey (Terraube *et al.* 2011). In this context, a reduction in the availability
70 of primary prey in the environment may contribute to reducing individual's breeding
71 performance, and potentially have broader implications for the entire population (Newton
72 1979, 1998).

73 The ground-nesting Black Harrier *Circus maurus* is a scarce raptor endemic to
74 southern Africa. Its population size has been estimated at less than 1,000 breeding individuals
75 and the species is currently considered Endangered in South Africa, Namibia and Lesotho,
76 which corresponds to its whole distribution range (Simmons *et al.* 2015, Taylor 2015). This

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medium-sized bird 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 confirmed as a small mammal specialist, with the Four-Striped Mouse *Rhabdomys pumilio*; hereafter "Striped Mouse") 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 explored. No quantitative data exist on the availability of the range of prey taken by this species over the landscape it occupies. Rainfall is considered as 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 Striped Mouse (Taylor & Green 1976, Jackson & Bernard 2006). In this context, higher winter rainfall would be expected to be associated with a greater abundance of small mammals. On the other hand, high temperatures are also known to induce a reduction of the activity of South African small mammals, such as the Striped Mouse (Nater *et al.* 2016). Therefore, high temperatures, e.g. those occurring at mid-day as the breeding season extends into summer, would be expected to be associated with a lower accessibility of small mammals.

In this paper, our aim was to investigate the spatial and temporal variations of diet of breeding Black Harriers in South Africa. Using a large data set of 1,679 identified prey from ca. 1,000 pellets collected at active nests during 2006-2015, we looked at temporal and regional variations of diet, and investigated diet variation according to winter rainfall and maximum temperatures. We hypothesized that the occurrence of small mammals in Black Harrier's 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 (-33.700° S, 18.45° E; -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 either as coastal or inland, depending on their location and altitude: coastal nests were defined as those within 15 km from the coast and with a maximal altitude of 100 mASL, and those located further than 15 km from the coast and with an altitude higher than 100 mASL 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 specific breeding pair. 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 (i.e. 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 when only fur, feathers or scales were found. However, for a sub-sample of pellets with fur only ($n = 105$), hair imprint analysis allowed us to identify if more than one small mammal species was present (see García-Heras *et al.* 2017).

We further estimated the relative biomass for each prey as follows: 1) for prey identified to species levels, using the average weight described for the species in Stuart and Stuart (2015); 2) for broader prey categories (e.g. “unidentified small mammals” or “unidentified birds”), using an estimated average weight, based on that of identified prey of the same taxonomic level (see García-Heras *et al.* 2017).

Pellet collection occurred between July-December in the coastal region and September-December in 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 as when the pellet was collected in the field). For simplicity, we henceforth refer to months of collection as “month”.

A total of 953 pellets was 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 analysis 2 pellets found in July (one in 2006 and one in 2011, totalling 6 identified prey) because they could not be confirmed to correspond to breeding birds. In the coastal region, pellets were collected in all study years, while 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. 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, 7 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 to 41 days old, and were camouflaged and covered with vegetation to avoid disturbing the breeding harriers 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 7 nests were monitored between 6 - 31 October. Cameras were either set to shoot an image every 5 seconds, or to record a 60 second video sequence upon movement detection (with a time lapse of 1 second between two consecutive videos), and active from sunrise until sunset (e.g. 06h00 – 19h59). We obtained a total of 1,557 videos and 90,692 minutes of recordings (527 ± 40.2 min per nest, range 397–665 min). 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

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those nests for which we had both pellets and cameras, diet identified with both methods correlated with each other when the proportion of unidentified prey in cameras was low (see Supplementary information). When the proportion of unidentified prey was high, the camera data became less reliable. We therefore preferred 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.

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 7 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 calculated 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 harriers. Monthly average daily maximum temperature data (°C) from the 7 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 ± 22 (SD) km.

Statistical analyses

We used R 3.2.3 (the R Foundation for statistical computing, 2015) for all statistical analyses.

Regional and seasonal variations in diet

We wanted to test the effects of month (seasonal variations), region, winter rainfall and maximum temperature on the occurrence of the different prey groups (small mammals, birds and reptiles) in Black Harrier diet. However, some of the above-mentioned variables are inter-linked, and could thus be collinear. So, we first investigated whether winter rainfall differed between years and regions, and whether maximum temperatures differed between years, regions and months. For this, we conducted Generalised Linear Mixed Models

(GLMMs), where 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 (10-level factor) and region (2-level factor: coastal vs. inland) were fitted as explanatory variables, while in the model for maximum temperature, year, region, month (continuous variable ranging from 8 -August- to 12 -December), and the interaction region x month were fitted as explanatory variables. In both models, 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 (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 for 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.

While “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 in order 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 of 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 then and we assumed that they represented diet during the previous month.

A stepwise backward procedure was performed for model selection (with the function `drop1`), where likelihood ratio χ^2 tests (LRT) on the residual sum of squares of models with and without interactions or individual variables were used for model selection (Zuur *et al.* 2009).

Inter-annual variations in diet with weather

To investigate 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 variations 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 logit link function; Bates *et al.* 2012), and the log of duration of the “recording time” fitted as an offset. “Recording time” was 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 from the same nest. We categorized recording hours (06h00-19h59) in three categories (hereafter referred as “daytime periods”) as follows: morning (06h00-10h59), midday (11h00-15h59) and evening (16h00-19h59). Daytime periods (3-level factor), region and their interaction were included as explanatory variables.

As above, a stepwise backward procedure was performed for model selection (with the function drop1), and likelihood ratio χ^2 tests (LRT) on the residual sum of squares of models with and without interactions or variables were used to select the best models (Zuur *et al.* 2009). All data are presented as means $\pm$ SE.

RESULTS

Temporal and spatial variations in weather

Winter rainfall varied significantly among 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 ($\chi^2_1 = 8.2$, $P = 0.004$; LS means $\pm$ SE: 23.0 ± 0.94 and 26.7 ± 0.90 for coastal and inland regions, respectively). The interaction month $\times$ region was not significant ($\chi^2_1 = 0.01$, $P = 0.91$). These results indicated that maximum temperature co-varied with region and month and these variables were therefore, collinear. Of all years in the inland region, 2008 was the hottest and wettest, and 2011 was the coolest and driest (Table 1).

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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); they were mostly replaced by birds and some reptiles (i.e. lizards). Indeed, the relative proportion of bird numbers and biomass in the diet doubled between September and December, when it reached 40% of the total biomass provisioned (Fig. 1b, d). By 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, c).

These differences in diet were further confirmed by GLMMs models, which showed a significant region $\times$ month interaction explaining the occurrence of small mammals in the diet (Table 2 and 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 x 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 $\pm$ SE: 0.68 ± 0.09) than in the inland region (LS means $\pm$ SE: 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 2), being greater inland (LS means $\pm$ SE: -0.81 ± 0.16) than along the coast (LS means $\pm$ SE: -1.60 ± 0.13), but 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 2, 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 x month; Table 2), 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 x 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 not explain reptile occurrence in the Black Harrier's 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 temperatures ($\chi^2_1 = 11.31$, $P = 0.0007$, slope: -0.18 ± 0.05), suggesting that the seasonal regional differences in diet could be linked with differences in maximum temperature. Accordingly, the occurrence of birds and reptiles increased with maximum temperature ($\chi^2_1 = 5.9$, $P = 0.01$, slope: $+0.16 \pm 0.06$ and $\chi^2_1 = 3.19$, $P = 0.07$, slope: $+0.12 \pm 0.06$, respectively).

Inter-annual variations in diet with weather

In the coastal region, inter-annual variations 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). Bird occurrence 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 explained by a significant interaction between region and daytime period (Table 3), indicating that diurnal patterns of provisioning differed significantly between regions. At coastal nests, provisioning rate was similar during mornings (0.81 ± 0.04 prey/hr) and midday (0.85 ± 0.04), and decreased slightly during evenings (0.65 ± 0.04). At inland nests, by contrast, 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 interaction region $\times$ daytime period, 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/hr) than in the inland region (0.53 ± 0.02 prey/hr).

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 3). At coastal nests, small mammals were delivered at a similar rate during mornings (0.48 ± 0.03) and midday (0.55 ± 0.03), but at a lower rate during evenings (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 evenings (0.37 ± 0.03); Fig. 4b). Overall, the small mammal provisioning rate was 63% greater in the coastal than in the inland region (0.49 ± 0.01 and 0.30 ± 0.01 , respectively).

Provisioning rates of birds also varied between regions and diurnally (Table 3). 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 3): reptiles were delivered about three time more often during mornings (0.070 ± 0.003), or midday (0.067 ± 0.003), than evenings (0.026 ± 0.001) (Fig. 4d).

Provisioning rates of non-identified items only varied among regions (Table 3), being more frequent along the coast (0.170 ± 0.005) than inland (0.100 ± 0.005), whereas 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. Interestingly, 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 first possible explanation for this seasonal shift in diet could be that inland breeders have more opportunities of 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 like Common Quails *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 than at 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 availability (i.e. abundance and or/ accessibility) of the Black Harriers primary prey (small mammals) in that region later in the breeding season.

Prey provisioning rate analyses showed that provisioning rates for 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 supports the idea that the reduced availability of the primary prey may be at least partly explained by temperature-mediated accessibility. Some studies have indeed demonstrated that the 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 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's 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 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 mammals' reproduction and their overall abundance. Indeed, the breeding season of the Striped Mouse is shorter (i.e. 3 months) in the succulent Karoo biome, where most inland Black Harriers nests are located, than in the Fynbos biome (i.e. 6 months), where coastal nests are located, essentially due to a milder the Mediterranean-like climate there (Mucina & Rutherford 2006).

Overall, our results support the idea that hotter temperatures reduce small mammal availability (either accessibility through diurnal rhythms, abundance through reduced mice 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 (RES, *personal observations*).

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, inter-annual 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 Striped Mice. Some studies have also shown that the 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 and, in turn, increases 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 harrier nests in this habitat. While winter rainfall probably interacts with temperature in explaining small mammal availability to inland harriers, our limited number of sample years for inland nests disallowed us investigating further inter-annual variation in diet there and its relation to both rainfall and temperature. But this should be contemplated 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 *Coturnix coturnix* in the succulent Karoo biome is greater following high winter rainfall (Taylor 2005; RES and F. Van der Merwe *personal observations*). 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 will be preferred by Black Harriers when available, and that their availability is also influenced by temperature, which further shapes diet composition.

Among specialist predators, when the availability of the primary prey species declines 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 in the inland than in the coastal region for clutch size and productivity (García-Heras *et al.* 2016). We suggest therefore, that the steeper seasonal decline observed inland is most likely associated with an overall decline in the availability of small mammals throughout the season there. A similar pattern has for example been found in Mauritius Kestrels *Falco punctuates* (Cartwright *et al.* 2014). In this 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). Future studies in 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, in order to explore this hypothesis.

Conclusions and conservation implications

This study provides evidence of a spatial and temporal (diurnal, seasonal and inter-annual) 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 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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Comentario [BAL5]: Quitamos esto?

References

Amar, A., Redpath, S. & Thirgood S. 2003. Evidence for food limitation in the declining Hen Harrier population in the Orkney Island, Scotland. *Biological Conservation*. **111**: 377-384.

521 | **Arroyo, B. & Garcia, J.T.** 2006. Diet composition influences annual breeding success of
522 Montagu's Harriers (*Circus pygargus*) feeding on diverse prey: capsule diet diversity was
523 positively related to nest failure in Montagu's Harriers. *Bird study*. **53**: 73-78.

524 **Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai,**
525 **B., Grothendieck, G. & Green, P.** 2012. Lme4: Linear mixed –effects models using S4
526 classes. R package ver. 0.999999-0.

527 **Bechard, M.J.** 1982. Effect of vegetative cover on foraging site selection by Swainson's
528 Hawk. *Condor*. **84**: 153-159.

529 **Cartwright, S.J., Nicoll, M.A., Jones, C.G., Tatayah, V. & Norris, K.** 2014. Agriculture
530 modifies the seasonal decline of breeding success in a tropical wild bird population.
531 *Journal of Applied Ecology*. **51**: 1387-1395.

532 **Cunningham, S.J., Madden C.F., Barnard, P. & Amar, A.** 2015. Electric crows:
533 powerlines, climate change and the emergence of a native invader. *Diversity and*
534 *Distribution*. **22**: 17-29.

535 **Curtis, O., Simmons, R.E. & Jenkins, A.R.** 2004. Black Harrier (*Circus maurus*) of the
536 Fynbos Biome, South Africa: a threatened specialist or an adaptable survivor? *Bird*
537 *Conservation International*. **14**: 233-245.

538 **Curtis, O.** 2005. Responses of raptors to habitat fragmentation: from individual responses to
539 population susceptibility. Masters thesis, University of Cape Town, South Africa.

540 **Elkins N.** 1983. Weather and bird behaviour. T & AD Poyser, Calton, UK.

541 **Ferrer M. & Negro J.J.** 2004. The near extinction of two large European predators: super
542 specialists pay a price. *Conservation Biology*. **18**: 344-349.

543 | **García-Heras, M-S., Arroyo, B., Mougeot, F., Amar, A. & Simmons, R.E.** 2016. Does
544 timing of breeding matter less where the grass is greener? Seasonal declines in breeding
545 performance differ between regions in an endangered endemic raptor. *Nature*
546 *Conservation*. **15**:23-45.

547 **García-Heras, M-S., Mougeot, F., Arroyo, B., Avery, G., Avery, M.D. & Simmons, R.E.**
548 2017. Is the Black Harrier *Circus maurus* a specialist predator? Assessing the diet of a
549 threatened raptor species endemic to Southern Africa. *Ostrich: Journal of African*
550 *Ornithology*, online. Doi: [10.2989/00306525.2016.1257515](https://doi.org/10.2989/00306525.2016.1257515)

551 **Haim, A., Van Aarde, R.J. & Zisapel, N.** 1998. Body Temperature daily rhythms in the
552 Striped Mouse *Rhabdomys pumilio*: the effects of α and β blockade. *Physiology and*
553 *Behaviour*. **63**: 889-893.

Con formato: Inglés (Reino Unido)

Con formato: Inglés (Reino Unido)

554 **Hockey, P.A.R., Sirami, C., Ridley, A.R., Midgley, G.F. & Babiker, H.A.** 2011.
 555 Interrogating recent range changes in South African birds: confounding signals from land
 556 use and climate change present a challenge for attribution. *Diversity and Distribution*. **17**:
 557 254 – 261.

558 **Jackson, C. & Bernard, R.T.F.** 2006. Variation in the timing of reproduction of the four-
 559 striped field mouse (*Rhabdomys pumilio*), in the Eastern Cape Province, South Africa.
 560 *African Zoology*. **41**: 301-304.

561 **Leckie, F.M., Arroyo, B., Thirgood, S.J. & Redpath, S.M.** 2008. Parental differences in
 562 brood provisioning by Hen Harriers (*Circus cyaneus*). *Bird Study*. **55**: 209-215.

563 **Lepage, D. & Lloyd, P.** 2004. Avian clutch size in relation to rainfall seasonality and
 564 stochasticity along an aridity gradient across South Africa. *Ostrich*. **75**: 259-268.

565 **Manning, J.** 2007. Field guide to Fynbos. Struik Publisher (Pty) Ltd, South Africa. p. 507.

566 **Meynard, C.N., Pilla, N., Perrigault, M., Caminade, P. & Ganem, G.** 2012. Evidence of
 567 environmental niche differentiation in the Striped Mouse (*Rhabdomys* sp.): inference from
 568 its current distribution in South Africa. *Ecology and Evolution*. **2**: 1008-1023.

569 **Mucina L. & Rutherford M.C.** 2006. The Vegetation of South Africa, Lesotho and
 570 Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, South
 571 Africa. p 808.

572 **Murgatroyd, M., Avery, G., Underhill, L. & Amar, A.** 2016. Adaptability of a specialist
 573 predator: the effects of land use on diet diversification and breeding performance of
 574 Verreaux's Eagles. *J. Avian Biol.* **47**: 001-012.

575 **Nater C., Canale C.I., Van Benthem K.J., Yuen C.H., Schoepf I., Pillay N., Ozgul A. &**
 576 **Schradin C.** 2016. Interactive effects of exogenous and endogenous factors on
 577 demographic rates of an African rodent. *Oikos*. **125**: 1838-1848.

578 **Newton, I.** 1979. Population ecology of raptors. T & AD Poyser, Berkhamsted, UK.

579 **Newton, I.** 1998. Population limitation in birds. Academic Press, London.

580 **Ogada, D.L.** 2009. Impacts of agriculture on the diet and productivity of Mackinder's Eagle
 581 Owls (*Bubo capensis mackinderi*) in Kenya. *Biotropica*. **41**: 485-492.

582 **Ontiveros, D., Pleguezuelos, J.M. & Caro, J.** 2004. Prey density, prey detectability and
 583 food habits: the case of Bonelli's Eagle and the conservation measures. *Biological*
 584 *Conservation*. **123**: 19-25.

585 **Perrin, M.R.** 1981. Notes on the activity of 12 species of Southern African rodents and a
 586 new design of activity monitor. *South African Journal of Zoology*. **16**: 248-258.

Con formato: Inglés (Reino Unido)

587 **Preston, C.** 1990. Distribution of raptor foraging in relation to prey biomass and habitat
588 structure. *Condor*. **92**: 107-112.

589 **Pyke, G.H., Pulliam, H.R. & Charnov, E.L.** 1977. Optimal foraging: a selective review of
590 theory and tests. *The Quarterly Review of Biology*. **52**: 137-154.

591 **Resano-Mayor, J., Hernández-Matías, A., Real, J., Moleón, M., Parés, F., Inger, R. &**
592 **Bearhop, S.** 2014. Mutli-scale effects of nestling diet on breeding performance in a
593 terrestrial top predator inferred from stable isotope analyses. *PLoS ONE*. **9**: e95320.

594 **Rosenberg K. & Cooper, R.J.** 1990. Approaches to avian diet analysis. *Studies in Avian*
595 *Biology*. **13**: 80-90.

596 **Robinson, B.G., Franke, A. & Derocher, A.E.** 2016. Weather-mediated decline in prey
597 delivery rates causes food-limitation in a top avian predator. *Journal of Avian Biology*
598 online (doi: [10.1111/jav.01130].)

599 **Rymer, T.L., Pillay, N. & Schradin, C.** 2013. Extinction or survival? Behavioral flexibility
600 in response to environmental change in the African Stripes Mouse (*Rhabdomys*).
601 *Sustainability*. **5**: 163:186.

602 **Schroeder E.L., Boal C.W. & Glasscock S.N.** 2013. Nestlings diets and provisioning rates
603 of sympatric golden-fronted and ladder-backed woodpeckers. *The Wilson Journal of*
604 *Ornithology*, 125: 188-192.

605 **Schlaich A.E., Klaassen R.H.G., Bouten W., Both C. & Koks B.J.** 2015. Testing a novel
606 agri-environment scheme based on the ecology of the target species, Montagu´s harrier
607 *Circus pygargus*. *Ibis*. 157: 713-721.

608 **Schradin, C. & Pillay, N.** 2004. The Stripped Mouse (*Rhabdomys pumilio*) from the
609 succulent Karoo, South Africa: a territorial group-living solitary forager with communal
610 breeding and helpers at the nest. *Journal of Comparative Psychology*. **118**: 37-47.

611 **Schulze, R.E.** 1997. Climate. In *Vegetation of Southern Africa* (Cowling, R. M., D. M.
612 Richardson, and S. M. Pierce, Editors). Cambridge University Press, Cambridge, UK. pp
613 21-42.

614 **Simmons, R.E.** 2000. *Harriers of the World: their behaviour and ecology*. Oxford University
615 Press, Oxford. pp 297-299.

616 **Simmons, R.E., Brown, C.J. & Kemper, J.** 2015. *Birds to watch in Namibia: red, rare and*
617 *endemic species*. Ministry of Environment & Tourism, Windhoek, Namibia.

Con formato: Inglés (Reino Unido)

- Simmons, R.E., Barnard, P., Dean W.R.J., Midgley, G.F., Thuiller, W. & Hughes, G.** 2004. Climate change and birds: perspectives and prospect from Southern Africa. *Ostrich: Journal of African Ornithology*. **75**: 295-308.
- Smith, K.G. & Rotenberry, J.T.** 1990. Quantifying food resources in avian studies: present problems and future needs. *Studies in Avian Biology*. **13**: 3-5.
- Stephens D.W., Brown, J.S. & Ydenberg R.C.** 2007. Foraging: behavior and ecology. University of Chicago Press, Chicago. p. 576.
- Steyn P.** 1982. Birds of Prey of Southern Africa. David Philip, Cape Town. p. 312.
- Stuart C. & Stuart M.** 2015. Stuart's field guide to mammals of Southern Africa including Angola, Zambia and Malawi. Hirt & Carter Cape (Pty) Ltd, Fifth Edition 2015. p. 456.
- Taylor, P.B.** 2005. Common Quail (*Coturnix coturnix*). In: Roberts birds of Southern Africa, Hockey, P. A. R., W. R. J. Dean, and P. G. Ryan. John Voelcker Bird Book Fund, Cape Town, South Africa. pp 75-76.
- Taylor, K.D. & Green, M.G.** 1976. The influence of rainfall on diet and reproduction in four African rodent species. *Journal of Zoology*. **180**: 367-389.
- Taylor, M., Peacock, F. & Wanless, R.** 2015. The 2015 Eskom Red data book of birds of South Africa, Lesotho and Swaziland. Birdlife South Africa Johannesburg.
- Terraube, J., Arroyo, B., Madders, M. & Mougeot, F.** 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos*. **120**: 234-244.
- The R foundation for statistical computing.** 2015." Wooden Christmas-Tree", copyright © Platform: x86_64-w64-mingw32/x64 (64-bit).
- Van der Merwe F.** 1981. Review of the status and biology of the Black Harrier. *Ostrich: Journal of African Ornithology*. **52**: 193-207.
- Widen, P.** 1994. Habitat quality for raptors: a field experiment. *J. Avian Biol.* **25**: 219-223.
- Zárybnická, M., Korpimäki, E. & Griesser, M.** 2012. Dark or short nights: differential latitudinal constraints in nestling provisioning patterns of a nocturnally hunting bird species. *PLoS ONE*. **7**: e36932.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M.** 2009. Mixed effects models and extensions in Ecology with R, in Statistics for Biology and Health. *Springer Science & Business Media*, LLC 2009. P 574.

651 Table 1. Average maximum temperature and rainfall per year (2006-2015) and for each
 652 region (coastal and inland).

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	Year	Average maximum temperature August-December $\pm$ SD	Average rainfall August-December $\pm$ SD
Coastal region	2006	16.8 $\pm$ 0.3	81.6 $\pm$ 9.5
	2007	23.6 $\pm$ 4.0	176.9 $\pm$ 48.4
	2008	21.6 $\pm$ 1.3	244.6 $\pm$ 0
	2009	22.0 $\pm$ 2.1	111.4 $\pm$ 55.1
	2010	21.9 $\pm$ 1.0	89.6 $\pm$ 45.6
	2011	21.1 $\pm$ 0.6	100.9 $\pm$ 53.0
	2012	23.9 $\pm$ 2.4	208.5 $\pm$ 37.2
	2013	20.5 $\pm$ 2.5	271.6 $\pm$ 4.3
	2014	24.7 $\pm$ 1.8	178.6 $\pm$ 2.3E-05
	2015	24.7 $\pm$ 1.4	102.8 $\pm$ 9.8E-06
Inland region	2006	27.1 $\pm$ 2.4	169.2 $\pm$ 86.5
	2008	29.4 $\pm$ 1.0 E-6	280.2 $\pm$ 8.8E-06
	2009	26.9 $\pm$ 0.4	280.2 $\pm$ 7.8E-6
	2011	26.8 $\pm$ 1.5	91.1 $\pm$ 49.7
	2013	26.8 $\pm$ 2.1	231.1 $\pm$ 69.9
	2014	28.2 $\pm$ 2.3E-6	127.2 $\pm$ 66.8

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Table 2. Results of the Generalized Linear Mixed Models (GLMMs) testing for variation in the occurrence of small mammals, birds and reptiles in the Black Harrier's diet. 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. DF: degree of freedom.

Dependent variables	Explanatory variables	DF	Chi-square	P
Small mammal occurrence				
	Month x Region	1	7.69	0.006
Bird occurrence				
	Region	1	28.83	< 0.0001
	Rainfall	1	3.12	0.08
Reptile occurrence				
	Month x Region	1	3.50	0.06

Table 3. Results of the Generalized Linear Mixed Models (GLMMs) testing for differences between daytime periods and regions in prey provisioning rates (prov. rate) to nestlings (all prey items, small mammals, birds, reptiles and unidentified items). 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. d.f.: degree of freedom.

Dependent Variables	Explanatory Variables	DF	Chi-square	P
Prey provisioning rate				
	Region x Daytime period	2	11.74	0.003
Small mammal provisioning rate				
	Region x Daytime period	2	12.67	0.002
Bird provisioning rate				
	Region x 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

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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) respectively show the occurrence and the percentage of biomass in the coastal region, whereas (b) and (d) respectively show the occurrence and the percentage of biomass in the inland region. For coastal regions, proportion of prey was calculated for 2006-2010 and 2012-2015, while 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= 1,679 total identified prey).

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 (grey dark 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.

Figure 3. Relationships between winter rainfall [sum of rainfall June-September (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.

Figure 4. Daytime variation in average ($\pm$ 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/hr 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).

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711 **FIGURE 1.**

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