Too hot to handle: How Martial Eagles (*Polemaetus bellicosus*) manage the heat in the Kruger National Park, South Africa

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ABSTRACT

Climate change poses a serious threat to biodiversity across the globe. Shifting weather patterns and increasing temperatures present serious challenges to species' ability to persist in an environment. However, how species react to changing climatic conditions can vary between species, with some species better able to adapt to such changes than others, either through physiological processes or behavioural adaptation. Changing climatic conditions can alter a species' ability to acquire the resources they need to survive, but the mechanism of how this occurs can be complex. For predatory species, in particular, we do not have a good understanding of how different climatic conditions may affect predator-prey interactions, which may be key to understanding how well a species can persist in the future.

The ability of predators to cope with a changing climate may be influenced by the level of specialism in their diet, with more generalist species expected to be better able to cope with changes in climate than more specialised species because they can in theory, switch between prey. By contrast, predatory species with more specialised diets may be more vulnerable to the effects of climate change, should the availability of their key prey species be strongly affected by climatic conditions, since they may have limited opportunities to switch to an alternative food source. However, empirically, we know little about how predator species switch between different prey types under different climate conditions.

In this study, we explore the influence of climate on the ability of a generalist predator, the Martial Eagle (*Polemaetus bellicosus*), to provision prey and how their diet varies with climate conditions. We installed cameras to remotely monitor nests in the Kruger National Park, where previous studies revealed a large population decline and where temperatures during the breeding season have increased dramatically over the last few decades. We recorded a total of 772 camera trap days (9312 hours) during the chick rearing period from 12 nests between 2018 to 2022. Cameras took photos every five minutes, and these photographs were then assessed to identify occurrences of prey deliveries (n=793). Where possible, prey items were identified down to the lowest possible taxonomic level (n = 751). We then explored how maximum daily temperature (T_{max}) and occurrence of rainfall (R_{day}) influenced prey provisioning and the overall biomass delivered to a nest per day. Prey provisioning rates peaked at around 1.4 items delivered on days with a T_{max} of 25°C but then declined with

increasing temperatures to around half that value when temperatures exceeded 40°C. However, despite fewer food items being delivered in hotter conditions, biomass delivered per day did not show a corresponding decline, remaining stable across the temperature gradient. These contrasting patterns were explained by the relationship between the average size of the prey items delivered in relation to temperature, with heavier prey items being delivered in hotter conditions. Thus, this species appeared to be able to buffer the negative influence of higher temperatures on prey captures by shifting to predate large prey items. To further explore these results, we assessed the delivery likelihood of each phylum of prey (reptiles, mammals or birds) in relation to climatic conditions. We found that in hotter conditions, the types of prey delivered shifted with fewer birds and more reptiles being delivered. Mammals on the other hand were not influenced by climatic variables. Reptile prey (principally monitor lizards, *Varanus* spp.) was significantly larger than bird prey, and explained the apparent increase in prey size at higher temperatures.

These results indicate that the dietary requirements of Martial Eagle may be potentially buffered from the effects of climate change through their ability to provision a wide diversity of prey. These differences are most likely due to these prey types having differing physiological and behavioural responses across the temperature gradient. However, the impact of dietary shifts such as this on Martial Eagles are not entirely clear, because it may be that reptile prey is lower quality compared to bird prey and this dietary shift may influence the fitness of the developing chicks and could have longer term impacts on their subsequent fitness, which would not be immediately evident without considerable further work.

INTRODUCTION

Climate change poses a significant and immediate threat to biodiversity as global temperatures continue to rise, leading to widespread ecological disruptions and habitat loss (Travis, 2003; Holyoak & Heath, 2016). Additionally, extreme weather events contribute to mass mortalities, thus, altering the abundance and distribution of species across habitats (Easterling et al., 2000). As a result, the rate of species extinction across all taxonomic groups is increasing, underscoring the severity of the crisis (Sinervo et al., 2010; Urban, 2015). However, the degree to which individual species are influenced by climate change is influenced by their sensitivity (degree to which the species is affected) and the adaptive capacity (the potential of the species to adjust) (Payne et al., 2023). A species' adaptive capacity includes the physiological and behavioural mechanisms they employ to cope with climatic changes, which are still relatively poorly understood (Boyles et al., 2011). Thus, recognizing whether climate change influences a species and assessing the degree to which a species exhibits physiological or behavioural plasticity to cope with change, is a crucial step for conservation action plans in the future (Martínez-Ruiz et al., 2023).

Rising temperatures and altered weather patterns can disrupt the suitability of habitats, forcing species to undergo population shifts in search of more favourable conditions (Mantyka-pringle, Martin & Rhodes, 2012; Holyoak & Heath, 2016; García-Palacios et al., 2018). The effects of these phenological shifts are not only restricted to space-use, but may also affect behavioural patterns across time (Blois et al., 2013). These shifts occur when a species is physiologically incapable of tolerating the new climatic extremes or lacks the required behavioural plasticity to adapt their behaviour to suit new climatic conditions (Redpath et al., 2002; Cunningham, Martin & Hockey, 2015; Conradie et al., 2019; Hall & Chalfoun, 2019). For example, in order to attain physiologically active body temperatures, heliothermic *Sceloporus* lizards need to bask in the sun, however, when temperatures exceed critical maximums, the lizards must retreat into refugia or risk heat-induced death. Concerningly, the extent of time spent in refugia will limit foraging, growth and reproduction rates, thus negatively influencing population growth rates and risking extinction (Sinervo et al., 2010). Additionally, in environments where critical maximum temperatures regularly exceed the historical average, species may struggle to acquire food at a suitable rate, either leading to immediate exodus, declines in fitness, cessation of breeding attempts or decreased breeding success, resulting in a steady population decline (Redpath et al., 2002; Cunningham, Gardner & Martin, 2021; Oswald & Conradie, 2023). For example, high daily maximum air temperature (T_{max}) significantly reduces weight gain of young Common Fiscal (*Lanius collaris*) nestlings, and the more frequently T_{max} exceeds critical temperature levels the lower the fledging body weight, which delays the timing of fledging, leading to an increased risk of predation (Cunningham et al., 2013). These various disruptions can have cascading effects on the interconnected relationships within ecosystems, for example, leading to changes in predator-prey dynamics (Jagielski et al., 2021).

The relationship between predators and their prey is sensitive to climate-induced changes (Riou et al., 2011; Terraube et al., 2015; Garcia-Heras et al., 2017). Predators play a fundamental role in ecosystems and are capable of influencing prey behaviour and abundance through top-down predator control (Laundré, Hernández & Ripple, 2010; Laundré et al., 2014; Atkins et al., 2017). To maintain fitness, predators are reliant on the availability of prey, which may be influenced by the density of prey (Higgins et al., 2021), the habitat structure (Preston, 1990; Thirgood et al., 2002) or the prey's behaviour (Sommers & Chesson, 2019), all three of which can in turn be influenced by climatic conditions. For example, declines in the primary prey of the Polar Bear (*Ursus maritimus*) because of sea ice melt, caused this generalist predator to shift its foraging behaviour to a more abundant prey, in this case, Common Eider eggs (*Somateria mollissima*). Although there are energetic benefits of eating eggs early in the season, the energetic cost of searching for eggs later in the season out-weighed the early-season benefits and results in a net energy decline (Jagielski et al., 2021). This scenario demonstrates the indirect effects of climate change on prey and subsequently on the predator, while, the direct effects of elevated temperatures include heat induced behavioural and physiological thermoregulation changes, which can be costly if increased water expenditure causes dehydration (Boyles et al., 2011) or adaptation involves reducing foraging time, which leads to body mass loss (Sharpe, Cale & Gardner, 2019). For instance, Jacky Winters (*Microeca fascinansi*) are unable to maintain body weight when exposed to temperatures which exceed 42°C, although, they are able to reduce the effects of extreme temperatures through behavioural thermoregulation (Sharpe, Cale & Gardner, 2019).

There are a few studies which suggest that climate change has both positive and negative effects on some bird populations (Crick, 2004). In Europe for instance, Collared Flycatchers (*Ficedula albicollis*) start breeding earlier and produce larger clutches after warmer, moist winters (Przybylo, Sheldon & Merilä, 2000). However, these earlier breeding attempts may be an example of phenological miscuing, a phenomenon where species mistime critical biological behaviour due to misinterpreting climatic cues (Crick, 2004). For example, Great Tits (*Parus major*) and Blue Tits (*P. caureleus*) time their breeding to coincide with the peak caterpillar prey emergence, to ensure that chicks receive sufficient food to develop (Perrins, 1991). Tits which commenced breeding before the caterpillar emergence were at a significant disadvantage to those which commenced slightly later (Perrins, 1991). Most bird studies, which focus on the impact of climate on diet, tend to concentrate on lower trophic levels (Pearce-Higgins, 2010; Burger et al., 2012). However, limited studies have highlighted the influence of climate on the diet of higher trophic levels, such as raptors (Garcia-Heras et al., 2017; Robinson, Franke & Derocher, 2017). There are several reasons to study raptors which include their wide distribution, long lifespan, their apex predatory role in the food-web and their suitability as flagship species for biodiversity (Martínez-Ruiz et al., 2023). In one study on the endangered Black Harrier (*Circus maurus*), the proportion of mammals found in the diet was significantly influenced by increasing maximum temperatures, thus creating a need to switch from their primary prey to alternate prey species as conditions got hotter (Garcia-Heras et al., 2017). The availability and accessibility of alternate prey is not always guaranteed, thus a change in diet may have knock on effects on population stability (Rutz & Bijlsma, 2006). Thus, diet analyses are an important component for tracking populations trends and are ideal for assessing climate related impacts, particularly when conducted on large, endangered raptors which require immediate conservation strategies.

Various methods have been used to study the diet of raptors, which all vary in costs, benefits and biases (Simmons, Avery & Avery, 1991; Lewis, Fuller & Titus, 2004). The relatively recent use of remote nest cameras has allowed several of these biases to be removed (Harrison et al., 2019), and has also enabled studies to explore diet niche separation between sexes (Poulin & Todd, 2006). Diet niche separation is not unusual and may be influenced by different habitat selection preferences (Elson, Schwab & Simon, 2007), different foraging behaviour (González-Solís, Croxall & Wood, 2000) and differences in the digestive system

(Markman et al., 2006). These differences in diet are often more noticeable in birds that exhibit larger sexual dimorphism (SD) or reverse sexual dimorphism (RSD), which is a phenomenon where the female is larger in size than the male, and in particular, this phenomenon is common amongst raptors (Temeles, 1985; Slagsvold & A. Sonerud, 2007). It has been proposed that SD evolved to limit diet niche overlap to exploit a broader base of smaller and larger prey during breeding (Krüger, 2005; Slagsvold & A. Sonerud, 2007). As a result, in species which exhibit RSD, the female is capable of provisioning larger prey than the male (Redpath et al., 2006; Hatfield, 2018; Panter & Amar, 2022). Thus, the benefits of this diet niche separation during the nestling stage of the breeding cycle may include an increased diet width, which has been linked to lower body conditions but ultimately, higher survival rates for White-tailed Eagle (*Haliaeetus albicilla*) nestlings (Nebel et al., 2023). Amongst raptors, the Martial Eagle (*Polemaetus bellicosus*) is Africa's largest eagle. Its ecology is relatively poorly understood due to their low breeding density (~1 pair per 140 km^2) and large (>100 km^2) home range size (Tarboton & Allan, 1984; Van Eeden et al., 2017). It is considered a generalist predator capable of preying on everything from large reptiles to medium-sized mammals to small game birds (Boshoff et al., 1990; Boshoff & Palmer, 1980; Tarboton & Allan, 1984). Furthermore, data from a GPS tracking study indicates that diet niche separation does occur in Martial Eagles, with females catching larger prey species than males (Hatfield, 2018). It has also been shown that females have a lower diet diversity than males, indicating that females are more specialised hunters (Hatfield, 2018).

The Martial Eagle is a species of conservation concern and was recently (2020) up-listed from globally vulnerable to endangered on the IUCN Red List of Threatened Species (BirdLife International, 2024). The global population, which occurs from Senegal across to Ethiopia and down to South Africa, has shown decreasing population trends over the past three generations (± 33 years) (Thiollay, 2006; BirdLife International, 2024; Shaw et al., 2024). A recent study examining trends across Africa suggest that this species may actually qualify for further up-listing to critically endangered based on a decline of over 80% over three generation lengths (Shaw et al., 2024). In South Africa, results from a comparison between the Southern African Bird Atlas Project (SABAP) 1 and SABAP 2 showed decreased reporting rates (proxy for abundance) over a twenty-year period (Amar & Cloete, 2018; Underhill & Brooks, 2014). Reasons for these population declines have been attributed to factors such as habitat loss, poisoning, pollution, drowning in reservoirs, electrocution and collision with energy infrastructure (Amar & Cloete, 2018; Herholdt & Kemp, 1997; Van Eeden et al., 2017). Martial Eagle reporting rates over the past 40 years within protected areas in Kenya have increased by 143%; however, reporting rates outside protected areas have declined by 63% and the overall population has declined by 26% (Ogada et al., 2022). Similar population trends have been identified in three other regions across Africa (Garbett et al., 2018; Shaw et al., 2024). Worryingly, the current known threats tend to be restricted to non-protected areas; thus, the drivers of population trends for this species in protected areas are still poorly understood. Climate change may be one of the widespread drivers of declines for this species, however, it's potential impact has not yet been explored.

This study aims to investigate the potential impact of climate change on the diet of Martial Eagles in the Kruger National Park (KNP) during the nestling period. We use data from camera traps set at Martial Eagle nests, coupled with local weather data to explore the influence of maximum daily air temperature (T_{max}) on the number of daily prey deliveries, the daily biomass delivered, and the type and size of prey items delivered to the nest. Furthermore, we explore these questions separately for the two sexes. We predict that when T_{max} increases prey provisioning rates will decline, either due to the behavioural changes of the prey, making these prey less available (e.g. greater use of thermal refuge, Cunningham, Martin & Hockey, 2015; Ma et al., 2023), or due to behaviour changes by the eagles (e.g. not hunting in hot conditions due to the threat of increased thermal loads). Lastly, we predict that when T_{max} increases, prey composition will shift from endothermic prey species (mammals and birds) which reduce activity during hotter conditions (Cunningham, Martin & Hockey, 2015; Cunningham, Gardner & Martin, 2021), towards ectothermic species (reptiles) which become more active in hotter conditions (Sinervo et al., 2010; Broeckhoven, Le Fras & Mouton, 2015).

METHODS

Study Area

This study was conducted in the Kruger National Park (KNP), the largest protected area in South Africa (Figure 1). The reserve falls within the Savanna Biome and is situated in the north-east of South Africa and is approximately 360 km from north to south (22°25'S; 31°13'E – 24°27'S; 31°31'E). The northern region is dominated by Mopaneveld which features a tree community comprised of *Colophospermun mopane*, *Combretum apiculatum* and *Terminalia sericea* (Mucina & Rutherford, 2006). The central and southern regions are situated on the Basalt and Granite Lowveld vegetation units which range from open to closed tree communities and include species such as *C. imberbe*, *C. zeyheri*, *Sclerocarya birrea*, *Senegalia nigrescense* and *Dichrostachys cinerea* (Mucina & Rutherford, 2006). The climatic conditions in the region are characterised by summer rainfall periods, where the mean annual rainfall is 633 mm in the south and 514 mm in the north (Mucina & Rutherford, 2006) (Figure 2). Mean annual temperatures vary from 20.9°C in the south to 21.2°C in the north (Mucina & Rutherford, 2006) (Figure 2).

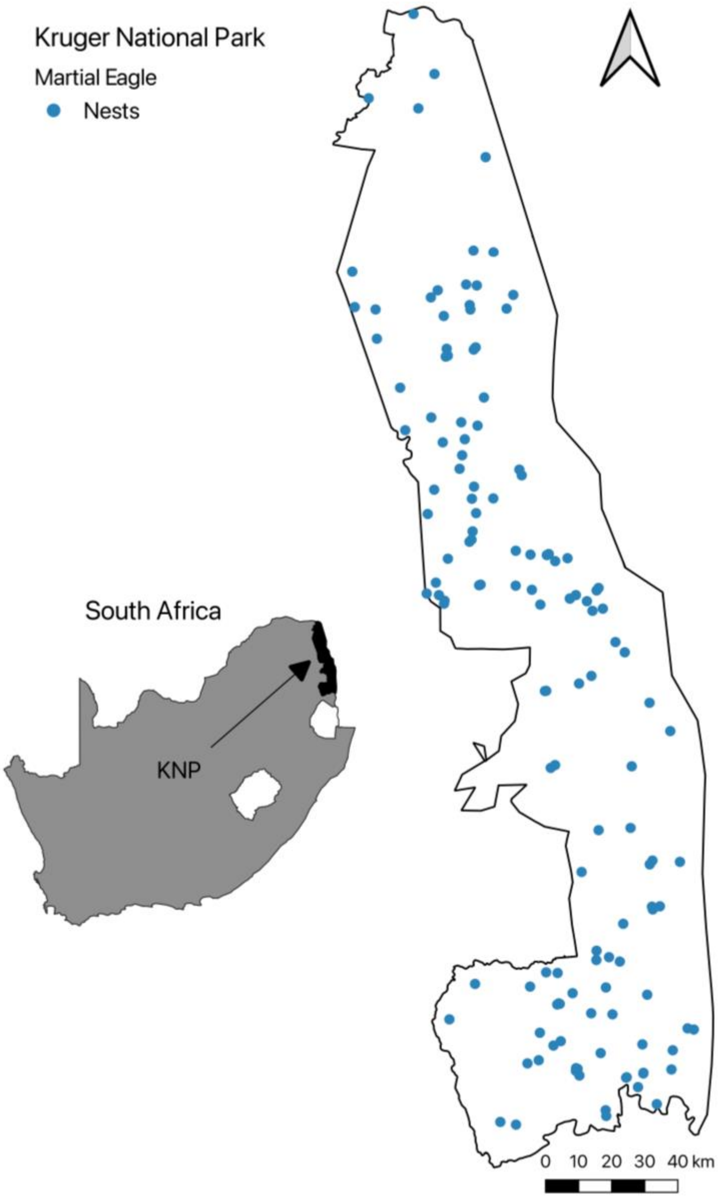

Figure 1. Map of the KNP showing all Martial Eagle nests (N = 134) found in KNP since research began on the species in 2012 (Van Eeden, 2017).

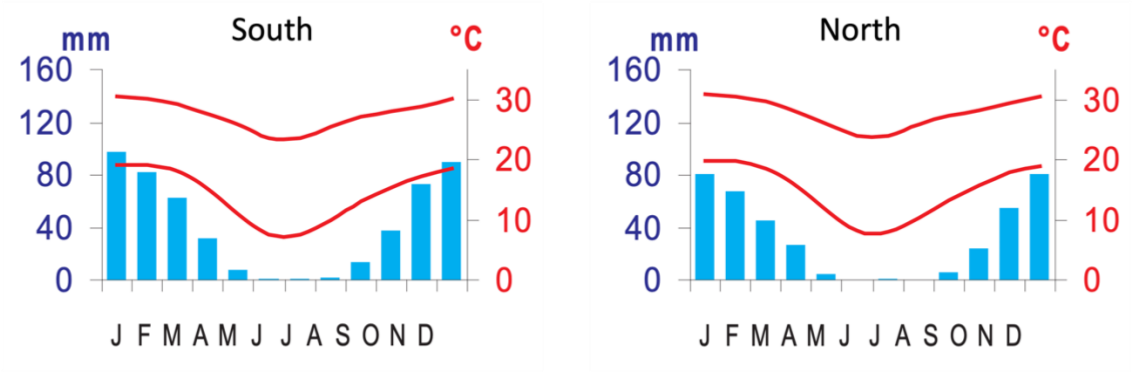

Figure 2. Mean annual rainfall and temperature values for two broad climatic regions in the KNP. The northern region is dominated by Mopaneveld while the southern region is granite lowveld Savanna (figure adapted from Mucina & Rutherford, 2006).

Remote Nest Monitoring

From March 2018 to December 2022, active Martial Eagle nests (N = 134) were located as part of a long-term population study (Van Eeden et al., 2017; Murgatroyd, Tate & Amar, 2023) (SANParks permits: AMAA165; UCT Ethics permit: 2019/V22AA). Nests believed to have been built by Martial Eagles due to the nest size, stick size and location in the tree (Murgatroyd, Tate & Amar, 2023), were checked for signs of activity at the start of the breeding season (March – May). A small action camera, connected via Bluetooth to a phone, and mounted on a 15 m extendable pole (+2 m for the handler) was used to check the contents of the nest. Nests which showed signs of activity such as adult Martial Eagle presence, fresh green leaf lining, fresh whitewash below the nest, presence of an egg or a chick on the nest were deemed active. Camera traps were installed at active nests either before laying or after hatching, and only in trees which were accessible and safe to climb (n = 36). Climbing was done using a 12 mm climbing rope, harness and ascending device. Certain tree species such as *C. mopane*, *C. imberbe*, *S. birrea*, *Diospyros mespiliformus*, *Schotia brachypetala* and *S. nigrescense* were suitable for climbing whilst branches of the *Philenoptera violacea* were known to break and were considered too dangerous to climb; thus, a coarse means of sample selection was used (Appendix 1). Once above the nest, a single remote camera (Browning Trail Cam (n = 13 nests) and Cuddeback Digital (n = 1 nest)) was then fastened to a branch and angled towards the nest. Typically, there is a limited number of branches above the nest capable of supporting the camera, thus, branches positioned approximately 1.5 – 2 m from the nest were preferred, regardless of the cardinal direction of the camera (Katzenberger et al., 2015; Tate, Bishop & Amar, 2016). The camera was then connected to an external 12v lithium-ion battery or a 12v solar-charged battery pack, which was then fastened to a branch below the nest. Cameras were set to capture an image of nest activity every 5-minutes from first light to last light, after which, they were set on motion activation with black flash to capture nocturnal images. Images were stored on a 256 GB SD-card, which was either replaced with an empty SD card after the chick hatched, downloaded every 60 days when the camera and battery pack were serviced, or retrieved along with the camera after the nestling had fledged.

Image Processing and Prey Identification

All camera trap images were individually analysed for prey content and grouped by territory and date. For the purpose of this study, only images taken during daylight hours were included (i.e. no nocturnal images were included because eagles do not provision food at night). Although the cameras captured the nest building and incubation stage of breeding, only the nestling stage was processed (n = 14 nests; 22 nests were not suitable for these analyses). Images were processed starting in the morning (~05h00) when the contents of the nest were clearly visible and ending in the evening when the contents of the nest were no longer visible (~18h00). If there was insufficient light to make out the contents of the nest, the image was not recorded in the dataset. Finally, days where the nest was recorded for less than 10 hours per day were excluded from the analyses.

All images were included in the database regardless of whether the image had a prey item or not. Images where no prey items were recorded received a “0” while only the first image with a new prey item received a “1”. These images were then grouped by day and the number of unique prey items recorded in the day were calculated (Appendix 1 & 2). All prey items, where possible, were identified down to the lowest taxonomic level (i.e. species or phylum) (Greene & Jaksić, 1983). Reference field guides were used when necessary (Hockey, Dean & Ryan, 2005). If a prey item could not be identified to species or phylum it was recorded as “unidentified” for that level. A species rarefaction curve was created using the ‘vegan’ package in R (Oksanen et al., 2019). The curve identifies if the diet diversity asymptote was reached using all the prey items in the sample.

Prey and Climate Data

All data from two nests where insufficient nesting days were captured during the breeding season were excluded. From the remaining 12 nests, all data where <45 % of the nest was visible in the photograph was excluded. This was where the camera moved and the view shifted away from the nest, therefore, it was no longer possible to confidently assess if or when a prey item was delivered to the nest.

As described above, Martial Eagles display reversed sexual dimorphism, whereby the female is larger than the male (Hatfield, 2018; Naude et al., 2019). Thus, when possible, the sex of the adult responsible for a prey delivery was identified. It was usually possible to discern the sex of the eagle from the images based on their tarsal size, and this could be confirmed occasionally when one of the two adult eagles at a nest was ringed with a metal SAFRing (n=4). For un-ringed pairs, differences in spot patterning on the legs and chest also helped to differentiate the sexes (Appendix 2). Lastly, behavioural differences were used to confirm the identity of the adult. At nests with ringed birds, only the females were recorded feeding the nestling while the males would land on the nest with food but would never attempt to feed the nestling. The female would also spend the majority of the day on the nest. Thus, it could be inferred that if a prey item was delivered some-time between two images (i.e. within a 5 minute interval), and if the female was present in both images, the male was very likely responsible for the prey delivery. When the nestling was older (40 - 70 days), the male would deliver a prey item and instantly depart, while the female would deliver a prey item and commence with feeding the nestling. Once the chick had fledged from the nest (~90 days for a male nestling and ~110 days for a female nestling), it became almost impossible to identify which adult delivered the prey item, as both adults would drop the prey and depart the nest, often with no photographic evidence of which adult delivered the prey. Thus, all data where the chick was older than 90 days was excluded, to eliminate any post-fledging provisioning behaviour from our analysis (i.e. once the chick had fledged but was still returning to the nest to feed).

Hourly temperature and rainfall data were obtained from the SAWS stations (2018) and ILeaf weather stations (ILeaf station climate data 2019 onwards). Readings were compiled from multiple weather stations around the KNP and when possible, climate data were used from the closest station to each nest (Appendix 1). In some instances, climate data were missing and, if available, data from the next closest station were used. There was relatively little rain as breeding occurred throughout winter and spring, so instead we converted the data to a binary value to represent rain fall day (R_{day}) (1 = rain occurring in at least one hour on a day; 0 = no rain occurring in any hours of a day). The highest recorded temperature (from the ~10 – 12 individual daytime hours), was assigned as the daily maximum temperature (T_{max}).

Estimating Prey Weights, Prey Proportions and Biomass

To estimate the biomass of prey delivered to the nest each day, the weight of each prey species was first estimated using the published weights for birds (Hockey, Dean & Ryan, 2005), mammals (Fairall & Braack, 1976; Skinner & Chimimba, 2005) and reptiles (Ciliberti et al., 2011). Prey were considered to be adults for the majority of prey species (Appendix 3). Thus, weight estimates were calculated from the average weight of adult females and adult males. For very large ungulates (>15 kg; e.g. Impala *Aepyceros melampus*) we assumed all prey were juveniles, whilst smaller ungulates (e.g. Steenbok *Raphicerus campestris*) were assigned an average weight calculated from given juvenile and adult or sub-adult weights (Appendix 3). Finally, both Rock Monitor *Varanus albigularis* and Water Monitor *V. niloticus* were assigned an average from both adult and sub-adult weights (Appendix 3); this was done to account for the large size variation in these prey items (Collar, Schulte & Losos, 2011). Lastly, the weights of unidentified prey items were assigned a mean value of all prey items (for unidentified phyla), the weighted mean of the individual phyla (for unidentified genus), or the weighted mean of all prey in the same genus (for unidentified species). Means were calculated by adding the weight estimates of all individuals (e.g. all individuals in the same genus were used for unidentified species) and then dividing the sum by the number of individuals in the sample.

However, whilst the above process estimated the weight of the prey items captured, we often observed that only a portion of the prey item was delivered to the nest, with smaller proportions of the prey items tending to be delivered for the larger prey species. Thus, in order to provide an improved estimate of the biomass that was delivered (i.e. available to the nestling), it was important to estimate the proportion of the prey items delivered to the nest and to explore whether prey size influenced these proportions. To explore this, we allocated each prey species to one of seven size classes based on weight (from very small to very large,

Appendix 3). For each of these seven prey-size classes, we estimated the proportion of the prey item that was delivered from the first observed image of each prey item (when the prey item was seen in multiple photos). For three of these classes (very small, large and very large), we did this for every prey item delivered to the nest, due to the relatively small number of items in these categories (Appendix 4). For the other four classes, we estimated proportions from a randomly selected sub-sample (~20% for each category). From these estimates we were able to calculate the average proportion of the prey that was delivered to the nest for the different size categories (Appendix 4), and by multiplying the category specific proportion by the weight of each prey species, we were able to estimate the biomass delivered per day. For example, a Helmeted Guineafowl (*Numida meleagris*) was assigned an average weight of 1,440 g (~1,380g male, 1,500g female) and a size class of ‘medium’ for which on average 78.67% of an item was delivered to the nest; Thus, each Helmeted Guineafowl would be a value of 1,133 g of biomass (1,440*0.7867).

Statistical Analyses

All statistical analyses were performed in R version 2023.06.0 (R Core Team, 2023). Generalised linear mixed models (GLMM) from the ‘lme4’ package (v. 1.1-35.1) were used (Bates et al., 2015) to explore the associations between prey deliveries (response variable), and our fixed effects of climatic variables (T_{max} and R_{day}) and the age of the chick (explanatory variables) (Appendix 5). Collinearity of the fixed effects were checked, but all correlations were negligible (Appendix 6). All explanatory variables were scaled by subtracting their value from the mean and dividing by the standard deviation. In all models, “nest” (a unique identifier for each nest) was used as a random term to account for the repeated daily measures of the same nest. The model selection method involved identifying non-linear relationships by including a quadratic term for each explanatory variable in the global model. Then, where quadratic terms were non-significant, they were removed from the final model. (Tate & Amar, 2017). The resulting models were considered the best fitting models to describe the relationship between the response variable and the explanatory variables (Appendix 5).

Relationship between Provisioning Rate and Weather

We explored if the number of prey items delivered per day was associated with T_{max} or R_{day}. For this analysis we fitted a GLMM with a Poisson distribution, with an offset fitted as the (log) of the total hours recorded each day (Appendix 5). This offset accounted for the fact that we had data from different months for which sunset and sunrise was not equal and thus the number of hours available for prey deliveries was not the same in each month. Additionally, we repeated this analysis for the number of prey items provisioned by the male and female Martial Eagle separately to test whether T_{max} or R_{day} (explanatory variables) influenced each sex differently. We also explored the relationship between the weather variables and if any prey was delivered on a day or not (e.g. regardless of if it was 1, 2, or 3, items). This was modelled as a binary prey response variable, using the same approach as the previous GLMM, but fit with binomial distribution and logit link function, where each day was assigned a score of 1, or 0, according to if any prey were delivered that day or not (Tate, Bishop & Amar, 2016). Next, we explored this same question, but for the two sexes separately. Lastly, we used the same model but explored prey delivery (binary measures) of each of the three prey phyla (mammal, bird and reptile) individually, this therefore, explored whether the probability of a prey type being delivered varied according to weather conditions.

Relationship Between Biomass, Prey Mass and Weather

The relationship between weather (T_{max} and R_{day}) and the total prey biomass delivered to the nest each day was analysed. A glmmTMB, from the 'TMB' package (version 1.1.8), fitted with a negative binomial distribution (family - nbinom2 (log)) was used to account for the zero-inflated nature of the biomass data (i.e. lots of days with zero biomass delivered) (Brooks et al., 2017). In addition to the weather variables and chick age, the square root of the total hours recorded was included as an explanatory variable to account for differences in day length.

To explore if the size of prey delivered was related to the weather, we fitted a linear mixed-effects model (LMER), with a Gaussian distribution from the 'lme4' package; We included T_{max}, R_{day} and the square root of the total hours as the explanatory variables and the (proportional) mass of prey items delivered to the nest as the response variable. Next, we explored whether the mass of prey delivered differed between the sexes, using an LMM model with a Gaussian distribution, fitted with "sex" (male or female) as the only explanatory variable. Estimated Marginal Means (EMMeans) were then calculated using the '*EMMeans*' package (v. 1.10.0) in R (Hall & Warner, 2020). EMMeans provides an estimate of the average response variable (mass proportion) for each level of the explanatory variable (sex). This function calculates the estimated marginal means along with standard errors and confidence intervals, allowing for a statistical comparison. Subsequently, a pairwise comparison between the two sexes was conducted to assess the differences in prey mass proportions delivered by male and female eagles.

Next, three separate analyses using an LMM model with a Gaussian distribution were used to assess the relationship between weather (T_{max} and R_{day}), and the mass of each of the three prey phyla. A *post hoc* ANOVA test, from the '*car*' package (v. 3.1-2), was used to test the significant differences among the three phyla. Finally, an LMER model with Gaussian distribution was used to explore whether species mass (proportion) was influenced by the phylum (reptiles, mammals, birds) as the only explanatory variable. EMMeans were then calculated to provide an estimate of the average response variable (species mass) for each level of the explanatory variable (phylum).

RESULTS

Between March 2018 and November 2022, a total of 36 camera traps were installed at active Martial Eagle nests, of which, 14 captured the nestling stage (Figure 3), which amounted to 291,471 images, grouped into daily time intervals from sunrise to sunset (n = 1,244 camera trap days). A total of 1,132 prey items were recorded, of which 1,082 prey items were recorded to the species level. Data were filtered for analytical purposes (i.e. two nests (number 10 and 14) were excluded with too few days (n = 3 days and n = 7 days respectively), days where cameras captured <45% of the nest were excluded (n = 2 days), days were the chick was >89 days old were excluded (n = 424), and days where too few hours recorded were excluded (n = 9 days) (Appendix 1). The sample size was reduced to 756 camera trap days from 12 nests ($\bar{x}$ days per nest = 63, SD = 23.4) (Appendix 1) (i.e. a recap of the data filtering process described in the Methods section).

A total of 793 prey items were recorded at our 12 nests ($\bar{x}$ prey per nest = 66, SD = 27.6), of which, 780 (98.4%) were identified to the phylum level and 751 (94.7%) were identified to the species level (Appendix 3). Birds made up the largest proportion of the prey items identified to the phylum level (47%), followed by mammals (33%) and then reptiles (21%). There was a total of 37 prey species identified in the diet, of which, the top 10 prey species made up ~85% (Figure 4, Appendix 3). The results of the species rarefaction curve indicate that the number of prey species recorded in the diet did not reach the asymptote, thus, more prey species could be expected if the sample size were to increase (Appendix 7).

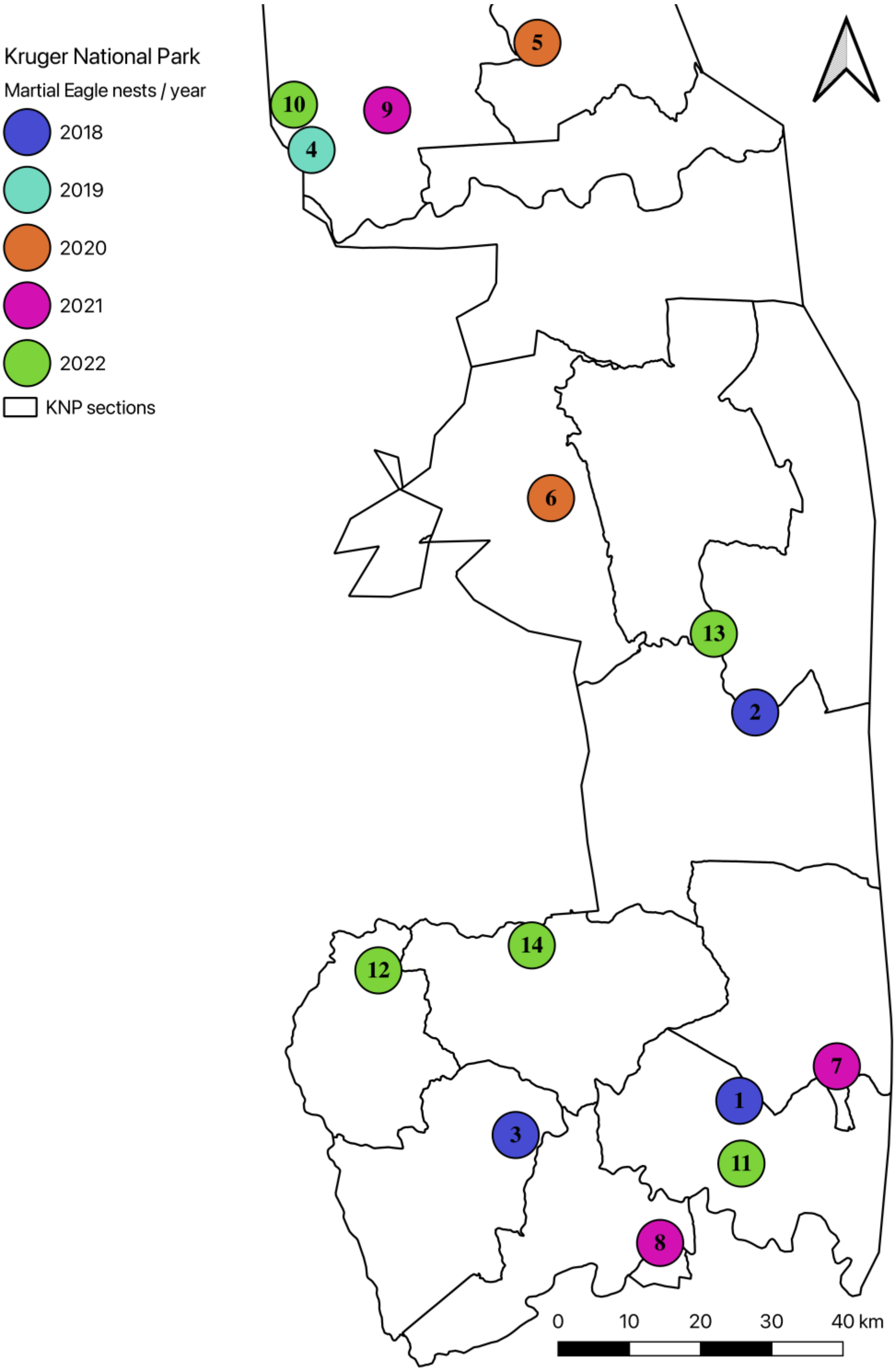

Figure 3. Locations of 14 Martial Eagle nests in the Kruger National Park that were monitored with camera traps from 2018-2022. The colour of the dots denotes the year in which the nest was monitored. Nest number 10 and 14 were excluded from the analyses due to a limited number of days sampled (see Appendix 1).

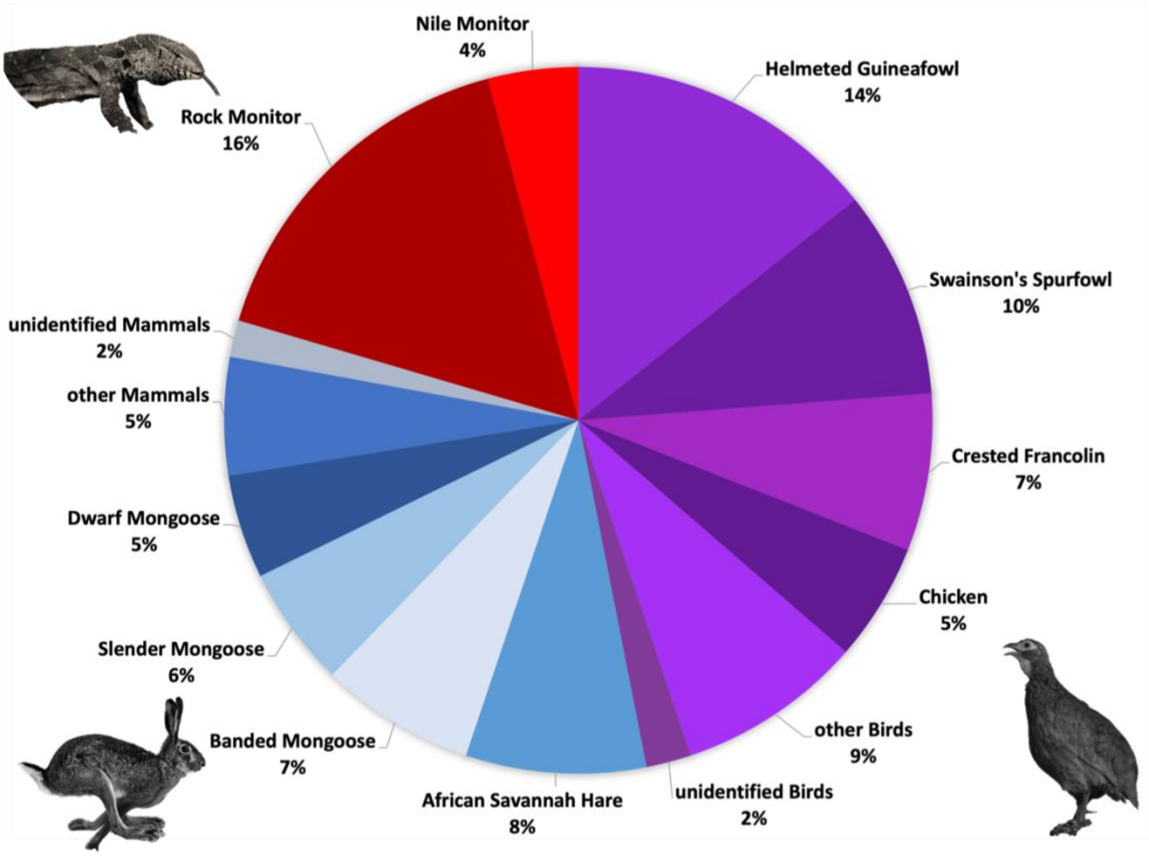

Figure 4. Combined prey composition identified to the phylum and species level from 12 Martial Eagle nests (n = 780). A total of 37 prey species were recorded in the diet, of which, the top 10 species made up ~85% of the prey items, identified to the species level.

At least one prey item was delivered on 74% of sample days, with no items being delivered on 26% of days (n = 201). There were 379 (49%) instances of 1 prey item, 166 (22%) instances of 2 items, 23 (3%) instances of 3, two instances of 4 and one instance of 5 prey items delivered on a single day (n = 772). In total, 599 prey items were delivered to the nest by the male and 146 were delivered by the female Martial Eagle (Figure 5); 48 prey items could not be ascribed to either adult. Birds were the most frequently delivered prey phyla delivered by males (54%), followed by mammals (29%) and reptiles (16%). Conversely, mammals were most frequently delivered by the female, (49%), followed by reptiles (38%) and birds (12%).

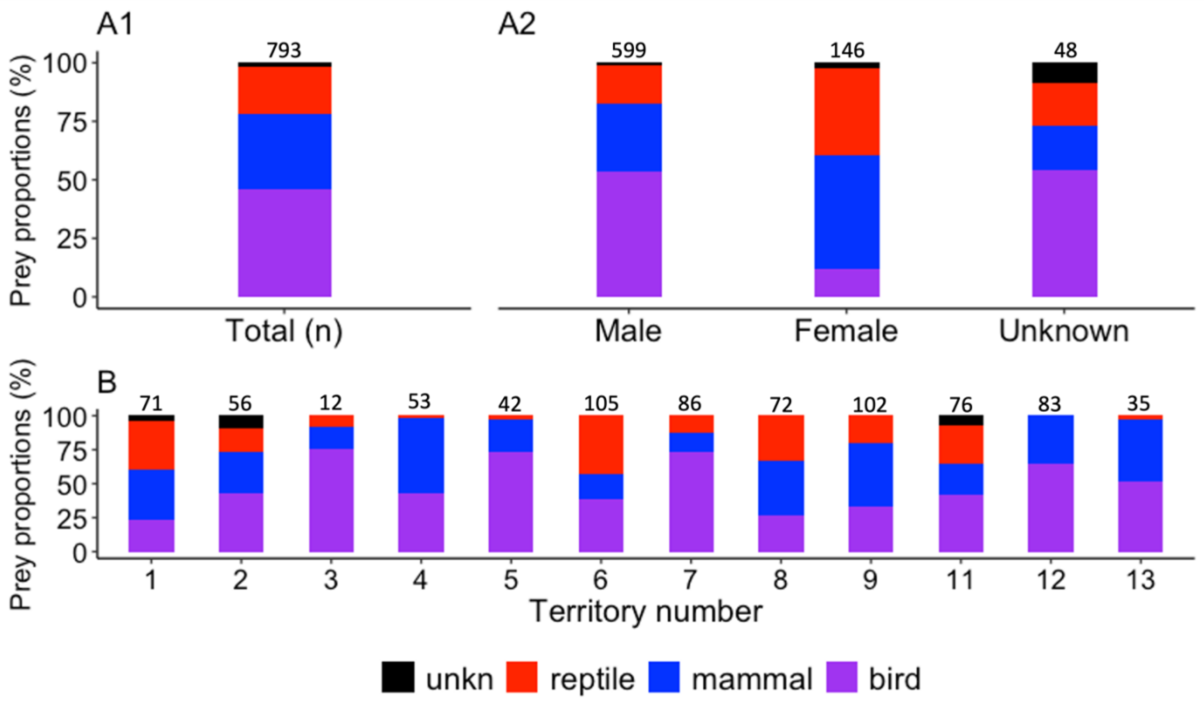

Figure 5. (A1) Total proportion of prey items delivered by Martial Eagles to a nest during the breeding season (n = 793). Birds account for 47%, mammals 33% and reptiles 21%. The sample size of prey items is recorded above each bar. (A2) Proportion of prey items delivered during the nestling stage of the breeding season (chick <90 days old) divided between male (n = 599) and female (n = 146) Martial Eagle. (B) Total proportions of prey items delivered to each of the 12 individual nests (see Figure 3 for more details).

Effect of Weather on Prey Delivery

The number of prey items varied from zero to a maximum of five items being delivered on one day. There was no influence of R_{day} and chick age, but the number of prey items delivered to the nest per day were significantly influenced by T_{max} (n = 772, $\chi^2 = 9.81$, df = 2, $P < 0.008$) (Figure 6). Examining these relationships separately by sex, we found that T_{max} had a negative linear influence on the number of prey items delivered by the male (n = 772, $\chi^2 = 6.50$, df = 1, $P = 0.01$) and a quadratic influence on the number of prey items delivered by the female Martial Eagle (n = 772, $\chi^2 = 6.42$, df = 2, $P = 0.04$). Chick age had a negative linear effect on the number of prey items delivered by the male ($\chi^2 = 7.2$, df = 1, $P = 0.007$) and a positive quadratic effect on the female ($\chi^2 = 28.5$, df = 2, $P < 0.0001$) (Figure 7).

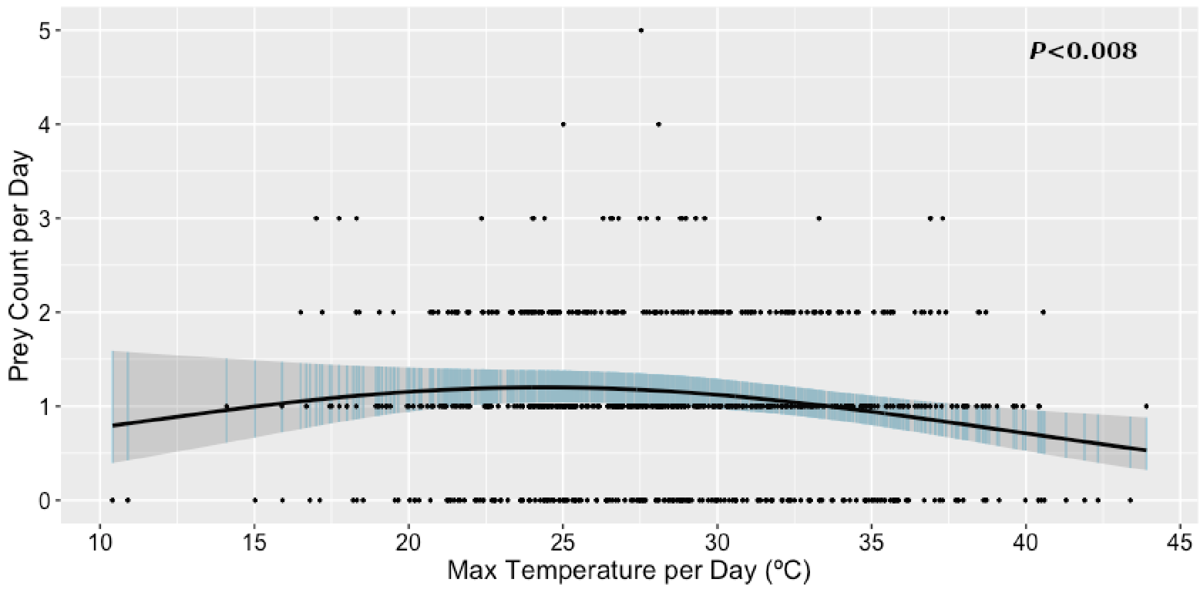

Figure 6. Average number of prey items (black line) (with 95% CI – grey bars) delivered to the nest per day across the T_{max} gradient. Also shown are the spread of the T_{max} samples (thin blue vertical lines) and prey count samples (black dots) across the temperature gradient.

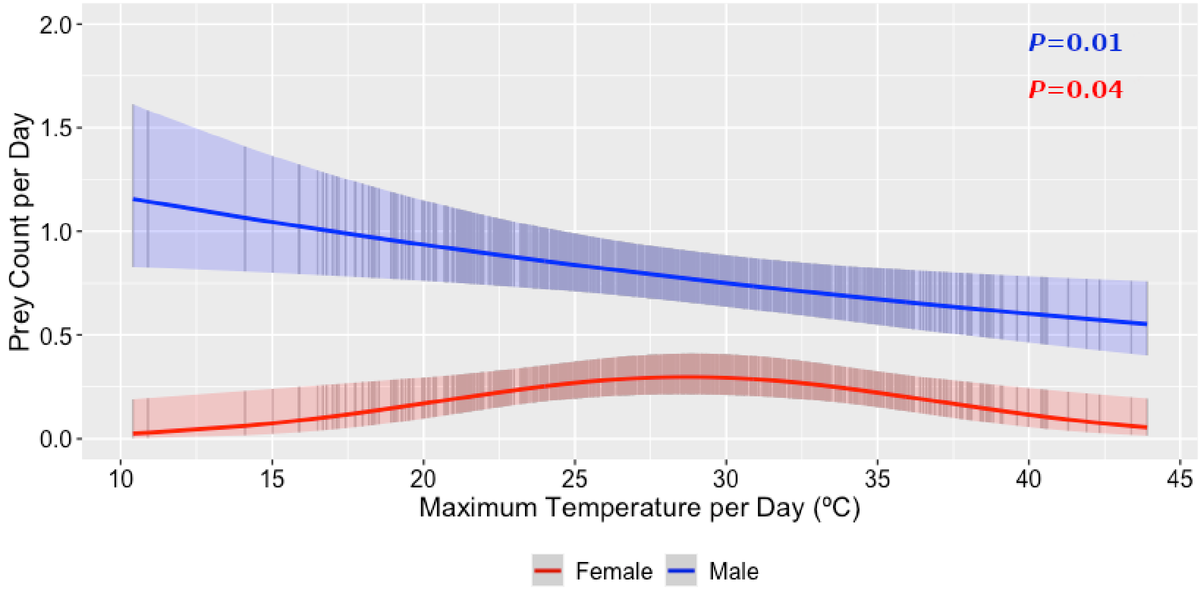

Figure 7. Influence of T_{max} on the number of prey items delivered to a nest per day by the adult male (blue) and female (red) Martial Eagles.

There was a significant quadratic relationship between the probability of a prey delivery (n = 760, χ^2 = 11.20, df = 2, $P < 0.004$) and temperature, with an increase from 40% at 10°C, peaking at around 80% at 26°C and then declining to <40% when T_{max} reached the maximum of 44°C (Figure 8). There was a weak negative linear effect of chick age but no effect of rainfall

(R_{day}) on the probability of prey being delivered. There was a significant linear influence of T_{max} (n = 722, χ^2 = 5.26, df = 1, *P* = 0.022) and negative influence of chick age (χ^2 = 8.14, df = 1, *P* = 0.004) on the probability of the male delivering a prey item. Likewise, there was a significant quadratic effect of T_{max} (n = 722, χ^2 = 8.43, df = 2, *P* = 0.015) and a significant quadratic effect of chick age on the probability of a female prey delivery (χ^2 = 28.09, df = 2, *P* < 0.0001) (Figure 9).

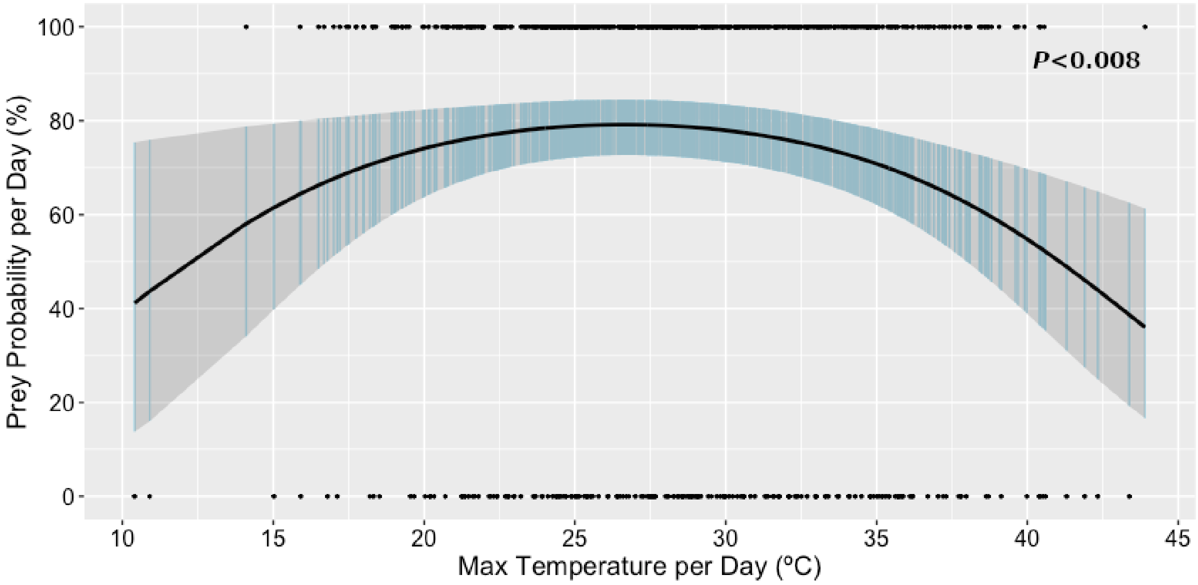

Figure 8. Relationship between Martial Eagle prey delivery (provisioning probability) per day across the T_{max} gradient (°C) throughout the nesting period (>90 days) of the breeding season in the KNP. The blue lines indicate the T_{max} data and the black dots indicate prey probability data used in the analysis.

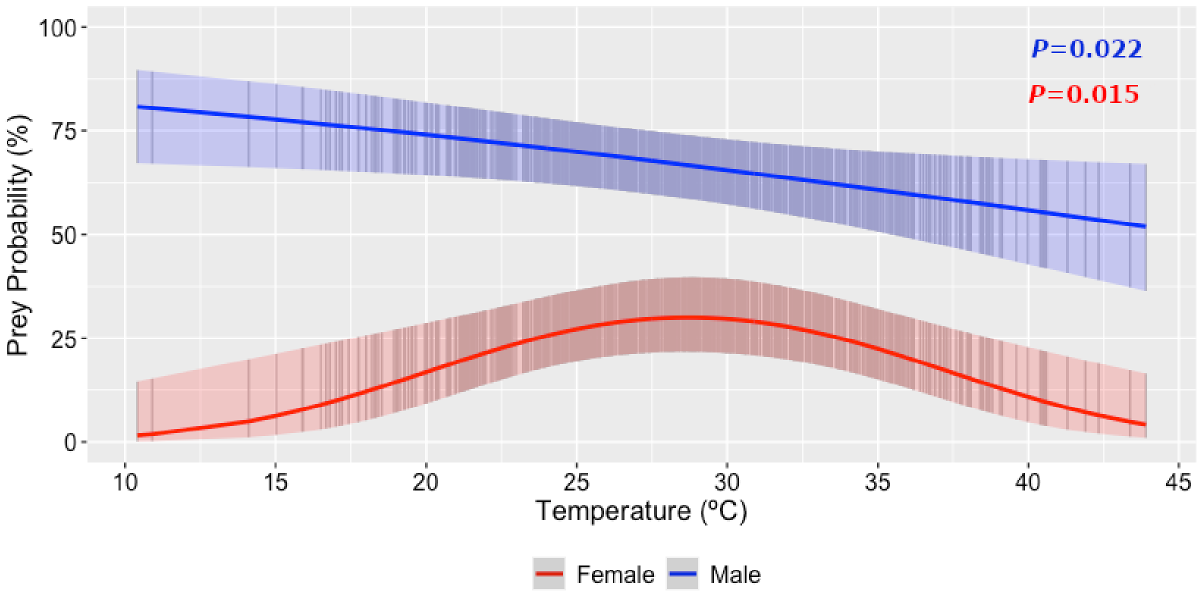

Figure 9. Probability estimates of adult male (blue) and female (red) Martial Eagle prey delivery (prey probability) across the T_{max} gradient in the KNP.

Effect of T_{max} on Biomass and Prey Mass

The results indicate that the biomass (g) delivered to the nest per day was not influenced by T_{max} (n = 760, $\chi^2 = 0.03$, df = 1, $P = 0.8$) (Figure 10). However, chick age had a weak quadratic effect and the total hours recorded per day had a positive linear effect on the biomass delivered ($\chi^2 = 4.07$, df = 1, $P = 0.043$). The amount of biomass delivered by the male was not influenced by T_{max} (n = 760, $\chi^2 = 0.24$, df = 1, $P = 0.63$); conversely, the amount of biomass delivered by the female was influenced significantly by T_{max} (n = 760, $\chi^2 = 7.5$, df = 2, $P = 0.024$) in a quadratic manner, with peak biomass delivered by females between approximately 30 – 35 (°C) (Figure 11).

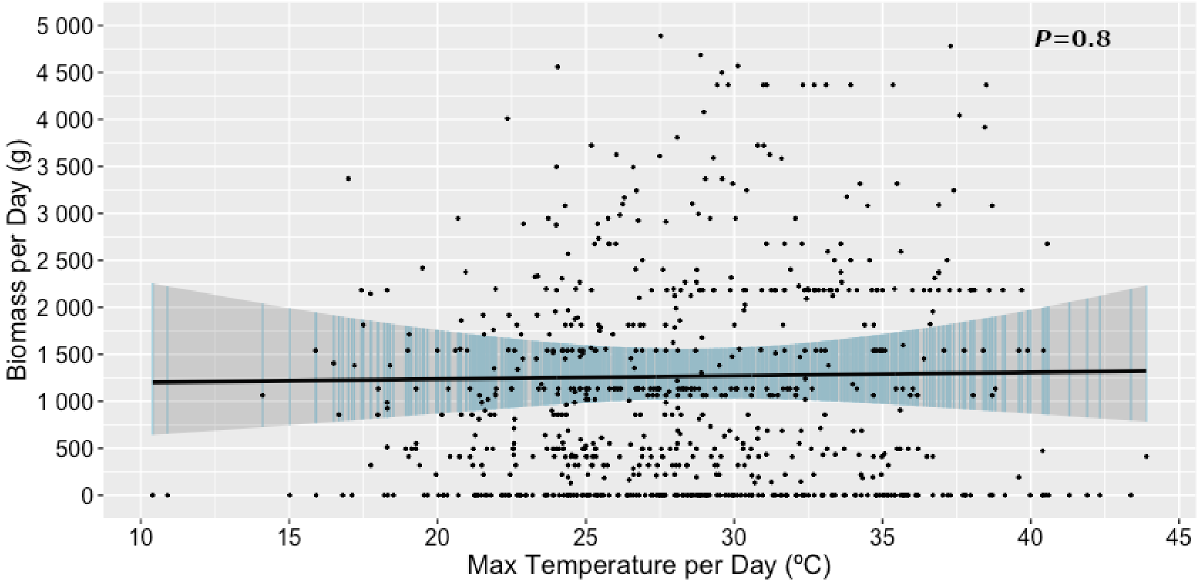

Figure 10. Relationship between the cumulative prey biomass (g) delivered to the nest (n=12) per day and the T_{max} per day, recorded in the KNP. Blue lines indicate the spread of T_{max} data and black dots indicate prey biomass data used in this analysis.

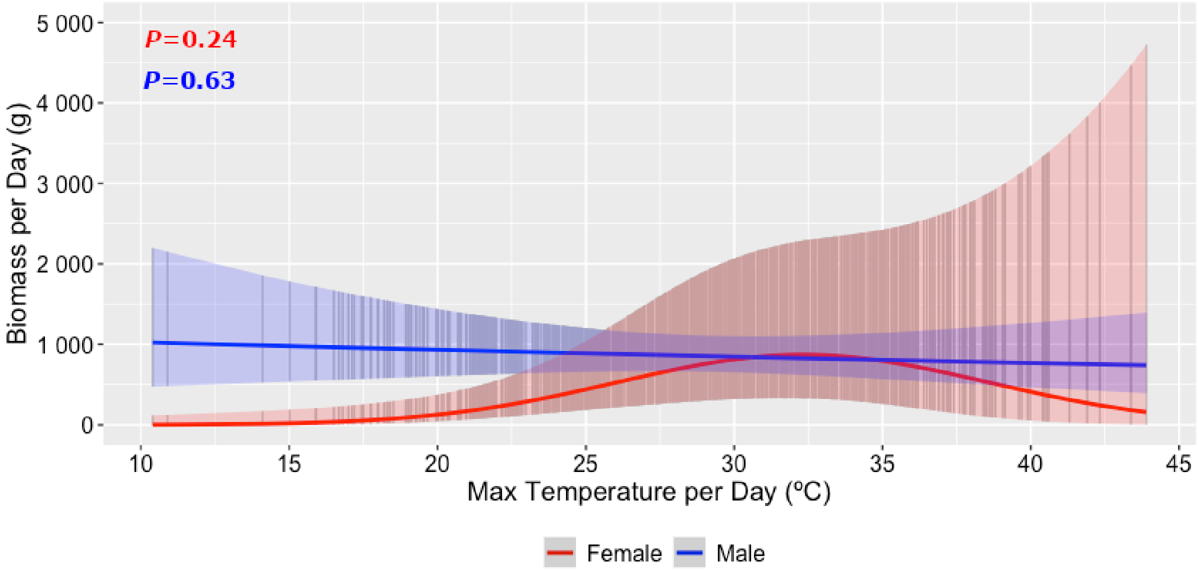

Figure 11. The influence of T_{max} on the quantity of prey biomass delivered by the male (blue) and female (red) Martial Eagle, to 12 nests in the KNP from 2018 to 2022. Vertical lines indicate the T_{max} data distribution.

The mass of prey items increased significantly in a linear fashion as T_{max} increased (n = 779, χ^2 = 28.80, df = 1, *P* < 0.0001) (Figure 12). Prey mass was not influenced by chick age, while total hours in a day had a positive linear influence on the mass of prey items delivered (χ^2 =

7.26, df = 1, P = 0.007). Male eagles provisioned significantly larger prey items as T_{max} increased (n = 585, χ^2 = 20.59, df = 1, $P < 0.0001$) with similar results for females (n = 146, χ^2 = 15.17, df = 1, $P < 0.0001$) (Figure 13). The total hours recorded per day significantly influenced male prey mass deliveries (χ^2 = 8.13, df = 1, P = 0.004) but did not influence females. R_{day} and chick age did not influence the mass of prey delivered by either sex. Estimated marginal means for each sex were calculated to explore the differences in prey mass between females and males. The estimated marginal mean prey mass for females was 1,512 grams (SE = 77.4), while for males, it was 951 grams (SE = 60.9). The 95% confidence interval for female prey mass ranged from 1,354 to 1,670 grams, and for males, it ranged from 818 to 1,085 grams. Pairwise comparisons between sexes revealed a significant difference in the prey mass, with females delivering significantly heavier prey items compared to males, with an estimated difference of 561 grams (SE = 62.1, t = 9.033, p < 0.001).

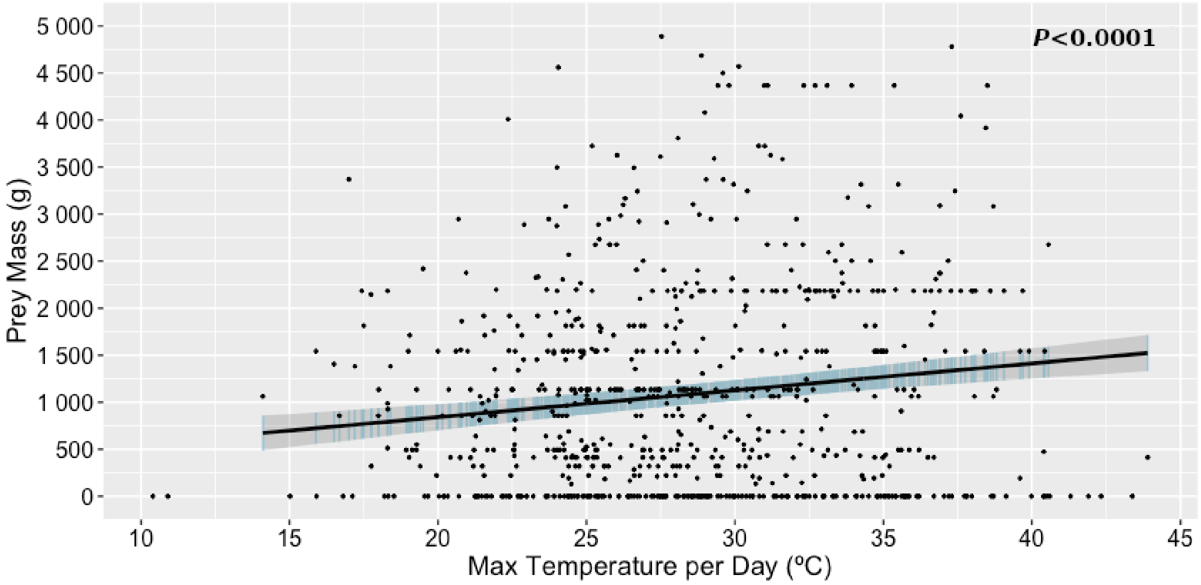

Figure 12. The relationship between T_{max} and the individual mass (g) of prey items (n = 779) delivered to the nest during daylight hours. Blue lines indicate the spread of T_{max} data and black dots indicate individual prey mass data used in this analysis.

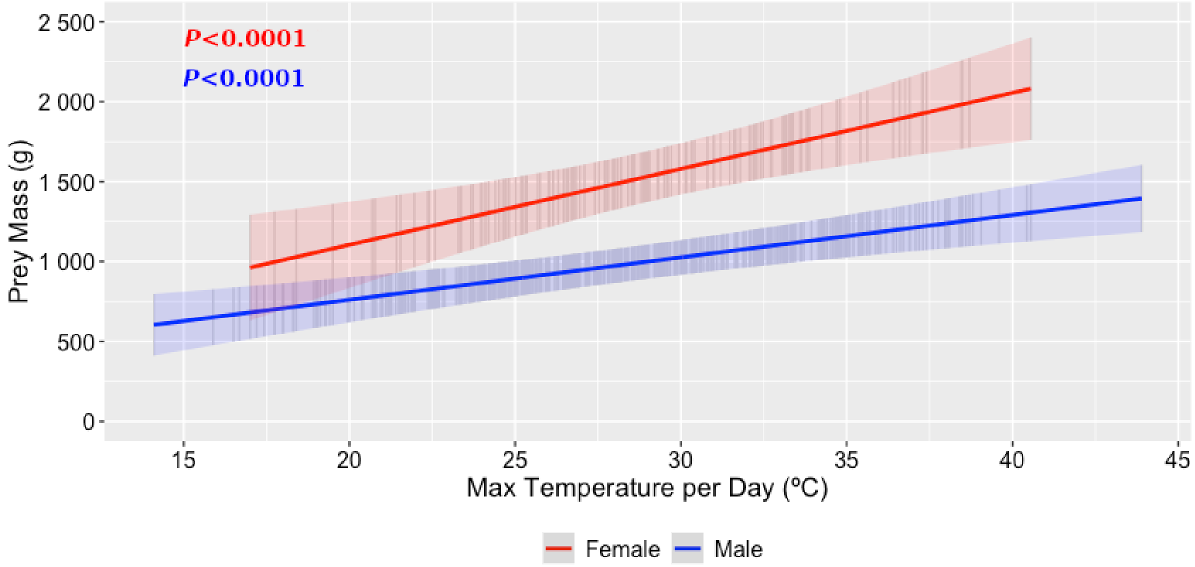

Figure 13. The relationship between T_{max} and the individual mass (g) of prey items delivered to the nest by the male and female Martial Eagle during daylight hours.

The results indicate that there was clear temperature-based variation in the prey delivery probabilities for each of the three prey phyla (mammals, birds and reptiles) (Figure 14). Mammals were least effected by T_{max}, although there was still a decline from ~35% probability of a mammalian prey delivery when T_{max} was lowest, to 25% at the highest T_{max} ($n = 748$, $\chi^2 = 0.65$, df = 1, $P = 0.42$). Bird deliveries increased from near 30% probability to ~54% when T_{max} increased to 22°C, after which they decreased to near ~2% at the maximum T_{max} ($n = 748$, $\chi^2 = 30.44$, df = 2, $P < 0.0001$). Lastly, reptiles showed a similar but more delayed trend, starting at ~1% probability of a reptilian prey delivery when T_{max} was <15°C and peaking at 30% when T_{max} reached 33°C but declining once again to ~17% at the highest T_{max} ($n = 748$, $\chi^2 = 11.98$, df = 2, $P < 0.003$).

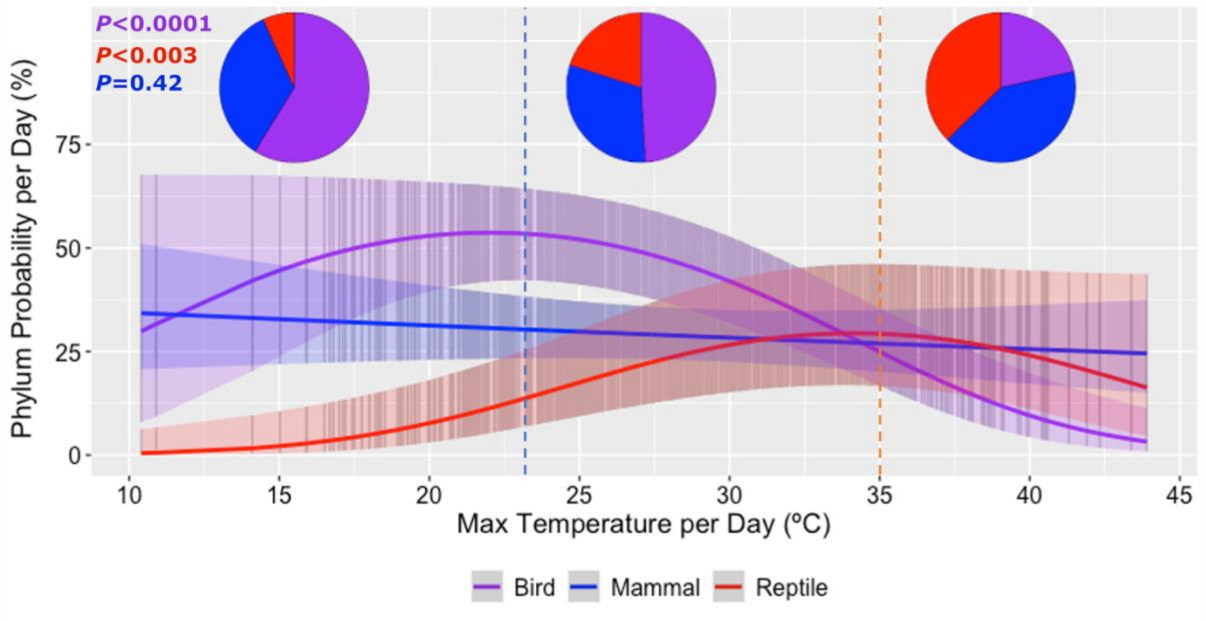

Figure 14. Probability estimates of adult Martial Eagle provisioning three different prey phyla (reptile, mammal and bird) across the T_{max} gradient (°C). The pie charts (from left to right) are the raw phylum proportions delivered between the lower T_{max} values (10°C – 22.9°C), mid T_{max} values (23°C – 34.9°C) and higher T_{max} values (>35°C), as indicated by the vertical blue and orange-dashed line. The shaded areas indicate the lower and upper 95% confidence intervals, while vertical lines indicate the T_{max} data distribution.

The likely driver of increasing species mass (T_{max}) was looked at but no significant association between T_{max} and the mass of reptiles, birds and mammals were found (n = 161, $\chi^2 = 2.41$, df = 1, $P = 0.12$; n = 358, $\chi^2 = 1.51$, df = 1, $P = 0.22$; n = 247, $\chi^2 = 1.46$, df = 1, $P = 0.23$) (Figure 15). 'EMMeans' for each phylum were calculated to further explore the differences in mass among bird, mammal, and reptile species. Birds exhibited a mean mass of 694 grams (SE = 40.1), while mammals had a mean proportion mass of 989 grams (SE = 43.4), and reptiles showed a mean proportion mass of 2,134 grams (SE = 50.3). Pairwise comparisons between phyla indicated significant differences in mass proportions. Birds had significantly lower mass proportions compared to mammals (estimate = -295 grams, SE = 38.7, $p < 0.001$) and reptiles (estimate = -1,439 grams, SE = 46.3, $p < 0.001$). Similarly, mammals had significantly lower mass proportions compared to reptiles (estimate = -1,144 grams, SE = 48.4, $p < 0.001$).

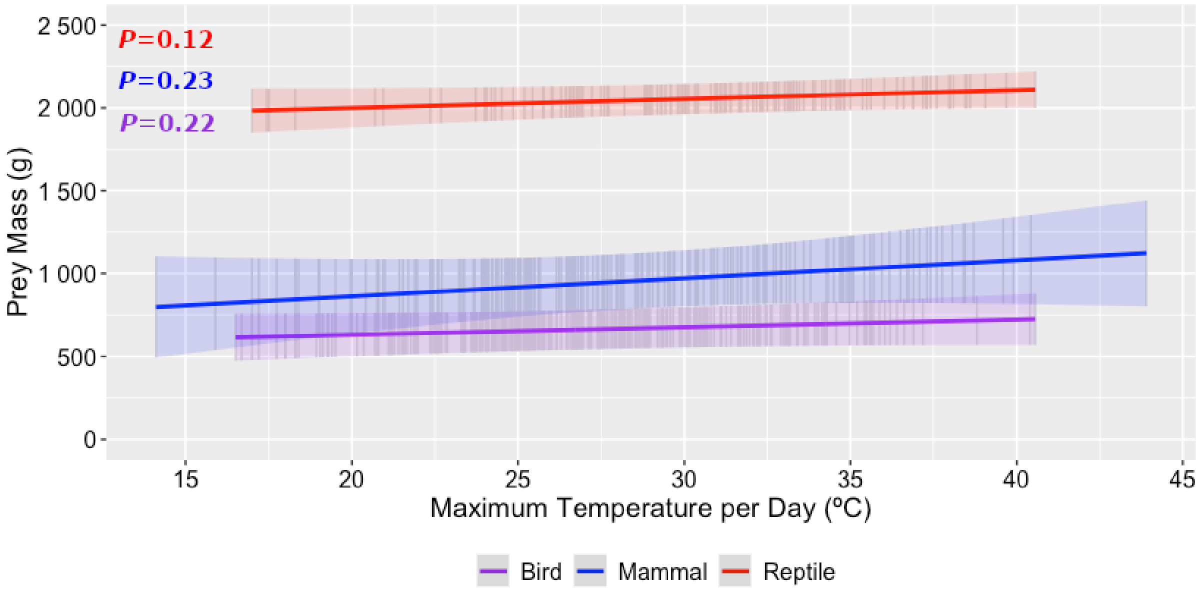

Figure 15. The influence of T_{max} on the mass (g) of each of the three prey phyla delivered to the nest during daylight hours. The grey lines in the 95% CI, indicate the temperature data available for each of the three phyla analyses.

DISCUSSION

Martial Eagle Diet

The diet of Martial Eagles in this study was comprised of three main prey phyla which included reptiles, mammals and birds. Almost 50% of the diet in the KNP is made up of birds, while 33% was made up of mammals and 21% reptiles. Other diet studies on Martial Eagle in South Africa (using prey remains) identified the same prey phyla, however, the proportions of each phylum differed. This may be a result of inherent biases associated with the older methods of diet sampling, such as prey collections or visual monitoring (Redpath et al., 2001). Diet studies in the Cape Province found that three quarters of the diet contained mammals, less than a quarter birds and a small proportion were made up of reptiles (Boshoff & Palmer, 1980). Subsequent studies a decade later revealed similar proportions of each prey phylum, although more mammals and fewer birds were recorded (Boshoff, Palmer & Avery, 1990). The arid Karoo habitat in the Cape Province differs greatly from the Savanna habitat in this study and the differences in diet are likely a function of prey species assemblages, which differ markedly between the two biomes. In the Transvaal, where habitat more closely resembles the KNP, the diet of eagles was made up of a similar proportion of birds (45%), although reptiles made up a larger proportion (38%) and mammals made up a smaller proportion (17%) (Tarboton, 1976). Our approach of using camera traps to identify prey items was able to eliminate many of the biases known to exist with diet studies which used more conventional methods of diet sampling (i.e. prey collection or visual monitoring) (Redpath et al. 2001).

More recently, a diet study which used web-based images of foraging Martial Eagles, found that reptiles make up 50% and birds make up ~17% of the diet in the North-east of South Africa (Naude et al., 2019). Although the results of this web-sourced sampling method closely matched estimates of prey composition with the study in the Maasai Mara (Hatfield, 2018), a comparison with our study reveals differing diet estimates. The reasons for this variation may be due to the time of data collection in this study (only breeding season) and the inclusion of post-fledging prey data in the web-based diet study. According to Naude et al. (2019), adult eagles were more likely to be recorded with birds, than juvenile eagles. Thus, by including juvenile prey samples, the diet estimates may have been biased towards non-bird prey items. Interestingly, the mammal composition estimates (25%) from the web-based study were comparable with the findings of our study. Furthermore, the results of our study indicate that Rock Monitor and Helmeted Guineafowl made up the largest proportion of the diet identified to the species level. Interestingly, these species were present in all the diet studies conducted across South Africa, highlighting the importance of these two species in the diet of Martial Eagles.

Influence of Weather on the Diet of Martial Eagles

Our results indicate that Martial Eagle prey delivery rates and prey composition are significantly influenced by maximum daily air temperature. We found that as T_{max} increased, provisioning rates decreased, and that prey composition shifted from birds and mammals towards reptiles and mammals, which confirmed our hypothesis. Thus, the foraging behaviour of Martial Eagles in the KNP is influenced by temperature, either due to shifts in foraging behaviour (e.g. they actively select different phyla on hotter days) or through shifts in prey availability, due to changes in prey thermoregulatory behaviour (van de Ven, McKechnie & Cunningham, 2019). Our analyses suggest that T_{max} was the most influential weather variable, while chick age had a moderate effect and R_{day} had little effect on Martial Eagle prey provisioning. These results show similar trends to that of another endangered raptor, the Black Harrier, whereby increasing temperatures significantly reduced the proportion of their primary prey, small mammals, in the diet; This could have been due to declines in mammal activity or abundance but ultimately the net result was a reduction in foraging efficiency (Garcia-Heras et al., 2017).

Our study found that on average, at least one prey item was delivered to the nest when T_{max} ranged between 15°C and 33°C. However, the mean quantity of prey items delivered to the nest declined below one item per day when T_{max} exceeded 33°C. This result could be explained by a trade-off between foraging efficiency and thermoregulatory behaviour, where instead of foraging, eagles make use of cooler microsites (Cunningham, Martin & Hockey, 2015), or are required to spend more time panting to cool down (van de Ven, McKechnie & Cunningham, 2019). Due to these behavioural adaptations, predators will attempt to compensate for a decline in prey quantity by switching to a higher quality prey (Hall & Chalfoun, 2018) or in some cases, larger prey (Palmer, Nordmeyer & Roby, 2004). Amongst the three prey phyla, bird meat is considered to have higher calorific content than both mammals and reptiles, thus, birds are considered to be the higher quality prey (Nagy, Girard & Brown, 1999).

We then explored whether the decrease in prey deliveries resulted in a decrease in biomass delivered to the nest. However, there was no evidence that T_{max} influenced the quantity of biomass delivered per day. An explanation for this result could include Martial Eagles exhibiting foraging behavioural plasticity, by selecting larger prey on hotter days. Alternatively, the relative availability of smaller prey decreased, which coincides with an increase in the availability of larger prey. We found that the average weights of all three prey phyla (reptiles, mammals and birds) differed significantly whereby the average weight of reptiles were double that of mammals and three times heavier than birds, which is a similar result to another Martial Eagle diet study (Naude et al., 2019).

We next looked to see whether T_{max} did in fact influence the size of the prey items delivered to the nest. The results indicate that eagles provision significantly heavier prey items as T_{max} increases, which was evident when we examined how each of the prey phyla were influenced across the T_{max} gradient. Birds were delivered significantly less than mammals and reptiles if T_{max} days were >34°C, while reptile deliveries increased significantly from 25°C upwards. A biological explanation for this may be that reptiles (ectotherms) are more likely to increase activity on hotter days due to their energetic reliance on temperature (Mendyk, Augustine &

Baumer, 2014). Conversely, the activity of birds is likely to decrease to cope with increasing temperatures (Cunningham, Martin & Hockey, 2015). Interestingly, mammals were the only phyla in the diet which were not influenced by T_{max}, although the probability of a delivery did decrease slightly across the T_{max} gradient. This suggests that mammal activity is influenced to a lesser extent by temperature, or that their retreat into refugia does not provide adequate cover from predation. Alternatively, we assessed the daily maximum temperatures on an hourly basis and found that days with high, moderate and low T_{max} values, all experienced similar temperatures in the early morning (Appendix 8). Thus, it is possible that mammals tend to be provisioned earlier in the morning, however, this analysis did not assess prey provisioning on an hourly time scale.

Sex-based Weather Influences

Next, we assessed whether the impact of T_{max} was sex related and found that the quantity of prey delivered by the male declined on hotter days. The reasons behind male prey declines may be due to reduced prey availability (i.e. birds are less active on hotter days). Alternatively, increased physiological or behavioural thermoregulation would reduce the amount of time dedicated to hunting, which is a phenomenon exhibited by other birds in arid environments (Cunningham et al., 2013). Females delivered the maximum number of prey items between the daily T_{max} of 27°C and 30°C, thus exhibiting a quadratic relationship with daily temperatures. This could be explained by the significance of the other explanatory variable, chick age. Young chicks are unable to thermoregulate and the female is required to keep the chick both warm and cool by either brooding or shading the chick during cold days and hot days respectively (Katzenberger et al., 2015). Thus, brooding behaviour could explain why females provisioned more prey on moderately warm days as opposed to very hot and cold days.

The influence of temperature on probability of a prey delivery differed significantly between male and female Martial Eagles. The differences in their provisioning rates may be explained by sex-based role separation during the breeding season. Like most other raptors, the role of the female is to brood and protect the nestling/s during the early stage of breeding, however, the female does commence with prey provisioning as the chick gets older (Poulin & Todd, 2006). Weather conditions can influence these sex-based roles, for instance, female Black Sparrowhawks (*Accipiter melanoleucus*) increase brooding behaviour during cold and wet weather conditions, thus limiting the amount of prey delivered to the nestling (Katzenberger et al., 2015). Likewise, increased T_{max} necessitated behavioural trade-offs for male Southern Yellow-billed Hornbills (*Tockus leucomelas*), where increased thermoregulation (e.g. panting) and time spent in cooler microsites, leads to a decrease in prey deliveries (van de Ven, McKechnie & Cunningham, 2019).

The results of this study indicate that female eagles provisioned significantly heavier prey than males. This result further enforces the findings of another Martial Eagle diet study in the Maasai Mara region of Kenya (Hatfield, 2018). Likewise, this provisioning division has been found in other large eagles such as the Harpy Eagle (*Harpia harpyja*) (Miranda, 2018). It is evident that sex-based diet niche separation is a mechanism by which Martial Eagles may reduce direct competition for the same food resources, whilst potentially increasing diet diversity. Importantly, is may also be a mechanism by which eagles buffer the effects of increased temperatures.

Contextualising Results

The physiological effects of reduced prey deliveries for developing Martial Eagle chicks remain unknown; however, decreased prey delivery rates in other species significantly influence the growth rate and size of fledglings, which has a large effect on the survival rate of first year birds (Martínez-Ruiz et al., 2023). For example, Manx Shearwater (*Puffinus puffinus*) chicks had lower fledging weights due to a decrease in the adult provisioning rate, as a direct result of warming sea surface temperatures and a simultaneous decline in prey quality (Riou et al., 2011). Similarly, the mortality rate of Hen Harrier (*Circus cyaneus*) chicks increased when the male prey delivery rates decreased due to the negative effect of low temperatures and high rainfall (Redpath et al., 2002). Lastly, the provisioning rate of American Kestrel (*Falco sparverius*) was not influenced by the abundance of prey items, however, they were influenced by the availability of prey in the environment, which was directly influenced by weather conditions and culminated in a reduced reproductive success (Dawson & Bortolotti, 2000).

In the future, it is predicted that climate change will lead to lizard population extinctions (Sinervo et al., 2010). Although our results indicate that Martial Eagle are capable of provisioning both Rock Monitor and Water Monitor during hotter T_{max} days, there was clear evidence of a decreasing likelihood of reptile prey deliveries on T_{max} days which exceed the

40°C threshold. This may be partly due to the physiological limitations of the lizards, which are unable to cope with extreme temperatures and tend to retreat into cool refuges or risk overheating and ultimately, death (Sinervo et al., 2010). However, the ecology and physiological behaviour of Rock Monitor and Nile Monitor differ. Nile Monitor have a lower body temperature which could be attributed to its use of riparian vegetation and water, which they use for thermoregulation and predator refuge (Bowker, 1984). Rock Monitor, much like Savannah Monitor (*V. exanthematicus*) have relatively long heating and cooling periods but heat faster than cooling (Bowker, 1984). According to Bowker (1984), Rock Monitor are thermophobic whilst Savannah Monitor, are thermophilic. These contrasting behavioural thermoregulatory mechanisms will have differing foraging implications for Martial Eagles.

In some situations, there have been shifts in prey selection which allow a species to offset the increased metabolism required to digest low quality prey (Boersma et al., 2016). Likewise, by selecting higher quality food, such as birds, animals may require less biomass and can afford to spend less time foraging in physiologically stressful temperatures and more time undertaking alternative behaviours such as brooding, shading or attending offspring (Hall & Chalfoun, 2018). Individuals that forage in riskier temperatures (i.e. higher temperatures which exert more physiological stress on an individual), will forage for higher quality prey. This is what is called "hazardous duty pay" which is an extension of fear-based modelling which looks at the trade-off between food and safety (Brown & Kotler, 2004).

The energetic cost and benefits associated with hunting and feeding on different prey phyla are unstudied in Martial Eagles. With this in mind, large protected areas slow down the impact of climate induced changes in arid environments (Loarie et al., 2009). This can be explained by increased biodiversity which is critical for maintaining ecosystem services (García-Palacios et al., 2018). The benefits of a diverse diet in this case may be problematic as the energetic costs may outweigh the benefits (Jagielski et al., 2021). However, since we do not know the nutritional qualities of each species, we are unable to differentiate high quality from low quality prey species. What is apparent is that the cost of searching for prey increases as prey availability decreases and search intensity increases. In this case, bird density (particularly within the order Galliformes) in Martial Eagle territories, may be higher at the start of the season and may naturally decline through predation attrition. Much like Polar Bears, which switch prey to meet their energetic demands, it may make energetic sense to focus on another prey phylum rather than increase the search intensity for birds.

Study Limitations

The body weights used for different prey species were estimated for the purpose of attempting to analyse the biomass delivered to the nest during the breeding season. The average weight of each species will vary across habitat types and seasons; However, biomass is a particularly important metric used for gauging the health and growth rate of the chick and for the purpose of these analyses, the weight estimates were deemed satisfactory. Furthermore, this study was only able to quantify the prey items delivered to the nest and is therefore unable to assess the total prey consumed by adult eagles or prey availability.

This study does not take in to account the impact of macro thermal relief, whereby hilly topography remains cooler while flat landscapes get hotter (Sears, Raskin & Angilletta, 2011), and this may not have been captured by the resolution of the weather data we used. Furthermore, the temporal resolution at which we performed these analyses may not have sufficiently captured all of the weather-related diet changes. Analyses conducted on an hourly time frame may produce more meaningful results which highlight how Martial Eagles provision food across the day (e.g. while temperatures are more suitable during the early mornings (Appendix 8).

Implications of Warming Climate for Martial Eagles

It is evident that the foraging behaviour of this generalist predator is significantly influenced by temperature and the degree to which they are influenced is mitigated by their diverse diet of mammals, reptiles and birds. This study which was conducted in the largest protected area in South Africa, has highlighted the importance of prey availability, not just of one prey phyla, but all of three of them. Given that biodiversity and prey abundance is generally lower outside protected areas, it is plausible to think that eagles outside protected areas are not able to buffer the physiological effects of increasing temperatures; which may ultimately cause a decrease in hunting success, breeding success and subsequent population declines.

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APPENDICES

Appendix 1. Martial Eagle nests monitored with camera traps from 2018 to 2022 in the KNP. Nest numbers correspond with study site map (see figure 3). Nest number 10 and 14 were excluded from the analysis due to a limited number of days sampled. Total hours (n = 9310), days (n = 756) and prey items (n = 793) recorded after filtering the data for analytical purposes. Provisioning rate calculated as the number of items delivered divided by the number of days recorded. Diet diversity (Shannon Diversity Index) per nest was calculated from the total identified species (n = 37) and total prey items identified to species level (n = 751). Distance calculated from each nest to the nearest weather station.

Nest No.	Nest code	Nest tree species	Date start	Date end	Total hours	Total days	Prey items	Provisioning rate per day	Number of species	Diet Diversity (Shannon Index)	Distance to weather station (km)
1	2011_05	*Senegalia nigrescens*	2018/08/05	2018/11/01	1049	72	71	0.99	14	2.02	32.1
2	2014_04	*Combretum imberbe*	2018/09/06	2018/10/14	493	39	56	1.44	11	1.94	34.3
3	2014_08	*Senegalia nigrescens*	2018/07/19	2018/07/28	116	10	12	1.20	5	1.47	28.3
4	2015_01	*Colophospermum mopane*	2019/06/12	2019/09/08	649	56	53	0.95	10	1.78	72.6
5	2011_20	*Combretum imberbe*	2020/05/10	2020/07/01	601	53	42	0.79	12	1.78	3.8
6	2018_06	*Senegalia nigrescens*	2020/08/16	2020/11/11	1109	88	105	1.19	15	1.91	17.6
7	2011_03	*Combretum imberbe*	2021/07/14	2021/09/23	850	72	86	1.19	12	1.71	5.0
8	2019_03	*Senegalia nigrescens*	2021/06/20	2021/09/04	890	77	72	0.94	13	2.00	10.2
9	2021_05	*Combretum imberbe*	2021/08/10	2021/11/06	1119	89	102	1.15	17	2.25	26.6
10	2020_12	*Colophospermum mopane*	2022/05/19	2022/06/22	-	-	-	-	-	-	-
11	2022_01	*Senegalia nigrescens*	2022/08/16	2022/11/07	1085	84	76	0.90	9	1.87	12.2
12	2022_18	*Sclerocarya birrea*	2022/06/25	2022/09/03	816	71	83	1.17	12	1.62	16.9
13	2022_22	*Senegalia nigrescens*	2022/07/22	2022/09/04	533	45	35	0.78	10	2.05	22.7
14	2022_23	*Sclerocarya birrea*	2022/07/25	2022/07/26	-	-	-	-	-	-	-

Appendix 2. A camera trap image of a Martial Eagle nest (number 8 – see Figure 3) showing the male Martial Eagle (Right) delivering a Rock Monitor (*V. albigularis*) to the nestling (centre) and female (Left). Note the male’s thin legs and crop and the females thick legs and spots extending to the base of the foot. Spot patterning was used to differentiate the male and the female from the same nest, although, each nest varied and in some cases different metrices were used to identify the individual (e.g. 1 adult was ringed, while another was missing a toe).

Appendix 3. Martial Eagle prey composition from 12 nests in the KNP. Units in parentheses after class, order and common name denote the proportional contribution of prey to the diet. The total indicates the total individual specimens in the diet. The age of each prey species was predicted before calculating the estimated mass of each species. The prey species were then categorised into 1 of 7 prey categories based on the mass of the species. Prey categories were then used to estimate the proportion of each prey item delivered to the nest. Mass was estimated using the average male and female weights as defined in the literature.

Phylum (%)	Order (%)	Common name (%)	Scientific name	Total	Mass (g)	Prey category	Prey age	Prey proportion (%)
Bird (46)	Galliformes (39)	Helmeted Guineafowl (14)	*Numida meleagris*	111	1440	medium	adult	78.67
		Swainson's Spurfowl (9)	*Pternistis swainsonii*	74	605	small - medium	adult	81.53
		Crested Francolin (7)	*Dendroperdix sephaena*	56	347	small	adult	92.01
		Natal Spurfowl (3)	*Pternistis natalensis*	23	450	small	adult	92.01
		Shelly's Francolin (<1)	*Scleroptila shelleyi*	4	468	small	adult	92.01
		Coqui Francolin (<1)	*Peliperdix coqui*	2	243	small	adult	92.01
		Chicken (Boschveld) (5)	*Gallus domesticus*	42	1088	medium	adult & juvenile	78.67
		Spurfowl sp.	-	2	473	-	-	-
		Unidentified (<1)	-	1	705	-	-	-
	Gruiformes (2)	Red-Crested Korhaan (2)	*Lophotis ruficrista*	15	675	small - medium	adult	81.53
		Black-Bellied Bustard (<1)	*Lissotis melanogaster*	1	1725	medium	adult	78.67
	Bucerotiformes (1)	Southern Red-billed Hornbill (<1)	*Tockus rufirostris*	5	139	very small	adult	92.93
		Southern Yellow-billed Hornbill (<1)	*Tockus leucomelas*	2	190	very small	adult	92.93
		African Grey Hornbill (<1)	*Lophoceros nasutus*	1	157	very small	adult	92.93
	Anseriformes (<1)	Egyptian Goose (<1)	*Alopochen aegyptiaca*	2	2110	small - medium	adult	81.53
	Charadriiformes (<1)	Spotted Thick-knee (<1)	*Burhinus capensis*	3	472	small	adult	92.01
		Double-banded Sandgrouse (<1)	*Pterocles bicinctus*	2	230	small	adult	92.01
		Water Thick-Knee (<1)	*Burhinus vermiculatus*	1	309	small	adult	92.01
	Columbiformes (<1)	Cape Turtle Dove (<1)	*Streptopelia capicola*	1	129	very small	adult	92.93
	Coraciiformes (<1)	Giant Kingfisher (<1)	*Megaceryle maxima*	1	363	small	adult	92.01

	Cuculiformes (<1)	Burchell's Coucal (<1)	*Centropus burchellii*	1	182	very small	adult	92.93
	Strigiformes (<1)	Spotted Eagle-Owl (<1)	*Bubo africanus*	2	645	small - medium	adult	81.53
	Unidentified (2)	-	-	13	688	-	-	-
Mammal (32)	Carnivora (18)	Banded mongoose (7)	*Mungos mungo*	55	1350	medium	adult	78.67
		Slender mongoose (6)	*Galerella sanguinea*	43	507	small - medium	adult	81.53
		Dwarf mongoose (5)	*Helogale parvula*	37	239	small	adult	92.01
		Large-spotted genet (<1)	*Genetta tigrina*	5	1876	medium	adult	78.67
		Unidentified (<1)	-	3	602	-	-	-
	Lagomorpha (8)	African savannah hare (8)	*Leupus saxatilis*	64	2075	medium - large	adult	74.21
	Artiodactyla (2)	Common duiker (1)	*Sylvicapra grimmia*	8	5967	very large	sub-adult & juvenile	38.60
		Steenbok (1)	*Raphicerus campestris*	6	5775	very large	adult & juvenile	38.60
		Impala (<1)	*Aepyceros melampus*	1	8128	very large	juvenile	38.60
		Bushbuck (<1)	*Tragelaphus scriptus*	1	6438	very large	juvenile	38.60
		Common reedbuck (<1)	*Redunca arundinum*	1	8960	very large	juvenile	38.60
	Rodentia (2)	Tree squirrel (2)	*Paraxerus cepapi*	17	193	very small	adult	92.93
		Springhare (<1)	*Pedetes capensis*	1	2840	medium - large	adult	74.21
	Hyracoidea (<1)	yellow-spotted rock hyrax (<1)	*Heterohyrax brucei*	1	1850	medium	adult	78.67
	Primates (<1)	Vervet monkey (<1)	*Cercopithecus pygerythrus*	1	4800	large	adult	50.00
	Unidentified (2)	-	-	10	1020	-	-	-
Reptile (20)	Squamata (20)	Rock monitor (16)	*Varanus albigularis*	127	2939	medium - large	adult & sub-adult	74.21
		Nile monitor (4)	*Varanus niloticus*	32	2442	medium - large	adult & sub-adult	74.21
		Giant plated lizard (<1)	*Matobosaurus validus*	2	907	small - medium	adult	81.53
Unidentified (2)	-	-	-	13	1183-	-	-	-

Appendix 4. Prey size categories sampled to determine the average proportion of the prey item delivered to the nest. Species were grouped into size categories based on the weight (g). The number of samples (N) was the total number of prey items delivered to the 14 nests before filtering the data for analytical purposes. The number of sampled (n) prey items made up either 20% or 100% for categories with a small sample size. The mean proportion of 25 sub-sampled items were calculated at random without replacement. The average proportion for the size category was calculated from 100 mean proportions.

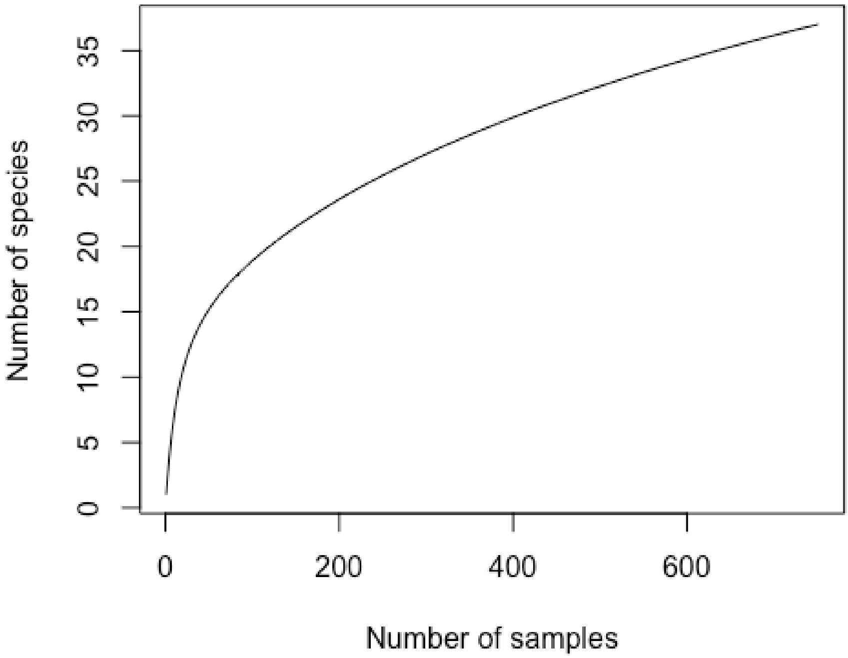
Size category	Samples (N)	Sampled (n)	Sampled (%)	Average proportion (%)
very small	31	31	100%	93%
small	179	36	20%	92%
small - medium	182	37	20%	82%
medium	257	52	20%	79%
medium - large	376	76	20%	74%
large	3	3	100%	50%
very large	27	27	100%	39%
extra large	1	1	100%	-
	1056	**263**	**24,91%**	

Appendix 5. Description of the model structures and response variables used to describe the climatic interactions with Martial Eagle prey. The ‘^2’ indicates that the variable was included as a quadratic term in the model, ‘s_’ indicates that the data were scaled, and ‘–‘ is non-applicable. All models were fitted with “territory” as the random effect. “R_{day}” is a binary variable, where rainfall on the day =1 and no rainfall =0. “chick_age” was recorded in days. “T_{max}” was the maximum daily temperature. The natural log of the Total Hours recorded each day (”tothours”) was used as a model offset where indicated. The square root of ”tothours” was also included as an explanatory variable where indicated.

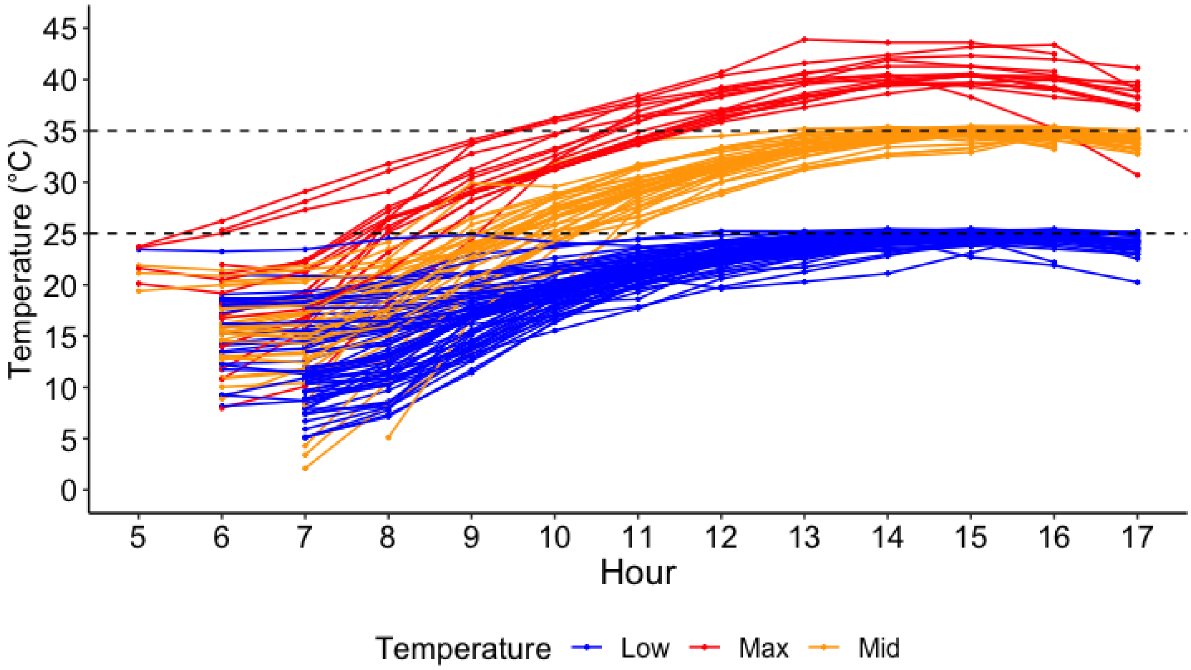
		Two vector response variable description				
Analysis	Response variable	Vector 1	Vector 2	Distribution (link)	Offset	Explanatory variables
1	Prey Count	-	-	Poisson	log(tothours)	R_{day} + s_chick_age^2 + s_ T_{max} ^2
	Male Prey Count	-	-	Poisson	log(tothours)	R_{day} + s_chick_age + s_ T_{max}
	Female Prey Count	-	-	Poisson	log(tothours)	R_{day} + s_chick_age^2 + s_ T_{max} ^2
2	Prey probability	Prey delivery	No prey delivery	binomial (logit)	glmerControl(optimizer = "bobyqa")	R_{day} + s_chick_age + s_ T_{max} ^2 + sqrt(tothours)
	Male Prey probability	Male delivery	No male delivery	binomial (logit)	glmerControl(optimizer = "bobyqa")	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)
	Female Prey probability	Female delivery	No female delivery	binomial (logit)	glmerControl(optimizer = "bobyqa")	R_{day} + s_chick_age^2 + s_ T_{max} ^2 + sqrt(tothours)
3	Biomass	-	-	nbinom2 (log)	-	R_{day} + s_chick_age^2 + s_ T_{max} + sqrt(tothours)
	Male Biomass	-	-	nbinom2 (log)	-	R_{day} + s_chick_age^2 + s_ T_{max} + sqrt(tothours)
	Female Biomass	-	-	nbinom2 (log)	-	R_{day} + s_chick_age^2 + s_ T_{max} ^2 + sqrt(tothours)
4	Prey mass	-	-	gaussian (identity)	-	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)
	Male Prey mass	-	-	gaussian (identity)	-	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)
	Female Prey mass	-	-	gaussian (identity)	-	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)
5	Reptile probability	Reptile delivery	No reptile delivery	binomial (logit)	glmerControl(optimizer = "bobyqa")	R_{day} + s_chick_age^2 + s_ T_{max} ^2 + sqrt(tothours)
	Bird probability	Bird delivery	No bird delivery	binomial (logit)	glmerControl(optimizer = "bobyqa")	R_{day} + s_chick_age + s_ T_{max} ^2 + sqrt(tothours)
	Mammal probability	Mammal delivery	No mammal delivery	binomial (logit)	glmerControl(optimizer = "bobyqa")	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)
6	Reptile prey mass	-	-	gaussian (identity)	-	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)
	Bird prey mass	-	-	gaussian (identity)	-	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)
	Mammal prey mass	-	-	gaussian (identity)	-	R_{day} + s_chick_age + s_ T_{max} + sqrt(tothours)

Appendix 6. A correlation matrix showing the collinearity of the four explanatory variables from the T-Max dataset.

Variables	T_{max}	Rain Day	Chick Age	Total Hour
T_{max}	1.000	NA	0.177	0.403
Rain Day	NA	1.000	0.010	-0.004
Chick Age	0.177	NA	1.000	0.548
Total Hours	0.403	NA	0.548	1.000



Appendix 7. A species rarefaction curve generated from 751 prey items collected at 12 territories and identified down to species level. The line indicates the number of species identified (n = 37). The curve trend indicates whether more species could be expected if the sample size increased. The general trend indicates that the number of species found in the diet has not yet reached the asymptote.



Appendix 8. Temperature records for each hour of the day. Temperatures were grouped according to the T_{max} of the day, for example: Low temperatures had a T_{max} of 25°C, Mid temperatures had a T_{max} of 35°C and Max temperatures had a T_{max} >= 40°C. There looks to be significant overlap in temperatures before 11h00 which may account for the overlap in prey phyla on both hot and cold days. Temperature data were extracted from the South African Weather Service (SAWS) stations for 2018 and ILeaf weather stations from 2019, onwards.