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Research article

Africa's overlooked top predator: Towards a better understanding of martial eagle feeding ecology in the Maasai Mara, Kenya

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Raptors exert top-down influences on ecosystems via their effects on prey population dynamics and community composition. Most raptors are sympatric with other predators, thus complicating our understanding of their relative influence in these systems. Estimates of kill rates and prey biomass recycling have been used as predation metrics that allow quantitative comparison among species and assessment of the relative role of single species within complex food webs. Few studies have produced findings of kill rates or prey biomass recycling for raptors. We used a supervised machine learning algorithm to behaviourally classify high resolution accelerometer informed GPS locations of tagged adult non-breeding martial eagles *Polemaetus bellicosus* in the Maasai Mara region of Kenya to estimate kill rates and prey biomass recycling. Eagle locations classified as feeding were clustered using distance and time thresholds to identify kills and calculate kill rates. Identified kill sites were quickly ground-truthed to confirm kills and identify prey species. We estimated kill rates for martial eagles at 0.59 kills day^{-1} for males and 0.38 kills day^{-1} for females, and we estimated biomass recycling per ground-truthed kill at 1796 g for males and 3860 g for females. From our sample of identified ground-truthed kills, 'gamebirds' was the most frequently recorded prey category for male eagles and 'small ungulates' was the most frequently recorded prey category for female eagles. These results position martial eagles close to sympatric mammalian top predators in trophic pyramids and provide evidence for their classification as a top predator.

Keywords: behaviour classification, biomass recycling, kill rate, *Polemaetus bellicosus*

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Introduction

Critical to our understanding of top predators and their roles in ecosystems is our ability to accurately determine kill rates, i.e., the rate at which predators acquire food, which is often expressed as the number of organisms killed and fed on by an individual or group within a given period (Vucetich et al. 2011). Kill rates are influenced by: 1) the nutritional requirements of an individual and the family unit they are provisioning (Mattisson et al. 2011, Cristescu et al. 2022), 2) the available prey species' size, nutritional quality, and abundance (Vucetich et al. 2011), 3) the age and experience of the predator (MacNulty et al. 2009) and 4) the length of time that a predator can spend feeding on a kill without being disturbed (Carbone et al. 2005, Dekker et al. 2012). Measuring kill rates for top predators has long been a challenge for ecologists, however, advances in global positioning system (GPS) cluster analyses and accelerometer-informed behavioural classification have greatly improved estimates, specifically for large mammalian top predators (Sand et al. 2008, Knopff et al. 2010, Merrill et al. 2010, Vucetich et al. 2012, Elbroch et al. 2018, Cristescu et al. 2022).

The kill rate of a top predator is one of the key variables used in predator–prey models to estimate how much prey biomass an individual predator or group of predators kills and recycles per unit time from an ecosystem. Quantifying prey biomass recycling provides insights into predator nutritional requirements and predator–prey dynamics which influence ecosystem function. Perhaps the best example of this comes from decades-long observations of moose *Alces alces* – wolf *Canis lupis* population dynamics on Isle–Royale in the US where wolve kill rates of moose have been found to be one of many complex factors that influence moose populations on this island (Nelson et al. 2011).

Although estimates of kill rates and prey biomass recycling of several mammalian top predators have been well-studied and quantified, kill rates and prey biomass recycling of top avian predators remain unknown (Norrdahl and Korpimäki 1995, 2000, Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998), especially when non-breeding. Hence their role in predator–prey dynamics is often elusive. Kill rates of avian top predators have been studied during breeding using behavioural watches and cameras at nest sites (Collopy 1984, López-López and Urios 2010, Debus 2011, Bassi et al. 2017), however, inferring individual kill rates and prey biomass recycling from these data is difficult. Sex-based behavioural roles (Collopy 1984, Bassi et al. 2017), the age of the nestlings (Collopy 1984), the need to deliver prey items of varying size and mass (Sonerud 1992) differences in prey detectability at nests (Rutz 2003), and the role of self-feeding by the provisioner (Sonerud 1992) create biases that can lead to both under and over-estimations of individual kill rates and prey biomass recycling.

One way to move beyond the biases associated with quantifying top avian predator kill rates and prey biomass recycling is to document these metrics during the non-breeding period, but this has proven to be challenging. Some studies have attempted to provide baseline non-breeding kill rate data for white-tailed eagles *Haliaeetus albicilla* (Nadjafzadeh et al. 2016), Bonelli's eagles *Aquila fasciata* (Moleón et al. 2011), and northern goshawks *Accipiter gentilis* (Kenward 1982). Unfortunately, the methods employed in these studies (i.e. behavioural watches and systematically searching home ranges for food remains and pellets) are impractical for many species, as raptors often have large home ranges and thus evade consistent observation. More importantly, analysis of pellets and prey remains do not always accurately reflect prey species composition, and therefore require supplemental, time-intensive direct observations to quantify inherent biases in diet estimation (Redpath et al. 2001, Rutz 2003).

Most studies exploring top avian predator foraging ecology and diet have focused on temperate regions (Brown and Watson 1964b). In more biodiverse, equatorial tropical regions, most raptor foraging and diet studies have been done at the nest and have focused on prey-deliveries and identification. In-depth studies on kill rates by birds of prey in the tropics are few (McClure et al. 2018, Buechley et al. 2019), particularly in predator-rich African savanna ecosystems where multiple top avian predators co-occur. Studies of predators generally in this region have largely excluded avian predator comparisons (Sinclair et al. 2003, Owen-Smith and Mills 2008), perhaps because of the lack of systematic research quantifying avian species predation patterns.

One of the top avian predators in most African savanna ecosystems is the martial eagle *Polemaetus bellicosus*; a large, sedentary, and long-lived species that occurs at varying but generally low population densities compared to most other birds of prey (Clark and Davies 2018). Now listed as endangered by the International Union for the Conservation of Nature (IUCN) (Birdlife International 2018), very little is known about martial eagle kill rates and prey biomass recycling, but their diet is known to vary widely and includes small gamebirds, small mammals, young bovids, warthog piglets, and monitor lizards (Boshoff et al. 1990, Naude et al. 2019). Martial eagles are known to exhibit reversed sexual dimorphism (RSD) and dietary studies have shown how RSD is correlated with differences in diet between the sexes, where larger females on average select for larger prey items (Hatfield 2018).

To improve our understanding of the role top avian predators can play within the diverse predator guilds of African savanna ecosystems, we used GPS transmitter-equipped martial eagles to quantify individual kill rates and estimate the biomass of live prey recycled from the ecosystem during the non-breeding season. This novel work represents the first attempt at calculating said predation metrics and allows for a comparative assessment of the martial eagle with other sympatric top predators.

Material and methods

Study area

The ~ 2500 km^2 Maasai Mara region (henceforth, Mara) in southwest Kenya (1°S and 34°–35° east, altitude ~ 1400 to

~ 1800 m a.s.l.) forms part of the greater Mara–Serengeti ecosystem. The study area comprises a reserve network of protected areas under both private and local government management. The Mara is characterized by a dynamic rainy season that occurs from November to June, peaking between November and December (short rains) and then again between March and May (long rains) (Bartzke et al. 2018). Annual rainfall varies widely but is typically between 600–900 mm (Bartzke et al. 2018). This landscape includes tall and short grassland, scrubland, woodland grassland, forest, and rocky hillsides (Oindo et al. 2003). The combination of a bimodal rainy season, deep nutrient-rich soils, and equatorial location makes the Mara one of the most ecologically productive and biodiverse savanna ecosystems in the world (Reid 2012). Thus, it is home to a diverse and densely populated fauna that is highlighted by the annual common wildebeest *Connochaetes taurinus* migration and the rich assemblage of predators that consume and recycle them.

Capture and tagging

From October 2016 to October 2019, we captured and released 21 adult martial eagles (13 males and 8 females), representing 16 breeding pairs, using a Bal Chatri trap (Berger and Mueller 1959). Adult eagles with known nest sites were targeted for capture. We inferred sex from body mass at capture ($F = \geq 4$ kg, $M = < 4$ kg) measured with a digital scale (Dr Meter ES-PS01, CHN) to the nearest 10 g and later confirmed sex through behavioural observations at nest sites while pairs were copulating, courting, or incubating.

Each captured eagle was fitted with a 27 g GPS with global system for mobile (GSM) and solar powered backpack transmitter attached with custom harnesses made with a Teflon™-like ribbon supplied by KoEco©. Transmitter casings had rounded edges with durable neoprene padding on the bottom and no external antenna, and the harness had a weak leather link included to facilitate drop off after ~ 4 years. The combined weight of transmitter and harness was ≤ 1% body mass of the smallest Martial Eagle caught during this study. Transmitters collected GPS location data throughout the full 24 h period on a dynamic, accelerometer-and-gyroscope-informed sampling schedule with time intervals ranging from 30 s to 1 h between locations (proprietary algorithm, madebytheo©). Time intervals shortened as continuous accelerometer movement energy (20 Hz) increased and transmitter tilt angle exceeded 70° to allow us to distinguish feeding action from flying and perching. Locations were collected in bursts of three, separated by 2 s intervals (henceforth, burst). In cloudy weather conditions, these solar-powered transmitters reverted to collecting four locations per day at six-hour intervals (05:00, 11:00, 17:00 and 23:00 h) (henceforth, low power periods).

Behaviour classification

To calculate daily activity budgets, we trained a random forest to classify transmitter GPS data into flight, feeding, and perching/other behaviours. Training data were collected by annotating GPS locations with behaviour labels from opportunistic observations of 8 of the 21 tagged martial eagles between 2017 and 2019 from a parked vehicle using binoculars and a spotting scope. Any movement through the air was 'flight,' and plucking or eating prey was 'feeding.' The third category 'perching/other' was predominantly perching and preening, but also included other largely stationary behaviours like walking. We chose these three behaviours as they are habitual, sustained, and distinctive, as well as practical to monitor in situ. Non-breeding season dates were defined for each mated pair based on field observations in combination with camera traps placed in nests to monitor chick rearing. The non-breeding period excluded nest-building, which we assumed to be the 30-day period prior to incubation. The non-breeding season resumed either when a breeding attempt failed or seven months after a chick had fledged the nest.

The random forest used two location-level features recorded by the transmitters, and we engineered six burst-level features that captured energy expenditure and tilt angle via changes in the sampling frequency. Burst-level features included times (sec) to previous and subsequent bursts, the maximum of these two times, distance (m) to previous and subsequent bursts, and the maximum of these two distances. The location-level features were speed (v, m sec^{-1}) as recorded by the transmitter, and altitude (z, meter). Altitude was the difference between the transmitter's height above mean sea level based on GPS and ground elevation (NASA JPL 2013). Because behavioural observation periods were temporally structured and dependent within-individual, we blocked training data by individual. Behavioural observations of two birds were set aside for testing, and observations of the remaining six birds were used to optimize hyperparameters with blocked cross-validation and to train the random forest using the R package 'randomForest' 4.6-14 (Liaw and Wiener 2002) and R ver. 3.6.3 (www.r-project.org). To estimate performance of the fitted random forest on the two test birds, we calculated a confusion matrix; the precision, recall, and F1 score of each behaviour; and the macro- and micro-averages of these performance metrics. We homogenized behaviour labels within each burst of GPS locations using a majority rule. We calculated daily activity time budgets by run-length encoding labelled bursts into activity bouts. The unlabelled periods between activity bouts were labelled as 'other/perching' if either the preceding or proceeding bout was 'other/perching'. Otherwise, the period was split evenly between feeding and flight following the order of activities. Of the 21 tagged Martial Eagles, 16 (10 males and 6 females, 14 pairs) had defined non-breeding periods that were behaviourally classified amounting to 5222 non-breeding bird-days, but we omitted 911 bird-days with transmitter low-power periods, leaving 4311 bird-days in our analysis (1371 female, 2940 male).

Kill rates and handling time

We clustered the behaviourally classified GPS locations into kills and estimated sex-specific kill rates and looked for sex differences in kill rates (per day), and handling time (time spent handling each kill). A kill cluster was defined as triplets of feeding bursts (at least nine locations) within 20 h and 500 m. These thresholds were informed by our field observations of martial eagles feeding during the non-breeding period. We observed martial eagles on several occasions sleeping with kills either held in their feet or on the ground close to their roost. On several occasions, we observed martial eagles returning to kills that had been left on the ground the previous evening. During our study, we never observed martial eagles dismembering and caching kills, nor has this been reported elsewhere, and they readily abandon large kills due to disturbance from kleptoparasites such as spotted hyenas *Crocuta crocuta* and tawny eagles *Aquila rapax*. Martial eagles moved mostly < 100 m with prey but were occasionally seen flying up to several hundred meters with prey seeking cover to feed. They were never seen to transport a kill more than 500 m between feeds, nor is this likely during the non-breeding season (Arnold 1954). We calculated the handling time of each predicted kill (excluding those within 20 h of a low-power transmitter period) by run-length encoding behaviour bouts in the kill cluster, and then summarized handling times within.

We estimated sex-specific kill rates and looked for sex differences in kill rates using the number of kills on 3863 bird-days, with 1241 bird-days of 6 females across 12 non-breeding seasons (i.e. we followed each individual for on average two non-breeding seasons), and 2622 bird-days of 10 males across 17 non-breeding seasons. We tested for sex differences in the handling time of 380 kills detected by our algorithm, with 75 kills by 5 females across 9 non-breeding seasons, and 305 kills by 10 males in 18 non-breeding seasons. We looked for sex differences in kill rates and handling times using generalized linear mixed-effects regression models fitted with the *glmer* function in R package 'lme4' (Bates et al. 2015). We used a Poisson model for kill rate, the number of kills detected by the algorithm per bird-day, and the kill rate model excluded days with low-power periods and the days preceding and proceeding low-power days. One non-breeding season was omitted entirely because all days either had low-power periods or were pre- or proceeded by a day with a low-power period.

We used an exponential model for handling time (minutes) and excluded kills that began within 20 h of a low-power period as part of the kill might have been missed due to low power. We omitted 2228 kills (487 by females and 1685 by males) because they began or ended within 20 h of a low-power period. Consequently, three non-breeding seasons were omitted entirely because they contained zero kills with known start or end times (ME16-1, ME19-1 and ME19-2).

In both models, the fixed effect was sex, and random intercepts were included for each individual's non-breeding season. We tested for sex differences in fitted mean kill rates and handling times using R package 'emmeans' (Lenth 2022). Individual summary statistics were calculated in R ver. 3.6.3 (www.r-project.org).

Field validation and prey species composition

We opportunistically ground-truthed the centroid of a predicted kill site within 72 h of the first location in the kill cluster. This rapid response enhanced the probability of finding small or scattered prey remains. In addition to two of the authors, 10 other experienced naturalists assisted with ground-truthing kills and were either trained prior to or guided through the process in real time over the phone. With a hand-held GPS or smartphone, we typically walked in increasingly large circles around the kill centroid, but search methods were slightly adapted to suit vegetation type, terrain, and wind direction. A kill was confirmed if we found part of a carcass, blood splatter, fresh bones, or three or more fresh pluckings (hair and feathers) of a single realistic prey species within 20 m of the kill centroid, but exceptions were made when strong winds clearly blew pluckings in a single direction > 20 m away from the feeding perch (Fig. 1).

Figure 1. Examples of evidence found at ground-truthed martial eagle kill locations in the Maasai Mara, Kenya. (A) A juvenile impala carcass killed by an adult female. (B) Pluckings of a white-bellied bustard *Eupodotis senegalensis* killed by an adult male.

In addition to ground-truthing predicted kills, we matched predicted kills to reports and social media posts of tagged martial eagles feeding (Fig. 2). Social media posts were gathered opportunistically but were most often found when one of the authors was 'tagged' in a relevant post or when #martialeagle was included in the social media post. We requested a photograph and brief description from the observer including date, time, and location, and then matched these attributes to predicted kills post hoc. We accepted precise times as well as time-periods such as morning (6:00–11:00 h), midday (11:00–14:00 h), and afternoon (14:00–19:00 h). For location, we asked for a GPS coordinate, a location pin sent from a smartphone, or a detailed description of the area including references to local landmarks.

Prey remains and photographs of prey remains were identified to genus or species level and when possible aged by two of the authors. Hare species remains were difficult to identify to species level and were assumed to be African savanna hare *Lepus victoriae* or cape hare *Lepus capensis*, the only two regularly occurring *Lepus* species in the Mara. Hyrax prey remains were also difficult to identify to species level and were assumed to be bush hyrax *Heterohyrax brucei*, the most common and widespread hyrax species in the Mara. Most gazelle prey remains could not be identified to species level and were assumed to be Thomson's gazelle *Eudorcas thomsonii* as they are the most common gazelle species in the Mara. The only other gazelle species that is present in the Mara is the larger Grant's gazelle *Nanger granti*. Each identified prey item was placed into one of the following prey categories for ease of comparison: gamebird, large bird, other bird, monitor, hare or hyrax, small carnivore, piglet, or small ungulate.

Prey biomass recycling

We estimated sex differences in prey biomass recycling per kill with an exponentially distributed mixed-effects linear regression model using the *glmer* function from R package 'lme4' (Bates et al. 2015). The fixed effect was sex of the martial eagle, and we included random intercepts for individual eagle. The response was average body mass in grams of prey items associated with predicted kills. The body mass of a prey item was determined using available literature on average live body mass of the prey species involved and rounded to the nearest 10 g. When only a range was provided for a species body mass in the literature the midrange was chosen as the prey body mass. Reported kills were excluded from this section of the analysis as we assumed that observations of citizen scientists were biased towards large prey items. Most prey items ground-truthed were assumed adults as when carcasses were found intact enough to age most prey items were aged as adult or close to adult size. Exceptions to this were impala *Aepyceros melampus*, bohor reedbuck *Redunca redunca*, Thomson's gazelle *E. thomsonii*, and common warthog *Phacochoerus africanus*, all of which were juveniles when carcasses were found intact enough to age. To derive body masses of these juvenile prey, we multiplied the birth or emergence mass of the species by a factor of 1.5. This factor was chosen as the resulting body masses reflected realistic live body masses for young ungulates preyed on by martial eagles and common warthog that were approximately one month old (Child et al. 1965, Roth 1965). We determined daily prey biomass recycling per martial eagle and per kilogram of martial eagle by estimating sex-specific average prey body mass multiplied by the estimated sex-specific daily kill rates divided by the average weight of adult male and female martial eagles within our study population.

Results

Behaviour classification

We observed the behaviour of eight adult martial eagles for a total of 26 h, 35 min and 54 s, during which the eagles spent

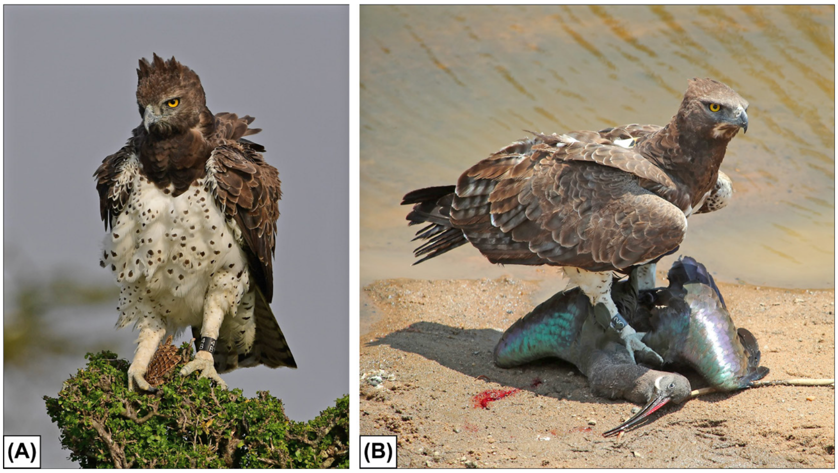

Figure 2. Example photographs of citizen science observations of tagged martial eagles feeding in the Maasai Mara, Kenya. (A) A tagged adult male feeding on a red-necked spurfowl. Report and photo courtesy of Jaana Eleftheriou and the African Impact Mara volunteer project. (B) A tagged adult male feeding on a hadada ibis *Bostrychia hagedash*. Report and photo courtesy of Marc Carniel and Steve Narasha.

17.2% of the time feeding, 14.9% flying, and 67.8% perching/other activities (Supporting information) and behaviourally labelled transmitter data to fit a random forest with the following hyperparameters: ntree = 500, mtry = 3, nodesize = 10, maxnodes = 32. The macro F1 score of the random forest was 0.94 indicating high precision and recall of the random forest (Table 1).

Kill rates and handling time

Our fitted Poisson regression model of kills per day estimated kill rates were 0.59 ± 0.04 kills per day (Mean ± SE, 95% CI: [0.52, 0.66]) for males, and 0.38 ± 0.03 kills per day (95% CI: [0.32, 0.45]) for females (Fig. 3). Our fitted exponential regression model of handling time estimated handling time at 248 ± 29.5 min (Mean ± SE, 95% CI: [197, 313]) for males, and 549 ± 108.8 min (95% CI: [372, 809]) for females (Fig. 3).

Field validation and prey species composition

We predicted and ground-truthed 96 kill locations (males = 58, females = 38) and found evidence of a kill at 89 of these sites (93%) (53 male, 36 female). We identified to genus or species level 81 prey items (51 male, 30 female) from the 89 kills that were successfully ground-truthed (Table 2).

We had 31 kills reported to our project (19 male, 12 female), and our algorithm detected 29 (94%) of these kills, and we identified all to genus or species level (Table 3). The two reported kills our algorithm failed to detect were small prey items (< 200 g) killed by male martial eagles: an adult corn crake *Crex crex* and a red-necked spurfowl pullet *Francolinus afer* (Taylor and Kirwan 2020). Of the 111 identified prey items from both ground-truthed predicted and reported kills, we recorded 26 different species with males killing 21 species and females killing 17 species. From the ground-truthed predicted kills, 'gamebirds' was the most frequently recorded prey category for male martial eagles (31 kills, 60%), with helmeted guineafowl being the most frequently recorded prey species (20 kills). 'Small ungulates' was the most frequently recorded prey category for female eagles (11 kills, 37%), with impala being the most frequently recorded species (7 kills, 23%).

Prey biomass recycling

From our fitted exponential regression model, we estimated biomass recycling per ground-truthed kill (mean ± SE) at 1796 ± 269 g (95% CI: [1338, 2410]) for males and 3860 ± 639 g (95% CI: [2791, 5338]) for females (Fig. 3). The estimated daily biomass killed by an adult male was 1060 g (~ 1 kg), and 1477 g for an adult female (~ 1.5 kg). The average weight (mean ± SE) of eagles within our study population was 3435 ± 40 g for males (n = 13) and 4718 ± 33 g for females (n = 8). The estimated prey biomass recycled per day per kg of male eagle was 309 g, and per kg of female eagle was 313 g.

Discussion

The presented kill rates and the estimated prey biomass recycled by martial eagles are the first attempt at quantifying the predatory and ecosystem service role of martial eagles in Africa's savanna ecosystems. Our findings provide insight into the role martial eagles play as predators as compared to more well-studied African mammalian top predators, particularly solitary hunters that include the leopard *Panthera pardus*, the cheetah *Acinonyx jubatus*, but also group hunters that include the lion *Panthera leo*, spotted hyena, and African wild dog *Lycaon pictus*.

The few studies on kill rates and prey biomass recycling of leopard and cheetah reveal that in most cases solitary kill rates are lower than martial eagles, but on average result in takes of much larger prey, therefore resulting in more prey biomass recycled and consumed per individual per day. In Namibia, leopard generally favored small ungulate prey, with a female averaging 1.6 kg day^{-1} about every five days (Stander et al. 1997). In Nepal, leopard generally favored medium sized ungulates, with single female leopard killing at intervals of ~ 6.7 days and consuming an average of 4 kg day^{-1} (Odden and Wegge 2009). Leopards in Iran generally

Table 1. Confusion matrix and performance statistics of behavioural classification by random forest.

		Predicted					
		Feed	Flight	Other	True positives	False negatives	Support
Observed	Feed	49	0	0	49	0	49
	Flight	0	57	0	57	0	57
	Other	5	0	15	15	5	20
	True negatives	72	69	106			126
	False positives	5	0	0			
		Performance					
		Precision	Recall	F1			
Class	Feed	0.91	1.00	0.95			
	Flight	1.00	1.00	1.00			
	Other	1.00	0.75	0.86			
Average	Macro	0.97	0.92	0.94			
	Micro	0.96	0.96	0.96			

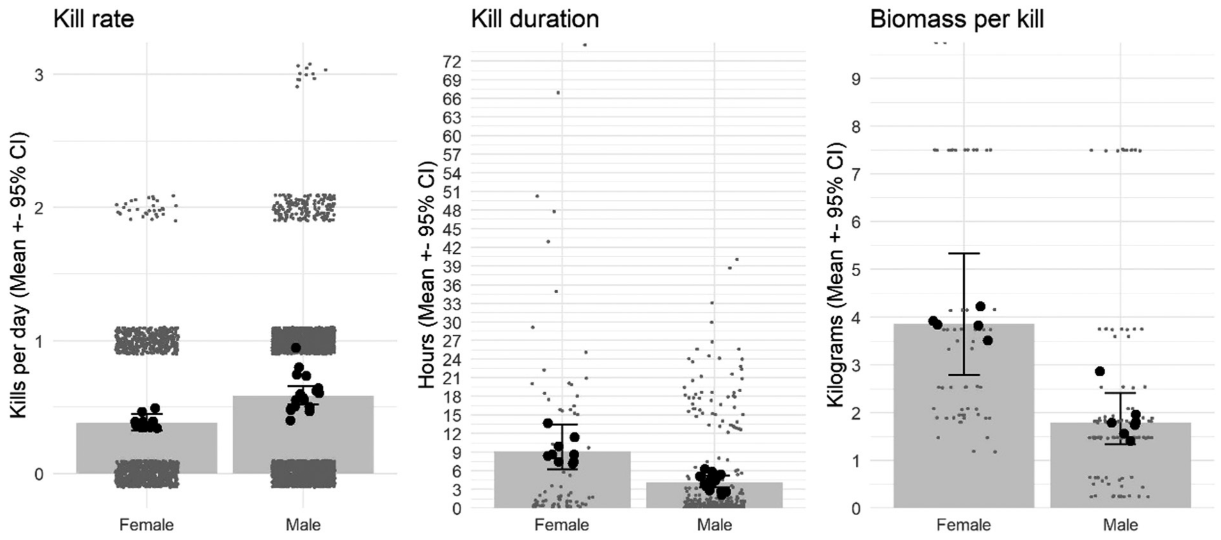

Figure 3. Sex differences in mean (grey bar) martial eagle kill rates (kills per day), kill durations (h), and biomass recycling per kill (kg). Non-overlapping 95% confidence intervals (black error bars) indicate significant differences between the sexes. Grey points are observations (data used to fit the model), and black dots are fitted individual means (i.e. random intercepts).

favored medium-sized ungulates, with a single male killing every ~ 9.1 days and consuming an average of 4.3 kg day^{-1} (Farhadinia et al. 2018). In South Africa, cheetah generally preferred medium-sized ungulates; a coalition of three male cheetah killed on average once every 3.5 days and each consumed 1.4 kg day^{-1} (Mills et al. 2004). The outlier in the reported leopard and cheetah kill rates is from Serengeti National Park, Tanzania where a female cheetah with two dependent cubs had a daily Thomson gazelle kill rate of close to one, and the adult female was estimated to consume 4 kg prey day^{-1} (Schaller 1968). Collectively, these findings indicate that an individual martial eagle recycles less biomass from ecosystems than leopard or cheetah. However, considering that adult female martial eagles are on average six times lighter than adult female leopard and cheetah (Caro 2013, Hunter et al. 2013), on a per kg basis, martial eagles almost certainly recycle more prey biomass than individual leopard and cheetah from African savanna ecosystems.

A per unit area calculation of prey biomass recycling (e.g. kg recycled per km^2) is ideally required for each species to best compare the ecosystem impact of leopard, cheetah, and martial eagles. To calculate these statistics, accurate population densities of all three species would need to be available from a single area. Unfortunately, to the best of our knowledge these data do not exist. Within the Mara, only cheetah population densities have been estimated accurately at approximately 1.31 individuals 100 km^{-2} (Femke Broekhuis and Gopalaswamy 2016). A study from neighboring Serengeti National Park estimated leopard population densities at 5.57 individuals 100 km^{-2} (Allen et al. 2020). Unfortunately, martial eagle population densities from the Mara remain unknown, but we expect them to be between those provided for leopard in Serengeti National Park and cheetah in the Mara (2–4 individuals 100 km^{-2}) as martial eagle annual home ranges within the Mara are approximately 175 km^2 (Hatfield 2018). These home ranges support two adult eagles, overlap to some degree with neighboring home ranges, and importantly also support an unknown number of dispersing juveniles, subadults and floaters.

Many studies that estimate kill rates for top mammalian predators provide an estimate of the number of ungulates removed per week by an individual predator. The puma *Puma concolor* is perhaps the best studied of these predators and a recent review of ungulate kill rates for pumas estimated that on average across all studies adult males kill approximately 0.84 ungulates per week and solitary adult females kill approximately 0.99 ungulates per week (Cristescu et al. 2022). Our dietary dataset showed that the most frequent prey item recorded for adult female martial eagles was young ungulates (Fig. 4). Solitary cheetah and leopard are also well known to disproportionately prey on ungulates; the primary difference with adult female martial eagles being the size of the ungulate (juvenile versus subadult/adult) (Hayward et al. 2006, Broekhuis et al. 2018). In this study, we estimated that 37% of the ground-truthed prey species killed by adult female martial eagles were juvenile ungulates. If we account for our kill rate of 0.38 kills per day and assume that this kill rate is maintained throughout the year, then female martial eagles make ~ 139 kills a year. If 37% of these kills are juvenile ungulates (~ 51 kills), then martial eagles are removing similar numbers of ungulates from the Mara as pumas in North America. If we assume that pumas are killing ungulates at similar rates to leopard and cheetah in African savanna ecosystems, then it is possible that an individual adult female martial eagle removes just as many ungulates annually as individual leopard and cheetah from African savanna ecosystems.

These comparisons with leopard and cheetah place martial eagles amongst the top predator guild of African savanna ecosystems, but do our results make physiological sense? Our work estimates that adult male martial eagles kill ~ 1 kg of

Table 2. Ground-truthed kill species and their estimated live body masses categorized by martial eagle sex and then sorted by frequency.

Prey species		Classification	Prey age	Estimated body mass	Number of male kills
Helmeted guineafowl	*Numida meleagris*	gamebird	Adult	1480 g (Martínez and Kirwan 2020)	15
Black-bellied bustard	*Lissotis melanogaster*	Gamebird	Adult	1970 g (Collar et al. 2021)	6
Impala	*Aepyceros melampus*	small ungulate	Juvenile	7500 g (Fairall 1969, Jarman and Jarman 1973)	5
Coqui francolin	*Campocolinus coqui*	gamebird	Adult	250 g (McGowan et al. 2021)	5
Thomson's gazelle	*Eudorcas thomsonii*	small ungulate	Juvenile	3750 g (Robinette and Archer 1971)	4
Red-necked spurfowl	*Pternistis afer*	gamebird	Adult	640 g (McGowan and Kirwan 2020a)	3
Banded mongoose	*Mungos mungo*	small carnivore	Adult	1880 g (Kingdon 2015a)	2
Common warthog	*Phacochoerus africanus*	piglet	Juvenile	1800 g (Child et al. 1965, Roth 1965)	2
Cape/scrub hare	*Lepus capensis/victoriae*	hyrax and hare	Adult	2540 g (Kingdon 2015d, e)	2
Red-winged francolin	*Scleroptila levaillantii*	gamebird	Adult	450 g (McGowan and Kirwan 2020b)	1
Domestic chicken	*Gallus gallus*	gamebird	Adult	1800 g (Magothe et al. 2012)	1
Bush hyrax	*Heterohyrax brucei*	hyrax and hare	Adult	2750 g (Kingdon 2015c)	1
Egyptian goose	*Alopochen aegyptiaca*	large bird	Adult	1920 g (Callaghan et al. 2020)	1
Hamerkop	*Scopus umbretta*	large bird	Adult	500 g (Elliott et al. 2020a)	1
Slender mongoose	*Herpestes sanguineus*	small carnivore	Adult	580 g (Kingdon 2015g)	1
White-tailed mongoose	*Ichneumia albicauda*	small carnivore	Adult	3600 g (Kingdon 2015h)	1
Unknown		NA	NA	NA	2

Prey species		Classification	Prey age	Estimated body mass	Number of female kills
Impala	*Aepyceros melampus*	small ungulate	Juvenile	7500 g (Fairall 1969, Jarman amd Jarman 1973)	6
Thomson's gazelle	*Eudorcas thomsonii*	small ungulate	Juvenile	3750 g (Robinette and Archer 1971)	5
Cape/scrub hare	*Lepus capensis/saxatilis*	hyrax and hare	Adult	2540 g (Kingdon 2015d, e)	4
Banded mongoose	*Mungos mungo*	small carnivore	Adult	1880 g (Kingdon 2015a)	3
Nile monitor	*Varanus niloticus*	monitor	Adult	1950 g (Ciliberti et al. 2011)	2
Bat-eared fox	*Otocyon megalotis*	small carnivore	Adult	4150 g (Kingdon 2015b)	2
Bush hyrax	*Heterohyrax brucei*	hyrax and hare	Adult	2750 g (Kingdon 2015c)	2
Black-headed heron	*Ardea melanocephala*	large bird	Adult	1180 g (Martínez-Vilalta et al. 2020)	1
Grey-crowned crane	*Balearica regulorum*	large bird	Adult	3500 g (Archibald et al. 2020)	1
White stork	*Ciconia ciconia*	large bird	Adult	3340 g (Elliott et al. 2020b)	1
Common warthog	*Phacochoerus africanus*	piglet	Juvenile	1800 g (Child et al. 1965, Roth 1965)	1
Serval	*Leptailurus serval*	small carnivore	Adult	9750 g (Kingdon 2015f)	1
Helmeted guineafowl	*Numida meleagris*	gamebird	Adult	1480 g (Martínez and Kirwan 2020)	1
Unknown		NA	NA	NA	6

prey per day and adult females ~ 1.5 kg per day. These values are higher than we expected as wild adult non-breeding golden eagles, a species whose physiology and energetics are roughly comparable to that of martial eagles, have been estimated to require 230 g of food a day to maintain body condition (Brown and Watson 1964a). The difference between our estimates for daily prey biomass killed and the physiological needs of an individual martial eagle can be explained due to wastage and kleptoparasitism. Wastage is the proportion of a carcass that is not eaten by a predator for various reasons. Brown and Watson (1964a, b) estimated that for small kills (such as gamebirds) wastage from golden eagles was < 20%, but that for larger kills (such as young ungulates), wastage could increase to > 50%. We can therefore assume that between 20–50% of all prey biomass captured by martial eagles would be wasted and left uneaten regardless of risk from kleptoparasites.

Although Brown and Watson (1964) observed that golden eagles in the wolf, brown bear *Ursus arctos* and Eurasian lynx *Lynx lynx* depleted Scottish Highlands were an uncontested top predator, most raptors coexist with a suite of avian and terrestrial competitors. In the Mara, martial eagles hunt in a predator rich environment with at least five species of aggressive kleptoparasites (lion, leopard, spotted hyena, black-backed jackal *Lupulella mesomelas*, and tawny eagle). We do not know how frequently martial eagle kills are lost to these species in the Mara, but given the open landscape and high kleptoparasite density (~ 100 kleptoparasites per 100 km^2

Table 3. Reported kill species sorted by martial eagle sex and frequency. The last column denotes whether our method detected the reported kill.

Prey species		Classification	Prey age	No. of male kills	No. of female kills	Kill/s detected?
Helmeted guineafowl	*Numida meleagris*	gamebird	Adult	5	1	Yes
Banded mongoose	*Mungos mungo*	small carnivore	Adult	2	2	Yes
Black-headed heron	*Ardea melanocephala*	large bird	Adult	2	0	Yes
Coqui francolin	Campocolinus coqui	gamebird	Adult	2	0	Yes
Common warthog	*Phacochoerus africanus*	piglet	Juvenile	1	1	Yes
Thomson's gazelle	*Eudorcas thomsonii*	small ungulate	Juvenile	1	1	Yes
Corn crake	*Crex crex*	small bird	Adult	1	0	No
Red-necked spurfowl	*Pternistis afer*	gamebird	Juvenile	1	0	No
Bush hyrax	*Heterohyrax brucei*	hyrax and hare	Adult	1	0	Yes
Scrub hare	*Lepus saxatilis*	hyrax and hare	Adult	0	1	Yes
Hadeda ibis	*Bostrychia hagedash*	large bird	Adult	1	0	Yes
White stork	*Ciconia ciconia*	large bird	Adult	0	1	Yes
Nile monitor	*Varanus niloticus*	monitor	Adult	0	1	Yes
Slender mongoose	*Herpestes sanguineus*	small carnivore	Adult	0	1	Yes
Bat-eared fox	*Otocyon megalotis*	small carnivore	Adult	1	0	Yes
White-tailed mongoose	*Ichneumia albicauda*	small carnivore	Adult	0	1	Yes
Impala	*Aepyceros melampus*	small ungulate	Juvenile	0	1	Yes
Kirk's dikdik	*Gallus gallus*	small ungulate	Adult	1	0	Yes
Bohor reedbuck	*Redunca redunca*	small ungulate	Juvenile	0	1	Yes

(Elliot and Gopalaswamy 2017, Mwampeta et al. 2021) we can expect this to occur frequently, especially for kills > 1 kg that cannot easily be flown into a tree or cover (Arnold 1954). Our own field observations support these conclusions, as one of the authors has witnessed a martial eagle abandoning a large kill to kleptoparasites.

It should be noted that our estimates of martial eagle kill rates and amount of prey biomass recycled are minimum values because our method only detected kills where sustained feeding occurred (feeding bouts > three bursts). Martial eagles rarely kill and feed on prey less than a few 100 g (Naude et al. 2019), yet we successfully detected two reported 250 g coqui francolin *Peliperdix coqui* kills (McGowan et al. 2021), therefore suggesting that our method's kill detection sensitivity may have only excluded unusually small prey items or kills that were disturbed or kleptoparasited before sustained feeding could occur.

Future work on martial eagle foraging behaviour should include relating kill rates to predator densities, prey densities and predation rates which would inform whether martial eagles play a role in regulating prey populations in African savanna ecosystems. This work should also incorporate martial eagle breeding data to fully understand the predatory impact of martial eagle family units on ecosystems. During breeding, female martial eagles are the primary incubator and chick caregiver, while males are the provisioner and for a period are responsible for feeding themselves, their mate, and their chick (Steyn 1973). We would hypothesize that male kill rates would rise dramatically during breeding to at least twice their non-breeding rates, while females we expect to decline as they are largely tied to the nest and only kill when they are food-stressed or when the nestling is capable of thermoregulating and self-defense.

Figure 4. An adult female martial eagle in the Maasai Mara, Kenya with a recently killed Thomson's gazelle juvenile.

Concluding remarks

High resolution accelerometer informed GPS satellite telemetry locations of martial eagles in the Mara Region allowed us to predictively model kill sites and rapidly deploy field crews to these areas, thereby greatly improving our understanding of feeding ecology of this endangered raptor. Our method of estimating kill rates and prey biomass recycling of individual martial eagles is a novel application of machine learning and behavioural classification and opens the door to others testing similar methods on other raptor species and comparing these raptors to sympatric carnivores. Estimates of kill rates and prey biomass recycling strongly suggest that martial eagles are top predators in African savanna ecosystems that deserve recognition in trophic pyramids alongside large terrestrial carnivores such as leopard and cheetah. Failure to account for martial eagles and other sympatric avian predators within African savanna ecosystems may bias our understanding of predation and ecosystem functioning. Moreover, this work has conservation consequences as the martial eagle is overall a poorly studied endangered species that is declining rapidly through large portions of its range (Amar et al. 2016, Birdlife International 2018). It is our hope that this work elevates the status of martial eagles as consequential predators in the eyes of ecologists, conservationists, and the public and provides momentum for conservation programmes and further studies on this species and its predatory behaviour.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v15dv423j (Hatfield et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Allen, M. L., Wang, S., Olson, L. O., Li, Q. and Krofel, M. 2020. Counting cats for conservation: seasonal estimates of leopard density and drivers of distribution in the Serengeti. – Biodivers. Conserv. 29: 3591–3608.

Amar, A., Cloete, D. and Whittington, M. 2016. Using independent nest survey data to validate changes in reporting rates of Martial Eagles between the Southern African Bird Atlas Project 1 and 2. – Ostrich 87: 1–5.

Archibald, G. W., Meine, C. D. and Garcia, E. 2020. Gray crowned-crane (*Balearica regulorum*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.grccra1.01.

Arnold, L. W. 1954. The Golden Eagle and its economic status, vol. 27. – US Fish and Willdife Service, Circular No. 27.

Bartzke, G. S., Ogutu, J. O., Mukhopadhyay, S., Mtui, D., Dublin, H. T. and Piepho, H. P. 2018. Rainfall trends and variation in the Maasai Mara ecosystem and their implications for animal population and biodiversity dynamics. – PLoS One 13: e0202814.

Bassi, E., Trotti, P., Brambilla, M., Diana, F., Sartirana, F., Galli, L. and Pedrotti, L. 2017. Parental investment in two large raptors breeding in a high prey density area. – J. Ornithol. 158: 549–559.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Berger, D. D. and Mueller, H. C. 1959. The Bal-Chatri: a trap for the birds of prey. – Bird Banding 30: 18–26.

Birdlife International 2018. Species factsheet: *Polemaetus bellicosus*. – https://datazone.birdlife.org/species/factsheet/martial-eagle-polemaetus-bellicosus.

Boshoff, A. F., Palmer, N. G. and Avery, G. 1990. Regional variation in the diet of martial eagles in the Cape Province, South Africa. – S. Afr. J. Wildl. Res. 20: 57–68.

Broekhuis, F. and Gopalaswamy, A. M. 2016. Counting cats: spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. – PLoS One 11: e0153875.

Broekhuis, F., Thuo, D. and Hayward, M. W. 2018. Feeding ecology of cheetahs in the Maasai Mara, Kenya and the potential for intra- and interspecific competition. – J. Zool. 304: 65–72.

Brown, L. H. and Watson, A. 1964a. The golden eagle in relation to its food supply. – Ibis 106: 78–100.

Brown, L. H. and Watson, A. 1964b. The golden eagle in relation to its food supply. – Ibis 106: 78–100.

Buechley, E. R., Santangeli, A., Girardello, M., Neate-Clegg, M. H. C., Oleyar, D., McClure, C. J. W. and Şekercioğlu, Ç. H. 2019. Global raptor research and conservation priorities: tropical raptors fall prey to knowledge gaps. – Divers. Distrib. 25: 856–869.

Callaghan, C. T., Brooks, D. M. and Pyle, P. 2020. Egyptian goose (*Alopochen aegyptiaca*). – In: Billerman, S. M. (ed.), Birds of the world. Cornell Laboratory of Ornithology.

Carbone, C., Frame, L., Frame, G., Malcolm, J., Fanshawe, J., FitzGibbon, C., Schaller, G., Gordon, I. J., Rowcliffe, J. M. and Du Toit, J. T. 2005. Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. – J. Zool. 266: 153–161.

Caro, T. 2013. *Acinonyx jubatus* Cheetah. – In: Kingdon, J. and Hoffman, M. (eds), Mammals of Africa volume V. Bloomsbury Publishing, pp. 187–196

Child, G., Sowls, L. and Mitchell, B. L. 1965. Variations in the dentition, ageing criteria, and growth patterns in warthog. – Arnoldia 1: 1–23.

Ciliberti, A., Berny, P., Delignette-Muller, M. L. and de Buffrénil, V. 2011. The Nile monitor (*Varanus niloticus;* Squamata: Varanidae) as a sentinel species for lead and cadmium contamination in sub-Saharan wetlands. – Sci. Total Environ. 409: 4735–4745.

Clark, W. S. and Davies, R. 2018. The martial eagle. – In: African raptors. Bloomsbury Publishing Plc, pp. 279–280.

Collar, N., Garcia, E. and Boesman, P. F. D. 2021. Black-bellied bustard (*Lissotis melanogaster*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology.

Collopy, M. W. 1984. Parental care and feeding ecology of golden eagle nestlings. – Auk 101: 753–760.

Cristescu, B., Elbroch, L. M., Dellinger, J. A., Binder, W., Wilmers, C. C. and Wittmer, H. U. 2022. Kill rates and associated ecological factors for an apex predator. – Mamm. Biol. 102: 291–305.

Debus, S. J. S. 2011. Parental time-budgets and breeding behaviour of the little eagle *Hieraaetus morphnoides* in northern New South Wales. – Corella 35: 65–72.

Dekker, D., Out, M., Tabak, M. and Ydenberg, R. 2012. The effect of kleptoparasitic bald eagles and gyrfalcons on the kill rate of peregrine falcons hunting dunlins wintering in British Columbia. – Condor 114: 290–294.

Elbroch, L. M., Lowrey, B. and Wittmer, H. U. 2018. The importance of fieldwork over predictive modeling in quantifying predation events of carnivores marked with GPS technology. – J. Mammal. 99: 223–232.

Elliot, N. B. and Gopalaswamy, A. M. 2017. Toward accurate and precise estimates of lion density. – Conserv. Biol. 31: 934–943.

Elliott, A., Garcia, E. and Boesman, P. F. D. 2020a. Hamerkop (*Scopus umbretta*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.hamerk1.01.

Elliott, A., Garcia, E. and Boesman, P. F. D. 2020b. White stork (*Ciconia ciconia*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.whisto1.01.

Fairall, N. 1969. Prenatal development of the Impala. – Koedoe 12: 97–103.

Farhadinia, M. S., Johnson, P. J., Hunter, L. T. B. and Macdonald, D. W. 2018. Persian leopard predation patterns and kill rates in the Iran-Turkmenistan borderland. – J. Mammal. 99: 713–723.

Hatfield, R. S. 2018. Diet and space use of the martial eagle (*Polemaetus bellicosus*) in the Maasai mara region of Kenya. – MSc thesis, Univ. of Kentucky, USA.

Hatfield, R. S., Davis, A. G., Buij, R., Cox, J. J., Kapila, S., Parmuntoro, L., Thomsett, S., Virani, M. Z., Njoroge, P. and van Langevelde, F. 2024. Data from: Africa's overlooked top predator: towards a better understanding of martial eagle feeding ecology in the Maasai Mara, Kenya. – Dryad Digital Repository, https://doi.org/10.5061/dryad.v15dv423j.

Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. and Kerley, G. I. H. 2006. Prey preferences of the leopard (*Panthera pardus*). – J. Zool. 270: 298–313.

Hunter, L., Henschel, P. and Ray, J. C. 2013. *Panthera pardus* Leopard. – In: Kingdon, J. and Hoffman, M. (eds), Mammals of Africa volume V. Bloomsbury Publishing, pp. 159–168.

Jarman, P. J. and Jarman, M. V. 1973. Social behavious, population structure and reproductive potential in Impala. – East Afr. Wildl. J. 11: 329–338.

Kenward, R. E. 1982. Goshawk hunting behaviour, and range size as a function of food and habitat. – J. Anim. Ecol. 51: 69–80.

Kingdon, J. 2015a. Banded mongoose *Mungos mungo*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, pp. 446–447.

Kingdon, J. 2015b. Bat-eared fox *Otocyon megalotis*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, p. 372.

Kingdon, J. 2015c. Bush hyrax *Hetrohyrax brucei*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, pp. 52–53.

Kingdon, J. 2015d. Cape hare *Lepus capensis*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, p. 309.

Kingdon, J. 2015e. Scrub hare *Lepus saxatilis*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, pp. 309–310.

Kingdon, J. 2015f. Serval *Leptailurus serval*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, pp. 398–400.

Kingdon, J. 2015g. Slender mongoose *Herpestes sanguineus*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, pp. 435–436.

Kingdon, J. 2015h. White-tailed mongoose *Ichneumia albicauda*. – In: Redman, N. (ed.), The Kingdon field guide to African mammals, 2nd edn. Bloomsbury Publishing Plc, pp. 439–440.

Knopff, K. H., Knopff, A. A., Kortello, A. and Boyce, M. S. 2010. Cougar kill rate and prey composition in a multiprey system. – J. Wildl. Manage. 74: 1435–1447.

Korpimäki, E. and Krebs, C. J. 1996. Predation and population cycles of small mammals: a reassessment of the predation hypothesis. – BioScience 46: 754–764.

Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. – Ecology 79: 2448.

Lenth, R. V. 2022. emmeans: estimated marginal means, aka least-squares means. – R package ver. 1.7.2, https://cran.r-project.org/package=emmeans.

Liaw, A. and Wiener, M. 2002. Classification and regression by randomForest. – R News 2: 18–22.

López-López, P. and Urios, V. 2010. Use of digital trail cameras to study Bonelli's eagle diet during the nestling period. – Ital. J. Zool. 77: 289–295.

MacNulty, D. R., Smith, D. W., Vucetich, J. A., Mech, L. D., Stahler, D. R. and Packer, C. 2009. Predatory senescence in ageing wolves. – Ecol. Lett. 12: 1347–1356.

Magothe, T. M., Okeno, T. O., Muhuyi, W. B. and Kahi, A. K. 2012. Indigenous chicken production in Kenya: I. Current status. – Worlds Poult. Sci. J. 68: 119–132.

Martínez, I. and Kirwan, G. M. 2020. Helmeted guineafowl (*Numida meleagris*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.helgui.01.

Martínez-Vilalta, A., Motis, A. and Kirwan, G. M. 2020. Black-headed heron (*Ardea melanocephala*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.blhher1.01.

Mattisson, J., Odden, J., Nilsen, E. B., Linnell, J. D. C., Persson, J. and Andrén, H. 2011. Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: can ecological research contribute to the development of a fair compensation system? – Biol. Conserv. 144: 3009–3017.

McClure, C. J. W., Westrip, J. R. S., Johnson, J. A., Schulwitz, S. E., Virani, M. Z., Davies, R., Symes, A., Wheatley, H., Thorstrom, R., Amar, A., Buij, R., Jones, V. R., Williams, N. P., Buechley, E. R. and Butchart, S. H. M. 2018. State of the world's raptors: distributions, threats, and conservation recommendations. – Biol. Conserv. 227: 390–402.

McGowan, P. J. K. and Kirwan, G. M. 2020a. Red-necked spurfowl (*Pternistis afer*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.renfra1.01.

McGowan, P. J. K. and Kirwan, G. M. 2020b. Red-winged francolin (*Scleroptila levaillantii*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.rewfra2.01.

McGowan, P. J. K., Kirwan, G. M. and Boesman, P. F. D. 2021. Coqui francolin (*Campocolinus coqui*). – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. and de Juana, E. (eds), Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA, https://doi.org/10.2173/bow.coqfra2.01.1.

Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P. and Frair, J. L. 2010. Building a mechanistic understanding of predation with GPS-based movement data. – Phil. Trans. R. Soc. B 365: 2279–2288.

Mills, M. G. L., Broomhall, L. S. and du Toit, J. T. 2004. Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? – Wildl. Biol. 10: 177–186.

Moleón, M., Sánchez-Zapata, J. A., Gil-Sánchez, J. M., Barea-Azcón, J. M., Ballesteros-Duperón, E. and Virgós, E. 2011. Laying the foundations for a Human-Predator conflict solution: assessing the impact of Bonelli's eagle on rabbits and partridges. – PLoS One 6: e22851.

Mwampeta, S. B., Wilton, C. M., Mkasanga, I. J., Masinde, L. M., Ranke, P. S., Røskaft, E., Fyumagwa, R. and Belant, J. L. 2021. Lion and spotted hyena distributions within a buffer area of the Serengeti-Mara ecosystem. – Sci. Rep. 11: 22289.

Nadjafzadeh, M., Hofer, H. and Krone, O. 2016. Sit-and-wait for large prey: foraging strategy and prey choice of White-tailed Eagles. – J. Ornithol. 157: 165–178.

NASA JPL 2013. NASA shuttle radar topography mission global 1 arc second [Data set]. – NASA EOSDIS Land Processes Distributed Active Archive Center, https://doi.org/10.5067/MEaSUREs/SRTM/SRTMGL1.003.

Naude, V. N., Smyth, L. K., Weideman, E. A., Krochuk, B. A. and Amar, A. 2019. Using web-sourced photography to explore the diet of a declining African raptor, the martial eagle (*Polemaetus bellicosus*). – Condor 121: 1–9.

Nelson, M. P., Vucetich, J. A., Peterson, R. O. and Vucetich, L. M. 2011. The Isle Royale Wolf–Moose Project (1958-present) and the wonder of long-term ecological research. – Endeavour 35: 31–39.

Norrdahl, K. and Korpimäki, E. 1995. Effects of predator removal on vertebrate prey populations: birds of prey and small mammals. – Oecologia 103: 241–248.

Norrdahl, K. and Korpimäki, E. 2000. Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predators. – Oikos 91: 528–540.

Odden, M. and Wegge, P. 2009. Kill rates and food consumption of leopards in Bardia National Park, Nepal. – Acta Theriol. 54: 23–30.

Oindo, B. O., Skidmore, A. K. and de Salvo, P. 2003. Mapping habitat and biological diversity in the Maasai Mara ecosystem. – Int. J. Remote Sens. 24: 1053–1069.

Owen-Smith, N. and Mills, M. G. L. 2008. Predator–prey size relationships in an African large-mammal food web. – J. Anim. Ecol. 77: 173–183.

Redpath, S. M., Clarke, R., Madders, M. and Thirgood, S. J. 2001. Assessing raptor diet: comparing pellets, prey remains, and observational data at hen harrier nests. – Condor 103: 184–188.

Reid, R. S. 2012. Savannas of our birth. – Univ. of California Press.

Robinette, W. L. and Archer, A. L. 1971. Notes on ageing criteria and reproduction of Thomson's Gazelle. – East Afr. Wildl. J. 9: 83–98.

Roth, H. H. 1965. Observations on growth and ageing of warthog, *Phacochoerus aethiopicus* (Pallas, 1766). – Mamm. Biol. 30: 367–380.

Rutz, C. 2003. Assessing the breeding season diet of goshawks *Accipiter gentilis*: biases of plucking analysis quantified by means of continuous radio-monitoring. – J. Zool. 259: 209–217.

Sand, H., Wabakken, P., Zimmermann, B., Johansson, O., Pedersen, H. C. and Liberg, O. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? – Oecologia 156: 53–64.

Schaller, G. B. 1968. Hunting behaviour of the cheetah in the Serengeti national park, Tanzania. – Afr. J. Ecol. 6: 95–100.

Sinclair, A. R. E., Mduma, S. and Brashares, J. S. 2003. Patterns of predation in a diverse predator–prey system. – Nature 425: 288–290.

Sonerud, G. A. 1992. Functional responses of birds of prey : biases due to the load-size effect in central place foragers. – Oikos 63: 223–232.

Stander, P. E., Haden, P. J., Kaqece, I. and Ghau, I. 1997. The ecology of asociality in Namibian leopards. – J. Zool. 242: 343–364.

Steyn, P. 1973. Magnificent martial. – In: Eagle days. Sable Press Ltd, pp. 75–86.

Vucetich, J. A., Hebblewhite, M., Smith, D. W. and Peterson, R. O. 2011. Predicting prey population dynamics from kill rate, predation rate and predator–prey ratios in three wolf-ungulate systems. – J. Anim. Ecol. 80: 1236–1245.

Vucetich, J. A., Huntzinger, B. A., Peterson, R. O., Vucetich, L. M., Hammill, J. H. and Beyer, D. E. 2012. Intra-seasonal variation in wolf *Canis lupus* kill rates. – Wildl. Biol. 18: 235–245.