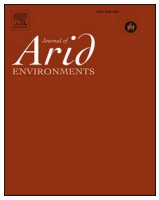
Journal of Arid Environments 227 (2025) 105331

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv



Feeding through the ages: Revisiting the diet of meerkats

Walter R. Jubber [a,c,*], Marta B. Manser [b,c,d], Andrea Fuller [a]

[a] Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Parktown, 2193, South Africa
[b] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[c] Kalahari Research Trust, Kuruman River Reserve, Van Zylsrus, 8467, Northern Cape, South Africa
[d] Mammal Research Institute, University of Pretoria, Hatfield, South Africa

ARTICLE INFO

Keywords:
Insectivore
Foraging
Kalahari
Dietary specialisation

ABSTRACT

We investigated the diet and foraging behaviour of a social carnivore, the meerkat (*Suricata suricatta*), living in stochastic dryland, and examined seasonal, as well as age-related variation in diet. Insecta constituted the highest percentage of prey eaten (88.4%), followed by Arachnida (5.7%), Diplopoda (4.3%), and Reptilia (1.1%). Within Insecta, Coleoptera (70.4%) was the most dominant prey order in the diet, followed by Lepidoptera and Hymenoptera. There was seasonal variation in the diet of meerkats, with the three main Coleoptera families eaten year-round, but higher consumption of Coleoptera adults in the wet season than in the dry season. We found that old adult meerkats (>24 months) consumed the most large-sized prey, while sub-adults (6–10 months) had the highest prey count of small adult Carabidae beetles. Yearlings (15–24 months) ate the highest percentage of Hepialidae caterpillars. Whether the high representation of Coleoptera in the meerkat diet reflects dietary opportunism associated with the relatively high abundance of Coleoptera, or specialisation in the diet regardless of abundance, remains to be determined.

1. Introduction

In drylands, where resources are often scarce and unpredictable, mammalian species have evolved remarkable physiological and feeding adaptations to survive and reproduce in these challenging environments (Rymer et al., 2016). An insectivorous diet is common in mammalian carnivores in drylands, with them having specialised foraging behaviours and adaptations to find, capture, and digest insect prey efficiently (Fox, 2011; Tarvin et al., 2023). One such carnivore occurring in the semi-and-arid landscapes of southern Africa is the meerkat (*Suricata suricatta*). Meerkats are diurnal foragers that mainly dig up subterranean prey items (Doolan and Macdonald, 1996; Turbé, 2006), which are located using a combination of olfactory and tactile sensory mechanisms (Glaser, 2006; Leclaire, 2017; Sörensen et al., 2019). In addition, they obtain a small percentage of their prey from the surface (Doolan and Macdonald, 1996). Two studies that analysed the stomach contents of meerkats in Botswana (Smithers, 1983) and the Free State, South Africa (Lynch, 1980), revealed that meerkats predominantly ate Coleoptera (larvae and adults, occurring in 58% of stomachs), followed by Lepidoptera (43%), Arachnida (21%), and Reptilia (5%) (Lynch, 1980; Smithers, 1983). In a study in the Kalahari in which meerkats were observed while foraging, Coleoptera (28%) and Hymenoptera (13%) were the prey items most frequently consumed by meerkats (Doolan and Macdonald, 1996).

Although studies of the meerkat diet have not extended over a full year, there appears to be seasonal variation in the diet. Examination of meerkat stomach contents sampled during winter in the open grasslands and bushveld of the Free State revealed that Coleoptera and Lepidoptera were favoured, followed by Isoptera (found in 27% of stomachs), Orthoptera (19%), and Diptera (15%). In summer, Coleoptera was eaten the most, followed by Isoptera (61%), Lepidoptera (53%), Orthoptera (47%) and Diptera (25%) (Lynch, 1980). Insect larvae (particularly Coleoptera) were the primary prey observed to be eaten by meerkats, but there was higher predation on pupae in April (autumn) and adult Coleoptera in the summer months of January and February, in comparison to other months of the year (Doolan and Macdonald, 1996). Hymenoptera were eaten in January and winter, while reptiles were preyed upon frequently from February to March and in July. In studies conducted as part of the long-term Kalahari Meerkat project (Clutton-Brock and Manser, 2016), which has been investigating cooperative behaviour in meerkats for over 30 years, changes were observed in the meerkat diet between the dry and wet seasons. There were more

* Corresponding author. Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Parktown, 2193, South Africa.
E-mail addresses: wrjubber@gmail.com (W.R. Jubber), marta.manser@ieu.uzh.ch (M.B. Manser), andrea.fuller@wits.ac.za (A. Fuller).

https://doi.org/10.1016/j.jaridenv.2025.105331
Received 22 March 2024; Received in revised form 20 January 2025; Accepted 20 January 2025
Available online 2 February 2025

larger-sized (reptiles, scorpions, and millipedes) and medium-sized (scorpions and solifuges) prey items consumed in the dry season, and a shift to mainly smaller-sized prey items (larvae and beetles) during the wet season (Barnard, 2000; Brotherton et al., 2001; Turbé, 2006).

Other factors that may influence the diet of individual meerkats are age and social status. Dominant and older individuals position themselves at the front of the group during foraging expeditions, which affords priority access to prey items (Barnard, 2000; Gall and Manser, 2018; Turbé, 2006). Older individuals follow predictable routes to optimise food patches, a behaviour attributed to the foraging experience, learned knowledge, and the ability to recognise environmental cues (Turbé, 2006). These behaviours collectively enhance older individuals' ability to maximise food intake while minimising foraging effort (Turbé, 2006). Younger and less experienced individuals, not leading the group, may benefit from increased forage time. As studies have shown that sub-adult meerkats, aged between 6 and 12 months old, have a lower foraging success than older adults, over 12 months old, possibly due to the lack of skill refinement needed to locate and capture prey (Barnard, 2000; Gall and Manser, 2018; Turbé, 2006).

Environmental factors also influence the foraging behaviour of meerkats (Brotherton et al., 2001; Clutton-Brock et al., 2001). High heat loads reduce foraging activity in meerkats, while low rainfall reduces food intake (Clutton-Brock et al., 1999; Doolan and Macdonald, 1996; Russell et al., 2002). These environmental factors impose direct physiological stress and reduce access to prey, impacting individual development and population dynamics. Increased air temperatures over the past few decades in the Kalahari have been associated with reduced individual growth rates and survival, which negatively impact the population stability (Paniw et al., 2019; Paniw et al., 2022, Van de Ven et al., 2019). Whether the diet of meerkats has changed in parallel with the increasing temperatures, either because of changing food availability or changes in foraging behaviour, is unknown.

The last study to focus on the diet of meerkats in the Kalahari was done more than 35 years ago, in 1987 (Doolan and Macdonald, 1996). While earlier studies describe some differences in the diet of meerkats at different times of the year, they have not shown how diet changes continuously across the year and whether it differs for meerkats in different age categories. Here we describe the diet and feeding behaviour of meerkats, in three different age categories, over 1 year at a ranch land site in the southern Kalahari where at any time 6–12 groups of habituated meerkats have been monitored for the last 30 years (Clutton-Brock and Manser, 2016).

The study focused on the diet and foraging behaviours of meerkats across seasonal variations in their dietary patterns, as well as diet differences in three distinct age categories. We recorded the meerkat diet over a year in the Kalahari, identifying the prey that individual meerkats caught and consumed. Our objectives included: (1) identifying prey items to the lowest taxonomic level possible, (2) seasonal change in meerkat diet, and (3) exploring how dietary preferences and foraging strategies varied among different age classes of meerkats. The research builds upon historical studies of meerkat diets by providing a comprehensive year-long perspective, revealing age-specific foraging strategies in the context of environmental variability.

2. Method

2.1. Study area

The study area was located at the Kalahari Research Centre (−26.978615°, 21.832148°), on the Kuruman River Reserve and adjacent lands. The study area is approximately 30 km west of Van Zylsrus in the Northern Cape of South Africa, within the centre of the meerkat's distribution range (Russell et al., 2002). The region experiences hot summers with rainfall typically from October to April and cold, dry winters. Over the past 12 years, mean annual rainfall was 266 mm, average summer daily air temperatures were 30.3 °C (maximum 44.2 °C), while winter air temperatures averaged 10.1 °C (minimum −11.9 °C; weather station data at the KRC). The study terrain comprised distinct macro-habitats as categorised by van Rooyen and van Rooyen (1998), including red dune sand shrub grassland - Duneveld typified by open savanna; Red Sand Woodland or Tree Savanna; White Calcareous Pan Flats characterised by limited grass cover within short shrubbery; Diatomous Fossil Riverbed dominated mainly by camelthorn trees (*Vachellia erioloba*); and undulating red sand grassland interspersed with grey camelthorn (*V. haematoxylon*), with raisin bush shrubs (*Grewia flava*).

2.2. Study animals

Our study was conducted over a year-long period, from June 2022 to May 2023, and we had access to habituated meerkat groups. Each meerkat group was located by a tracking VHF collar placed on one of the dominant meerkats, and each meerkat individual was identified by a unique hair dye spot (Jordan et al., 2007). Over 95% of all meerkat individuals are known from birth and monitored as soon as they emerge from the burrow while remaining individually identifiable, which allowed us to separate them into the relevant age categories, pups (up to 3 months), juveniles (3–6 months), sub-adults (6–12 months), and adults (≥12 months), with the adult category further divided into yearlings (12–24 months) and old adults (>24 months) (Brotherton et al., 2001; Clutton-Brock et al., 1998; Clutton-Brock and Manser, 2016, Thornton, 2008).

We followed six habituated meerkat groups covering a range of group sizes (mean group size: 18 individuals, range: 9 to 27) and occupying a diverse variety of habitats including duneveld, red sand woodland, white calcareous pan flats, and diatomous fossil riverbed (van Rooyen and van Rooyen, 1998). We excluded juveniles that still solicit food assistance from helpers and meerkats aged 11–14 months to differentiate sub-adults from experienced adults. We, therefore, only followed subjects of the following ages: 1) sub-adults aged 6–10 months, 2) yearlings aged 15–24 months, and 3) older adults, which are primarily dominant individuals, older than 24 months of age. Each studied group contained at least two individuals from each specified age category.

2.3. Foraging observations

We observed one or two meerkat groups each week, visiting a single group for a total of one or two days in that week, with a mean of five groups per month. Observations were conducted in the morning, starting from when the meerkats began foraging after leaving the sleeping burrow to about midday when meerkats typically rested and sometimes retreated to burrows. Each focal observation was conducted for 20 min per individual, with typically six individual meerkats being observed in a morning session (two per age category, the weekly mean: 6 individuals across all age categories). The result was a total sample size of 312 focal observations (sub-adults = 93, yearlings = 101, old adults = 118). On average, we conducted 27 (range:19 to 36, ±7 SD) individual focal observations per month, 7.8 (±2.2 SD) observations per month for sub-adult meerkats, 8.4 (±2.1 SD) observations for yearlings, and 9.8 (±3.1 SD) for old adults. Over the study year, 140 unique individuals were observed (102 h and 44 min of observation, across 65 distinct focal observation sessions). As the meerkats aged throughout the study, some of them were reclassified into different age categories.

When conducting the foraging observations, we recorded how meerkats searched for prey items, including forage dig, tracking prey as it moved below ground or following its burrow route to locate the prey item, root chewing, and surface foraging when prey items were eaten directly above or just below the ground surface. A committed forage bout was defined as any dig for a prey item lasting longer than 2 s, during which we recorded prey type and size (small, medium, large), the number of prey items consumed within the single forage bout, and the

handling method employed by the meerkat. Prey size was graded in relation to the meerkat mouth breadth and number of chews: small (comfortably fitting within the mouth, 5 or fewer chews), medium (1.5 times the mouth breadth, 6–15 chews), and large (exceeding 1.5 times the mouth breadth, more than 15 chews) (Brotherton et al., 2001; Turbé, 2006; Barnard, 2000; Thornton, 2008). Video recordings were captured using a GoPro Hero 9 mounted on a telescopic pole with a remote control, positioned approximately 10–20 cm from the head of individual meerkats. We used video recordings of committed meerkat foraging bouts to document their duration and assist with prey identification. Forage bout duration was determined from when the digging started until the individual ceased and changed its behaviour or moved at least 10 cm away to initiate a new forage dig. If an individual meerkat ceased its foraging activity for a period exceeding 5 min, due to activities such as guarding, babysitting, alarm responses, or collective behavioural dynamics, the observation session was stopped. An alternative individual within the same age category was then selected. Data from observation sessions that were terminated early were kept, with the reason for cessation. If the same individual became available for observation later, it was reconsidered for observation, based on the session time remaining and the need to focus on all age classes.

2.4. Prey identification

Prey was identified by one person (WJ) during observations. To verify and confirm the identification of any less familiar species, video recordings were taken during the forage bouts and abandoned prey items were collected and preserved in 96% ethanol. The specimens sampled formed a reference collection to assist with confirming identification made during field observations. Prey items were predominantly abandoned due to alarm calls in response to a predator, inter-group interactions or weather-related disturbance (such as rain and strong gusts of wind). In addition, we conducted periodic quadrat sampling digs (of standardised dimensions measuring 50 cm by 50 cm × 30 cm deep) in regions where meerkats frequently foraged. The specimens retrieved from these excavations were catalogued into the reference collection and cross-referenced to assist in confirming the identification of prey through observations and video footage. Other researchers at the study site contributed to prey identification by collecting discarded prey items still sufficiently intact for identification. These prey items were checked with the reference collection or added if not yet catalogued. Any video or photographs of prey items were used in combination with previously sampled and preserved prey specimens. Where needed, keys derived from the literature and relevant experts were consulted to assist with identifying and confirming prey items to the lowest possible taxa. Some prey items could not be identified, either because of their small size or because the prey item was not visible to the observer before it was consumed. Overall, the prey item consumed could not be identified in 48% of feeding bouts.

2.5. Statistical analyses

We used generalised linear mixed models (GLMMs) with a negative binomial error distribution to account for overdispersion in prey count data (Table 1). All models were implemented in *R version 4.3.2* (R Core Team, 2023) using the *glmmTMB* package (Brooks et al., 2017). Prey counts were used as the response variable, while percentages were calculated for figures and interpretations. Observations were pooled per individual meerkat, factor, and category as required, with individual meerkat identity or focal observation session included as random effects to account for repeated measures and shared environmental or temporal influences. Unobserved combinations or sparse data for certain categories were excluded to ensure statistical robustness and interpretability. For example, missing combinations of prey size and age category, as well as individuals with no observations in specific prey categories, were omitted. Adjustments were noted in the models while retaining sufficient data to maintain analytical integrity.

To analyse the contributions of different prey taxa to the meerkat diet, prey counts were summed for each 20-min focal observation and grouped by taxonomic classification (class, order, family). Duplicate prey items consumed within the same foraging bout were excluded to avoid artificially inflating counts, but distinct prey types consumed within the same bout were recorded separately. GLMMs were fitted with prey counts as the response variable and taxonomic level as the fixed effect. At the family level, Gryllidae was excluded from the model due to incomplete predation records, although observations of prey capture attempts were retained.

Seasonal dietary patterns and the consumption of prey life stages were examined by summing prey counts for selected families with fewer than 10 prey items or less than 1% of the total counts. Counts were analysed across wet (November–April) and dry (May–October) seasons. For this analysis, GLMMs included a two-way interaction between prey family and season as fixed effects, with Hepialidae excluded because it was consumed only in the wet season. A separate model investigated the relative abundance of larval versus adult Coleoptera (Carabidae, Tenebrionidae, Scarabaeidae) across seasons using a three-way interaction between life stage, family, and season, while pupae were excluded due to low frequency. Finally, life stage preferences for Formicidae (adults and pupae) across seasons were analysed using a two-way interaction between life stage and season. Prey counts were the response variable, with individual meerkat identity included as the random effect in all seasonal models.

Age-related dietary differences were examined across three age categories: sub-adults, yearlings, and old adults. In the first analysis,

Table 1
Description of the models used for the meerkat diet analysis.

	Model ID	Response variable	Sample size (Observations)	Sample size (unique individuals)	Fixed effects model structure	Adjustments and justifications
1	Class	Prey counts	840	140	Prey class	Zeros included for all 6 prey classes.
2	Order	Prey counts	2520	140	Prey order	Zeros included for all 18 prey orders.
3	Family	Prey counts	4480	140	Prey family	Zeros included for all 33 prey families.
4	Seasonality	Prey counts	10080	140	Season x prey families	Observations reflect 9 families × 4 life stages × 2 seasons. Missing combinations retained as zeros.
5	Coleoptera family life stages	Prey counts	1104	131	Prey life stage x season x Coleoptera	Observations reduced due to unobserved combinations of family × life stage × season and 9 individuals with no Coleoptera consumption.
6	Formicidae life stages	Prey counts	560	140	Season x life stage	
7	Age-related diet difference	Prey counts	355	65	Age categories x prey families	Sparse data excluded for specific prey families and age categories.
8	Prey size across age categories	Prey counts	454	65	Age categories x prey sizes	Missing data for prey size × age category combinations resulted in reduced observations.
9	Foraging strategies	Prey counts	189	65	Foraging strategy	

prey counts were modelled using GLMMs with a two-way interaction between prey family and age category as fixed effects. In a second analysis, differences in prey size (small, medium, large) across age categories were tested using GLMMs with a similar two-way interaction. For both models, the focal observation session was included as the random effect. To analyse the different foraging strategies used by meerkats (direct digging, tracking, root chewing, surface foraging), prey counts were summed for each strategy per individual. A GLMM was fitted with foraging strategy as the fixed effect and focal observation session as the random effect.

Model diagnostics were performed using the *DHARMa* package (Hartig, 2022). To evaluate the uniformity of the residuals, we applied the *Kolmogorov-Smirnov (KS) test* (Massey, 1951), where p-values indicated whether the residuals significantly deviated from the expected distribution. Furthermore, we examined dispersion through the *DHARMa* nonparametric test, which compares the standard deviation of the observed residuals to that of simulated residuals, detecting instances of over- or under-dispersion. (Table A1). The significance of specific categorical terms was assessed by likelihood ratio tests, and post-hoc pairwise comparisons across factor levels were conducted using the *emmeans* package (Lenth, 2023), with p-values adjusted using the *Benjamini-Hochberg* method to control the false discovery rate (Benjamini and Hochberg, 1995). The variance explained by the fixed effects, and by the fixed and random effects combined are reported as the marginal and conditional R^2, respectively.

2.6. Ethics

Ethics clearance was received from the University of Witwatersrand Animal Research Ethics Committee (2022)/07/05/B, and research and collection permit FAUNA 0041/2023 was obtained from Northern Cape Nature Conservation. The Kalahari Research Centre, where the study was conducted, already had the relevant, ethics permits from the University of Pretoria (NAS003/2022), and relevant research and section 20 permits from the Department of Agriculture, Land Reform and Rural Development (12/11/1/8/MG (2272)).

3. Results

3.1. Meerkat diet across taxonomic levels

In our year-long study, we identified 84 different prey categories within six major taxonomic classes, including 18 orders, 33 families, and 43 genera (Table A2). Of the six classes, Insecta contributed the highest percentage of prey counts in the meerkat diet (88.4%, n = 1110 prey counts), followed by Arachnida (5.7%, n = 71) and Diplopoda (4.3%, n = 54)) (Fig. 1a). The only observed vertebrate class preyed upon by meerkats was Reptilia, constituting 1.1% (n = 14) of prey counts in the diet. The examination of prey to the level of the order indicated that, within the Insecta, most of the prey eaten by meerkats was Coleoptera (70.4%, n = 805 counts), with declining prey counts of Lepidoptera (7.5%, n = 86), Hymenoptera (5.4%, n = 62). Scorpiones (4.9%, n = 56) and Spirostreptida (4.7%, n = 54) formed the dominant Arachnida and Diplopoda components, respectively eaten by meerkats. Other orders comprised less than 1.5% of the prey counts in the diet (Fig. 1b–Table A2). Given the bias towards Coleoptera, the three families making up the highest dietary percentage were Coleopteran representatives (Fig. 1c). Carabidae was predated the most by meerkats at 35.5% (n = 353 counts), followed by Tenebrionidae at 25.1% (n = 249), and Scarabaeidae at 11.4% (n = 249). Other families that were frequently eaten by meerkats were Odontopygidae (4.4%, n = 44), Hepialidae (5.3%, n = 53), and Formicidae (5.6%, n = 56). The two scorpion families contributed less than 5% of the prey counts in the diet, with Buthidae contributing 2.3% (n = 23) and Scorpionidae 2.1 % (n = 21) counts. Gekkonidae was the predominant Reptilia family eaten, comprising 0.9% (n = 9).

The GLMM results showed that meerkats ate Insecta more than all other classes, with the contrasts showing that meerkats had strong preferences for Insecta over Arachnida (GLMM contrast: 2.90, $p < 0.001$), Diplopoda (GLMM contrast: 3.23, $p < 0.001$), and Reptilia

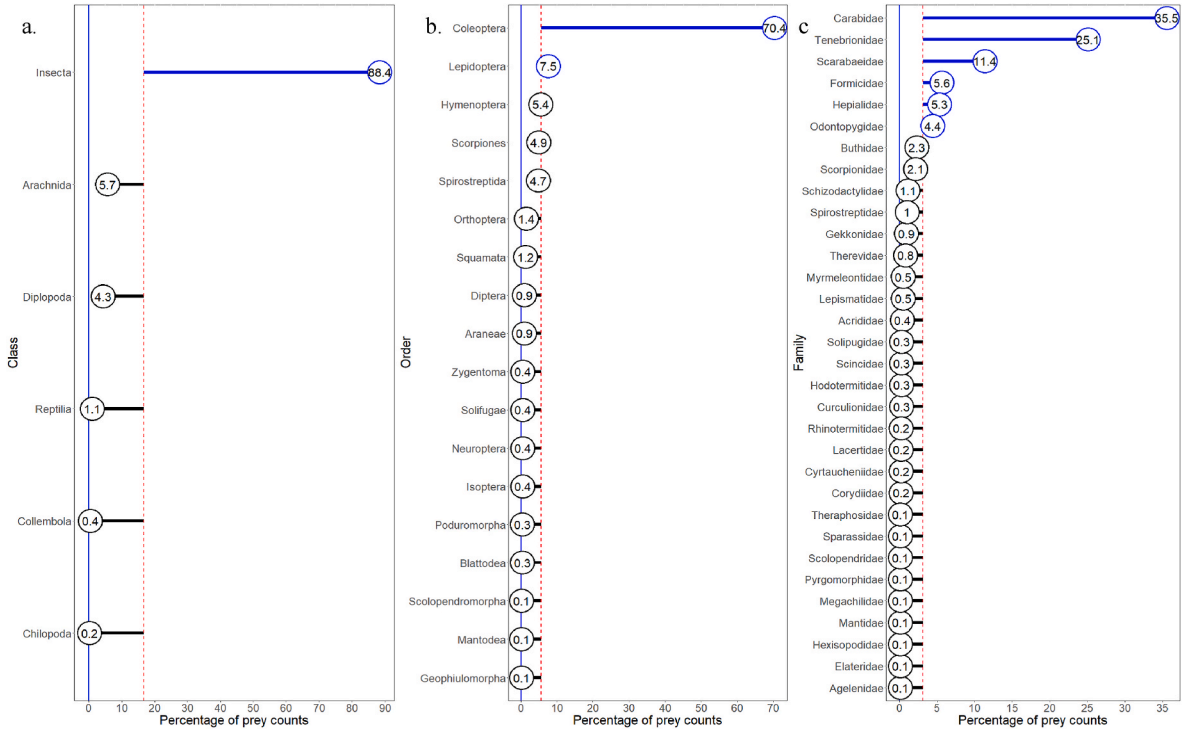


Fig. 1. Proportion (in percentage) of prey counts in the meerkat diet according to class (a), order (b), and family (c). The red dashed vertical lines mark the expected prey-category percentage if all categories were eaten equally at the class (16.7%), order (5.6%), and family (3.1%) levels. Prey categories to the right of the mean are relatively overrepresented (blue), and those to the left are relatively underrepresented (black).

(GLMM contrast: 4.71, $p < 0.001$) (Tables A3 and A4). At the order level, Coleoptera was consumed significantly more than Lepidoptera (GLMM contrast: 2.62, $p < 0.001$) and Hymenoptera (GLMM contrast: 2.78, $p < 0.001$). At the family level, meerkats ate Carabidae more than other Coleoptera families, followed by Tenebrionidae and Scarabaeidae.

3.2. Seasonal variation in meerkat diet and by life stage of prey

In the dry season, two prey families, Schizodactylidae (GLMM contrast wet - dry: 1.45, SE = 0.84, p-value = 0.083) and Scorpionidae (GLMM contrast wet - dry: 0.95, SE = 0.57, p-value = 0.093), were eaten more by meerkats than in the wet season (Table 2 and Table A5). For the two scorpion families, Buthidae were eaten more often by meerkats than Scorpionidae. However, there was no statistical difference between the wet and dry seasons in the prey counts of Buthidae (GLMM contrast in Table A5), though counts of both families were highest in October compared to all other months of the year (Fig. 2c). Meerkats ate more of the millipede family Odontopygidae than Spirostreptidae (GLMM contrast in Table A5: 1.49, SE = 0.41, p-value = 0.001), with higher prey counts of Odontopygidae in the latter part of the wet season and the start of the dry season (Fig. 2, GLMM contrast wet - dry: 1.24, SE = 0.47, p-value = 0.008). Meerkats only ate the larvae of Hepialidae during the wet season (Fig. 2b).

Meerkats fed on adult Carabidae beetles throughout the year, with the highest prey counts during the wet season (Fig. 2a). Throughout the year, meerkats had a higher number of prey counts of both Scarabaeidae and Tenebrionidae larvae compared to the other prey families. The highest prey counts of both adult Scarabaeidae (post-hoc GLMM estimate: 1.63, SE: 0.67, p = 0.015) and adult Tenebrionidae (post-hoc GLMM estimate: 2.64, SE: 0.64, $p < 0.0001$) were during the wet season. Meerkats fed more on adult Coleoptera in the wet season compared to in the dry season (GLMM contrast dry–wet: 1.50, SE = 0.32, p-value = <0.0001), while there was no significant difference in the seasonal predation of Coleoptera larva by meerkats (Tables A5 and A6).

Meerkats ate Formicidae prey predominantly in the wet season (GLMM contrast wet - dry: 1.34, SE = 0.43, p-value = 0.002) (Fig. 2b–Table A5. & A6), with Formicidae pupae eaten more often than the adults. Formicidae prey counts increased from the end of the dry season, peaking in the wet season.

3.3. Age-related variation in diet

3.3.1. Diet differences across the age categories

The diet composition was generally similar across the different age categories of meerkats, particularly in terms of the prey family's meerkats ate. However, differences were observed in the number of prey items consumed from specific families, in particular between old adults and sub-adults (Fig. 3). Sub-adults consumed small adult Carabidae beetles more often than other meerkat age groups (GLMM estimates in Table 3: 1.50, CI = 1.27 to 1.73, p-value = <0.001). Yearlings, on the other hand, consumed more Hepialidae caterpillars compared to meerkats in the other two age categories. Old adult meerkats had higher prey counts for most other prey families, consuming greater numbers of adult Tenebrionidae (n = 105) than either yearlings (n = 73, GLMM contrast in Table A7: 0.44, SE = 0.18, p-value = 0.05) or sub-adults (n = 71). Further, old adult meerkats ate more Scarabaeidae larvae (n = 59) than yearlings (n = 26) and sub-adults (n = 28).

3.3.2. Age-related variation in prey size

Small-sized prey was eaten most often by all age classes of meerkats. Sub-adults had the highest prey counts for small-sized prey items (Fig. 4, (Table 4 and Table A7)) and ate less medium and large-sized prey items than did old adult meerkats (GLMM estimate: 1.30, CI = 1.09 to 1.50, p-value = <0.001). In contrast, yearlings (GLMM estimate: 0.32, CI = −0.01 to −2.00, p-value = 0.045) had the lowest prey counts for large prey. Across the age categories, old adult meerkats had the highest prey counts of medium and large-sized prey items.

3.4. Foraging strategies

Meerkats dug up most of their prey: 96.1% of all prey counts were acquired through digging (n = 4806), while 3.9% were captured on the surface (n = 195, GLMM Table 5). Meerkats used three methods to excavate prey: direct digging (73%, n = 3666), tracking prey as it moved

Table 2
GLMM results for seasonality and prey families in the meerkat diet.

Predictor	Response variable: Prey counts					
	Estimate	Std. error	CI (lower)	CI (upper)	Statistic	p-value
Intercept [dry: Carabidae]	−1.49	0.22	−1.92	−1.07	−6.87	**<0.001**
Season [wet]	0.15	0.29	−0.41	0.71	0.52	0.604
Prey family [Buthidae]	−2.87	0.42	−3.69	−2.04	−6.8	**<0.001**
Prey family [Formicidae]	−2.74	0.41	−3.55	−1.93	−6.66	**<0.001**
Prey family [Odontopygidae]	−3.01	0.44	−3.88	−2.15	−6.85	**<0.001**
Prey family [Scarabaeidae]	−1.35	0.33	−1.99	−0.71	−4.13	**<0.001**
Prey family [Schizodactylidae]	−3.06	0.45	−3.93	−2.18	−6.85	**<0.001**
Prey family [Scorpionidae]	−2.48	0.39	−3.24	−1.72	−6.39	**<0.001**
Prey family [Spirostreptidae]	−3.78	0.58	−4.92	−2.65	−6.52	**<0.001**
Prey family [Tenebrionidae]	−0.25	0.29	−0.82	0.32	−0.86	0.391
Season [wet] × Prey family [Buthidae]	0.07	0.58	−1.07	1.21	0.12	0.905
Season [wet] × Prey family [Formicidae]	1.19	0.52	0.18	2.21	2.3	**0.021**
Season [wet] × Prey family [Odontopygidae]	1.09	0.55	0.02	2.17	1.99	**0.047**
Season [wet] × Prey family [Scarabaeidae]	0.22	0.44	−0.64	1.09	0.51	0.613
Season [wet] × Prey family [Schizodactylidae]	−1.6	0.88	−3.33	0.13	−1.81	0.071
Season [wet] × Prey family [Scorpionidae]	−1.1	0.63	−2.34	0.14	−1.73	0.083
Season [wet] × Prey family [Spirostreptidae]	0.09	0.77	−1.42	1.59	0.11	0.909
Season [wet] × Prey family [Tenebrionidae]	−0.11	0.41	−0.9	0.69	−0.27	0.788

Random effects		Model fit	
Component	Estimate	Metric	Value
Residual variance (σ^2)	3.42	Marginal R^2	0.315
Variance (Individual) (τ00)	0.77	Conditional R^2	0.44
Intraclass Correlation Coefficient (ICC)	0.18		
Number of individuals (N)	140		
Observations	10080		

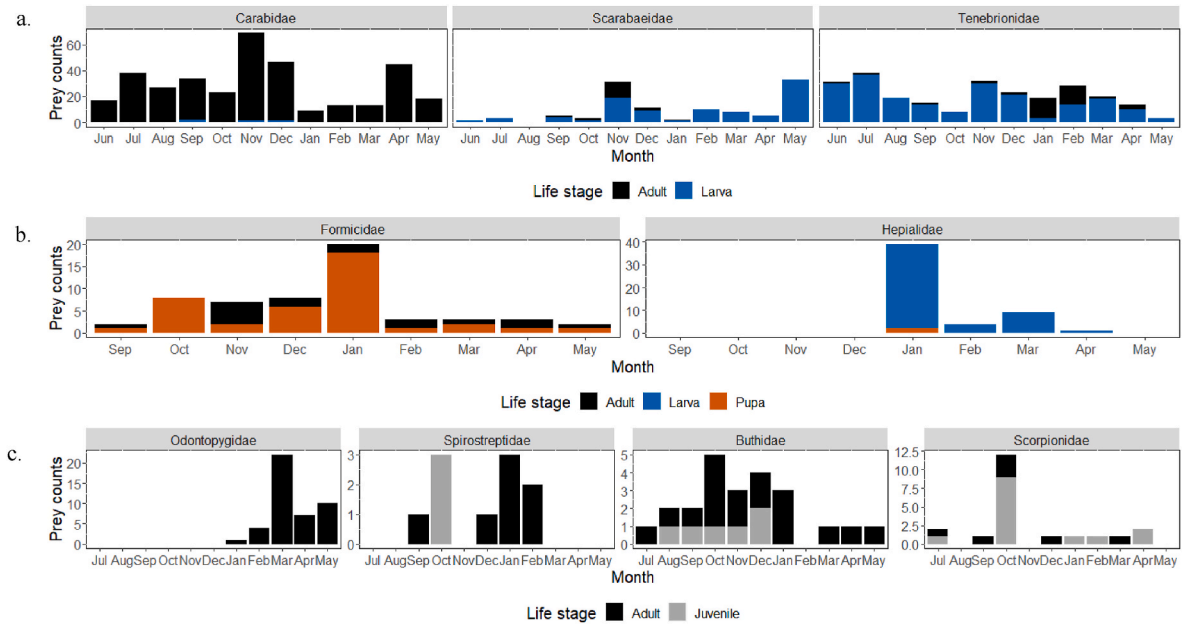


Fig. 2. Number of individual prey counts of the main eaten prey families by meerkats by month, to show predation peaks and declines across the year. The months of May to October represent the dry season, while November to April signifies the wet season. a. The upper panel shows Coleoptera families: Carabidae, Scarabaeidae and Tenebrionidae. b. The middle panel shows the other Insecta families: Formicidae and Hepialidae. c. The lower panel shows the Diplopoda families: Odontopygidae and Spirostreptidae, and Scorpiones families: Buthidae and Scorpionidae. Different life stages of prey items are represented as adult in black, larva in blue, pupa in orange, and juvenile in grey.

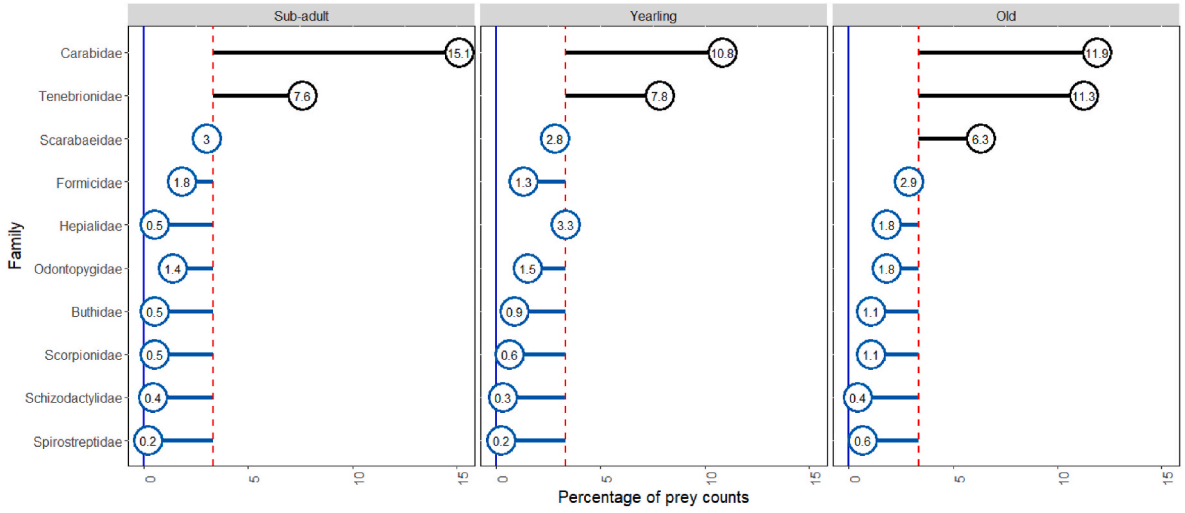


Fig. 3. Proportion (in percentage) of prey counts of prey items by the regularly eaten prey family in the different meerkat age categories: a) sub-adult (6–10 months), b) yearlings (adults 15–24 months), and c) old (adults >24 months). Percentages indicate the dietary contribution of each prey family within the total diet for each age category. The dashed red vertical line (3.7%) marks the expected prey-category percentage if all categories were eaten equally. Prey families above the mean are depicted in black, and those below the mean in blue.

underground (22%, n = 1086), and exposing and chewing open roots of certain shrubs (*Indigofera* spp. and *Justicia* spp.) to consume Hepialidae (ghost moth) larvae (1.1%) (Fig. 5). About a quarter (23%) of the fast-moving Tenebrionidae larvae (n = 58) were tracked before being captured, while some Carabidae beetles were also tracked, but less often (13%, n = 49) compared to being directly dug up (79%, n = 288). Meerkats mainly captured and ate Spirostreptidae by digging them up (77%, n = 10), while 23% (n = 3) were captured either just below or on the ground surface.

4. Discussion

As shown by previous studies, and supported by our study, meerkats are insectivores (88.4% of the prey counts were insects), with insectivores being defined as animals with over 50% of the diet consisting of Insecta (Pineda-Munoz et al., 2016; Pineda-Munoz and Alroy, 2014; Pollard and Puckett, 2021; Doolan and Macdonald, 1996). Within Insecta, meerkats primarily consumed Coleoptera, as shown previously (Doolan and Macdonald, 1996; Lynch, 1980; Smithers, 1983). In our study, Coleoptera accounted for 70.4% of the meerkat diet. In comparison, the observational study by Doolan and Macdonald (1996) found that Coleoptera made up 27.5% of the meerkat diet, while stomach

Table 3
GLMM results for age-related dietary differences.

Predictor	Response variable: Prey counts					
	Estimate	Std. error	CI (lower)	CI (upper)	Statistic	p-value
Intercept [sub-adult: Carabidae]	1.5	0.12	1.27	1.73	12.55	**<0.001**
Age category [yearling]	−0.3	0.17	−0.62	0.03	−1.8	0.071
Age category [old]	−0.36	0.16	−0.67	−0.04	−2.24	**0.025**
Prey family [Buthidae]	−1.36	0.5	−2.33	−0.38	−2.73	**0.006**
Prey family [Formicidae]	−0.99	0.3	−1.57	−0.41	−3.35	**0.001**
Prey family [Hepialidae]	−0.42	0.55	−1.5	0.66	−0.76	0.445
Prey family [Odontopygidae]	−0.78	0.34	−1.46	−0.11	−2.29	**0.022**
Prey family [Scarabaeidae]	−1.15	0.24	−1.62	−0.67	−4.7	**<0.001**
Prey family [Schizodactylidae]	−0.81	0.59	−1.96	0.34	−1.39	0.165
Prey family [Scorpionidae]	−0.92	0.52	−1.94	0.09	−1.78	0.075
Prey family [Spirostreptidae]	−1.42	0.77	−2.94	0.09	−1.84	0.066
Prey family [Tenebrionidae]	−0.63	0.18	−0.98	−0.28	−3.54	**<0.001**
Age category [yearling] × Prey family [Buthidae]	0.49	0.64	−0.77	1.75	0.76	0.445
Age category [old] × Prey family [Buthidae]	0.63	0.62	−0.59	1.85	1.02	0.31
Age category [yearling] × Prey family [Formicidae]	−0.1	0.45	−0.99	0.78	−0.23	0.819
Age category [old] × Prey family [Formicidae]	0.54	0.39	−0.21	1.3	1.4	0.16
Age category [yearling] × Prey family [Hepialidae]	0.91	0.62	−0.3	2.12	1.48	0.14
Age category [old] × Prey family [Hepialidae]	0.46	0.63	−0.78	1.71	0.73	0.465
Age category [yearling] × Prey family [Odontopygidae]	0.81	0.49	−0.15	1.77	1.65	0.098
Age category [old] × Prey family [Odontopygidae]	0.79	0.47	−0.12	1.71	1.7	0.09
Age category [yearling] × Prey family [Scarabaeidae]	0.41	0.35	−0.28	1.09	1.17	0.243
Age category [old] × Prey family [Scarabaeidae]	0.91	0.31	0.3	1.51	2.94	**0.003**
Age category [yearling] × Prey family [Schizodactylidae]	−0.22	0.86	−1.91	1.46	−0.26	0.795
Age category [old] × Prey family [Schizodactylidae]	−0.42	0.79	−1.97	1.14	−0.52	0.601
Age category [yearling] × Prey family [Scorpionidae]	0.01	0.69	−1.35	1.36	0.01	0.989
Age category [old] × Prey family [Scorpionidae]	0.28	0.64	−0.97	1.52	0.43	0.665
Age category [yearling] × Prey family [Spirostreptidae]	0.36	1.1	−1.79	2.51	0.33	0.745
Age category [old] × Prey family [Spirostreptidae]	0.83	0.91	−0.94	2.61	0.92	0.358
Age category [yearling] × Prey family [Tenebrionidae]	0.06	0.25	−0.44	0.55	0.23	0.814
Age category [old] × Prey family [Tenebrionidae]	0.55	0.24	0.08	1.02	2.29	**0.022**

Random effects	Model fit		
Component	Estimate	Metric	Value
Residual variance (σ^2)	0.42	Marginal R^2	0.241
Variance (Individual) (τ00)	0.1	Conditional R^2	0.396
Intraclass Correlation Coefficient (ICC)	0.2		
Number of individuals (N)	65		
Observations	355		

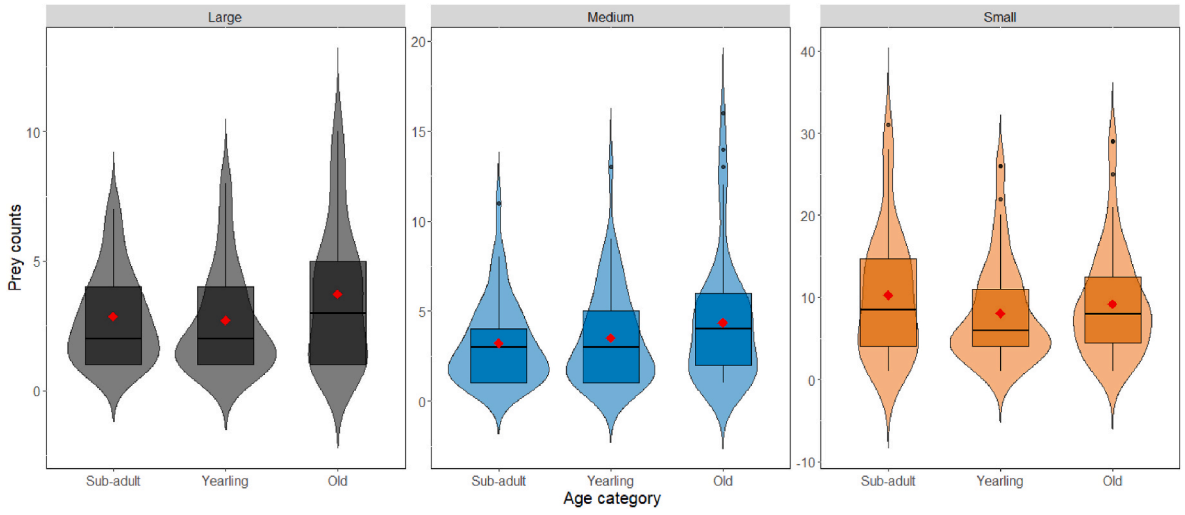


Fig. 4. Violin plots of prey count of different prey sizes (large = black, medium = blue, and small = orange) by meerkat age category (sub-adult = 6–10 months, yearlings = 15–24 months, and old adults = > 24 months). The red point in the violin and box plot depicts the model-predicted means, and the box plot is representative of the median, quartiles, and outliers.

analysis studies by Lynch (1980) and Smithers (1983) found 58% and 91% occurrence, respectively (Table A8). Whether the high percentage of Coleoptera in the diet reflects dietary opportunism, with Coleoptera being abundant in the Kalahari (Åström, 2003), or dietary specialisation regardless of abundance, remains to be determined. We also found that meerkats primarily dug up their prey, while surface foraging was done to a lesser extent and likely was more opportunistic, as shown previously in other studies (Glaser, 2006; Leclaire, 2017; Sörensen et al., 2019;

Table 4
GLMM results for age-related differences in prey item size.

Predictor	Response variable: Prey counts					
	Estimate	Std. error	CI (lower)	CI (upper)	Statistic	p-value
Intercept [old, large]	1.3	0.11	1.09	1.5	12.16	**<0.001**
Age category [sub-adult]	−0.26	0.16	−0.57	0.05	−1.62	0.105
Age category [yearling]	−0.32	0.16	−0.63	−0.01	−2	**0.045**
Prey size [medium]	0.16	0.14	−0.12	0.44	1.11	0.269
Prey size [small]	0.91	0.13	0.65	1.16	6.87	**<0.001**
Age category [yearling] × prey size [medium]	0.1	0.22	−0.32	0.52	0.47	0.64
Age category [sub-adult] × prey size [medium]	−0.04	0.22	−0.48	0.39	−0.2	0.841
Age category [yearling] × prey size [small]	0.18	0.2	−0.2	0.57	0.93	0.353
Age category [sub-adult] × prey size [small]	0.37	0.2	−0.02	0.76	1.85	0.065

Random effects	Model Fit		
Component	Estimate	Metric	Value
Residual variance (σ^2)	0.38	Marginal R^2	0.372
Variance (Individual) (τ00)	0.04	Conditional R^2	0.429
Intraclass Correlation Coefficient (ICC)	0.09		
Number of individuals (N)	65		
Observations	454		

Table 5
GLMM results for foraging strategies used by meerkats to locate prey items.

Predictor	Response variable: Prey counts					
	Estimate	Std. error	CI (lower)	CI (upper)	Statistic	p-value
Intercept [dug]	3.35	0.07	3.2	3.49	44.90	**<0.001**
Foraging strategies [root chewed]	−1.49	0.25	−1.99	1	−5.87	**<0.001**
Foraging strategies [surface]	−2.20	0.12	−2.44	1.96	−18.07	**<0.001**
Foraging strategies [tracked]	−1.47	0.11	−1.69	1.26	−13.41	**<0.001**

Random effects	Model Fit		
Component	Estimate	Metric	Value
Residual variance (σ^2)	0.29	Marginal R^2	0.706
Variance (Individual) (τ00)	0.06	Conditional R^2	0.757
Intraclass Correlation Coefficient (ICC)	0.17		
Number of individuals (N)	65		
Observations	189		

Doolan and Macdonald, 1996; Turbé, 2006). Additionally, meerkats actively dug to expose roots and then chewed the roots open to prey upon Hepialidae larvae and actively pursued and tracked the movements of fast-moving Tenebrionidae larvae before excavating and consuming them.

Our analysis of the diet of meerkats revealed that the three most common beetle families in the meerkat diet – Carabidae (36% of prey counts), Tenebrionidae (25%), and Scarabaeidae (11%) – were eaten throughout the year. Meerkats ate the adults of the smaller Carabidae genera year-round, with increased prey counts during the wet season compared to the dry season. Large Tenebrionidae larvae were an important part of the meerkat's diet during the dry season and the start of the wet season. A previous study on a different population (about 300 km away, in the Kgalagadi Transfrontier Park) found that meerkats ate a lower number of Tenebrionidae larvae in the dry season compared to the wet season, which the authors suggested could be due to the larvae digging deeper and being more difficult to capture (Doolan and Macdonald, 1996). We also found that primarily adult Tenebrionidae were eaten in the wet season. Scarabaeidae larvae were eaten at the start of the dry season, but predation on these larvae declined over the peak of the dry season, possibly due to larval dormancy and pupation (Davis et al., 2008). Meerkats ate adult Scarabaeidae (Woolly Chafer beetles *Sparrmannia flava* being the main prey species) mostly at the start of the wet season (September to January), which likely reflects increased adult beetle emergence for reproduction, coinciding with seasonal rainfall.

Hymenoptera were eaten the most during the wet season by meerkats, consistent with the findings of Doolan and Macdonald (1996). Further in the wet season, there was increased predation on Formicidae (ant) pupae than in the dry season, while meerkats avoided adult Formicidae. Meerkats, like American black bears (*Ursinus americanus*; Auger et al., 2004), may prefer ant pupae to adult ants, due to the lack of chemical and anatomical defences, lower fibre content, and a higher nutrient concentration in the pupae. As also found by Doolan and Macdonald (1996), we found relatively low predation by meerkats on Reptilia and Scorpiones. Reptiles appeared to be opportunistic prey for meerkats, except for the family Gekkonidae (particularly barking geckoes, *Ptenopus garrulus*), which were actively dug up and consumed as these geckos became more active at the end of the dry season (Turbé, 2006). In contrast, Smithers (1983) reported a higher percentage of reptiles in meerkat stomach samples (13%) in Botswana. The difference in the findings between our studies may reflect Smither's smaller sample size, or short study duration with opportunistic feeding by meerkats at the time of his study.

In our study, Scorpiones were eaten by meerkats mainly at the start of the wet season, most likely due to increased scorpion activity during the warmer months of the year (Engelbrecht, 2023). The low predation rate of Scorpiones (less than 5%) is similar to that found by Doolan and Macdonald (1996), in contrast to the 21% in the meerkat stomach analyses in the Free State, South Africa (Lynch, 1980), and 35% in Botswana (Smithers, 1983). The higher occurrence in stomach samples as compared to our study could be due to different sampling periods and regional variation. Meerkats eating scorpions may provide a key nutritional benefit for meerkats after the dry season, as scorpions are nutrient-rich (with high amounts of proteins and fats, and low levels of carbohydrates) and have a high moisture content (Abulude et al., 2006; Turbé, 2006).

Meerkats also preyed upon millipedes more often towards the end of the wet season and the start of the dry season. A previous study found that millipedes (which comprise 40% unsaturated fatty acids and 25% protein) were eaten most frequently during the dry season, possibly also as a means for meerkats to meet their nutritional requirements at that time of year (Enghoff et al., 2014; Turbé, 2006). Within the long-term meerkat project spanning more than 30 years, it has been recorded that meerkats occasionally consumed Isoptera and preyed upon *Mus indutus* (desert pygmy mouse) when their population increased as a result of optimal environmental conditions. These patterns were not observed in the year of our study, emphasising the importance of conducting dietary studies over multiple years to account for varying climatic and environmental conditions.

We further compared the diets of meerkats of different ages and

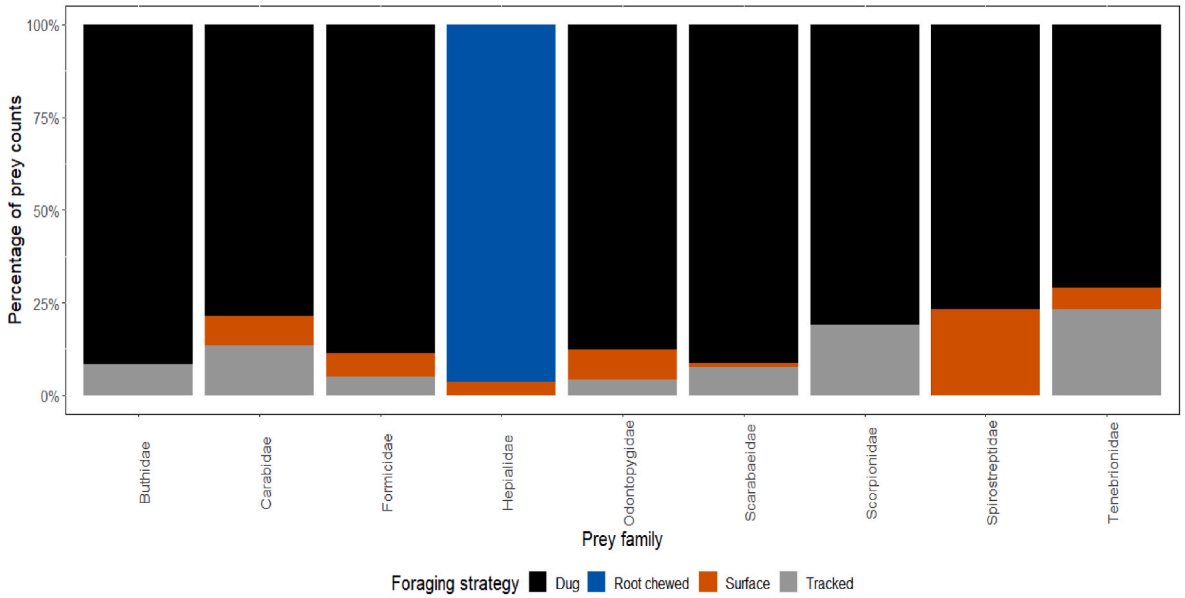


Fig. 5. The various foraging strategies used by meerkats (dug = black, root chewed = blue, surface for surface foraged = brown, tracked = grey) to search for and capture the main prey families.

found that although the diet composition was similar across the three studied age categories, there were differences in prey counts with certain prey families. Sub-adult meerkats ate the highest number of small-sized prey items, particularly small Carabidae beetles. Yearling meerkats fed more on the Hepialidae caterpillars inside roots and had the lowest prey counts for large-sized prey. Old adult meerkats had the highest prey counts for medium and large-sized prey items and their representative prey families (Tenebrionidae, Scarabaeidae, Scorpionidae, Buthidae, and Spirostreptidae). While there have been comparisons of diet across ages for other vertebrates, including reptiles (Platt et al., 2006; Prior et al., 2015), fish (Alves et al., 2021), and birds (Marugán-Lobón and Chiappe, 2022), there have been very few studies on diet changes in mammals across age. In a study of diet changes with age in European hedgehogs (*Erinaceus europaeus*), it was found that older animals were more selective and ate fewer small prey items (under 0.05 g) but consumed more larger prey items (over 2 g), compared to younger individuals. A shift in dietary selection among older individuals likely indicates improved foraging efficiency (Dickman, 1988). In another study on meerkats, older meerkats were found to consume three times more large prey items than their younger counterparts, which aligns with our findings (Barnard, 2000). However, while we observed age-related dietary differences, we did not directly measure foraging efficiency.

A limitation of our study was the restriction of focal observations to the mornings. The diet of meerkats may differ in the afternoons, particularly if meerkats change their foraging behaviour and diet because of factors that change across the day, such as environmental temperature, or if prey item availability changes across the day. We also may not have documented some prey categories that were consumed as a consequence of the difficulty in identifying all prey items, particularly when they were eaten within the excavated dig site or too quickly without being seen. It would have also been beneficial to conduct long-term invertebrate abundance sampling within the various macro-habitats and regions frequented by the meerkats. The invertebrate abundance sampling would have allowed for prey selectivity index analyses to be performed to gain a deeper insight into foraging patterns and preferences.

Our research on the meerkat diet has provided detailed insights into their dietary habits and foraging strategies, contributing to a deeper understanding of their diet in relation to seasonal changes and age-related foraging skills of individuals. Studies such as ours are important as climate change is negatively impacting invertebrates, leading to a decrease in arthropod diversity (Bastida et al., 2019; Prather et al., 2013), with likely impacts on the diet of meerkats. In the southern Kalahari, air temperatures have increased by 1.5 °C over the last two decades, in parallel with reduced meerkat survival and growth (Paniw et al., 2022; Van de Ven et al., 2019). Soil invertebrates in arid environments may face greater thermal and hydration stress than those in more mesic areas, which may further impact the invertebrate populations (Prather et al., 2013) that meerkats rely on. Future research on the diet of meerkats should extend data collection over a full day and include measurements on prey availability, to allow for a more comprehensive understanding of changes in diet and prey item selectivity across the day. Additionally, conducting diet studies over multiple years would allow us to better understand how seasonal and climatic changes influence meerkat foraging strategies and dietary choices. Furthermore, understanding the relationship between macro-habitats and the diet across meerkat groups may provide valuable insights into how changes in prey availability may affect meerkat populations and their seasonal movements.

CRediT authorship contribution statement

Walter R. Jubber: Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Marta B. Manser:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Andrea Fuller:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Funding sources

We are grateful for the financial support provided by the University of Zurich to M.B.M. and Cambridge University to Tim Clutton-Brock (T.C.-B). as well as the MAVA Foundation, the Zoo Zurich, and the Exekias and Irene Staehelin foundations, for their long-term investment in the Kalahari Research Centre, and Kalahari Meerkat Project run at this field site. Additionally, we are grateful to the European Research Council, European Union's Horizon 2020 research and innovation program, no. 742808 for the finances awarded to T.C.-B., and the Human Frontier

Science Program (RGP0051/2017, RGP0051/2019) for meerkat research.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thanks are extended to the Kalahari Research Trust and the Kalahari Meerkat Project for granting access to their facilities and the habituated animals on and around the Kuruman River Reserve. We are also indebted to the local farmers for their cooperation and for granting access to their land. We thank the numerous managers, volunteers, students, and researchers whose efforts facilitated the collection and curation of the extensive long-term data essential to this project and thank Karin Krüger-Jubber, Jack Thorley, Shay Rotics, Peter Kamerman, Maria Paniw and Lily Johnson-Ulrich for their valuable input and support. Special thanks are to Prof Tim Clutton-Brock, for his support and foundational contributions to the study. We also acknowledge the University of Witwatersrand, School of Physiology, and the University of Pretoria, Mammal Research Institute, for their support in facilitating this research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2025.105331.

Data availability

The data that has been used is confidential.

References

Abulude, F.O., Ogunkoya, M.O., Esiet, B.O., Oni, J.O., 2006. Studies on scorpion (*Androctonus australis*): nutritional and anti-nutritional factors. J. Entomol. 3, 156–160. https://doi.org/10.3923/je.2006.156.160.

Alves, G.H.Z., Figueiredo, B.R.S., Manetta, G.I., Benedito, E., 2021. Ontogenetic diet shifts: an additional mechanism for successful invasion of a piranha species in a neotropical floodplain. An. Acad. Bras. Cienc. 93 (4). https://doi.org/10.1590/0001-3765202120190868.

Åström, J., 2003. Insect Communities in Southern Kalahari, Botswana – Abundance and Diversity in Relation to Land Management. MSc Thesis. Uppsala University.

Auger, J., Ogborn, G.L., Pritchett, C.L., Black, H.L., 2004. Selection of ants by the American black bear (Ursinus americanus). Western North American Naturalist 64 (2), 166–174.

Barnard, J.A., 2000. Costs and Benefits of Group Foraging in Cooperatively Breeding Meerkats. *PhD Thesis, Emmanuel College*.

Bastida, F., Eldridge, D.J., Abades, S., Alfaro, F.D., Gallardo, A., García-Velázquez, L., García, C., Hart, S.C., Pérez, C.A., Santos, F., Trivedi, P., Williams, M.A., Delgado-Baquerizo, M., 2019. Climatic vulnerabilities and ecological preferences of soil invertebrates across biomes. Mol. Ecol. 29, 752–761. https://doi.org/10.1111/mec.15299, 2020.

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: a practical and powerful approach to multiple testing. J. Roy. Stat. Soc. B 57 (1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x.

Brooks, E.M., Kristensen, K., Benthem, J., van, K., Magnusson, A., Berg, W.C., Nielsen, A., Skaug, J.H., Mächler, M., Bolker, M.B., 2017. glmmTMB Balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. The R Journal 9 (2), 378. https://doi.org/10.32614/rj-2017-066.

Brotherton, P.N.M., Clutton-Brock, T.H., O'Riain, M.J., Gaynor, D., Sharpe, L., Kansky, R., McIlrath, G.M., 2001. Offspring food allocation by parents and helpers in a cooperative mammal. Behav. Ecol. 12 (5), 590–599. https://doi.org/10.1093/beheco/12.5.590.

Clutton-Brock, T.H., Brotherton, P.N.M., Russell, A.F., O'Riain, M.J., Gaynor, D., Kansky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G.M., Small, T., Moss, A., Monfort, S., 2001. Cooperation, control, and concession in meerkat groups. Science 291 (5503), 478–481. https://doi.org/10.1126/science.291.5503.478.

Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrathm, G., Chadwick, P., Brotherton, P.N.M., O'Riain, J.M., Manser, M., Skinner, J.D., 1998. Costs of cooperative behaviour in suricates (Suricata suricatta). The Royal Society 265 (1392), 185–190. https://doi.org/10.1098/rspb.1998.0281.

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D., Brotherton, P.N.M., 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. J. Anim. Ecol. 68 (4), 672–683. https://doi.org/10.1046/j.1365-2656.1999.00317.x.

Clutton-Brock, T.H., Manser, M.B., 2016. Meerkats: Cooperative Breeding in the Kalahari. Cambridge University Press, Cambridge, pp. 294–317. https://doi.org/10.1017/CBO9781107338357.009.

Davis, A.L.V., Frolov, A.V., Scholtz, C.H., 2008. The African Dung Beetle Genera. Protea Book House, Pretoria. ISBN: 978-1-8-86919-244-0.

Dickman, C.R., 1988. Age-related dietary change in the European hedgehog, *Erinaceus europaeus*. J. Zool. 215 (1), 1–14. https://doi.org/10.1111/j.1469-7998.1988.tb04881.x.

Doolan, S.P., Macdonald, D.W., 1996. Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. J. Zool. 239 (4), 697–716. https://doi.org/10.1111/j.1469-7998.1996.tb05472.x.

Engelbrecht, I., 2023. Field Guide to Scorpions of South Africa. Struik Nature, Cape Town.

Enghoff, H., Manno, N., Tchibozo, S., List, M., Schwarzinger, B., Schoefberger, W., Schwarzinger, C., Paoletti, M.G., 2014. Millipedes as food for humans: their nutritional and possible antimalarial value - a first report. Evid. base Compl. Alternative Med. https://doi.org/10.1155/2014/651768, 2014.

Fox, B.J., 2011. Review of small mammal trophic structure in drylands: resource availability, use, and disturbance. J. Mammal. 92 (6), 1179–1192. https://doi.org/10.1644/10-MAMM-S-227.1.

Gall, G.E.C., Manser, M.B., 2018. Spatial structure of foraging meerkat groups is affected by both social and ecological factors. Behav. Ecol. Sociobiol. 72 (5). https://doi.org/10.1007/s00265-018-2490-x.

Glaser, A., 2006. Prey Detection and Foraging Strategies in Meerkats (*Suricata suricatta*). *Diploma thesis*. University of Zurich.

Hartig, F., 2022. DHARMa: Residual diagnostics for hierarchical (multi-Level/mixed). https://CRAN.R-project.org/package=DHARMa.

Jordan, N.R., Cherry, M.I., Manser, M.B., 2007. Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. Anim. Behav. 73 (4), 613–622. https://doi.org/10.1016/j.anbehav.2006.06.010.

Leclaire, S., 2017. Recognition of prey odor in wild meerkats. Chemoecology 27 (2), 85–90. https://doi.org/10.1007/s00049-017-0229-1.

Lenth, R.V., 2023. _emmeans: Estimated marginal means, aka least-squares means_. https://CRAN.R-project.org/package=emmeans.

Lynch, C., 1980. Ecology of the suricate, *Suricata suricatta*, and yellow mongoose, *Cynictis penicillata*, with special reference to their reproduction, 14. Memoirs of the National Museum of Bloemfontein, pp. 1–144.

Marugán-Lobón, J., Chiappe, L.M., 2022. Ontogenetic niche shifts in the Mesozoic bird *Confuciusornis sanctus*. Curr. Biol. 32 (7), 1629–1634.e2. https://doi.org/10.1016/j.cub.2022.02.010.

Massey, Jr.F.J., 1951. The Kolmogorov-Smirnov test for goodness of fit. J. Am. Stat. Assoc. 46, 68–78. https://doi.org/10.1080/01621459.1951.10500769.

Paniw, M., Duncan, C., Groenewoud, F., Drewe, J.A., Manser, M., Ozgul, A., Clutton-Brock, T., 2022. Higher temperature extremes exacerbate negative disease effects in a social mammal. Nat. Clim. Change 12 (3), 284–290. https://doi.org/10.1038/s41558-022-01284-x.

Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T., Ozgul, A., 2019. Life history responses of meerkats to seasonal changes in extreme environments. Science 363 (6427), 631–635. https://doi.org/10.1126/science.aau5905.

Pineda-Munoz, S., Alroy, J., 2014. Dietary characterization of terrestrial mammals. Proc. Biol. Sci. 281 (1789). https://doi.org/10.1098/rspb.2014.1173.

Pineda-Munoz, S., Evans, A.R., Alroy, J., 2016. The relationship between diet and body mass in terrestrial mammals. Dryad. https://doi.org/10.5061/dryad.br45b.

Platt, S.G., Rainwater, T.R., Finger, A.G., Thorbjarnarson, J.B., Anderson, T.A., McMurry, S.T., Rainwater, T.R., 2006. Food habits, ontogenetic dietary partitioning and observations of foraging behaviour of Morelet's crocodile (*Crocodylus moreletii*) in Northern Belize. Herpetol. J. 16 (3), 281–290.

Pollard, M.D., Puckett, E.E., 2021. Evolution of degrees of carnivory and dietary specialization across Mammalia and their effects on speciation. bioRxiv 2021, 460515. https://doi.org/10.1101/2021.09.15.460515, 09.15.

Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Wolts, M., Block, C.P., Del Toro, I., Ho, C. K., Kominoski, T., Newbold, T.A.S., Parsons, S., Joern, A., 2013. Invertebrates, ecosystem services and climate change. Biol. Rev. 88 (2), 327–348. https://doi.org/10.1111/brv.12002.

Prior, B., Booth, D.T., Limpus, C.J., 2015. Investigating diet and diet switching in green turtles (*Chelonia mydas*). Aust. J. Zool. 63 (6), 365–375. https://doi.org/10.1071/ZO15063.

R Core Team, 2023. R: A Language and Environment for Statistical. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from. http://www.R-project.org/.

Russell, A.F., Clutton-Brock, T.H., Brotherton, P.N.M., Sharpe, L.L., Mcilrath, G.M., Dalerum, F.D., Cameron, E.Z., Barnard, J.A., 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. J. Anim. Ecol. 71 (4), 700–709. https://doi.org/10.1046/j.1365-2656.2002.00636.x.

Rymer, T.L., Pillay, N., Schradin, C., 2016. Resilience to droughts in mammals: a conceptual framework for estimating vulnerability of a single species. Q. Rev. Biol. 91 (2), 133–176. https://doi.org/10.1086/686810.

Smithers, R.H., 1983. The Mammals of Southern Africa Subregion. University of Pretoria Press, Pretoria.

Sörensen, I., Amundin, M., Laska, M., 2019. Meerkats (*Suricata suricatta*) are able to detect hidden food using olfactory cues alone. Physiol. Behav. 202, 69–76. https://doi.org/10.1016/j.physbeh.2019.02.002.

Tarvin, R.D., Pearson, K.C., Douglas, T.E., Ramírez-Castañeda, V., Navarrete, M.J., 2023. The diverse mechanisms that animals use to resist toxins. Annu. Rev. Ecol. Evol. Systemat. 54, 283–306. https://doi.org/10.1146/annurev-ecolsys-102320, 2023.

Thornton, A., 2008. Social learning about novel foods in young meerkats. Anim. Behav. 76 (4), 141–1421.

Turbé, A., 2006. Foraging Decisions and Space Use in a Social Mammal, the Meerkat. *PhD thesis, Trinity College*.

Van de Ven, T.M.F.N., Fuller, A., Clutton-Brock, T.H., 2019. Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat. Funct. Ecol. 34 (1), 194–202. https://doi.org/10.1111/1365-2435.13468.

van Rooyen, N., van Rooyen, M.W., 1998. Vegetation of the south-western arid Kalahari: an overview. Trans. Roy. Soc. S. Afr. 53 (2), 113–140. https://doi.org/10.1080/00359199809520381.