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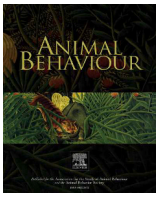

The ontogeny of foraging in meerkats, a cooperatively breeding mongoose

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Delayed reproductive life histories characterize many singular cooperative breeders, where the onset of first breeding is often delayed beyond adulthood. These delays are commonly attributed to factors including inbreeding avoidance and reproductive suppression, but an additional possibility is that the slow development of foraging skills constrains successful reproduction because of its energetic demands. While this explanation for delayed breeding has found limited support, there is evidence in some cooperative breeders of relatively long foraging ontogenies that could influence reproduction. To investigate whether delays in foraging skill acquisition might contribute to delays in a cooperatively breeding mammal's reproductive life-history, we analysed age-related changes in the foraging behaviour of meerkats, *Suricata suricatta,* in the Kalahari Desert. Kalahari meerkats are primarily insectivorous, although they also predate some small vertebrates and forage most of their prey by digging them up from below ground. We found that age-related increases in the rate of prey capture and in the size of the prey consumed level off at 9 months old, although improvements in foraging efficiency continue until individuals are around 1 year of age. Sex and dominance status had little effect on foraging performance. Our results indicate that meerkats' foraging skills mature around the onset of adulthood, well before dominance is usually acquired, the point at which successful breeding commonly begins. As a result, the acquisition of foraging skills is unlikely to delay the onset of successful breeding in meerkats. Instead, the maturation of foraging performance is more closely aligned with the age at which individuals' growth begins to asymptote, suggesting their foraging ontogeny may be constrained by physical traits.

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The delayed onset of breeding is characteristic of singular cooperative breeders, where a single dominant breeding pair monopolize the reproduction of their groups, while resident subordinates seldom breed, even after reaching adulthood (Koenig & Dickinson, 2016). Delayed breeding in cooperative breeders is commonly attributed to a combination of factors including a lack of access to unrelated breeding partners and reproductive suppression by the dominant breeder, as well as philopatric benefits or environmental constraints that delay the dispersal of subordinates to form new breeding units (Cooney & Bennett, 2000; Hackländer et al., 2003; Hatchwell, 2009; Jennions & Macdonald, 1994). It has also been suggested that delayed breeding could result from the time needed to develop the skills necessary for successful reproduction, referred to as the 'skills hypothesis' (Brown, 1987; Cockburn, 1998; Selander, 1964). However, studies investigating whether philopatric helpers acquire parental skills for future reproduction by providing alloparental care have provided little evidence supporting this hypothesis (Chesterton et al., 2024; Khan & Walters, 1997; Koenig & Walters, 2011). Rather than being constrained by parental skills, the onset of breeding may instead be constrained by the slow development of foraging skills, which are essential for meeting the energetic demands of reproduction (Brown, 1987; Cockburn, 1998). This idea is supported by a study of the cooperatively breeding white-winged choughs,

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Corcorax melanorhamphos, where the long period required to develop proficiency in complex foraging behaviours is thought to increase care requirements, extend nutritional dependence and delay both dispersal and reproduction (Heinsohn, 1991; Heinsohn et al., 1988).

Foraging is a key component of animal lives, providing the energy essential for both survival and reproduction (Boggs, 1992). It is also an important energy source for growth, and variation in foraging performance influences individual growth trajectories (Morey & Reznick, 2001) with downstream effects on adult size (Soulsbury et al., 2008), which can affect both competitiveness and fecundity (Haley et al., 1994; Hodge et al., 2008; Rusu & Krackow, 2004). Despite the importance of foraging for these processes (Jeanniard-du-Dot et al., 2017), individuals are rarely born with fully developed foraging skills and must instead learn the cognitive and motor skills required for proficient foraging (Herrel & Gibb, 2006). The complexity of a species' foraging niche can strongly influence the duration of foraging development because of the increased time it takes to develop the morphological and experiential traits required to successfully exploit more complex niches (Marchetti & Price, 1989; Schuppli et al., 2012). Examples of these traits include the physical strength needed by carnivores that engage in high-risk prey hunting (Purwandana et al., 2016) or the cognitive abilities required by species whose foraging involves tool use (Patterson et al., 2016). Factors such as social structure and postweaning provisioning are also associated with variation in the length of skill development (Schuppli et al., 2012). As a result, the rate of foraging skill acquisition varies widely across taxa, with consequences for the timing of key life-history events (Bekoff et al., 1984).

Since the energetic demands of reproduction are usually large, it might be expected that adult-level foraging performance is acquired before the onset of reproduction. This is the case in many mammals, where adult-level foraging is commonly acquired prior to the onset of breeding (Carvajal & Schuppli, 2022; Schuppli et al., 2012) and, in birds too, the maturation of foraging abilities and the timing of first reproduction are often closely correlated (Marchetti & Price, 1989; Schuppli et al., 2012). However, the rate at which different mammal species acquire foraging competence varies. While many reach adult-level foraging ability around weaning (Lonsdorf et al., 2021; Schuppli, Forss, et al., 2016; Stone, 2006), others take longer to develop their foraging skills (Holekamp et al., 1997; Koster et al., 2020). Longer periods of foraging skill development have been associated with delays in life-history events, with these longer foraging ontogenies often associated with more complex niches. For example, in orangutans, *Pongo* spp., contrasts between species found the acquisition of adult-level feeding rates took longer in a more complex foraging niche, which was associated with a delayed age of weaning (Schuppli, Forss, et al., 2016). In other species, the period of foraging development is long enough to impose energetic constraints that can delay the timing of reproductive processes. In Javan slow loris, *Nycticebus javanicus*, for example, feeding rates for difficult to access nectar continue to develop into adulthood and are associated with dispersal being delayed beyond sexual maturity (Maynard et al., 2021). Similarly, in some capuchin monkeys, *Cebus* spp., extended periods of time are required to learn how to exploit difficult-to acquire food items (Gunst et al., 2010), which is suggested to explain their long juvenile periods and delayed reproductive onset (Eadie, 2015).

To date, studies of extended foraging ontogenies and their consequences in mammals have focused on species that occupy the most complex foraging niches, such as primates (Koster et al., 2020; Schuppli, Graber, et al., 2016), and carnivores that feed on prey larger than themselves (Holekamp et al., 1997; MacNulty et al., 2009), which have some of the longest observed foraging ontogenies. However, among the cooperatively breeding mongooses, there is also some indication that longer foraging ontogenies may be present, such as the presence of extractive foraging, which is commonly regarded as a complex form of foraging. For instance, banded mongooses, *Mungus mongo*, extract encased insects by throwing them against anvils (McAuliffe & Thornton, 2012; Müller, 2010). Meanwhile, in meerkats, *Suricata suricatta*, it is reported that individuals' foraging efficiency continues to improve past the age of nutritional independence (Thornton, 2008a), yet the potential consequences of this for their reproductive life-history have received comparatively little attention.

Here, we investigate the foraging ontogeny of meerkats, a cooperatively breeding mammal, and explore how it relates to their growth and the timing of their reproductive life-history, using a 4-year longitudinal dataset collected between 1996 and 2001. Meerkats live in closely related groups that in our population can reach sizes of up to 50 individuals but average 14 individuals, and consist of a dominant pair and subordinate helpers (Clutton-Brock & Manser, 2016). Subordinate helpers express a range of cooperative behaviours, some of which are altruistic, such as babysitting and the provisioning of pups (Clutton-Brock et al., 2000, 2001), while others, including vigilance and territory defence, provide direct immediate benefits to all group members (Dyble et al., 2019; Rauber & Manser, 2017). Though subordinate females try to breed, they are reproductively supressed by the dominant female, who monopolizes reproduction and produces over 80% of their group's pups (Clutton-Brock et al., 2010; Griffin et al., 2003). Only a small proportion of meerkats acquire a dominant position during their lifetime, and both sexes can acquire behavioural dominance in either their natal group or following dispersal (Hodge et al., 2008; Spence-Jones et al., 2021). While females can hold reproductively viable dominance positions in their natal group or a dispersed group (Duncan et al., 2018; Hodge et al., 2008), males can only acquire dominant breeding positions after dispersing (Spong et al., 2008) because of inbreeding avoidance and the rarity of female immigration. Dispersal is commonly delayed until after adulthood, which is reached around 1 year of age, and as a result, the acquisition of breeding status and the onset of successful reproduction in meerkats often occurs 1–2 years after reaching physiological reproductive maturity.

Kalahari meerkats are generalist foragers, primarily consuming invertebrates, but their diet also includes small vertebrates and some vegetation (Doolan & Macdonald, 1996). While some prey is caught on or just below the surface, most is located relatively deep below the surface and requires focused digging involving both forelimbs to shift sand and capture prey. Digging bouts can last several minutes, and can involve moving amounts of sand exceeding their body mass (Barnard, 2000). After birth, meerkat pups are kept below ground, relying on lactation for nutrition (Scantlebury et al., 2002). At around 30 days of age, pups emerge from their birth burrow and begin foraging with the group, at which point they start to be weaned and all group members start to provision them with food until they reach nutritional independence around 90 days old (Clutton-Brock et al., 2001). During the provisioning period, the pups' own foraging behaviour undergoes substantial development (Thornton, 2008a), facilitated by both social learning and teaching (Thornton, 2008b; Thornton & Clutton-Brock, 2011; Thornton & McAuliffe, 2006), but they do not achieve adult-level foraging proficiency by the time they reach nutritional independence. Their foraging skills continue to improve between nutritional independence and adulthood (Barnard, 2000; Thornton, 2008a), but it is unclear exactly when their foraging proficiency matures or how this relates to the timing of meerkats' reproductive life-histories.

In this study, we aimed to investigate the foraging ontogeny of meerkats with four objectives. (1) First, we characterized the age-related changes in foraging behaviour to determine the age at which meerkats' foraging skills mature. (2) With age accounted for, we assessed whether the foraging performance of dominant individuals was greater than that of subordinates. (3) We also tested for the presence of sex-differences in foraging behaviour, expecting them to be absent because of the lack of pronounced sexual dimorphism in meerkats. (4) Finally, we assessed the relative timing of the acquisition of breeding status and individuals' growth in our population in relation to the characterized ontogeny of meerkats foraging behaviour to gauge potential associations.

METHODS

Study System

This study was based on focal watches of foraging meerkats of known age at the Kalahari Meerkat Project (KMP) in the Southern Kalahari between December 1996 and December 2000. This population has been followed continuously since 1993 over an area approximately 50–60 km^2 on the Kuruman River Reserve and neighbouring farms in the Northern Cape, South Africa (26°58'S, 21°49'E). Most individuals in the study population were identified by unique dye marks and habituated to the presence of researchers, allowing observation to within a few metres. Across the course of the project groups were visited 3–4 days a week and followed for 3–4 h in the morning, after leaving the burrow to forage, and for 1–2 h in the evening before returning to the burrow. During these visits, data were collected on group composition, dominance interactions, individual reproductive status, body mass and several forms of behavioural data.

Focal Data Collection

Focal follows were conducted continuously throughout the 4-year study period, with an average of 67 h of focal observations collected per month (Fig. S1). Therefore, the coverage of the focal data encompassed entire years, capturing both summer and winter, as well as periods of reproduction and pup rearing, including pup provisioning. Focal data were collected from 12 distinct groups during the study period (Fig. S1), with groups being visited approximately two mornings a week for focals while they were being followed. In selecting the order of individual focal follows, observers ensured that no individual was followed more than twice per session and not consecutively without a break between follows to ensure even data spread across the population. Beyond this, the order that individuals were followed was chosen at random. Each focal watch aimed to collect 20 min of behavioural observation and were focused on behaviours involved in searching for and acquiring food while individuals were in a foraging context (see Table 1 for details of foraging behaviours and Table S1 for the full ethogram). If individuals switched to performing nonforaging-related behaviours for more than 2 min (such as burrow excavation or sentinel behaviour), the focal was paused until they resumed foraging. All focal follows were conducted by trained field researchers using PSION mark2 personal organizers programmed with a bespoke data collection software coded in ODB.

Quantification of foraging metrics

During a focal, digging in the pursuit of food was recorded once an individual had started digging in the same location for at least 2 s. Each digging bout was considered to be complete either when digging animals successfully caught prey and begun chewing, when they stopped digging without catching prey, or when they changed digging site (hind legs have moved more than 20 cm). All handling time prior to the food entering the mouth counted towards the digging bout duration (e.g. rolling millipedes or beetles in the sand). Some digging bouts were interrupted by another behaviour (e.g. predator alarms), which were recorded before digging was resumed at the same site. For these analyses, we considered these disrupted digs as a single bout and combined the digging durations (excluding the interrupting behaviour). To differentiate between prey caught on or just below the surface and prey that was caught as the result of concerted digging effort, we distinguished between digging bouts that lasted more than 5 s, which we refer to from now on as dig bouts, with all other prey caught referred to as surface prey from now on. When a prey item was found, the size, identity and number of prey items found was recorded (Table 2, Table S2). Prey found on the surface was recorded in the same fashion. Most prey capture events resulted in the acquisition of a single prey item (88.4%). However, when meerkats forage on ants/termites, this usually involves foraging just below the surface at a nest and can result in over 100 tiny prey items being foraged in a single bout. To avoid biasing our data towards this prey type, our analyses of prey capture quantified the number of successful pursuits, not individual items acquired.

To investigate the ontogeny of foraging behaviour, we quantified various indices of foraging performance using the focal data. First, to calculate the amount of prey caught, we calculated the 'prey capture rate' for each focal watch—the number of prey capture events as a function of the total duration of observation. To quantify the efficiency of prey capture from digs, we calculated the number of successful digs of >5 s where prey was caught as a function of the total time spent digging, which we refer to as 'digging efficiency'. To further break this down and assess the contributions of effort and skill to efficiency, we also quantified the proportion of successful pursuits near/on the surface versus those from digs ('surface prey'), the proportion of the focal watch spent on digs ('digging effort') and the proportion of digs that resulted in prey capture ('digging success'). To investigate how individual commitment to single dig bouts varied, we also analysed dig duration at the bout level ('dig bout duration').

To explore dietary variation, we also quantified the proportion of the diet that consisted of larger-sized prey (prey that did not fit

Table 1
Ethogram of foraging related behaviours recorded in focal follows

Code	Behaviour	Description
FO	Digging for food	Digging below surface layer for food in single location (that is, greater than 20 cm distance from last dig) for more than 2 s
RF	Redigging for food	Resuming digging for food in the same location as prior to an interrupting behaviour
TF	Termite feeding	Picking up termites from the surface. Not used for ant or ant larvae foraging just below the surface.
NO	Other activity	Any behaviour not assigned in the ethogram. This includes moving between feeding sites, visual scanning and scratching for prey within the top surface layer

An ethogram detailing all behaviours recorded can be found in the supplementary material (Table S1).

Table 2
Definitions of aggregated prey categories

Prey category	Percentage of prey	Prey items
Ants and termites	5.41	Ants, termites, ant larvae, ant pupae
Beetles	14.80	Adult-stage Coleoptera
Caterpillars	0.78	Larval-stage Lepidoptera
Eggs	0.03	All eggs from vertebrate species
Larvae	23.25	Insect larvae, from all clades where not otherwise identifiable as Lepidoptera or ant larvae
Millipedes	0.41	All identifiable millipede species
Other invertebrates	1.80	All other invertebrate species
Plants	0.26	Bulbs, berries and other vegetation
Pupae	3.85	Insect pupae from all clades where not identified as ant pupae
Scorpions	1.81	All scorpion species
Unidentified	46.39	Any prey items not identified during observation
Vertebrates	1.21	All vertebrate species including various amphibian, reptile and mammalian species

Prey categories used in analysis based upon all recorded observations ($N = 90\,179$), with their prevalence in our sample reported.

wholly in a meerkats mouth; Table S2), as well as the composition of prey caught (Table 2). Of the 90 179 observed prey captures, 53.6% of the prey were identified and categorized into broad taxonomic categories (Table 2), with the remainder labelled as unidentified prey. Being generalists, meerkats feed on a range of prey, but some are rarely foraged and are consequently difficult to analyse reliably. We therefore restricted analyses of the composition of prey caught to prey types that constituted greater than 1% of the populations observed prey caught (Table 2).

Calculating life-history events

To contextualize the foraging ontogeny of meerkats within their physical development and reproductive life-history, we used data from across the history of the project (1997–2024) to investigate the time at which various developmental and life-history milestones occurred. To characterize the overall growth trajectory of meerkats and the development of morphology likely to be important for foraging, we modelled age-related changes in body mass, a proxy for the development of size and strength, in addition to front claw length, an important morphological trait for the pursuit and processing of prey. Body mass was measured at the beginning of morning visits prior to foraging, using electronic scales to the nearest gram. Front paw measurements were taken from the left paw while ventrally flexed. The distance from the dorsal side of the flexed wrist to both the base and the tip of claw was measured, and front claw length was calculated as the difference of these two measures. These morphometric measurements were taken using callipers on routine captures from 2010 onwards as part of longitudinal lifetime sampling of individuals that occurred approximately every 3–6 months involving anaesthesia via isoflurane (for detailed capture protocol, see Dantzer et al., 2017).

For reproductive life-history, we identified their age of sexual maturity and the age at which they started to consistently reproduce successfully. We estimated the age of sexual maturity as the age at which individuals first displayed evidence of sexual activity. In males this was the age at which they were first seen roving at another group—a behaviour associated with trying to achieve mating opportunities outside the group. For females, we used the age at which they were first seen to be visibly pregnant (pregnancies were visibly identifiable approximately 30-days post-conception). As successful reproduction was largely limited to dominant breeders, we calculated the onset of consistent successful reproduction as the mean age at which individuals acquired their first dominant position. As males cannot successfully reproduce in their natal group because of inbreeding avoidance, we only considered males that had dispersed and acquired dominance outside of their natal group for these calculations.

Statistical Analysis

To assure the quality and representativeness of the focal follows, we limited our sample of focals to those with between 15 and 25 min of behavioural observation. As our study was focused on the ontogeny of foraging after nutritional independence, we constrained our sample set to individuals older than 3 months who were born in our population and therefore were of known age. Given the sparseness of data at older ages and to reduce the impact of any senescent effects, we also limited our sample to individuals younger than 5 years, the age at which senescence in body mass and reproduction commence (Thorley et al., 2020). This resulted in a sample set of 9919 focals from 324 individuals (160 males and 164 females), collected across the 4 years of focal observation for 12 groups (Fig. S1). In total, 26 of these individuals were dominant at some point during the study period, with the remaining 298 individuals being subordinates throughout. Individuals were on average followed across nine distinct months (range 1–40 months), covering an average total time span (from an individual's first focal follow to their last) of 11 months (range 0–46 months).

The different components of foraging behaviour were analysed using generalized additive mixed models (GAMMs). The 'prey capture rate' was modelled using a negative binomial distribution with the number of prey capture events fitted as the response variable and the observation duration fitted as an offset to control for sampling effort. 'Digging efficiency' was also modelled using a negative binomial distribution with number of successful dig bouts as the response term, and the overall time spent committed to dig bouts included as an offset, making the number of successful bouts a function of individual digging effort. 'Digging effort', 'digging success', 'proportion of surface prey' and the size of prey items were fitted as proportions in models with a Tweedie error distribution, capturing the zero-bound and right skewed nature of these data. To model the 'dig bout duration', digs were analysed at the bout level. For purposes of computational efficiency, given the size of the bout-level dataset, $N = 205\,376$ bouts, these data were Box–Cox ($\lambda = -0.424$) transformed and modelled with a Gaussian error distribution. Finally, to investigate age-related changes in the types of prey caught, we modelled the proportion of each prey type caught per focal independently using GAMMs with a Tweedie distribution.

To characterize age-related changes in meerkats foraging behaviour, age was fitted as a smooth term using thin plate regression splines in our GAMMs with K set to 12 to allow for flexibility in the age response while avoiding overfitting. To check that the choice of knots adequately captured age-related patterns in our models, we extracted model residuals and fitted them in generalized additive models with age included as a smoothed

effect (Table S3). To identify periods of significant change in foraging trajectory, we extracted the first derivatives of each age smooth using the method of finite differences ('gratia' package, Simpson, 2024). Periods of significant change were considered those regions where the CIs of first derivative did not cross zero (Fig. S2). For plots of smooth effects (Figs 1, 2, S3 and S4), simultaneous CIs were calculated and plotted (Simpson, 2018).

For our models on foraging behaviour at the level of individual focal watches, we also investigated the effects of dominance status and sex, including them as fixed effects in the models. In all models, to control for environmental and seasonal variation we included the breeding year (July to June) as a random smooth and the day of the breeding year as a cubic cyclic spline ($K = 8$; Fig. S4). Additionally, to control for any variation caused by differences in the social environment, we included group size in models, testing for both linear and quadratic effects (Fig. S5). Group size was taken as the number of nutritionally independent individuals (age > 3 months) in the group on the day of the focal and was scaled by mean centring and division by 2 SDs when included in models (Gelman, 2008). For our models of diet composition, we did not include any individual or social fixed effects, as we had no a priori expectations for how these factors might affect diet. Random smooths were also included for individual and group identity in all models. For the model of the duration of individual digs a random smooth for the unique focal was also included (grouping all bouts from a single focal). Full model outputs for all GAMMs are presented in the supplementary materials (Table S4–S11).

Growth in meerkats can be modelled using a biphasic monomolecular curve that captures the approximately linear growth until nutritional independence (3 months old) and the decelerating growth thereafter (English et al., 2012). We used this curve to describe age-related changes in body mass. However, unlike previous treatments (English et al., 2012), we did not control for environmental factors. We restricted our analyses to individuals that survived beyond 6 months of age and who had more than 10 mass measurements across their lifespan ($N = 2274$). This decision ensured that we had enough measurements across an individual's life span to estimate asymptotic mass accurately. We also restricted measurements to those collected on nonvisibly pregnant subordinate individuals before 4 years of age to remove the influence of senescence, pregnancy related mass gains and post-dominance growth on the curve (Huchard et al., 2016; Thorley et al., 2020). Given the large number of measurements collected across lifespan (mean measurements per individual = 236), we were able to fit individual-level growth curves, allowing all growth parameters to vary between individuals by fitting random intercepts for each parameter in the nonlinear mixed effects model.

Front claw measurements were taken from individuals starting at nutritional independence, with subsequent measurements at approximately 3- to 6-month intervals. Since measurements were only started at nutritional independence, we modelled claw growth with a monophasic monomolecular curve. Given the resolution of sampling (individuals = 1220, mean measurements per individual = 3), we fitted a population-level curve and did not consider any individual-level random effects. To assess the ability of the monomolecular curve to accurately model front claw length, we visually compared the estimated growth curve to estimates from a linear mixed effects model, in which age was divided into 3-month windows and fitted as a categorical variable with individual ID as a random intercept.

All statistical tests were performed in the R statistical environment, version 4.2.3 (R Core Team, 2023). Generalized additive mixed models were fitted with the 'mgcv' package (Wood et al., 2016), and model diagnostics and visualizations were facilitated using the packages 'mgcViz' (Fasiolo et al., 2020), 'gratia' (Simpson, 2024) and 'DHARMa' (Hartig, 2024). Linear regressions were fitted using the package 'glmmTMB' (Brooks et al., 2017), and growth models were fitted using the 'nlme' package (Pinheiro, Bates & R Core Team, 2024).

Ethical Note

To minimize the impacts of our research on the study animals, efforts were made to habituate all individuals to our presence, and behavioural data collection was conducted at a distance whereby our presence did not disturb and affect the behaviour of our focal individual. To reduce direct contact, for the collection of weights, individuals were coaxed onto scales using egg crumbs. For identification marks, dye was applied using long paint brushes to maintain distance from the animal. Additionally, to limit any effects of repeated captures, the project aimed to limit the maximum number of captures per year to four with a gap of 3 months, except in extenuating circumstances. In general, individuals were rarely caught more than three times a year. The long-term data used in this study were collected under permits granted by the ethics committee of the University of Pretoria, South Africa (EC047-16, EC010-13 and SOP029-12) and adhered to the standards outlined in the ASAB/ABS guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB Ethical Committee & ABS Animal Care Committee, 2012).

RESULTS

Development of Foraging Behaviour

All components of foraging showed age-related changes beyond nutritional independence (3 months, representing the age at which pups were no longer regularly fed by other group members). The number of successful prey pursuits per focal ('prey capture rate': estimated degrees of freedom (edf) = 6.775, F = 6.253, $P < 0.001$; Fig. 1a) and the proportion of large-sized prey (edf = 6.291, $F = 7.248$, $P < 0.001$; Fig. 1b) increased significantly until around 9 months of age. After this point, the effect of age on these foraging metrics plateaued and no further substantial periods of age-related change were detected (Fig. S2). The proportion of prey found near the surface, rather than from dig bouts, also increased with age ('surface prey': edf = 3.512, $F = 7.634$, $P < 0.001$; Fig. 1c), and the rate of increase began to decline after 1 year and age-related changes were no longer significant after 15 months (Fig. 1c).

The efficiency with which individuals acquired prey from digs also improved, so that the rate of prey capture for a given amount of digging increased with age, before plateauing at around 12 months ('digging efficiency': edf = 5.687, F = 12.224, $P < 0.001$; Fig. 1d). Except for a brief period of further improvement in efficiency after 24 months of age, there was little age-related change in foraging efficiency after 12 months (Figs 1d and S2). Improvements in 'digging efficiency' occurred partly because the proportion of digging bouts that were successful increased from independence until around 14 months, where it also plateaued ('digging success': edf = 4.682, F = 10.178, $P < 0.001$; Fig. 1e), with no significant changes detected thereafter, and partly due to the duration of single digs decreasing across the first year of life before levelling off ('dig bout duration': edf = 5.402, F = 18.88, $P < 0.001$; Fig. S6). This trend was observed in digs that failed to acquire prey, as well as in successful digs for small and large prey (Fig. S7). The total proportion of the focal invested in dig bouts declined with age until around 14 months before plateauing ('digging effort': edf = 6.881, F = 13.419, $P < 0.001$; Fig. 1f). However, there was a

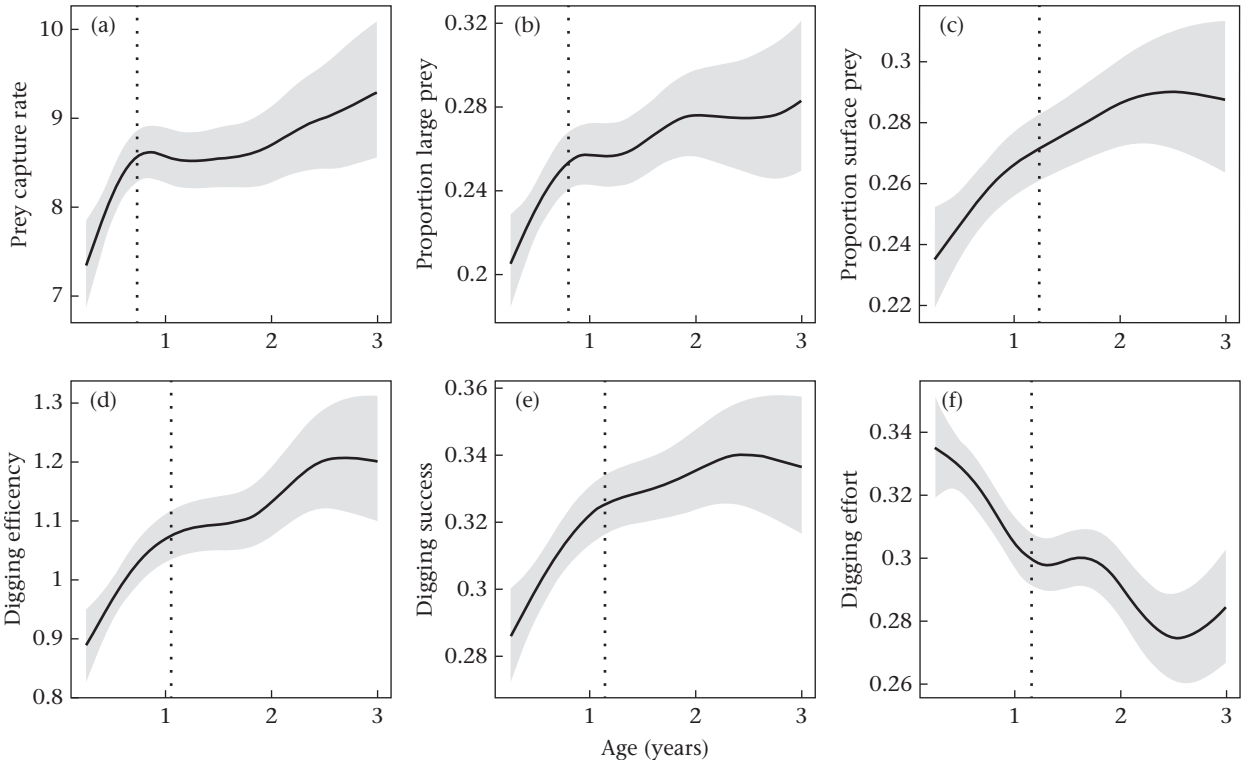

Figure 1. The population-level effect of age on the number of successful captures per focal (a), the proportion of large prey caught (b), the proportion of prey found on the surface (c), the number of successful digs per min of digging (d), the proportion of successful digs per focal (e) and the proportion of the focal spent on digs (f). Mean estimates plotted (solid lines) with 95 % simultaneous CIs (shaded ribbon). Estimates are from generalized additive mixed models (GAMMs) with random smooths and other smoothed effects zeroed, and covariates held at their mean or reference level. Plots restricted to the first 3 years of lifespan to focus on early life changes (see Fig. S3 for full range), and the age at which the smooth first transitioned from a significant period of change to not significant was highlighted (dotted line, Fig. S2).

subsequent period of significant change in foraging between the ages of 2−3 years, where the time invested in long digs decreased again, before subsequently increasing towards its original level (Figs 1f and S2).

The composition of prey caught by meerkats also changed as they aged. Larvae, which constituted the largest identifiable component, comprised an increasingly larger proportion of prey caught (edf = 4.845, F = 3.243, $P = 0.003$; Fig. 2a), while beetles, representing the second largest component, decreased with age (edf = 4.915, F = 8.998, $P < 0.001$; Fig. 2a). There were also changes in the rarer prey items, with the proportion of vertebrates approximately doubling over the first year of life (edf = 5.528, F = 10.394, $P < 0.001$; Fig. 2b), and the proportion of scorpions also increasing with age (edf = 3.182, F = 4.210, $P = 0.002$; Fig. 2b). We did not detect significant age-related patterns in the other prey types (Table S11).

The Influence of Dominance and Sex on Foraging Behaviour

Dominance status had little to no effect on foraging behaviour once age was controlled for. Specifically, there was no clear status difference in 'digging efficiency', 'prey capture rate', or the size of captured prey (Table 3). Similarly, there was no significant effect of dominance status on 'digging effort', 'digging success' (Table 3) or 'surface prey'.

We also found no sex differences in foraging behaviour. The effect size of sex in models of 'digging success', 'digging effort', 'digging efficiency' and 'prey capture rates' was small, and in all cases not statistically significant (Table 3). Similarly, the proportion of surface prey did not differ between the sexes, nor did the proportion of prey caught consisting of larger prey items (Table 3).

Timing of Growth and Reproductive Milestones

The mean age at which female meerkats first showed visible signs of pregnancy was 1.5 years, and males were also first seen visiting other groups in search of breeding opportunities (roving) at 1.5 years (Fig. 3a). The acquisition of dominance and the onset of successful breeding occur later: the mean age of dominance acquisition was 2.3 years for females and 2.9 years for males (Fig. 3b). However, there was considerable variation between individuals in the ages at which these events occurred: 10% of individuals in our population displayed evidence of reproductive activity before adulthood (Figs 3a), and 10% of dominants had acquired their positions by 1.2 years and 1.6 years of age in females and males, respectively (Fig 3b). Body mass growth began to level off after adulthood, and 95% of growth was completed by 17 months (Fig. 3c). The growth of front claws stopped earlier, and by 12 months, front claws had reached their asymptote (Fig 3d).

Our estimates of the completion of growth were broadly aligned with the age at which meerkats acquired adult-level foraging proficiency (Figs 1 and 3). Front claw growth stopped at around the time at which digging efficiency first plateaued (Figs 1d and 3d), and the decline in digging effort levelled off as body mass began to level off (Figs 1f and 3c). Additionally, individuals appeared to reach adult-level foraging performance by the onset of mean sexual maturity, with the earliest occurrences of reproductive activity observed around the time that foraging performance plateaued (Figs 1 and 3a). Some individuals acquired dominance not long after their foraging development was completed, but it is unlikely that these processes are directly linked, since the average dominant had been foraging at adult levels for 1 or 2 years before acquiring their status (Figs 1 and 3b).

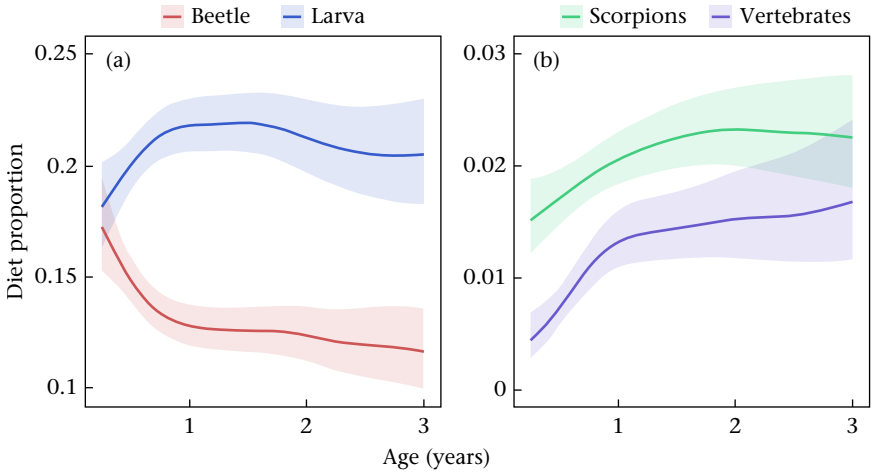

Figure 2. The significant population-level effects of age on the composition of meerkat's diet. Prey categories split across plots according to the proportion of the diet they constitute, from largest (a) to smallest (b). Plots restricted to the first 3 years of lifespan to focus on early life changes. Mean estimates plotted (solid lines) with 95 % simultaneous CIs (shaded ribbon). Estimates are from generalized additive mixed models (GAMMs) with all other smooth effects zeroed.

DISCUSSION

In this study, we aimed to characterize the foraging ontogeny of meerkats and investigate how this is associated with the timing of their reproductive life-history and growth. Our results show that foraging skills in meerkats increase rapidly throughout the first year of their life, after which few age-related changes in foraging performance were observed, at least until 5 years of age, when our analyses stopped. The 'prey capture rate' and the proportion of larger-sized prey caught increased from nutritional independence at 3 months and reached adult levels at 9 months of age. Most other aspects of foraging behaviour matured around 12 months. The 'dig bout duration' continued to decline with increasing age, as did the cumulative amount of time committed to digs ('digging effort'), while the probability of prey being successfully caught from digs increased ('digging success') and consequently the overall efficiency of prey capture from digs increased with age ('digging efficiency'). Moreover, up until 15 months of age meerkats gained a greater portion of their prey from on or near the surface ('surface prey') without needing to commit to long and energetically costly digs.

The composition of prey caught by meerkats also changed with age over the first year of life. The proportion of larvae (the commonest identifiable component in meerkats prey) increased as did the number of vertebrates and scorpions. In contrast, the prevalence of adult-stage beetles declined as their age increased. These changes in the composition of prey caught could have reflected increases in foraging skill, or morphological changes across development that allowed individuals to better pursue certain prey types more effectively as they aged. For example, prey such as adult-stage beetles may be found closer to the surface and easier to catch, whereas larvae may be present deeper below the ground and benefit from a more developed morphology to access. Additionally, scorpions are a dangerous, venomous prey and vertebrates such as lizards and burrowing skinks are fast moving, making them harder to catch and possibly handle. In addition, as they are less prevalent prey, individuals likely have less opportunity for learning, potentially resulting in a longer period of skill development for these prey types.

We also investigated whether the social status and sex of individuals affected their foraging performance. After age-related changes in foraging performance were controlled, we found little evidence of any difference in the foraging performance between subordinate and dominant meerkats. Similarly, there was no evidence of any sex differences in foraging, which is consistent with the absence of pronounced body-mass dimorphism between the sexes in meerkats (Huchard et al., 2014).

To date, there has been limited support for delayed breeding in cooperative breeders resulting from the time required to learn the skills necessary for reproduction as suggested by the skills hypothesis (Chesterton et al., 2024; Cockburn, 1998; Koenig & Walters, 2011). Similarly, we find no evidence that foraging skill development influences the timing of breeding in meerkats. Instead, our results showed that foraging ability matures before dominance is commonly acquired in meerkats. Nor were there any clear differences in foraging success between subordinates and dominants. This suggests that neither the delayed onset of breeding nor the failure of subordinates to breed regularly in meerkats is a result of constraints imposed by the development of foraging skills. Instead, the absence of regular reproduction by subordinates appears to be a function of other processes, including the absence of unrelated breeding males in their group, the eviction of older subordinate females by the dominant female and high rates of infanticide of their pups by pregnant group members

Table 3
Fixed effect estimates from generalized additive mixed models of different indices of foraging

Parametric term	Prey capture rate	Prey size	Surface proportion	Digging efficiency	Digging success	Digging effort
Dominance status	0.054 (0.032)	−0.058 (0.048)	0.008 (0.044)	0.047 (0.038)	−0.024 (0.027)	−0.012 (0.024)
Sex	0.026 (0.017)	0.011 (0.023)	−0.025 (0.021)	0.023 (0.021)	0.010(0.015)	0.014 (0.013)
Group size	0.010 (0.022)	**0.108 (0.033)**	**0.092 (0.032)**	**−0.086 (0.026)**	**−0.089 (0.020)**	**0.053 (0.016)**
Group size^2	**0.152 (0.24)**	–	–	**0.130 (0.028)**	**0.102 (0.021)**	–

The reference level for the categorical fixed effects sex and dominance status were 'female' and 'dominant', respectively. Parametric effect for scaled group size presented, with scaling performed via mean centring and division by 2 SDs. Estimates and SEs are presented, and fixed effects with P values < 0.05 are highlighted in bold. Full model output tables with smooth effects, including the smoothed effects of age, can be found in the Supplementary Material.

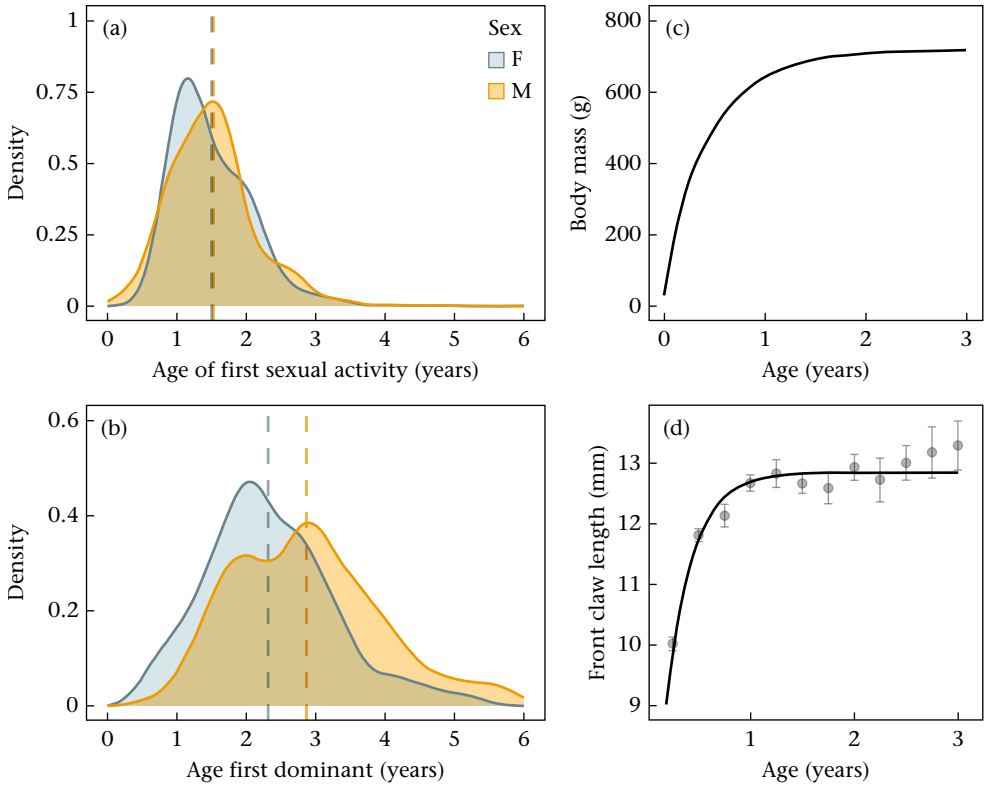

Figure 3. Plots of the age at which meerkats reach different reproductive and growth milestones. The distributions of the age of first evidence of sexual activity (a), and the age at first dominance (b) for males (orange) and females (blue), with sex-specific means shown by the dashed line. The estimated growth curve for body mass (c) and front claw length (d) are shown by the black line, for model parameter estimates see Table S12. For the plot of front claw length, the mean estimates from a linear mixed effects model in which age was binned into 3-month intervals is also plotted, along with the 95 % CIs (grey dots with error bars).

(Clutton-Brock et al., 2010; Griffin et al., 2003; Young et al., 2006). Similar mechanisms appear to constrain subordinate reproduction in many other singular cooperative breeders (Cooney & Bennett, 2000; Creel et al., 1992; Hackländer et al., 2003; Jennions & Macdonald, 1994; Nelson-Flower et al., 2018).

In showing that meerkats' foraging performance matures around adulthood, our results deviate from the general pattern seen in mammals, where adult levels of foraging performance are usually acquired earlier, around nutritional independence (Schuppli et al., 2012). We suspect that the longer development of foraging performance in meerkats is partly attributed to most prey being dug up from below the surface, which can involve shifting substantial amounts of sand (Barnard, 2000), and is therefore likely to be constrained by individuals' body size and strength. This is supported by our results showing that the maturation of foraging performance coincides with the asymptotes of body mass and front claw growth because where species foraging ability are determined by morphological traits the development of their foraging performance often tracks their growth (MacNulty et al., 2009; Purwandana et al., 2016). Meerkats must also locate and identify prey hidden below the surface using mechanisms such as olfaction to discriminate between food types (Leclaire, 2017; Sörensen et al., 2019), so their foraging ability may also be linked to the development of this sense. Similar patterns are seen in primates that predate invertebrates embedded in woody substrates, where it is also thought that the morphological and cognitive constraints on their ability to locate and extract hidden prey are responsible for observations of slower foraging skill development (Gunst et al., 2010), and of greater prevalence in the diets of adults (Mallott et al., 2017). In contrast, where such constraints on the catching of invertebrate prey are not apparent (e.g. foraging invertebrates from among foliage), there is evidence that foraging skills develop more rapidly (Stone, 2006).

In conclusion, our results show that the delayed onset of reproduction in meerkats is not associated with the nature of their foraging ontogeny. Instead, the development of foraging proficiency in meerkats aligns with their growth trajectories and sexual maturation, which may reflect their ancestral onset of breeding prior to the evolution of cooperative breeding. Therefore, characterising the foraging ontogenies of other closely related solitary mongoose species would shed further light into the meerkat's ancestral foraging condition and its interplay with their reproductive life history. Our results also suggest that insectivory of below surface prey may be physically constrained, which could result in longer foraging ontogenies; especially for smaller species and species whose prey are found deeper below the surface where the physical constraints might be more pronounced. Further studies on terrestrial foragers of fossorial prey would be interesting not only to confirm this effect, but also to test whether it transfers to other dietary niches.

Author Contributions

Chris Duncan: Writing – original draft, Formal analysis, Conceptualization, Visualization, Data curation. **Zoe Turner:** Data curation, Writing – original draft, Formal analysis, Conceptualization. **David Gaynor:** Writing – review & editing, Software, Methodology. **Jack Thorley:** Methodology, Writing – review & editing. **Tim Vink:** Writing – review & editing, Data curation. **Tim Clutton-Brock:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

Data Availability

Data and the code to run analyses and produce figures are available through Mendeley Data at https://doi.org/10.17632/zgdc9bxjm4.2.

Declaration of Interest

The authors declare no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123302.

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