

Intergenerational effects of maternal androgens on vocal ontogeny and developmental plasticity in a cooperatively breeding mammal

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ABSTRACT

Developmental plasticity, the ability to adapt one's phenotype to environmental cues, is crucial during early-life stages and can affect fitness. Despite significant androgenic variation between females of select species, the impact of maternal hormones on offspring ontogeny in wild mammals has been rarely investigated. Here, we rely on natural and experimentally induced variation in androgen action between dominant and subordinate female meerkats, *Suricata suricatta*, to examine plasticity of vocal development in their offspring. Meerkats are cooperatively breeding mongooses that have a rich vocal repertoire. We recorded calls produced at distinct developmental stages by offspring from dominant and subordinate control mothers that naturally differ in absolute androgen concentrations and from dominant treated mothers that had received an androgen-receptor blocker in late gestation. Using call types as indicators, we found that the offspring of dominant control mothers had a robust vocal trajectory, even under adverse environmental conditions; following full nutritional dependence, their vocal development was accelerated relative to that of other offspring. Conversely, offspring from both subordinate control and dominant antiandrogen treated mothers suffered ontogenetic delays; they showed distinct sex differences in trajectory and a greater sensitivity to socio-ecological influences. Antiandrogen-exposed offspring also showed atypical early call usage. These findings provide rare evidence of the potential for maternal androgens to mediate mammalian offspring development in accordance with demands of the socio-ecological environment.

1. Background

Developmental plasticity refers to an organism's ability to adapt its physical or physiological characteristics in response to environmental cues perceived during critical periods of growth and maturation (Taborsky, 2017). Considering the relatively brief duration of these periods, early-life adaptations can have a disproportionate impact on an individual's survival and reproductive success (Lindström, 1999). Although genetic inheritance plays a foundational role in shaping these

adaptations, the maternal phenotype significantly influences them through epigenetic, intergenerational effects (Mousseau and Fox, 1998; Weaver et al., 2004; Wolf and Wade, 2009). One major pathway for such effects is via prenatal exposure to maternal hormones, which can occur *in ovo* (Groothuis et al., 2019; von Engelhardt and Groothuis, 2011), *in utero*, or postnatally through maternal milk (Edwards et al., 2021; Power and Schulkin, 2013). In mammals, exposure to steroid hormones, including glucocorticoids and sex hormones, during sensitive stages of development can induce permanent organisational effects that shape the

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individual's morphology, behaviour, and hormonal responsiveness throughout the lifespan (Arnold, 2017; Phoenix et al., 1959; Wallen, 2009). These wide-ranging and enduring outcomes underline the maternal endocrine milieu as a powerful influence on offspring development and, ultimately, fitness.

Among these key hormones, androgens (of testicular, fraternal or maternal origin) play a crucial role in mammalian sexual differentiation (Arnold, 2020; Arnold, 2017; Jost, 1970), influencing genital development and physical attributes, as well as sex differences in the brain and the central nervous system (Arnold, 2020; Forger et al., 2016; Knudsen, 2004). Androgens thus affect cognitive and behavioural traits (Dloniak et al., 2006; Goy, 1988; Herman and Wallen, 2007; Wallen and Hassett, 2009), from spatial and social cognition (Aspesi et al., 2023; Herman and Wallen, 2007) to communication (Bowers et al., 2014; Pasch et al., 2011; Tomaszycycki et al., 2005; Tomaszycycki et al., 2001)—skills that are particularly vital in early life for acquiring resources and navigating social interactions. Beyond shaping morphology and impacting offspring growth rates (Huber et al., 2017; Smith et al., 2010; Sun et al., 2012), androgens are also suspected of playing a role in the organism's susceptibility to environmental factors. Proposed mechanisms include the upregulation of neural plasticity, interactions with other endocrine systems influencing metabolism and growth (Davies et al., 2024) and their impact on the ontogeny of temperament (Del Giudice et al., 2018). Whereas androgens can contribute to canalisation (Waddington, 1942), constraining developmental trajectories and phenotypic variation (Matsushita et al., 2018; Phoenix et al., 1959), some have suggested that androgens may also increase developmental plasticity, particularly in traits like aggression (Del Giudice et al., 2018). Their pleiotropic effects may thus confer both adaptive benefits and fitness costs, as highlighted by the Immunocompetence Handicap Hypothesis (Folstad and Karter, 1992; Roberts et al., 2004), which links androgens to several detrimental effects (e.g. immunosuppression (Trigunaité et al., 2015)), as evidenced in meerkats (*Suricata suricatta*) by enhanced ectoparasite abundance (Smyth et al., 2018; Smyth-Kabay et al., 2024). These widespread effects of androgens are typically from testicular sources and examined in males; here, our focus will be on the role of maternal androgens in the vocal development of both sexes.

In altricial young, such early offspring-carer signalling is crucial for survival and resource acquisition because it plays a key role in mediating opposing fitness interests, such as parent-offspring conflict (Godfray, 1995a; Kuijper and Johnstone, 2018) or sibling competition (Godfray, 1995b; Muller and Groothuis, 2013). Previous research has established the influence of maternal androgens on early offspring vocal communication; however, the scope and nature of the findings differ substantially between taxa. In avian species, research has been mostly focused on the functional implications of maternally derived yolk androgens on early offspring-carer signalling. Notably, the influence on begging behaviour strongly suggests adaptive significance (Bebbington and Groothuis, 2021; Noguera et al., 2013), with direct implications on nestling fitness (Boncoraglio et al., 2006; Eising and Groothuis, 2003; Noguera et al., 2013; Ruuskanen and Laaksonen, 2013; von Engelhardt et al., 2006). In contrast, mammalian research on the effects of maternal androgens on vocal behaviour has been primarily focused on mechanistic questions about sexual differentiation. For instance, experimental manipulations in rhesus macaques (*Macaca mulatta*) highlight how androgen exposure interacts with offspring sex and the timing of exposure, which varies considerably in viviparous species. Administration of androgens to mothers during early, but not late, gestation masculinises female vocalisations, whereas androgen receptor ('AR') blockade feminises male vocalisations (Tomaszycycki et al., 2001). Conversely, androgen exposure during late gestation leads to masculinised agonistic vocalisations (or screams) in daughters and hyper-masculinised screams in sons (Tomaszycycki et al., 2005). In Sprague-Dawley rats (*Rattus norvegicus domestica*), that are born in a particularly altricial state, the organisational window extends postnatally; direct administration of exogenous androgens to neonates eliminates the previously observed

sex difference in calling rates by modulating expression of *Foxp1* and *Foxp2* (Bowers et al., 2014), transcription factors in brain regions involved in development, motor control and vocal communication (Fisher and Scharff, 2009). Lastly, in humans, foetal testosterone, measured via amniocentesis, correlates with vocabulary size in early development (Lutchmaya et al., 2001), consistent with the prenatal impact of androgens on communicative skills. Whereas these studies provide compelling evidence for the importance of androgens on vocalisations, they leave the functional implications of early vocal behaviour and ontogeny, particularly in the context of offspring-carer signalling, relatively underexplored.

Here, we test both the masculinising role of maternal androgens on the vocal ontogeny of wild meerkats, and its potential functional significance. The meerkat is a social, cooperatively breeding mongoose, that lives in groups of 3–49 mostly related individuals, which include a single dominant pair; all other members of both sexes and all ages are subordinate. The dominant pair typically secures most of the reproductive opportunities with the group, such that both sexes show significant reproductive skew (Clutton-Brock, 2001a). Nonetheless, subordinate females are physically capable of breeding and occasionally do so (Barrette et al., 2012; Clutton-Brock, 2001b; Drea et al., 2021). Meerkats represent a particularly interesting case for the study of epigenetic, intergenerational effects via prenatal exposure to maternal androgens (Drea and Davies, 2022). Firstly, in this matriarchal society, all adult females naturally express raised androgen concentrations or show physiological 'masculinisation' (Davies et al., 2016). Secondly, dominant females express higher androgen concentrations than do subordinate females (Clutton-Brock et al., 2006), creating the basis for a natural experiment. Exceptionally, outside of reproductive phases, the circulating testosterone concentrations of dominant females are equivalent to those of male conspecifics, even exceeding them during pregnancy (Davies et al., 2016). Thirdly, the females' status-related difference in androgen concentrations is particularly pronounced in late gestation (Davies et al., 2016; Drea et al., 2021), which represents the critical period for mammalian sexual differentiation of behaviour (Despres et al., 1984; Goy, 1988; Thornton et al., 2009). Fourthly, although the extent to which maternal hormones reach the embryo remains unclear for most species (but see (Yalcinkaya et al., 1993)), previous research in meerkats has shown that late-term maternal androgens transmit to the developing offspring and exert lasting effects on various traits (e.g., competitive aggression (Drea et al., 2021), endocrine development, growth (Davies et al., 2024), health and survivorship (Smyth-Kabay et al., 2024)) in a manner that predictably reflects natural or experimentally induced variation. Lastly, offspring care is provided by all group members, thereby minimising the potential for maternal androgenic influences to be confounded by socialisation (Drea et al., 2021). Indeed, helper contributions to food provisioning are not influenced by relatedness or maternal status (Clutton-Brock et al., 2004; Clutton-Brock et al., 2001), although dominant females contribute less than do subordinates after weaning (Clutton-Brock et al., 2004; Rotics et al., 2023). Eventually, male helpers disperse voluntarily, whereas female helpers are often forcefully evicted by the dominant female (Clutton-Brock and Manser, 2016; Young et al., 2007; Young et al., 2006). The status-dependent differences in female androgen concentrations facilitate dominance acquisition and reproductive control and, despite the associated costs of reduced health and survival in juvenile offspring (Smyth-Kabay et al., 2024), could ultimately promote fitness along dominant matriline (Clutton-Brock et al., 2006; Drea et al., 2021; Drea and Davies, 2022).

The offspring undergo distinct developmental stages (Fig. 1A), each marked by specific call types (Fig. 1B). Born altricial, pups remain underground at the natal den for the first three to four weeks of life, entirely dependent on milk and adult care (Clutton-Brock and Manser, 2016; Doolan and Macdonald, 1999). As they begin joining the foraging group, they use various types of begging calls to solicit food and compete for access to providers (Brotherton, 2001; Hodge et al., 2007; Manser

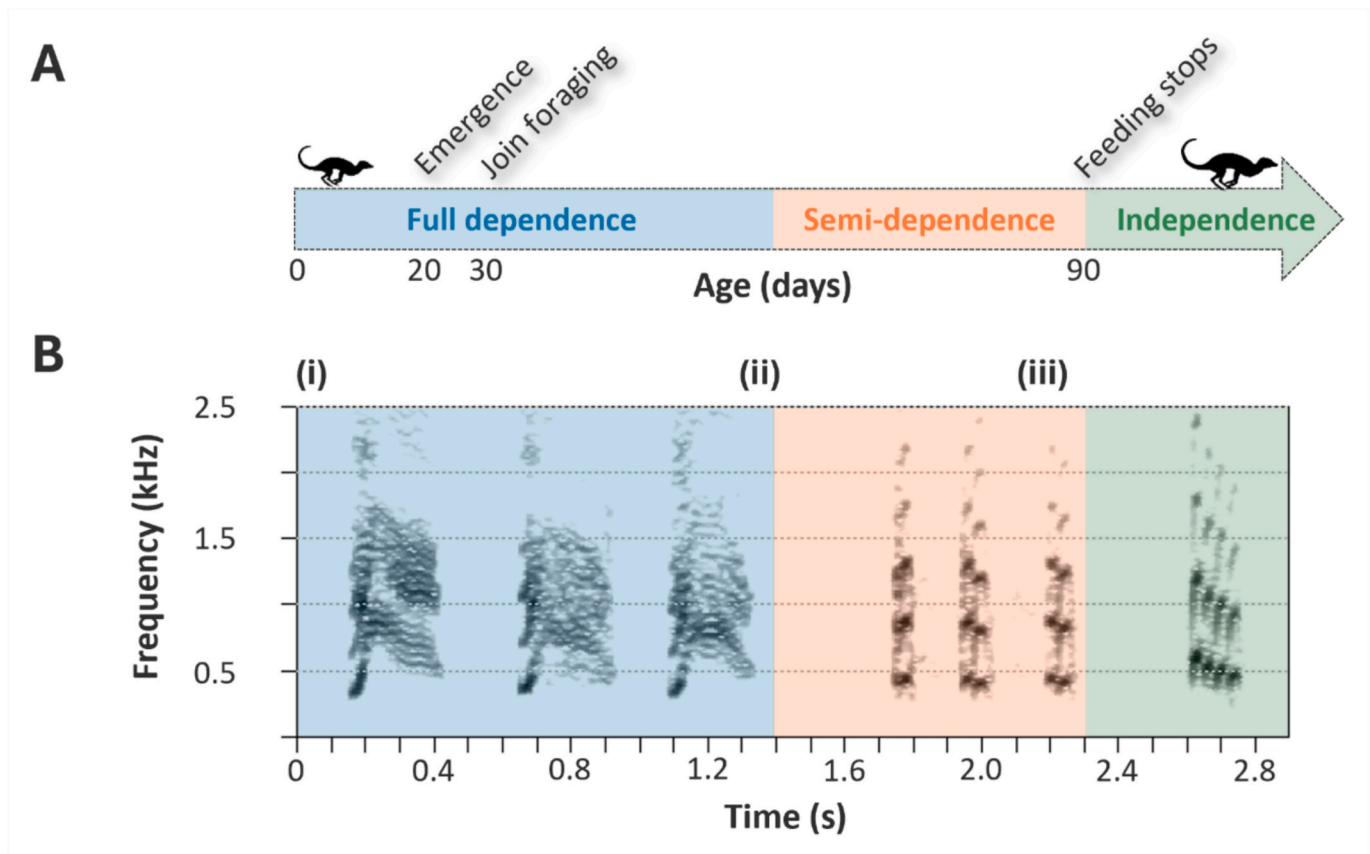


Fig. 1. Meerkat ontogeny and corresponding vocalisations. Panel A illustrates the developmental timeline from birth underground to nutritional independence, comprising three phases: full nutritional dependence (blue), semi-dependence (orange) and full independence (green). Panel B shows representative spectrograms of (i) repeat calls, (ii) digging calls, and (iii) a single close call, indicating their acoustic structure across frequency (kHz) and time (s) with background colours matching the predominant developmental phase of production.

and Avey, 2000). Initially, offspring continuously emit ‘repeat calls’ (Fig. 1Bi) to increase general provisioning (Kunc et al., 2007). When a nearby helper finds prey, pups switch from repeat to ‘high-pitched calls’ to direct food allocation (Kunc et al., 2007; Manser et al., 2008). With increasing independence, repeat calls are gradually replaced by ‘digging calls’ (Fig. 1Bii), allowing pups to practice foraging while staying close to adult helpers, who still occasionally provide food (Kunc et al., 2007; Madden et al., 2009; Thornton, 2008). Furthermore, repeat calls gradually cease to trigger a provisioning response from helpers, prompting pups to shift their strategy from begging to self-sufficient foraging (Madden et al., 2009). At full nutritional independence around the age of three months (Brotherton, 2001; Doolan and Macdonald, 1996), young meerkats transition from the pup vocal repertoire to the adult vocal repertoire (Manser and Avey, 2000), mainly producing contact calls or ‘close calls’ (Fig. 1Biii) to maintain group cohesion during foraging (Engesser and Manser, 2022).

To assess the intergenerational effects of maternal androgens on vocal development, we recorded three distinct call types (repeat, digging and close calls) in meerkat offspring born to dominant and subordinate control mothers (hereafter ‘DC’ and ‘SC’ offspring, respectively), as well as offspring of dominant treated mothers (hereafter ‘DT’ offspring). For a period of three weeks in later gestation, DT mothers had received flutamide, an AR blocker that crosses the placental barrier (Neri et al., 1972). Numerous studies in mammals, including meerkats, confirm that this treatment effectively blocks the temporary or activation effects of androgens in mothers during the treatment period, as well as the permanent or organisational effects of androgens in their offspring (Clemens, 1978; Drea et al., 2021; Drea et al., 1998; Gladue and Clemens, 1980; Thornton et al., 2009; Wallen, 2005). We thus

examined vocal development across three maternal conditions—hereafter ‘treatments’—(DC, SC, and DT, reflecting high androgen, lower androgen and blocked androgen, respectively) by tracking age-related changes in call occurrence and overall call proportions.

Individual fitness in meerkats is closely linked to early growth rates and body mass at nutritional independence (English et al., 2013; Russell et al., 2007; Russell et al., 2002), and larger group sizes (i.e., more helpers) buffer against adverse environmental conditions during development (Clutton-Brock, 2001a; Duncan et al., 2021; Groenewoud and Clutton-Brock, 2021). Additionally, maternal endocrine effects can shape sex-specific developmental trajectories (e.g. Dantzer et al., 2019)). We thus investigated how maternal treatment interacted with offspring sex and socio-ecological factors to shape vocal development. Specifically, we assessed the influence of body condition (using body mass offset as a proxy), group size and competition levels—defined as number of helpers per offspring and number of offspring per group. We also included rainfall as a proxy for insect abundance (Hodge et al., 2009), given that the study took place during a prolonged drought (Davies et al., 2024) and that provisioning increases with resource availability (Clutton-Brock et al., 2002). By exploring these interactions, we aimed to provide insight into the adaptive significance of maternal androgens on vocal development and plasticity.

If the early vocalisations of meerkats are androgen dependent, we would predict (a) the developmental trajectories—i.e., the ontogenetic change in relative proportions of call types—to differ between DC and SC pups, and between DC and DT pups, reflecting the offspring’s exposure to different androgen conditions (i.e., DC > SC ≥ DT). Given the enhanced begging intensity that occurs with increased yolk androgens in avian species (Eising and Groothuis, 2003; Schwabl, 1996), we also

might expect (b) DC offspring to have higher repeat call proportions compared to SC and DT offspring, especially within the first weeks of foraging. If, as previously suggested (Del Giudice et al., 2018), androgen exposure enhances developmental plasticity by increasing responsiveness to environmental conditions, we would expect (c) the call proportions of DC pups to be most strongly influenced by socioecology. Lastly, considering faster initial weight gain in offspring of dominant mothers (Davies et al., 2024), we would anticipate systematic differences in the timing of key developmental transitions, i.e. from full- to semi-nutritional dependence and from semi-dependence to full-nutritional independence. Explicitly, we would anticipate (d) DC pups to transition most rapidly between developmental stages. Such an effect could owe to a competitive advantage in securing access to helpers, or to faster acquisition of foraging skills based on potential androgenic effects on motoneurons, spatial cognition or general persistence, as seen in other species (Archer, 1977; Fargo et al., 2009; Forger et al., 2018; Jones and Watson, 2005; McConnell et al., 2012; Welker and Carré, 2015). We address the first three predictions by analysing each call type separately, while also considering the potential influence of sex and socio-ecological variables, followed by a comparison across call types to evaluate the fourth prediction regarding developmental pace.

2. Methods

2.1. Ethics statement

Research protocols were approved by the Institutional Animal Care and Use Committee (IACUC) of Duke University (Protocol Registry Numbers A17109-06 and A143-12-05) and the Animal Use and Care Committee of the University of Pretoria (EC074-11, SOP029-12, EC010-13, and EC047-16). Additionally, the study was conducted under permits issued by the Northern Cape Province Department of Environment and Nature (Conservation Permit Numbers FAUNA 263/3/2012, FAUNA 050/2013, FAUNA 192/2014, and FAUNA 1020/2016). All data collection adhered to the ASAB/ABS (2012) Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

2.2. Study site

The study, which was conducted between November 2011 and July 2014, involved wild but habituated meerkat groups that are part of the long-term Kalahari Meerkat Project ('KMP') at the Kuruman River Reserve ('KRR'; 26°58' S, 21°49' E) in the southern Kalahari Desert, South Africa. All of the animals were microchipped and visually and individually identifiable via dye-marks on their fur (Clutton-Brock et al., 1998). Additionally, one or two individuals per group were fitted with radio collars to facilitate locating groups (Jordan et al., 2007). The animals were habituated to close observation (<2 m), regular weighing, and sound recordings (Manser and Avey, 2000). An onsite weather station (CR200 datalogger; Campbell Scientific) records different climatic variables, including daily precipitation and air temperatures.

2.3. Subjects and maternal antiandrogen treatment

The focal animals were the offspring of three categories of females: dominant control (DC, $N_{\text{offspring}} = 37$) and subordinate control (SC, $N_{\text{offspring}} = 28$) females, as well as dominant treated females (DT, $N_{\text{offspring}} = 15$) that had received an antiandrogen in the third trimester of gestation. Between November 2011 and April 2015, 11 pregnant dominant females from 11 groups were implanted subcutaneously with two, steadily dissolving antiandrogen pellets (21-day flutamide release, ~15 mg/kg/day; 300 mg, Innovative Research of America, Sarasota, FL) using a minimally invasive procedure (Drea et al., 2021), as required by the KRR for pregnant females in this harsh environment. The treatment regimens for pellet implantation and appropriate controls (i.e. for handling and anaesthesia, but not placebo) had been previously

validated (delBarco-Trillo et al., 2016). The timing of the implant was chosen to target the last 21 days of the 70-day gestation period, during the foetus' increased sensitivity to organisational effects on behaviour as reported in other species (Despres et al., 1984; Goy, 1988; Thornton et al., 2009). All treated animals were monitored before, during, and after treatment and no adverse effects were detected (Drea et al., 2021). Various anticipated consequences of the effective androgen receptor blockade in the offspring of treated mothers have been reported elsewhere (Davies et al., 2024; Drea et al., 2021; Smyth-Kabay et al., 2024).

From the 11 treated pregnancies, one female aborted, and 10 litters were born, from which five were lost before or shortly after emergence, resulting in the inclusion of the remaining five litters in the study (DT, Table 1). To ensure full age-range coverage for offspring by maternal treatment and sex, the control sample (DC, SC) included additional subjects born during the study period and therefore differs from those originally reported (Drea et al., 2021). For the extraction of call data, we included all recordings from the DT offspring but selected a subsample based on available recordings of DC and SC offspring that were matched to the sex ratio of the DT treatment to achieve a balanced dataset (DC, $N_{\text{offspring}} = 20$; SC, $N_{\text{offspring}} = 20$, DT, $N_{\text{offspring}} = 15$; Table 1: Full sample).

2.4. Focal recordings and call data extraction

From February 2012 to July 2014, we conducted monthly recordings of offspring vocalisations ($N_{\text{recordings}} = 746$), from emergence of all pups in a litter from the natal burrow until nutritional independence, up to the age of four months (age in days: mean = 87.1, SD = 28.0, min = 31, max = 130). We followed the focal offspring from a close distance (0.2–1 m) using a directional microphone (Sennheiser ME66 with windshield Rainhardt, W200) connected to a solid-state recorder (Marantz PMD661, Marantz Japan Inc.; sampling frequency 48 kHz, 24 bits accuracy) for a period of 5–10 min depending on call rate and external events. With a second hand-held microphone and additional sound channel, the observer recorded the focal animal's behaviour, to ensure the identity of the calling individual for later analyses, the call context and the distance to nearby individuals. If possible, recordings were carried out during two separate foraging sessions within a few days to minimise contextual and environmental influences. Because the sample size decreased over time as offspring disappeared from the group or died (max age in days: mean = 112.2, SD = 23.2), the number of recordings per focal animal varied (mean $N = 9.3$, SD = 6.5, range = 1–25).

Using Adobe Audition (Version 22.4, Adobe Inc), we annotated all sound recordings from our subsample (Table 1; Full sample, $N_{\text{recordings}} = 491$), identifying call types based on their sound and respective spectrograms. Each subject contributed an average of 8.9 total recordings (SD = 5.75), with an average of 3.1 recordings per month (SD = 1.30), ensuring sufficient representation across individuals. First, we split each sound file into 1-min periods. Then, within each period, we marked ten calls produced in a sequence and labelled each one by respective call type (repeat, digging, close) for a maximum of five separate 1-min periods resulting in a maximum of 50 calls per file. We excluded the infrequent high-pitched call, that temporally overlaps with the production of repeat calls.

2.5. Metadata

From the long-term database of the KMP we calculated the size and composition of each group at the time of audio recording by averaging the individual sightings of the preceding week (aged in days: pups $\leq 130 \leq$ juveniles $\leq 180 \leq$ sub-adults $\leq 365 \leq$ adults) and we used the morning body mass measurements from the same period to calculate the average mass of each subject. For our analyses, we calculated the cumulative rainfall (mm) from the month (30 days) preceding the dates of our observations.

Table 1
 Subject demographics and sample sizes. Shown are the number of subjects included in the study, along with sex ratio, number of litters, number of groups, and total recording numbers. Mean litter size reflects the number of pups per litter at the time of emergence, which may differ from the number of offspring included in the analyses at specific age ranges. Also shown are mean group size, the mean number of pups and adults in the group, mean body mass offset (%), mean normalised competition score, and mean monthly rainfall (mm), each reported with their respective standard deviations (SD), calculated from the corresponding subsamples.

Maternal treatment	Sample size (n)		Mean ± SD				n pups	n adults	Body mass offset (%)	Normalised competition score	Rainfall (mm/month)
	Individual (F/M)	Groups	Litters	Recordings	Litter size	Group size					
Dominant control (DC)	20 (11/9)	10	10	157	3.85 ± 0.86	14.4 ± 8.34	3.59 ± 1.45	12.9 ± 7.21	-0.42 % ± 13.3 %	0.13 ± 0.16	22.4 ± 21.4
Subordinate control (SC)	20 (10/10)	7	9	157	3.87 ± 0.54	20.1 ± 6.53	4.17 ± 1.45	18.5 ± 5.66	-1.65 % ± 9.41 %	0.08 ± 0.04	11.4 ± 9.73
Dominant treated (DT)	15 (8/7)	5	5	177	3.01 ± 0.43	21.4 ± 9.26	3.41 ± 1.20	18.5 ± 8.73	-1.04 % ± 11.6 %	0.11 ± 0.20	16.0 ± 21.3
Full sample	55 (29/26)	13	25	491	3.55 ± 0.75	18.73 ± 8.69	3.71 ± 1.40	16.71 ± 7.80	-1.04 % ± 11.55 %	0.11 ± 0.15	16.58 ± 18.96
Analyses sample	55 (29/26)	13	25	481	3.55 ± 0.75	18.80 ± 8.70	3.69 ± 1.39	16.79 ± 7.79	-1.03 % ± 11.52 %	0.10 ± 0.15	16.32 ± 18.55

As body mass is highly correlated with age and influenced by environmental stressors such as droughts (Dimac-Stohl et al., 2018), we modelled the expected mass for the subjects as function of age, sex and rainfall while controlling for ID. We then used the offset (%) between the expected and average body mass as a proxy for the physical condition of the offspring. To incorporate the ratio of adults and pups within a group while accounting for both the relative availability of helpers (adult/pup ratio) and the absolute number of competitors (N pups), we defined a competition score (CS) using the reciprocal of the adult/pup ratio and the number of pups in the group: $\frac{1}{\frac{N \text{ adults}}{N \text{ pups}}} * N \text{ pups}$.

For comparison across conditions and to add robustness, we normalised CS (hereafter ‘CSN’), with lower values indicating less competition: $CSN = \frac{CS - \min CS}{\max CS - \min CS}$

2.6. Statistical analyses

We used a Bayesian framework to analyse our data, accounting for the relatively small sample sizes and enabling the inclusion of posterior distributions as priors in future analyses. We specified all multilevel models using the ‘brms’ package (Bürkner, 2017) in R (R Core Team, 2024). Throughout the analysis, we visually inspected chain trace plots and confirmed all $\hat{R}s = 1.00$ to ensure model convergence (Brooks et al., 2011). We evaluated model fit and performance through posterior predictive checks and verified a large effective sample size to ensure the reliability of the estimates (Bürkner, 2017; Kruschke, 2015; Vehtari et al., 2021). As the continuous predictors were on different scales, we standardised values to facilitate comparisons of their magnitudes.

To estimate body mass at the time of data collection, we applied a Gaussian multilevel model using ‘mass’ as the response variable (Supplementary Table S1, Supplementary Fig. S1). We fitted this model with a total of $N = 3053$ weight measurements from all 55 subjects up to 140 days old (Female $N = 1514$; Male $N = 1539$), incorporating scaled ‘age’, cumulative 30-day ‘rainfall’, and ‘sex’, as population-level effects (PLE). We set individual identity as a group-level effect (GLE) and defined weakly informative, half-normal priors (i.e. normal(0, 0.5), lower bound = 0) for the predictors and a weakly informative prior centred on zero (i.e. normal(0,1)) for the intercept. We then used these model estimates to calculate the percentage difference (hereafter body mass offset) between expected and averaged measured mass for further analysis.

For the main analysis of call proportions, we only included recordings containing at least one call bout (i.e., min calls = 10) and complete predictor values (Table 1: Analyses sample). To investigate the relationship between maternal treatment effects and call dynamics, we used a multivariate model with a zero-inflated beta-binomial distribution, binomial response structure and logit-link function. Unlike a compositional model, which imposes a fixed-sum constraint, this approach allows predictors to affect call types independently while accounting for correlations between call types, continuous proportions and overdispersion. In addition, the binomial response automatically down-weights samples with fewer total call counts. We incorporated individual identity nested within litter identity as GLEs and used weakly informative priors centred on zero (i.e., normal(0,1)) for the intercept and all PLEs. Because our focus is on ontogeny, the formula for each call type included the three-way interaction of maternal treatment, age, and sex as well as the three-way interactions of treatment, age and each of our continuous predictors (body mass offset, CSN, group size, rainfall) as PLEs. Age terms were pre-determined based on ontogenetic call dynamics (linear for repeat and close calls; linear and quadratic for digging calls). We tested the three-way interactions of treatment and age with body mass, group size, CSN, or rainfall for non-linearity in separate models beforehand, selecting the relation with the greater predictive power based on expected log pointwise density (ELPD) scores from approximate leave-one-out cross-validation (LOO; (Vehtari et al., 2017)). Despite the model’s complexity, diagnostics confirmed result

reliability, and predictor reduction minimally decreased uncertainty but substantially lowered predictive performance, supporting the final model as the best balance of complexity and explanatory power (Bürkner, 2017; Kruschke, 2015; Vehtari et al., 2021).

We then examined two key transitions between nutritionally determined developmental phases: from full- to semi-dependence (when digging call proportions exceed repeat call proportions) and from semi- to full-independence (when close call proportions exceed digging call proportions). Additionally, we identified the age at which digging call proportions peaked, marking the onset of self-sufficiency. To determine these ages, we extracted posterior predictions from the multivariate model, generating call proportion estimates across ages 1–180 days,

with continuous predictors (body mass offset, CSN, group size, rainfall) held at sample means. To ensure that proportions summed to 1, we normalised values per age and identified the first age at which the higher-proportion call type exceeded the lower-proportion type by ≥ 0.01 using direct threshold-based extraction. We propagated uncertainty by drawing 100 posterior samples per subject directly from the fitted model and excluded samples where any age was < 30 or > 180 days to ensure biological validity. Next, we analysed variation in developmental timing using the distribution of sampled transition ages as the response variable in a log-normal Bayesian hierarchical model with an identity-link function. Individual identity was included as GLE to account for repeated sampling within individuals. Maternal

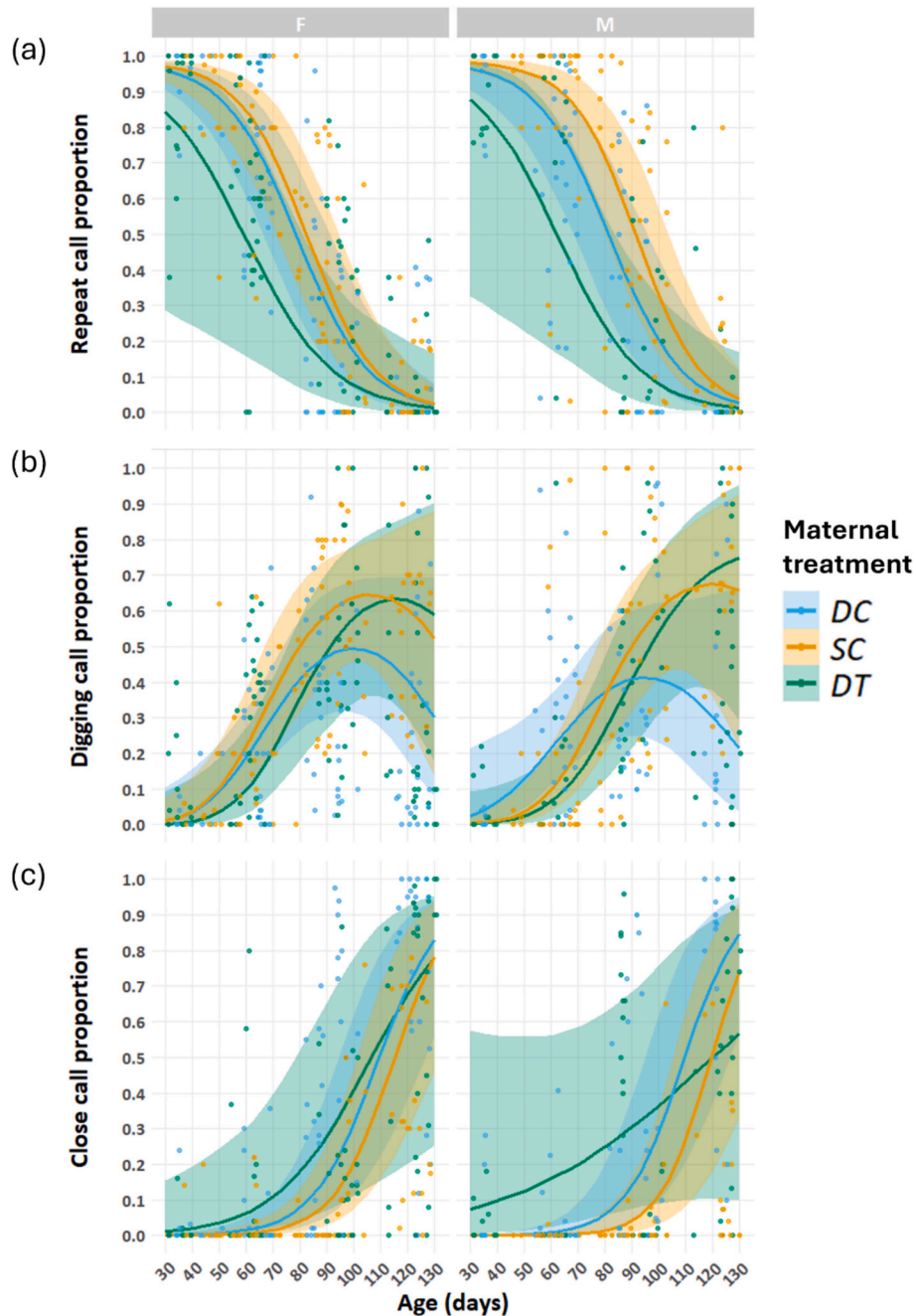


Fig. 2. Estimated proportions from a multivariate model for (a) repeat calls, (b) digging calls and (c) close calls over the course of meerkat ontogeny (from 30 to 130 days of age), for offspring differentiated by maternal treatment (dominant control, DC, blue; subordinate control, SC, orange; dominant treated, DT, green) and while additional predictors were kept constant at the sample mean. Panels differentiate offspring by sex (female, F; male, M). Dots show original observations; ribbons represent the 95 % equal-tailed credible intervals (CrI). $N = 481$; R^2 (and CrI) = (a) 0.73, (0.67, 0.78); (b) 0.45, (0.37, 0.54); (c) 0.75, (0.69, 0.81).

treatment, sex, and their interaction were included as PLEs. We applied weakly informative priors (normal(0,1)) for the intercept and PLEs.

To determine the explained variance of our models, we calculated the LOO-adjusted Bayesian R^2 (Bürkner, 2017). To evaluate the strength of an effect, we first calculated the Probability of Direction ('pd'), representing the proportion of the posterior distribution aligned with the median sign (Makowski et al., 2019b). We then determined the probability of practical significance ('ps') using the 'bayestestR' package (Makowski et al., 2019a), setting the threshold as the percentage of the posterior distribution beyond the Region of Practical Equivalence ('ROPE') where an effect is considered negligible (Kruschke, 2018; Makowski et al., 2019a). We used the 'emmeans' package (Lenth, 2024) to contrast slopes for call proportions and estimate marginal means (EMMs) for transition ages across and within maternal treatment and sex to identify differences between offspring groups. Additionally, we estimated and contrasted EMMs for call proportions at three key ages—30 days for repeat calls, 75 days for digging calls, and 120 days for close calls—respectively representing the beginning, middle, and end of vocal ontogeny. For significant socioecological effects, we further tested for differences based on maternal treatment by calculating posterior probabilities ($\Pr(\beta > 0)$ or $\Pr(\beta < 0)$) using the 'hypothesis()' function (Bürkner, 2017)

We consider $\text{pd.} \geq 95\%$ as strong evidence for the direction of an effect (Makowski et al., 2019b), while $\text{ps} \geq 0.85$ is used as an additional indicator of practical significance. We report 95% credible intervals (CrIs) in all plots and tables to reflect uncertainty. In the results section, we report the estimated coefficients as indicators of effect size on the logit scale.

3. Results

3.1. Repeat calls

Repeat call proportions declined substantially over ontogeny ($\text{age} \hat{\beta} = -2.15$, $\text{pd.} = 100\%$, $\text{ps} = 1.00$), with maternal treatment modulating these trajectories through interactions with the included socioecological influences (Fig. 2a, Supplementary Table S2, Supplementary Fig. S2). Specifically, post-hoc tests (Supplementary Table S3) showed a weaker reduction of repeat call proportions with increasing body mass offset by SC and DT offspring compared to DC offspring (DC - SC: $\Pr(\beta < 0) = 0.99$; DC - DT: $\Pr(\beta < 0) = 0.99$; SC:age:body mass offset $\hat{\beta} = 0.45$, $\text{pd.} = 94.51\%$, $\text{ps} = 0.83$; DT:age:body mass offset $\hat{\beta} = 0.47$, $\text{pd.} = 95.81\%$, $\text{ps} = 0.86$). SC offspring also showed a weaker decline in repeat call proportions with increasing group size than did DC and DT offspring (DC - SC: $\Pr(\beta < 0) = 0.96$; SC - DT: $\Pr(\beta > 0) = 0.99$; SC:age:group size $\hat{\beta} = 0.83$, $\text{pd.} = 99.09\%$, $\text{ps} = 0.97$), and weaker non-linear declines with group size² than did DC offspring (DC - SC: $\Pr(\beta < 0) = 0.99$; SC:age:group size² $\hat{\beta} = 0.90$, $\text{pd.} = 99.47\%$, $\text{ps} = 0.98$). Although competition was associated with reduced repeat call proportions (DT: competition $\hat{\beta} = -0.60$, $\text{pd.} = 97.25\%$, $\text{ps} = 0.89$; age:competition² $\hat{\beta} = 0.87$, $\text{pd.} = 93.43\%$, $\text{ps} = 0.89$), posterior probabilities did not strongly support differences across groups. In contrast, rainfall effects varied by maternal treatment, with DT offspring showing a stronger reduction in repeat call proportions than did SC offspring (SC - DT: $\Pr(\beta > 0) = 0.91$; DT:rainfall $\hat{\beta} = -0.49$, $\text{pd.} = 97.56\%$, $\text{ps} = 0.89$). When all environmental predictors were held at the sample mean, contrasts between slopes did not provide strong evidence for overall group differences in the rate of change (Supplementary Table S4; all $\text{pd.} < 95\%$, $\text{ps} < 0.85$).

In addition to these maternal and environmental influences, sex differences emerged at the beginning of ontogeny. EMM contrasts at 30 days (Supplementary Table S5) indicated that within sexes, DC and SC females had higher repeat call proportions than did DT females (DC > DT: $\text{pd.} = 91.21\%$, $\text{ps} = 0.89$; SC > DT: $\text{pd.} = 94.46\%$, $\text{ps} = 0.93$). Among males, SC offspring showed the highest repeat call proportions (DC < SC: $\text{pd.} = 90.54\%$, $\text{ps} = 0.87$; SC > DT: $\text{pd.} = 97.41\%$, $\text{ps} = 0.97$),

whereas DT males produced the lowest proportions (DC > DT: $\text{pd.} = 88.55\%$, $\text{ps} = 0.86$). Between the sexes, regardless of maternal treatment, males showed a less steep decline in repeat call proportions over ontogeny than did females (age:male $\hat{\beta} = 0.55$, $\text{pd.} = 92.58\%$, $\text{ps} = 0.84$). SC females also produced lower proportions at 30 days than did SC males (SC F < SC M: $\text{pd.} = 92.61\%$, $\text{pd.} = 0.88$), further emphasizing early sex-specific differences in call patterns.

3.2. Digging calls

Similar to repeat calls, maternal treatment influenced the ontogenetic trajectories of digging calls through its interaction with socioecological factors (Fig. 2b, Supplementary Table S6, Supplementary Fig. S3). Digging call proportions followed a strong curvilinear relationship with age, initially increasing (age $\hat{\beta} = 0.74$, $\text{pd.} = 99.61\%$, $\text{ps} = 0.98$) before declining sharply later in ontogeny (age² $\hat{\beta} = -0.75$, $\text{pd.} = 99.34\%$, $\text{ps} = 0.97$). Depending on maternal treatment, competition (SC:competition $\hat{\beta} = -0.72$, $\text{pd.} = 94.88\%$, $\text{ps} = 0.89$; SC:competition² $\hat{\beta} = -0.83$, $\text{pd.} = 96.68\%$, $\text{ps} = 0.92$; DT:age:competition $\hat{\beta} = -0.73$, $\text{pd.} = 99.80\%$, $\text{ps} = 0.99$; DT:age:competition² $\hat{\beta} = 1.08$, $\text{pd.} = 97.07\%$, $\text{ps} = 0.94$; DT:age²:competition $\hat{\beta} = -0.82$, $\text{pd.} = 91.96\%$, $\text{ps} = 0.86$) and rainfall (DT:age:rainfall² $\hat{\beta} = -0.53$, $\text{pd.} = 98.76\%$, $\text{ps} = 0.93$; DT:age²:rainfall $\hat{\beta} = -1.03$, $\text{pd.} = 98.30\%$, $\text{ps} = 0.96$) exerted varying effects on digging call proportions; however, posterior probabilities (Supplementary Table S7) only confirmed that SC offspring responded more strongly to rainfall than did SC offspring (SC - DT: $\Pr(\beta > 0) = 0.99$).

Sex further modulated the linear age patterns of digging call proportions across maternal treatment groups (SC:age:male: $\hat{\beta} = 0.93$, $\text{pd.} = 98.91\%$, $\text{ps} = 0.97$; DT:age:male: $\hat{\beta} = 0.65$, $\text{pd.} = 97.48\%$, $\text{ps} = 0.92$), which became more evident in the slope contrasts (Supplementary Table S8): Within sexes, DC females increased digging call proportions more slowly than did DT females (DC < DT: $\text{pd.} = 95.44\%$, $\text{ps} = 0.90$). Likewise, DC males showed the slowest increase in digging call proportions compared to both SC and DT males (DC < SC: $\text{pd.} = 99.51\%$, $\text{ps} = 0.99$; DC < DT: $\text{pd.} = 99.74\%$, $\text{ps} = 0.99$). Between sexes, SC females increased their digging call proportions more slowly than did SC males (SC F < SC M: $\text{pd.} = 97.76\%$, $\text{ps} = 0.92$); however, at 75 days of age (Supplementary Table S9), representing mid-ontogeny, SC females produced higher digging call proportions than did SC males (SC F > SC M: $\text{pd.} = 97.19\%$, $\text{ps} = 0.92$), suggesting strong sex specific effects in SC offspring.

3.3. Close calls

Maternal treatment effects in interaction with the socio-ecological environment also shaped the developmental trajectory of close calls, which followed a strong linear trajectory over ontogeny, with proportions increasing consistently with age (age: $\hat{\beta} = 2.46$, $\text{pd.} = 100\%$, $\text{ps} = 1.00$) (Fig. 2c, Supplementary Table S10, Supplementary Fig. S4). Specifically, post-hoc tests (Supplementary Table S11) confirmed that DT offspring produced lower close call proportions with increasing competition compared to DC offspring (DC - DT: $\Pr(\beta < 0) = 0.99$; DT: age:competition²: $\hat{\beta} = 0.54$, $\text{pd.} = 99.54\%$, $\text{ps} = 0.96$) but showed a stronger increase in close call proportions with increasing group size compared to both DC and SC offspring (DC - DT: $\Pr(\beta < 0) = 0.90$; SC - DT: $\Pr(\beta < 0) = 0.93$; SC:age:group size: $\hat{\beta} = 0.59$, $\text{pd.} = 94.71\%$, $\text{ps} = 0.87$; DT:age:group size: $\hat{\beta} = 0.82$, $\text{pd.} = 97.56\%$, $\text{ps} = 0.94$; DT:group size²: $\hat{\beta} = 0.33$, $\text{pd.} = 96.79\%$, $\text{ps} = 0.81$). Conversely, DT offspring showed a strong negative response in close call proportions to increasing rainfall, whilst DC and SC offspring were not reliably affected by this proxy for prey abundance (DC - DT: $\Pr(\beta > 0) = 0.96$; DT:age:rainfall: $\hat{\beta} = -0.68$, $\text{pd.} = 97.70\%$, $\text{ps} = 0.93$), with SC offspring showing a similar pattern (SC - DT: $\Pr(\beta > 0) = 0.92$).

Sex differences further shaped close call trajectories ($DT:age:male: \hat{\beta} = -1.14$, $pd. = 99.88\%$, $ps = 0.99$), with the divergent slopes indicating a pronounced effect of maternal treatment on DT offspring (Supplementary Table S12). Within sexes, both DC and SC males showed a stronger increase in close call proportions than did DT males ($DC > DT$: $pd. = 99.80\%$, $ps = 0.99$; $SC > DT$: $pd. = 99.66\%$, $ps = 0.99$). Between sexes, DT males also showed a significantly weaker increase in close call proportions compared to DT females ($DT F > DT M$: $pd. = 99.90\%$, $ps = 0.99$), resulting in higher proportions by DT females at 120 days of age ($DT F > DT M$: $pd. = 94.63\%$, $ps = 0.90$), representing late ontogeny (Supplementary Table S13).

3.4. Transitional ontogeny across calls

The age at which meerkat offspring transitioned from full-nutritional dependence to semi-nutritional dependence was indicated by a proportional change in call types, specifically when repeat call proportions were exceeded by digging call proportions (Fig. 3a, Supplementary Table S14, Supplementary Fig. S4). This transition was significantly modulated by maternal treatment, occurring earliest in DT offspring ($DT \hat{\beta} = -0.09$, $pd. = 96.55\%$, $ps = 0.95$), followed by DC and SC offspring.

EMM contrasts confirmed this pattern (Supplementary Table S15), as DT females were younger at the time of transition than were DC and SC females ($DC > DT$: $pd. = 96.55\%$, $ps = 0.95$; $SC > DT$: $pd. = 93.77\%$, $ps = 0.91$) and DT males transitioned significantly earlier than did DC and SC males ($DC > DT$: $pd. = 99.68\%$, $ps = 0.99$; $SC > DT$: $pd. = 99.99\%$, $ps = 1.00$). Among SC offspring, SC females were younger at the time of transition than were their male littermates ($SC F < SC M$: $pd. = 98.07\%$, $ps = 0.97$). SC males were also older than DC males at the transition to

semi-dependence ($DC < SC$: $pd. = 90.06\%$, $ps = 0.86$).

The age at which digging call proportions were at their peak was strongly influenced by both maternal treatment and by offspring sex ($SC:male \hat{\beta} = 0.08$, $pd. = 96.28\%$, $ps = 0.94$; $DT:male \hat{\beta} = 0.16$, $pd. = 99.90\%$, $ps = 1.00$) (Fig. 3b, Supplementary Table S16, Supplementary Fig. S5). EMM contrasts (Supplementary Table S17) showed that DC offspring reached their peak digging calls at the youngest age, both among females ($DC < SC$: $pd. = 98.20\%$, $ps = 0.96$; $DC < DT$: $pd. = 99.30\%$, $ps = 0.98$) and males ($DC < SC$: $pd. = 100\%$, $ps = 1.00$; $DC < DT$: $pd. = 100\%$, $ps = 1.00$). Both SC and particularly DT males, relative to their sisters, showed an age delay in producing peak digging call proportions ($SC F < SC M$: $pd. = 99.52\%$, $ps = 0.99$; $DT F < DT M$: $pd. = 100\%$, $ps = 1.00$).

Lastly, the age at which meerkat offspring transitioned from semi-nutritional to full-nutritional independence occurred when digging call proportions were exceeded by close call proportions (Fig. 3c, Supplementary Table S18, Supplementary Fig. S6). This transition age was significantly influenced by both maternal treatment and sex ($SC:male \hat{\beta} = 0.11$, $pd. = 98.72\%$, $ps = 0.98$; $DT:male \hat{\beta} = 0.12$, $pd. = 98.96\%$, $ps = 0.98$). Based on their calls (Supplementary Table S19), DC offspring transitioned sooner to full independence than did SC and DT offspring of both sexes (females: $DC < SC$: $pd. = 99.99\%$, $ps = 1.00$; $DC < DT$: $pd. = 99.83\%$, $ps = 1.00$; males: $DC < SC$: $pd. = 100\%$, $ps = 1.00$; $DC < DT$: $pd. = 100\%$, $ps = 1.00$). Moreover, both SC and DT males reached nutritional independence significantly later than their sisters ($SC F < SC M$: $pd. = 99.26\%$, $ps = 0.98$; $DT F < DT M$: $pd. = 99.25\%$, $ps = 0.99$).

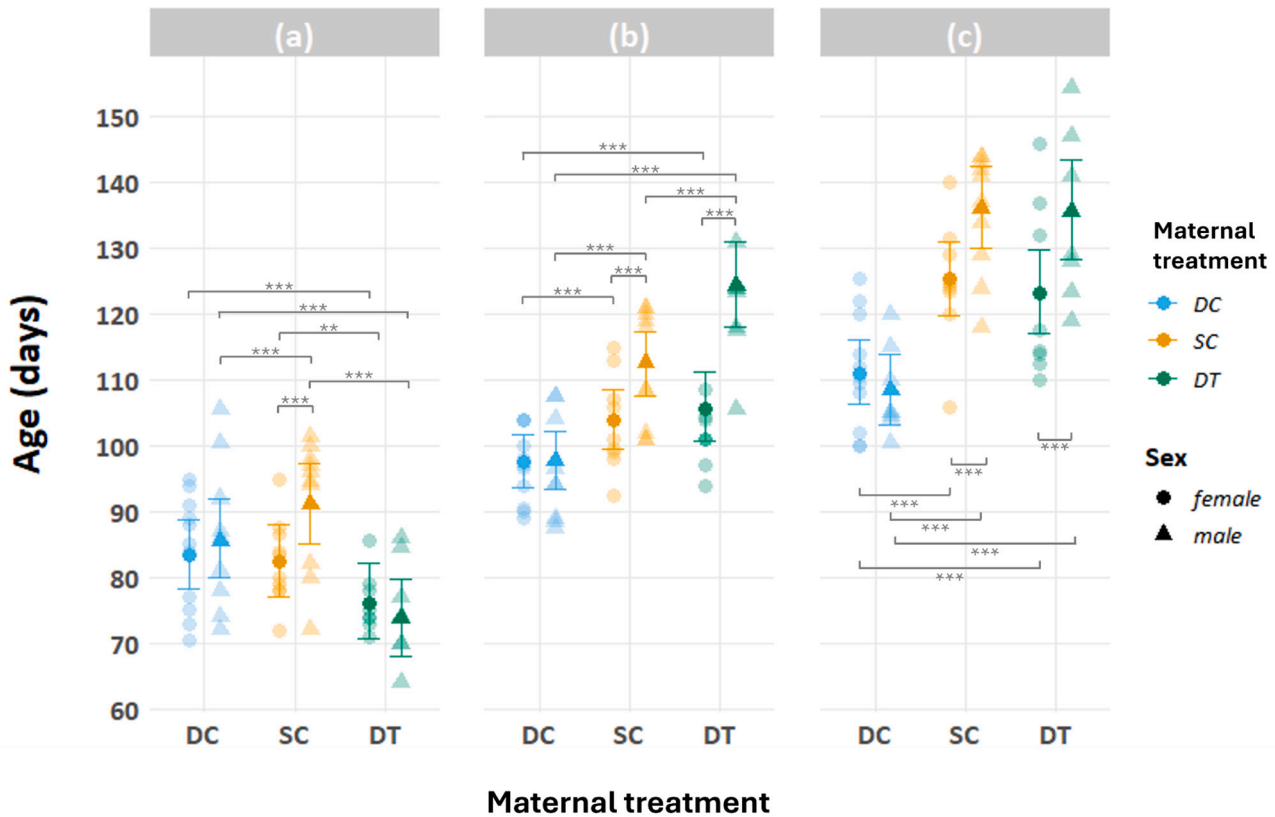


Fig. 3. Estimated marginal means of meerkat offspring age (in days) when (a) digging call proportions exceeded repeat call proportions, (b) digging call proportions were at their peak and (c) close call proportions exceed digging call proportions. Offspring are differentiated by maternal treatment (dominant control, DC, blue; subordinate control, SC, orange; dominant treated, DT, green) and sex (female, filled circles; male, filled triangles). Transparent icons represent predicted median transition ages for each subject ($N = 55$) based on the posterior samples ($N_{a,b} = 5499$, $N_c = 4924$). Whiskers depict 95 % equal-tailed credible intervals. Contrasts with high probabilities of direction (pd) are indicated by brackets (** $pd. \geq 95\%$, * $pd. \geq 90\%$).

4. Discussion

The natural variation in androgen concentrations between dominant and subordinate female meerkats, along with the experimental administration of an AR blocker to dominant females during late gestation, offered a unique framework for examining how hormonal masculinisation shapes early vocalisations in wild meerkats. Based on the distinct phases of meerkat vocal ontogeny, as reflected by the proportion of call-type usage, we observed accelerated development in the offspring of dominant control (DC) mothers, with less variable trajectories even under adverse socio-ecological conditions. By comparison, the offspring of subordinate control (SC) and dominant treated (DT) mothers showed a slower pace of vocal development, with significant sex differences in trajectory and significant influence of social factors and prey availability. Organisational effects of maternal androgens were thus evident in the ontogeny and plasticity of offspring vocalisations, with further mediation by the socio-ecological environment.

Based on previous research on the impact of maternal androgens on offspring aggression (Drea et al., 2021) and both endocrine and physical development (Davies et al., 2024) in meerkats, we anticipated (a) that the developmental trajectories of vocalisations, defined as changes in call proportions over ontogeny, would differ among DC, SC, and DT pups, reflecting their varying prenatal androgen milieu and their competitiveness, with the strongest differences potentially expected between DC and DT offspring (i.e., $DC > SC \geq DT$). Although we expected differences across all call types, our findings confirmed the strongest divergence between DC and DT offspring in digging and close call trajectories, whereas SC offspring followed a more variable trajectory, with some similarities to both DC and DT offspring depending on the call type and socio-ecological conditions. Still, consistent with predictions, repeat call proportions within each sex were lowest in DT offspring. As independent foraging increased, vocal patterns aligned most closely with the predicted extremes of prenatal androgen action. For instance, digging call proportions increased more rapidly, but substantially later in DT than in DC offspring. Additionally, DT males showed smaller increases in close call proportions over time compared to DC and SC offspring of either sex, and to their sisters, indicating a clear divergence in male vocal trajectories due to prenatal AR blockade. Together, these results suggest that the organising actions of androgens are involved in shaping the developmental trajectories of meerkat vocalisations in both sexes.

Sex differences in vocal development varied across offspring groups, potentially suggesting some variability in the strength, timing, or susceptibility of vocal features to organisational effects of maternal androgens. Pregnancy alters maternal androgen concentrations in meerkats (Davies et al., 2016; Drea et al., 2021), including of both androstenedione and testosterone, which can play differential roles, as seen in the offspring of other species in which females are physiologically masculinised (Grebe et al., 2019). Furthermore, although the disruption of organisational effects owing to prenatal androgen blockade may alter early vocal development, later activational effects of hormones could still contribute to sexually differentiated vocal behaviour (Alward et al., 2018; Watts, 2020). Nonetheless, the lack of sex differences in DC offspring supports previous findings that elevated prenatal androgen exposure can diminish or eliminate sex differences in early vocal behaviour by masculinising female calls (Tomaszycki et al., 2005; Tomaszycycki et al., 2001; von Engelhardt et al., 2006).

During the phase of full nutritional dependence, we expected (b) DC offspring, given their increased levels of aggression and competitiveness (Drea et al., 2021), to produce higher repeat call proportions compared to SC and DT offspring. In line with findings in avian species, in which yolk androgens enhance the begging behaviour of nestlings (Eising and Groothuis, 2003; Schwabl, 1996), we indeed observed higher repeat call proportions in the offspring of DC compared to those of DT mothers when we examined the sexes separately. DC offspring showed substantially reduced repeat call proportions with improved body condition,

whilst SC and DT offspring maintained their begging efforts, possibly reflecting a compensatory strategy to secure resources due to reduced competitiveness. In line with this reduction, SC males had the highest repeat call proportions throughout ontogeny and showed a delayed developmental trajectory. Additionally, SC offspring maintained high begging levels in larger groups, relying more on prolonged adult investment than did DC offspring. DT offspring, by comparison, produced the fewest repeat calls, which may suggest a more rapid developmental pace and initially constrained maturation in DC and SC offspring; yet, DT offspring further reduced begging under higher competition, indicating greater social vulnerability. Their strong response to rainfall also suggests they benefitted the most from increased prey availability and subsequent helper generosity (Clutton-Brock et al., 2002), likely struggling to elicit provisioning under less favourable conditions.

Accordingly, DT offspring transitioned to semi-dependence earliest, potentially due to ineffective begging or an inability to secure enough food in competitive environments, pushing them to forage independently sooner than was observed in DC or SC offspring. Their earlier transition may alternately reflect a physiological acceleration, as DT offspring showed peak insulin-like growth factor-1 (IGF-1) expression and grew faster than SC offspring initially (Davies et al., 2024), which could have facilitated a more rapid shift toward independent foraging. However, their prolonged use of digging calls alongside the earlier but weaker increase in close calls suggests that this transition was not accompanied by an immediate increase in foraging competence, reflecting challenges in food acquisition, which is highly competitive in meerkats (Hodge et al., 2009). Although the mechanism behind the indicated lack of efficiency in DT offspring remains unclear, AR blockade may have prevented the activation of androgen-mediated processes, such as those typically associated with increased persistence or perseverance (Archer, 1977; Welker and Carré, 2015). Thus, while these findings are compelling in suggesting differential organisational effects of androgens on vocal development between our three study groups, additional research on the finer details of vocalisations is needed, such as examining call durations or rates and acoustic properties, as these can significantly influence the provisioning response of adult meerkats (Madden et al., 2009; Manser et al., 2008; Manser and Avey, 2000).

In addition to the organising effects of androgens, the observed similarities and variations in developmental trajectories among DC, SC, and DT offspring were further shaped by the socio-ecological environment, as already evidenced by the differential impact on repeat call proportions. Whereas rainfall had no substantial effect on the digging call trajectory of DC offspring, SC offspring responded more strongly to this proxy for prey abundance than did DT offspring. Also, group size did not affect close call proportions in DC offspring but impacted the trajectory of close calls in SC and particularly DT offspring, providing further evidence of reduced dependence on adult provisioning and greater self-sufficiency in offspring of dominant control females. With increased rainfall, close call proportions were generally higher in all offspring across maternal treatments, aligning with previously reported increases in growth rates throughout development (English et al., 2014); however, DT offspring showed a strong, negative developmental response to rainfall, potentially implying reduced foraging competence. Increased competition (as indicated by fewer available helpers per offspring and more pups in the group) was associated with a significant reduction in close call emergence in DT compared to DC offspring, further suggesting that DT offspring struggled to become self-sufficient when competition was high. Thus, the younger age at which DC offspring, particularly males, reached full nutritional independence suggests that litters of dominant mothers might be better equipped to thrive in such competitive environments. A similar status-related advantage has been previously described in female spotted hyaenas (*Crocuta crocuta*), in which dominant dams, relative to subordinate dams, express greater androgen concentrations and produce offspring that show increased aggression, presumably with downstream fitness

consequences for the offspring (Dloniak et al., 2006).

While these findings suggest that the vocal ontogeny of DC offspring is more robust than that of peers exposed prenatally to reduced androgen action, and less influenced by external socio-ecological factors such as group size or rainfall, they contradict prediction (c) of increased plasticity in DC offspring due to higher androgen exposure, as proposed by Del Giudice and colleagues (Del Giudice et al., 2018). Instead, the robustness observed in DC offspring may offer significant advantages in the harsh and unpredictable environment of meerkats, enabling them to maintain a consistent developmental trajectory even under challenging conditions. This stability suggests that rather than exhibiting a higher sensitivity to the environment, offspring of dominant mothers show enhanced developmental canalisation, i.e., a robust phenotype in spite of genetic or environmental variation (Waddington, 1942). This canalisation likely reflects an adaptive strategy in which the offspring of the matriarchal line are best equipped to reliably reach critical milestones such as nutritional independence. In cooperative breeders, achieving nutritional independence earlier enhances the survival prospects of the offspring and increases maternal fitness by freeing up resources and helpers for subsequent litters (Dantzer et al., 2019; Russell and Lummaa, 2009). Conversely, the greater plasticity observed in SC, and to a more variable extent, in DT offspring could represent an alternative developmental strategy for the offspring of mothers that express reduced androgen action, allowing such offspring to adjust their developmental pace to fluctuating socio-ecological conditions. This flexibility may help compensate for lower aggressiveness by enabling these offspring to optimise their growth and development according to the environmental contexts they encounter.

In young meerkats, investment in foraging is mediated by available energy reserves and general body condition (Thornton, 2008). Therefore, our last expectation was for (d) an accelerated developmental pace in DC offspring and more relaxed trajectories in SC and DT offspring due to less efficient begging during the phase of nutritional dependence and poorer foraging skills. Our findings partially support the prediction, as DC offspring were significantly younger than SC and DT pups when reaching peak digging call proportions and they became nutritionally independent earlier than did SC and DT offspring. Thus, DC offspring showed a faster rate of development after, but not before, progression to semi-dependence. Their initially slower transition relative to DT offspring may reflect early developmental constraints associated with elevated prenatal androgens (Davies et al., 2024), but this delay could also have contributed to their more robust trajectory later on. Considering that androgens can enhance spatial memory (Jones and Watson, 2005; McConnell et al., 2012), affect motor neurons (Fargo et al., 2009; Forger et al., 2018), and increase persistence (Archer, 1977; Welker and Carré, 2015), our findings suggest that DC pups might be better equipped to rapidly acquire and refine foraging skills than are SC and DT offspring, potentially offsetting any initial trade-offs. Yet, despite greater male than female testosterone concentrations at this early age (Davies et al., 2024), SC and DT males reached peak digging call proportions later and took longer to become nutritionally independent than their female littermates. Nevertheless, sons of SC mothers already showed a substantial delay in the transition to semi-dependence, aligning more closely with organisational effects of androgens rather than with concurrent effects of circulating androgen concentrations, further highlighting the role of maternal androgens in shaping developmental trajectories.

By examining the distinct developmental stages and corresponding call types of young meerkats, our study sheds light on how status-related differences in hormonal masculinisation influence both the ontogeny of vocalisations and their integrated developmental trajectories. In this cooperatively breeding mammal, the offspring of DC mothers, exposed to higher androgen concentrations prenatally, showed accelerated postnatal development and canalised vocalisation patterns, likely enhancing their fitness in both favourable and adverse conditions. In contrast, offspring of SC and DT mothers displayed a slower

developmental pace, marked by pronounced sex differences and greater flexibility in response to the social environment—possibly as an adaptive strategy to reduced prenatal androgen exposure. AR-blockade in utero altered postnatal developmental trajectories in DT offspring, leading to an initial divergence from SC and DC but a gradual shift toward SC-like patterns, with less distinct developmental phases. These findings provide rare insight into how maternal androgen exposure interacts with socio-ecological factors to shape developmental plasticity, influencing mechanisms of female sexual selection and intrasexual competition. The stability of the developmental trajectory and earlier nutritional independence observed in the offspring of dominant control females may confer competitive advantages crucial for reproductive success, potentially outweighing health costs (Smyth-Kabay et al., 2024). This study highlights the adaptive significance of maternal effects in shaping competitive traits in offspring and contribute to a deeper understanding of selective pressures in social mammals.

CRediT authorship contribution statement

Britta Walkenhorst: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Ines Braga Goncalves:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Christine M. Drea:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Marta B. Manser:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) utilised ChatGPT for tasks such as grammar and spelling checks to proofread the text. Following the use of this tool/service, the author(s) carefully reviewed and edited the content as necessary and take full responsibility for the integrity and accuracy of the final publication.

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Declaration of competing interest

We have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2025.105814>.

[org/10.1016/j.yhbeh.2025.105814](https://doi.org/10.1016/j.yhbeh.2025.105814).

Data availability

R analysis code and study data can be downloaded from <https://tinyurl.com/WalkenhorstEtAl20251>

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