

1 **Dispersal-induced social stress prolongs gestation in wild meerkats**

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18 **Abstract**

19 In the majority of mammals, gestation length is relatively consistent and seldom
20 varies by more than 3%. In a few species, females can adjust gestation length by
21 delaying the development of the embryo after implantation. Delays in embryonic
22 development allow females to defer the rising energetic costs of gestation when
23 conditions are unfavourable, reducing the risk of embryo loss. Dispersal in mammals
24 that breed cooperatively is a period when food intake is likely to be suppressed and
25 stress levels are likely to be high. Here we show that pregnant dispersing meerkats
26 (*Suricata suricatta*), which have been aggressively evicted from their natal group and
27 experience weight loss and extended periods of social stress, prolong their gestation
28 by means of delayed embryonic development. Repeated ultrasound scans of wild,
29 unanaesthetised females throughout their pregnancies showed that pregnancies of
30 dispersers were on average 6.3% longer and more variable in length (52-65 days) than
31 those of residents (54-56 days). The variation in dispersers shows that, unlike most
32 mammals, meerkats can adapt to stress by adjusting their pregnancy length by up to
33 25%. By doing so, they potentially rearrange the costs of gestation during adverse
34 conditions of dispersal and enhance offspring survival.

35 **Introduction**

36 Gestation length is relatively invariable in most mammalian species [1] and although
37 flexibility to adjust this energetically demanding period would be adaptive in
38 unpredictable environments, only few species have been shown to possess such
39 flexibility [2,3]. For example, in wild California leaf-nosed bats (*Macrotus*
40 *californicus*), low body temperature slows the rate of embryonic development [4]; and
41 in the short-tailed fruit bat (*Carollia perspicillata*), stressful lab conditions impede

42 prenatal development [5]. Bat species have a more variable gestation length as a
43 consequence of delayed post-implantation embryonic development and can prolong
44 their gestation by up to 50% [4–7]. The ability to delay embryonic development could
45 be adaptive when food is scarce or predation rates are likely to be high [5]. Stress
46 induced retardation of development would maximise the amount of time offspring
47 spend in the safest stage of development (cf., safe harbour hypothesis) [8] and defer
48 the steeply rising energetic demands of the final quartile of gestation [9], reducing the
49 risks of embryo loss.

50 Mammals can adjust gestation length by either delaying implantation of the blastocyst
51 or by delaying the post-implantation development of the embryo [3,10]. Delayed
52 implantation occurs in nine mammalian orders (Diptrotodontia, Dasyuromorphia,
53 Eulipotyphyta, Cingulata, Carnivora, Rodentia, Chiroptera, Lagomorpha,
54 Cetartiodactyla) and allows mating when both male and female are in peak physical
55 condition [3,10]. It has been shown to be dependent on maternal [11], environmental
56 [12], and social [13] factors. The fact that delayed implantation has been observed in
57 a wide range of taxa shows its ecological significance and suggests that it has evolved
58 independently several times [14]. While delayed implantation is common in
59 mammals, delayed development has only been observed in ten bat species and little is
60 known about its ecological function [3].

61 Here we show that cooperative meerkats exhibit variable gestation length due to
62 delayed post-implantation development. Meerkats live in groups of 2-50 individuals
63 with a dominant pair that monopolises most of the reproduction and several closely
64 related subordinate helpers [15,16]. The dominant female aggressively evicts
65 subordinate females when subordinates are pregnant. Evictees either abort their
66 pregnancy (stress-induced reproductive suppression) and return to their group [17], or

67 permanently disperse in multiple-member coalitions to establish a new group and
68 often bring their pregnancies to term [18,19]. Most dispersing females are pregnant at
69 eviction, but those who are not typically conceive with roaming males soon after
70 eviction [20]. One coalition member attains dominance in the new group, while the
71 remaining coalition members remain subordinate [19]. Aggression at eviction and
72 costs associated with dispersal increase acute stress levels (as measured by faecal
73 glucocorticoids) as well as reduce foraging efficiency and body mass [17,21]. Despite
74 these high dispersal costs, dispersing meerkats try to bring their pregnancies to term
75 to rapidly augment their new group [18,19]. We hypothesised that gestation is delayed
76 in females experiencing stressful social conditions during eviction and dispersal.

77 **Methods**

78 *Study population*

79 We followed 44 groups of habituated wild meerkats between September 2013 and
80 January 2019 at the Kalahari Meerkat Project (KMP) located on the Kuruman River
81 Reserve (26° 59' S, 21° 50' E) in South Africa. One individual per resident group
82 carried a VHF collar as part of the long-term activities at the KMP (Biotrack Ltd,
83 Wareham, UK: 23 g) [22]. We fitted VHF collars to subordinate females immediately
84 after eviction from the resident group (Holohil Systems Ltd, Ontario, Canada: 25 g,
85 ~3.5 % of meerkat body mass). To mount the collars, individuals were sedated using a
86 mixture of isoflurane and oxygen in compliance with the KMP protocol [22].
87 Dispersing and resident individuals were tracked every 4-7 days by means of VHF
88 telemetry. We only considered pregnancies where pups were born successfully. This
89 could be guaranteed by observing lactation marks on the mother and other group

90 females that helped with nursing (pups stay hidden under ground for the first four
91 weeks of life).

92 *Visual pregnancy assessment*

93 Meerkats were habituated to the presence of people (<1 m) and trained to climb onto a
94 portable weighing scale allowing for regular weight measures to corroborate the
95 visual pregnancy assessment. Abdominal swelling and weight gain become apparent
96 28 days after conception [23] (Fig. S1), and we so measured the onset of 96
97 pregnancies in 46 dispersers and 258 pregnancies in 103 residents. We identified
98 parturition from a sudden change in abdominal shape and weight loss [23] (Fig. S1).

99 Some evicted females lost their pups after birth and returned to their natal groups.
100 Hence, the same female may have been evicted and pregnant multiple times.
101 Therefore, some dispersers – and some residents, having multiple pregnancies
102 throughout their lives – were included in the analysis more than once. On average, we
103 included 2.1 pregnancies per female in dispersers (SD=1.5, min-max=1-7) and 2.5
104 pregnancies per female in residents (SD=2.5, min-max=1-13).

105 *Ultrasound scans*

106 Because abdominal swelling is not an unequivocal measure of pregnancy stage, we
107 used sequential transcutaneous ultrasound scans to precisely monitor 13 additional
108 pregnancies, i.e., 8 dispersers and 5 residents (Table S1). We trained animals to hold
109 upright still for the scanning procedure by providing small amounts of water and egg
110 (Fig. S2). We performed scans using an ultrasound probe (Linear array L742,
111 SonoScape Ltd, Nanshan, China) and water-based lubricant. The procedure could
112 usually be executed every 4-7 days without the need for anaesthesia, and we

113 identified time of implantation and measured relevant gestational features of
114 embryonic development until parturition (Fig. 1, Fig. S5-11, Table S2). On the
115 earliest ultrasound scans where we could detect pregnancies, the embryonic vesicle
116 containing amniotic fluid was visible and embedded in the decidua (Fig. 1a). Shortly
117 after, we could identify the embryonic structure in form of a hyperechogenic, grain of
118 rice-like mass and the early formation of the endotheliochorial placenta, confirming
119 successful implantation of the early embryo [24]. We hereafter refer to these earliest
120 observations of implanted embryos as time of implantation.

121 We measured the outer diameter of the embryonic vesicle as an estimate of total
122 embryonic size (Fig. S3) using the Zeiss ZEN blue software (Zeiss GmbH, Jena,
123 Germany). To define a standardised time of implantation, we selected three
124 pregnancies for which embryonic vesicle diameter on the day of earliest detection was
125 smallest (<0.4 cm, Table S1) and signs of implantation present. From these three
126 pregnancies we obtained an average embryo development curve starting with the day
127 of implantation using the *loess* function in R, version 4.1.2 [25] (Fig. S4). We then
128 used the average development curve to backdate implantation of pregnancies with
129 embryonic vesicle diameter >0.4 cm on the day of earliest detection (Fig. S4). On
130 average, the earliest-detection embryo size was 0.58 cm (interquartile range=0.54-
131 0.61 cm, min-max: 0.30-0.86 cm) when the conceptuses were still spherical. We only
132 used pregnancies with earliest-detection embryo size <1 cm to reduce noise arising
133 from different angles of non-spherical scan cross-sections (Fig. S5). Where possible,
134 we obtained negative scans a few days prior to implantation to back up our estimate
135 (Table S1-2). Around parturition, we visited animals every other day and could
136 therefore estimate birth dates with ± 1 day accuracy.

137 *Palpation*

138 We observed two additional pregnancies by palpation during the captures of two
139 dispersing females under anaesthesia (Table S1). By touching the animals' abdomen,
140 we could identify the embryo palps and confirm the pregnancies previously observed
141 by visual assessment. The identification of the embryos was done in collaboration
142 with a veterinarian (S. Patterson, Royal Veterinary College, University of London,
143 UK). We estimated the size of the embryo to be at least 0.9 cm at the time of
144 palpation (i.e., max. measure of embryonic vesicle diameter on early ultrasound
145 images), as it would be unlikely to detect palps smaller than this size. We backdated
146 the time of implantation with the above-described method. Embryos may have been
147 larger at the time of palpation, but we used a conservative measure to avoid
148 overestimation of pregnancy length.

149 *Statistical analysis*

150 *Visual assessment* - We used a linear mixed effects model (LMM) in the R package
151 *lme4* [26] with log-transformed gestation time (Δt first abdominal swelling-
152 parturition) as response (right-skewed distribution) to test the difference between
153 dispersers (n=96) and residents (n=258). In addition, we investigated the influence of
154 social status (dominant vs. subordinate, see SI Text) and number of prior pregnancies
155 on development time. It was suggested that parity [5] and competition between social
156 ranks can affect pregnancy length [27]. To ensure that covariates were not correlated
157 with each other, we calculated variance inflation factors for the model coefficients
158 [28], none were correlated (max VIF=1.28). We used individual identity as a random
159 intercept term.

160 *Ultrasound and palpation* - Here, we used a nonparametric Kruskal-Wallis test (KW)
161 in the basic R environment to test the difference in gestation length (Δt implantation-
162 parturition) between dispersers ($n_{\text{ultrasound}}=8 + n_{\text{palpation}}=2$) and residents ($n_{\text{ultrasound}}=5$).
163 To confirm that the two pregnancies detected by palpation did not bias the ultrasound
164 results, we performed a second KW without the palpation pregnancies to investigate
165 the difference between dispersers and residents. We performed a third KW to test for
166 differences in gestation length between dominant, subordinate, and lone females. We
167 used non-parametric tests because the data were not normally distributed and did not
168 use random terms to avoid overfitting. However, except for two individuals of which
169 each had two pregnancies (Table S1), all pregnancies were from different individuals
170 originating from seven different natal groups.

171 **Results**

172 Both methods – visual and ultrasound – showed that, on average, dispersing females
173 had longer pregnancies than resident females (Fig. 2). Based on visual assessment,
174 dispersers had an average post-assessment (i.e., abdominal swelling) development
175 time of $45.1 \pm \text{SE } 1.6$ days while that of residents was 39.3 ± 0.7 days (Est=0.12,
176 SE=0.04, $p < 0.005$, Table S3). The ultrasound scans revealed that dispersers can
177 indeed prolong their pregnancies by means of delayed embryonic development, with
178 an average post-implantation duration of 57.9 ± 1.39 days in dispersers versus
179 54.6 ± 0.16 days in residents (Chi=4.17, $p = 0.041$, Table S3). Post-implantation periods
180 ranged from 52 to 65 days in dispersers and from 54 to 56 days in residents. Gestation
181 was on average longer when measured with ultrasound because embryos could be
182 detected on average one week before first abdominal swelling was visible. Based on
183 ultrasound, on average dispersers prolonged their post-implantation time by 6.3%.

184 With the shortest observed post-implantation period being 52 days and the longest
185 being 65 days (Table S1), we observed a maximum difference of 13 days or 25%.
186 Although the longest recorded pregnancy (65 days) was identified by palpation, the
187 second-longest pregnancy was nearly as long (62 days) and was identified by
188 ultrasound. When excluding the two pregnancies identified by palpation, the
189 difference in gestation length between dispersers and residents was still marginally
190 significant, i.e., the p-value was below 0.1 (Chi=2.91, p=0.088, Table S3).
191 There was a positive correlation between gestation length and number of previous
192 pregnancies (Est=0.02, SE=0.01, p=0.004) and there were no differences in gestation
193 length between dominant, subordinate (Est=-0.01, SE=0.04, p=0.729), and lone
194 females (Est=0.14, SE=0.10, p=0.150, Table S3). The analysis based on ultrasound
195 confirmed that there was no difference between dominants and subordinates
196 (Chi=0.25, p=0.885, Table S3).

197 **Discussion**

198 Our ultrasonographic assessment confirms that the observed delay in meerkat
199 pregnancies was due to delayed post-implantation embryonic development. The most
200 likely explanation of the observed flexibility in embryonic development is that it is a
201 mechanism to allow pregnant females under adverse conditions to delay and spread
202 the energetic costs of gestation [4,5], which increase rapidly in the last month of
203 pregnancy [9]. There is evidence that eviction and dispersal have substantial costs in
204 meerkats, including low foraging efficiency, body-condition loss, and increased
205 glucocorticoid levels [17,21]. Stress and malnutrition are therefore likely causes to
206 delay the increasing energetic demands of the final stages of gestation in dispersing
207 meerkats, which could improve the chances of giving birth to successful offspring

208 upon settlement. An alternative, non-adaptive explanation is that embryonic
209 development is slowed down as a by-product of reduced food intake and limited
210 investment into embryo growth.

211 Adaptation of pregnancy length to reproductive conflict may be a common trait in
212 social mongooses, as subordinates of the cooperatively breeding banded mongoose
213 (*Mungo mungo*) give birth earlier and synchronise parturition with the dominant
214 female to avoid infanticide [27]. Older and more dominant females conceive a few
215 days before their younger group members, but all females usually give birth on the
216 same day. By delaying mating, younger females may gain access to high-quality
217 males after these males have finished mating with the older females in the group.
218 Alternatively, delayed oestrus in younger females may reflect their latency in reacting
219 to the behavioural or pheromonal cues of dominant females that enter oestrus. While
220 it is unclear which mechanism is responsible for reduced gestation length in
221 subordinate females of banded mongooses, the reduction seems to be caused by
222 reproductive conflict within the group. As such, variable gestation length in both
223 meerkats and banded mongooses is an adaptation of subordinate females to
224 reproductive suppression.

225 Our findings suggest that meerkats can adjust their pregnancy length in response to
226 reproductive suppression (i.e., eviction) and dispersal. Increased stress during eviction
227 [17] and dispersal [21] may have led to a temporary arrest or decreased rate of
228 embryonic development [5]. In other species where gestational delays have been
229 documented, these appear to depend on abiotic stressors such as food availability or
230 temperature [4,29]. In meerkats, however, gestational delays seem to be initiated by
231 stressful evictions and are therefore socially induced. Dispersal-related external

232 factors such as low foraging rate, unfamiliar landscapes, and increased predation
233 pressure are likely to add to the costs of social stressors.

234 In addition, retarded embryonic development could be responsible for stress-induced
235 pregnancy failure in form of embryonic absorption and foetal abortions in evicted
236 meerkats [17,30], as delayed development has been suggested to facilitate
237 reabsorption of the embryo [31]. A stress-related mechanism to abort or prolong
238 pregnancies in evicted meerkats may be adaptive, offering the potential to end or
239 extend a pregnancy depending on whether a female returns to the natal group or
240 disperses and starts a new group. If a female disperses, deferring the cost of gestation
241 may increase the chance of giving birth successfully, and consequently of new group
242 establishment as the success of new groups depends on their rapid augmentation.

243 Our study is the first confirmed observation of delayed post-implantation embryonic
244 development in mammals outside of the Chiroptera. There is, however, some
245 indication of delayed embryonic development in armadillos (*Dasypus novemcinctus*)
246 [32] and Antarctic fur seals (*Arctocephalus gazella*) [29]. Considering its high
247 adaptive value, delayed embryonic development may also occur in other mammalian
248 species, yet it is hard to prove due to the inherent difficulty of determining
249 implantation date in wild animals [33].

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268 **Data and code**

269 Data and code supporting this manuscript are available
270 <https://doi.org/10.5061/dryad.stjq2c6r> [34]. Data include ultrasonographic images of
271 13 pregnancies.

272 Additional figures and methodological details are provided in the electronic
273 supplementary material <https://doi.org/10.6084/m9.figshare.c.6706344>.

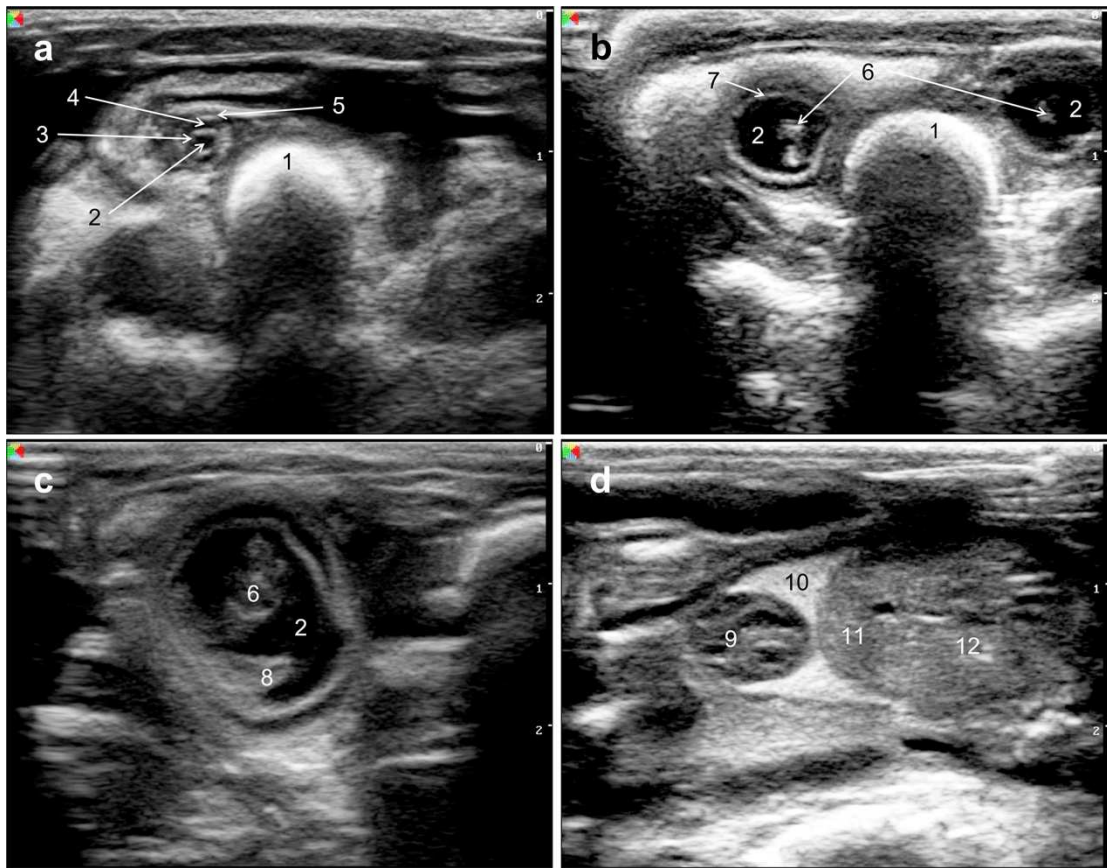
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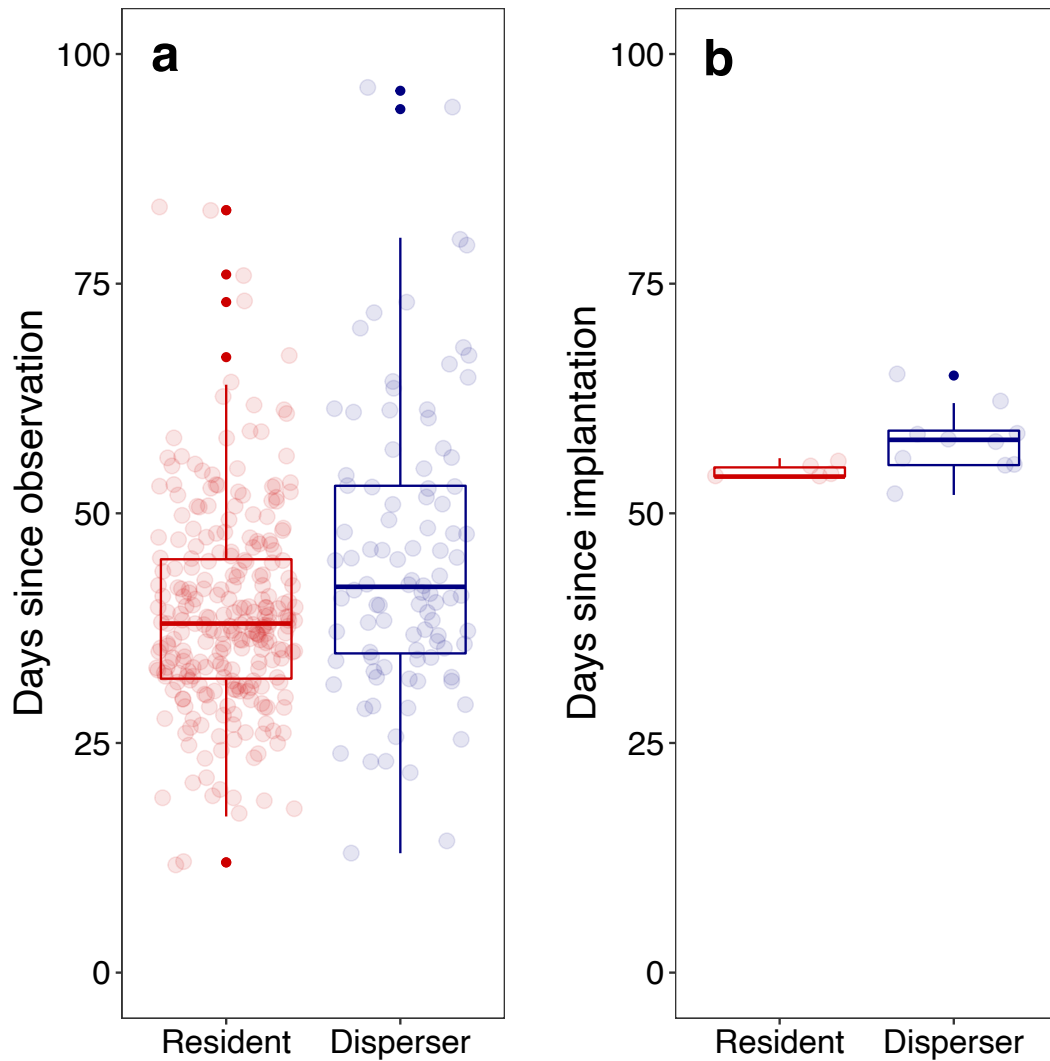
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359

360 **Fig. 1. Cross-sectional ultrasound scans of embryos during developmental stages**
 361 **of a meerkat gestation.** Embryonic development 0 days (a), 6 days (b), 12 days (c),
 362 and 36 days (d) after implantation. 1 = maternal spine, 2 = amniotic fluid, 3 =
 363 hyperechogenic mass, 4 = thickened placenta ring, 5 = outline uterus, 6 = embryo, 7 =
 364 embryonic vesicle, 8 = yolk sac, 9 = embryonal heart, 10 = lungs, 11 = liver, 12 =
 365 intestines. **a,** The early embryo has just implanted in the decidua. **b, c,** The embryo
 366 and yolk sac are clearly visible inside the amniotic cavity. **d,** The embryo has become
 367 large and its organs are detectable. The scales along the right picture margins are
 368 given in centimetres.



369

370 **Fig. 2. Variation in gestation length between resident and dispersing meerkats. a,**
 371 **Days between first observed abdominal swelling in the field and parturition. b, Days**
 372 **between implantation date estimate and parturition based on ultrasound. Boxplots**
 373 **show median and interquartile range, error lines show values within 1.5 times**
 374 **interquartile range, transparent points show raw data. Gestation length was on average**
 375 **longer when measured with ultrasound because we detected pregnancies earlier.**