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3

4 **Competitive growth in a cooperative mammal**

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22

23

24 In many animal societies where hierarchies govern access to reproduction, the social rank of
25 individuals is related to their age and weight¹⁻⁵ and slow-growing animals may lose their place
26 in breeding queues to younger ‘challengers’ who grow faster than they do^{5,6}. The threat of
27 being displaced might be expected to favour the evolution of competitive growth strategies,
28 where individuals increase their own rate of growth in response to increases in the growth of
29 potential rivals. While growth rates have been shown to vary in relation to changes in the
30 social environment in several vertebrates including fish^{2,3,7} and mammals⁸, it is not yet known
31 whether individuals increase their growth rates in response to increases in the growth of
32 particular reproductive rivals. Here we show that, in wild Kalahari meerkats (*Suricata*
33 *suricatta*), subordinates of both sexes respond to experimentally induced increases in the
34 growth of same-sex rivals by raising their own growth rate and food intake. In addition, when
35 individuals acquire dominant status, they show a secondary period of accelerated growth
36 whose magnitude increases if the difference between their own weight and that of the heaviest
37 subordinate of the same sex in their group is small. Our results show that individuals adjust
38 their growth to the size of their closest competitor and raise the possibility that similar plastic
39 responses to the risk of competition may occur in other social mammals, including domestic
40 animals and primates.

41

42 Recent studies have revealed the extent to which aspects of the social environment can affect
43 growth in several vertebrates. In some social fish, the risk of conflict with dominant
44 individuals reduces the growth rates of subordinates^{2,3,7} while, in some mammals, prenatal
45 growth increases in response to physiological stress levels in pregnant mothers in high-density
46 environments⁸. However, studies have not yet investigated whether adolescents or adults can
47 adjust their growth rates in relation to changes in the size of specific rivals who may displace
48 them in reproductive queues. In many cooperatively breeding mammals, subordinates of both

49 sexes queue for reproductive opportunities in breeding groups, sometimes for several years^{5,9}.
50 Rank in these queues is usually determined by relative age and weight, and previous research
51 has produced some evidence of strategic adjustments in growth. In mole-rats and meerkats,
52 adult females that acquire the dominant breeding position commonly show a period of
53 secondary growth¹⁰⁻¹² which may allow them to increase their fertility or consolidate their
54 status^{5,13}. Here, we describe experiments that investigate whether subordinate meerkats
55 queuing for breeding opportunities also engage in competitive growth.

56

57 Meerkats live in groups of 3–50 individuals where 90% of reproduction is monopolised by a
58 single dominant pair⁵. Subordinates of both sexes contribute to costly cooperative activities,
59 including pup-feeding, babysitting and raised-guarding¹⁴. Within groups, subordinates of the
60 same sex are ranked in a hierarchy based on age and weight¹⁵. If the breeding female dies, the
61 oldest and heaviest subordinate typically replaces her, and subordinate females occasionally
62 displace breeders⁵. Unlike females, most males leave their natal groups voluntarily when they
63 are 2–4 years old in small parties of 2-6 individuals, and attempt to displace males in other
64 groups^{5,16}. If they are successful, the oldest and heaviest male in the party may often assume
65 the breeding position. If they are successful, the oldest and heaviest male usually assumes the
66 breeding position^{5,16}. Data presented here are derived from a twenty-year study of wild
67 meerkats that has encompassed more than sixty groups in which all individuals were
68 recognisable. Most individuals were trained to climb onto electronic balances and were
69 weighed three times a day (dawn; after three hours of foraging; and dusk) on approximately
70 ten days a month throughout their lives⁵. Changes in the weight of individuals between the
71 beginning and end of morning foraging sessions provide a measure of their food intake.

72

73 Using 14 groups of habituated meerkats, we manipulated the growth of subordinates of both
74 sexes by provisioning particular individuals and measuring effects on the growth and food
75 intake of individuals of the same sex immediately above them in the age-related hierarchy.
76 We identified pairs of same-sex littermates belonging to two distinct age classes: juveniles
77 (aged 4–7 months), who had recently reached nutritional independence (n=12 female and 19
78 male litters from 12 groups), and young adults (aged 12–24 months), who had reached sexual
79 maturity and were able to compete for any breeding vacancies that occurred⁵ (n=8 female and
80 9 male litters from 14 groups). In each pair, we fed the lighter individual, later referred to as
81 the ‘challenger’, with half a hard-boiled egg twice per day for three months. We subsequently
82 compared the growth of unfed littermates, referred to as ‘challenged’ individuals, with those
83 of unfed control individuals of the same age from other litters over the same period (Extended
84 Data Figure 1).

85

86 Challenged individuals of both age classes responded to increases in the growth of fed
87 challengers by increasing their average weight (both in absolute terms and relative to controls)
88 over the course of the experiment. Growth from the start to the mid-point of the experiment
89 was greater in challenged than in control individuals (Figure 1a-b; juveniles: two sample
90 Welch t-test, n=32 challenged and 72 control individuals, $t=4.17$, $P<10^{-4}$; adults: n=18
91 challenged and 18 age- and sex-matched control individuals, paired t-test, $t=2.10$, $df=17$,
92 $P=0.050$), generating a difference in the average weight of challenged and control individuals
93 halfway through the experiment (juveniles: n=32 challenged and 83 control individuals,
94 $504.3\pm68.2\text{g}$ vs. $438.5\pm73.2\text{g}$, two-sample Welch t-test, $t=4.54$, $P<10^{-4}$, adults: pairwise
95 weight difference= $40.7\pm51.06\text{g}$, paired t-test, $t=3.38$, $df=17$, $P=0.003$). Differences in growth
96 were, however, no longer detectable in the second half of the experiment (Juveniles: n=27
97 challenged and 74 control individuals, two-sample Welch t-test, $t=0.22$, $P=0.825$; adults:

98 paired t-test, $t=-24.23$, $df=17$, $P=0.059$), suggesting that challenged individuals may not be
99 capable of sustaining accelerated growth over extended periods. In both age classes, the
100 growth of challenged individuals over the first half of the experiment was positively
101 correlated with the growth of their fed challenger (Extended Data Figure 2, Extended Data
102 Table 1), suggesting that challenged individuals adjusted their growth response to the growth
103 of their rival. Increases in the growth of challenged individuals were associated with increases
104 in food intake: food intake was greater for challenged than for control individuals in the first
105 half of the experiment (Figure 1c-d, juveniles: $n=32$ challenged and 86 control individuals,
106 two-sample Welch t-test, $t=2.17$, $P=0.033$, adults: paired t-test: $t=2.80$, $df=16$, $P=0.013$), but
107 not in the second half (Juveniles: $n=29$ challenged and 83 control individuals, two-sample
108 Welch t-test, $t=1.19$, $P=0.240$; adults: paired t-test: $t=-0.16$, $df=16$, $P=0.876$).

109

110 Social mechanisms other than competitive growth could conceivably contribute to increases
111 in the growth of challenged animals, but we were unable to find any evidence that this was the
112 case. It is unlikely that potential increases in the contributions of fed challengers to
113 cooperative activities in the first half of experiment reduced the contributions of challenged
114 animals and so increased their weight gain. First, juveniles contribute little to cooperative
115 activities, so accelerated growth in challenged juveniles cannot be mediated by changes in
116 cooperative behaviour. Second, challenged adults maintained their investment in raised-
117 guarding and pup-feeding in the same period relative to control animals (Wilcoxon signed-
118 rank paired-test, raised-guarding: $V=52$, $df=17$, $P=0.156$, pup-feeding: $V=30$, $df=14$,
119 $P=0.095$). Finally, adult fed challengers increased their contributions to raised guarding but
120 not to pup-feeding (Wilcoxon signed-rank paired-test: raised-guarding: $V=143$, $df=17$,
121 $P=0.013$, pup-feeding: $V=67$, $df=14$, $P=0.719$).

122

123 Additional analyses suggest that adults that acquire dominant positions may also adjust their
124 growth rates in a strategic fashion. In both sexes, the lifetime breeding success of dominant
125 meerkats depends on the length of time they hold the dominant position⁵ which, in females,
126 increases with the difference between their own weight and the weight of the heaviest
127 subordinate of the same sex⁵. Since subordinates engage in competitive growth, we examined
128 whether individuals that have recently acquired the dominant position adjust the magnitude of
129 their subsequent increase in weight to the relative weight of their closest rival. We first
130 analysed whether newly dominant males and females increase their growth rate following
131 dominance acquisition by comparing their weight in the month prior to dominance acquisition
132 and in the four months following dominance acquisition. New dominants of both sexes
133 increased in weight after acquiring dominance (analysis of variance with repeated measures,
134 effect of month post-dominance acquisition on weight: $F_{4,184}=16.81$, $P<10^{-4}$, Figure 2a,
135 Extended Data Figure 3a). The extent of growth following dominance acquisition did not
136 differ between the sexes (analysis of variance with repeated measures, interaction between sex
137 and month post-dominance acquisition: $F_{4,184}=1.22$, $P=0.31$) and occurred primarily in the
138 two months following dominance acquisition (see Extended Data Table 2 for the results of the
139 post-hoc tests). This growth response may not solely reflect improved access to resources, as
140 food intake remained constant in both sexes during the same period (analysis of variance with
141 repeated measures, effect of month post-dominance acquisition on food intake: $F_{4,112}=0.34$,
142 $P=0.850$, and interaction between sex and month post-dominance acquisition: $F_{4,112}=0.09$,
143 $P=0.986$, Extended Data Figure 3b).

144

145 The growth of new dominants in the five months following dominance acquisition was more
146 pronounced when the heaviest same-sex subordinate was closer to their own weight at the
147 time of dominance acquisition (Linear Model, estimate±SD=-0.76±0.27, $F_{1,36}=7.69$, $P<0.01$,
148 Figure 2b and Extended Data Table 3). There was no significant sex difference in this
149 accelerated growth (Extended Data Table 3). Rapid post-dominance growth exacerbated
150 existing weight differences between dominants and same-sex subordinates, with the result that
151 most established dominants were the heaviest individual of their sex in their group (females:
152 58% of groups, males: 68%). While similar periods of growth after dominance acquisition in
153 female naked mole-rats have been interpreted as a way of enhancing fecundity^{11,12,17}, the
154 presence of strategic growth adjustments to the relative size of rivals in dominant meerkats of
155 both sexes suggests that these increases may serve to consolidate their status and prolong their
156 breeding tenure^{5,13}.

157

158 Our findings suggest that subordinates can track changes in the growth and size of potential
159 competitors, perhaps using physical contact as well as visual, vocal or olfactory cues, and
160 react by adjusting their own growth. While the physiological correlates of increased growth
161 rates in challenged individuals are not yet known, hormonal changes associated with
162 heightened threat of competition may increase growth and food intake. Acceleration in growth
163 following dominance acquisition is probably associated with the sudden lifting of
164 reproductive suppression and a re-orientation of life-history strategy. The hormonal profile of
165 dominant meerkats is distinct from that of subordinates, with higher plasmatic levels of
166 oestradiol and progesterone in breeding females and of cortisol in breeders of both
167 sexes^{10,18,19}. Sex steroids are known to regulate the production of critical actors in the
168 insulin/growth factor pathway in the mammalian reproductive tract and associated tissues²⁰,
169 which may result in the up-regulation of anabolic genes involved in growth. Strategic

170 increases in growth rates could be constrained by energy and fitness costs²¹. Allocation of
171 additional resources to growth by challenged individuals may depress immune function and
172 reduce longevity as a result of increases in oxidative stress and telomere shortening²² while
173 increases in time spent foraging may raise predation risk, which is high in meerkats²³.

174

175 Our results suggest that competitive growth may represent an important component of the
176 developmental strategy of individuals. Recognition of this process may alter classic
177 perspectives on mechanisms of social competition, which frequently suggest that the
178 phenotype of interacting individuals determines the outcome of competitive interactions
179 rather than vice versa. As reproductive queues are widespread in social mammals and the size
180 and weight of individuals often affect their status and breeding success²⁴, competitive growth
181 may occur in many other social species, possibly including domestic mammals, nonhuman
182 primates and humans.

183

184 **References and Notes**

- 185 ¹ Hoogland, J L, *The black-tailed prairie dog: social life of a burrowing mammal*. (University
186 of Chicago Press, Chicago, 1995).
- 187 ² Buston, P. M., Social hierarchies: size and growth modification in clownfish. *Nature* **424**, 145
188 (2003).
- 189 ³ Heg, D., Bender, N., and Hamilton, W. D., Strategic growth decisions in helper cichlids. *Proc.*
190 *R. Soc. Lond. Ser. B-Biol. Sci.* **271**, S505 (2004).
- 191 ⁴ Spong, G F, Hodge, S J, Young, A J, and Clutton-Brock, T H, Factors affecting reproductive
192 success of dominant male meerkats. *Mol Ecol* **17**, 2287 (2008).
- 193 ⁵ Clutton-Brock, T. H. et al., Intrasexual competition and sexual selection in cooperative
194 mammals. *Nature* **444** (7122), 1065 (2006).
- 195 ⁶ Reeve, H. K. , Peters, J. M., Nonacs, P., and Starks, P. T., Dispersal of first “workers” in
196 social wasps: causes and implications of an alternative reproductive strategy. *Proc Natl Acad*
197 *Sci USA* **95**, 13737 (1998).
- 198 ⁷ Wong, M. Y. L., Munday, P. L., Buston, P. M., and Jones, G. P., Fasting or feasting in a fish
199 social hierarchy. *Curr Biol* **18**, R372 (2008).
- 200 ⁸ Dantzer, B. et al., Density triggers maternal hormones that increase adaptive offspring growth
201 in a wild mammal. *Science* **340**, 1215 (2013).

202 9 Hauber, M. E. and Lacey, E. A., Bateman's principle in cooperatively breeding vertebrates:
203 The effects of non-breeding alloparents on variability in female and male reproductive
204 success. *Integr. Comp. Biol.* **45** (5), 903 (2005).
205 10 Russell, A. F. et al., Adaptive size modification by dominant female meerkats. *Evolution* **58**,
206 1600 (2004).
207 11 Young, A. J. and Bennett, N. C., Morphological divergence of breeders and helpers in wild
208 damaraland mole-rat societies. *Evolution* **64**, 3190 (2010).
209 12 Dengler-Crish, C. M. and Catania, K.C., Phenotypic plasticity in female naked mole-rats after
210 removal from reproductive suppression. *J Exp Biol* **210**, 4351 (2007).
211 13 Clutton-Brock, T., Structure and function in mammalian societies. *Phil Trans R Soc B* **364**,
212 3229 (2009).
213 14 Clutton-Brock, T. H. et al., Evolution and development of sex differences in cooperative
214 behavior in meerkats. *Science* **297**, 253 (2002).
215 15 Thavarajah, N. K., Fenkes, M., and Clutton-Brock, T.H., The determinants of dominance
216 relationships among subordinate females in the cooperatively breeding meerkat. *Behaviour*
217 **151**, 89 (2014).
218 16 Doolan, S. P. and Macdonald, D. W., Dispersal and extra-territorial prospecting by slender-
219 tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *J Zool* **240**, 59 (1996).
220 17 O'Riain, M J et al., Morphological castes in a vertebrate. *Proc Natl Acad Sci USA* **97**, 13194
221 (2000).
222 18 Carlson, A. A. et al., Hormonal correlates of dominance in meerkats (*Suricata suricatta*).
223 *Horm Behav* **46** (2), 141 (2004).
224 19 Young, A. J., Monfort, S. L., and Clutton-Brock, T. H. , The causes of physiological
225 suppression among female meerkats: a role for subordinate restraint due to the threat of
226 infanticide? *Horm Behav* **53**, 131 (2008).
227 20 Dantzer, B. and Swanson, E. M., Mediation of vertebrate life histories via insulin-like growth
228 factor-1. *Biol Rev* **87**, 414 (2012).
229 21 Arendt, J.D., Adaptive intrinsic growth rates: An integration across taxa. *Q Rev Biol* **72**, 149
230 (1997).
231 22 Metcalfe, N. B. and Monaghan, E.P., Compensation for a bad start: grow now, pay later?
232 *Trends Ecol Evol* **16**, 254 (2001).
233 23 Clutton-Brock, T. H. et al., Predation, group size and mortality in a cooperative mongoose,
234 *Suricata suricatta*. *J Anim Ecol* **68**, 672 (1999).
235 24 Clutton-Brock, T. and Huchard, E., Social competition and selection in males and females.
236 *Philosophical Transactions of the Royal Society B-Biological Sciences* **368**, 20130074 (2013).
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251

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255 information is available at www.nature.com/reprints. Correspondence and requests for
256 materials should be addressed to ehuchard@gmail.com.

257

258 **Figure legends**

259

260 **Figure 1. Competitive growth in subordinates.** Boxplots showing the growth (individual
261 weight difference between the start and mid-point of the experiment) (panels a, b) and food
262 intake (average morning weight gain in the first half of experiment) (panels c, d) of unfed,
263 ‘challenged’ individuals (light grey boxes) and of their fed ‘challengers’ (dark grey boxes)
264 relative to control individuals (white boxes) in juveniles (panels a, c) and adults (panels b, d).
265 Whiskers comprise all data points. Numbers below the boxes indicate the number of
266 individuals.

267 **Figure 2. Competitive growth in dominants.** Panel a: example growth trajectories of a male
268 and female during their transition to dominance. Panel b: adjustment of growth following
269 dominance acquisition in response to social competition in 20 males and 25 females. Dots
270 show the raw values (grey for females, black for males) of dominant weight gain within the
271 150 days following dominance acquisition as a function of weight difference to the heaviest
272 same-sex subordinate (measured at dominance acquisition). The dotted line shows the
273 predicted values of the linear model (results presented in Extended Table 3) and standard
274 deviations of the predicted values are delineated by shaded areas.

275 **Methods**

276 **Study site and population**

277 Data were collected between 1996 and 2013 as part of a long-term study of wild meerkats at
278 the Kuruman River Reserve, South Africa. The site experiences a hot–wet season (October–
279 April) and a cold–dry season (May–September), with extensive inter-annual variation in
280 rain²³. Rainfall was measured daily (in millimetres) using a standard gauge²⁵. Details about
281 the site and population are published elsewhere^{5,14,23}.

282 Meerkats were habituated to humans and individually recognizable by dye marks.
283 Groups were visited about three times a week, so life-history events (births, deaths,
284 emigrations, changes in dominance) were known to an accuracy of about 3 days (refs 5, 14).
285 Pregnancy status was inferred from parturition date and affects female weight from the
286 midpoint of gestation, lasting approximately 70 days (ref 26). Females were considered
287 pregnant from 40 days before parturition or from the first day of detectable pregnancy in cases
288 where abortions occurred. Dominant individuals were identified by their behaviour towards
289 group-mates^{4,5}. They scent-marked more frequently than subordinates, and asserted their
290 dominance over others by anal marking, by rubbing them with their chin, and more rarely by
291 attacking and biting them. Changes in dominance were immediately recognizable, as they
292 were often preceded by a short period (hours to days) of intense fighting, and were
293 accompanied by dramatic changes in behaviour in the contesting individuals. Previous genetic
294 work has shown the absence of incestuous matings within groups⁴. If all immigrant males die,
295 a natal male may become socially dominant in his group. Natal dominant males do not mate-
296 guard the dominant female, which is often their mother, and regularly conduct extraterritorial
297 forays for mating opportunities²⁷. These males (77/166 dominant males in our dataset) were
298 excluded from analyses.

299 **Weight measures**

300 Individuals were trained to climb onto a laboratory balance in return for drops of water or
301 crumbs of hard-boiled egg, allowing us to record body weight to an accuracy of 1 g. Although
302 individuals were often weighed three times a day, we only used data collected in the morning
303 right after emergence from the burrow and before foraging, to avoid noise created by variation
304 in foraging success throughout the day²⁵. Food intake, or morning weight gain, was calculated
305 as the difference between weight collected before foraging activity started, and weight
306 collected after about 3 h of foraging¹⁰.

307 **Cooperative behaviour**

308 Three cooperative activities are regularly performed by male and female meerkats¹⁴: (1)
309 babysitting newborn pups, where an individual stays at the burrow while the rest of the group
310 forages; (2) feeding pups that are old enough to join foraging trips (approximately 1–3 months
311 old); and (3) raised-guarding, where an individual ceases foraging and climbs to a raised
312 position to watch out for potential dangers. The occurrence of babysitting, pup-feeding and
313 raised-guarding was recorded *ad libitum* as events during observation sessions, allowing
314 quantification of relative rates of helping per individual: that is, the number of occurrences of
315 one cooperative behaviour performed by one individual relative to the total number of
316 occurrences of that behaviour in the group over a given period.

317 **Competitive growth experiment**

318 From 2010 to 2013, we conducted a set of 3-month feeding experiments on adults aged 310–
319 870 days and on juveniles aged 111–215 days to investigate whether unfed littermates
320 (challenged individuals) would increase their growth rate in response to experimentally
321 elevated growth rates of their fed siblings (challengers). We identified pairs containing at least
322 two same-sex littermates and fed the individual that was lightest (or as heavy as its sibling)
323 when the experiment started (mean weight difference (\pm s.d.) in juveniles: 9.8 ± 30.6 g; in
324 adults: 29.9 ± 28.2 g). The fed individuals received half an egg twice daily four times a week
325 for 3 months. Competitive growth has never been described previously, so no prior
326 information was available for power analyses to establish adequate sample sizes. For 17 fed
327 adults including 8 females, the shortest feeding bout lasted 55 days and the mean \pm s.d.
328 feeding duration was 84 ± 11 days. For 31 fed juveniles including 12 females, the shortest
329 feeding bout lasted 21 days and the mean \pm s.d. feeding duration was 76 ± 21 days. For one
330 adult female litter and one juvenile male litter, there were three same-sex siblings and the two
331 lightest individuals were very close in weight (that is, their average weight difference was
332 lower than 10 g in the 15 days preceding the experiment); one of them was fed, and the two
333 unfed siblings were included in the cohort of challenged individuals. Experiments were
334 interrupted when a pregnancy was detected in an experimental female (fed or unfed), and
335 corresponding data were excluded from analysis. In other cases where the experiment was
336 aborted (for example, if an individual disappeared), data collected during the shortened period
337 were included in analyses; note that for three juvenile dyads, food supplementation lasted
338 respectively 21, 23 and 26 days, so these individuals were excluded from all calculations
339 related to measures describing the second half of the experiment. Observations and weighing

340 sessions were not subjected to blinding, because weight gained by fed individuals during the
341 experiment was often detectable by observers.

342

343 **Statistical analysis**

344

345 To investigate the effect of feeding individuals on the growth of their unfed same-sex
346 littermate, we first calculated the growth and food intake, averaged over the first or the second
347 half of the experiment for challenged individuals, challengers and control individuals. Growth
348 was calculated as the individual difference between weight recorded immediately before the
349 start of the experiment and at the mid-point of the experiment (45 days), or as the individual
350 change in weight from the mid-point to the end of the experiment (90 days). Food intake,
351 calculated in terms of morning weight gain, was averaged for each individual, over days 5–45
352 of the experiment (the first 4 days were excluded to allow for potential adjustments in
353 challenged individuals) and then over experimental days 45–90. We compared these measures
354 across challenged and control individuals using two-sample Welch's *t*-tests (for juveniles) and
355 paired *t*-tests (for adults) after checking that variance was homogeneous across groups using
356 Levene tests ($P > 0.05$ in all cases). We focused on the contrast between challenged and
357 control individuals: significantly higher growth in challenged individuals over controls would
358 provide experimental evidence for competitive growth, defined as an elevated increase in
359 growth in response to the challenge of a fed rival. Control individuals were selected as any
360 individual from the population during the experimental period (2010–2013) that had a lighter
361 same-sex littermate in their group at the age at which supplemental feeding started in
362 experimental groups (120 days in juveniles, 1 year in adults), to match criteria used to identify
363 unfed individuals in experimental dyads (Extended Data Fig. 1). In adults, where
364 heterogeneity in the age at the start of the experiment was considerable (361–772 days,
365 mean \pm s.d. = 496.7 ± 112.9 days), each challenged individual was matched to the same-sex
366 individual of the control cohort that was closest in age (differences in birth dates between
367 challenged individuals and their matched control were small: 2–32 days,
368 mean \pm s.d. = 11.2 ± 8.4) and present in the population at the time of the experiment.
369 Matching each experimental individual with a same-age and same-sex control in this way
370 allowed us to control for environmental variation that might otherwise have introduced noise
371 when comparing the weight and growth of individuals that underwent a supplementation at
372 different periods (e.g. during the dry versus the wet season). Individual weight before the

373 experiment was averaged across the 15 days preceding the experiment; weight at mid-point
374 was averaged across days 45–60 of the experiment; and weight at the end of the experiment
375 was averaged across experimental days 90–105.

376 It was not possible to select such matched control individuals in juveniles, however, as
377 there was no control litter born shortly before or after experimental litters in several cases.
378 Small age differences can introduce important noise when comparing weights among
379 juveniles, because growth rates are relatively high between 4 and 7 months of age, compared
380 with later ages²⁵. In the juvenile cohort, age at the start of the experiment was very
381 homogeneous (range: 111–128 days of age, mean \pm s.d. = 122.3 \pm 4.7), so matching
382 experimental dyads with control individuals by age was deemed less necessary. Individual
383 weight records were averaged across 95–110 days of age (before experiment); 170–185 days
384 of age (after about 45 days of experiment); and 215–230 days of age (after about 90 days of
385 experiment), and growth was calculated between these time points.

386 We further ran a linear model investigating the relationship between the growth of
387 challenged individuals and the growth of their fed challenger to test whether the growth
388 responses of challenged individuals were adjusted to the weight gain of their fed challenger.
389 Growth was the response variable, and was calculated as the weight difference between the
390 start and the mid-point of the experiment (since the above analyses suggested that competitive
391 growth was highest at this time). Explanatory variables included sex, age at start of
392 experiment and cumulative rainfall in the previous 9 months, which was previously found to
393 influence the growth of individual meerkats²⁵. Results and sample sizes are presented in
394 Extended Data Table 1 and Extended Data Fig. 2.

395

396 We investigated the influence of the experiment on pup-feeding and raised-guarding rates in
397 the adult cohort only, because helping is rare before 6 months of age¹⁴. We did not consider
398 babysitting because fewer than half of the experimental groups exhibited babysitting during
399 the experiment. For each observation session, we measured the observed proportion of raised-
400 guarding events performed by the focal individual relative to the total number of events
401 recorded for the group. We then calculated individual deviation from the proportion expected
402 under the null hypothesis, where each individual contributes equally, calculated as the inverse
403 of the number of helpers in the group. We averaged this deviation across all observation
404 sessions for each individual during the first half of the experiment (10–120 sessions per
405 individual, median = 19). Thus, mean deviation gives an indication of the extent of

406 cooperative behaviour relative to average contributions in the group: individuals with a larger,
407 more positive deviation have higher cooperative behaviour. We compared the mean
408 deviations between challenged individuals and their matched controls using paired Wilcoxon
409 signed-rank tests, as the response variable was not normally distributed. We used the same
410 approach to test for differences in individual contributions to pup-feeding between challenged
411 and control individuals.

412

413 When investigating changes in weight following dominance acquisition, we considered
414 individuals that maintained dominance for at least 6 months, to avoid biasing the sample
415 towards short and unstable tenures. We averaged weight records for each individual ($n = 42$
416 females and 30 males) across the 30 days preceding dominance acquisition (labelled ‘month
417 0’) and then across days 0–30, 30–60, 60–90 and 90–120 following dominance acquisition
418 (respectively labelled ‘months 1, 2, 3 and 4’). Weights recorded during pregnancies were
419 excluded. We then retained only individuals with no missing data in any of these five 1-month
420 blocks ($n = 21$ females and 27 males) to ensure a balanced design. Thus, we could evaluate
421 the significance of weight differences between 1-month blocks using a repeated-measures
422 analysis of variance with multiple factors. Factors included sex, proximity to dominance
423 acquisition (with five levels: month 0, 1, 2, 3 and 4) and the interaction between sex and
424 proximity to dominance acquisition, to test if the temporal dynamics of post-dominance
425 growth differed between males and females. Post-hoc tests were conducted using paired t -
426 tests with adjusted P values to compare within-individual changes in weight before
427 dominance acquisition to each of the 4 months after acquisition; as well as between each
428 month of the 4-month period following acquisition of dominance. A Bonferroni correction
429 was applied to correct for multiple testing. These results are presented in Extended Data Fig.
430 3a and Extended Data Table 2.

431 We compared changes in food intake (measured as morning weight gain) following
432 dominance acquisition using the same approach. As described above, we retained only
433 individuals with no missing data in any of the five 1-month blocks ($n = 9$ females and 21
434 males) to evaluate the significance of differences in food intake between 1-month blocks
435 using a repeated-measures analysis of variance with multiple factors. As above, factors
436 included were sex, proximity to dominance acquisition and their interaction. These results are
437 illustrated in Extended Data Fig. 3b.

438

439 To investigate the effect of competition on growth following dominance acquisition, we ran a
440 linear model, with weight gain within 150 days following dominance acquisition (calculated
441 as weight 150 days after dominance acquisition minus weight at dominance acquisition, each
442 averaged across all weights for 10 days before and after the time-point of interest) as our
443 response variable. We focused on a 5-month period after dominance acquisition, because
444 previous analyses had revealed that growth rates were elevated in the 2 to 4 months following
445 dominance acquisition. We included all new dominant females that retained dominance for
446 longer than 6 months and had at least one subordinate female in their group that was older
447 than 6 months when they became dominant. Six months is the age of the youngest female that
448 ever reached dominance. Weights recorded during pregnancies were excluded. We included
449 all new dominant males that had at least one non-natal subordinate male in their group that
450 was older than 6 months when they became dominant. Natal subordinate males were not
451 considered as rivals because they hardly ever reproduce or fight for dominance⁴. Explanatory
452 variables included sex, rainfall (averaged over the 150 days following dominance acquisition),
453 a sinusoidal term describing season of dominance acquisition²⁵, age at dominance acquisition,
454 and absolute weight difference with the same-sex rival (that is, heaviest subordinate at the
455 time of dominance acquisition). In addition, the interaction between sex and absolute weight
456 difference with the same-sex rival tested whether the effect of the weight difference with the
457 main rival differed between sexes. We used the absolute value of weight difference because
458 graphical exploration of the data suggested that dominant growth rates increase when the
459 main same-sex rival is either slightly heavier or slightly lighter, but not when the rival is much
460 lighter or much heavier. In cases where a rival is much heavier but fails to win fights over
461 dominance, he or she may have poor competitive abilities for other reasons and may not
462 represent a threat to the dominant. The results and sample sizes are presented in Extended
463 Data Table 3.

464

465 **Additional references of the section describing methods**

466 ²⁵ English, S., Bateman, A. W., and Clutton-Brock, T. H., Lifetime growth in wild
467 meerkats: incorporating life history and environmental factors into a standard growth
468 model. *Oecologia* **169**, 143 (2012).

469 ²⁶ Sharp, S. P., English, S., and Clutton-Brock, T. H., Maternal investment during
470 pregnancy in wild meerkats. *Evol. Ecol.* **27**, 1033 (2013).

- 471 ²⁷ Young, A. J., Spong, G., and Clutton-Brock, T. H., Subordinate male meerkats
472 prospect for extra-group paternity: alternative reproductive tactics in a cooperative
473 mammal. *Proc R Soc B* **274**, 1603 (2007).
- 474 ²⁸ R Development Core Team (2015). R: A language and environment for statistical
475 computing. R Foundation for Statistical Computing, Vienna, Austria. URL
476 <http://www.R-project.org/>.

477 **Extended data Figure legends**

478 **Extended data Figure 1. Diagram depicting the experimental design.** Juvenile
479 experiments were conducted from 15/12/2010 to 19/08/2012, and adult experiments from
480 28/03/2011 to 20/07/2013. Each horizontal line represents longitudinal weight data collected
481 from an experimental group. Thick orange lines represent unfed, challenged individuals and
482 blue lines represent fed challengers. Thick green lines represent control individuals, which
483 were animals of the same sex and age-range from the same population over the same period
484 (2010–2013). Red boxes indicate the 3-month experimental windows of food
485 supplementation, which spanned different time periods for different dyads (allowing us to
486 disentangle experimental effects from environmental and seasonal effects on weight) and, for
487 the adult experiment, occurred any time between 310 and 870 days of age. F: female, M:
488 male. Note that the x-axis is not drawn to scale, to facilitate comparison of the design between
489 the juvenile and adult cohorts. The meerkat icon was downloaded from PhyloPic:
490 <http://phylopic.org>, with credit to Michael Keeseey.

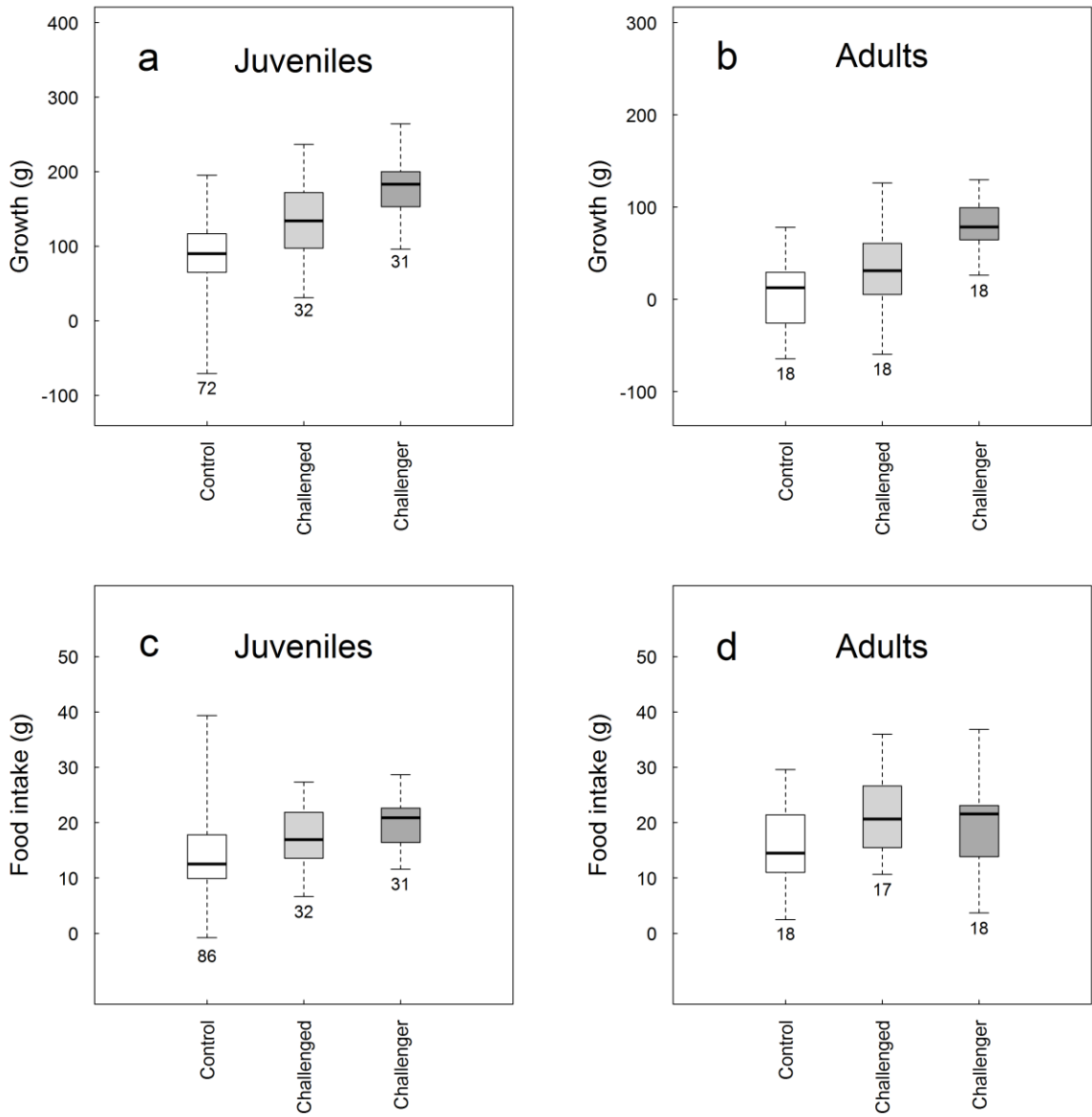
491 **Extended data Figure 2. Relationship between the growth of the challenged individual**
492 **and the growth of its fed challenger. a, Juveniles; b, adults.** Thirty-two juvenile and 17
493 adult experimental pairs were included. Growth was calculated as the individual weight
494 difference between the start and mid-point of the experiment. Dots show the raw values (grey
495 for females, black for males). The dotted line shows the predicted values of the linear model
496 (results presented in Extended Table 1) and standard deviations of the predicted values are
497 delineated by shaded areas.

498 **Extended Data Figure 3. Changes in weight and food intake in new dominant females**
499 **(grey boxes, $n = 42$) and males (black boxes, $n = 30$).** **a, Weight; b, food intake.** Boxplots
500 show the raw values, averaged for each individual during the month preceding dominance
501 acquisition (labelled '0'), as well as during the 1st, 2nd, 3rd and 4th months post-dominance

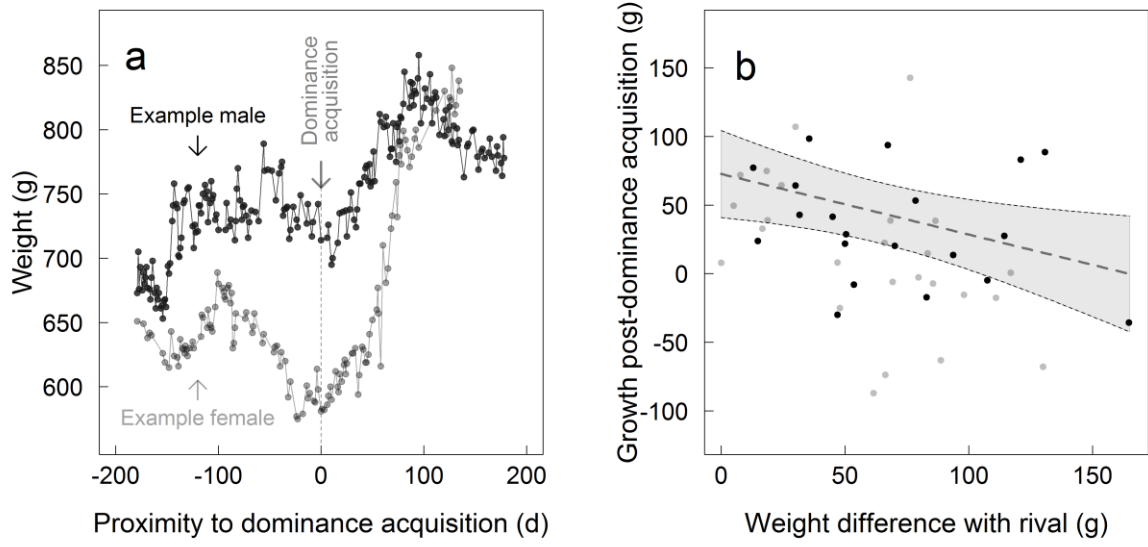
502 acquisition (respectively labelled '1', '2', '3' and '4'). Whiskers show all data points that are
503 no further away from the box than half the interquartile range.

504

505



508 **Figure 2**



509

510

511 **Extended Data Table legends**

512 **Extended Data Table 1. Results of linear models investigating the relationship between**
513 **the growth of challenged individuals and their fed challengers in juveniles and adults.**

514 The response variable is the growth of the challenged individual, calculated as the individual
515 weight difference between the start and mid-point of the experiment. The juvenile model
516 includes 12 females and 20 males and the value of the model adjusted R^2 is 0.65. The adult
517 model includes 8 females and 9 males and the value of the model adjusted R^2 is 0.61. Est.:
518 Estimate, SD: standard deviation.

519 **Extended Data Table 2. Results of the posthoc paired t-tests investigating temporal**
520 **changes in weight following dominance acquisition.** Pairwise comparison tests were

521 conducted after the repeated measures ANOVA to compare within-individual changes in
522 weight between the month preceding dominance acquisition (labelled '0') and the four
523 months (labelled '1' to '4') following dominance acquisition, as well as between each of the
524 four months post-dominance acquisition. A Bonferroni correction was applied to correct for
525 multiple testing.

526 **Extended Data Table 3. Results of the linear model investigating changes in body weight**
527 **within 150 days following dominance acquisition in relation to absolute weight**
528 **difference with the heaviest same-sex subordinate.** This analysis includes 25 females and

529 20 males. The value of the model adjusted R^2 is 0.21. Est.: Estimate, SD: standard deviation,
530 and F-value: F-statistic of an F-test.

531

532

533

Extended Data Table 1.

Variable	Est.	SE	DF	F-value	P-value
JUVENILES					
Growth of fed challenger (g)	1.068	0.17	27	39.43	<10 ⁻⁴
Sex	-14.178	8.50	27	2.78	0.107
Age	0.726	0.94	27	0.59	0.448
Rainfall	0.012	0.09	27	0.02	0.897
ADULTS					
Growth of fed challenger (g)	0.916	0.24	12	14.72	0.002
Sex	6.143	13.99	12	0.19	0.668
Age	-0.164	0.06	12	7.16	0.020
Rainfall	0.205	0.08	12	7.19	0.020

Extended Data Table 2.

		Proximity to dominance acquisition (months)			
		df=47 for all tests			
		1	2	3	4
Proximity to dominance acquisition (months)	0	t=4.34, p<0.001	t=5.83, p<10 ⁻⁴	t=7.28, p<10 ⁻⁴	t=5.09, p<10 ⁻⁴
	1	–	t=3.52, p<0.001	t=3.94, p=0.003	t=2.63, p=0.115
	2	–	–	t=0.90, p=1.000	t=0.14, p=1.000
	3	–	–	–	t=0.78, p=1.000
	4	–	–	–	–

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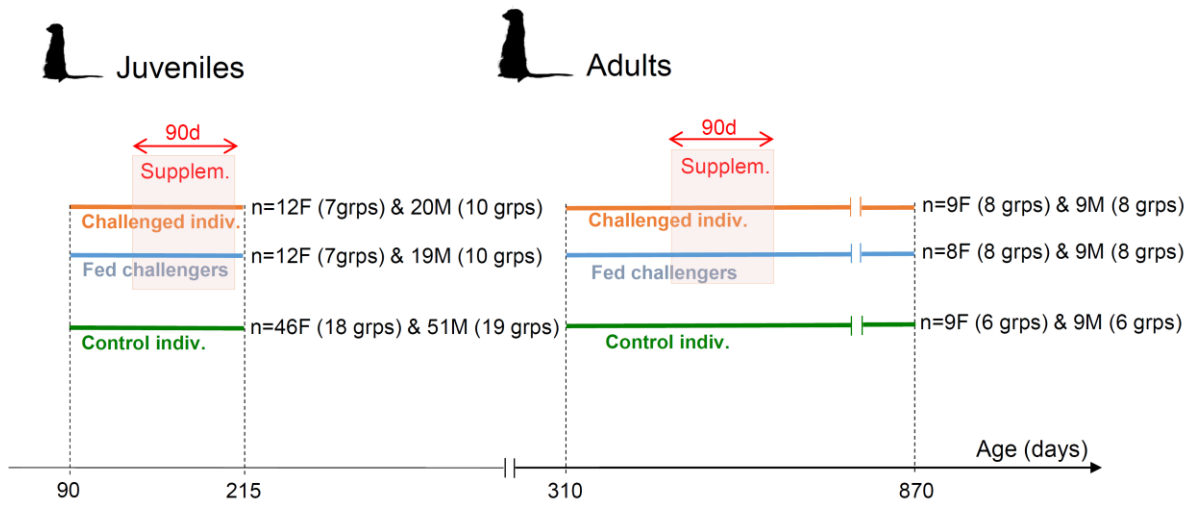
Extended Data Table 3.

Variable	Est.	SE	DF	F-value	p-value
Age at dominance acquisition (days)	-0.030	0.02	36	2.59	0.117
Sex (reference: female)	-5.541	28.75	36	0.04	0.848
Rainfall (mm)	-0.270	0.11	36	5.65	0.023
Seasonality	5.425	11.04	36	0.24	0.626
Weight gap with main rival (g)	-0.758	0.27	36	7.69	0.009
Sex : weight gap with main rival	0.597	0.39	36	2.29	0.139

539

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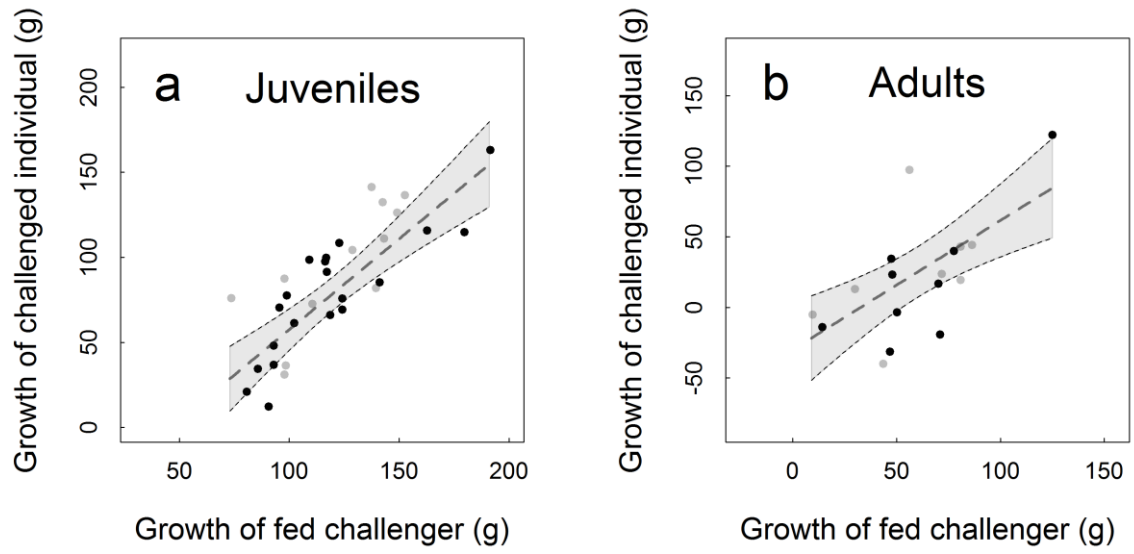
541 **Extended Data Figure 1**



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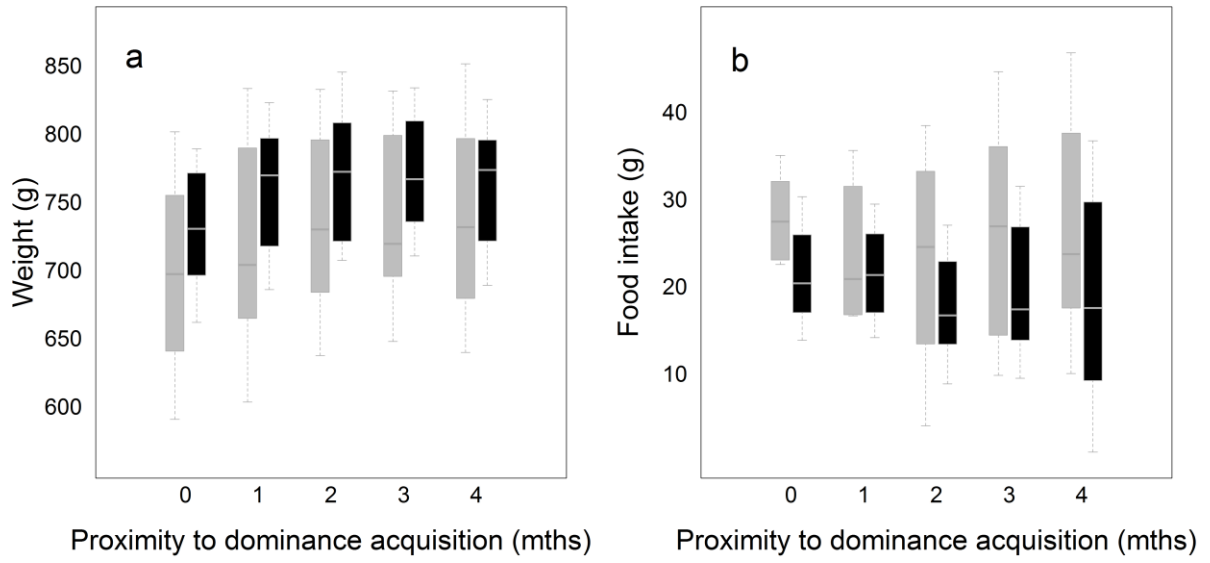
544 **Extended Data Figure 2**



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547 **Extended Data Figure 3**



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