Title
Deferred Benefits of Dominance for Natal Males in a Cooperative Breeder

Authors

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Short Title
Deferred benefits of dominance for natal males

1 **Abstract**
2 In many co-operatively breeding mammals, an unrelated dominant pair monopolises reproduction in the
3 social group while subordinates help to raise their offspring. In Kalahari meerkats (*Suricata suricatta*),
4 dominant males are usually immigrants while dominant females are natal animals that have not left the group
5 where they were born. However, in around 20% of cases, a natal male acquires and holds the dominant
6 position – despite being closely related to the dominant female. Natal dominant males seldom mate within
7 their group (either with the dominant female or with subordinate females) and the benefits they accrue from
8 acquiring and maintaining the dominant position are not obvious. Here, we describe the circumstances in
9 which natal males acquire dominance and explore the possible benefits they gain by comparing the life
10 history, growth and behavioural differences between natal dominants, natal subordinates, and immigrant
11 dominants in wild groups. We show that natal dominant males do not appear to obtain any survival,
12 nutritional or reproductive benefits from their status while they remain in the natal group. However, after
13 dispersing from their natal group, they have a higher chance of acquiring dominant status in another breeding
14 group, suggesting that acquiring dominance in their natal group has deferred direct fitness benefits for male
15 meerkats.

16

19

20 **Introduction**

21

22 In group-living mammals, male social dominance is often associated with increased access to breeding
23 females and increased reproductive success (Smith, 1993; Røed et al., 2002; Huang, Wey and Blumstein,
24 2011; Clutton-Brock, 2016). These reproductive benefits are particularly striking in singular co-operative
25 breeders where a single dominant pair monopolises reproduction in each group (Hauber and Lacey, 2005);
26 for example, in Kalahari meerkats *Suricata suricatta*, immigrant dominant males typically father at least
27 three-quarters of pups born to the resident dominant female (Griffin et al., 2003). In some cases, however,
28 dominance is taken by an individual who may gain fewer reproductive benefits from the position, such as a
29 natal male related to all breeding females in the group. This entails not only energetic investment in
30 competing for and maintaining dominance, but also potentially delaying dispersal from the natal group - and
31 therefore forgoing reproductive opportunities elsewhere, a seemingly maladaptive strategy from the
32 perspective of maximising lifetime reproductive fitness.

33

34 Remaining with the group after reaching maturity - despite a lack of reproductive opportunities - occurs in
35 multiple species, typically co-operative breeders (e.g. Sparkman et al., 2011; Kingma et al., 2017; Ha Suh et
36 al., 2020) or those otherwise living in family groups (e.g. Woodroffe, Macdonald and Silva, 1995; Ekman,
37 Bylin and Tegelström 1999; Parsons et al., 2009; Wong, 2010; McHugh et al., 2011; Dillard and Maigret,
38 2017). This delayed dispersal is commonly associated with indirect fitness benefits (i.e. helping relatives to

39   survive and breed; Creel and Rabenold, 1994; Green and Hatchwell, 2018) and/or non-reproductive benefits

40   which enhance survival or growth (Stacey and Ligon, 1991; Green and Cockburn, 2001; Sparkman et al.,

41   2011): access to group-controlled resources (Alexander, 1974), familiarity with local conditions (Funston et

42   al., 2003), and social cooperation (Dobson, Smith and Gao, 1998; Burland et al., 2001). Delayed dispersal

43   may also be context-dependent, with individuals remaining in their natal group until resources, territories, or

44   breeding opportunities become available, or constraints such as predation pressure are lifted (Bowler and

45   Benton, 2004; Payne, Mazzucco and Dieckmann, 2011).

46

47   Natal dominant individuals of the usually-dispersing sex, however, also incur the costs of competing for and

48   maintaining social dominance despite the (assumed) absence of a reproductive benefit. Taking dominance

49   may involve risks of injury or death in competitive encounters, energy expenditure in defending the position,

50   and heightened levels of glucocorticoids (see Creel, 2001; Carlson et al., 2004; Creel et al., 2013; Smyth et

51   al., 2016). There are, however, potential non-reproductive benefits to holding dominance (Silk, 2007; Ang

52   and Manica, 2010), such as protection from predation (Hall and Fedigan, 1997), increased access to

53   resources (Barton, 1993; Stahl et al., 2001), or access to preferred roosting or sleeping sites (Napper et al.,

54   2013).

55

56   Kalahari meerkats are a classic cooperative breeding system, with substantial reproductive gains of taking

57   dominance in both sexes (Hauber and Lacey, 2005; Spong et al., 2008) - and correspondingly fierce

58   competition for the position, often incurring high costs (see Carlson et al., 2004; Hodge et al., 2008; Smyth

59   and Drea, 2016; Smyth et al., 2018). Typically, a dominant female is natal to the group, while male

60   dominants are unrelated immigrants (joining groups either singly or as part of a coalition) who may take

61   dominance following the death/disappearance of the previous dominant male, or may actively displace an

62   incumbent (Clutton-Brock and Manser, 2016). However, around 20% of all dominant male meerkats are

63   natal individuals: closely related to the resident dominant female and to other females in the group (who are

64   typically her daughters or sisters), and hence unlikely to breed with them (Nielsen, 2012; O'Riain et al.,

65   2000). Given the apparent costs of dominance to these males and the absence of reproductive benefits, it is

66   unclear how they benefit from taking and maintaining natal dominance (Smyth and Drea, 2016), particularly

67   when contrasted against the potential reproductive benefits of dispersing (Doolan and Macdonald, 1996).

68

69   Here we use data from a long-term study of wild meerkat groups to investigate the possible benefits and

70   costs to males of acquiring and maintaining dominance status in their natal group. We begin by

71   characterising the circumstances in which a natal male takes dominance. We then identify and investigate

72   five potential benefits of natal dominance relative to natal subordinate or immigrant dominant males: (1)

73   direct reproductive fitness (more pups fathered overall while dominant), (2) indirect fitness (increased

74   reproductive output of groups, regardless of the father's identity), (3) energetic (increased growth rate), (4)

75   survival (decreased probability of death or disappearance), and (5) deferred/long-term benefits (increased

76   reproductive output later in life (overall or while dominant), higher probability of successful emigration, or

77   increased probability of taking dominance elsewhere).

78

79   Given the suggested absence of within-group reproductive behaviour in natal dominants and the potential for

80   non-reproductive benefits of dominance, we predict that natal dominant males gain neither direct nor indirect

81   reproductive fitness benefits from their position, but that they may show improved weight gain or survival

82   relative to both immigrant dominant males - who must invest more resources in guarding and mating with

83   the dominant female - and to equivalent subordinate males. We also predict that natal dominants may accrue

84   longer-term benefits from holding the position, such as increased probability of achieving dominance in

85   other groups, or increased reproductive output later in life.

86

87

88   **Methods**

89

90   *Study population*

91   Data were collected from wild meerkats as part of a long-term study based at the Kuruman River Reserve,

92   South Africa between Oct 1993 and Feb 2017 (see Clutton-Brock et al., 1999; Clutton-Brock and Manser,

93   2016). Eight to fifteen groups (subject to group extinction/creation dynamics) were visited at least 3 times

94   per week to record group membership, life history events, behavioural observations, and to weigh

95   individuals. Each meerkat was identifiable throughout life using a subcutaneous transponder inserted soon

96   after birth and/or a regularly-replenished unique dye mark. Relatedness between individuals was estimated

97   using a combination of field pedigree (e.g. observed maternity) and genetic pedigree (where field data were

98   absent or inconclusive; see Spong et al., 2008 for methods).

99

100   *Characterisation of dominance*

101   The dominance status of individuals was based on behavioural observations: dominant male meerkats are

102   typically characterised by regular marking of substrate, aggressive interactions with other males, and may

103   guard the dominant female during her oestrus periods (Thavarajah, Fenkes and Clutton-Brock, 2014;

104   Clutton-Brock and Manser, 2016). Age at the start/end of dominance was calculated for males with known

105   birth dates. 284 bouts of male dominance were identified in total, involving 219 individual males at 69

106   different groups.

107

108   For all analyses, adult males (≥12 months old) were classed into one of four categories depending on their

109   position and natal status in the group at the time: Natal Dominant, Immigrant Dominant, Natal Subordinate,

110   and Immigrant Subordinate. Males with unknown birth groups (born outside the study population) were

111   classed as immigrants and assumed to be adult, since males rarely emigrate before reaching maturity (in this

112   study, of 398 males whose age at first emigration was known, only 7.5% were <12 months of age).

113

Reproductive benefits

Reproductive benefits of holding dominance were assessed using the rate of pup paternity both within and outside the group for individual males in all male classes, as well as the frequency with which males left the group to search for breeding opportunities elsewhere ('roving'). Paternity was established using genetic analysis from tail-tip samples taken after pup emergence (generally within 2 weeks of birth, see Spong et al., 2008 for further details and methods). This generated 1368 pups with fathers assigned with >70% confidence. It is expected that, since not all meerkat groups in the area were under study, the numbers of pups sired by individuals outside their own group are an underestimate. The status of the father (membership status in pup's birth group, natal and dominance status in home group) was assessed in the two weeks surrounding estimated conception date (75 days before birth; see analysis in Appendix 1). Pups fathered by immigrant subordinate males (n=131 pups) were excluded from this as they are not relevant to the current analysis.

To control for differing amounts of time spent in each natal/dominance class, the 'number of pups fathered' was standardised by total meerkat-days in each class for each individual; only males who had spent 30+ days in a class were included for this analysis (n=635 males, fathering a total of 879 pups). Estimates of the frequency with which males left their usual group and searched for breeding opportunities elsewhere ('roving') were obtained using recorded disappearances and reappearances of males within groups. Potentially missed events were controlled for by standardising roving rates using the total number of 'seen days' for each male (i.e. recorded sightings of the individual within the dominance/natal class). Two metrics were used: 'number of roving bouts per seen day' and 'number of days between roving bouts'.

Indirect fitness benefits

Average whole-group breeding success ('pups born per month') was calculated for each group using all emerging pups that were born within the group during the male's dominance period (regardless of the identity of the mother or father). The per-adult-female rate of pup production in the group was also calculated to control for group size effects. Periods where the group did not have a dominant male were also included. Only dominant males with a tenure over two months (n=224) or periods where a group went without a dominant for over two months (n=10) were included in this analysis to avoid over-representation of the impact of a previous dominant male.

Energetic benefits

To assess rates of growth, weights obtained in the field before foraging began for the day were used in calculating average monthly weights for each individual (with known birth date) in each male class. Only instances where an individual had been weighed five or more times in a given month of age were used (n=1441 months over 105 individuals for Immigrant Dominants, n=411 months over 48 individuals for Natal Dominants, n=8937 months for 719 individuals for Natal Subordinates). Average monthly weight changes

151 (both absolute and as a percentage of the start-of-month weight) were calculated for males using the
152 difference between average weights in the first and last week of a given calendar month.

153

154 The dynamics of weight change around dominance acquisition were examined by comparing the average
155 weights of the future dominant male and a littermate brother (n=13 immigrant dominant-subordinate pairs,
156 n=7 natal dominant-subordinate pairs) in the fortnight surrounding the date of dominance acquisition and the
157 fortnight surrounding the date two months before dominance acquisition.

158

159 *Survival benefits*
160 Survival probabilities were calculated on a per-month-of-age basis. The proportion of males surviving each
161 month of age (as a percentage of the total males seen for each month of age) was compared between classes.
162 Percentage survival was calculated using both 'all disappearances from the population' (including
163 individuals who disappeared and were not seen again), and using only 'confirmed survival/deaths' (i.e. only
164 including males seen again and those confirmed dead).

165

166 *Deferred benefits*
167 Four potential aspects of long-term benefits of natal dominance were investigated: emigration/immigration
168 behaviour of natal males, probability of acquisition of dominance upon immigration into a non-natal group,
169 lifetime reproductive success of males, and reproductive success of groups based on the dominant male's
170 previous dominance experience (see 'indirect fitness benefits').

171

172 'First dispersal' was taken as the date at which a male was first recorded as emigrating from his natal group
173 (n=398 males) and did not include males who disappeared from their natal group and were not seen again.
174 First emigration weights and ages were compared between natal males who had previous dominance
175 experience (even if they did not hold the position at the time of their dispersal: n=26) vs. no previous
176 dominance experience (n=372). Where available, average weight of males within a two-week period
177 surrounding immigration to a new group (n=204) was also compared between males with differing
178 dominance experience (natal: n=9; immigrant; n=14, both natal & immigrant n=3; no previous dominance
179 experience n=178). These analyses should be taken with caution due to the relatively small representation of
180 males with previous dominance experience within the sample.

181

182 Factors affecting probability of an immigrant male taking dominance were investigated using instances of
183 immigrant dominance acquisition where at least two immigrant males were present in the group during the
184 dominance takeover period (n=111 dominance takeover events). A male was considered 'present' during the
185 takeover period if he had been seen with the group in the period between one week before the previous
186 dominant was recorded as having lost dominance and the date on which the next dominant was recorded. All
187 immigrant males present (excluding the previous dominant) were included as potential candidates for
188 acquiring dominance, regardless of age (n=413 individuals). A male was considered to be successful in

189 competing for dominance if he was the next recorded dominant of the group, regardless of how long the
190 group went without a dominant male in the interim.

191

192 Lifetime reproductive success (total number of pups fathered, regardless of the mother's identity) was also
193 calculated for each male with a known birth date who reached adulthood before death or disappearance from
194 the population (n=758 males), split by the male's dominance experience during his (recorded) lifetime (Natal
195 only, Immigrant only, Both, Subordinate). The correlation between lifetime reproductive success and the
196 proportion of an individual's life spent as a natal/immigrant dominant was also investigated for males who
197 achieved each type of dominance (n=54 natal dominants, n=109 immigrant dominants).

198

199 *Statistical Methods*
200 All analyses were performed using packages in R v.3.5.1 (R Core Team, 2018). Unless otherwise indicated,
201 means are reported in association with their standard error. Metrics were typically compared between male
202 classes (natal dominant, immigrant dominant, natal subordinate). Metrics were typically compared between
203 males/groups/classes using generalized linear models (GLM) or Kruskal-Wallis tests with post-hoc Dunn
204 tests between pairs of classes as appropriate (package "PMCMR"; Pohlert, 2014). Where only two classes
205 were compared, Mann-Whitney U tests were used.

206

207 Where there were repeated measures for individuals (e.g. per-month paternity rates within a class; roving
208 rates within a class; per-month average weight gain; average weight by age), Generalised Linear Mixed
209 Models (GLMM; package "lme4", Bates et al., 2015; package "glmmTMB", Brooks et al., 2017; package
210 "MuMIn", Bartoń, 2018) were used and individual ID was set as a random factor. The significance of male
211 class was ascertained using likelihood ratio tests (LRT) of the full model against a null model excluding
212 male class, and post-hoc Tukey tests enabled statistical comparisons between classes (package "multcomp";
213 Hothorn, Bretz and Westfall, 2008).

214

215 Factors affecting the probability of successful acquisition of dominance by an immigrant male were assessed
216 using GLMM with binomial error and logit link function. The average weight of the male in the two weeks
217 surrounding the dominance change and previous dominance experience were included as fixed effects, and
218 group ID was included as a random effect. Male age was correlated with weight (rho=0.44, $t_{(347)}$=9.168,
219 p<0.001) and hence was not included in the model.

220

221 **Results**

222

223 *Characterisation of dominance*
224 Natal males acquired the dominant position in their group in 57 of 284 cases (20.1%) of dominance
225 acquisition by males (see figure 1). In 43 of these 57 cases (75.4%) of natal dominance, the male was closely
226 related to the dominant female (sibling, half-sibling or offspring). Natal males rarely took dominance if

227   another immigrant subordinate male was already present in the group when the previous dominant male died

228   or disappeared: a natal male took the dominant position in only 17 out of 163 such cases.

229

230   Natal dominant males acquired dominant positions significantly younger than immigrant males (Wilcoxon

231   rank sum: W=5253.5, p=0.002; immigrant dominant mean 41 ± 1.4 months, natal dominant mean 33 ± 1.3

232   months), and also ended dominance significantly younger (Wilcoxon rank sum: W=5447.5, p<0.001;

233   immigrant dominant mean 52 ± 1.9 months, natal dominant mean 40 ± 1.6 months). They did not have

234   significantly different periods of tenure than immigrant males (average tenure period 341 days ± 426,

235   Wilcoxon rank sum: W=7276, p=0.146).

236

237   *Reproductive benefits*

238   As expected, immigrant dominant individuals had the highest overall rates of paternity while in their class

239   (Figure 2), fathering approximately 82% of pups with known paternity. While rates of paternity were

240   significantly different between classes overall ($\chi^2_{(2)}$=24.053, p<0.001), this was mainly driven by the higher

241   paternity of immigrant dominants relative to all other classes of male. Natal dominants did not father more

242   offspring overall than natal subordinates (Tukey contrast: p=0.991) while in their class. We found that only

243   15 pups out of 1368 with known parentage (1.1%) were the product of breeding between parent/offspring or

244   (half-) sibling pairs (8 litters out of 395; 2.0% of litters), which is in accord with previous studies (Griffin et

245   al., 2003; Clutton-Brock, 2016) and illustrates the lack of breeding opportunities for natal males.

246

247   Natal dominant males (n=55) resembled natal subordinate males (n=753) in their roving behaviour: they

248   were not significantly different to natal subordinates in terms of roving bouts per seen day (0.05± 0.001

249   bouts per seen day: Tukey contrast: p=0.649) or inter-roving intervals (average inter-roving interval =

250   38.7±0.88 days: Tukey contrast: p=0.965). Although natal dominant and natal subordinate males visited

251   other groups significantly more than immigrant dominant males (n=115; average roving bouts per seen day =

252   0.01± 0.001 days, LRT: $\chi^2_{(2)}$=196.96, p<0.001; average inter-roving frequency = 75.1± 12.59 days, LRT:

253      $\chi^2_{(2)}$=49.349, p<0.001 contrasts: Tukey contrasts all p<0.001), rates of pups fathered in groups other than

254   their own (i.e. as a result of roving) did not differ significantly between classes of male (LRT: $\chi^2_{(2)}$=4.2963,

255   p=0.117).

256

257

258   *Indirect fitness benefits*

259   Rates of pup production by females within groups (regardless of the father's identity) were unaffected by the

260   natal status (or complete absence) of the dominant male; there were no significant differences in per-monthly

261   rates of pup production between groups with a natal dominant (n=41), immigrant dominant (n=183), or no

262   dominant male (n=10), both in absolute terms (KW $\chi^2_{(2)}$=0.106, p=0.949) and when standardized by the

263   number of adult females present in the group (KW $\chi^2_{(2)}$=2.898, p=0.235).

264

265 *Energetic benefits*

266 There was no evidence of consistent differences in foraging success between natal dominant and natal

267 subordinate males: average monthly weight gain did not differ significantly between the classes of males

268 when age was controlled for (absolute weight gain LRT: $\chi^2_{(4)}$=5.052, p=0.282; percentage weight gain LRT:

269 $\chi^2_{(4)}$=4.4761, p=0.345).

270

271 However, both natal and immigrant dominants were substantially heavier than their subordinate counterparts

272 when matched for age (see figure 3). This weight difference was not evident between littermate pairs two

273 months before one took dominance (Wilcoxon signed rank: V=136, p=0.131) but was significant at the point

274 of dominance acquisition (Wilcoxon signed rank: V=166, p=0.011; individuals taking dominance were on

275 average 34g heavier than subordinate brothers) for both natal and immigrant dominant males (no significant

276 difference between the two natal classes of dominant male; ANOVA: $F_{(1, 18)}$=0.858, p=0.367).

277

278 *Survival benefits*

279 There was no evidence that holding the dominant position affected a male's chances of survival while they

280 remained in their natal group. The probability of within-group survival in any given month of the lifespan of

281 males did not differ significantly between classes of males, with age, or with the interaction between the two

282 (GLM: $F_{(5, 173)}$=0.667, p=0.649).

283

284 Although the probability of permanent disappearance from the population in any given month of a male's

285 dominance tenure did not differ significantly between natal and immigrant dominants (p=0.888), natal

286 dominants were significantly less likely to be found dead (as opposed to simply disappearing from the group)

287 than immigrant dominants (Wilcoxon signed rank: V=38, p=0.041: natal dominant average per-month

288 survival: 99.4 ± 0.29%, immigrant dominant average per-month survival: 98.5 ± 3.06%).

289

290 *Deferred benefits*

291

292 Individuals who had held a natal dominance position before their first emigration from their group emigrated

293 at a significantly older age (natal dominants, n=26, 1265±64 days, natal subordinates, n=404, 745±16 days;

294 Wilcoxon rank sum: W=8398, p<0.001) and higher weight (natal dominants 749±15g, natal subordinates

295 664±6g, Wilcoxon rank sum: W=6201.5, p<0.001) than their subordinate counterparts; these two factors

296 were significantly correlated (Spearman's rank correlation: ρ=0.449, p<0.001). This difference was reflected

297 in the weights of males upon immigration into a group, which were significantly different between males

298 with differing previous dominance experience (KW $\chi^2_{(3)}$=8.0887, p=0.044) - males with natal dominance

299 experience were significantly and considerably heavier on average than males with no previous experience

300 (natal dominance experience, 746±21g, no dominance experience, 628±12g; Dunn post-hoc p=0.034).

301

302   Males who had held a natal dominance position were more likely to acquire dominance positions in other

303   groups after successful dispersal from their natal group: when multiple immigrant males were present in an

304   established group, an individual's probability of taking dominance was enhanced if he had previous

305   dominance experience even when weight was controlled for (LRT: $\chi^2_{(3)}$=15.284, p=0.002; see figure 4). In

306   accordance with previous studies (Russel et al., 2004; Thavarajah et al., 2014), weight (p<0.001) was also

307   found to be a significant predictor of an immigrant male's success in acquiring dominance within the full

308   model, with heavier males more likely to take dominance.

309

310   Lifetime reproductive success did depend on the dominance history of the male (KW $\chi^2_{(3)}$=138.690,

311   p<0.001). However, males who were only ever natal dominants did not have significantly higher average

312   lifetime reproductive success than males who were never dominant (Dunn post-hoc p=0.714; 2.91 ± 2.29

313   pups). Males who were both natal and immigrant dominants within their lifetime were equivalent to

314   immigrant-only dominants in the total number of pups fathered (Dunn post-hoc p=0.714; 7.59 ± 3.53 pups).

315   While the proportion of life spent as an immigrant dominant was positively correlated with number of pups

316   fathered (rho=0.645, $t_{(107)}$=8.738, p<0.001), the proportion of life spent as a natal dominant was not ($t_{(52)}$=-

317   1.065, p=0.292).

318

319   The dominance experience of the male did not appear to affect the reproductive success of the group as a

320   whole: there was no significant difference in the per-monthly pup production of groups based on the

321   previous dominance experience (or lack thereof) of the dominant male (KW $\chi^2_{(3)}$=4.296, p=0.231).

322

323

324   **Discussion**

325

326   Our results provide an unusual example of the deferred benefits of social status within animal groups. We

327   find that natal male meerkats do not gain immediate benefits of dominance in terms of direct or indirect

328   reproductive success (both within- and outside-group), growth, or survival. However, males that acquire

329   dominance natally appear to be in a stronger position to disperse and achieve dominance elsewhere, which

330   has positive long-term effects on their reproductive success and supports a deferred benefit of this life history

331   strategy.

332

333   We do not find evidence within this study of any immediate reproductive benefits of holding the dominant

334   position for natal male meerkats. Natal dominant males reproduce within their group extremely rarely

335   (Figure 2) and so do not gain the classic reproductive benefits associated with a dominant position; their

336   reproductive behaviour is more similar to natal subordinates (i.e. they engage in 'roving' attempts at other

337   groups and have generally low breeding success overall). We also found no indication of indirect benefits of

338   natal dominance for males: group reproductive rate (and therefore the reproduction of a natal male's kin) is

339   unaffected by the status - or indeed complete absence - of a dominant male.

340

341 We also see no evidence of direct non-reproductive benefits of holding the position: natal dominant males

342 showed neither increased growth rate nor improved survival probability relative to natal subordinates while

343 group-bound. The latter result is consistent with previous results indicating that out-of-group mortality

344 generates status-related survival differences in this study population (Cram et al., 2018). This implies that the

345 behavioural assertions over subordinates seen in dominant males (e.g. aggressive behaviour; Thavarajah et

346 al., 2014) do not translate directly into, for example, improved foraging success or access to safer locations

347 within the group - although it should be noted that the conditions of the study site (particularly frequent

348 presence of observers) might reduce the incidence of predation within this population (Clutton-Brock et al.,

349 1999).

350

351 It is possible that natal dominant males suffer relatively few costs of competing for and maintaining the

352 position when compared to their immigrant equivalents. The exact costs of holding dominance for male

353 meerkats are relatively unknown compared to females (e.g. Carlson et al., 2004; Hodge et al., 2008; Smyth

354 and Drea, 2016; Smyth et al., 2018) but may be lower: unlike in females, dominant male meerkats do not

355 differ in testosterone or cortisol levels from their same-sex subordinates (Carlson et al., 2004; Davies et al.,

356 2017). While some costs are likely to remain – such as investment in dominance-maintaining behaviours like

357 substrate marking and aggression towards same-sex subordinates - others may be reduced for natal dominant

358 males. Notably, natal dominants do not seem to invest heavily in guarding breeding females, as the presence

359 of a natal dominant does not decrease the reproductive success of the group. These potential reductions in

360 resource or metabolic cost, however, do not appear to generate direct benefits: natal dominant males are no

361 heavier than their immigrant counterparts.

362

363 Weight is valuable in competitive interactions in meerkats (Russel et al., 2004; Thavarajah et al., 2014). It

364 might be expected that achieving high weight is a benefit of acquiring dominance, but we find that a weight

365 advantage is a cause - rather than a consequence - of dominance acquisition in both natal and immigrant

366 males. This investment in weight gain in order to be competitive carries potential long-term costs (Metcalfe

367 and Monaghan, 2001; Huchard et al., 2016; Cram et al., 2018), making it even more paradoxical from the

368 perspective of a natal individual who has seemingly little to gain from successfully competing for the

369 position. This may be why natal dominant males rarely take the position over an immigrant male present in

370 the group, who has stronger motivation to pay any costs of competing for the position. While there is

371 currently no evidence in meerkats for a role of the dominant female in determining the outcome of

372 dominance competition in males (and therefore favouring a close relative), natal males may also compete

373 less fiercely for the position - and hence risks of injury or death during dominance competition between natal

374 males may be lower than for immigrant males.

375

376 We find, however, that natal dominant males appear to gain benefits from their position which only manifest

377 once they have left it. Dispersal is costly for meerkats (Maag et al., 2019); the relatively high age and weight

of natal dominant male meerkats at their first emigration likely put them at an advantage when attempting to leave, immigrate and take dominance in other groups (Doolan and Macdonald, 1996; Spong et al., 2008). It is noteworthy that natal dominant males emigrate from their group later than the average for natal subordinate males, and at around the same time (42 months) that subordinate male mass reaches an asymptote (see fig. 3) - implying that natal subordinate males may otherwise be forced to leave their group earlier than would be optimal. Becoming a natal dominant may enable individuals to time their eventual dispersal to align with optimal environmental conditions, such as periods of abundant resources or when viable mating or dominance opportunities arise (Bowler and Benton, 2004; Payne et al., 2011). Males with previous natal dominant experience also appear to have higher probability of taking dominance once they have joined a group as an immigrant, independently of their weight advantage. The exact factors underlying this cannot be determined within this study, but may involve practice of aggressive and assertive behaviours over other group members, or previous establishment of dominance within any coalition of co-dispersing males.

To our knowledge, ours is the first study to examine the presence of dominant individuals who do not gain reproductive benefits from the position within a cooperatively-breeding species. The value to a natal male meerkat of gaining experience of dominance early in life highlights that individuals may gain more than just reproductive benefits through a socially dominant position, even when these reproductive benefits are substantial - and that they may be enough to justify the costs of taking and holding dominance alone. Our results also shed light on the complexity of factors affecting social status within these groups, which appear to be affected not only by current factors (such as weight) but also by previous experience in other contexts. Given the apparent long-term benefits, the phenomenon of non-breeding dominance may not be unique to meerkats, but may also be found in other cooperative species or those with hierarchical groups and single-sex dispersal: a possible 'short-cut' to the top of a hierarchy upon immigration to a new group.

Previous studies identifying non-reproductive benefits of natal philopatry (e.g. Rood, 1990; Stacey and Ligon, 1991; Ekman et al., 1999; Green and Cockburn, 2001; Sparkman et al., 2011; Wong, 2010; Nelson-Flower et al., 2018) have often focused on immediate benefits: indirect fitness through helping relatives to breed, access to resources or other condition-improving factors such reciprocal grooming from group members, or reduced mortality (such as group-based protection from predation). Our study highlights an additional factor: knowledge and experience gained in a 'safe' environment which can be used to increase reproductive fitness later in life - a finding which mirrors previous work finding that experience as a non-breeding helper provides knowledge of nest-site quality which may be beneficial for future breeding attempts in long-tailed tits (*Aegithalos caudatus*, Hatchwell et al., 1999). Long-term and downstream consequences of behavioural strategies are, by nature, often difficult to capture in observational research; however, our results show that they may be an additional potential factor when determining the evolutionary costs and benefits of behavioural strategies.

Ethical Statement

Our work was approved by the Animal Ethics Committee of the University of Pretoria (no. EC010-13) and by the Northern Cape Department of Environment and Nature Conservation (FAUNA 1020/2016), and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

References

Alexander, R. D. (1974) The Evolution of Social Behaviour. *Annual Review of Ecology and Systematics* 5 (1), 325-383

Ang, T. Z., Manica, A. (2010) Benefits and Costs of Dominance in the Angelfish *Centropyge bicolor*. *Ethology* 116, 855-865

Barton, R. A. (1993) Sociospatial mechanisms of feeding competition in female olive baboons, *Papio anubis*. *Animal Behaviour* 46 (4), 791-802

Bartoń, K. (2018) MuMin: Multi-Model Inference. R package version 1.42.1 https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67 (1), 1-48

Bowler, D. E., Benton, T. G. (2004) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80, 205-225

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., Bolker, B.M. (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9 (2), 378-400

Burland, T. M., Barratt, E. M., Nichols, R. A., Racey, P. A. (2001) Mating patterns, relatedness and the basis of natal philopatry in the brown long-eared bat, *Plecotus auritus*. *Molecular Ecology*, 10, 1309-1321

Carlson, A. A., Young, A. J., Russell, A. F., Bennett, N. C., McNeilly, A .S., Clutton-Brock, T. H. (2004) Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Hormones and Behaviour* 46, 141-150

Clutton-Brock, T. H., Gaynor, D., McIlrath, G. M., Maccoll, A. D. C., Kansky, R., Chadwick, P., Manser, M., Skinner, J. D., Brotherton, P. N. M. (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* 68, 672-683

Clutton-Brock, T. H. (2016) Mammal Societies. Chichester: John Wiley & Sons, Inc.

Clutton-Brock, T. H, Manser, M. (2016) Meerkats: cooperative breeding in the Kalahari. In: Koenig, W. D., Dickinson, J. L., editors. (2016) Cooperative Breeding in Vertebrates. Cambridge: Cambridge University Press. p. 294-317.

Cram, D. L., Monaghan, P., Gillespie, R., Dantzer, B., Duncan, C., Spence-Jones, H. C., Clutton-Brock, T. H. (2018) Rank-Related Contrasts in Longevity Arise from Extra-Group Excursions Not Delayed Senescence in a Cooperative Mammal. *Current Biology* 28 (18), 1-6

Creel, S. (2001) Social dominance and stress hormones. *Trends in Ecology & Evolution* 16(9), 491-497

Creel, S., Dantzer, B., Goymann, W., Rubenstein, D. R. (2013) The ecology of stress: effects of the social environment. *Functional Ecology* 27, 66-80

Creel, S. R., Rabenold, K. N. (1994) Inclusive fitness and reproductive strategies in dwarf mongooses. *Behavioral Ecology* 5 (3), 339-348

Davies, C. S., Smyth, K. N., Greene, L. K., Walsh, D. A., Mitchell, J., Clutton-Brock, T. H., Drea, C. M. (2017) Exceptional endocrine profiles characterise the meerkat: sex, status, and reproductive patterns. *Scientific Reports* 6, 35492

510 Dillard, J. R., Maigret, T. A. (2017) Delayed dispersal and prolonged brood care in a family-living beetle.
511 *Journal of Evolutionary Biology* 30, 2230-2243

513 Dobson, F. S., Smith, A. T., Gao, W. X. (1998) Social and ecological influences on dispersal and philopatry
514 in the plateau pika (Ochotona curzoniae). *Behavioral Ecology* 9 (6), 622-635

516 Doolan, S. P., Macdonald, D. W. (1996) Dispersal and extra-territorial prospecting by slender-tailed
517 meerkats (*Suricata suricatta*) in the south-western Kalahari. *Journal of Zoology* 240 (1), 59-73

519 Ekman, J., Bylin, A., Tegelström, H. (1999) Increased lifetime reproductive success for Siberian jay
520 (*Perisoreus infaustus*) males with delayed dispersal. *Proceedings of the Royal Society B* 266, 911-915

522 Funston, P. J., Mills, M. G. L., Richardson, P. R. K., van Jaarsveld, A. S. (2003) Reduced dispersal and
523 opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology* 259, 131-142

525 Green, D. J., Cockburn, A. (2001) Post-fledging care, philopatry and recruitment in brown thornbills.
526 *Journal of Animal Ecology* 70, 505-514

528 Green, J. P., Hatchwell, B. J. (2018) Inclusive fitness consequences of dispersal decisions in a cooperatively
529 breeding bird, the long-tailed tit (*Aegithalos caudatus*). *PNAS* 115 (47), 12011-12016

531 Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., McIlrath, G., Gaynor, D., Kansky, R., O'Riain, J.,
532 Clutton-Brock, T. H. (2003) A genetic analysis of breeding success in the cooperative meerkat (*Suricata*
533 *suricatta*). *Behavioral Ecology* 14 (4), 472-480

535 Hall, C. L., Fedigan, L. M. (1997) Spatial benefits afforded by high rank in white-faced capuchins. *Animal*
536 *Behaviour* 53 (5), 1069-1082

538 Ha Suh, Y., Presendorfer, M. B., Tringali, A., Bowman, R., Fitzpatrick, J. W. (2020) Investigating social and
539 environmental predictors of natal dispersal in a cooperative breeding bird. *Behavioral Ecology* 31 (3), 692-
540 701

542 Hatchwell, B. J., Russell, A. F., Fowlie, M. K., Ross, D. J. (1999) Reproductive Success and Nest-Site
543 Selection in a Cooperative Breeder: Effect of Experience and a Direct Benefit of Helping. *The Auk* 116 (2),
544 355-363

546 Hauber, M. E., Lacey, E. A. (2005) Bateman's Principle in Cooperatively Breeding Vertebrates: The Effects
547 of Non-breeding Alloparents on Variability in Female and Male Reproductive Success. *Integrative and*
548 *Comparative Biology* 45 (5), 903-914

550 Hodge, S. J., Manica, A., Flower, T. P., Clutton-Brock, T. H. (2008) Determinants of reproductive success in
551 dominant female meerkats. *Journal of Animal Ecology* 77, 92-102

553 Hothorn, T., Bretz, F., Westfall, P. (2008) Simultaneous Inference in General Parametric Models.
554 *Biometrical Journal* 50 (3), 346-363

556 Huang, B., Wey, T. W., Blumstein, D. T. (2011) Correlates and Consequences of Dominance in a Social
557 Rodent. *Ethology* 117 (7), 573-585

559 Huchard, E., English, S., Bell, M. B. V., Thavarajah, N., Clutton-Brock, T. H. (2016) Competitive growth in
560 a cooperative mammal. *Nature* 533, 532-534

562 Kingma, S. A., Komdeur, J., Burke, T., Richardson, D. S. (2017) Differential dispersal costs and sex-biased
563 dispersal distance in a cooperatively breeding bird. *Behavioral Ecology* 28 (4), 1113-1121
564

Maag, N., Cozzi, G., Bateman, A., Heistermann, M., Ganswindt, A., Manser, M., Clutton-Brock, T., Ozgul, A. (2019) Cost of dispersal in a social mammal: body mass loss and increased stress. *Proceedings of the Royal Society B* 286 (1896), 20190033

McHugh, K. A., Allen, J. B., Barleycorn, A. A., Wells, R. S. (2011) Natal philopatry, ranging behaviour, and habitat selection of juvenile bottlenose dolphins in Sarasota Bay, Florida. *Journal of Mammalogy* 92 (6), 1298-1313

Metcalfe, N. B., Monaghan, P. (2001) Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* 16 (5), 254-260

Napper, C. J., Sharp, S. P., McGowan, A., Simeoni, M., Hatchwell, B. J. (2013) Dominance, not kinship, determines individual position within the communal roosts of a cooperatively breeding bird. *Behavioural Ecology and Sociobiology* 67 (12), 2029-2039

Nelson-Flower, M. J., Wiley, E. M., Flower, T. P., Ridley, A. R. (2018) Individual dispersal delays in a cooperative breeder: Ecological constrains, the benefits of philopatry and the social queue for dominance. *Journal of Animal Ecology* 87 (5), 1227-1238

Nielsen, J. F. (2012) The evolutionary genetics of meerkats (*Suricata suricatta*). Ph.D. The University of Edinburgh.

O'Riain, M. J., Bennett, N. C., Brotherton, P. N. M., McIlrath, G., Clutton-Brock, T. H. (2000) Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats (*Suricata suricatta*). *Behavioral Ecology and Sociobiology* 48 (6), 471-477

Parsons, K. M., Balcomb III, K. C., Ford, J. K. B., Durban, J. W. (2009) The social dynamics of southern resident killer whales and conservation implications for this endangered population. *Animal Behaviour* 77 (4), 963-971

Payne, J. L., Mazzucco, R., Dieckmann, U. (2011) The evolution of conditional dispersal and reproductive isolation along environmental gradients. *Journal of Theoretical Biology* 273 (1), 147-155

Pohlert, T. (2014) The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). R package, <URL: https://CRAN.R-project.org/package=PMCMR>

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rood, J. P. (1990) Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour* 39, 566-572

Røed, K. H., Holand, Ø., Smith, M. W., Gjøstein, H., Kumpula, J., Nieminen, M. (2002) Reproductive success in reindeer males in a herd with varying sex ratio. *Molecular Ecology* 11 (7), 1239-1243

Russel, A. F., Carlson, A. A., McIlrath, G. M., Jordan, N. R., Clutton-Brock, T. (2004) Adaptive size modification by dominant female meerkats. *Evolution* 58, 1600-1607

Silk, J. B. (2007) The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B* 362, 539-559

Smith, D. G. (1993) A 15-year study of the association between dominance rank and reproductive success of male rhesus macaques. *Primates* 34 (4), 471-480

Smyth, K. N., Greene, L. K., Clutton-Brock, T. H., Drea, C. M. (2016) Androgens predict parasitism in female meerkats: a new perspective on a classic trade-off. *Biology Letters* 12 (10), 20160660

622	Smyth, K. N., Drea, C. M. (2016) Patterns of parasitism in the cooperatively breeding meerkat: a cost of
623	dominance for females. *Behavioral Ecology* 27 (1), 148-157
624
625	Smyth, K. N., Caruso, N. M., Davies, C. S., Clutton-Brock, T. H., Drea, C. M. (2018) Social and endocrine
626	correlates of immune function in meerkats: implications for the immunocompetence handicap hypothesis.
627	*Royal Society Open Science* 5, 180435
628
629	Sparkman, A. M., Adams, J. R., Steury, T. D., Waits, L. P., Murray, D. L. (2011) Direct fitness benefits of
630	delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). *Behavioral Ecology* 22, 199-205
631
632	Spong, G. F., Hodge, S. J., Young, A. J., Clutton-Brock, T. H. (2008) Factors affecting the reproductive
633	success of dominant male meerkats. *Molecular Ecology* 17 (9), 2287-2299
634
635	Stacey, P.B., Ligon, D. J. (1991) The Benefits-of-Philopatry Hypothesis for the Evolution of Cooperative
636	Breeding: Variation in Territory Quality and Group Size Effects. *The American Naturalist* 137 (6), 831-846
637
638	Stahl, J., Tolsma, P. H., Loonen, M. J., Drent, R. H. (2001) Subordinates explore but dominants profit:
639	resource competition in high Arctic barnacle goose flocks. *Animal Behaviour* 61 (1), 257-264
640
641	Thavarajah, N. K., Fenkes, M., Clutton-Brock, T. H. (2014) The determinants of dominance relationships
642	among subordinate females in the cooperatively breeding meerkat. *Behaviour* 151 (1), 89-102
643
644	Wong, M. Y. L. (2010) Ecological constrains and benefits of philopatry promote group-living in a social but
645	non-cooperatively breeding fish. *Proceedings of the Royal Society B* 277, 353-358
646
647	Woodroffe, R., Macdonald, D. W., Silva, J. (1995) Dispersal and philopatry in the European badger, *Meles*
648	*meles*. *Journal of Zoology* 237 (2), 227-239
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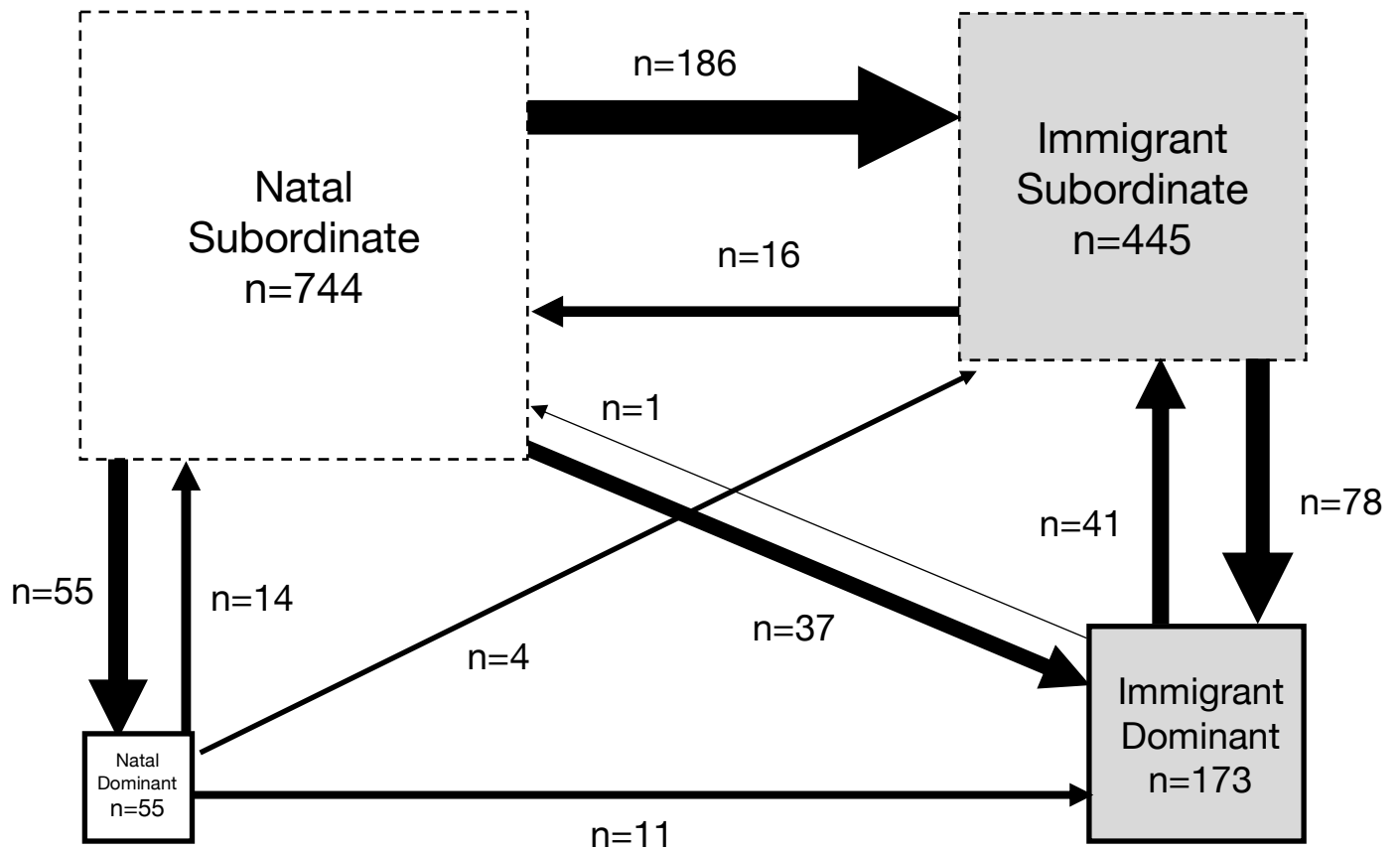661
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Figure 1 - Frequency of class occupancy and transitions between male classes in meerkats. Numbers indicate individuals who spent >30 days in that class (within box) or made the transition between two classes (arrows), each of which they spent >30 days in. In total 55 out of 759 known adult male meerkats spent >30 days as a natal dominant (with 2 individuals having two separate bouts of dominance in their natal group), and one-fifth of these went directly on to become immigrant dominants in another group.

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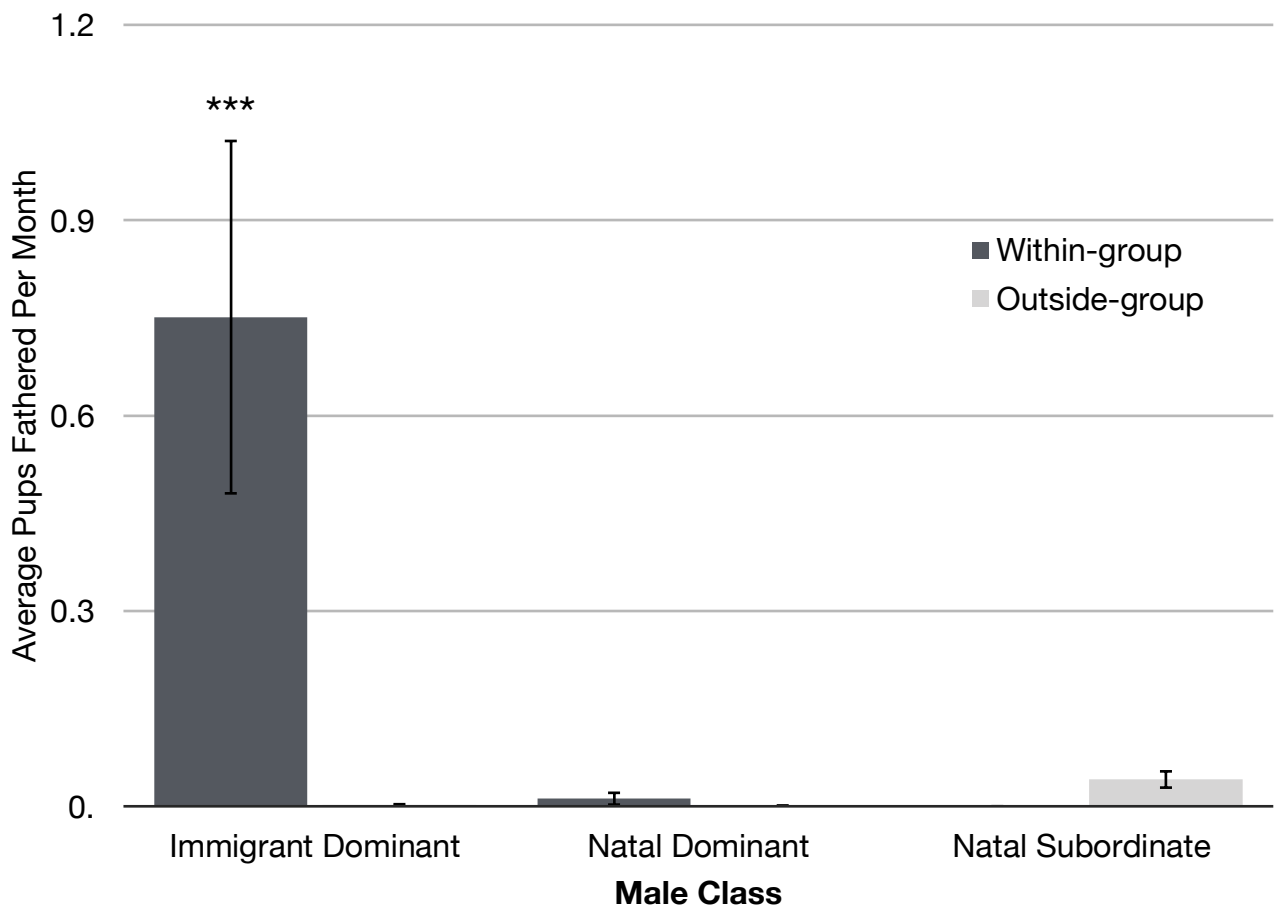738
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Figure 2 - Average per-monthly rates of emerging pups fathered for individual male meerkats of each class (immigrant dominant n=149; natal dominant n=54; natal subordinate n=478), showing the fitness benefits of holding an immigrant dominant position relative to other positions in the group. Only males who were in a class for a month or more were included in this analysis. Male class significantly affected the total pups fathered per month (χ^2 (2)=24.053, p<0.001), as well as the within-group pups fathered per month (χ^2 (2)=27.074, p<0.001), but did not significantly affect outside-group pups fathered per month ((χ^2 (2)=4.2963, p=0.117)

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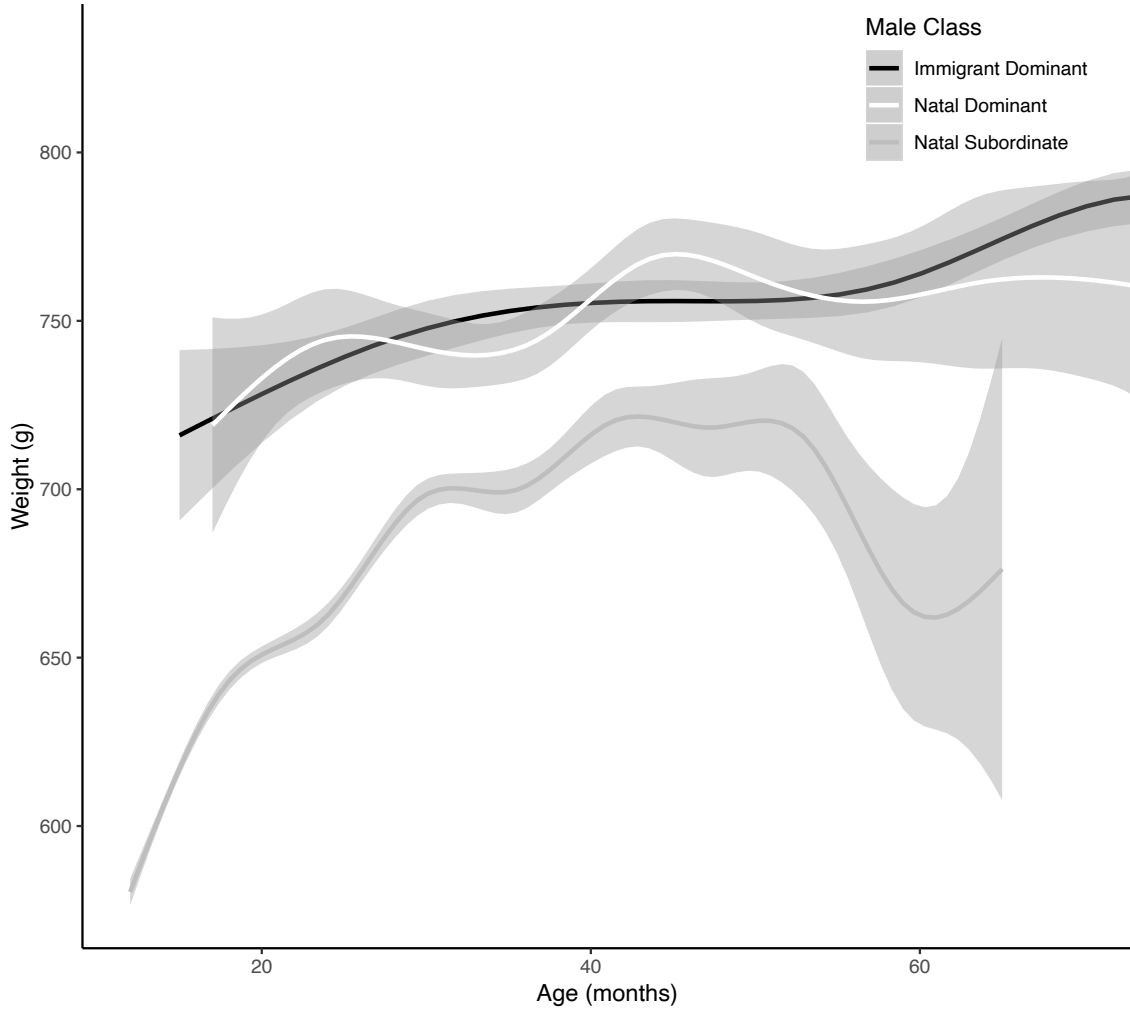797
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Figure 3 - Average per-monthly weight for males within the three classes (loess smoothed conditional mean with 95% C.I.), showing lower per-monthly weights (and apparent senescence in terms of body mass) for natal subordinates when compared with both immigrant and natal dominant males. Both natal and immigrant dominant males were significantly heavier than natal subordinate males (Likelihood ratio test: χ^2_4=2004.5, p<0.001; Tukey contrasts: Natal Dominant – Natal Subordinate p<0.001, Immigrant Dominant – Natal Subordinate p<0.001)
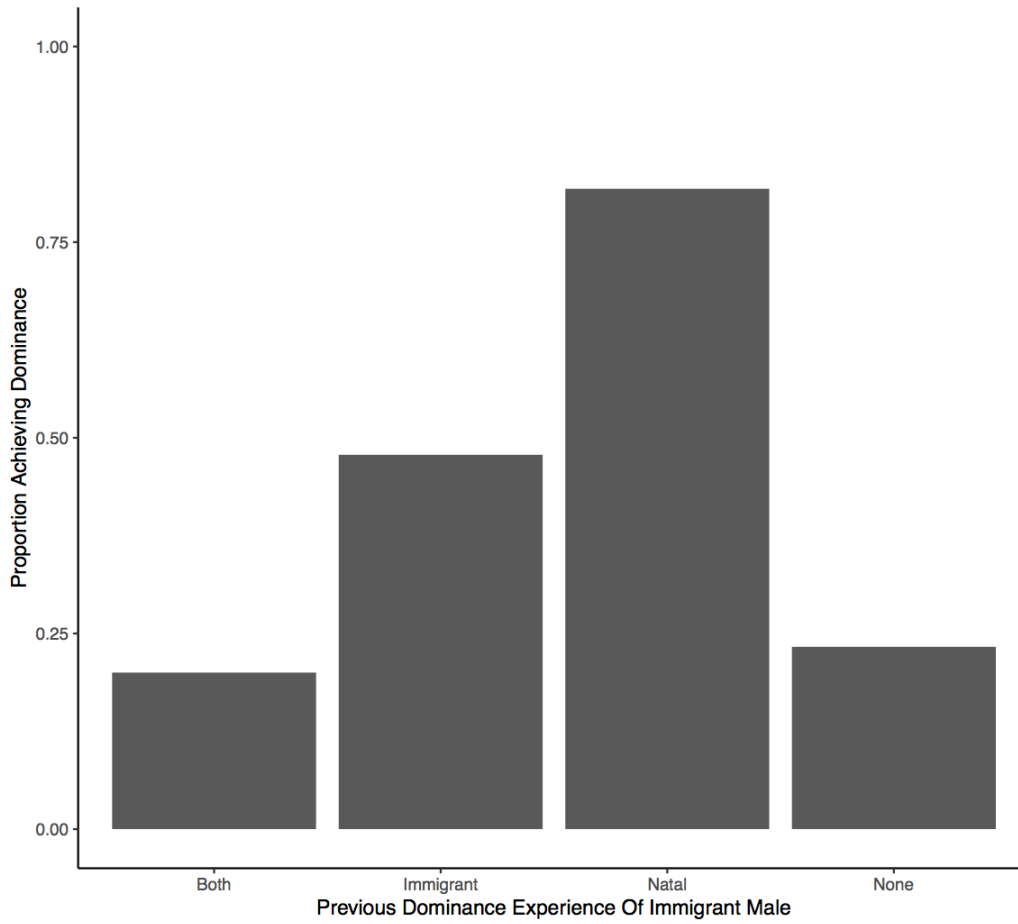
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Figure 4 - The proportion of immigrant males with each type of dominance experience who went on to become group dominant, having been present in the group when the position became available (natal dominance experience n=11; immigrant dominance experience n=46; natal & immigrant dominance experience n=5; no dominance experience n=322).