


Deferred benefits of dominance for natal males in a cooperative breeder, the Kalahari meerkat

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Introduction

In group-living mammals, male social dominance is often associated with increased access to breeding females and increased reproductive success (Smith, 1993; Røed *et al.*, 2002; Huang, Wey & Blumstein, 2011; Clutton-Brock, 2016). These reproductive benefits are particularly striking in singular cooperative breeders where a single dominant pair monopolizes reproduction in each group (Hauber & Lacey, 2005); for example, in Kalahari meerkats *Suricata suricatta*, immigrant dominant males typically father at least three-quarters of pups born to the resident dominant female (Griffin *et al.*, 2003). In some cases, however, dominance is taken by an individual who may gain fewer reproductive benefits from the position, such as a natal male related to all breeding females in the group. This entails not only energetic investment in competing for and

Abstract

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

maintaining dominance, but also potentially delaying dispersal from the natal group – and therefore forgoing reproductive opportunities elsewhere, a seemingly maladaptive strategy from the perspective of maximizing lifetime reproductive fitness.

Remaining with the group after reaching maturity – despite a lack of reproductive opportunities – occurs in multiple species, typically cooperative breeders (e.g. Sparkman *et al.*, 2011; Kingma *et al.*, 2017; Ha Suh *et al.*, 2020) or those otherwise living in family groups (e.g. Woodroffe, Macdonald & Silva, 1995; Ekman, Bylin & Tegelström, 1999; Parsons *et al.*, 2009; Wong, 2010; McHugh *et al.*, 2011; Dillard & Maigret, 2017). This delayed dispersal is commonly associated with indirect fitness benefits (i.e. helping relatives to survive and breed; Creel & Rabenold, 1994; Green & Hatchwell, 2018) and/or non-reproductive benefits which enhance survival or growth (Stacey & Ligon, 1991; Green & Cockburn, 2001;

Sparkman *et al.*, 2011): access to group-controlled resources (Alexander, 1974), familiarity with local conditions (Funston *et al.*, 2003), and social cooperation (Dobson, Smith & Gao, 1998; Burland *et al.*, 2001). Delayed dispersal may also be context-dependent, with individuals remaining in their natal group until resources, territories or breeding opportunities become available, or constraints such as predation pressure are lifted (Bowler & Benton, 2004; Payne, Mazzucco & Dieckmann, 2011).

Natal dominant individuals of the usually dispersing sex, however, also incur the costs of competing for and maintaining social dominance despite the (assumed) absence of a reproductive benefit. Taking dominance may involve risks of injury or death in competitive encounters, energy expenditure in defending the position and heightened levels of glucocorticoids (see Creel, 2001; Carlson *et al.*, 2004; Creel *et al.*, 2013; Smyth *et al.*, 2016). There are, however, potential non-reproductive benefits to holding dominance (Silk, 2007; Ang & Manica, 2010), such as protection from predation (Hall & Fedigan, 1997), increased access to resources (Barton, 1993; Stahl *et al.*, 2001) or access to preferred roosting or sleeping sites (Napper *et al.*, 2013).

Kalahari meerkats are a classic cooperative breeding system, with substantial reproductive gains of taking dominance in both sexes (Hauber & Lacey, 2005; Spong *et al.*, 2008) – and correspondingly fierce competition for the position, often incurring high costs (see Carlson *et al.*, 2004; Hodge *et al.*, 2008; Smyth & Drea, 2016; Smyth *et al.*, 2018). Typically, a dominant female is natal to the group, while male dominants are unrelated immigrants (joining groups either singly or as part of a coalition) who may take dominance following the death/disappearance of the previous dominant male or may actively displace an incumbent (Clutton-Brock & Manser, 2016). However, around 20% of all dominant male meerkats are natal individuals: closely related to the resident dominant female and to other females in the group (who are typically her daughters or sisters) and hence unlikely to breed with them (O’Riain *et al.*, 2000; Nielsen, 2012). Given the apparent costs of dominance to these males and the absence of reproductive benefits, it is unclear how they benefit from taking and maintaining natal dominance (Smyth & Drea, 2016), particularly when contrasted against the potential reproductive benefits of dispersing (Doolan & Macdonald, 1996).

Here, we use data from a long-term study of wild meerkat groups to investigate the possible benefits and costs to males of acquiring and maintaining dominance status in their natal group. We begin by characterizing the circumstances in which a natal male takes dominance. We then identify and investigate five potential benefits of natal dominance relative to natal subordinate or immigrant dominant males: (1) direct reproductive fitness (more pups fathered overall while dominant), (2) indirect fitness (increased reproductive output of groups, regardless of the father’s identity), (3) energetic (increased growth rate), (4) survival (decreased probability of death or disappearance) and (5) deferred/long-term benefits (increased reproductive output later in life (overall or while dominant), higher probability of successful emigration or increased probability of taking dominance elsewhere).

Given the suggested absence of within-group reproductive behaviour in natal dominants and the potential for non-reproductive benefits of dominance, we predict that natal dominant males gain neither direct nor indirect reproductive fitness benefits from their position, but that they may show improved weight gain or survival relative to both immigrant dominant males – who must invest more resources in guarding and mating with the dominant female – and to equivalent subordinate males. We also predict that natal dominants may accrue longer-term benefits from holding the position, such as increased probability of achieving dominance in other groups, or increased reproductive output later in life.

Methods

Study population

Data were collected from wild meerkats as part of a long-term study based at the Kuruman River Reserve, South Africa between October 1993 and February 2017 (see Clutton-Brock *et al.*, 1999; Clutton-Brock & Manser, 2016). Eight to fifteen groups (subject to group extinction/creation dynamics) were visited at least 3 times per week to record group membership, life history events and behavioural observations, and to weigh individuals. Each meerkat was identifiable throughout life using a subcutaneous transponder inserted soon after birth and/or a regularly replenished unique dye mark. Relatedness between individuals was estimated using a combination of field pedigree (e.g. observed maternity) and genetic pedigree (where field data were absent or inconclusive; see Spong *et al.*, 2008 for methods).

Characterization of dominance

The dominance status of individuals was based on behavioural observations: dominant male meerkats are typically characterized by regular marking of substrate, aggressive interactions with other males, and may guard the dominant female during her oestrus periods (Thavarajah, Fenkes & Clutton-Brock, 2014; Clutton-Brock & Manser, 2016). Age at the start/end of dominance was calculated for males with known birth dates. 284 bouts of male dominance were identified in total, involving 219 individual males in 69 different groups.

For all analyses, adult males (≥ 12 months old) were classed into one of four categories depending on their position and natal status in the group at the time: Natal Dominant, Immigrant Dominant, Natal Subordinate and Immigrant Subordinate. Males with unknown birth groups (born outside the study population) were classed as immigrants and assumed to be adult, since males rarely emigrate before reaching maturity (in this study, of 398 males whose age at first emigration was known, only 7.5% were < 12 months of age).

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 S1). 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 standardized 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 standardizing 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 2 months ($n = 224$) or periods where a group went without a dominant for over 2 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 (both absolute and as a percentage of the start-of-month weight) were

calculated for males using the difference between average weights in the first and last week of a given calendar month.

The dynamics of weight change around dominance acquisition were examined by comparing the average weights of the future dominant male and a littermate brother ($n = 13$ immigrant dominant-subordinate pairs, $n = 7$ natal dominant-subordinate pairs) in the fortnight surrounding the date of dominance acquisition and the fortnight surrounding the date 2 months before dominance acquisition.

Survival benefits

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

Deferred benefits

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

'First dispersal' was taken as the date at which a male was first recorded as emigrating from his natal group ($n = 398$ males) and did not include males who disappeared from their natal group and were not seen again. First emigration weights and ages were compared between natal males who had previous dominance experience (even if they did not hold the position at the time of their dispersal: $n = 26$) versus no previous dominance experience ($n = 372$). Where available, average weight of males within a 2 weeks period surrounding immigration to a new group ($n = 204$) was also compared between males with differing dominance experience (natal: $n = 9$; immigrant; $n = 14$, both natal & immigrant $n = 3$; no previous dominance experience $n = 178$). These analyses should be taken with caution due to the relatively small representation of males with previous dominance experience within the sample.

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

considered to be successful in competing for dominance if he was the next recorded dominant of the group, regardless of how long the group went without a dominant male in the interim.

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

Statistical methods

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

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

Factors affecting the probability of successful acquisition of dominance by an immigrant male were assessed using GLMM with binomial error and logit link function. The average weight of the male in the 2 weeks surrounding the dominance change and previous dominance experience were included as fixed effects, and group ID was included as a random effect. Male age was correlated with weight ($\rho = 0.44$, $t_{(347)} = 9.168$, $P < 0.001$) and hence was not included in the model.

Results

Characterization of dominance

Natal males acquired the dominant position in their group in 57 of 284 cases (20.1%) of dominance acquisition by males (see Fig. 1). In 43 of these 57 cases (75.4%) of natal dominance, the male was closely related to the dominant female (sibling, half-sibling or offspring). Natal males rarely took dominance if another immigrant subordinate male was already

present in the group when the previous dominant male died or disappeared: a natal male took the dominant position in only 17 out of 163 such cases.

Natal dominant males acquired dominant positions significantly younger than immigrant males (Wilcoxon rank sum: $W = 5253.5$, $P = 0.002$; immigrant dominant mean 41 ± 1.4 months, natal dominant mean 33 ± 1.3 months) and also ended dominance significantly younger (Wilcoxon rank sum: $W = 5447.5$, $P < 0.001$; immigrant dominant mean 52 ± 1.9 months, natal dominant mean 40 ± 1.6 months). They did not have significantly different periods of tenure than immigrant males (average tenure period 341 days \pm 426, Wilcoxon rank sum: $W = 7276$, $P = 0.146$).

Reproductive benefits

As expected, immigrant dominant individuals had the highest overall rates of paternity while in their class (Fig. 2), fathering approximately 82% of pups with known paternity. While rates of paternity were significantly different between classes overall ($\chi^2_{(2)} = 24.053$, $P < 0.001$), this was mainly driven by the higher paternity of immigrant dominants relative to all other classes of male. Natal dominants did not father more offspring overall than natal subordinates (Tukey contrast: $P = 0.991$) while in their class. We found that only 15 pups out of 1368 with known parentage (1.1%) were the product of breeding between parent/offspring or (half-) sibling pairs (8 litters out of 395; 2.0% of litters), which is in accord with previous studies (Griffin *et al.*, 2003; Clutton-Brock, 2016) and illustrates the lack of breeding opportunities for natal males.

Natal dominant males ($n = 55$) resembled natal subordinate males ($n = 753$) in their roving behaviour: they were not significantly different to natal subordinates in terms of roving bouts per seen day (0.05 ± 0.001 bouts per seen day; Tukey

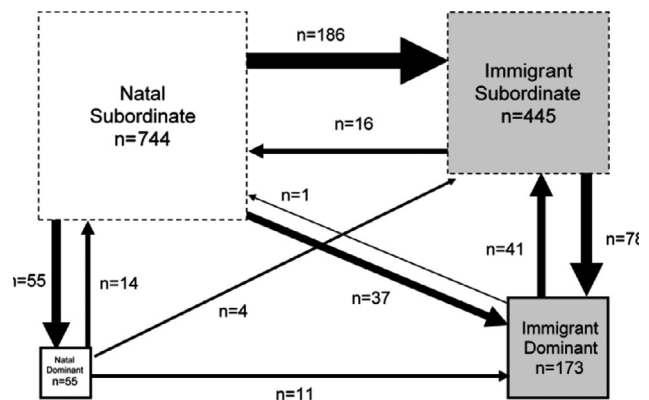


Figure 1 Frequency of class occupancy and transitions between male classes in meerkats. Numbers indicate individuals who spent >30 days in that class (within box) or made the transition between two classes (arrows), each of which they spent >30 days in. In total 55 out of 759 known adult male meerkats 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.

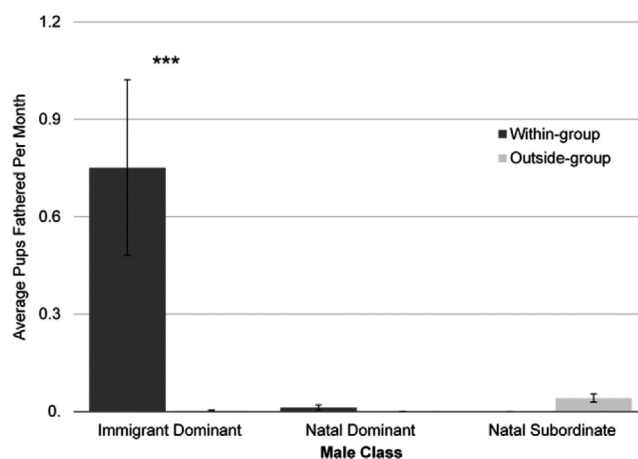


Figure 2 Average per-monthly rates of emerging pups fathered for individual male meerkats of each class (immigrant dominant $n = 149$; natal dominant $n = 54$; natal subordinate $n = 478$), showing the fitness benefits of holding an immigrant dominant position relative to other positions in the group. 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 ($\chi^2_{(2)} = 24.053$, $P < 0.001$), as well as the within-group pups fathered per month ($\chi^2_{(2)} = 27.074$, $P < 0.001$), but did not significantly affect outside-group pups fathered per month ($\chi^2_{(2)} = 4.2963$, $P = 0.117$).

contrast: $P = 0.649$) or inter-roving intervals (average inter-roving interval = 38.7 ± 0.88 days: Tukey contrast: $P = 0.965$). Although natal dominant and natal subordinate males visited other groups significantly more than immigrant dominant males ($n = 115$; average roving bouts per seen day = 0.01 ± 0.001 days, LRT: $\chi^2_{(2)} = 196.96$, $P < 0.001$; average inter-roving frequency = 75.1 ± 12.59 days, LRT: $\chi^2_{(2)} = 49.349$, $P < 0.001$ contrasts: Tukey contrasts all $P < 0.001$), rates of pups fathered in groups other than their own (i.e. as a result of roving) did not differ significantly between classes of male (LRT: $\chi^2_{(2)} = 4.2963$, $P = 0.117$).

Indirect fitness benefits

Rates of pup production by females within groups (regardless of the father's identity) were unaffected by the natal status (or complete absence) of the dominant male; there were no significant differences in per-monthly rates of pup production between groups with a natal dominant ($n = 41$), immigrant dominant ($n = 183$) or no dominant male ($n = 10$), both in absolute terms (KW $\chi^2_{(2)} = 0.106$, $P = 0.949$) and when standardized by the number of adult females present in the group (KW $\chi^2_{(2)} = 2.898$, $P = 0.235$).

Energetic benefits

There was no evidence of consistent differences in foraging success between natal dominant and natal subordinate males: average monthly weight gain did not differ significantly between the classes of males when age was controlled for (absolute weight gain LRT: $\chi^2_{(4)} = 5.052$, $P = 0.282$; percentage weight gain LRT: $\chi^2_{(4)} = 4.4761$, $P = 0.345$).

However, both natal and immigrant dominants were substantially heavier than their subordinate counterparts when matched for age (see Fig. 3). This weight difference was not evident

between littermate pairs 2 months before one took dominance (Wilcoxon signed rank: $V = 136$, $P = 0.131$) but was significant at the point of dominance acquisition (Wilcoxon signed rank: $V = 166$, $P = 0.011$; individuals taking dominance were on average 34 g heavier than subordinate brothers) for both natal and immigrant dominant males (no significant difference between the two natal classes of dominant male; ANOVA: $F_{(1, 18)} = 0.858$, $P = 0.367$).

Survival benefits

There was no evidence that holding the dominant position affected a male's chances of survival while they remained in their natal group. The probability of within-group survival in any given month of the lifespan of males did not differ significantly between classes of males, with age, or with the interaction between the two (GLM: $F_{(5, 173)} = 0.667$, $P = 0.649$).

Although the probability of permanent disappearance from the population in any given month of a male's dominance tenure did not differ significantly between natal and immigrant dominants ($P = 0.888$), natal dominants were significantly less likely to be found dead (as opposed to simply disappearing from the group) than immigrant dominants (Wilcoxon signed rank: $V = 38$, $P = 0.041$: natal dominant average per-month survival: $99.4 \pm 0.29\%$, immigrant dominant average per-month survival: $98.5 \pm 3.06\%$).

Deferred benefits

Individuals who had held a natal dominance position before their first emigration from their group emigrated at a significantly older age (natal dominants, $n = 26$, 1265 ± 64 days, natal subordinates, $n = 404$, 745 ± 16 days; Wilcoxon rank sum: $W = 8398$, $P < 0.001$) and higher weight (natal dominants 749 ± 15 g, natal subordinates 664 ± 6 g, Wilcoxon

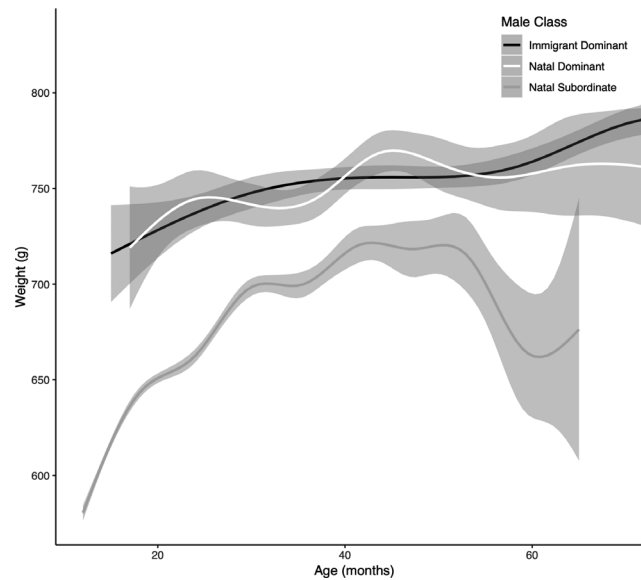


Figure 3 Average per-monthly weight for males within the three classes (loess smoothed conditional mean with 95% C.I.), showing lower per-monthly weights (and apparent senescence in terms of body mass) for natal subordinates when compared with both immigrant and natal dominant males. Both natal and immigrant dominant males were significantly heavier than natal subordinate males (Likelihood ratio test: $\chi^2_{(4)} = 2004.5$, $P < 0.001$; Tukey contrasts: Natal Dominant – Natal Subordinate $P < 0.001$, Immigrant Dominant – Natal Subordinate $P < 0.001$).

rank sum: $W = 6201.5$, $P < 0.001$) than their subordinate counterparts; these two factors were significantly correlated (Spearman's rank correlation: $\rho = 0.449$, $P < 0.001$). This difference was reflected in the weights of males upon immigration into a group, which were significantly different between males with differing previous dominance experience (KW $\chi^2_{(3)} = 8.0887$, $P = 0.044$) – males with natal dominance experience were significantly and considerably heavier on average than males with no previous experience (natal dominance experience, 746 ± 21 g, no dominance experience, 628 ± 12 g; Dunn *post hoc* $P = 0.034$).

Males who had held a natal dominance position were more likely to acquire dominance positions in other groups after successful dispersal from their natal group: when multiple immigrant males were present in an established group, an individual's probability of taking dominance was enhanced if he had previous dominance experience even when weight was controlled for (LRT: $\chi^2_{(3)} = 15.284$, $P = 0.002$; see Fig. 4). In accordance with previous studies (Russel *et al.*, 2004; Thavaraiah *et al.*, 2014), weight ($P < 0.001$) was also found to be a significant predictor of an immigrant male's success in acquiring dominance within the full model, with heavier males more likely to take dominance.

Lifetime reproductive success did depend on the dominance history of the male (KW $\chi^2_{(3)} = 138.690$, $P < 0.001$). However, males who were only ever natal dominants did not have significantly higher average lifetime reproductive success than males who were never dominant (Dunn *post hoc* $P = 0.714$; 2.91 ± 2.29 pups). Males who were both natal and immigrant dominants within their lifetime were equivalent to immigrant-only dominants in the total number of pups fathered (Dunn

post hoc $P = 0.714$; 7.59 ± 3.53 pups). While the proportion of life spent as an immigrant dominant was positively correlated with number of pups fathered ($\rho = 0.645$, $t_{(107)} = 8.738$, $P < 0.001$), the proportion of life spent as a natal dominant was not ($t_{(52)} = -1.065$, $P = 0.292$).

The dominance experience of the male did not appear to affect the reproductive success of the group as a whole: there was no significant difference in the per-monthly pup production of groups based on the previous dominance experience (or lack thereof) of the dominant male (KW $\chi^2_{(3)} = 4.296$, $P = 0.231$).

Discussion

Our results provide an unusual example of the deferred benefits of social status within animal groups. We find that natal male meerkats do not gain immediate benefits of dominance in terms of direct or indirect reproductive success (both within- and outside-group), growth or survival. However, males that acquire dominance natively appear to be in a stronger position to disperse and achieve dominance elsewhere, which has positive long-term effects on their reproductive success and supports a deferred benefit of this life history strategy.

We do not find evidence within this study of any immediate reproductive benefits of holding the dominant position for natal male meerkats. Natal dominant males reproduce within their group extremely rarely (Fig. 2) and so do not gain the classic reproductive benefits associated with a dominant position; their reproductive behaviour is more similar to natal subordinates (i.e. they engage in 'roving' attempts at other groups and have generally low breeding success overall). We also found no

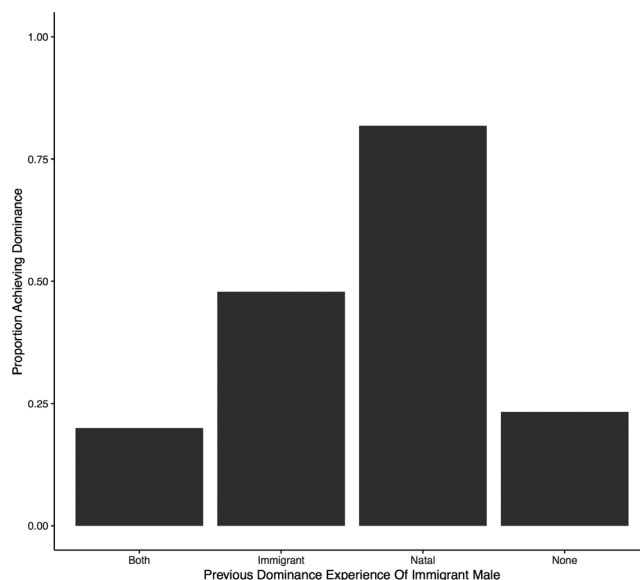


Figure 4 The proportion of immigrant males with each type of dominance experience who went on to become group dominant, having been present in the group when the position became available (natal dominance experience $n = 11$; immigrant dominance experience $n = 46$; natal & immigrant dominance experience $n = 5$; no dominance experience $n = 322$).

indication of indirect benefits of natal dominance for males: group reproductive rate (and therefore the reproduction of a natal male's kin) is unaffected by the status – or indeed complete absence – of a dominant male.

We also see no evidence of direct non-reproductive benefits of holding the position: natal dominant males showed neither increased growth rate nor improved survival probability relative to natal subordinates while group-bound. The latter result is consistent with previous results indicating that out-of-group mortality generates status-related survival differences in this study population (Cram *et al.*, 2018). This implies that the behavioural assertions over subordinates seen in dominant males (e.g. aggressive behaviour; Thavarajah *et al.*, 2014) do not translate directly into, for example, improved foraging success or access to safer locations within the group – although it should be noted that the conditions of the study site (particularly frequent presence of observers) might reduce the incidence of predation within this population (Clutton-Brock *et al.*, 1999).

It is possible that natal dominant males suffer relatively few costs of competing for and maintaining the position when compared to their immigrant equivalents. The exact costs of holding dominance for male meerkats are relatively unknown compared with females (e.g. Carlson *et al.*, 2004; Hodge *et al.*, 2008; Smyth & Drea, 2016; Smyth *et al.*, 2018) but may be lower: unlike in females, dominant male meerkats do not differ in testosterone or cortisol levels from their same-sex subordinates (Carlson *et al.*, 2004; Davies *et al.*, 2017). While some costs are likely to remain – such as investment in dominance-maintaining behaviours like substrate marking and aggression towards same-sex subordinates – others may be reduced for natal dominant males. Notably, natal dominants do

not seem to invest heavily in guarding breeding females, as the presence of a natal dominant does not decrease the reproductive success of the group. These potential reductions in resource or metabolic cost, however, do not appear to generate direct benefits: natal dominant males are no heavier than their immigrant counterparts.

Weight is valuable in competitive interactions in meerkats (Russel *et al.*, 2004; Thavarajah *et al.*, 2014). It might be expected that achieving high weight is a benefit of acquiring dominance, but we find that a weight advantage is a cause – rather than a consequence – of dominance acquisition in both natal and immigrant males. This investment in weight gain in order to be competitive carries potential long-term costs (Metcalf & Monaghan, 2001; Huchard *et al.*, 2016; Cram *et al.*, 2018), making it even more paradoxical from the perspective of a natal individual who has seemingly little to gain from successfully competing for the position. This may be why natal dominant males rarely take the position over an immigrant male present in the group, who has stronger motivation to pay any costs of competing for the position. While there is currently no evidence in meerkats for a role of the dominant female in determining the outcome of dominance competition in males (and therefore favouring a close relative), natal males may also compete less fiercely for the position – and hence risks of injury or death during dominance competition between natal males may be lower than for immigrant males.

We find, however, that natal dominant males appear to gain benefits from their position which only manifest 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 & 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 & 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 & Ligon, 1991; Ekman *et al.*, 1999; Green & Cockburn, 2001; Wong, 2010; Sparkman *et al.*, 2011; Nelson-Flower *et al.*, 2018) have often focussed on immediate benefits: indirect fitness through helping relatives to breed, access to resources or other condition-improving factors such as 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.

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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.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Meerkat pregnancy length.