The Importance of Being Beta: Female Succession in a Cooperative Breeder

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In singular cooperative breeders few females breed successfully, but those that acquire dominant positions can achieve high levels of breeding success, leading to strong selection for traits that enable individuals to acquire and maintain dominance status. However, little is known about the process by which females acquire dominant breeding status or the traits that enable them to do so. Female meerkats can acquire dominance either by inheritance after the death of the previous dominant, displacing the incumbent dominant or at the foundation of a new group. Here we investigate the possible fitness benefits associated with these different routes to dominance and the traits that affect an individual's probability of acquiring dominance via these routes. We found that all routes to dominance have similar fitness benefits and that when a dominance vacancy arose, weight was the main determinate of succession, with age still influencing within group succession and the eldest subordinate female, the beta, often succeeding to dominance. Since the chance that subordinate females will acquire dominance is also positively correlated with the duration of their tenure in the beta position, we tested whether beta females adjust their growth or cooperative behaviour to avoid eviction and increase their tenure length as the beta. However, there is no indication that betas employ either strategy to increase their tenure. Given that the differing routes to dominance have equivalent fitness pay-offs and are triggered stochastically, selection probably favours flexibility rather than strategies that commit individuals to a specific route.

Key Words: cooperative breeders, dominance acquisition, dominants, reproductive success, strategic growth, succession

Introduction

In many cooperatively breeding mammals, a single dominant female virtually monopolises reproduction in each group and her offspring are reared by other group members that seldom breed successfully (Bennett & Faulkes, 2000; Clutton-Brock & Manser, 2016; Creel & Creel, 2002; Hackländer, Möstl, & Arnold, 2003; Rood, 1990; Saltzman, Digby, & Abbott, 2009). Since most females never acquire dominance, while those that do may maintain their position for several years and may breed several times a year, variance in the lifetime breeding of females is unusually high and frequently exceeds that of males (Clutton-Brock et al., 2006; Hauber & Lacey, 2005), generating strong selection among females for characteristics and strategies that enhance their ability to acquire and maintain dominant positions (Clutton-Brock et al., 2006; Clutton-Brock & Huchard, 2013; English, Huchard, Nielsen, & Clutton-Brock, 2013).

Age based hierarchies where individuals queue for dominance occur in many mammalian societies, including African elephants, *Loxodonta africana* (Archie, Morrison, Foley, Moss, & Alberts, 2006), chimpanzees, *Pan troglodytes* (Foerster et al., 2016) and free-ranging dogs, *Canis lupus familiaris* (Bonanni et al., 2017), as well as in several cooperatively breeding mammals, such as the dwarf mongooses, *Helogale parvula*, wolves, *Canis lupus* and wild-dogs, *Lycaon pictus* (Creel, 2005; Creel, Creel, Wildt, & Monfort, 1992). Although the weight and condition of individuals are commonly correlated with their status (Veiberg, Loe, Mysterud, Langvatn, & Stenseth, 2004; Vervaecke, Roden, & De Vries, 2005) few studies have been in a position to investigate their effects on the likelihood of status acquisition itself. One exception is a study of captive house mice, *Mus domesticus*, where the weight rank of individuals at group formation was positively related to their probability of acquiring high status (Rusu & Krackow, 2004).

While an individual’s ability to acquire high status can increase as they age and grow, individuals can also find themselves subject to higher levels of aggression and eviction from the group should they threaten the status (Buston, 2003a) or reproductive monopoly of higher ranking individuals (Cant, Hodge, Bell, Gilchrist, & Nichols, 2010; Thompson et al., 2016; Young et al., 2006). In some social fish species that show size related hierarchies, individuals queuing for the dominant position reduce their rate of growth when they approach the weight of the individual in the rank above them in the hierarchy. This serves to reduce the frequency with which they are threatened, attacked or evicted, maximising their chances of remaining in the group and, eventually, of succeeding to the dominant breeding position (Buston, 2003b; Heg, Bender, & Hamilton, 2004; Wong, Munday, Buston, & Jones, 2008). The "pay-to-stay" hypothesis suggests an alternative mechanism for appeasing dominants, by which subordinate individuals increase cooperative effort to compensate their increasing cost to the dominant (Balshine-Earn, Neat, Reid, & Taborsky, 1998). Evidence of such a mechanism has been reported in cichlids, *Neolamprologus pulcher* (Bruintjes & Taborsky, 2008) and paper wasps, *Polistes dominula* (Grinsted & Field, 2017). While weight-based dominance hierarchies are observed in many social mammals (Veiberg et al., 2004) and the aggressive eviction of subordinate females by older dominants occurs in some (Kappeler & Fichtel, 2012; Pope, 2000), no mammalian studies have yet investigated whether individuals modify their growth rates or levels of cooperation to minimise conflict with the dominant.

Here, we examine the factors affecting succession to the dominant position in female Kalahari meerkats, *Suricata suricatta*, and investigate whether individuals modify their growth rates or cooperative behaviour to avoid aggression and increase their chances of remaining in their natal group and acquiring dominance status. Kalahari meerkats live in breeding groups of up to 50 individuals, including a single dominant breeding pair and an approximately equal number of subordinates of each sex that help to rear the offspring of the breeding pair (Clutton-Brock et al., 2001; Clutton-Brock & Manser, 2016; Doolan & Macdonald, 1999). After a successful birth, one or two individuals will stay at the burrow to babysitting the pups each day until they start foraging (T. H. Clutton-Brock et al., 2000), at which point group members will provision them with food items until they reach nutritional independence at around 90 days (Carter, English, & Clutton-Brock, 2014; Clutton-Brock et al., 2002). Older subordinate females occasionally attempt to breed but rarely do so successfully and the resident dominant female is usually the mother of over three quarters of all young born in her group and may hold tenure for more than 10 years, producing up to three litters a year (Clutton-Brock et al., 2001; Griffin et al., 2003; Young & Clutton-Brock, 2006). Subordinate females are tolerated by the resident dominant female in their group until they are at least two years old but almost all are forcibly evicted by the dominant female before they are four years old (Clutton-Brock et al., 1998; Young et al., 2006). Evicted females leave alone or in small coalitions that sometimes establish new breeding groups with dispersing males from other groups (Young, 2003).

Female meerkats may acquire a dominant position either in their natal group or in a group they dispersed and founded, and do so either by inheriting after the death of the previous dominant female; by displacing (and usually evicting) the existing dominant female or at the founding of a new breeding group with a male(s) that have dispersed from another group (Clutton-Brock & Manser, 2016). Previous work has shown that the probability that individual females will acquire dominant status during their lifespan is associated with the status of their mothers (Hodge, Manica, Flower, & Clutton-Brock, 2008), their growth rates as pups (English et al., 2013) and the level of investment by helpers during their own development (Russell, Young, Spong, Jordan, & Clutton-Brock, 2007). In this study we describe the relative frequency with which females acquire dominant breeding status, the breeding tenure and success of individuals that acquire dominance in different ways and the traits that affect the ability of females to acquire dominant status. The oldest subordinate female, the beta, is usually dominant to other subordinate females (Thavarajah, Fenkes, & Clutton-Brock, 2014) and is more likely to acquire the dominant position after the death of an existing dominant female in her group than other group members (Clutton-Brock et al., 2006; Hodge et al., 2008). The eldest subordinate is commonly the heaviest subordinate and also at the highest risk of eviction by the dominant (Clutton-Brock, Hodge, Flower, Spong, & Young, 2010). Subordinate females in several species that queue for the dominant position have been reported to reduce their growth or increase their contributions to cooperative activities to reduce the chance of eviction and maintain their position within group (clown fish, *Amphiprion percula*, Buston, 2003b; paper wasps, *Polistes dominula*, Grinsted & Field, 2017; cichlids, *Neolamprologus pulcher*, Heg et al., 2004; gobies, *Paragobiodon xanthosomus*, Wong et al., 2008). Therefore, we investigated whether subordinate female meerkats in the beta position reduced their growth or increased their contribution to cooperative behaviour.

Methods

Study Site and Population

This research was conducted using data collected in the course of a long-term study of wild meerkats in the Southern Kalahari Desert. The study area was located on the Kuruman River Reserve and surrounding farms (26°58′S, 21°49′E), South Africa; covering a range of 50-60km^2 (Cozzi, Maag, Börger, Clutton-Brock, & Ozgul, 2018). Data were collected between July 1995 and March 2017, on average at any month 215 individuals (range: 46-359) composing 15 groups (range: 6-25) were followed. Almost all individuals in our study groups could be observed from less than two meters and each animal was given a distinct dye mark to allow for visual identification. After pups emerge from the burrow almost all were caught to insert a subcutaneous transponder and take a tissue sample (Hodge et al., 2008; Spong, Hodge, Young, & Clutton-Brock, 2008). Immigrants into our population were processed in this way as soon as they were able to be caught. Samples were subsequently genotyped in order to assign genetic parentage (Spong *et al* ,2008) and were then used to construct a multi-generational pedigree (Nielsen, 2012). All groups were visited 3-5 times a week throughout the year and observed for 3-4 hours a day. Behavioural data were recorded *ad libitum* over the course of these observations. Detailed records were kept of the life histories of all individuals in our study population, including their birth dates (±1-2 days), their membership of different groups, pregnancies, lactation, offspring survival, dominance interactions, condition and age at death. Almost all individuals could be weighed regularly by enticing them onto electronic scales using crumbs of hardboiled egg. During these visits group members were weighed to the nearest gram shortly after dawn when the group first emerged from its sleeping burrow, three hours after the animals began foraging and shortly before they entered their sleeping burrow at the end of the day (Clutton-Brock & Manser, 2016).

Identification of female dominance

The dominance status of females was determined from the frequency and direction of aggressive and submissive interactions directed at other females within their group as well as from the relative frequency of anal marking, which is substantially higher in dominants than subordinates (Thavarajah, Fenkes, & Clutton-Brock, 2014). The dominant female was dominant to all other females in the group and, in most cases, to all males, too. The period that a dominant female holds their position we refer to as bout of dominance, the start date for a dominance bout was set as the first day on which clear and consistent one directional dominance relationships were observed between the new dominant and all other females. The end date was either the day on which a dominant died (due to our usual practice of radio-collaring all dominant females, death can usually be positively identified) or the day on which a dominant female was displaced by another group member. Only females that were born in our study population (n=1111) were included in analyses so their dispersal status, age and other characteristics could be reliably determined. During our study period a total of 167 bouts of dominance at 68 groups were observed, for females born in the population. Dispersal distances for females are short (Maag, Cozzi, Clutton-brock, Manser, & Ozgul, 2018), thus dispersing females rarely settle outside or far from our study area. Whilst they are often incorporated into the study population, inevitably some individuals leave our study population and are not observed acquiring dominance. Therefore, we likely underestimate the frequency of dispersed dominants.

Previous work has identified age as the main determinant of the outcome of antagonistic interactions among subordinates, with weight dictating outcomes between individuals of the same age (Thavarajah, Fenkes, & Clutton-Brock, 2014). Therefore, we defined a beta individual as the eldest subordinate in the group each month and where several individuals from the same litter were present in the top age rank, we assumed that the heaviest individual in the litter was the beta. To avoid the possibility that individuals who were absent for most of the month were assigned beta status, individuals had to be present for more than 33% of group observations per month to be recorded as occupying the beta role. Following English et al (2013), only females born between 01/01/1997 and 02/03/2014 were included in the analysis of beta females (02/03/2014 represents 1126 days before the end of our sampling period which is the age at which 75% of dominants had acquired their position; this restriction helps to reduce bias caused by including individuals who had not yet had sufficient time to acquire dominance). The lower date limit was the point at which the group data coverage reached a level allowing for beta positions to be tracked reliably and accurately at a monthly resolution. Our approach resulted in a sample set consisting of 917 females who could have held a beta position, we further restricted this to individuals that lived beyond a year, reducing our sample to 648 females.

Ethical Note

The majority of data used in this study was observational and the handling necessary for weighing, tissue sampling or attaching collars was kept to a minimum. All data collection protocols and methodologies were approved by the Animal Ethics Committee of the University of Pretoria.

Statistical Analyses

All analyses were conducted in the statistical environment R, version 3.3.3 (R Core Team, 2017). To conduct multiple regressions, linear mixed effect models (LMER) and generalized mixed effects models (GLMM) were utilized. This allowed for the fitting of random terms to account for repeat sampling. Only random terms that explained greater than zero variance were maintained in models. These models were fitted using the R package glmmTMB (Magnusson et al., 2017). When GLMMs were used to model count data these models were fitted with a negative binomial error distribution and a log link to account for overdispersion (Hilbe, 2011). Additionally, when there was variation in observation time within data-sets, a variable representing sampling effort or period was fitted as an offset within the model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Collinearity of fixed terms was tested in models using variance inflation factors (Table A1-3), applying a threshold value of three revealed no collinear terms in any model (Zuur et al., 2009). Quadratic terms were fitted in models when an expected quadratic relationship was confirmed by preliminary diagnostic plotting. Stepwise backwards removal and reintroduction of non-significant terms was used for model simplification and to check for missed significant terms (Crawley, 2013). Full models were presented except when only one fixed term was of interest, in which case the coefficients for that term of interest were presented and the full model included in the supplementary material.

__Contrasting paths to dominance__

As in many other social mammals, female meerkats that leave their natal group rarely join established breeding groups with only three observed cases of females immigrating into another group. Dominance could be acquired in either an individual's natal group or in a new group they had formed post dispersal, and via three methods: inheritance, displacement or foundation. Subordinate females could consequently acquire dominance by one of five routes: (1) natal inheritors acquired dominance status in their natal group following the death of a previous dominant; (2) natal displacers also acquire dominance status in their natal group after displacing (and usually evicting) the previous dominant; (3) dispersed founders left their natal groups and subsequently founded a new breeding group and immediately acquired dominant status there; (4) dispersed displacers were founding members of a new breeding group and subsequently displaced a dominant female that succeeded dominance before them; and (5) dispersed inheritors were founding members of a new breeding group and subsequently inherited the breeding position there after the death of the previous incumbent.

To investigate differences in the acquisition age, age at tenure loss and length of tenure, in relation to where and by what method individuals acquired dominance, LMERs were used with group ID fitted as a random effect. When analysing the age an individual acquired dominance, acquisition routes as opposed to method was used to allow for distinction between individuals utilising the same acquisition methods in natal vs dispersal groups. To fulfil assumptions of normality, acquisition age was square root transformed, tenure length was transformed by the 5th root and the age at tenure loss was log transformed.

We used two measures to compare the reproductive success of dominant females that acquired their status via different routes: the number of offspring produced during the tenure of dominance that reached nutritional independence (90days) and the number of offspring that reach adulthood (365days). Both measures were fitted as response variables in separate GLMMs with negative binomial error distributions with a log link and tenure length in days fitted as an offset and group ID as a random effect. The offspring of dominant females were identified using a combination of our genetic pedigree and field observations. In these analyses, restricted our sample to dominant females born in our population that had a confirmed tenure end as well as a tenure long enough to conceive and produce emergent pups (> 90 days), giving a sample size of 104 distinct dominance tenures. To investigate the effect of the route to dominance on reproductive success, location (Dispersal vs Natal) and method (Inheritance vs Foundation vs Displacement) of acquisition were fitted as categorical predictors in the GLMMs.

Factors determining the acquisition of status

A binomial proportions test was used to test whether individuals that held a beta status were more likely to acquire dominance than those that did not at any point in their lifetime. We subsequently summed the total number of months betas held their status over their life time and investigated the relationship between length of beta tenure and the probability of acquiring dominance, using a GLMM with a binomial error distribution and a logit link. Total months spent as a beta was fitted as a predictor variable, whether they acquire dominance as a binomial response variable and their natal group as a random effect.

To model proximate factors influencing the probability of a subordinate female acquiring dominance when an acquisition opportunity arose, we used GLMs with a binomial error structure and a logit link. Each method of acquisition was modelled separately to investigate possible differences in the traits determining dominance between the methods. We included every subordinate female of six months or older who was present in the group in the month prior to the acquisition event as a competitor. Individuals were then assigned a binary value as to whether they acquired dominance in the acquisition event which was fitted as the response variable. Weight and age relative to the heaviest and oldest competitors present along with an individual's pregnancy status prior to the event were included as predictor variables. The weight of individuals was calculated as the mean pre-foraging morning weight for a period of 14 days before and 7 days after the acquisition event. Whether the possible successor was the daughter of the previous dominants and their relatedness coefficient relative to the dominant female were fitted as predictor variables in the model for natal inheritance. In the displacement model natal status within the group and whether the successor was the sibling of the previous dominant were included as categorical predictor variables.

Characteristics of Betas

The growth rate of all beta individuals was measured for each month of their tenure as the difference in mean morning weights for the first and the last seven days of the month. To identify any possible adjustments in growth in response to conspecific weights, the beta's growth rate was fitted as the response variable in a LMER with their difference in weight to the dominant and to the next eldest subordinate (gamma) at the beginning of the month, included as fixed effects. Age, cumulative rainfall for the two months prior and the weight of the beta at the start of the month were controlled for by including them as fixed effects. Rainfall was calculated using the data from the Global Precipitation Climatology Project dataset provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at https://www.esrl.noaa.gov/psd/ on 13th December 2017 (Adler et al., 2003). The year, month and identity of the beta were included as random effects to control for repeat sampling. Months where individuals were pregnant were excluded from the data set as their state was expected to have a confounding effect on growth. Initially for our sample consisted of 2274 month periods with a beta present, however sub-setting this for only periods where we have growth rates for the beta, weight measures for both the dominant and the gamma females, and the target individuals were not pregnant, reduced the sample for this analysis to 938 month periods consisting of 194 distinct beta females.

To assess the contributions of beta individuals to cooperative activities relative to those of other subordinates, we measured their contributions to pup provisioning and babysitting on a per litter basis. Litters born across our entire study period were included in the analyses. All females older than 6 months present during the helping period for a litter were included in the analysis, with the beta female classified as described above, and subordinates classified as females present in the group that are neither the beta or Dominant female. During a babysitting period, the group was usually visited every morning and most evenings to identify the babysitting individuals, therefore contributions to babysitting were calculated as the number of half days spent babysitting between the birth of the litter and the time the pups started foraging. Individual contributions to pup provisioning were calculated as the number of food items contributed by each individual recorded between the day the pups started foraging and when the period of peak provisioning ended 45 days later. Babysitting contribution and pup provisioning contributions were fitted as response variables in separate GLMMs with a negative binomial error distribution and a log link, with rank as a two-level factor (beta vs sub) included as a predictor. The number of half days the group were observed during babysitting was included as an offset and, for pup provisioning, the total minutes of behavioural observation recorded during the provisioning period was also included as an offset. The identity of the individuals and the litter were fitted as random effects. Age, mean morning weight and mean group size (individuals older than 6 months) were included as predictor variables in both models and the mean number of pups present was included as a predictor variable in just the provisioning model. Quadratic terms for age and weight were included in the babysitting model, whilst quadratic terms for weight, group size and pup number were included in the provisioning model. These analyses included 491 babysat litters constituting 2317 periods of babysitting from 739 individuals and 464 provisioned litters constituting 2276 periods of pup feeding for 708 individuals.

Results

Contrasting paths to dominance

152 (21%) of the 723 females born into our study population that reached adulthood (12 months) acquired a dominant position in our study population at some stage during their lives. Almost all of these acquired the dominant position when they were over a year old though some did not do so until they were over three years old. The chances that females would acquire dominance increased as they grew older, although the number of females acquiring dominance declined after the age of 30 months (Figure 1).

Of the 152 individuals that acquired dominance, thirteen had two distinct bouts of dominance during their lifetime. Nine (69%) of those dispersed to acquire dominance in a new group from the group in which they first acquired a dominant position. Just over half of all individuals acquired their first dominance position in their natal group while slightly under half acquired a dominant position after dispersing from their natal group (Table 1). Inheritance was the most common method of acquisition (49%, *N* = 74) overall while displacing an existing dominant was the least common (20%, *N* = 31; Table I). Acquisition of a dominant position immediately after founding a new group was the second most common acquisition method (31%, *N* = 31; Table 1).

Individuals that acquired dominance in their natal group, did so earlier in life than those that acquired dominance after dispersal (LMER: $F_{1,106} = 29.37$, $P < 0.001$) and the differences in age of acquisition between different routes were significant (LMER: $F_{4,103} = 9.264$, $P < 0.001$; Figure 2). Displacers were not significantly older than individuals that acquired dominance by inheritance but were closer in age to the dominants they displaced than were inheritors, with the age gap between displacers and the individuals they displaced being smaller than that between inheriting successors and the previous dominant (LMER: $F_{1,75} = 10.71$, $P = 0.002$). Individuals that acquired dominance in their natal group, also lost their tenure at an earlier age than individuals who acquired dominance after dispersal (LMER: $F_{1,90} = 12.8$, $P < 0.001$).

Mean duration of tenure of dominant status for females was 20.1±24 months (median = 9.2 months, range = 0.2 – 125.7 months; see Figure 3). There was no significant difference between the tenure lengths of individuals that acquired dominance in their natal group and those that acquired dominance after dispersal (LMER: $F_{1,90} = 0.035$, $P = 0.853$) or between individuals that acquired dominance via different methods (LMER: $F_{2,89} = 0.665$, $P = 0.522$). There was also no significant relationship between individual's reproductive success and the method by which they acquired their position of dominance or the location of their dominance bout (Table 2).

Factors affecting the acquisition of dominance

Of the 648 females born in the population within the sample period that survived to adulthood, 308 (49%) had held a beta position for at least a month. Individuals that acquired a beta position held beta status for a mean total of eight months (median = 5, range = 1 – 40 months). Of the individuals that held a beta position in our sample ($N = 308$), 55 (18%) acquired dominance status in their natal group, 34 (11%) died before doing so and 219 (71%) were evicted by the dominant female in their group or disappeared suddenly. Of those that were evicted 49 (22%) acquired dominance in a newly founded group. Individuals that never held a beta position, ($N = 340$) had a significantly lower probability of acquiring dominance than those that had done so (binomial proportions test: $N1 = 308$, $N2 = 340$, $X_2 = 79.4$, $P < 0.001$), with only 20 (6%) acquiring a position of dominance at any stage in their lives. Of the 20 individuals that had never held a beta position who subsequently acquired dominance, two were cases where the group's beta died just before the acquisition event (making them effectively the beta in the acquisition event), two had a beta in poor health at the acquisition event and four dispersed to found a new group as the eldest in their coalition. The remaining twelve had to acquire dominance by out-competing older individuals for dominance.

The tenure of Beta females affected the probability that they would acquire dominance status and the more months individuals spent in the beta position, the greater were their chances of acquiring dominance (Effect = 0.031 ± 0.015, z-value = 2.12, *P* = 0.034; Figure 4). In groups where several adult subordinate females were present, 85% (64/75) of dominant females that died or were displaced were succeeded by the oldest female group member. Similarly, 89% (48/54) of females that acquired dominance after dispersal, in a group of which they were a founding member had been the beta female at some point in their natal group.

The weight of subordinates relative to that of other potential contenders is an important proximate factor in determining their chances of acquiring the dominant position, with the heaviest subordinate being most likely to succeed and an individual's chances of acquisition decreasing the greater the weight difference between them and the heaviest subordinate (Table 3). An individual's age also affected their chances either of inheriting dominance or of displacing the previous incumbent. However, this was not the case in new groups founded by dispersing females (Table 3). In most cases where the oldest competing subordinate acquired dominance either by inheritance or by displacement, they were the heaviest subordinate female in the group (77%, 44/58). Also, in 73% (11/15) of cases where the oldest subordinate outcompeted another subordinate of the same age they had a weight advantage. In displacement and inheritance acquisition when the oldest subordinate was outcompeted for dominance by a younger female, the younger female had a weight advantage over the older subordinate 55% (6/11) of the time. Other traits, such as pregnancy and relatedness to the previous dominant, did not significantly influence the probability of individuals acquiring dominance, either in their natal group or after founding a new group (Table 3).

Most dominant females that die are succeeded by their daughters (45.1%; 37/82) or siblings (30.5%; 25/82). When dominant females are displaced before their death, this is most commonly by a sibling (57%, 20/35) and usually occurs within the first year of their tenure (77%, 27/35). However, irrespective of this we found no effect of relation to the previous dominant on success at competing for dominance vacancies (Table 3).

Strategies for maximising beta tenure

Since dominant females are more likely to evict subordinates that pose a risk to their reproductive potential (Clutton-Brock, Hodge, Flower, Spong, & Young, 2010), we investigated whether beta females reduced their growth rates relative to the weight of the dominant female after acquiring beta status or increased their contributions to cooperative behaviour. However, there was no evidence that subordinates that acquired beta status either reduced their growth rates or increased their contributions to cooperative behaviour. Among 242 individuals that acquired beta status that we analysed, there was no significant reduction in growth over the 1137 months they held their positions relative to either the weight of the next oldest subordinate (t-value = -0.37, $P = 0.71$) or the dominant female (t-value = 1.72, $P = 0.09$) at the start of the month. There was also no indication that individuals holding beta status increased their contributions to cooperative activities after other predictors of cooperative effort had been controlled for. No significant effect of the rank of females on relative contributions to babysitting (z-value= -0.51, $P = 0.61$) or on pup provisioning (z-value = -0.06, P value = 0.9) was found (See SM for full models).

Discussion

We found that most dominant female meerkats acquire their status either through inheritance in their natal group or through the founding of a new breeding group and establishing themselves as the dominant female. A smaller proportion acquired dominance by displacing the incumbent dominant (Hodge *et al.*, 2008; Sharp and Clutton-Brock, 2011). Individuals that acquire dominance in their natal group do so at an earlier age than those that disperse before acquiring dominance, but neither tenure length nor reproductive output vary consistently in relation to the route to dominance. When dominant females die or are displaced, they are usually replaced by the heaviest and oldest female in their group and a female's chances of acquiring dominance are related to the length of time she occupies the beta position. However, we find no evidence that beta females either restrict their growth rate or increase their cooperative care of the dominants offspring to prolong their tenure.

The later age at which individuals acquire dominance in groups other than their natal group is due to such opportunities only becoming available after eviction, the risk of which increases with age (Clutton-Brock et al., 1998). This raises the questions as to why individuals do not voluntarily disperse at an earlier age and seek extra-group dominance, especially when potential breeding partners present themselves in the form of prospecting males (Young et al., 2007). One benefit of subordinates maintaining group residency (philopatry) is the possibility of future direct fitness benefits gained by inheriting the breeding position and/or territory of their current group, which has been reported to drive patterns of philopatry and dispersal in common lizards, *Lacerta vivipara* (Ronce, Clobert, & Massot, 1998) and paper wasps, *Polistes dominulus* (Leadbeater, Carruthers, Green, Rosser, & Field, 2011). The selective eviction in meerkats of older high-ranking subordinate females creates social mobility with lower ranking subordinates increasing hierarchical rank and probability of inheritance over time. Social mobility is reported to play an important role in individuals maintaining group residence in Tibetan macaques, *Macaca thibetana* (Sun, Xia, Sun, Sheeran, & Li, 2017)., and is likely an important driver of philopatry in meerkats too as it leads to the future probability of natal dominance acquisition being more evenly distributed across the hierarchy. Conversely, in societies where eviction is infrequent or absent, and hierarchies are stagnant, the benefits of philopatry decline with subordinate rank as probability of dominance acquisition declines. In such cases younger low ranking subordinates with little prospect of natal succession voluntarily disperse in search of reproductive dominance or a higher rank position (Nelson-Flower, Wiley, Flower, & Ridley, 2018; Rood, 1987), sometimes acquiring positions of dominance earlier in life than those that remain in their natal groups (Rood, 1990).

Whilst natal dominants acquire dominance at an earlier age, they do not experience longer tenures than individuals that disperse and acquire dominance later in life. This appears to be due natal dominants also losing dominance at an earlier age, which as dominance tenures most commonly end in death suggests that the fate of dominants is determined by a maximum dominance span not a maximum life span. This is in line with evidence of the cumulative physiological costs of dominance and reproduction (Blount, Vitikainen, Stott, & Cant, 2016; Cram, Blount, & Young, 2015; Sapolsky, 2005) and supports recent analysis of meerkats showing dominant mortality being driven by accelerated senescence (Cram et al., 2018). This is likely why even though the availability of different routes to dominance vary with age, the fitness benefits do not differ between them. While some social species do incur fitness costs dependent on the route to dominance utilised, often in the forms of reduced survival and reproductive rates (Ekman & Griesser, 2018; Georgiev et al., 2016; Sparkman, Adams, Steury, Waits, & Murray, 2011), these costs tend to be associated with early dispersal or intense competition for alpha status when invading groups. Neither of these issues are faced by subordinate female meerkats, who disperse only after reproductive maturity and then form a new group rather than invading existing stable groups.

The fact that individuals that hold a beta position are more likely to acquire dominance in their lifetime, especially in relation to their increasing tenure, is likely due to an increased probability of experiencing a dominance vacancy whilst being the prime successor. This is partially corroborated by our analyses of the proximate factors dictating succession, which indicate that age relative to other subordinate females is an important indicator of who acquires dominance when a within group vacancies arise (inheritance and displacement). Which is in line with research depicting age-based dominance hierarchies where females queue for dominance in a number of social species (Archie et al., 2006; Creel, 2005; Foerster et al., 2016). However, we also find that an individual's weight relative to other subordinates is an important proximate factor in determining acquisition of dominance, a result only previously reported in a captive study of house mice (Rusu & Krackow, 2004). Whilst this can be partially explained by weight differences resolving dominance competitions between same aged competitors (Thavarajah et al., 2014), our results also indicate that younger subordinates with a weight advantage are sometimes able to outcompete older subordinates. This raises two possibilities, either weight is playing a more important role in determining the subordinate hierarchical rank than expected or dominance vacancies are not queued for but instead actively competed over when they arise. As age has no significant effect on acquisition at the foundation of a new group, any age stratified queue for dominance present in the natal group seems not to be conserved over dispersal, with an individual's weight instead dictating dominance acquisition. Distinguishing whether succession is dictated by an individual's proximate traits or a predetermined hierarchical position remains unclear. Therefore, future studies should focus on characterising the subordinate hierarchy, the traits dictating its ordering, and the importance of hierarchical position versus proximate traits at the time of succession in determining who acquires dominance.

We find no evidence that females in the beta position adjust their growth or cooperative effort in an attempt to increase the length they hold position within their group. In species that have been reported to employ similar tactics to maintain group residency, the exposure to particularly high ecological constraints is suspected to drive the evolution of these tactics (Buston, 2003a; Wong et al., 2008) and the expression of them has been related to the severity of these constraints (Bergmüller, Heg, &

Taborsky, 2005; Grinsted & Field, 2017). Whilst meerkats are exposed to ecological constraints in the form of dispersal costs (Young & Monfort, 2009; Young et al., 2006) and variable extra-group reproductive opportunities (Maag et al., 2018), these don't appear to be prohibitively high, with our results finding similar numbers of subordinates acquiring dominance by dispersing as we do acquiring dominance in their natal group and with no apparent fitness costs. As we find weight is an important predictor of dominance acquisition, which is likely to be reduced by these strategies, investing in them would compromise an individual's ability to compete for a dominance position should an opportunity arise. Furthermore, subordinate cooperation in meerkats is not mediated by dominant aggression (Dantzer et al., 2017; Santema & Clutton-Brock, 2012), an indicative trait of species exhibiting "pay-to-stay" mechanisms (Bruintjes & Taborsky, 2008), which combined with our results suggest that subordinate female meerkats do not "pay-to-stay", with cooperative appeasement not being viable.

In conclusion, we find that with no clear fitness advantages to certain pathways to dominance, female meerkats do not employ strategies to maximise their chances of natal succession. We suggest that unless there are particularly high costs or benefits associated with certain routes to dominance, there will not be selection for strategies to acquire dominance by specific routes. When highly stochastic events such as the death of an incumbent dominant or forced dispersal dictate the occurrence of opportunities to acquire dominance, subordinate females benefit from flexibly reacting to any opportunities that arise rather than adopting strategies that favour one route over another.

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Tables and Appendices

Table 1: Proportions of dominance acquired via different routes

Acquisition Method	Frequency (Individuals)	Proportion of Acquisitions (%)
Natal		
Inheritance	67	44.1
Displacement	16	10.5
Total	**83**	**54.6**
Dispersal		
Founder	47	30.9
Inheritance	7	4.6
Displacement	15	9.9
Total	**69**	**45.4**

In cases where an individual held multiple positions of dominance, only their first position was counted.

Table 2: The reproductive success for dominance bouts depending on where and how dominance was acquired.

Model Term	**Estimate ± SE**	**z-value**	***P***
# Pups Reaching Nutritional Independence			
Acquisition Location (Dispersed)			
Natal	-0.15 ± 0.23	-0.67	0.50
Acquisition Method (Displacement)			
Foundation	-0.33 ± 0.25	-1.33	0.18
Inheritance	-0.33 ± 0.23	-1.42	0.16
# Pups Reaching Adulthood			
Acquisition Location (Dispersed)			
Natal	-0.11 ± 0.30	-0.38	0.71
Acquisition Method (Displacement)			
Foundation	-0.30 ± 0.34	-0.88	0.38
Inheritance	-0.38 ± 0.31	-1.22	0.22

Modeled using a GLMM with a negative binomial error distribution and a log link, tenure length was controled for as an offset in the model and group identity was fitted as a random effect. The reproductive output of 103 distinct dominance bouts at 41 groups were included in these models.

Table 3: Factors influencing which subordinate acquires the dominant position during different types of acquisition event.

Model Term	Estimate ± SE	z-value	*P*
Natal Inheritance (GLM)			
Relative Weight	**-2.32 ± 0.57**	**-4.05**	**<0.001**
Relative Age	**-1.71 ± 0.54**	**-3.16**	**0.002**
Relatedness Coefficient	1.69 ± 2.37	0.73	0.47
Daughter (Y/N)	-0.72 ± 0.54	-1.33	0.18
Pregnant (Y/N)	0.03 ± 0.46	0.077	0.93
Group Foundation (GLM)			
Relative Weight	**-2.19 ± 0.69**	**-3.15**	**0.002**
Relative Age	-1.01 ± 0.58	-1.75	0.080
Pregnant (Y/N)	-0.23 ± 0.55	-0.41	0.68
Displacement (GLM)			
Relative Weight	**-3.34 ± 0.90**	**-3.70**	**<0.001**
Relative Age	**-1.08 ± 0.52**	**-2.09**	**0.037**
Natal (Y/N)	0.84 ± 0.77	1.08	0.28
Sibling	0.42 ± 0.71	0.58	0.56
Pregnant (Y/N)	0.84 ± 0.77	0.38	0.71

Modelled using General Linear Models with a binomial error structure and logit link. Significant variables highlighted in bold. For the inheritance model 249 possible dominants from 54 acquisition events were included; for the founding model 124 possible dominants from 34 events and for the displacement model 101 possible dominants from 22 events.

Table A1: Variance inflation factors calculated for the explanatory variables included in the GLM exploring the factors influencing who acquires dominance during a natal inheritance (Table 3).

Fixed Effects	**GVIF**
RelativeAge	1.928
RelativeWeight	2.218
Relatedness	2.342
Preg	1.165
Daughter	2.334

Table A2: Variance inflation factors calculated for the explanatory variables included in the GLM exploring the factors influencing who acquires dominance at the foundation of a new group (Table 3).

Fixed Effects	**GVIF**
RelativeAge	1.925
RelativeWeight	2.091
Preg	1.162

Table A3: Variance inflation factors calculated for the explanatory variables included in the GLM exploring the factors influencing who acquires dominance during a displacement event (Table 3).

Fixed Effects	GVIF
RelativeAge	1.261
RelativeWeight	1.340
Preg	1.192
Sibling	1.124
Status	1.441

Table A4: Factors influencing the growth rate of a beta female.

Model Term	Estimate ± SE	z-value	*P*
Age (Months)	**3.50 ± 1.56**	**1.90**	***0.025***
Weight Relative to Dominant	2.94 ± 1.71	1.72	*0.085*
Weight Relative to Gamma	-0.46 ± 1.22	0.37	*0.71*
Rainfall	**6.47 ± 2.02**	**3.20**	***0.001***
Start Weight	**-11.74 ± 2.19**	**5.36**	***<0.001***

The growth rate of a beta female modelled using a GLMM with a guassian distribution. Significant factors highlighted in bold. The year, month and the indentitiy of the beta individual were included as random terms. Growth rates over 938 months from the tenures of 194 distinct beta individuals were included in the model. Significant terms in bold.

Table A5: Factors influencing subordinate babysitting contribution

Model Term	Estimate ± SE	z-value	*P*
Age (Months)	**0.42 ± 0.04**	**9.31**	***<0.001***
Age^2 (Months)	**-0.28 ± 0.04**	**7.08**	***<0.001***
Rank (Sub vs Beta)	-0.04 ± 0.04	0.51	*0.61*
Average Weight	**0.08 ± 0.02**	**3.35**	***<0.001***
Average Weight^2	**-0.12 ± 0.01**	**11.22**	***<0.001***
Group Size	**-0.33 ± 0.02**	**16.71**	***<0.001***

The babysitting contribution of individuals for a litter modelled using a GLMM with a negative binomial distribution and a logit link. The identity of the babysitter and the identity of the litter being babysat were included as random terms. The maximum number of half days an individual could have been babysitting was included as an offset. 2317 individual babysitting periods for 491 litters representing 739 distinct babysitters were included in this model. Significant terms in bold.

Table A6: Factors influencing subordinate pup provisioning effort

Model Term	Estimate ± SE	z-value	*P*
Age (Months)	**-0.06 ± 0.05**	**3.08**	***0.002***
Average Weight	**-0.07 ± 0.02**	**3.67**	***0.0002***

Average Weight^2	**-0.11 ± 0.01**	**11.81**	***<2e-16***
Group Size	**-0.38 ± 0.03**	**14.63**	***<2e-16***
Group Size^2	**0.09 ± 0.02**	**3.99**	***6.70e-05***
Mean Litter Size	**0.36 ± 0.09**	**3.97**	***7.09e-05***
Mean Litter Size^2	**-0.29 ± 0.04**	**3.22**	***0.001***
Rank (Sub vs Beta)	-0.002 ± 0.04	0.06	*0.95*

The the pup provisioning effort of individuals for a litter modelled using a GLMM with a negative binomial distribution and a logit link. The identity of the provisioner and the litter being provisioned were included as random terms in the model. The total number of minutes of behavioural observation over the provisioning period were included as an offset. 2276 provisioning periods of 708 individuals for 464 litters were included in this model. Significant terms in bold.

Figure Legends

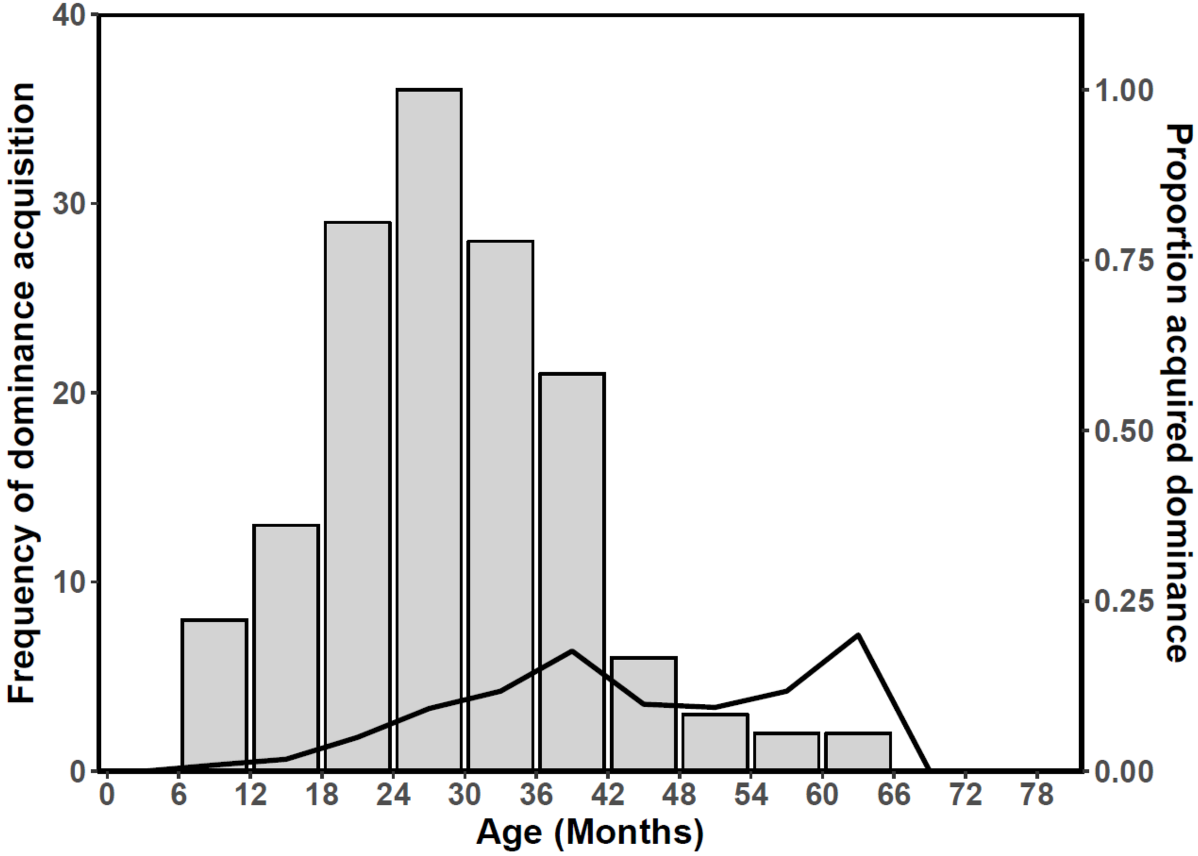

Figure 1: Frequency of subordinate females acquiring dominance relative to age (grey bars). Proportion of subordinate females that acquired dominance at an age relative to the number of subordinates that survived to that age (black line). Only individuals first bouts of dominance were included in this figure.

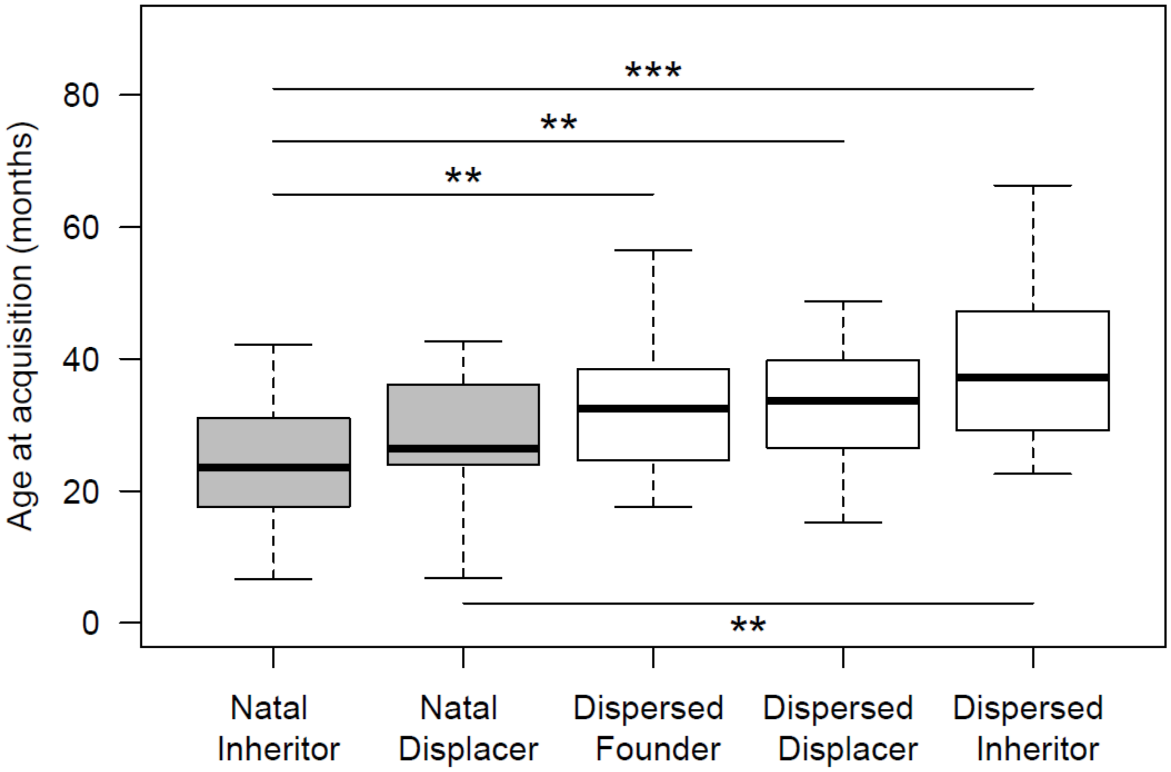

Figure 2: The age at which dominant females acquired their dominance in days relative to where (Natal = grey, Dispersed = white) and how they acquired their dominance: Natal Inheritor (*N* = 68), Natal Displacer (*N* = 16), Dispersed Founder (*N* = 54), Dispersed Displacer (*N* = 19) and Dispersed Inheritor (*N* = 11). Horizontal lines represent the median, the limits of the boxes represent the upper and lower quartiles and the limits of the whiskers represent the minimum and maximum values with outliers excluded. Significant differences were derived using a LMER with group included as a random effect (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

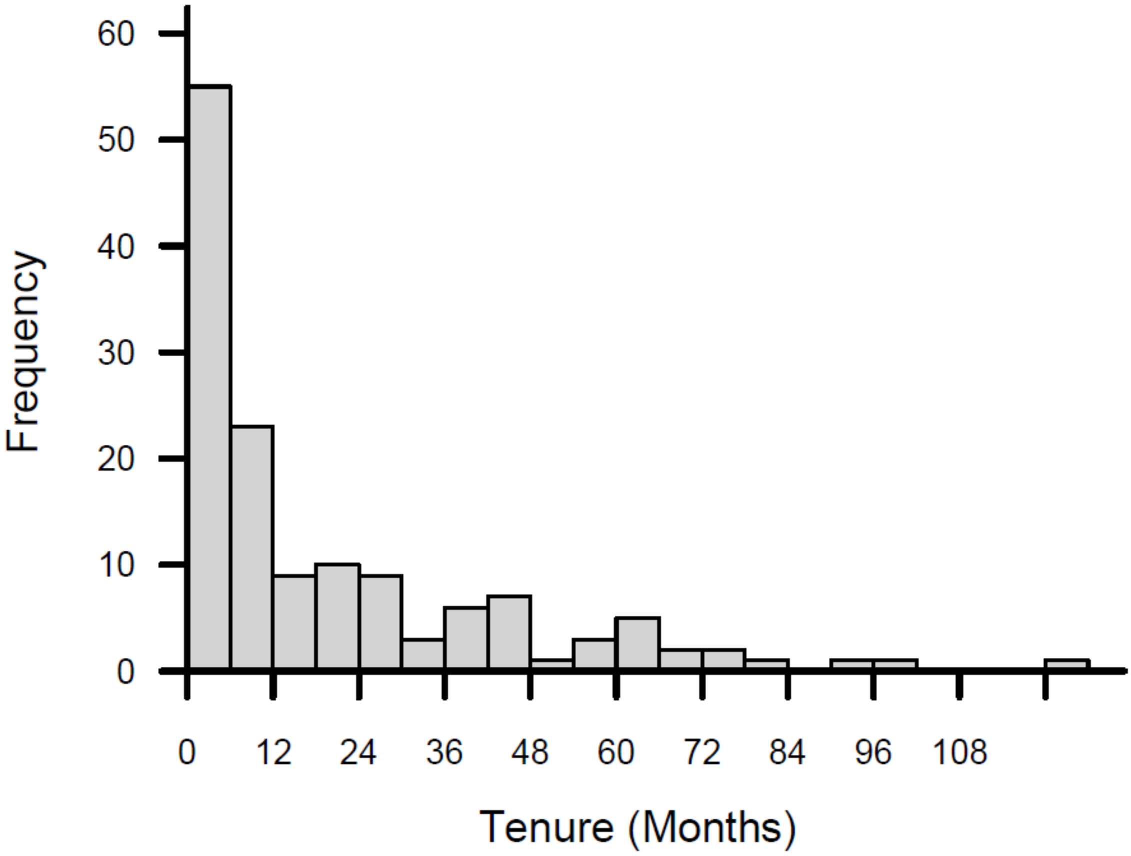

Figure 3. Frequency distribution of the duration of dominance bouts.

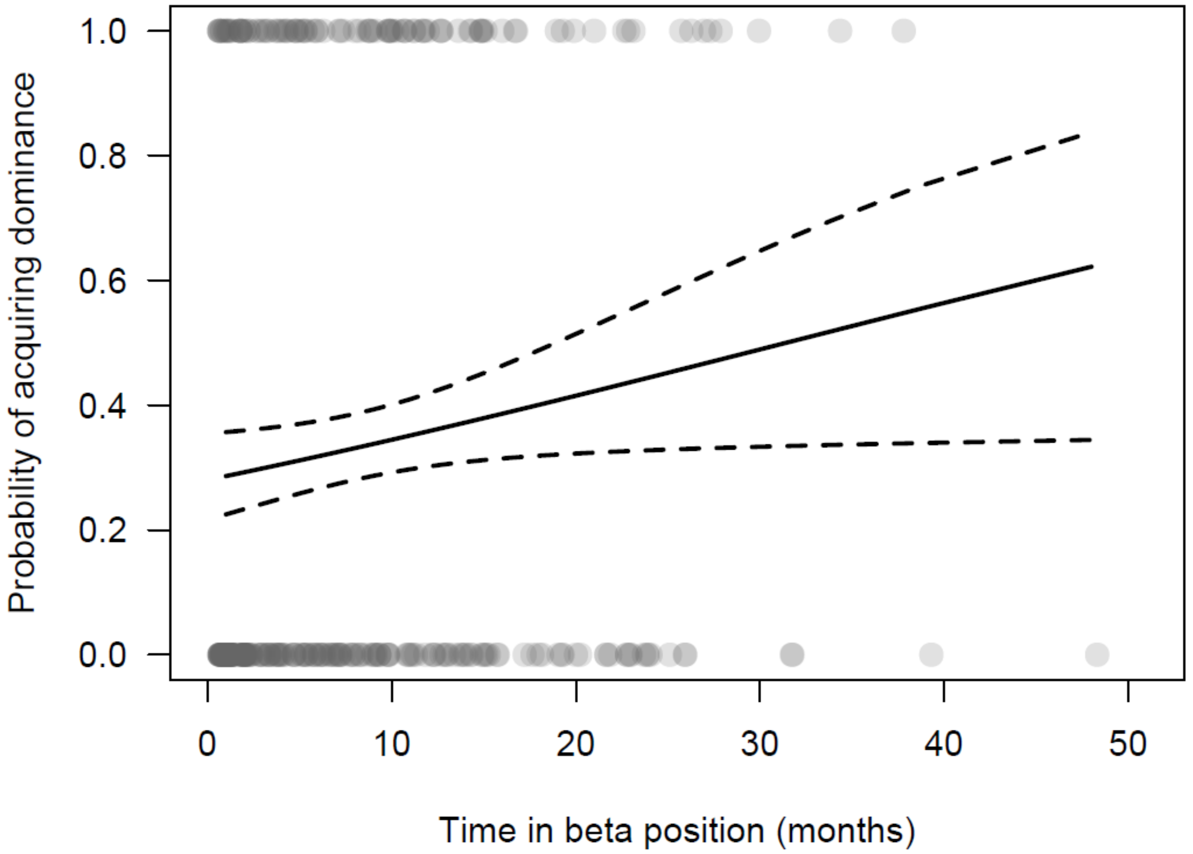

Figure 4: Relationship between the total number of months in a beta position during an individual's lifetime and their probability of acquiring dominance. Fitted effect (solid line), 95% confidence intervals (dashed lines) and raw data (transparent grey points) from a GLMM with acquisition of dominance as a binary response variable and months as a beta as a predictor variable. Jitter applied to raw data points on the x-axis to improve clarity. 308 individuals that survived beyond a year and held a beta position for at least a month were included in this model with their natal group fitted as a random effect.