

The acquisition and maintenance of dominance in
male and female cooperatively breeding meerkats,
Suricata suricatta

Christopher Ian Macdonald Duncan



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Preface

This thesis is purely the result of my own work, and nothing has been undertaken in collaboration except where stated at the start of each chapter. The total length of the text does not exceed 60,000 words. No part of this thesis has been submitted to any other university in application for a higher degree.

Chris Duncan
December 2021

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Summary

In group-living species with strong reproductive skew, acquiring a position of dominance is often essential for maximising fitness, and where the frequency of lifetime dominance acquisition is low, substantial variation in fitness among individuals can arise. However, even among dominant individuals there is still substantial variance in fitness attainment, driven by processes such as the maintenance of status, fecundity, and fertility. In this thesis, to understand better the variation in fitness among individuals, I use 26 years of long-term data to investigate the acquisition of dominance and the subsequent maintenance of status and group persistence in a population of cooperatively breeding meerkats, *Suricata suricatta*, located in the Southern Kalahari. In Chapters 3 and 4, I characterise the distinct routes that subordinates of both sexes pursue to acquire dominance. While there is variation in the frequency that certain dominance routes are used, I find no substantial differences between routes in the traits that determine the acquisition of dominance, the length of tenures or the reproductive success of dominants. In Chapter 5, I distinguish between the reproductive consequences of intrasexual competition from within and outside the group for dominant males. This reveals that while resident immigrant subordinate males compete with the dominant male for reproduction, they also buffer against reproductive competition from outside the group, thereby offsetting their reproductive costs. In Chapter 6, I investigate the factors that influence the maintenance of both sexes' dominance tenures, while accounting for the distinct causes of tenure loss. I show that heavier dominants are more likely to maintain their position and that dominants of both sexes experience similar levels of within-group intrasexual competition, with increasing numbers of resident competitors increasing the risk of displacement. In addition, dominant males are uniquely vulnerable to extra-group takeovers and resident subordinate males appear to aid in the defence of the group, with higher numbers of subordinate males reducing takeover risk. Furthermore, males are also distinct from female dominants in that a substantial number abandon their dominance, a process that I find is associated with the availability of reproductive opportunities within the group. Finally in Chapter 7, I characterise the processes influencing group persistence, which is important for both the maintenance of a dominant's tenure and ensuring the persistence of their lineage. I show that groups

can persist for over a decade and that maintaining a large group size is essential for maximising group longevity. I also find that an endemic form of tuberculosis, *Mycobacterium suricattae*, plays a considerable role in the failure of groups, being associated with the failure of most long lived groups in the population.

Publications

Publications arising from thesis:

Duncan, C. Gaynor, D. Clutton-Brock, T. (2018) 'The importance of being beta: female succession in a cooperative breeder', *Animal Behaviour*, 146, p113-122

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Chapter 1: Introduction

In many group-living species, holding high social rank confers benefits that can increase individual fitness (Cowlshaw & Dunbar 1991; Stockley & Bro-Jørgensen 2011). This is particularly the case in more despotic species, such as cooperative breeders, where reproduction is strongly skewed towards a single dominant individual or group of dominants (Koenig & Dickinson 2016). In societies with high reproductive skew, it is often essential for individuals to acquire dominant positions to successfully reproduce, however, to maximise fitness, individuals must maintain as long and productive dominance tenures as possible. Consequently, there will not only be strong selection on the traits important for acquiring dominance, but also for traits that maximise their reproductive success as a dominant. In this thesis I investigate the ways in which both male and female meerkats, *Suricata suricatta*, can acquire dominance, and the processes that influence the maintenance and productivity of their tenures. In this chapter I discuss more broadly the consequences of dominance, how individuals acquire dominance and the different processes that influence the productivity of dominance tenures, before describing the biology of my study species and then detailing the specific aims and scope of this thesis.

Dominance systems and their consequences

Group-living species exhibit a diversity of dominance systems ranging from despotic or group-dominant systems where an individual or subset of individuals are clearly dominant over a number of subordinates of indistinguishable rank (Sasaki *et al.* 2016), to more egalitarian systems where consistent dominance relations among individuals are weaker or absent (Cashdan 1980; Crisp *et al.* 2021). However, comparative studies across the animal kingdom suggest that dominance systems most commonly tend towards steep linear hierarchies, where each individual occupies a clearly defined rank and is dominant to all individuals ranking below them and subordinate to all higher ranking individuals (McDonald & Shizuka 2013; Shizuka & McDonald 2015). Dominance hierarchies are ultimately the summation of individual dominance relationships between group members (Chase & Seitz 2011). Dominance relationships result from repeated contests between conspecifics over controllable resources. These take the form of either physically aggressive interactions (Palaoro & Briffa 2017) or honest displays of quality and motivation (Allen *et al.* 2016) and the winner is commonly the individual with the greatest resource holding potential (Rudin & Briffa 2012).

As dominance systems arise from competition over limited resources, it is often the case that individuals of high social rank experience benefits associated with their status. These benefits can take

the form of priority access to foraging sites (Murray *et al.* 2006) or prey carcasses (Frank 1986), as well as spatial positions with the lowest predation risk (Ron *et al.* 1996) or high-quality nesting sites (Hurst 1987). These advantages can increase the survival and reproductive success of dominant individuals, leading to greater fitness for dominants relative to subordinates (Stockley & Bro-Jørgensen 2011; Clutton-Brock & Huchard 2013). The magnitude of these benefits varies widely across species, and where dominants employ strategies that limit subordinate reproduction, considerable contrasts in rank related fitness can occur. For example, in many polyandrous species and cooperatively breeding species, one dominant female monopolises reproduction within a group producing many tens of offspring across their lifespan whilst most subordinate females seldomly breed successfully at any stage in their lifespan (Hauber & Lacey 2005; Clutton-Brock *et al.* 2006). However, even in species where the rank related differences in reproduction are less extreme and more linear (Holekamp *et al.* 1996), if individuals can maintain their status for long periods, large differences in lifetime fitness can occur (Clutton-Brock & Huchard 2013). As a result of the impact dominance can have on individual fitness, there is considerable interest in understanding the routes through which individuals acquire dominance.

Routes to acquiring dominance

Dominant breeding positions may be acquired through many distinct routes, and individuals can vary in both where and how they acquire dominance. Where individuals acquire dominance usually varies in relation to whether individuals remain within their natal group or choose to disperse in search of dominance. Dispersal is often sex-biased, and in birds, females are commonly the more dispersive sex (Clarke *et al.* 1997), while in group-living mammals it is commonly males that will disperse in search of dominance and breeding opportunities following sexual maturation (Greenwood 1980; Lawson Handley & Perrin 2007). Female mammals on the other hand are often philopatric, pursuing breeding positions in their natal groups and remaining resident for life. However, there are exceptions to these rules (Lawson Handley & Perrin 2007; Clutton-Brock & Lukas 2012), for example in chimpanzees, *Pan troglodytes*, and marmosets, *Callithrix jacchus*, males will often remain in their natal groups their entire lives while females disperse (Muller *et al.* 2009; Yamamoto *et al.* 2014). Furthermore, while it is often the case that individuals will follow one sex-specific dispersal route, in many species the dispersal behaviours within a sex may vary with some individuals remaining in their natal groups while others disperse (Rood 1990; Clutton-Brock & Lukas 2012; Davidian *et al.* 2016).

Variation in individual decisions to disperse has generally been related to variance in individual condition, with dispersal being limited to better quality individuals who are able to weather the

associated costs (Bowler & Benton 2005). However, it is also the case that individuals can be highly plastic in their dispersal behaviour, making decisions that maximise fitness. Dispersal decisions can be influenced by a variety of factors including ecological constraints (Nelson-Flower *et al.* 2018), the availability and quality of mates (Packer & Pusey 1987; Höner *et al.* 2007), as well as the composition and genetic structure of groups (Rood 1987).

Following dispersal, individuals can pursue a position of dominance in various locations (Rood 1987; Raihani *et al.* 2010). Where dispersing individuals meet members of the opposite sex they may join together forming a new breeding group (Cant *et al.* 2016; Maag *et al.* 2018). The ability of dispersers to form new groups will largely be a function of the density of opposite sex floating individuals available to form a group with, and the availability of empty territories for the new group to settle within. Alternatively, dispersing individuals may migrate into an already established group (Davidian *et al.* 2016; Teichroeb & Jack 2017), however, resident individuals are often resistant to the immigration of additional same-sex competitors. Therefore, individuals may need to disperse in large coalitions to forcefully overcome resistance from residents (Young 2003), or join the group at the bottom of the social hierarchy, reducing the cost their presence imposes on residents. Additionally in some facultatively group-living species, individuals may avoid joining other individuals and instead settle on a territory as a solitary breeder (Hill *et al.* 2015).

How an individual competes for dominance can also vary. In some cases, individuals may wait in a subordinate position for stochastic processes to remove higher ranking individuals generating dominance vacancies. Where individuals queue for dominance, inheritance of the vacancy will be determined by a succession rule, such as the oldest or largest individuals inherits, and subsequently all individual ranks will shift according to the rule and there will be little competition (Buston 2003b; Archie *et al.* 2006; Wong *et al.* 2008). However, the creation of a dominance vacancy can also destabilise the hierarchy, triggering intense competition among group members, with the individual with the highest resource holding potential commonly acquiring dominance (Foerster *et al.* 2016). Under these circumstances there will be strong selection on the traits that determine acquisition, examples of which include weapon size, fatness, body mass and social support (Rusu & Krackow 2004; Vervaecke *et al.* 2005; Vullioud *et al.* 2019). Alternatively, rather than waiting for a vacancy to arise subordinate individuals can instead directly challenge more dominant individuals for their position (Sharp & Clutton-Brock 2011b). Displacing higher ranking individuals is likely to be costly and may be limited to individuals whose competitive ability substantially exceeds the dominant they are challenging. Following a successful challenge, the subordinate challenger and incumbent dominant will switch ranks, and in some cases the new dominant may actively evict the previous dominant from the social group (Jack & Fedigan 2004).

Within a species the presence of multiple dispersal strategies and methods for competing for dominance results in the existence of a diverse range of routes to dominance. This raises questions as to whether some routes to dominance generate greater fitness returns than others (Walters & Garcia 2016), and if so why? Furthermore, it is important to know why individuals pursue certain routes to dominance. Do individuals preferentially pursue an optimal route that offer greater fitness returns while others represent a “best-of-a-job” strategy for lower quality individuals (Josi *et al.* 2021), or are individuals flexibly responding to their environment and condition to pursue the most fruitful route to breeding status (Davidian *et al.* 2016)?

Determinants of fitness in dominants

The potential reproductive benefits of acquiring dominance are well understood, however, even among dominants substantial variation in fitness can occur, especially where reproduction is highly skewed, and dominants can hold long tenures. The levels of fitness dominants acquire is a function of the variance components of their tenure reproductive success: the length of their tenure and the productivity of their tenure. The productivity of a dominant’s tenure is a function of the rate at which offspring are produced and the survival of these offspring. Variation in the rates at which dominants produce successful offspring can result from differences in individual phenotype, such as condition (Kruuk *et al.* 1999), as well as their social environment with the levels of intrasexual competition a dominant experiences often an important determinant of successful reproduction (Sharp & Clutton-Brock 2011a; Lardy *et al.* 2013). The acquisition of high social rank does not guarantee complete reproductive control, and even in species with high levels of reproductive skew it is rare for complete reproductive monopolies to exist (Clutton-Brock & Isvaran 2006; Lambert *et al.* 2018). Often subordinate individuals will still compete for access to reproduction, adopting alternative strategies that will be costly to the dominant. Particularly costly examples of intrasexual competition include subordinate males sneaking successful mating with breeding females (Alberts *et al.* 2006; Kappeler & Port 2008; Lardy *et al.* 2012), or subordinate females committing infanticide of the dominant’s offspring to create breeding opportunities for themselves (Young & Clutton-Brock 2006). A number of theories have been proposed to explain the loss of reproductive monopoly by dominants (e.g. concessions, Reeve *et al.* 1998), however empirical evidence to date largely supports the limited-control hypothesis (Engh *et al.* 2002; Port *et al.* 2018), whereby dominants try to exert complete reproductive control but are constrained in their ability to do so by factors including the number of breeding females, the levels of intrasexual competition and their phenotypic quality (Clutton-Brock 1998; Port & Kappeler 2010; Dubuc *et al.* 2011).

The length of time an individual can maintain their position of dominance also exerts a strong influence over lifetime reproductive success, and in species with long tenures, tenure length can explain a substantial amount of between individual variance in lifetime reproductive success (Hodge *et al.* 2008; Pusey 2012; Lukas & Clutton-Brock 2014; Lardy *et al.* 2015). In some species dominant individuals hold their position until death, therefore, the length of tenure is determined by largely stochastic processes such as predation and disease (Ronget *et al.* 2017). Dominants can also be challenged for their position and overthrown, with the probability of being displaced being determined by the levels of intrasexual competition they are exposed to, and their ability to suppress subordinates (Jack & Fedigan 2004; Lardy *et al.* 2012; Pines *et al.* 2015). Finally, dominants may also voluntarily abandon their position, commonly by dispersing from their group. The abandonment of position tends to be associated with individuals trying to maximise their fitness, resulting from reduced breeding opportunities in their resident group relative to other neighbouring groups (Packer & Pusey 1987; Höner *et al.* 2007). Dominants are commonly exposed to a multitude of distinct threats to their tenure, and the factors influencing tenure loss are likely to vary with the cause of tenure loss, possibly even having contrasting effects. Consequently, to understand the maintenance of tenure it is essential to use analyses that account for competing causes of tenure loss.

Dominance in the cooperative breeders

Some of the most despotic dominance systems observed in nature are those of the singular cooperative breeders. Cooperative breeders are present across the animal kingdom including, but not limited to, birds (Hatchwell 2009), mammals (Creel *et al.* 1993; Clutton-Brock & Manser 2016; Faulkes & Bennett 2016), and fish (Taborsky 2016). Singular cooperatively breeding species are characterised by the presence of strong reproductive skew towards a single dominant breeding pair and the presence of subordinate helpers that provide alloparental care for the dominant's offspring (Koenig & Dickinson 2016). There are multiple possible causes of the observed reproductive skew, including an absence of unrelated breeding partners for natal subordinate helpers (O'Riain *et al.* 2000). However, a common feature of cooperative breeders that appears to play a considerable role in driving the extreme levels of skew is the reproductive suppression of subordinates by dominant individuals. In females this can take the form of behavioural suppression, with dominant females evicting reproductively mature subordinates and killing their offspring (Gilchrist 2006; Clutton-Brock *et al.* 2010), or physiological suppression, whereby the presence of dominants appears to suppress the fertility of subordinates (Faulkes & Abbott 1996). For males, reproductive suppression commonly

takes the form of mate guarding, with dominant males often able to monopolise reproduction by focusing guarding efforts on dominant females during oestrus (Cant *et al.* 2016).

In addition to high levels of reproductive skew, dominants in cooperative breeders can hold status for long periods producing a substantial number of offspring during their lifetime, generating considerable variance in fitness (Hauber & Lacey 2005). Consequently, there is intense competition from subordinates to acquire dominance and subordinates will commonly also attempt to breed at a cost to the dominant (Clutton-Brock *et al.* 2008; Lardy *et al.* 2015). In addition, subordinates may employ alternative strategies such as male subordinates roving at other groups to acquire mating opportunities, generating additional sources of competition for resident males (Young *et al.* 2007). As a result, a dominant's fitness appears particularly sensitive to the levels of intrasexual competition they experience, with a dominant's ability to maintain their status and reproductive monopoly often appearing to decline as the numbers of subordinate competitors increase (Hodge *et al.* 2008; Spong *et al.* 2008; Lardy *et al.* 2012, 2013).

When considering competition in cooperative breeders it is important to also account for relatedness. Group-living in many cooperative breeders is believed to have resulted from the evolution of delayed dispersal in a monogamous ancestor (Federico *et al.* 2020), resulting in high relatedness within groups, but not between groups (Griffin *et al.* 2003; Dyble & Clutton-Brock 2020). Relatedness is not only important for the evolution of cooperative behaviours through inclusive fitness benefits (West *et al.* 2021), but is also likely to mediate competition among conspecifics, with kinship being associated with affiliation and tolerance (Wahaj *et al.* 2004; Chakrabarti *et al.* 2020). When inclusive fitness is considered, the relatedness between dominants and subordinates will influence both the costs and benefits of competition for both individuals. Therefore, the motivation for individuals to compete with the dominant and the tolerance of competition by dominants, are likely to vary for different categories of competitors dependant on their kinship with the dominant. Consequently, to understand the realisation of competition within cooperative breeders, it is critical to understand kinship relationships between dominants and their competitors.

Ultimately, to understand the distribution of fitness in cooperative breeders we must understand both how individuals acquire dominance and subsequently maintain long and productive tenures. Therefore, in this thesis I aim to investigate the acquisition and maintenance of dominance in meerkats, *Suricata suricatta*, a cooperatively breeding species of mongoose. I use a dataset collected over the last 26 years by the Kalahari Meerkat Project on multiple groups of wild living meerkats in the Southern Kalahari. The length and breadth of this study makes it ideal for investigating dominance as the entire tenures of multiple dominants in multiple groups have been documented,

and in most cases both the acquisition and loss of dominance was observed. In addition, the consistent high-resolution collection of life history, social, morphological, and genetic data, allows for the investigation of the dynamics of dominant's social and individual characteristics and their impact on tenure productivity. Consequently, this is an ideal dataset to investigate the phenotypic and social differences between dominants and how these factors drive the observed variance in reproductive success.

Biology of meerkats

Meerkats, *Suricata suricatta*, are a species of singular cooperatively breeding mongoose distributed across southern Africa (Figure 1.1a). Meerkats are a highly social mammal that form stable fixed membership groups that can consist of up to 50 individuals (Figure 1.1b). Commonly inhabiting semi-arid open habitats, meerkats are adapted for foraging in sandy substrates with long claws that aid in digging up fossorial prey (van Staaden 1994). While meerkats are omnivorous, feeding on food items ranging from vegetation to small mammals, they are primarily insectivorous with most of their diet composed of larvae, pupae, and scorpions. Being a relatively small member of the carnivora clade, meerkats are subject to both terrestrial predators, including caracals and snakes; and aerial predators, including medium to large raptors. In response to such a diverse array of predators, meerkats have evolved cooperative guarding behaviours that operate in concert with a comprehensive range of vocalisations that can convey the type and threat level of observed predators to group mates (Manser *et al.* 2002).



Figure 1.1: (a) Range distribution of meerkats generated by the IUCN in 2008 (shaded orange area) plotted on a Stamen terrain map of southern Africa. (b) The meerkat group Van-Helsing performing an alarm response to a small raptor flying above.

The environment meerkats inhabit is highly seasonal and their breeding is largely constrained to wetter and warmer periods (Groenewoud & Clutton-Brock 2021). Depending on how long favourable conditions last, female meerkats can reproduce multiple times within a breeding season due to their short gestation (~70days) and postpartum oestrus; giving birth to litters consisting of on average 3.93 young (range: 1 – 7; Hodge *et al* 2008). Following parturition, the litter will be kept below ground in the burrow, being babysat, and provisioned through lactation by their mother and other allolactating subordinate females (English *et al.* 2010; MacLeod *et al.* 2013). After around three weeks the pups will emerge from the burrow and soon start foraging with the group, at which point group members will provision them with food items at a decreasing rate until they reach nutritional independence at around three months (Russell *et al.* 2002). Between three and six months of age individuals are considered juveniles, while largely nutritionally independent they are still too young to contribute properly to cooperative efforts within the group. After 6 months individuals are classified as sub-adults, in this age category individuals can theoretically become sexually active, although this is rare and sub-adults are unlikely to actively pursue reproductive opportunities. As sub-adults, individuals will also start to contribute substantially to cooperative efforts by providing alloparental care and investing in guarding. At one year of age individuals are considered adults and have largely completed their developmental growth trajectory and their growth rates decline as they approach asymptotic mass (English *et al.* 2012). As adults, individuals will still contribute to cooperative activities within the group, however, they will also start to pursue direct fitness by attempting to reproduce, with the likelihood of reproductive activity increasing with age (Young *et al.* 2006, 2007).

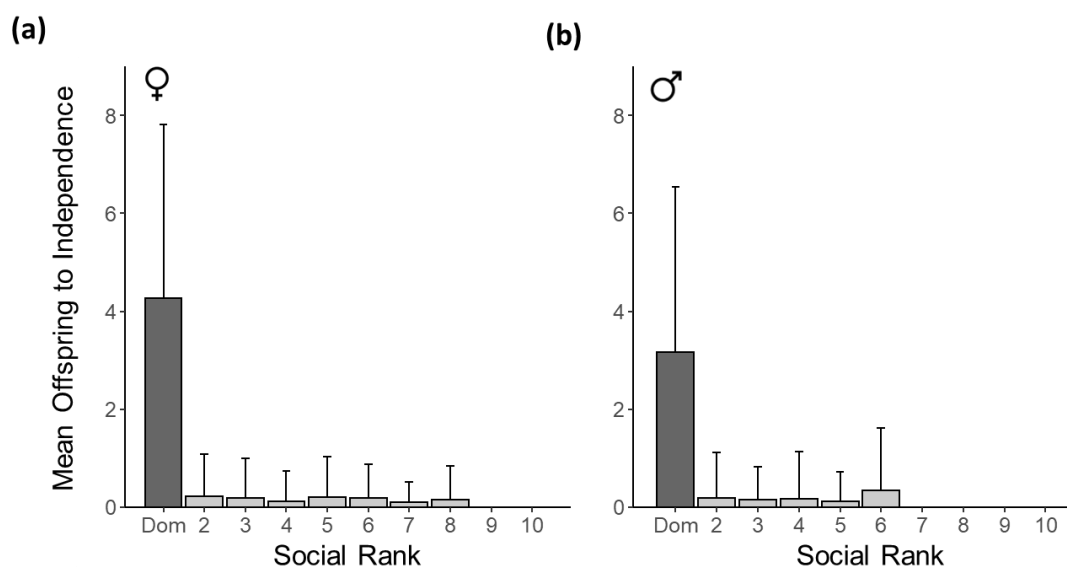


Figure 1.2: Visualisations of the reproductive skew present in meerkats. The rate at which both females (a) and males (b) produced offspring that survived to independence in relation to their dominance status with subordinates subdivided by age rank. For males the data were restricted to immigrant individuals, as natal males rarely reproduce due to inbreeding avoidance. Reproduction was measured between October-March, the period of highest reproduction which could be considered the breeding season.

As singular cooperative breeders the reproduction of meerkat groups is highly skewed towards a dominant breeding pair (Figure 1.2a, b), who can monopolise over 80% of the group's reproduction (Griffin *et al.* 2003; Clutton-Brock *et al.* 2006). The rest of the group is comprised of subordinate helpers who are usually the siblings or offspring of the dominant pair. Subordinates express a range of cooperative behaviours including providing altruistic alloparental care for offspring born in the group such as: allolactation, pup provisioning and babysitting (Clutton-Brock *et al.* 2001a). In addition, they also express cooperative behaviours that provide group benefits such as the excavation of burrows and bolt holes, as well as guarding against predators (Clutton-Brock *et al.* 1999b; Duncan *et al.* 2019). However, while subordinate meerkats invest heavily in cooperative behaviours they are reproductively suppressed by the dominant pair. Subordinate females do become pregnant, yet they rarely successfully produce pups, as they are subject to intense aggression from dominant females and even eviction from the group, which can trigger abortion or force subordinates to give birth away from the group where the litter is unlikely to survive (Clutton-Brock *et al.* 2008, 2010). Subordinate males are not subject to the same levels of aggression as subordinate females, however, by mate guarding the dominant female during oestrus, the dominant male is largely able to exclude subordinate males from mating opportunities (Spong *et al.* 2008).

Most residents within meerkat groups have either parent-offspring or sibling relationships, resulting in high mean intra-group relatedness ($r = 0.35$, Dyble & Clutton-Brock 2020). Therefore, the recipients of both alloparental and group benefit cooperative behaviour share substantial amounts of genetic material with the co-operator, which results in the individuals expressing cooperative behaviours deriving considerable inclusive fitness gains (Clutton-Brock & Manser 2016). It is likely that the extremely high levels of within group relatedness are what allows meerkats to ignore recipient relatedness and express altruistic behaviours indiscriminately (Duncan *et al.* 2019), as even randomly directing cooperative behaviours will rarely result in the possibly maladaptive direction of cooperation towards unrelated recipients. However, meerkat helpers are also likely to gain direct fitness benefits through the expression of altruistic alloparental behaviours because of increases in group size. Larger groups confer a wide range of benefits including, increased likelihood of winning intergroup interactions (Dyble *et al.* 2019), reduced predation risk (Courchamp *et al.* 1999), larger dispersing coalitions (Young 2003) and presumably better quality groups for subordinates to acquire dominance within.

Considering the high levels of reproductive skew, it is essential for meerkats to acquire a dominant position during their lifetime to maximise their fitness. The route to dominance for subordinate meerkats can vary both in location and method. Both male and female meerkats can acquire a position of behavioural dominance in their natal groups. However, for males natal

dominance is not reproductively viable (Spence-Jones *et al.* 2021), as all breeding females are their kin who will avoid mating with them due to inbreeding avoidance (Griffin *et al.* 2003). Therefore, to acquire reproductive dominance males must disperse, and therefore in this thesis I restrict the analyses of male dominants to immigrant dominants. In contrast, natal dominant females can rely on roving males to provide mating opportunities in the absence of unrelated resident males until a new migrant male arrives to provide them with a breeding partner. Both sexes may disperse in search of dominance positions. In males dispersal is voluntary and males will regularly rove in search of breeding opportunities before permanently dispersing (Young 2003; Mares *et al.* 2014). For subordinate females dispersal is involuntary and facilitated by the dominant female evicting them during her pregnancy (Clutton-Brock *et al.* 2010), which temporarily excludes them from the group and exposes them to dispersal opportunities (Maag *et al.* 2018). Both sexes usually disperse in same sex coalitions consisting of members of their previous group, and when two opposite sex coalitions meet there is a chance they will settle and form a new group. In addition, males have an alternate dispersal route and rather than found a new group they may forcefully migrate into an established group. Migrant males will commonly displace the incumbent dominant from their position and evict resident adult males not part of their coalition (Mares *et al.* 2012). Following successful migration, one member of the dispersal coalition will assume dominance following a brief period of competition and all other coalition members will assume subordinate positions. When resident within a group, subordinates of both sexes have two options for acquiring dominance. They can either wait for stochastic processes to remove the incumbent creating a vacancy for them to compete for, or they can actively challenge the dominant for their position and try to displace them (Spong *et al.* 2008; Sharp & Clutton-Brock 2011b).

Age appears to be the most important determinant of who succeeds to dominance positions when a vacancy arises in both sexes (Hodge *et al.* 2008; Spong *et al.* 2008). Although, in females, body mass also appears important, determining who acquires dominance when multiple age-matched competitors are present (Hodge *et al.* 2008). These results are further supported by age and weight determining the outcomes of antagonistic interactions among subordinate females in a similar fashion (Thavarajah *et al.* 2014). However, following the acquisition of dominance there is still a substantial amount of variation in the lifetime reproductive success attained. A breakdown of the variance components of lifetime reproductive success, reveals that in both sexes their tenure length as a dominant and their rate of reproduction largely explains the reproductive success individuals will accrue across their tenure. While the survival of their offspring has a relatively small impact on dominant's lifetime reproductive success (Hodge *et al.* 2008; Spong *et al.* 2008). Previous studies suggest that variation in these components of lifetime reproductive success is likely to result from

both differences in an individual's phenotype and social environment, with intrasexual competition playing an important role (Hodge *et al.* 2008; Spong *et al.* 2008).

Thesis aims and scope

The importance of acquiring dominance for maximising fitness in both sexes is well understood in meerkats (Clutton-Brock *et al.* 2006), and the different ways they can acquire dominance have been documented in both sexes. Yet, the consequences of utilising different routes to dominance remains to be investigated in meerkats. Due to the requirement for high-resolution long-term data, few studies of wild animals have been able to investigate the variation in fitness between different routes to dominance. However, the studies that do exist suggest that the fitness prospects of dominance can vary both in relation to where and how individuals acquire dominance (Walters & Garcia 2016; Josi *et al.* 2021), and that individuals can respond plasticly to these differences (Davidian *et al.* 2016). Therefore, understanding the differences among the routes to dominance may provide insight into the processes driving the variance in reproductive success among dominant meerkats. In Chapters 3 and 4, I investigate the characteristics of the different routes to dominance in male and female meerkats, and test whether these result in differential fitness outcomes depending on the route to dominance an individual pursues.

Following the acquisition of dominance, meerkats are still subject to intrasexual competition, and it is rare for a dominant to completely monopolise all group reproduction during their tenure. This loss of reproductive monopoly appears to be due to energetic constraints on the dominant's ability to suppress subordinates (Dubuc *et al.* 2017), with the increasing numbers of resident subordinate competitors negatively affecting the likelihood of male and female dominants successfully reproducing (Hodge *et al.* 2008; Spong *et al.* 2008). However, dominant males are unique in that they also experience competition from outside the group, with extra-group males that rove at groups sometimes able to successfully mate with a resident female and acquire paternity within the group (Young *et al.* 2007; Mares *et al.* 2014). Evidence of subordinate males investing in the defence of the group against these extra-group rovers generates a potential trade-off for dominant males (Mares *et al.* 2012). Feasibly the presence of subordinate males may reduce the likelihood of extra-group paternity, which could offset the costs they impose on the dominant by competing for mating opportunities within the group. To investigate this trade-off, in Chapter 5, I distinguish between extra-dominant paternities resulting from resident immigrant males and extra group males, modelling the effects of the numbers of resident males on the probability of dominants losing paternity to these two categories of competitor. Furthermore, to understand the role of relatedness in mediating

competition I calculated and contrasted pairwise pedigree relatedness for dominants, male competitors and offspring born during a dominant's tenure.

In meerkats, maintaining long dominance tenures is critical for maximising fitness and the length of a dominant's tenure explains >50% of the variance in life-time reproductive success among dominants (Hodge *et al.* 2008; Spong *et al.* 2008). Several factors have been associated with variation in dominant tenure lengths including individual condition and the levels of intrasexual competition present within a group (Hodge *et al.* 2008; Spong *et al.* 2008). However, to understand how these factors influence tenure length it is important to first account for the causes of tenure loss in dominants. A variety of distinct processes can result in dominants losing tenure, and without accounting for these, the mechanisms through which traits are operating to influence the maintenance of dominance cannot be deciphered. In addition, factors can have variable and even contrasting effects on different causes of dominance loss that are obscured when tenure loss is considered as a single process. Furthermore, individual traits and their social environment commonly vary temporally, both seasonally and across an individual's life as they age, and to gauge the true impact of these factors on the ability of dominants to maintain tenure, their temporal variation must be considered. Therefore, in Chapter 6, the factors influencing the tenure maintenance of dominant meerkats of both sexes are investigated; using time-varying competing risk models that allow for tenure loss to be modelled in a cause specific manner.

Beyond the maintenance of status, the persistence of the group is also important for a dominant's fitness, since in some social species the persistence of both the group and the dominant breeding pair are intrinsically linked, and following the death of a breeder the group will lose cohesion and disintegrate (e.g. wolves, *Canis Lupus*, Borg *et al.* 2015; and African wild dogs, *Lycaon pictus*, Woodroffe *et al.* 2020). However, in other species where positions of dominance are inherited and groups persist beyond the lifetime of one breeder, the persistence of the group is also essential for the maintenance and proliferation of a dominant's lineage. Not only does the persistence of the group conserve a dominant's matriline, as dominance positions are inherited by offspring and grand-offspring, but also the longer a group persists the more likely they are to produce successful dispersal units that spread the lineage to new groups. To understand the influence of group persistence on a dominant's fitness, one must first understand the nature of group failure within a species. To address this gap in our knowledge, in Chapter 7, I characterise the different causes of group failure in meerkats and investigate the impact of both sociodemographic and environmental factors on the persistence of groups. These analyses will also provide important information for understanding the demography of group-living species, as the persistence and failure of groups is likely to have important impacts on the vital rates of a population. This will especially be the case in species with high reproductive skew,

such as meerkats and other cooperative breeders, where groups start to become functionally equivalent to breeding units.

Chapter 2: Study area and methodology

Study site

Meerkats are distributed widely across Southern Africa south of Angola, tending to inhabit arid, open environments such as savannahs and shrubland, while being absent from true deserts such as the Namib desert in Namibia (van Staaden 1994). The meerkats studied for this thesis were a wild population studied by the Kalahari Meerkat Project since 1993; living in the Southern Kalahari Desert, a semi-arid savannah located towards the centre of the meerkats geographic range. The population occupied a mean range of 50-60 km² within the study area situated on the Kuruman River Reserve and surrounding farms, located approximately 20 km south of Botswana in Northern Cape, South Africa (Figure 2.1a). The study area is centred on the Kuruman River (Figure 2.1b), a fossil river that flows once every few decades following extreme rainfall events. The riverbed is flanked by calcareous flats that are primarily populated with low lying shrubs and bushes, such as *drie doring*, *Tribulus terrestris* (Figure 2.2a). These calcareous flats also extend away from the riverbed in tributary like shapes for many kilometres and can also be found as isolated pans throughout the wider study area. While trees rarely grow on the calcareous flats, along the banks of the river, large trees can be found in relatively high density. Beyond the flats, the dominant habitats of the study area are red sands, characterised by their substrate of loose ferrous sands that are populated by sparsely distributed savannah grasses and desert adapted trees (e.g. *Vachellia erioloba*, Camel Thorn). However, following periods of intense rainfall the coverage and density of the savannah grasses can increase dramatically, transforming the desert into a grassland for a brief period. Closer to the river the red sands take the form of dune fields running approximately north-south, however as you move further away from the river the variation in topography declines and the habitat transitions to flat sandy plains (Figure 2.2b).

Pastoral farming is the primary land use for the study area and the wider Kalahari located within South Africa. In addition to cattle and sheep, a variety of indigenous antelope species are also grazed in sizeable herds on the land. As a result, the land is divided by fences into large enclosures to restrict the movement of herds. While the movements of smaller mammals, including meerkats, are not restricted by these fences, the movement of larger terrestrial predators ranging from lions to black backed jackals is limited. Restricted movement combined with the persecution that predators face from farmers means that the prevalence of terrestrial predators in the study area is exceptionally low. While some persecution of raptors has been reported in the South African Kalahari, they are still

abundant in the study area and meerkat predations in the population come primarily from aerial sources.

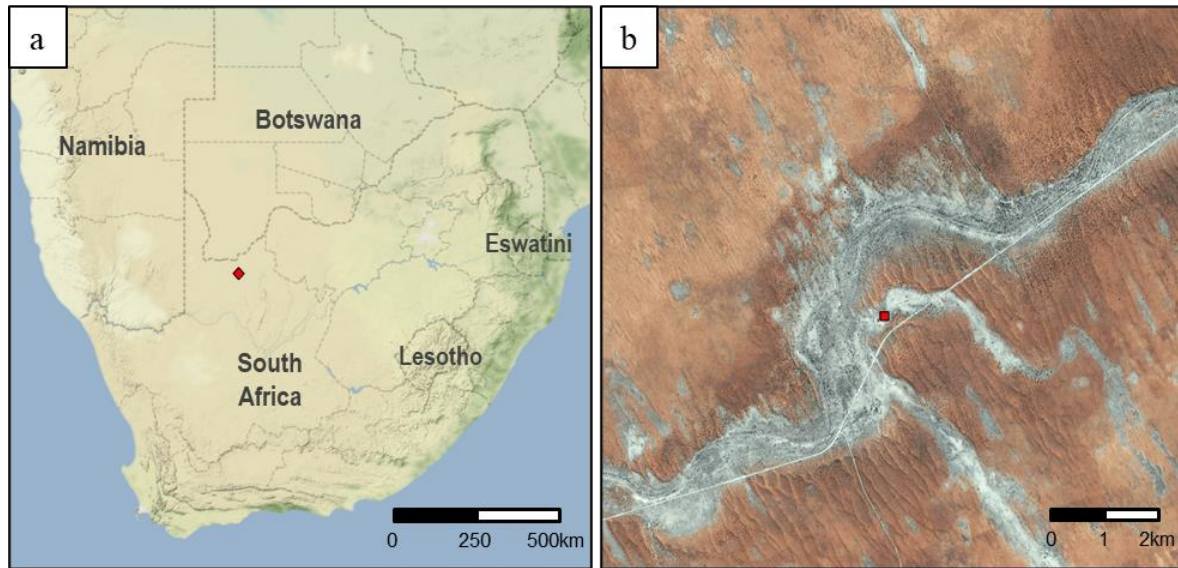


Figure 2.1: (a) Location of study site (red diamond) on a terrain map of southern Africa provided by Stamen maps, with manually annotated country labels. (b) Satellite image of the study area with the field station marked (red square), provided by Google maps.

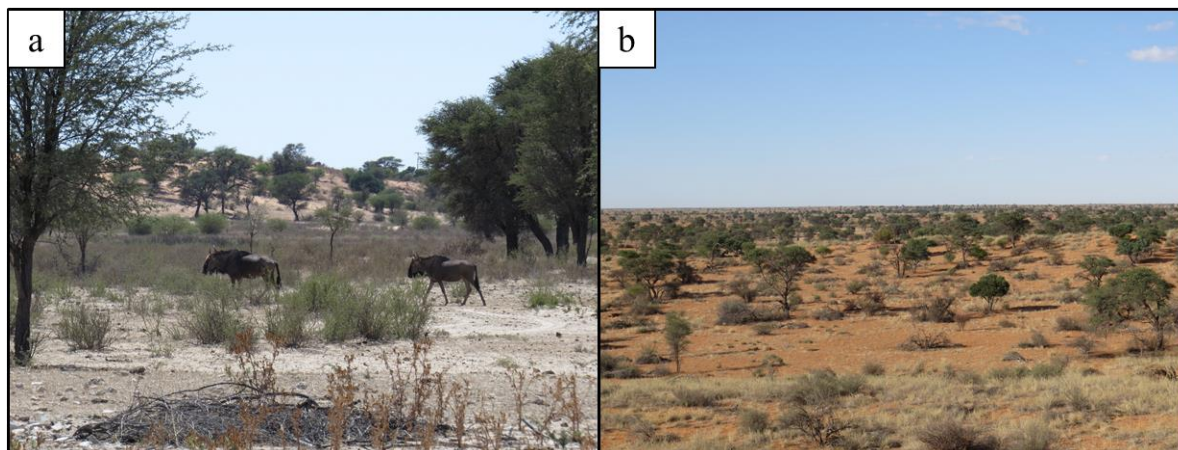


Figure 2.2: (a) Calcareous riverine flats that begin to transition into red sand dunes in the background, with resident wildebeest also pictured. (b) Red sand flats populated with sparsely distributed savannah grasses and trees.

Climate

The Kalahari is a semi-arid savannah region receiving between 100 - 500mm of rainfall per annum, with the southern regions where the study area is located being the driest. Rainfall tends to fall in large amounts over short periods of time and occurs seasonally in the summer months between October and April, with winter months being extremely dry (May to September; Figure 2.3b). However, in addition to seasonal variation in rainfall there is also considerable variation between years. The Standardised Precipitation Index (SPI), a drought index, reveals that over the course of the project (1993 - 2021), as well as experiencing considerably wetter periods (Figure 2.4), there have been five

periods dry enough to be classified as droughts ($SPI < -2$, Mckee *et al.* 1993). Droughts in the Kalahari are associated with the arrestment and failure of reproduction as well as increases in mortality for numerous species, and in the meerkat project population contractions in population size of between 30-50% have been associated with these drought periods (Figure 2.4, Figure 2.5a).

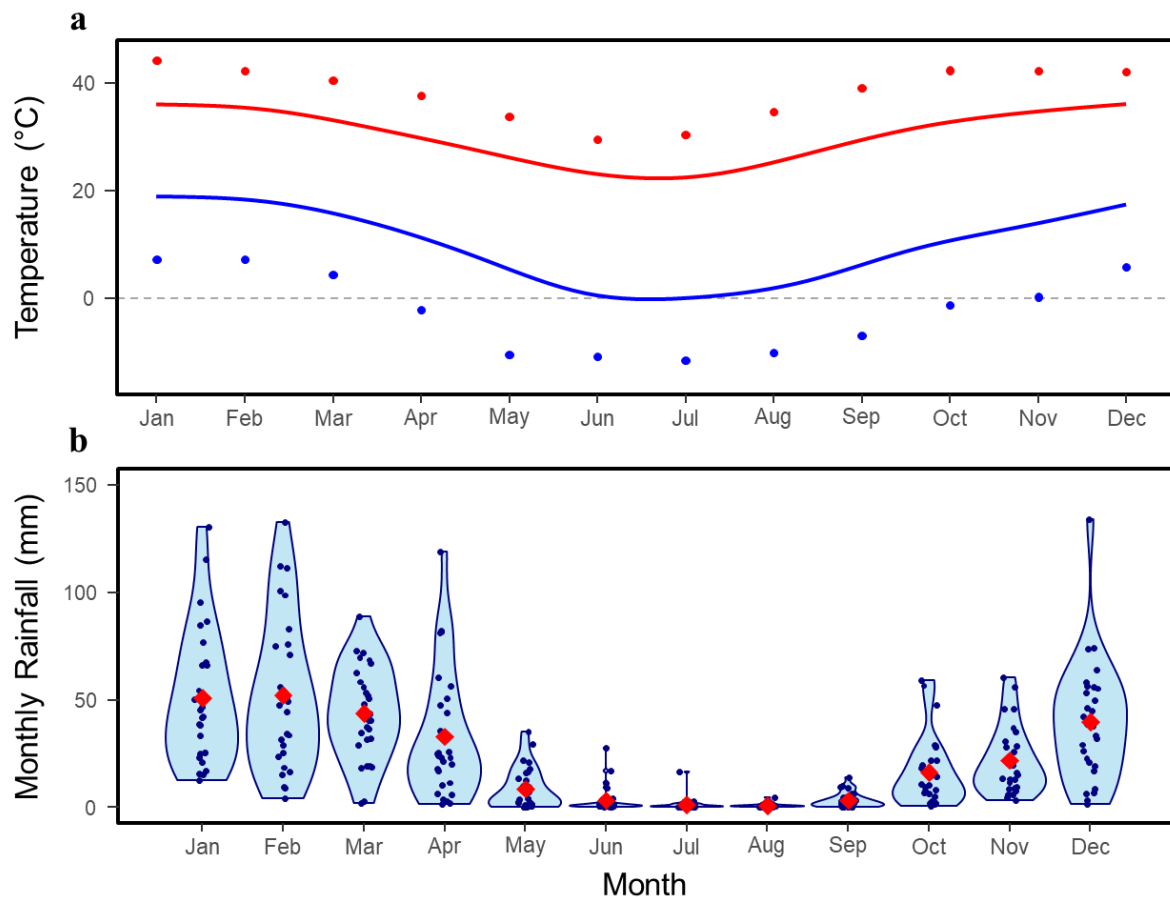


Figure 2.3: (a) Variation in minimum and maximum temperatures (°C) across the year. Smoothed Loess curves (solid lines) were fitted to daily minimum (blue) and maximum (red) temperature readings recorded by an onsite weather station between 2009 and 2021. The highest (red) and lowest (blue) recorded temperatures in a given month are also plotted (solid points). (b) Mean monthly rainfall (mm) across the year (red diamonds), calculated from monthly rainfall estimates (navy points) from 1993 – 2020 generated from remote sensed satellite data for the study area. The distribution of the data is characterised using violin plots at a monthly level.

Temperature is also highly seasonal in the Kalahari, fluctuating between extreme highs of over 40°C in the middle of the day in summer and lows below -10°C during winter nights (Figure 2.3a). In the height of winter (June to August), temperatures can fluctuate by over 20°C over the course of the day, ranging from below 0°C in the early mornings to around 20°C by midday. While summer months are considerably warmer with minimum temperatures being around 20°C, the daily fluctuations are still large with the midday temperatures tending to exceed 35 °C. Trends in recent years indicate that the Kalahari is getting hotter, with mean maximum temperatures and minimum temperatures

increasing significantly in recent years (van Wilgen *et al.* 2016). The impacts of extreme temperature on the behaviour and condition of species inhabiting the Kalahari are well documented (van de Ven *et al.* 2020a, b), therefore if these trends continue, negative impacts on the demographic rates of these species are expected (Paniw *et al.* 2019).

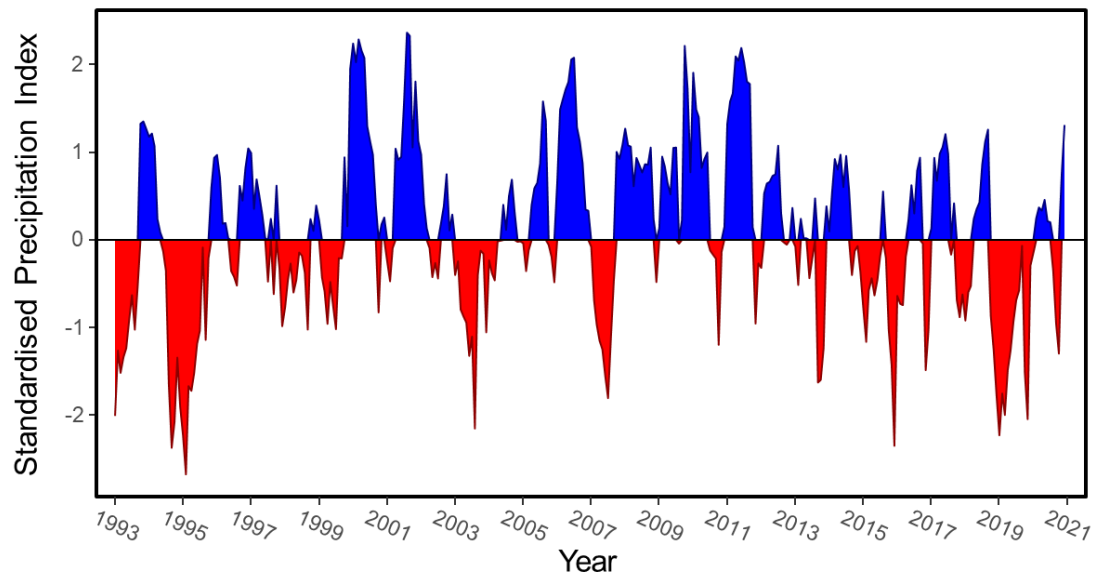


Figure 2.4: The Standardised Precipitation Index (SPI) for the study area from 1993 - 2021. The SPI represents how the cumulative rainfall for the previous 6 months deviates from the mean expected rainfall. Periods with SPI < 0 (red) are drier than expected and periods with SPI > 0 are wetter than expected. Periods in which SPI drop below -2 are commonly considered droughts (Mckee *et al.* 1993). SPI was calculated using remoted sensed rainfall data for the study area from 1970 until 2021.

Population

Research on meerkats in the study area commenced in 1993 when the first meerkat groups were habituated and followed. In the early years of the project, most new groups recruited to the study population were already established wild groups that required habituation. However, as the study progressed most new groups resulted from the dispersal and formation of new groups by habituated individuals that settled within the study area. During the first decade of the project, the number of individuals and groups followed increased steadily as the project grew. However, from the early 2000s onwards between 10-20 groups have been consistently followed at any one point in time (Figure 2.5b), with the number of individuals being followed ranging between 100 – 360 individuals (Figure 2.5a). In total 3615 unique individuals and 98 distinct groups have been followed, with the birth and formation dates known for most individuals (88%) and groups (63%).

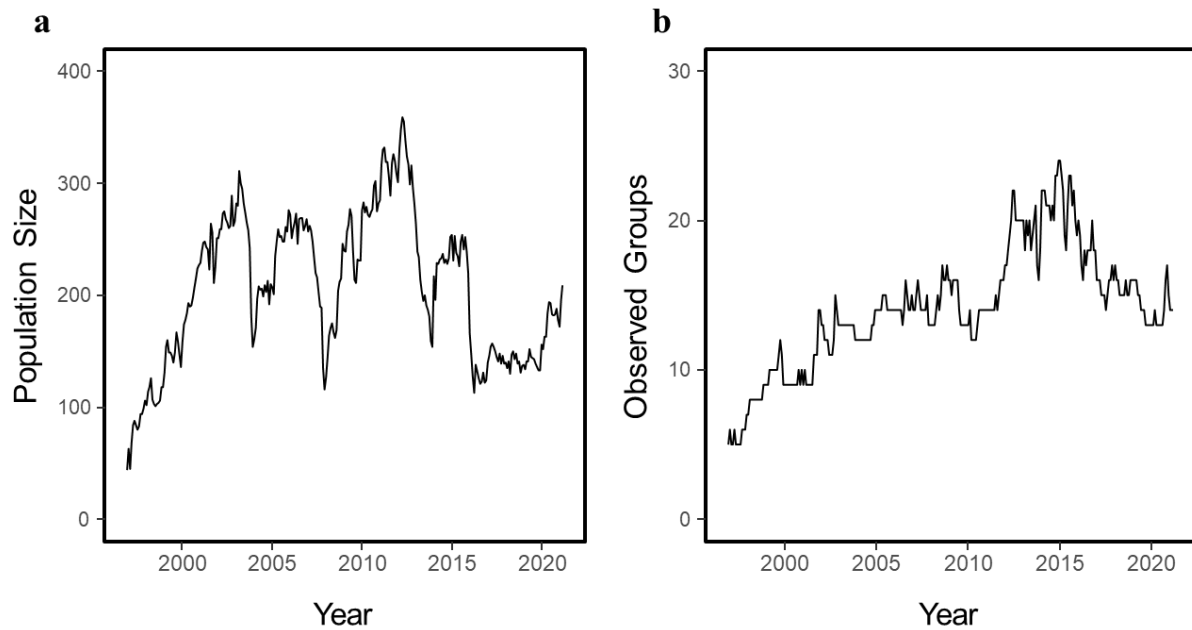


Figure 2.5: (a) The total number of meerkats and (b) distinct social groups observed each month at the project from 1996 until 2021.

Data Collection

Group monitoring

To track each meerkat group one resident individual was fitted with a VHF collar (Figure 2.6a), that could be tracked from 2 km away across flat ground using a Telonics VHF receiver and aerial. The collar was preferentially fitted to the dominant females as they were the most consistently resident within the group, as males would leave for periods of time to rove for mating opportunities and subordinate females were vulnerable to eviction from the group. The VHF collars were only fitted to individuals for whom the collars weight was less than 5% of their own weight and previous studies have shown that the collars neither impaired foraging efficiency nor increased their predation risk (Golabek *et al.* 2008).

Groups were visited 3-4 days a week for “full sessions” and followed for between 3-5 hours in the morning and 1-2 hours in the evening, this involved the collection of data on individual life-history, behaviour, and weights. To prevent groups being unobserved for longer than a day, additional shorter visits were undertaken where only life-history data were collected. Concerted efforts were made to habituate all individuals in the population to the presence of observers, and except for briefly resident wild migrants, most individuals could be approached to within a few metres without altering their behaviour. This allowed for individuals to be given unique identifying markings either using black hair-dye or haircuts. Care was taken to make sure all individuals within the population had unique marks

to enable the accurate identification of individuals making extra-group excursions. Individuals were also fitted with RFID readable pit-tags as soon as they were able to be captured, allowing for identification of individuals even when individual dye marks cannot be maintained such as when subordinates are absent from their group for extended periods.

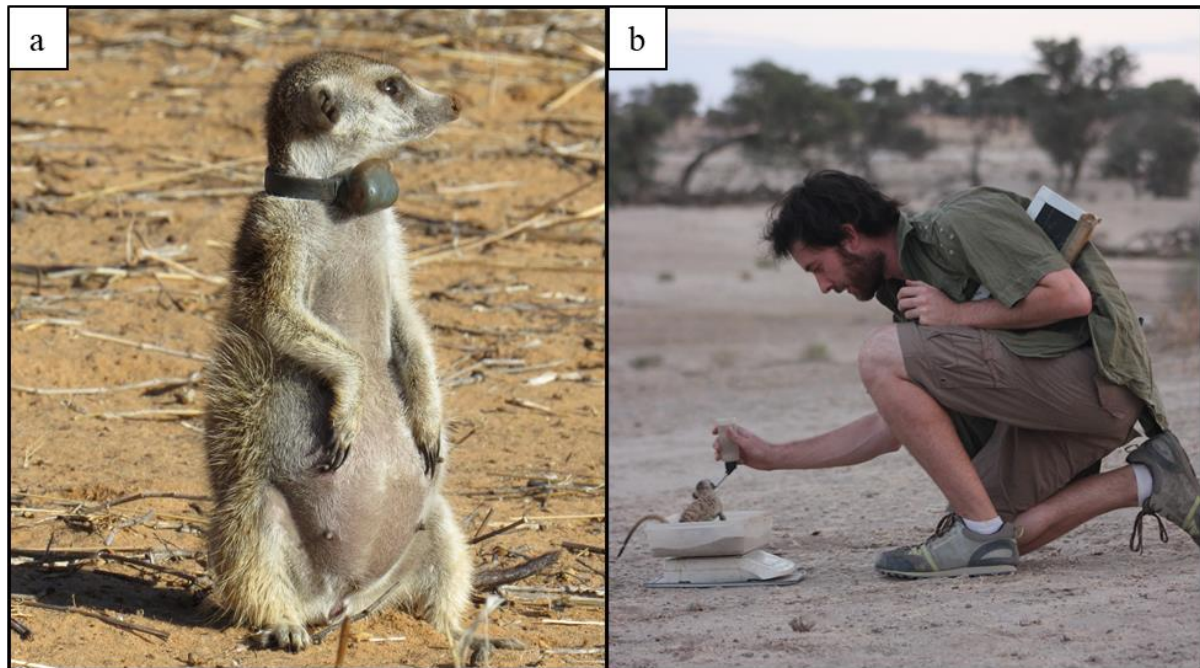


Figure 2.6: (a) Picture of a pregnant dominant female meerkat with a VHF collar. (b) Picture of weights being collected, with the meerkat being coaxed onto the scale using a water bottle.

Life history data

When groups were visited a full census of group membership was taken and a variety of individual specific life-history details were recorded. During sessions, group membership was continuously monitored and any individuals that left or returned to the group were recorded. Additionally, any interactions with other groups or extra-group individuals were recorded along with the identities of the non-focal individuals or groups. The reproductive status of all individuals was assessed with definite and suspected pregnancies recorded, as well as the presence of sandy rings around nipples that indicate lactation. Mate guarding and other behaviours indicative of oestrus were also recorded. Non-ritualised dominance behaviours such as individual contests were monitored, allowing for the stability of hierarchies to be monitored and dominance changeovers to be tracked. Finally, all individuals were checked for signs of health-related issues such as injuries and fatigue; with particular attention paid to clinical signs of tuberculosis (TB), including lymphatic swellings and persistent skin lesions.

Behavioural data collection

Behavioural data were collected whenever groups were visited for full data collection sessions. Group behaviour was monitored for 3 hours in the morning after the commencement of foraging and for an hour in the evening prior to the end of foraging. The primary form of behavioural observation, referred to as *Ad-Libertum* collection, involved the observer recording the occurrence of specific behaviours and the time they were observed. During *Ad-Libertum* sampling observers move around the group trying to spread their observation effort as evenly as possible across all group members during the data collection session. Although, as meerkat groups commonly forage at close proximity in open habitats, it is often the case that all or most of the group are visible to the observer. A variety of behaviours were recorded with focus on cooperative behaviours, including guarding and pup provisioning, as well as social interactions, including grooming, competition, and ritualised dominance. *Ad-Libertum* sampling has been consistently recorded on all habituated groups for most of the project's existence, with only a few minor changes to the behavioural ethogram over the course of the study. In addition to *Ad-Libertum* sampling, both focal observations and behavioural scan sampling have been conducted. However, these additional forms of data collection have been largely conducted in association with specific experiments and not across the length of the project. Prior to 2017 all behavioural data collection was conducted using PSION personal organisers MARK2 with a bespoke program designed for each collection methodology. Due to hardware and software constraints, all behavioural data collection since 2017 has moved to programs designed using the Pendragon software and deployed on tablets running the Android OS.

Assignment of dominance

Dominant individuals and dominance in this thesis refers to either the alpha breeding male or female meerkats in established groups. Established groups are defined as a continuous association between males and female meerkats. Dominant individuals could be identified from the frequency and direction of aggressive and submissive interactions directed at other same-sex members within their group as well as from the relative frequency of anal marking, which is substantially higher in dominants than subordinates (Thavarajah *et al.* 2014). Dominant individuals were dominant to all other same-sex members of their groups, and would direct ritualised dominance behaviours at subordinate individuals and would also receive ritualised submissive behaviours (Kutsukake & Clutton-Brock 2006). Dominance is also associated with morphological and physiological differences. Following acquisition, dominants of both sexes undergo a secondary period of accelerated growth (Huchard *et al.* 2016), and females experience increases in both their body length and skull width (Russell *et al.*

2004). This does not necessarily mean dominants are always the heaviest member of their sex within the group, and dominants of both sexes undergo senescence, declining in weight after 5-6 years of age (Thorley *et al.* 2020). There are also hormonal differences associated with dominance in meerkats, and dominants of both sexes tend to have higher circulating levels of cortisol, and dominant females have higher levels of testosterone than subordinate females (Carlson *et al.* 2004; Davies *et al.* 2016).

The period that a dominant holds their position is referred to as a bout of dominance. The start of an individual's dominance bout is defined as the date from which they were clearly dominant to other same-sex residents within the established group, asserting dominance to all other competitors and receiving submissions in return. The defined end of a dominant's tenure depended on the cause of dominance loss. Tenure was set at either the date the dominant died, emigrated from the group, when a conspecific took over the position of dominance, or when the group failed. Dominant meerkats rarely undertake excursions away from the group (Cram *et al.* 2018), especially female dominants. However, brief absences from the group are observed, often either in association with a failure of spatial cohesion in the group or due to the dominant pursuing out-group breeding opportunities. In addition, a dominant's tenure can also be disrupted by periods of hierarchical instability where the certainty of their position is unclear, resulting either from the immigration of new individuals or the outbreak of competition with resident same sex individuals challenging them for their social status. While these periods of instability and absence from the group may perturb a dominant's tenure, unless the perturbation resulted in a changeover in dominance, a dominant's tenure is considered continuous throughout these periods.

Weights

For full data sessions all individuals are weighed three times, first in the morning as they emerged from the burrow and prior to foraging, second following three hours of foraging and finally in the evening following the cessation of foraging. Individuals were coaxed onto scales using crumbs from a mashed hardboiled egg or water dispensed from an animal feeding bottle (Figure 2.6b). Except for specific feeding experiments (Huchard *et al.* 2016), individuals were only given tiny amounts of egg or water to get them onto the scales to avoid influencing their growth or behaviour. Following their first emergence from the burrow, young meerkats are exposed to egg so they can acquire a taste for it which usually lasts throughout their life. Efforts were made to weigh all group members and over the course of the project over 1.5 million weights have been collected. Subsequently there are multiple weights per week throughout the lifespan of many individuals born in the population, with 85% of the individuals observed in the population for longer than a week having more than two

weights per week on average across their observed lifespan (mean = 5.35, range 0 – 13.34). The weights are collected using Sartorius scales that can measure weights at a resolution of 1 gram and can weigh objects up to 2 kilograms. For all analyses in this thesis, I used morning weights to calculate individual body mass, usually averaged over a defined period. The mean weekly morning weight rate of individuals in the population was 2.29 (range = 0 – 6.22) weights per week across their lifespan. Additionally for females, I excluded weight values from when they were visibly pregnant to avoid conflating pregnancy related growth with individual condition.

Parentage assignment

Historically, genetic pedigrees have been generated for the meerkat population on multiple occasions across the 26-year history of the project. First, Griffin *et al.* (2001) developed a panel of 12 polymorphic microsatellites loci, including 9 cloned directly from meerkats and 3 from other carnivores, for the purposes of describing the reproductive skew and genetic structure of meerkat groups (Griffin *et al.* 2003). Following this Spong *et al.* (2008) expanded the number of loci that meerkats were genotyped at to 14 for analyses on the lifetime reproductive success of dominant males. Additionally, this work also resulted in research on the role of prospecting and extra-group paternity in generating fitness for subordinate males (Young *et al.* 2007). Most recently Nielsen (2012) expanded the number of microsatellite markers to 18 and re-genotyped all available historical samples. Using a combination of MASTERBAYES and COLONY2, parentage was assigned for sampled individuals resident within the population between 1993 and 2011. Since 2011, at approximately yearly intervals all individuals sampled at the project have been genotyped at the 18 microsatellite loci specified by Nielsen and have had their parentages assigned using COLONY2. Initially, the genotyping and parentage analysis was carried out by Josephine Pemberton at the University of Edinburgh, although since 2017 Glauco Camenisch at the University of Zurich has taken over this work.

To assign individual parentage, tissue samples were obtained from tail tips taken in the field and stored in ethanol. Samples were taken for individuals born in the population soon after they first emerged from the burrow post birth, and for individuals who migrated into the population, as soon as they were habituated enough to be caught. DNA was extracted from the tail tips and individuals were then genotyped at 18 distinct microsatellite loci (Nielsen 2012). Based on the individual microsatellite markers the program COLONY2 was then used to assign parentages, which were used to create a multigenerational pedigree of the population. For the parentage analysis a list of candidate fathers and mothers was supplied to COLONY2. For the assignment of paternity all males observed in the population within 2 weeks of estimated conception were considered candidate fathers. For

maternity assignment, where a single female gave birth, she was assigned as the candidate mother, however, when multiple females gave birth to a mixed litter, all observed pregnant females were included as candidate mothers.

For the analyses included in this thesis I restricted the sample to parentages assigned with $\geq 80\%$ confidence, with the exception of parentage assigned by half sibling inference where confidence values are not supplied. Furthermore, I also excluded a few erroneous parentage assignments where individuals were either assigned themselves as a parent ($n=6$) or where the assigned parent was either too young to be a prospective parent or was born after their supposed offspring ($n=41$). Some individuals had their parentage assessed multiple times as new genetic data was added. Where there was disagreement in the assigned parentage, I used the parents assigned in the most recent analysis. Additionally, in cases where maternity could not be assigned genetically, yet only one female was observed to be pregnant in the group, maternity was assigned to this female. Finally, when parentage could not be assigned, the parent was likely an unsampled individual either within or outside our population. In COLONY2, as both parentage and sibship are assessed, in some cases sibship can infer the existence of an unsampled parent who were assigned a unique identifier and are referred to as a dummy parent (Nielsen 2012).

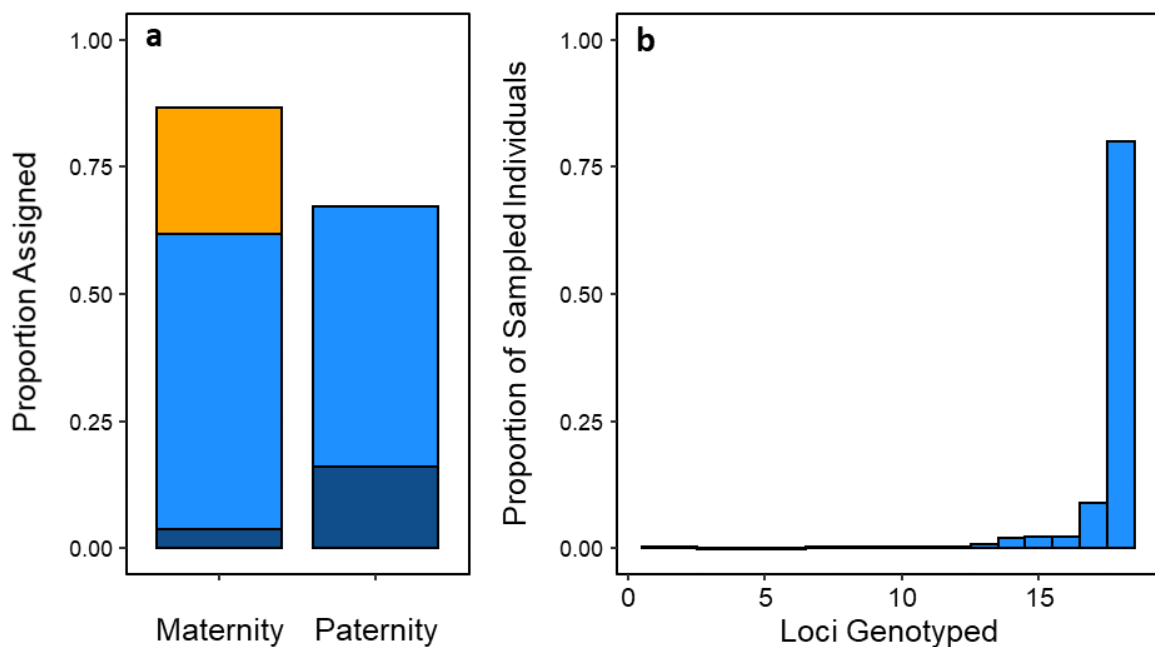


Figure 2.7: (a) Stacked bar plot of the proportion of individuals observed within the population with their maternity and paternity assigned. Stacked bars are differentiated based on whether parentage was genetically assigned to an individual within the population (light blue), genetically assigned to a dummy individual (dark blue) or inferred based on field observations (orange). (b) Bar plot of the proportion of sampled individuals related to the number of loci genotyped.

The current genetic sample at the project includes individuals observed up until and including August 2019, for which a substantial number have had their parentage assigned (Figure 2.7a). During this period 3193 pups were born into the population, of which 2579 were captured, sampled, and genotyped (Figure 2.7b). Of these genotyped individuals 2140 individuals were successfully assigned maternities, including only 57 dummy mothers. Supplementing the genetically assigned maternities with field observations where there was only one observably pregnant female at the group who could be the mother, maternity was able to be assigned for 96% of pups born into the population (3062/3193). Paternity was successfully assigned for 2346 of the genotyped pups, however the number of dummy assignments was higher for paternity, with 509 paternities being assigned to dummy individuals. Due to the large number of possible candidate fathers for any reproductive event, including both resident and extra group males, field observations could not be used to supplement paternity assignments. Therefore, paternity was only able to be assigned for 74% of the pups born into the population.

Of the 3615 individuals observed during the study prior to August 2019, 422 were born outside of the study population. These individuals either migrated into an observed group or were resident at a newly discovered group that was habituated and incorporated into the study population. Of these 422 individuals 182 were captured, sampled, and genotyped, with maternities being assigned for 112 individuals and paternities for 116 individuals. As would be expected for an individual born outside the population, most parentages were assigned to dummy individuals: 80 assigned dummy mothers and 75 dummy fathers.

Climatic data

For this thesis I used remote sensed rainfall measurements provided by the NOAA Global Precipitation and Climatology Project (GPCP). This dataset was generated by merging multiple satellite-based estimates of precipitation combined with numerous rain gauge measurements sourced globally (Adler *et al.* 2003, 2018). The GPCP monthly product provides monthly rainfall estimates at a 2.5° longitude/latitude resolution. This dataset provides measurements from 1997 up until 2021, covering the entire history of the study population. On site weather was first measured manually from 1993 until 2007 using a potometer and then from 2009 onwards using an onsite weather station. Due to the lack of coverage and consistency in collection for the projects history I did not use the onsite rainfall data for my analyses. However, the onsite rainfall data has been used for ground truthing and has confirmed the viability of using the GPCP dataset to capture the rainfall patterns the study population experiences (Paniw *et al.* 2019; Groenewoud & Clutton-Brock 2021). The onsite weather

station also records hourly temperature readings in addition to daily minimum and maximum temperature readings

Ethical Note

The data used in this thesis was collected as part of the long-term data collection at the Kalahari Meerkat project which consists primarily of observational data, and where handling was necessary for weighing, or captures to take tissue samples, PIT tag, and attach collars, it was kept to a minimum. All data collected at the project were approved by the Animal Ethics Committee of the University of Pretoria, South Africa (EC010-13), and the Northern Cape Department of Environment and Nature Conservation, South Africa (FAUNA1020/2016).

Data Processing

Over the course of the meerkat project, a multitude of field researchers have monitored groups and contributed to the core project dataset. All data-collectors undertake field training and monitoring, however, to reduced possible observer bias, efforts were made to rotate researchers across groups, so all groups were monitored by a variety of researchers. The recording of life history data was based on a consensus system, whereby the recording of a life history event (e.g. pregnancy, dominance acquisition etc.) required agreement between multiple researchers visiting the group. For example, recording an individual pregnancy required three different researchers on consecutive visits to the group to be convinced of the pregnancy based on visual signs, at which point the pregnancy was recorded and the first date at which visual signs were observed was noted. The synthesis and recording of life-history data from researcher's field observations was overseen by a specially trained life-history researcher, whose role was to ensure the consistency and application of the project's life-history event definitions. Furthermore, the life-history data were checked monthly by the project manager who replicated the synthesis of life-history data and corroborated it against the recordings in the database. While originally life-history data were recorded in Excel sheets, in 2011 the data were transferred to a relational database stored in Microsoft Access where additional automated data-checks were implemented to maintain the integrity and logic of the individual dataset.

For this thesis, I derived and constructed all datasets from the relational database, either using SQL scripts or R, with additional data-checking and cleaning carried out. Specifically, I manually processed datasets of dominants and groups, checking all records against the original field observations and auxiliary datasets, to ensure consistency in the definitions of dominance and groups,

as detailed in the following data chapters. Furthermore, to identify and categorise the processes of dominance acquisition and loss, as well as the failure of groups, I undertook a resynthesis of the original field observations in combination with life-history records and associated comment-data. Finally, to incorporate the impacts of TB into this thesis, I generated new datasets detailing periods of group-level clinical infection. These TB datasets resulted from the synthesis of data on individual mortality, the original comment-based field observations and individual health records pattern matched and filtered for terms associated with TB. Combining these different data-sources highlighted periods of possible infection that I then manually verified and recorded as periods of clinical TB.

Statistical analyses

All statistical analyses in this thesis were conducted within the R statistical environment (Team 2017a), using the most recent Microsoft R open distribution at the time the analyses were conducted ($\leq 4.0.2$). Prior to modelling, the distributions of the response variable and fixed effects were visualised and variance inflation factors (VIF) were calculated to pre-emptively identify possible collinearity issues among fixed effects (Zuur *et al.* 2009). Variance inflation factors greater than three were considered problematic and requiring further investigation.

For frequentist analyses the R package *glmmTMB* was used for the fitting of both linear (LM) and generalised linear models (GLM), as well as their multilevel forms: linear mixed effect models (LMM) and generalised linear mixed effect models (GLMM). In addition to being able to fit models with a wide range of distributions, *glmmTMB* also provide numerous methods for accounting for over-dispersed and zero-inflated data (Brooks *et al.* 2017). Model residual diagnostic checks were carried out using the package *DHARMa* (Hartig 2017), which provided tools for checking the model's goodness-of-fit and for diagnosing problems such as zero-inflation and dispersion.

For Bayesian analyses, models were fitted using the package *brms* (Bürkner 2018). Models were run using 4 chains of 3000 iterations including 1000 warm-up iterations. Adequate chain mixing was assessed using visualisations and all model parameters were checked for adequate sampling (rhat < 1.01). Posterior predictive checks were conducted for all models using a combination of functions from the *brms*, *loo*, *bayesplot* and *shinybayes* packages (Team 2017b; Vehtari *et al.* 2017; Bürkner 2018; Gabry *et al.* 2019). The posterior distribution was sampled and contrasted against the raw data to confirm that the model adequately captured the distribution of the raw data. The posterior predictive checks were combined with Leave-One-Out Cross-Validation (LOO) generated LooAIC to determine the distributions that best fitted the data. Furthermore, I extracted Pareto-K values for each observation to check for overly influential outliers ($K > 0.7$). In most situations I used LOO to contrast

the fits of different models, however in rare cases where LOO did not perform well, k-fold cross-validation was utilised (Vehtari *et al.* 2017).

Survival analyses in this thesis were conducted using the package *Survival* to fit non-parametric and semi-parametric models (Therneau 2020), and the package *flexsurv* for the fitting of parametric models (Jackson 2016). The package *flexsurv* allowed for parametric survival models to be fitted within a multistate framework, however for the fitting of semi- and non-parametric survival models within a multistate framework the package *mstate* was utilised (de Wreede *et al.* 2011). In all survival models, datapoints were censored when they disappeared from the study or were still present at the end of the study without the event of interest having occurred. When covariate survival analyses were conducted, the semi-parametric Cox-proportional hazard model was used. The assumption of the non-proportionality of hazards was checked for all Cox-proportional hazard models, and where non-proportionality was observed, interactions with time were included to account for this. Furthermore, the beta-residuals were checked to identify possible outliers that were driving or masking fixed effects.

Chapter 3: The acquisition of dominance in female meerkats

This chapter was written for Animal Behaviour:

Duncan, C. Gaynor, D. Clutton-Brock, T. (2018) 'The importance of being beta: female succession in a cooperative breeder', *Animal Behaviour*, 146, p113-122

Abstract

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. In this chapter, I 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. I 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, I tested whether beta females adjust their growth or cooperative behaviour to avoid eviction and increase their tenure length as the beta. However, there was 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.

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 (Rood 1990; Bennett & Faulkes 2000; Creel & Creel 2002; Hackländer *et al.* 2003; Saltzman *et al.* 2009; Clutton-Brock & Manser 2016). 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 (Hauber & Lacey 2005; Clutton-Brock *et al.* 2006), 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 *et al.* 2013).

Age based hierarchies where individuals queue for dominance occur in many mammalian societies, including African elephants, *Loxodonta africana* (Archie *et al.* 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 dwarf mongooses, *Helogale parvula*, wolves, *Canis lupus* and wild-dogs, *Lycaon pictus* (Creel *et al.* 1992; Creel 2005). Although the weight and condition of individuals are commonly correlated with their status (Veiberg *et al.* 2004; Vervaecke *et al.* 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 (Young *et al.* 2006; Cant *et al.* 2010; Thompson *et al.* 2016). 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 *et al.* 2004; Wong *et al.* 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 *et al.* 1998). Evidence of such a mechanism has been reported in cichlids, *Neolamprologus pulcher* (Bruitjes & 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 (Pope 2000; Kappeler & Fichtel 2012), no mammalian studies have yet investigated whether individuals modify their growth rates or levels of cooperation to minimise conflict with the dominant.

In this chapter I examine the factors affecting succession to the dominant position in female 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. 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 *et al.* 2008), their growth rates as pups (English *et al.* 2013) and the level of investment by helpers during their own development (Russell *et al.* 2007). Here I 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 *et al.* 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 also the heaviest subordinate and at the highest risk of eviction by the dominant (Clutton-Brock *et al.* 2010). Subordinates 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 the 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, I investigated whether subordinate female meerkats in the beta position reduced their growth or increased their contribution to cooperative behaviour.

Methods

The analyses in this chapter were conducted using the long-term data collected in the study area between July 1995 and March 2017. On average, at any month 215 individuals (range: 46-359) composing 15 groups (range: 6-25) were followed. Only females that were born in the study population ($n=1111$) were included in analyses so their dispersal status, age and other characteristics could be reliably determined. During the 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 *et al.* 2018), thus dispersing females rarely settle outside or far from the study area. Whilst they are often incorporated into the study population, inevitably some individuals leave the study area and are not observed acquiring dominance. Therefore, the frequency of dispersed dominants is likely to be underestimated.

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 *et al.* 2014). Therefore, I 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, I 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 the 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. This approach resulted in a sample set consisting of 917 females who could have held a beta position, I further restricted this to individuals that lived beyond a year, reducing the sample to 648 females.

To conduct multiple regressions, linear mixed effect models (LMM) and generalized mixed effects models (GLMM) were utilized. This allowed for the fitting of random terms to account for repeat sampling. 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 *et al.* 2009). Collinearity of fixed terms was tested in models using variance inflation factors, 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).

Contrasting routes 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; (4) dispersed displacers were founding members of a new breeding group and subsequently displaced a dominant female that held dominance before them; and (5) dispersed inheritors were founding members of a new breeding group and subsequently inherited the breeding position following 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, LMMs were used with group ID fitted as a random effect. When analysing the age an individual acquired dominance, acquisition routes as opposed to method were 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.

I 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 (90 days) and the number of offspring that reach adulthood (365 days). 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 the genetic pedigree and field observations. In these analyses, the sample was restricted to dominant females born in the 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. I subsequently summed the total number of months betas held their status over their lifetime 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, I 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. I 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. Variance inflation factors (VIF) for these models indicated there was no problematic multicollinearity among the predictor variables, even relative weight and age (Table 3.1).

Table 3.1: Variance inflation factors calculate for the explanatory variables included in the GLM exploring the factors influencing who acquires dominance during natal inheritance, displacement, and group foundation.

Fixed Effects	GVIF		
	Inheritance	Displacement	Foundation
Relative Age	1.928	1.261	1.925
Relative Weight	2.218	1.340	2.091
Relatedness	2.342	NA	NA
Pregnancy Status	1.165	1.192	1.162
Daughter	2.334	NA	NA
Sibling	NA	1.124	NA
Natal Status	NA	1.441	NA

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 LMM 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 when individuals were pregnant were excluded from the data set as their state was expected to have a confounding effect on growth. Initially the sample consisted of 2274 month periods with a beta present, however sub-setting this for only periods where there were 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, I measured their contributions to pup provisioning and babysitting on a per litter basis. Litters born across the 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 nor 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 routes to dominance

152 (21%) of the 723 females born into the study population that reached adulthood (12 months) acquired a dominant position in the 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 3.1).

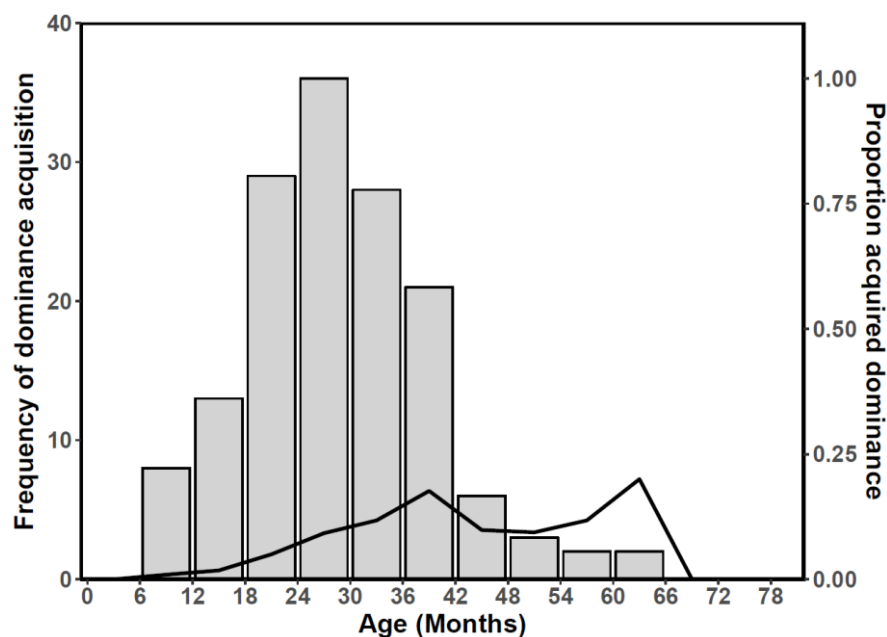


Figure 3.1: Frequency of subordinate females acquiring dominance relative to age (grey bars). Proportion of subordinate females that acquired dominance at an age relative to the number of subordinates that survived to that age (black line). Only individuals first bouts of dominance were included in this figure.

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 3.2). 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 3.2). Acquisition of a dominant position immediately after founding a new group was the second most common acquisition method (31%, $N = 47$; Table 3.2).

Table 3.2: Proportions of dominance acquired via different routes

Acquisition Method	Frequency (Individuals)	Proportion of Acquisitions (%)
<i>Natal</i>		
Inheritance	67	44.1
Displacement	16	10.5
Total	83	54.6
<i>Dispersal</i>		
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.

Individuals that acquired dominance in their natal group did so earlier in life than those that acquired dominance after dispersal (LMM: $F_{1,106} = 29.37$, $P < 0.001$) and the differences in age of acquisition between different routes were significant (LMM: $F_{4,103} = 9.264$, $P < 0.001$; Figure 3.2). 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 between inheriting successors and the previous dominant (LMM: $F_{1,75} = 10.71$, $P = 0.002$). Individuals that acquired dominance in their natal group, also lost their tenure at an earlier age than individuals who acquired dominance after dispersal (LMM: $F_{1,90} = 12.8$, $P < 0.001$).

The mean tenure length of dominant females was 20.1 ± 24 months (median = 9.2 months, range = 0.2 – 125.7 months; Figure 3.3). 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 (LMM: $F_{1,90} = 0.035$, $P = 0.853$) or between individuals that acquired dominance via different methods (LMM: $F_{2,89} = 0.665$, $P = 0.522$). 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 3.3).

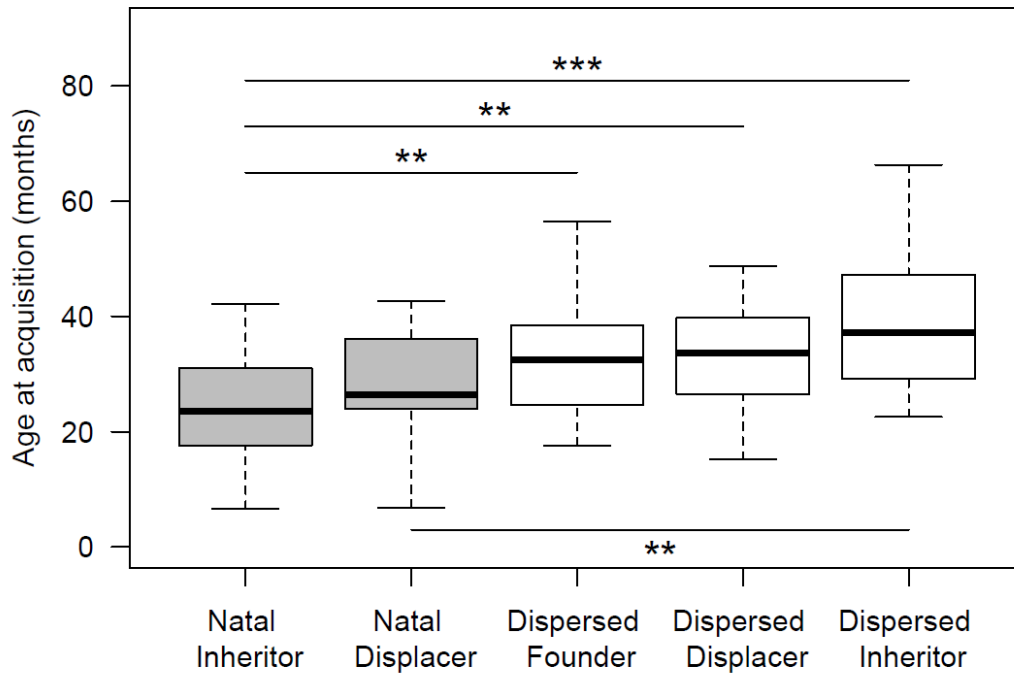


Figure 3.2: The age at which dominant females acquired their dominance in days relative to where (Natal = grey, Dispersed = white) and how they acquired their dominance: Natal Inheritor ($N = 68$), Natal Displacer ($N = 16$), Dispersed Founder ($N = 54$), Dispersed Displacer ($N = 19$) and Dispersed 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 LMM with group included as a random effect (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

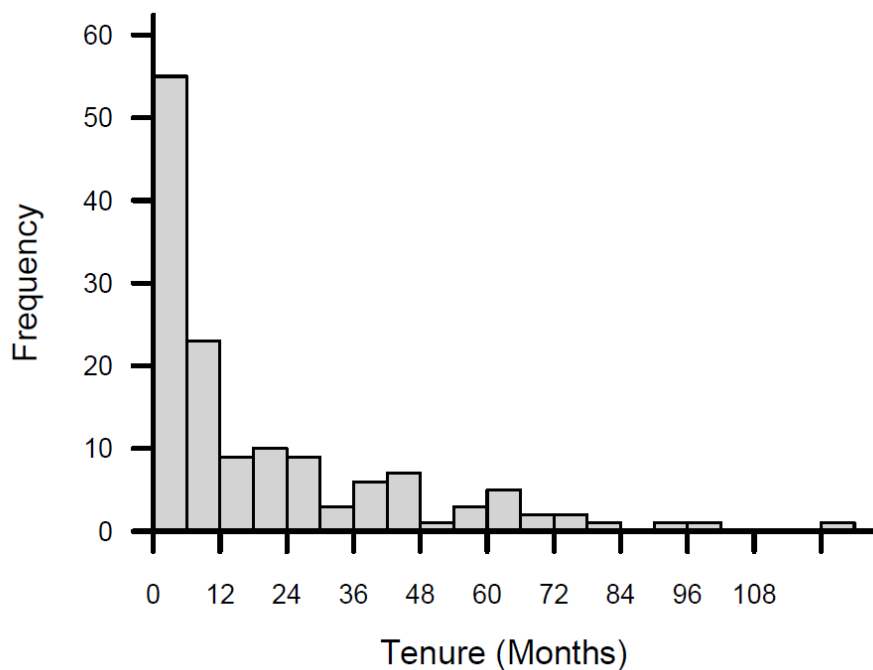


Figure 3.3. Frequency distribution of the duration of dominance bouts.

Table 3.3: The reproductive success for dominance bouts depending on where and how dominance was acquired.

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

Modeled using a GLMM with a negative binomial error distribution and a log link, tenure length was controlled 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.

Factors affecting the acquisition of dominance

Of the 648 females born in the population within the sample period that survived to adulthood, 308 (48%) 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 my 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 3.4). 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.

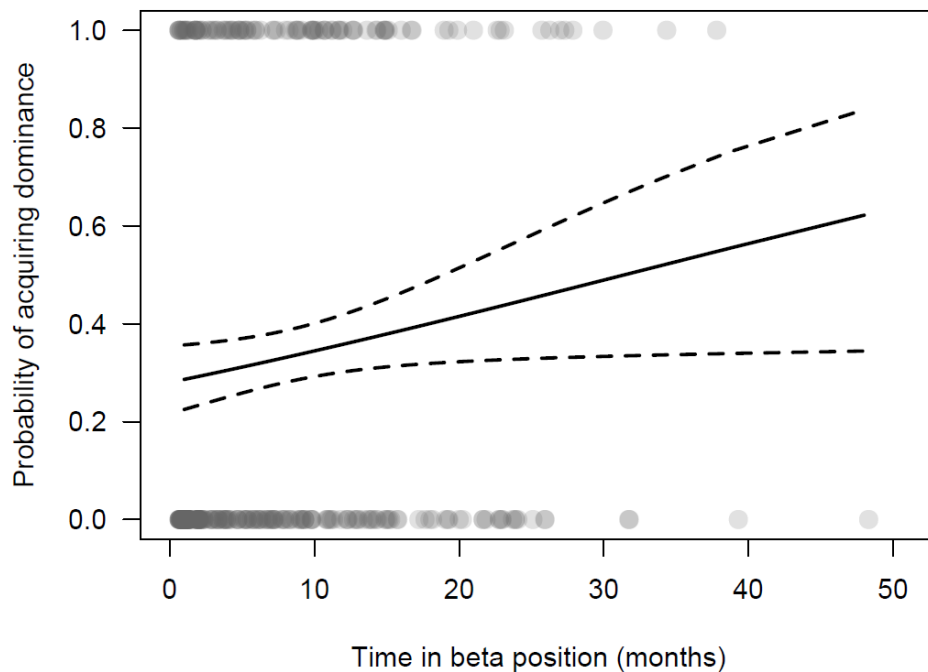


Figure 3.4: Relationship between the total number of months in a beta position during an individual's lifetime and their probability of acquiring dominance. Fitted effect (solid line), 95% confidence intervals (dashed lines) and raw data (transparent grey points) from a GLMM with acquisition of dominance 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.

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 3.4). 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 3.4). 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 (76%, 44/58). Also, in 73% (11/15) of cases where a 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 3.4).

Most dominant females that die are succeeded by their daughters (45%; 37/82) or siblings (31%; 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 I found no effect of relation to the previous dominant on success at competing for dominance vacancies (Table 3.4).

Table 3.4: Factors influencing which subordinate acquires the dominant position during different types of acquisition event.

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

Strategies for maximising beta tenure

Since dominant females are more likely to evict subordinates that pose a risk to their reproductive potential (Clutton-Brock *et al.* 2010), I 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 were 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 (Table 3.5). 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, $P = 0.61$, Table 3.6) or on pup provisioning (z-value = -0.06, P value = 0.9, Table 3.7) was found.

Table 3.5: Factors influencing the growth rate of a beta female.

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

The growth rate of a beta female modelled using a GLMM with a Gaussian distribution. Significant factors highlighted in bold. The year, month and the identity 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 3.6: Factors influencing subordinate babysitting contribution

Model Term	Estimate \pm SE	z-value	P
Age (Months)	0.42 \pm 0.04	9.31	<0.001
Age² (Months)	-0.28 \pm 0.04	7.08	<0.001
Rank (Sub vs Beta)	-0.04 \pm 0.04	0.51	0.61
Average Weight	0.08 \pm 0.02	3.35	<0.001
Average Weight²	-0.12 \pm 0.01	11.22	<0.001
Group Size	-0.33 \pm 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 3.7: Factors influencing subordinate pup provisioning effort

Model Term	Estimate \pm SE	z-value	P
<i>Age (Months)</i>	-0.06 \pm 0.05	3.08	0.002
<i>Average Weight</i>	-0.07 \pm 0.02	3.67	0.0002
<i>Average Weight²</i>	-0.11 \pm 0.01	11.81	<2e-16
<i>Group Size</i>	-0.38 \pm 0.03	14.63	<2e-16
<i>Group Size²</i>	0.09 \pm 0.02	3.99	6.70e-05
<i>Mean Litter Size</i>	0.36 \pm 0.09	3.97	7.09e-05
<i>Mean Litter Size²</i>	-0.29 \pm 0.04	3.22	0.001
<i>Rank (Sub vs Beta)</i>	-0.002 \pm 0.04	0.06	0.95

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.

Discussion

In this chapter, I 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, I find no evidence that beta females either restrict their growth rate or increase their cooperative care of the dominant's offspring to prolong their beta tenure.

The later age at which individuals acquire dominance in groups other than their natal group is due to dispersed dominance 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; Mares *et al.* 2014). 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 *et al.* 1998) and paper wasps, *Polistes dominulus* (Leadbeater *et al.* 2011). The selective eviction in meerkats of older high-ranking subordinate females creates social mobility with the hierarchical rank and probability of inheritance increasing for lower rank subordinates over time. Social mobility is reported to play an important role in individuals maintaining group residence in Tibetan macaques, *Macaca thibetana* (Sun *et al.* 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 (Rood 1987; Nelson-Flower *et al.* 2018), 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 to 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 (Sapolsky 2005; Cram *et al.* 2015; Blount *et al.* 2016) 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 (Sparkman *et al.* 2011; Georgiev *et al.* 2016; Ekman & Griesser 2018), 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 the individuals that hold a beta position tend 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 my analyses of the factors dictating succession, which indicate that age relative to other subordinate females is an important indicator of who acquires dominance when vacancies arise within a group (inheritance and displacement). This is in line with research depicting age-based dominance hierarchies where females queue for dominance in a number of social species (Creel 2005; Archie *et al.* 2006; Foerster *et al.* 2016). However, I also find that an individual's weight relative to other subordinates is an important 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), my 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 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 traits at the time of succession in determining who acquires dominance.

In addition, I 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 *et al.* 2005; Grinsted & Field 2017). Whilst meerkats are exposed to ecological constraints in the form of dispersal costs (Young *et al.* 2006; Young & Monfort 2009) and variable extra-group reproductive opportunities (Maag *et al.* 2018), these don't appear to be prohibitively high, with these results finding similar numbers of subordinates acquiring dominance by dispersing as well as acquiring dominance in their natal group and with no apparent fitness costs. As 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 (Santema & Clutton-Brock 2012; Dantzer *et al.* 2017), an indicative trait of species exhibiting "pay-to-stay" mechanisms (Bruintjes & Taborsky 2008), which combined with these results suggest that subordinate female meerkats do not "pay-to-stay", with cooperative appeasement not being viable.

In conclusion, these results show no clear fitness advantages of certain routes to dominance, female meerkats do not employ strategies to maximise their chances of natal succession. I 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.

Chapter 4: The acquisition of dominance in male meerkats

Abstract

There are often multiple routes individuals can pursue to acquire dominance, which may influence the levels of fitness individuals attain from their dominant position. In this chapter, I investigate the different routes to dominance for male meerkats, *Suricata suricatta*, and whether they are associated with consistent differences in tenure and breeding success. Male meerkats can acquire dominance following dispersal either by founding a new group or by forcefully taking over an established group. However, some males assume a subordinate position following dispersal and may pursue dominance either by displacing the incumbent dominant or by inheriting dominance following the incumbent's death or dispersal. I show that the size and composition of a dominant male's group at the start of their tenure varies across dominance routes, however, contrasting routes to dominance appear to have no effect on the tenure length or breeding success of dominants. Ultimately, in the absence of variation in the benefits and constraints of distinct dominance routes, I suspect males will follow a flexible strategy pursuing the routes to dominance which stochastically present themselves during their lifespan.

Introduction

In many group-living species acquiring dominance is key to successfully reproducing (Ellis 1995), resulting in considerable differences in the fitness acquired by dominants and subordinates (Clutton-Brock *et al.* 2006). However, even among dominant individuals there is still substantial variation in lifetime reproductive success (LRS) (Hodge *et al.* 2008). Variation in a dominant's LRS can result from heterogeneity in individual traits that influence reproductive success, often termed individual quality. Phenotypic traits including individual size, morphology, and immunological profile linked to variation in the components of reproductive success: breeding tenure and breeding rate (Buston & Elith 2011; Breuer *et al.* 2012; Saino *et al.* 2012). In addition, high levels of stochasticity in the variance components of LRS can drive among individual variation, with individuals LRS being a function of their "luck, not pluck" (Snyder & Ellner 2018). However, it is also possible that variance in a dominant's reproductive success may derive from the different routes an individual can pursue to acquire dominance (Walters & Garcia 2016; Josi *et al.* 2021), which could be considered distinct dominance types or tactics.

Distinct routes to dominance have been well documented in many species, with individuals varying in both where (natal vs dispersed) and how (queueing vs displacement) they acquire dominance (Rood 1990; Raihani *et al.* 2010; Foerster *et al.* 2016). However, few studies have been able to investigate the consequences of these routes to dominance for individual fitness. Should the initial group size and composition vary consistently among dominance routes (Rood 1990), it is probable that differences in LRS will occur, as they can have considerable influence on the tenure lengths and productivity of breeders (Riehl 2011; Creel & Creel 2015; Lardy *et al.* 2015). Indeed, in the spotted hyena, *Crocuta crocuta*, population of the Ngorongoro Crater, the number and quality of breeding females a male has access to varies between their natal and neighbouring groups, and individuals appear to assess these characteristics and pursue breeder status where prospective fitness gains are highest (Davidian *et al.* 2016). In addition, the costs of competing for dominance can vary with the route to dominance, for example it is likely that actively competing for dominance and trying to overthrow an incumbent will be more energetically demanding than queueing for vacancies. Should these energetic demands be high, it can permanently compromise an individual's condition (Lardy *et al.* 2012), thereby reducing their ability to reproduce successfully and maintain their position (Georgiev *et al.* 2016). Beyond providing a possible explanation for differences in the LRS of dominants, understanding the characteristics of different dominance routes will also provide insight into social dynamics and allow for predictions to be made about the strategies individuals will pursue for acquiring dominance.

To document the ways in which males acquire dominance and whether the different routes to dominance influence the tenure length and reproductive success of dominant males, I utilise 26-years of long-term data collected on wild dominant male meerkats, *Suricata suricatta*. Meerkat groups are composed of a dominant breeding pair who monopolise the majority of the group's reproduction (> 80%, Hodge *et al.* 2008; Spong *et al.* 2008), and a number of reproductively suppressed subordinate helpers (Clutton-Brock *et al.* 2001b, 2010), who are commonly either the offspring or siblings of the dominant pair (Griffin *et al.* 2003). Subordinate males can gain inclusive fitness by providing alloparental care to the offspring of dominants who are commonly kin (Clutton-Brock & Manser 2016), however, to maximise fitness in the presence of strong reproductive skew, individuals must acquire a position of dominance during their lifespan. While males can acquire dominance within their natal groups (Spence-Jones *et al.* 2021), these tenures are unproductive as resident females are usually their relatives and will refuse to breed with them to avoid inbreeding (Griffin *et al.* 2003). Therefore, to acquire reproduction, males must prospect for mating opportunities at neighbouring groups (Young *et al.* 2007), or permanently disperse in search of a dominant breeding position, either individually or as part of a coalition usually consisting of natal group mates (Young 2003).

Following dispersal, there are four distinct routes to dominance (Spong *et al.* 2008). Firstly, individuals can acquire dominance immediately after dispersing, either by founding a new group ("founder dominant"), or by migrating into an established breeding group, evicting resident males and taking over dominance ("migrant dominant"). However, male meerkats often disperse in multi-male coalitions and individuals that do not acquire dominance will commonly remain within the group as immigrant subordinates. These immigrant subordinates can then either acquire dominance by challenging and displacing the incumbent dominant ("displacer dominant"), or by queueing and inheriting dominance following a stochastic event which removes the incumbent dominant ("inheritor dominant").

In this chapter, I first investigate the distinct routes to dominance and characterise the group size and composition dominants utilising different routes experience. Specifically, I expect the dominant of newly founded groups to inhabit smaller groups than dominants in established groups and for displacer and inheritor dominants to have lower numbers of immigrant males and reproductively viable unfamiliar females. Both group size and composition influences a dominant individuals reproductive success and the risk of certain causes of tenure loss (Courchamp *et al.* 1999; Hodge *et al.* 2008; Spong *et al.* 2008). I therefore investigate the potential consequences of any variation in social environment by analysing the tenure lengths and reproductive success of dominant males in relation to their dominance route. Finally, I investigate the intrinsic and social characteristics that determine the acquisition of dominance to assess whether the constraints of acquiring

dominance vary between routes. In addition to individual age (Spong *et al.* 2008), I also predict that body mass will play a role in dominance acquisition, as competitions over dominance are often intense and aggressive. For dispersing dominants (migrants and founders), coalition size is also likely to be a constraint. While founder dominants only compete with other male coalitions, migrant dominants need to have coalitions larger than the number of resident males to successfully takeover a group (Young 2003); therefore, I predict that migrant dominance will be limited to males in large coalitions.

Methods

For this chapter I use long term data collected between August 1995 and August 2019. As males that acquire dominance within their natal groups rarely breed, I restrict the analyses in this chapter to immigrant dominant males. During this period 258 bouts of dominance held by immigrant males were observed, which constituted 205 unique individuals due to the occurrence of individuals holding multiple distinct tenures in a lifetime. Of these dominance bouts I was able to accurately identify the route taken to acquiring dominance in 223 cases. The route to dominance for the 35 remaining bouts could not be identified either because the individual was already holding dominance when first observed, or because of low observation resolution resulting in events being missed and lack of contextual information allowing inferences to be made with confidence.

Variation in group size and composition

To quantify the social environment dominant males experienced at the beginning of their tenures I investigated differences in both group size, the number of immigrant subordinate males and the numbers of resident unfamiliar females among the routes to dominance. Unfamiliar females being those born prior to the immigration of the dominant male, who are likely to be unrelated to him and therefore a viable breeding partner. The distributions of group size were left skewed and restricted to non-negative values and was therefore analysed using Bayesian models fitted with gamma distributions. Both the number of immigrant subordinate males and the number of unfamiliar females were modelled using a negative binomial distribution to account for the possibility of zero values. The mean group size, calculated as individuals 6-months and older, and the number of distinct unfamiliar females and immigrant subordinate males observed in the first month of tenure were fitted as response variables in the models with the route to dominance included as a 4-level categorical predictor variable. To assess how these group characteristics varied across tenure these models were refitted for dominants after one and two years of tenure. Pairwise comparisons of the different routes to dominance were calculated using the *emmeans* (Lenth 2002) package and drawn from the posterior distribution of the models. The sample size for the group size and immigrant subordinate males' models was 175 at the start of tenure, 74 at one year and 31 at two years. For the model of unfamiliar females, the sample at the start of tenure was 170, 67 at one year and 30 after two years of tenure.

Modelling dominants acquisition age, tenure length and reproductive success

To model the influence of dominance route on the age at which males acquired their position and on their tenure length, I used Bayesian models with a gamma distribution. This distribution accounted for the non-normality of these left-skewed data and the fact it is biologically impossible for age or tenure length to have values lower than zero. For the analysis of acquisition age, the dataset was restricted to include only those dominants of known birth date. Additionally, for individuals that held multiple dominance tenures in their lifetime, only the first bout of dominance was included in the analysis (N = 118). In the model the dominant's age when they first acquired dominance was fitted as the response variable. For the model of a dominant's tenure length, all dominance bouts that had ended prior to the end of the study period were included, including those of males born outside the population (N = 209). Analyses restricting the dataset to only dominant males born within the population were conducted and produced results in concordance with the larger dataset. The length of a dominant male's tenure in months was fitted as the response variable in these models. In both the acquisition age and tenure length models, the dominance route was fitted as a four-level categorical predictor variable with displacer dominants fixed as the reference level. The model was refitted multiple times with the other routes set as the reference and additional contrasts where the confidence intervals did not cross the reference level (zero) were reported.

Variation in the reproductive success of dominant males in relation to their dominance route was modelled using a Bayesian hurdle model with a negative binomial distribution. Other distributions suitable for modelling count data were tested, including Poisson distributions and zero-inflated models, however posterior predictive checks and Leave-One-Out Cross-Validation indicated negative binomial hurdle models best captured these data. The hurdle model consisted of two components, first the zero inflated component that modelled the likelihood of an individual having no offspring, equivalent to a binomial model, and the second component, a zero-truncated negative binomial model, that modelled the number of offspring produced by individuals that experienced non-zero reproductive success. The reproductive success of a dominant male was quantified as the number of pups conceived within their tenure that survived to independence (90 days) and were genetically assigned as offspring. Conception was set at 70 days prior to birth, the estimated mean gestation time of meerkats (Spong *et al.* 2008). The dataset was limited to dominants who had been genetically sampled and had held their position for longer than a month to allow time for conception. Furthermore, to prevent underestimating dominants reproductive success, the sample was limited to tenures where over 90% of the pups born within the group have been genotyped. Consequently, the sample in this model consisted of 145 bouts of dominance, of which 71 produced offspring to independence sired by the dominant male. In addition, a dominants length of tenure has been shown

to strongly effect reproductive success in meerkats and a number of other species (Clutton-Brock *et al.* 2006), therefore I also included tenure length in both components of the model, as a fixed effect in the zero-inflated model and as an offset in the zero-truncated model.

Modelling the effects of age and weight on dominance acquisition

To identify the impact of individuals age and weight on the acquisition of dominance, and whether these varied between routes, Bayesian binomial models were fitted including whether a competitor successfully competed for the dominance position fitted as the response variable. Each of the four distinct routes to dominance were modelled independently. Potential competitors for the dominance position were limited to immigrant males, as it is rare for natal males to successfully compete for dominance when immigrant males are present. When a dominance changeover occurred following an immigration event (migrant dominant), males that migrated into the group with the future dominant or prior to the conclusion of the dominance competition were included in the model as potential competitors. For competition over dominance following the formation of a new group (founder dominants), males who migrated into the group prior to the resolution of the dominance competition were included as competitors, except for a small number of males who briefly joined and left the newly formed group prior to the immigration of the eventual dominant, that were excluded. For competition to inherit a vacant dominant position (inheritor dominant) or to acquire dominance following the displacement of an incumbent dominant (displacer dominant), all males resident in the week prior to acquisition of dominance were included as competitors except for the previous incumbent dominant. In addition, where dominance was acquired through displacement, the age and body mass of the new dominant was compared to that of the previous dominant using paired t-tests.

In all the binomial models of dominance competition a unique identifier for the specific acquisition event was included as a random effect, and only acquisition events where there was more than one possible competitor were included. A competitors age (months) and body mass (grams) were transformed relative to heaviest and eldest competitor present in the competition and fitted as fixed effects, with the oldest and heaviest individuals having their values set to zero. As age and body mass commonly exhibit strong correlations, variance inflation factors (VIF) were calculated, and the correlations of posterior predictive samples were visually inspected.

Results

Of the 906 males born into the population that reach adulthood, 130 (14%) were observed to acquire a position of dominance. However, this is an underestimate as some males will have dispersed outside of the population to acquire dominance. For all the adult males that resided within the population, including those that migrated into the study area, 18% held a position of dominance within their observed lifespan. Assuming the rate of migration into and out of the population are broadly equal, this is a more accurate estimate of the true rate of dominance acquisition.

Frequency of dominance routes

Most males born in the population that held dominance acquired their first observed position immediately following successful dispersal (75/130, 58%), either after migrating into an established group (55/75) or founding a new group (20/75). Of the males that migrated into established groups, only 38% had to challenge and takeover dominance from an incumbent dominant. The other 62% of immigrant dominants migrated into groups with a vacant dominance position, where the previous incumbent had either died or abandoned the group prior to the immigration of the new dominant. These vacancies did not remain open for long with the new male dominant migrating into the group on average 19 days after the end of the previous dominant's tenure (median = 6 days, range: 0 - 151 days).

Out of the 130 individuals observed to hold dominance, 43 (33%) individuals acquired dominance after first dispersing to a subordinate position, with a coalition mate initially acquiring the position of dominance. Individuals subsequently acquired dominance by either challenging and displacing their coalition mate from the dominance position (23/43, 53.5%), or inheriting dominance following the death or migration of the previous dominant (20/43, 46.5%). Finally, for 12 (9%) of the individuals observed to hold dominance their method of acquisition could not be determined.

Does social environment vary with dominance route?

At the beginning of tenure, displacer dominants experienced the largest group sizes compared to all other dominants (Figure 4.1a). In contrast, founder dominants had smaller group sizes than all other dominants (Figure 4.1a, Appendix I Figure 1). Males that acquired dominance through inheritance or immigration, experienced similar group sizes at the start of tenure, being smaller than displacers groups, but larger than founders. As tenures progressed the variance in group size within

routes increased, and while the mean group size of displacers stayed constant, dominants that utilised other routes experienced an increase in group size. Resulting in group size differences between routes becoming absent by the second year of dominance (Figure 4.1a, Appendix I Figure 1).

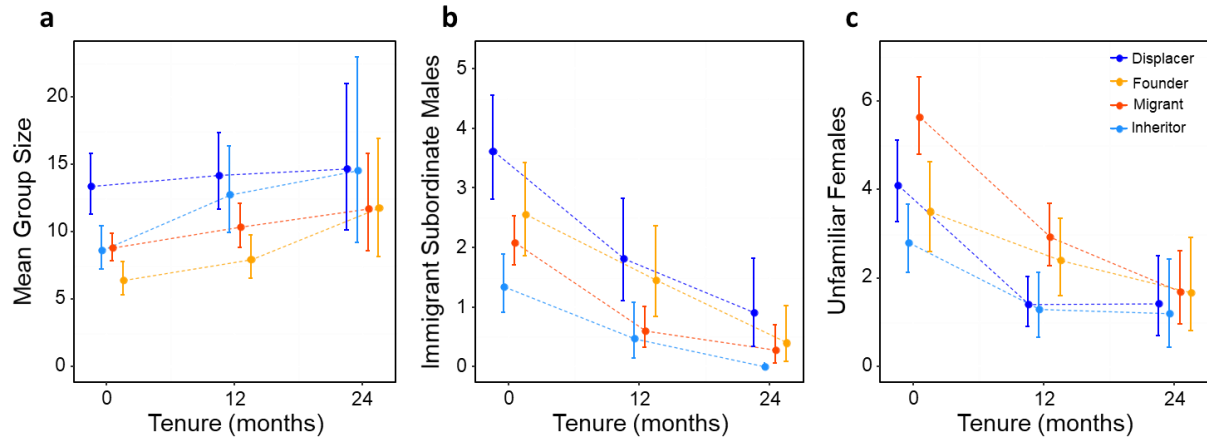


Figure 4.1: Mean estimates (points) and 95% credible intervals (error bars) for group size (a), the number of immigrant subordinate males (b) and the number of unfamiliar females (c) in relation to the route to dominance (see legend) measured at zero months, 12 months, and 24 months of tenure. Mean estimates and credible intervals generated using Bayesian models with gamma (a) and negative binomial distributions (b, c). Pairwise contrast drawn from the posterior distribution are available in Appendix I figures 1, 2, and 3.

The number of immigrant subordinate males resident following acquisition of dominance did not vary between founder or migrant dominants (Figure 4.1b). However, displacer dominants had considerably more immigrant subordinate males than dominants of other routes, in contrast to inheritor dominants who had considerably fewer resident immigrant subordinate males (Figure 4.1b). The number of immigrant subordinate males declined as tenure progressed and after two years, dominants commonly had no subordinate immigrant males resident within their group, in particular no inheritor dominants had a resident immigrant subordinate two years into their tenure (Figure 4.1b, Appendix I Figure 2).

The number of unfamiliar females resident in the group at the start of tenure also varied depending on the route utilised to dominance, with migrant dominants having access to more unfamiliar females at the start of their tenure than dominants that utilised other routes (Figure 4.1c). In contrast, inheritors had the lowest number of unfamiliar females, having substantially lower numbers than both migrant and displacer dominants. The number of unfamiliar females declined as tenure progressed, levelling off at around one female, which was usually the dominant female. Displacer and Inheritor dominants levelled off at one unfamiliar female first and had fewer unfamiliar females than founder and migrant dominants after one year of tenure. Additionally, migrant dominants lost unfamiliar females at a faster rate than founder dominants, and subsequently they had similar numbers of resident unfamiliar females after one year of tenure. After two years of tenure, the

number of unfamiliar females resident in the groups of all dominants declined to around one and there was no difference in relation to dominance route (Figure 4.1c, Appendix I Figure 3).

Does acquisition age and tenure length vary with dominance route?

The age at which individuals acquired their first observed dominance position varied dependant on the route they utilised (Figure 4.2a, Appendix I Figure 4), with displacers tending to acquire dominance later in life, particularly compared to migrants (Estimate [CI 95%]: 0.2 [0.02 – 0.40]) and inheritors (Estimate [CI 95%]: 0.3 [0.07 – 0.54]). However, the age at which males acquired their dominance position had little effect on how long they held their position of dominance for (Log-Normal model: Estimate [CI 95%]: 0.05 [-0.23 – 0.33]). This could explain why the route an individual utilised to acquire dominance had little effect on the length of their tenure (Figure 4.2b), with all pairwise contrasts crossing zero (Appendix I Figure 5). While there is some indication that migrants experienced shorter tenures (Figure 4.2b), this appears to be driven by stronger left skew compared to the other routes to dominance, with a greater proportion of migrant dominants experiencing particularly short tenures. When analyses were restricted to dominants that held position for at least 3 months, in-line with previous analyses on meerkats (Spong *et al.* 2008), these differences in tenure length among the different routes to dominance are no longer tangible (Appendix I Figure 5).

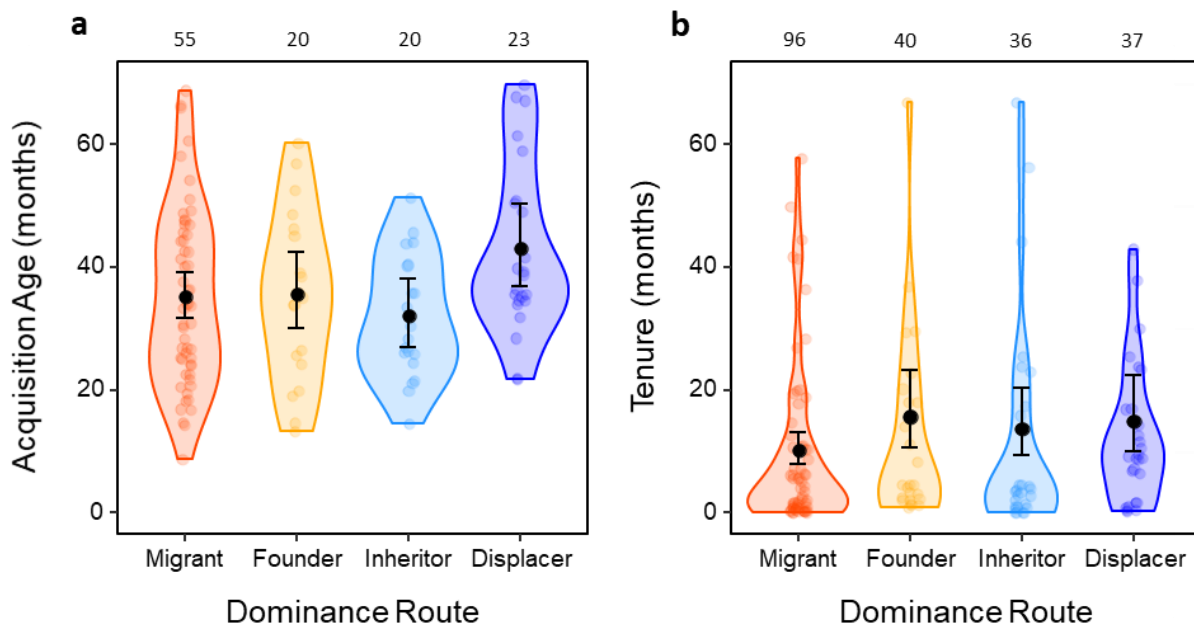


Figure 4.2: Violin plots with accompanying raw data plotted (translucent points) for the (a) age at acquisition and (b) tenure length of dominant males' dependant on how they acquired dominance. Estimated means and 95% credible intervals (black points and error bars) generated from gamma distributed models are also plotted. Sample sizes for each dominance route labelled at the top of the figure.

Does reproductive success vary with dominance route?

Depending on their route to dominance there were differences in the likelihood of a dominant male successfully siring a pup that survived to independence. Displacer dominants were considerably less likely to experience tenures that had zero reproductive success, even with tenure controlled for (Figure 4.3a, Appendix I Figure 6). There were no obvious differences in the likelihood of experiencing zero reproduction during a dominance bout between the other routes to dominance. When dominant males who sired at least one offspring to independence were compared, there was no difference in the rates of reproductive success dominant males acquired in relation to their route to dominance (Figure 4.3b, Appendix I Figure 6). When the two components of the hurdle model are combined, it appears that displacers are likely to experience increased reproductive success early in tenure, although, as tenure progresses the difference will disappear, and the reproductive success of long tenured dominants is unlikely to be influenced strongly by their route to dominance (Figure 4.3c).

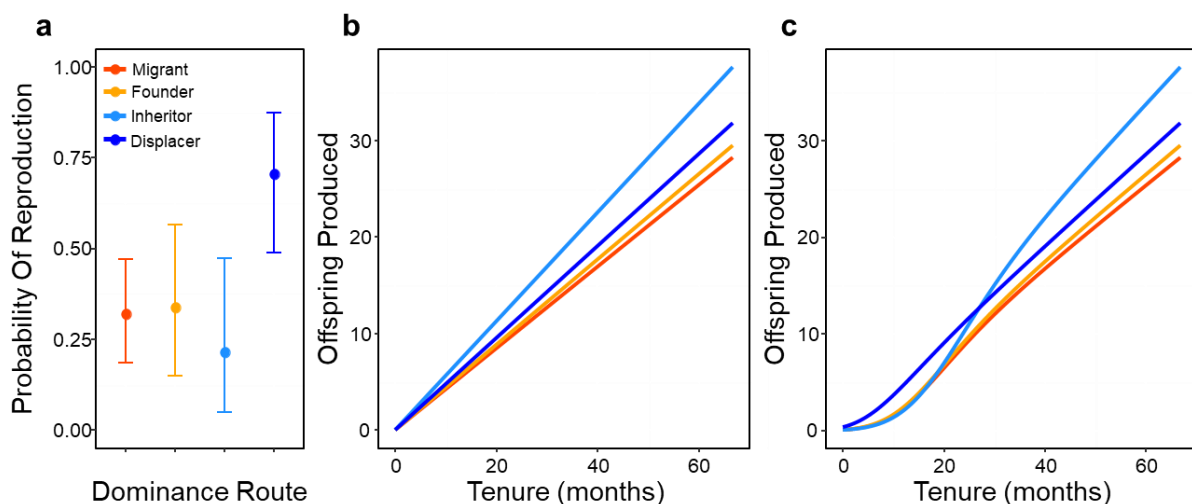


Figure 4.3: Model predictions from a negative binomial hurdle model investigating the effect of dominance route (see legend) on reproductive success. (a) The predicted probability (points) of a dominant conceiving at least one pup that survived to independence during their tenure, with accompanying 95% credible intervals (error bars). Tenure was fixed at 285 days, the median tenure length of dominance bouts in the sample. Model estimates were subtracted from one to give probability of reproduction rather than zero-probability. (b) The predicted number of pups conceived that survived to independence relative to tenure length, for dominants that conceived at least one pup surviving to independence. (c) The estimated combined effect of both components of the hurdle model.

Traits determining the acquisition of dominance via different routes

Both age and weight were important predictors of dominance acquisition, with the eldest and/or heaviest competitors most likely to acquire dominance irrespective of the dominance route, except for inheritor dominants (Figure 4.4, Table 4.1). Weight did not have as clear an effect on inheritor dominance acquisition when compared to age, however, sample sizes were small for inheritance and the direction of the effect suggests heavier individuals are more likely to inherit

dominance (Table 4.1). Variance inflation factors and residual inspection indicated an absence of multicollinearity between relative age and relative weight. However, while models fitted with both terms included produced qualitatively similar results to univariate models of age and weight, the increases in standard error and reductions in effect size suggests that the models were struggling to disentangle these two effects. This is likely to be a result of the high frequency that successful dominance competitors are both the heaviest and oldest competitors. It is possible that both traits play an important role in determining dominance acquisition, however, a larger sample of age matched comparisons are needed to confirm this. Finally, although heavier competitors were more likely to succeed to dominance during a displacement, they were not considerably heavier than the incumbent dominant they displaced (paired t-test: $N = 24$, mean difference = 23 grams, $P = 0.11$).

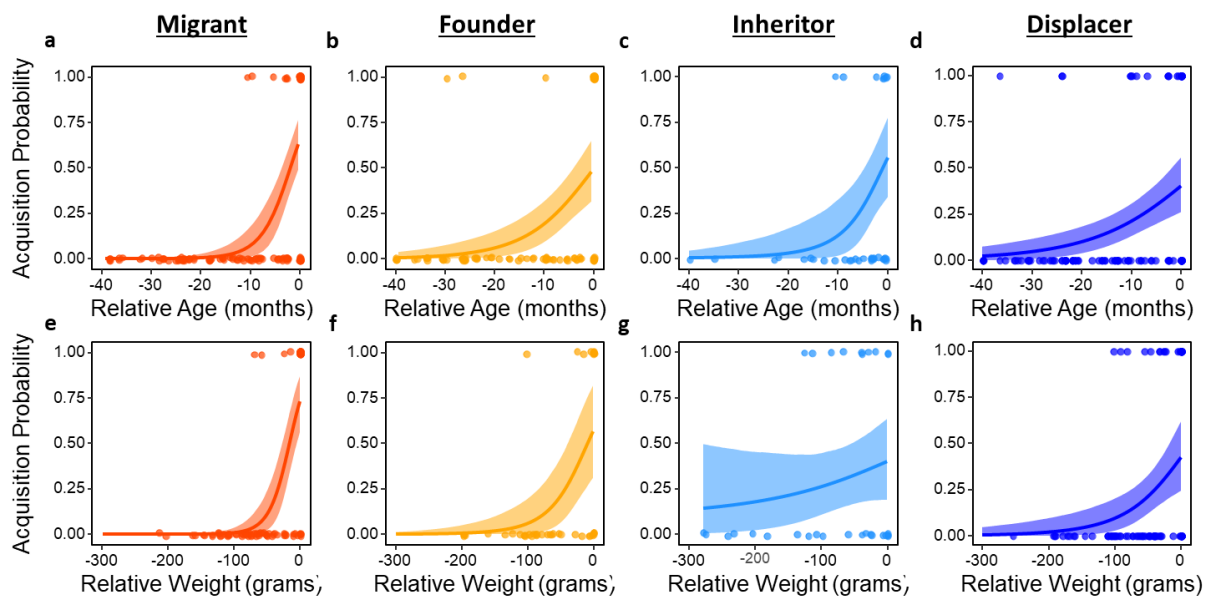


Figure 4.4: The predicted probability of dominance acquisition dependant on relative age (a,b,c,d) and relative weight (e,f,g,h) for the different routes to dominance, including: migrant (a,e), founder (b,f), inheritor (c,g) and displacer (d,h) dominants. The prediction range for these plots were limited to -40 to 0 months for age and -300 g to 0 g for relative weight. This was to improve visual clarity and allow for comparability between plots, some extremely young and lighter individuals who did not acquire dominance are excluded from the plots. Predicted mean effects (solid lines) and credible intervals (shaded ribbons) were extracted from route and covariate specific binomial models.

Table 4.1: Fixed effects for univariate models of dominance acquisition.

Route	Term	Events	N	Estimate	95% CI
<u>Migrant</u>	Age	35	132	11.24	6.54 – 17.23
	Weight	26	88	7.54	4.60 – 11.40
<u>Founder</u>	Age	21	96	4.44	2.31 – 7.25
	Weight	11	50	9.29	3.58 – 16.83
<u>Inheritor</u>	Age	14	43	5.11	1.61 – 9.89
	Weight	11	36	1.18	-0.53 – 3.22
<u>Displacer</u>	Age	25	124	2.92	1.40 – 4.69
	Weight	18	89	3.46	1.27 – 6.10

Events refer to the number of succession events within the dataset and N refers to the total number of competitors.

Discussion

The results in this chapter show that in meerkats the characteristics of a dominant's group varied in relation to their dominance route. Displacer dominants had larger group sizes and a greater number of subordinate immigrant males resident at the beginning of their tenures, whilst founder dominants had the smallest group sizes and migrant dominants had access to the greatest number of reproductively viable females at the start of their tenures. However, these differences degraded over time and after two years of dominance there were no tangible differences in group characteristics between dominance routes. These early tenure differences in social environment did not appear to result in variation in the fitness prospects of dominance routes, with neither tenure length nor reproductive rate showing a difference between routes. Furthermore, the requirements to successfully compete for dominance were also largely consistent across routes, with both age and weight positively influencing acquisition probability, and the average coalition size of migrant and founder dominants being equal.

There were no consistent differences in the tenure length or reproductive success dominant males experienced in relation to their dominance route, and this suggests that no single route is the optimal dominance strategy, while others represent the "best-of-bad-job" (John 1993; Josi *et al.* 2021). It was surprising no differences in dominants' fitness were found while consistent differences in group characteristics were observed, especially considering that both group size and composition have been found to influence dominant's tenure lengths and reproductive rates in meerkats (Hodge *et al.* 2008; Spong *et al.* 2008), and other cooperative breeders (Lardy *et al.* 2015; Keynan & Ridley 2016).

The absence in route specific fitness differences may result from the observed changes in dominant males group characteristics over time. As individual tenure progressed, the differences in group characteristics dissipated, likely because of stochastic demographic processes and environmental noise. Consequently, the differences in reproductive rate and the probability of tenure end associated with group characteristics will also dissipate, and early tenure differences in fitness will begin to be averaged out. Therefore, fitness differences between dominance routes driven by group characteristics may be limited to early in tenure and only of substantial consequence in species where males have short tenures. Furthermore, the highly variable and skewed distribution of tenure lengths suggests the presence of reasonably high levels of individual stochasticity (Snyder & Ellner 2018). In the presence of high stochasticity, the effects of social environment on reproductive success would need to be particularly strong to generate fitness differences between dominance routes (Cam *et al.* 2016), which may not be the case in meerkats.

Additionally, different group characteristics can also have contrasting effects on fitness components, that when summated may result in similar fitness attainment across dominance routes. For example, dominant displacer males experience larger groups and should subsequently benefit from increased rates of female reproduction and reduced rates of paternity loss (Hodge *et al.* 2008; Spong *et al.* 2008). This potentially explains why I find an increased likelihood of displacer dominants successfully breeding early in tenure. However, displacer dominants are also exposed to higher numbers of immigrant males who negatively affect their tenure and reproductive success (Spong *et al.* 2008), which could cancel out the benefits of larger group sizes. Conversely, while dominants utilising other dominance routes inhabited smaller groups, they also had fewer resident competitors and therefore experience lower levels of intrasexual competition. Similar contrasting effects also explain the parity of lifetime reproductive success among natal and dispersed breeding males in spotted hyenas, for while dispersed breeders have access to more breeding females, natal breeding males have priority of access to higher quality females (Davidian *et al.* 2016). Therefore, where certain routes to dominance result in larger group sizes, this can also mean higher levels of costly competition, and consequently may not necessarily be a more advantageous route to dominance.

In the absence of fitness differences between distinct dominance routes, it might be expected that individuals choose routes based on the requirements associated with acquiring dominance via different routes. The route to breeding individuals pursue can be determined by their phenotypic traits (Bowler & Benton 2005), for example, whether female striped mice, *Rhabdomys pumilio*, in arid environments pursue a solitary or communal breeding tactic is determined by their body mass (Hill *et al.* 2015). However, in meerkats this appears unlikely as I find both individual age and weight were likely to be important for acquiring dominance irrespective of the route used, indicating the traits necessary to acquire dominance are correlated across routes. Furthermore, while coalition size is important for successful dispersal (Young 2003; Maag *et al.* 2018), the absence of a difference in the coalition sizes of migrant and founder dominants indicates that access to both routes of dominance are similarly constrained by coalition size. Therefore, while individuals' phenotypic traits and coalition sizes are likely to determine the likelihood of acquiring dominance, they won't necessarily influence the route to dominance used.

That coalition size did not vary between migrant and founder dominants is surprising. I suspect that this is because rather than forcefully invading and overthrowing incumbent dominants, most migrant dominant males follow the path of least resistance and migrate into groups where the dominant position is vacant. Similar patterns have been described in other cooperative breeders, where individuals more commonly disperse into vacancies as opposed to aggressively taking over groups with incumbent breeders (Raihani *et al.* 2010; Yamamoto *et al.* 2014). When competing for

vacancies in established groups the main competition for coalitions of migrating males is not resident males trying to defend their group, but rather other rival coalitions looking for dominance vacancies, as is the case for males founding new groups. Therefore, migrant dominance appears to more commonly be an opportunistic route to dominance as opposed to a specialised strategy limited to males in large dispersing coalitions.

In the absence of differences in fitness prospects or the traits necessary to compete for dominance, male meerkats should flexibly pursue which ever route to dominance will maximise their likelihood of acquiring dominance. Therefore, to understand male decisions on the routes they take to dominance and subsequently the frequency distribution of different dominance routes, future work should look at how the propensity of males to use certain routes varies within their sociodemographic environment. It is likely that the rates of migrant and founder dominants acquiring dominance will be a function of the availability of dominance vacancies in established groups, and the density of evicted females. Evidence of male meerkats prospecting efforts being correlated with evicted female density provides some support for this (Mares *et al.* 2014). These effects will also be important for immigrant subordinates, dictating whether they undergo secondary dispersal or queue within their group for dominance, with the levels of intrasexual competition likely to determine whether they will challenge the incumbent for dominance or wait to inherit.

In conclusion I show that there are no strong differences in either the tenure length or reproductive success that male dominants experience in relation to the route to dominance. This suggests that no single route is the optimal dominance strategy, with the others representing the “best-of-bad-job”. Instead, it is likely that the dominance route male meerkats utilise is largely a function of whatever routes stochastically present themselves, which in turn will be influenced by sociodemographic processes that will determine the availability of routes in their surrounding environment. Therefore, to maximise their probability of acquiring dominance individuals should invest in maintaining their condition and exposing themselves to as many opportunities as possible through prospecting.

Chapter 5: The trade-offs in reproductive competition for dominant male meerkats

Abstract

In group-living species where subordinate males successfully compete for reproduction with dominants, the dominant male's tolerance of subordinates represents a conundrum. One possibility is that by contributing to group defence, subordinate males reduce paternity from extra-group sources offsetting the proportion of paternity they take. In this chapter, I use 23-years of data on cooperatively breeding meerkats to investigate how the numbers of resident immigrant subordinate males influence the levels of paternity dominants lose to extra and intra-group males. Excluding the offspring of familiar females who will not reproduce with dominants to avoid inbreeding, dominant males still lost paternity of the offspring of reproductively viable females to both subordinate and extra-group males. I found that as the numbers of immigrant subordinates increased, so too did the portion of paternity they took. However, increasing numbers of subordinate immigrants also reduced the levels of paternity dominant males lost to extra-group males. Ultimately, dominant males only began to experience considerable reductions in paternity when exposed to five or more resident immigrant males. Immigrant subordinates were also commonly related to the dominant, therefore these costs are reduced by the inclusive fitness acquired from paternity lost to subordinates relative to unrelated extra-group males. Furthermore, subordinate paternity was largely limited to the lower quality and less numerous offspring of subordinate females. When these factors and the costs associated are considered it is likely that the benefits of subordinate immigrants outweigh their costs, which may explain why dominant males tolerate their presence.

Introduction

For dominant males in multi-male group-living species, the presence of subordinate competitors often generates costs. Where subordinate males are unrelated to the resident breeding females, they will commonly compete for mating opportunities, reducing the dominant male's reproductive monopoly. The reproductive costs of subordinate males often increase with their numbers (Alberts *et al.* 2006; Lardy *et al.* 2012), as the dominant males become increasingly energetically constrained and unable to exclude multiple males from breeding opportunities, especially when there are high numbers of females and their oestrus is synchronised (Altmann 1962; Kappeler & Port 2008; Dubuc *et al.* 2011; Lambert *et al.* 2018). Subordinate males can also be a threat to a dominant's social status, and should the resource holding potential of a subordinate substantially exceed the dominant, the subordinate may challenge and displace them from their position (Hasegawa & Kutsukake 2014; Bonanni *et al.* 2017).

Given the potential cost subordinate males can impose on the dominant male, it is worth considering why their presence is tolerated. Though it could be that the costs of excluding subordinates from the group are too high, it is also possible that subordinates confer benefits to the lifetime reproductive success of dominants that outweigh their costs. One way subordinate males can do this is to increase the breeding rate of dominant males (Snyder-Mackler *et al.* 2012), for example, by increasing the number of breeding females they can control within their group (Chowdhury *et al.* 2015) or by increasing the survival of the dominant male's offspring (Feh 1999). Alternatively, where dominant males face competition from extra-group sources, they can benefit from subordinate males contributing to the communal defence of the group (Feh 1999; Mares *et al.* 2012). By defending against extra-group males, subordinates can reduce the risk of takeovers, increasing the dominant male's breeding tenure and subsequently increasing their lifetime reproductive success (Port *et al.* 2010; Lukas & Clutton-Brock 2014). In addition, subordinate investment in group defence could also reduce the rate of extra-group paternity, and where the reduction in extra-group paternity exceeds the portion of paternity taken by resident subordinate males it may benefit dominants to tolerate subordinates. This is especially the case in species where resident male relatedness is high (Dyble & Clutton-Brock 2020), as from the perspective of inclusive fitness, the successful reproduction of related subordinates will be less costly for dominants compared to unrelated extra-group males.

When measuring the impact of subordinate males on dominant reproductive success, it is important to account for additional constraints on dominant males' access to breeding opportunities, as these can confound the perceived effect of subordinates on dominant male reproduction. Female mate choice in the context of inbreeding avoidance is a commonly observed constraint on the access

of males to breeding opportunities, where females refuse to breed with close relatives (Clutton-Brock & McAuliffe 2009; Sanderson *et al.* 2015). For example, natal males born in species with philopatric females are commonly unable to breed due to high relatedness to resident females and must subsequently disperse in search of breeding opportunities (O’Riain *et al.* 2000; Höner *et al.* 2007). However, even for immigrant male dominants, as their tenure progresses, unrelated females will die and be replaced by daughters recruiting into breeding positions. Subsequently, their pool of available breeding females will decline along with their reproductive success (Wikberg *et al.* 2017); which can drive secondary dispersal in long tenured breeding males (Höner *et al.* 2007). Therefore, where inbreeding avoidance is in action and extra-pair males reproduce with females related to the dominant male, this should not necessarily be considered a cost to the dominant male as these females would not have bred with them anyway.

To determine whether tolerating subordinate males benefits the dominant male, the impact of subordinates on both the dominant’s reproductive rate and tenure length must be characterised. Firstly, in this chapter, I utilise data from a long-term study on a wild population of cooperatively breeding meerkats, *Suricata suricatta*, to investigate the cost and benefits of subordinate males for the reproductive success of dominant males. Then in Chapter 6, I investigate the impact of subordinate males on the maintenance of dominant male tenures and finally in Chapter 8, I synthesise these results aiming to understand meerkat dominant male’s tolerance of subordinates. In meerkat groups, reproduction in both sexes is skewed strongly towards a dominant male and female (Clutton-Brock *et al.* 2006), however they do not completely monopolise reproduction and subordinates of both sexes attempt to breed; sometimes producing successful litters that survive beyond emergence. Behavioural dominance can be acquired by both male and female meerkats in their natal groups (Chapter 3, Spence-Jones *et al.* 2021). Yet, while natal dominant females are reproductively active (Chapter 3), it is rare for natal dominant males to reproduce within their groups due to inbreeding avoidance (O’Riain *et al.* 2000). Therefore, to acquire reproductively viable positions of dominance male meerkats must disperse (Spong *et al.* 2008).

Males commonly disperse in coalitions consisting of related males from the same natal group and following successful immigration the males that do not acquire dominance will remain resident as immigrant subordinates. These immigrant subordinate males continue to compete with the dominant male during their tenure, challenging them for reproductive opportunities and sometimes even displacing them from their position of dominance (Chapters 4 & 6). In addition to within group competition, dominant male meerkats are also at risk from extra group males roving for opportunities to reproduce with resident females (Young *et al.* 2007) or the possibility of taking over the group from the incumbent male (Mares *et al.* 2012). Consequently, as the levels of intra-sexual competition

increase, inferred by increases in roving male encounters and the numbers of resident subordinate competitors, the probability of dominant males siring offspring decline (Spong *et al.* 2008). However, the amount of paternity dominants lose is also influenced by maternal status, and dominant males are considerably less likely to lose paternity of the litters of dominant females compared to subordinate females (Griffin *et al.* 2003).

In this chapter I investigate how the presence of subordinate immigrant males influence the reproduction of immigrant dominant males. Evidence suggests that dominant females are more likely to seek extra-pair paternity as their relatedness to the dominant males increases (Leclaire *et al.* 2013). Therefore, I first quantify the impact of inbreeding avoidance on dominant male access to breeding females. Restricting analyses to the offspring of females with whom dominant males can breed, I then investigate the costs and benefits of subordinate immigrant males in relation to dominant male reproduction. I predict that increasing numbers of subordinate males will have a negative effect on dominant male paternity probability. However, as subordinate male meerkats invest in group defence against extra group males (Mares *et al.* 2012), I hypothesise that the subordinate male's reproductive cost will be offset by their presence having a negative effect on the probability of roving males acquiring paternity within the group. Finally, I examine the pairwise relatedness of the dominant and offspring born to extra-dominant fathers, to test my expectation that the offspring of resident subordinate immigrants will be more highly related to the dominant than the offspring of roving males. This would indicate that within-group extra pair paternity is less costly for the dominant male compared to extra-group paternities.

Methods

The work in this chapter comprises long-term data collected between December 1996 and August 2019. Of the 1524 males observed during this period, 245 held a position of dominance during their observed lifetime, of which 198 were genotyped at more than eight loci. While natal males can hold dominance, it is rare for them to successfully breed within their group due to inbreeding avoidance (O’Riain *et al.* 2000). Therefore, I excluded natal dominants resulting in a sample of 160 individuals. Males can hold multiple distinct positions of dominance during their lifespans, and the sample consists of 214 bouts of dominance. During the tenures of the sample of dominants, 2074 pups were born that survived to emergence, of which 1781 were genotyped at more than eight loci, allowing for assessment of paternity. In line with previous studies on meerkats, litter conception was set to 70 days prior to birth, the estimated mean gestation length (Spong *et al.* 2008).

Paternity assignment

Individual tissue samples were obtained from tail tips taken in the field and stored in ethanol. Samples were taken for individuals born in the population soon after they emerged from the burrow post birth, and for individuals who migrated into the population, as soon as they were habituated enough to be caught. DNA was extracted from the tail tips and individuals were genotyped at 18 microsatellite loci. Genetic parentage was then assigned using the program COLONY2 (Jones & Wang 2010) as first described in Nielsen (2012). For the assignment of paternity all males within the population were considered candidate fathers, as extra-group roving males as well as resident males could be the father (Young *et al.* 2007). Where paternity could not be assigned to a population male, but the existence of a genetic father could be inferred, a dummy father was assigned by COLONY2. To confirm that unassigned paternity or paternity assigned to dummy fathers represented paternity by unsampled extra-group roving males and not unsampled resident males, I limited the analyses to only pups conceived where all resident males had been genotyped. Furthermore, to identify the dominance status of mothers and their familiarity to the dominant male I restricted the sample to pups with an identifiable mother. These restrictions reduced the sample from 1781 pups to 1541 pups. Subsequently all genotyped offspring were categorised based on whether they were sired by the dominant male, a resident subordinate male or an extra-group roving male.

For the estimation of pairwise relatedness, I used the assigned parentages to generate a multi-generational pedigree using the package *gggroups* (Nilforooshan & Saavedra-Jiménez 2020). I limited the estimations of relatedness to dominant males born within the population to maximise the accuracy of these estimates, as parentage was likely to have been assigned for these individuals.

Furthermore, they were also likely to have their ancestry characterised for multiple generations, this allows for finer scale estimates of relatedness.

Accounting for the impact of inbreeding avoidance on dominant male paternity

First, I investigated the possible impact of breeder kinship and inbreeding avoidance on constraining dominant males access to breeding females. As there is not strong evidence for fine scale kin discrimination in meerkats, I used the familiarity of the litters mother with the dominant male as a proxy of kinship meerkats might use. I defined familiar mothers as those born after the immigration of the dominant male into the group, as there is a high probability of these females being kin of the dominant male. In contrast, unfamiliar females, defined by being born prior to the male's immigration, are unlikely to be related to the dominant male. To confirm this assumption, I used the multi-generational pedigree to calculate the dominant male's relatedness to both familiar and unfamiliar mothers. I then assessed the distribution of paternity between dominant males, subordinate males, and extra-group roving males in relation to the familiarity of the mother. The effect of mother familiarity on the distribution of paternity was considerable (see results in this Chapter) and I therefore limited analyses to only pups born to unfamiliar mothers (1364 pups from 376 Litters).

Modelling the effects of immigrant subordinate males on paternity distribution

To investigate the effects of subordinate immigrant male numbers on the likelihood of dominant males losing paternity to resident subordinates (subordinate paternity model) and extra-group roving males (rover paternity model), I first modelled both sources of extra-dominant paternity separately. While most meerkat litters born are sired by a single male, some did contain mixed paternity (34/376, 9%). Binomial Bayesian models were initially fitted to account for mixed litters; however, posterior predictive checks indicated the models struggled to capture the raw data even with zero-inflation terms fitted. Therefore, I opted to fit simpler Bayesian models with a Bernoulli distribution which produced results that were qualitatively the same. These Bernoulli models essentially estimated the likelihood of a male siring one or more pups within a litter. The response variable for the model of subordinate male paternity was set to 1 where at least one pup in the litter was fathered by a resident subordinate male and 0 where no pups were fathered by a resident subordinate male. Similarly for the extra-group roving male paternity model, the response variable was set to 1 where at least one pup was fathered by a roving male and 0 where no pups were fathered by roving males.

In both the subordinate paternity and the rover paternity model a fixed effect for the number of immigrant subordinate males was included, along with fixed effects for the duration of the dominant male's tenure at conception, the size of the group and the dominance status of the litter's mother, as well as a random effect for the dominant males individual ID (Table 5.1). Furthermore, a quadratic term was fitted for immigrant subordinate number to test for the presence of non-linear effects, in particular whether the effect of changes in subordinate immigrant numbers diminish at high immigrant subordinate numbers. To investigate whether the numbers of reproductive viable females influenced the likelihood of extra-dominant individuals acquiring paternity, I fitted a term for the number of resident unfamiliar females in the model of subordinate paternity and a term for the number resident adult females in the rover paternity model (Table 5.1). In addition, to see whether natal males might also contribute to the defence of the group, I included a term for the number of resident natal males in the rover paternity model. Finally, a group's level of contact with extra-group individuals has been shown to influence the probability of dominant male paternity loss, therefore I accounted for this term in the model of rover paternity (Table 5.1). To assess potential multicollinearity the relationship between all fixed effects were visualised with pairs plots and variance inflation factors were calculated (VIF), with a $VIF > 3$ considered problematic. Where problematic multicollinearity was expected, I refitted the models with the collinear terms fitted independently and contrasted the model fits using Leave-One-Out Cross-Validation (LOO, Vehtari *et al.* 2017).

Finally, to investigate how the effect of subordinate immigrants on the likelihood of both subordinate and rover paternity combines to influence dominant male paternity, I used multinomial Bayesian models. The response variable was comprised of three components, the number of pups in a litter fathered by the dominant male, resident subordinate immigrants and extra-group males. The number of pups genotyped in the litter was included as the number of trials. The fixed effects included in the best fitting models of subordinate male and rover paternity were included in the multinomial model and the model was rerun with the reference level changed to allow all contrasts to be reported. When the dominant male's ID was included as a random effect in the multinomial model, PSIS-LOO values indicated the presence of a problematic number of influential datapoints. Further investigation revealed that these issues predominantly arise from random effect levels with a single data point, for which PSIS-LOO methods can have issues handling (Vehtari *et al.* 2017). Therefore, I assessed model fit using k-fold cross validation and contrasted the model against a multinomial model with no random effects. K-fold cross validation indicated that including a random effect resulted in a considerably better fitting model ($\Delta\text{elpd} \pm \text{SE} = -273.8 \pm 47.8$), therefore I kept the random effect in the model.

Table 5.1: Descriptions of fixed effects included in models

Term	Code	Mean (Range)	SD	Description
Maternal Status	MS			The dominance status of the mother (dominant vs subordinate)
Encounters	ENC	1.4 (0 - 19)	2.9	Number of encounters with an extra-group male
Tenure	T	16.3 (0 – 62)	14.5	The number of months the dominant male had held their position for at time of conception
Group Size	GS	8.8 (1 - 29)	5.1	The number of individuals aged 6 months and older resident in the group.
Immigrant Males	IM	1.2 (0 - 15)	2.1	Number of resident subordinate males not born within the group
Natal Males	NM	2.7 (0 - 15)	3.0	Number of resident subordinate males born within the group aged 6 months and older
Adult Females	AF	4.0 (0 - 15)	2.5	Number of adult females resident within the group
Unfamiliar Females	UF	3.3 (0 - 17)	3.6	Number of resident females born prior to the immigration of the dominant male.

Results

Reproduction was strongly skewed towards dominant males, who sired 63% (1119/1781) of the genotyped pups that were conceived during their tenures. To allow for within-group and extra-group extra-pair paternity to be distinguished, the sample was restricted to pups conceived when all resident immigrant males were genotyped, of which dominant males sired 66% of pups. Of the pups not sired by dominant males, most were sired by extra-group males (28%, 438/1581), with subordinate males siring a smaller proportion (6%, 102/1581) (Figure 5.1). Of the pups sired by subordinate males, except for one pup sired by a natal male, all pups were sired by immigrant subordinates.

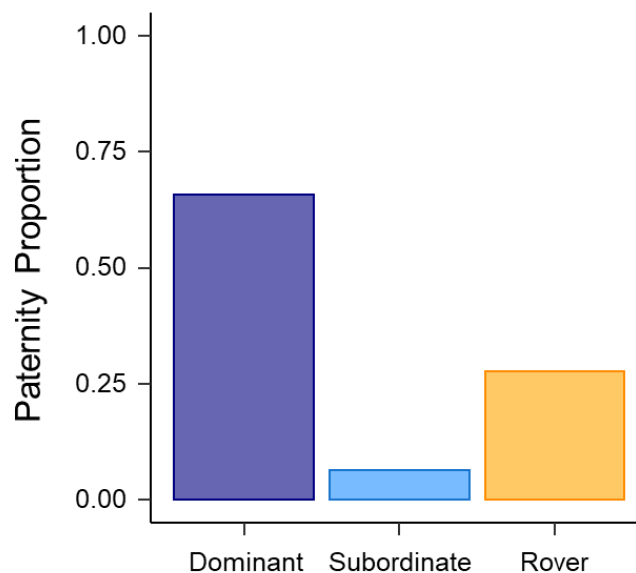


Figure 5.1: Proportion of pups born during the tenure of dominant males sired by dominant males (navy), resident subordinate males (light blue), and extra-group roving males (orange),

Does inbreeding avoidance constrain dominant male access to breeding females?

The familiarity of mothers, whether they were born before or after the incumbent dominant male's immigration, exerted a considerable influence on the distribution of paternity. 96% (170/177) of the pups born to familiar females were sired by extra-group roving males (Figure 5.2a), accounting for 40% of all observed extra-group paternity. Dominant males and subordinate immigrants fathered only 4 and 3 pups of familiar females respectively. In contrast, dominant males sired 74% (1013/1364) of the pups born to unfamiliar females, who were resident when they migrated into the group. However, roving extra-group males only sired 19% (255/1364) of unfamiliar females' offspring and subordinate immigrants only sired 7% (96/1364) (Figure 5.2b). Pair-wise relatedness estimates

confirmed familiarity as a good proxy of kinship for the dominant male, with familiar mothers being highly related to the dominant male (mean $r = 0.37$, median $r = 0.5$), especially when compared to unfamiliar mothers (mean $r = 0.07$, median $r = 0.04$). These results are strong evidence that dominant males are constrained from reproducing with familiar females due to inbreeding avoidance. Therefore, losing paternity of the pups of familiar females should not be considered a consequence of intrasexual competition and I subsequently exclude them from further analyses.

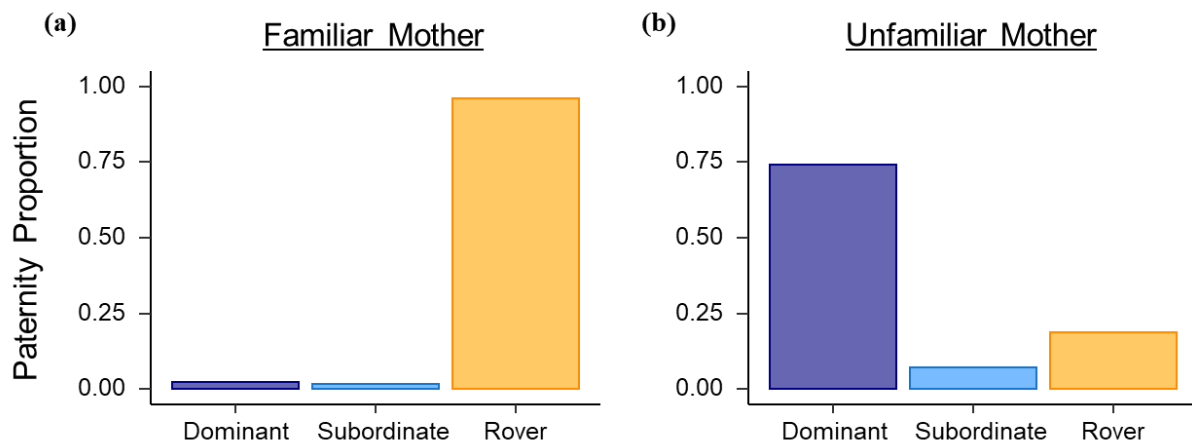


Figure 5.2: Proportion of pups born to females familiar (a) and unfamiliar (b) to the dominant male during their tenure sired by dominant males (navy), resident subordinate males (light blue), and extra-group roving males (orange).

Impact of maternal status on the distribution of paternity

With the sample restricted to the offspring of females unfamiliar to the dominant male, the impact of maternal status was still in concordance with previous studies on the population (Figure 5.3a, b). Dominant females produced a greater number of successful litters than subordinates, producing 85% (321/376) of the litters in the sample. Dominant males acquired paternity of a greater proportion of the offspring of dominant females, siring 78% of their offspring, compared to siring 45% of subordinate female offspring (Figure 5.3a, b). In contrast, roving males sired only 17% (196/1181) of the offspring of dominant females, and immigrant subordinate males sired even less (54/1181, 5%). However, a considerable proportion of the offspring of subordinate females were sired by subordinate immigrant males (42/182, 23%) and roving males (59/182, 32%).

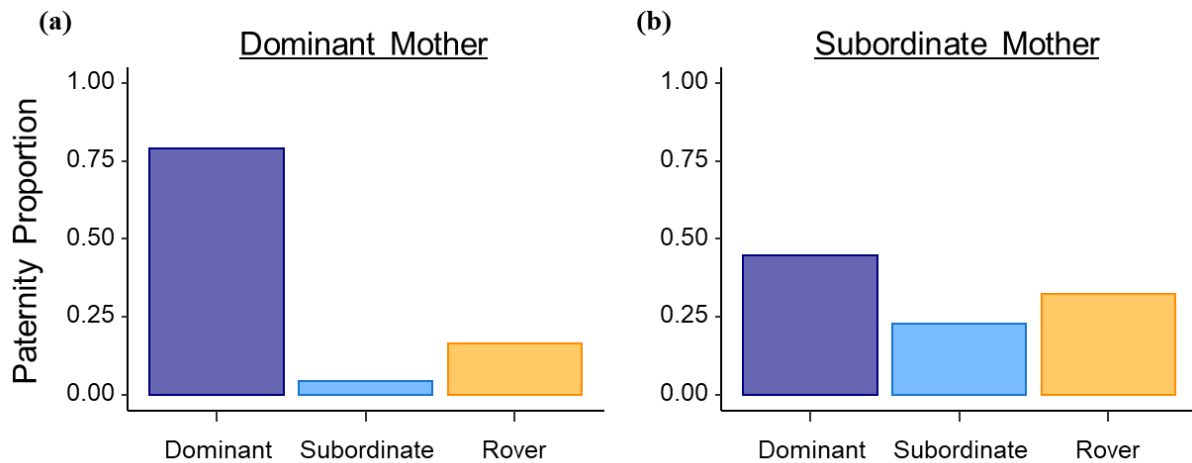


Figure 5.3: Proportion of pups born to dominant females (a) and subordinate females (b) during the tenure of a immigrant dominant male, sired by dominant males (navy), resident subordinate males (light blue), and extra-group roving males (orange).

Do subordinate paternity rates increase with subordinate immigrant numbers?

To measure the costs of subordinate immigrants, the likelihood of them siring at least one offspring within the litters of females unfamiliar to the dominant male was modelled. As the number of subordinate male immigrants increased, the probability of dominant males losing paternity to subordinate males also increased (Figure 5.4a, c). Similarly, the longer a dominant male held their tenure, the less likely they were to experience paternity loss to subordinate males (Figure 5.4a).

Group characteristics also appeared to influence the likelihood of subordinate immigrants acquiring paternity. Group size exerted a negative effect on the likelihood of immigrant subordinates fathering offspring (Figure 5.4a). There was also evidence that the number of unfamiliar females had a positive effect on subordinate paternity probability (Estimate [95%CI] = 1.36 [-1.84 – 4.62]), although the 95% credible intervals crossed zero for this effect and model comparison indicated its inclusion resulted in a worse fitting model ($\Delta\text{elpd} \pm \text{SE} = -1.4 \pm 1.0$), consequently it was dropped as a fixed effect. While variance inflation factors indicated an absence of multicollinearity among the group characteristics, pairs plots of the model indicated some level of correlation among group size, unfamiliar female number, and the number of immigrant subordinate males. However, comparing models with these covariates fitted separately and together revealed that rather than competing for the same variance, modelling these covariates together revealed the presence of masked effects.

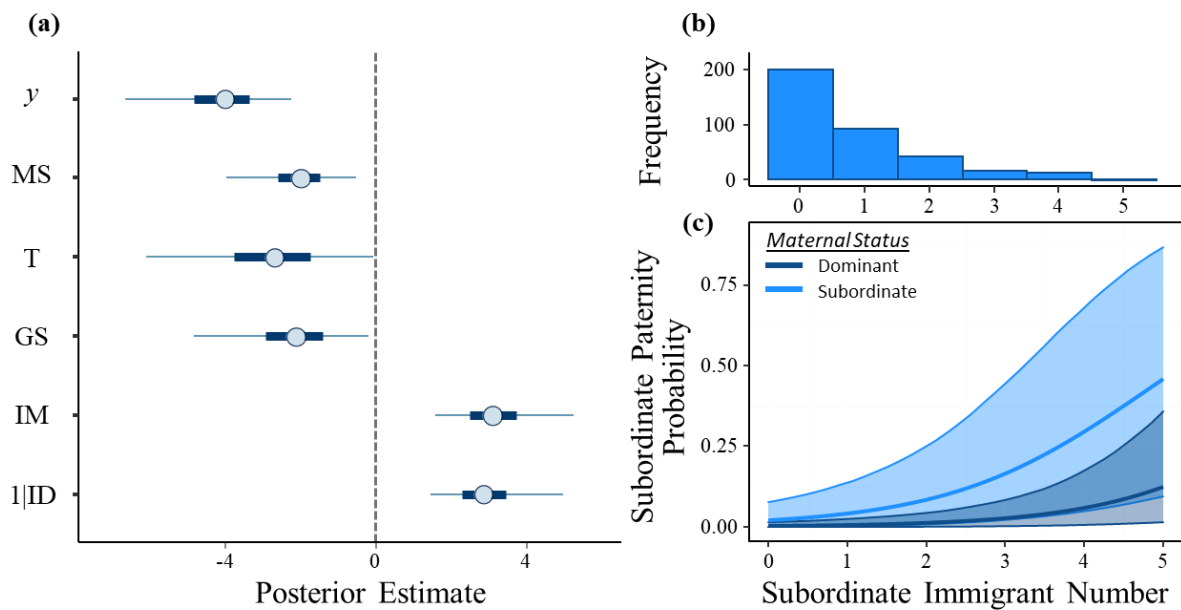


Figure 5.4: (a) Effect size plot for the model of subordinate male litter paternity, including the estimated median effect size (point) as well as the 50% (thick line) and 95% (thin line) credible intervals for the following model parameters: the intercept (y), maternal dominance status (MS), tenure (T), group size (GS), immigrant subordinate number (IM) and dominant identity as a random effect (1|ID). (b) Histogram showing the distribution of the number of subordinate immigrants. (c) The probability of subordinate males siring pups within the litters of dominant (dark blue) and subordinate (light blue) females dependant on the number of subordinate immigrant males resident within the group. Thick lines represent the median estimated probability and the shaded areas bound by thin lines represent the 95% credible interval. For plots (b) and (c), the visualisation was limited to between 0 and 5 subordinate immigrants, which is where 96.8% of the raw data lies, as the data beyond 5 subordinate immigrants is too sparse and the uncertainty too large for meaningful interpretation. All estimates and credible intervals were drawn from the posterior distribution of a Bayesian multilevel model fitted with a Bernoulli distribution.

Do subordinate immigrants reduce the levels of extra-group paternity?

To investigate the possible benefits of subordinate immigrants, the likelihood of extra-group males siring at least one offspring within a litter was modelled. Visualisation of the raw data and a linear regression revealed no apparent effect of immigrant subordinate number on extra-group roving male paternity (Estimate [95%CI] = 0.23 [-0.54 – 0.99]). However, with the number of immigrant subordinates fitted as a quadratic and the identity of the dominant male accounted for as a random effect, the probability of extra-group males siring offspring within a litter decreased as the number of immigrant subordinates increased (Figure 5.5a, c). While the quadratic nature of this effect suggests the direction of the effect could be reversed at higher numbers of subordinate immigrants, the data are too sparse (Figure 5.5b) and the uncertainty too great at this end of the distribution to draw any conclusions with confidence.

Dominant males were also less likely to lose paternity to roving males in the litters of dominant females (Figure 5.5a, c). Furthermore, there was evidence that the longer a dominant male held their tenure, the less likely they were to lose paternity to roving males. However, there was some

uncertainty around the effect of tenure with the 95% credible intervals marginally crossing zero (Figure 5.5a). In contrast, the numbers of encounters a group had with roving males increased the likelihood of the dominant male losing some paternity within the litter to rovers (Figure 5.5a).

Except for immigrant subordinate male number, there were no clear effects of group characteristics on the probability of rover paternity. Due to high levels of multicollinearity, group size had to be fitted separately from the number of adult females and number of natal males. However, neither group size, natal male number or adult female number had convincing effects, with parameter median estimates close to zero and 95% credible intervals extending considerably either side of zero. Furthermore, model comparisons using LOO, indicated that the inclusion of these measures of group size and composition resulted in models with a poorer fit (group size: $\Delta\text{elpd} \pm \text{SE} = -0.9 \pm 0.9$; group composition: $\Delta\text{elpd} \pm \text{SE} = -2.5 \pm 0.6$). Therefore, they were not included in the final model (Figure 5.5a).

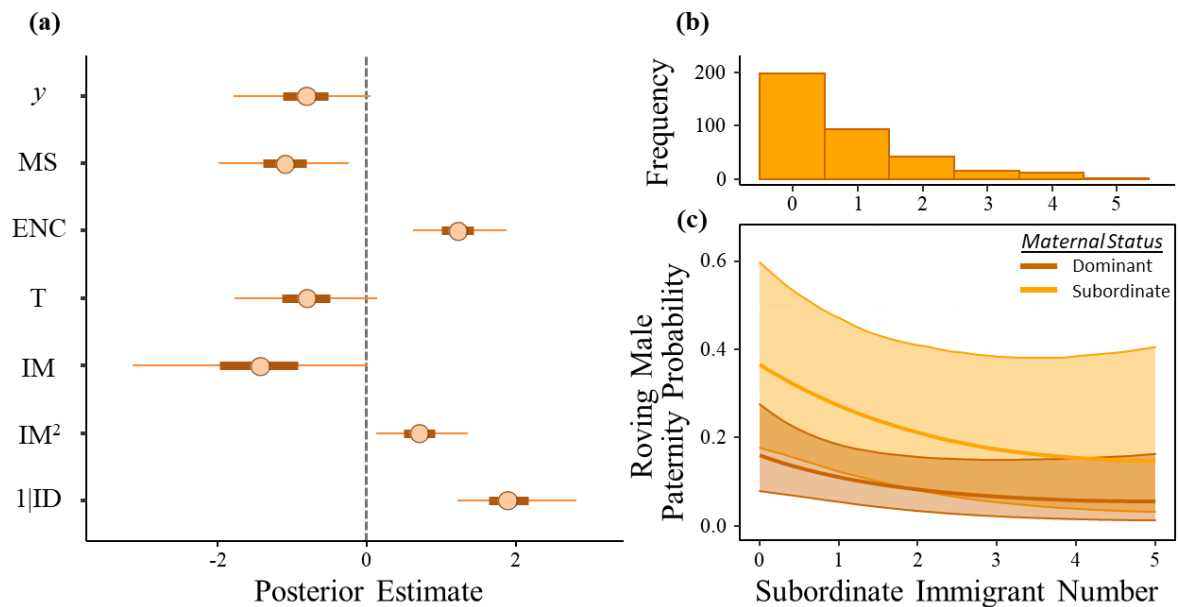


Figure 5.5: (a) Effect size plot for the model of extra-group rover litter paternity, including the estimated median effect size (point) as well as the 50% (thick line) and 95% (thin line) credible intervals for the following model parameters: the intercept (y), maternal dominance status (MS), encounter number (ENC), tenure (T), immigrant subordinate number fitted as a quadratic (IM & IM²) and dominant identity as a random effect (1|ID). (b) Histogram showing the distribution of the number of subordinate immigrants. (c) The probability of extra-group roving males siring pups within the litters of dominant (dark orange) and subordinate (light orange) females dependent on the number of subordinate immigrant males resident within the group. Thick lines represent the median estimated probability and the shaded areas bound by thin lines represent the 95% credible interval. For plots (b) and (c), the visualisation was limited to between 0 and 5 subordinate immigrants, which is where 96.8% of the raw data lies, as the data beyond 5 subordinate immigrants is too sparse and the uncertainty too large for meaningful interpretation. All estimates and credible intervals were drawn from the posterior distribution of a Bayesian multilevel model fitted with a Bernoulli distribution.

The total impact of subordinate immigrants on dominant male paternity

The results of the subordinate and roving male paternity models were broadly replicated by the multinomial model (Table 5.2, Figure 5.6a, b). However, fitting a quadratic term for the number of subordinate immigrants on the probability of subordinate paternity in multinomial model resulted in a better fitting mode ($\Delta\text{elpd} \pm \text{SE} = -25.2 \pm 24.3$), which was not the case for the model just looking at subordinate paternity probability (Figure 5.4). In addition, the effects of tenure on both subordinate and rover paternity weakened, and the credible intervals crossed zero (Table 5.2). In contrast, the effect of group size strengthened, and the credible intervals no longer crossed zero for its effect on both subordinate and rover paternity (Table 5.2).

The estimated median paternity probabilities from the multinomial model suggest that the negative effect of subordinate immigrants on dominant male paternity does not become apparent until more than three subordinate immigrants are present (Figure 5.6). This is due to subordinate immigrants simultaneously reducing the levels of rover paternity, therefore partially offsetting their negative effect on dominant paternity (Figure 5.6a, b). Furthermore, it is important to note the importance of maternal status, with the impacts of subordinate immigrant males most apparent for the paternity of subordinate female offspring, where both roving males and subordinate immigrants steal a substantial amount of paternity (Figure 5.6a, b).

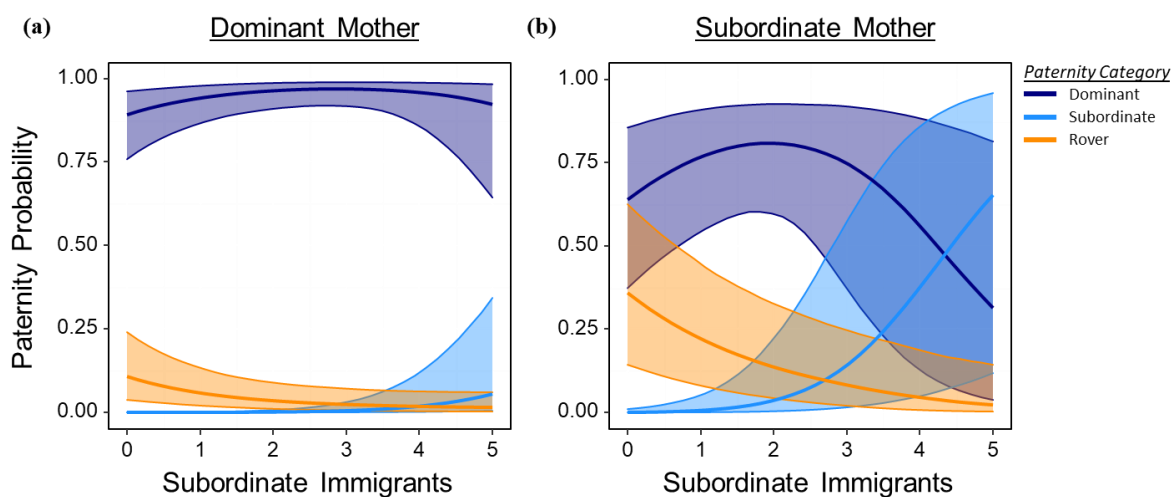


Figure 5.6: The probability of dominant (navy), subordinate (light blue) and roving males (orange) siring the pups of (a) dominant and (b) subordinate females in relation to number of subordinate immigrant males resident in the group. Median estimated probabilities (thick lines) and 95% credible intervals (shaded ribbons bound by thin lines) were drawn from the posterior sample of a multilevel Bayesian model fitted with a multinomial distribution and all continuous fixed effects were set to their sample medians. For plots (c) and (d), the visualisation was restricted to between 0 and 5 subordinate immigrants, which is where 96.8% of the raw data lies, as the data beyond 5 subordinate immigrants is sparse and the uncertainty too large for meaningful interpretation.

Table 5.2: Estimated covariate effects for the Bayesian multinomial model of litter paternity. Dominant male paternity was set to the reference level, so all reported covariate effects are relative to dominant paternity. Parameters mean estimates, standard error and 95% credible intervals presented, with estimates in bold where the credible intervals do not cross zero.

	Subordinate Paternity			Rover Paternity		
	Estimate	SE	95% CI	Estimate	SE	95% CI
y	-5.49	1.31	-8.26 – -3.14	-1.46	0.57	-2.63 – -0.41
MS	-3.65	0.7	-5.09 – -2.33	-0.59	0.35	-2.29 – -0.90
T	-2.37	1.48	-5.29 – 0.48	-0.63	0.41	-1.43 – 0.17
GS	-3.12	1.15	-5.59 – -1.07	-0.73	0.36	-1.45 – -0.03
ENC	-0.99	0.68	-2.41 – 0.23	1.01	0.21	0.60 – 1.44
IM	6.49	1.43	3.95 – 9.46	-2.2	0.79	-3.78 – -0.71
IM ²	-1.14	0.47	-2.14 – -0.14	1.03	0.32	0.43 – 1.68
1 ID	5.14	0.9	3.64 – 7.19	3.80	0.58	2.81 – 5.10

Parameter codes: the intercept (y), maternal dominance status (MS), encounter number (ENC), tenure (T), immigrant subordinate number fitted as a quadratic (IM & IM²) and dominant identity as a random effect (1|ID). R-hat values were equal 1 for all model parameters, and all parameters were adequately sampled by the model (>20%).

As expected, subordinate immigrants that acquired paternity in litters tended to be highly related to the dominant male, being on average more related than half-siblings (mean $r = 0.32$, median $r = 0.31$). This relatedness is significantly higher than the relatedness between dominant males and the extra-group males who sired offspring at the group, with a mean r of 0.08 (median $r = 0$, Wilcoxon-test, $W = 1037$, $p < 0.001$), although this is an underestimate as unsampled males from outside the population are assumed to be completely unrelated ($r = 0$) which is unlikely to be true. However, even if the sample is limited to extra-group fathers within the population, they are still significantly less related to the dominant male (mean $r = 0.18$, median $r = 0.07$, Wilcoxon-test: $W = 849.5$, $p < 0.001$). Consequently, when subordinate immigrants reproduced with unfamiliar females, dominant males gained inclusive fitness being on average 0.22 related to the resultant offspring (median $r = 0.23$). In contrast, when extra-group males bred with unfamiliar females, dominant males were only on average 0.08 related to the offspring (median $r = 0$). Unexpectedly, while almost all pups born to familiar females are the result of extra-group paternity, the offspring were still reasonably highly related to the dominant male (mean $r = 0.22$, median $r = 0.25$). This results from the mothers often being the daughters of the dominant male and suggests that extra-group paternity could provide inclusive fitness benefits for the dominant male in the context of related breeding females. This will, however, be contingent on familiar female reproduction not interfering with the successful reproduction of unfamiliar breeding females.

Discussion

The results in this chapter show that subordinate immigrant males successfully compete with the dominant male for unfamiliar females' reproduction, and that the probability of subordinate immigrant males fathering offspring increases with the numbers of subordinate immigrants. However, the overall proportion of the offspring subordinate males sire is relatively low (7%), and largely restricted to the offspring of subordinate females. Furthermore, the results suggest that as the numbers of subordinate immigrants increased the likelihood of extra-group roving males siring offspring decreased. This decline in extra-group paternity partially offsets the costs of subordinate immigrants, with these results suggesting that subordinate immigrants only begin to have substantially negative impacts on dominant males when they are present in uncommonly high numbers (>3 subordinate immigrants). Additionally, the cost of subordinate immigrants is likely to be further offset by kinship, as subordinate immigrants are more highly related to the dominant male than extra-group males. Therefore, inclusive fitness gains will result in subordinate immigrant paternity being less costly relative to paternity by extra-group males.

My results highlight the importance of considering the dominant males access to breeding females before impacts of intrasexual competition on dominant male paternity. Similarly to natal male meerkats (O'Riain *et al.* 2000), inbreeding avoidance appears exerts a strong influence on the availability of breeding females for immigrant dominant male meerkats. As when females born after the immigration of the dominant male reproduced, dominant males rarely sired the offspring. These familiar females are highly related to the dominant male and are often his daughters. Therefore the inability of dominant males to father their young supports previous suggestions of inbreeding avoidance influencing dominant male paternity (Griffin *et al.* 2003; Leclaire *et al.* 2013). When females avoid breeding with the dominant male due to relatedness, they will likely seek additional mating opportunities such as roving extra-group males. Consequently, inbreeding avoidance can have a considerable effect on the levels of extra-group paternity dominant males experience, being responsible for 40% of the extra-group paternity in meerkats. Accounting for these cases where dominant males are constrained in their access to certain females is essential, as extra-dominant offspring produced by these females do not represent the outcome of intrasexual competition and should not necessarily be considered a cost to the dominant male. In fact, as familiar females are often the kin of the dominant male, their mating with extra-group males generates inclusive fitness for the dominant male, which could benefit them should the reproduction of familiar females not interfere with the reproductive success of other breeders within the group.

Dominant male mate choice could also be at play in meerkats, possibly explaining why rates of extra-dominant paternity are lower among the offspring of dominant females relative to subordinate females (Griffin *et al.* 2003; Spong *et al.* 2008). Where a dominant male's ability to control female reproduction is constrained, such as in large multi-male multi-female groups (Alberts & Altmann 2012; Cant *et al.* 2016) or where multiple females synchronise oestrus (Altmann 1962), it will benefit them to direct their reproductive efforts towards the breeding females that will produce the greatest fitness return. Evidence for this is seen in species where dominant males appear to maximise their reproductive success by focusing mate guarding on more fecund females (Gesquiere *et al.* 2007; Emery Thompson & Wrangham 2008) or older females who are more likely to reproduce successfully (Mainguy *et al.* 2008; Nichols *et al.* 2010). Focusing mating efforts on the dominant females would make sense for male meerkats, with subordinate females who are not only less likely to produce litters that reach emergence due to reproductive suppression by the dominant female (Clutton-Brock *et al.* 2008, 2010), but their successful offspring are also of lower quality, experiencing reduced survival and a lower probability of acquiring dominance later in life (Russell *et al.* 2002). To assess possible mate-choice in male meerkats, future studies should investigate and contrast the behavioural responses of dominant males to oestrus in both subordinate and dominant females.

These results suggest that dominant males' reproductive opportunities are limited to unfamiliar females, who are usually unrelated to them. Therefore, when investigating the costs of competition with intra and extra-group males, only the offspring of unfamiliar females should be considered. However, even for the offspring of unfamiliar females, dominant male meerkats lost a portion of their paternity to immigrant subordinates and extra-group males.

The probability of subordinate male paternity increased with increasing numbers of immigrant subordinates, which supports my hypothesis that the negative effect of subordinate immigrants on dominant male paternity (Spong *et al.* 2008) is a function of direct reproductive competition. This could result from a swamping effect where it is physically impossible for a dominant to simultaneously suppress multiple subordinates or the increasing energetic costs of suppressing greater numbers of subordinates that compromises a dominant's competitive ability. That dominant's agonistic interaction rates increase in groups with higher numbers of immigrant subordinates suggests that subordinates could be energetically costly in meerkats (Kutsukake & Clutton-Brock 2008). In addition, research on alpine marmots, another cooperatively breeding mammal, shows that a dominant's body mass declines in the presence of higher numbers of subordinates which entails considerable fitness consequences (Lardy *et al.* 2012). However, the reproductive cost of subordinates is not always additive; in redfronted lemurs beyond the initial cost of associating with a subordinate male, the proportion of extra-dominant paternity does not increase with subordinate numbers

(Kappeler & Port 2008; Port *et al.* 2010). Where the cost of subordinates is not additive, the benefit subordinates confer need only exceed the initial cost of multi-male association for dominant male tolerance to be selected for, and with no additional cost of tolerating multiple subordinates the size of multi-male associations may be particularly large, being constrained by environmental rather than social conditions.

In the context of subordinate males aiding in the defence of breeding females and territories, most research has focused on how the presence of subordinates can extend the tenure length of dominants by reducing extra-group takeover risk. However, fewer studies have looked at the possible benefits subordinates could have for the dominant male's reproductive rate (Snyder-Mackler *et al.* 2012; Chowdhury *et al.* 2015), and none to my knowledge have looked at whether subordinate male investment in group defence could reduce the levels of extra-group paternity. My results show that in systems where prospecting males compete for reproduction, the presence of subordinate immigrant males can reduce the levels of extra-group paternity. This reduction in extra-group paternity partially offsets the reproductive costs subordinates inflict by competing for within group reproduction. The overall levels of dominant paternity only appear to decline when more than four subordinate immigrants are present and substantial reductions in paternity appear with uncommonly high numbers of subordinate immigrants, although data here is sparse so the true costs are unclear.

The reduction in extra-group paternity associated with the increasing numbers of subordinate male immigrants is likely due to the active role they take in the defence of the group against extra-group males (Mares *et al.* 2012). Interestingly, natal subordinate males who are also observed to aid in group defence do not appear to reduce the rates of extra-group paternity. This indicates that there is perhaps a difference in the motivation of natal subordinates or the quality of defence they provide. Additionally, the presence of subordinate males does not always have a neutral or negative effect on the levels of extra-group paternity (Launhardt *et al.* 2001), with the rates of extra-group paternity increasing with the numbers of subordinate males in both the alpine marmots, *Marmota marmota* (Cohas *et al.* 2006), and superb fairy wrens, *Malurus cyaneus* (Mulder *et al.* 1994). This suggests, that where subordinates do not aid in group defence, the loss of control over breeding females precipitated by increasing numbers of subordinates also benefits extra-group males by increasing the ease with which they can acquire mating opportunities.

Finally, when considering the different sources of competition dominant males face, it is important to consider their relatedness to competitors, with kinship being associated with tolerance and affiliation both within (Wahaj *et al.* 2004) and between groups (Bebbington *et al.* 2017; Humphries *et al.* 2021), in addition to being a principal factor in the evolution of altruism and cooperatively

breeding systems more widely (West *et al.* 2021). In meerkats the relatedness of within group competitors is much greater than extra group males. Subsequently the costs of losing reproduction to subordinate males versus extra-group males will be lower, as subordinate reproduction will still provide inclusive fitness to the dominant as the produced offspring will likely be 2nd or 3rd order kin. The same is also true for the subordinate immigrant males who will lose inclusive fitness should extra-group males outcompete the dominant for paternity, which could be a factor driving subordinate contributions to group defence. This in turn might also explain why in some species where resident males are not highly related, subordinate male numbers have no effect or sometimes even increase the levels of extra-group paternity (Cohas *et al.* 2006), as investing in costly group defence behaviours (Feh 1999; Mares *et al.* 2012); that conserve the dominant's reproductive monopoly will confer no fitness benefits.

In conclusion, while the presence of subordinate males can be costly for dominants, a variety of benefits conferred by subordinate residency have been identified that could compensate their residency cost and select for dominant male tolerance and the evolution of multi-male groups. Here I describe another benefit subordinates can provide in situations where dominant males face extra-group competition for breeding opportunities, with the presence of increasing numbers of subordinates reducing the levels of extra-group paternity at the group. I expect this behaviour to be common in species where there is high relative kinship among male residents and cooperative defence of breeding females will provide inclusive fitness benefits for all. However, this trade-off in reproductive competition is unlikely to completely explain male tolerance and a number of other factors are likely to be at work. Therefore, future work should try to incorporate the cost and benefits of subordinates in multiple domains in addition to trying to account for the potential costs of subordinate suppression.

Chapter 6: The drivers of dominance loss in male and female meerkats

This chapter was written for publication and is currently in preparation for submission:

Duncan, C. Thorley, J, B. & Clutton-Brock, T. Sex differences in the causes of dominance loss in cooperatively breeding meerkats. (In Prep)

Abstract

The acquisition and maintenance of dominance status can have important consequences for the lifetime fitness of individuals in many group-living species. To date, research on social animals has concentrated principally on the characteristics of individuals that help them to acquire dominance, rather than on how individuals maintain their status and why they eventually lose it. Using 26 years of data on the cooperatively breeding meerkat, *Suricata suricatta*, where a single breeding-pair virtually monopolise reproduction in each group, I compare the different ways in which males and females lose their dominance status and examine the factors that prolong or curtail the dominance tenure in each sex. In meerkats, the reproductive tenure of males is shorter than that of females because males can lose dominance in a greater variety of ways. While dominants of both sexes are challenged and displaced by same-sex group members at similar rates, dominant males suffer an additional threat of takeovers from out-of-group competitors. In addition, the death of their breeding partner causes males to leave their group, whereas dominant females that lose their partner maintain their status. Differences in the factors constraining tenure in the two sexes are likely to occur in many other breeding systems and can lead to sex differences in lifetime breeding success and to contrasts in the selection pressures operating on females and males.

Introduction

In many group-living species, the acquisition and maintenance of high social rank is key to acquiring fitness. Individuals that acquire high rank can experience increased rates of reproductive success (Holekamp *et al.* 1996; Nichols *et al.* 2010) and in extreme cases a single dominant individual can be responsible for almost all the group's reproductive output (Rood 1990; Clutton-Brock *et al.* 2006), generating high levels of reproductive skew. Where reproductive skew is high, the length of time an individual holds a position of dominance will be equivalent to their breeding tenure and the longer they hold dominance the greater the lifetime reproductive success they will acquire (Clutton-Brock, 1988; Merilä & Sheldon, 2000; Newton, 1989). Under these circumstances there will be unusually large differences in lifetime breeding success between individuals and strong selection pressures favouring traits associated with the acquisition and maintenance of high social status.

Some of the most extreme examples of variation in lifetime breeding success among vertebrates occur in singular cooperative breeders (Koenig & Dickinson 2016), where a single dominant pair typically monopolise a group's reproductive output, and subordinate group members help to rear the offspring of dominants, often gaining indirect benefits by doing so (Solomon & French 1997; Clutton-Brock *et al.* 2006). In these species subordinates rarely breed either as a result of reproductive suppression by dominant individuals, or a lack of unrelated breeding partners, or both (Clutton-Brock *et al.*, 1998; Gilchrist, 2006; Saltzman, Digby, & Abbott, 2009) and individuals of both sexes compete intensely for dominant positions. Once individuals have acquired dominant status in a group, they are seldom displaced by subordinate members of their group (Rood, 1990; Sharp & Clutton-Brock, 2011), even when they are emaciated and the costs of challenging should be low (Creel 2001). Dominants therefore can hold long tenures and subsequently produce large numbers of offspring across their lifespan.

In social mammals, the traits that allow individuals to acquire dominant status commonly include aspects of their own phenotype, such as their age, mass and weapon size (Berger & Cunningham 1998; Vervaecke *et al.* 2005; Archie *et al.* 2006), as well as aspects of their social environment, such as the number and status of allies that support them in conflicts with other group members (Hasegawa & Kutsukake 2014; Vullioud *et al.* 2019). Similar traits are likely to influence a dominant's ability to maintain their position, yet this has received comparatively little attention. Dominant individuals can lose their position in several ways including mortality, displacement by same sex competitors, or the abandonment of their position. However, current research has focused on the factors that influence tenure length without accounting for the different possible causes of dominance loss, or have only considered dominance loss in a single context, such as intrasexual competition.

Intrasexual competition can have considerable consequences for the maintenance of a dominant's tenure, and depending on the source of competition, the presence of same sex competitors can be either a cost or a benefit. Where dominants are at risk of displacement from within their group, the presence of increasing numbers of resident competitors can have a negative effect on tenure length. This is the case for male dominants in some polygynous species (Setchell *et al.* 2006), and the dominants of both sexes in the cooperatively breeding alpine marmots, *Marmota marmota* (Lardy *et al.* 2011, 2013), and meerkats, *Suricata suricatta* (Hodge *et al.* 2008; Spong *et al.* 2008). However, threats of displacement can come from outside the group in the form of same-sex dispersing individuals or coalitions seeking to invade and takeover the group (Marty *et al.* 2017a). Where extra-group individuals represent a threat, resident competitors can aid in the defence of the group (Feh 1999), reducing the risk of a takeover and thereby increasing the tenure lengths of the incumbent dominants (Port *et al.* 2010; Nagy *et al.* 2012; Snyder-Mackler *et al.* 2012).

In species where dominants can be displaced from both inside and outside their group, the presence of resident competitors is likely to have complex effects on the tenures of dominants. More generally, it will seldom be the case that dominants lose their tenure by only a single route, and the factors affecting the duration of tenure will often be multifaceted. Therefore, to gain a comprehensive understanding of the determinants of dominance tenure length, it is necessary to identify the different causes of dominance loss, and examine the factors driving dominance loss in a cause-specific manner.

In this chapter, I use the long-term dataset collected on wild meerkats to investigate the factors that limit the tenure of dominant breeding females and males in wild meerkats. In meerkats the dominant breeding pair produce most offspring born in the group (Hodge *et al.* 2008; Spong *et al.* 2008) and only a small proportion of the adult population ever acquire dominance. Subsequently, competition over vacancies is intense with older and heavier individuals most likely to win struggles for the breeding position, as shown in Chapters 3 and 4. Subordinate females can acquire dominant positions either within their natal group, or by dispersing to found a new group with males that have dispersed from other groups (Chapter 3, Maag *et al.* 2018). Males, however, must disperse to acquire a dominant position with breeding opportunities either by founding a new group or migrating into an established group (Spong *et al.* 2008). For dominants of both sexes a considerable proportion of variation in the lifetime reproductive success is attributable to variation in their tenure length (Hodge *et al.* 2008; Spong *et al.* 2008). Females have longer tenures than males and show higher reproductive variance (Clutton-Brock *et al.* 2006). Previous work has suggested that intrasexual competition and the loss of breeding partners may play important roles in determining tenure lengths, and that variation in these processes between sexes could drive the observed sex differences in tenure length (Hodge *et al.* 2008; Spong *et al.* 2008). However, without accounting for the specific causes by which

tenures end, or the temporal variation of traits across lifespan, it is difficult to draw conclusions about the mechanisms determining tenure length or the extent to which they vary between sexes.

To investigate the maintenance of dominance status and the factors affecting tenure duration in both sexes, I first aimed to identify the causes of tenure end and compare their prevalence across tenure in both males and females. Secondly, I use a cause-specific approach to identify the individual and social factors influencing the probability of tenure end. Specifically, I examine the effects of within group competitors, testing whether different categories of competitors (natal vs immigrant) have contrasting effects on tenure length. In addition, I also examine the effects of available breeding opportunities on the propensity of dominants to abandon their position of dominance and for subordinates to compete for positions of dominance. Finally, I synthesise the results of these analyses to uncover the processes driving the observed sex differences in dominant's tenure lengths.

Methods

This chapter used data collected between August 1994 and August 2019 during which the tenures of dominants were observed in 92 meerkat groups. Dominance is behaviourally distinct with all same-sex group members receiving assertions of dominance and reciprocating with ritualised submissive behaviour (Kutsukake & Clutton-Brock 2006). Dominant individuals also display scent marking behaviours at much higher frequencies than subordinates, and in females, the incumbent dominant regularly evicts other females in her group and engages in infanticide of non-descendant offspring. The start of a dominance tenure was defined as the point at which the individual was clearly observed asserting dominance and receiving submissions from all possible competitors. As dominant females can breed irrespective of whether they acquired dominance in their natal group or in a group they dispersed to, I included all female tenures in analyses, while for males, I restricted these analyses to only include the tenures of immigrant dominants, because males acquiring dominance in their natal group do not reproduce while group-bound. In total the sample consisted of 205 males and 201 females who have been observed to hold positions of dominance, with some holding more than one position of dominance during their lifetime

Females lose their position of dominance either by dying ('mortality'), or through displacement by a subordinate female from within the group who successfully challenges and displaces them (Sharp & Clutton-Brock, 2011). Males can likewise lose their position through mortality or displacement from within the group. However, males are also vulnerable to displacement by out-of-group males who will invade the group, often in coalitions, and evict the resident dominant and other potential resident male competitors. To avoid confusion going forwards, displacement from outside the group will be referred to as a "takeover", and only displacement from within the group as "displacement". Males also sometimes abandon their position of dominance, leaving the group permanently or for extended periods of time, allowing another male to move into the vacant position. The collapse of groups due to a break down in social cohesion also results in the loss of dominance for both sexes, however, this is a rare occurrence.

To investigate the different ways in which male and female meerkats lose dominance, I utilised survival analyses in a multistate framework. Specifically, I performed competing fates analyses, a type of multistate model that allows for individuals to transition from a stable state to multiple competing absorbing states. Fate-specific survival analyses often induce bias into their models by either truncating or censoring individuals of a known end date who suffer a fate not being analysed. Multistate models correct for these biases by modelling all fates within a single framework. In my models, individuals transition from a state of dominance to a state of lost dominance via one of

multiple routes, with each different route being treated as a separate absorbing state. In addition to the fates of interest, dominance loss via group collapse was included as an absorbing state to avoid censoring bias, but the factors contributing to group collapse were not explicitly investigated due to small sample sizes ($N = 9$ and 17 in females and males respectively), and the causes of group failure are investigated in detail in Chapter 7.

Causes of dominance loss

I first characterised patterns of dominance loss in meerkats over time with parametric survival models (Appendix II Table 1). The sample was restricted to tenures where the start of tenure was observed, to allow for accurate calculation of tenure length ($N = 410$). To test for sex differences, sex was fitted as a binary fixed effect to all distributional parameters. To investigate tenure end in cause specific manner, the sexes were modelled independently, and the sample was further restricted to tenures where the cause of tenure loss could be identified. While in most cases the cause of tenure loss could be accurately identified, in some cases dominants disappeared and the cause of tenure loss could not be inferred (Males = 27, Females = 1). In females it is rare for dominants to leave their groups and they tend to remain resident following displacement; therefore, disappearance can often be inferred as mortality. However, in males, the multiple causes of tenure loss can make it impossible to accurately infer the cause of tenure loss for disappeared dominants. As the disappearance of male dominants is more likely to be associated with abandonment and mortality, my estimates of the frequency of abandonment and death are likely to be slightly underestimated. However, this will not bias the models looking at the cause specific drivers of tenure loss. Following these restrictions, the sample consisted of 194 male tenures and 188 female tenures, representing 157 unique males and 174 unique females that acquired dominance. Of these, the tenures of 14 male and 24 female dominants were censored, as they were either still dominant at the end of the study or where observation of their group ceased before they lost their position.

To characterise the general patterns of dominance loss across time, dominance tenure was first modelled without accounting for the cause of dominance loss. The different sexes were first modelled independently to identify the survival distribution of best fit; the sexes were then modelled together to test for sex differences. Subsequently, to characterise the different causes of tenure loss I conducted a competing fates analysis for each sex. Royston-Palmer spline models were used for the competing fates analysis to allow for variation in the distributions of the different causes of tenure loss to be captured. Model selection was guided by AIC for small sample sizes and plots of the

predicted survival and hazard curves alongside the raw data were used for the confirmation of good model fit.

Factors driving dominance loss

To test how individual, social, and environmental factors influence a dominants' likelihood of losing their position, in a fate-specific manner, I refitted the competing fates models with time-varying semi-parametric Cox proportional hazard models. As competing fate models allow for the fitting of transition specific covariates, the same covariates can vary in the strength and direction of their effect across different transitions. In my case, all covariates were fitted as transition-specific and were only fitted to transitions where I *a priori* hypothesized an effect. Where model selection was required, AIC was used to determine the best fitted model. An assumption of the Cox-proportional hazards model is that covariates are proportional, meaning their effect remains constant across time. I controlled for instances where covariates violated this assumption by fitting a temporal interaction (*time:covariate*, Fox & Weisberg, 2011). For comparability of effect sizes, all continuous variables were scaled by 2 standard deviations as per Gelman (2008), and binary covariates were mean centred.

Dominance tenures were broken up into one-month periods, with covariates of interest taken as the monthly mean. After excising periods with missing data, my sample for males consisted of 2010 one-month periods from 182 dominance bouts with 146 observed tenure ends. For females there were 2910 one-month periods from 172 dominance bouts with 146 observed tenure ends. Covariates included mean body mass, mean group size (Individuals older than 6 months) and the mean number of competitors within the group, the latter defined as the number of same sex-subordinates older than one year of age within the group (the approximate lower bound of reproduction in wild meerkats). In males competitors were further distinguished between natal competitors born within the group and immigrant competitors who had migrated into the group, fitting both as separate terms and comparing the fit of this model against a model with competitor count included as a single variable. Body mass for females was calculated with pregnancy weights included to maximise sample size, though all analyses were repeated on a reduced dataset where pregnancy weights were excluded to check conformity. Where there were discrepancies in the results with and without pregnancy weights, additional analyses were conducted to disentangle the effect of pregnancy on tenure fates (Appendix III Figure 2). I also included covariates to capture changes in the social environment faced by dominants: for both sexes a binary term noted if the dominant individual's breeding partner had died within the previous three months, and for females I also included a term indicating whether foreign males had migrated into the group either during the current or previous month. Finally, for

males I included a term for whether there were still resident females who were born before the dominant male immigrated into the group (“unfamiliar females”), as these females are likely to be unrelated to the dominant male and represent viable breeding females.

Mortality in meerkats can be separated into two constituent types, mortality due to ‘stochastic’ processes such as predation, and mortality in association with disease which in the population is most commonly attributable to a species-specific strain of tuberculosis (TB), *Mycobacterium suricatta*. The pathology of TB takes the form of grossly enlarged lymph nodes that rupture to form open sores, and the continued progression of TB often precedes periods of terminal decline (Patterson *et al.* 2017). Using these symptoms, some of which are considered pathognomonic, I was able to identify disease related mortality among individuals. Additionally, across the course of the study a euthanasia protocol was in place for individuals experiencing late-stage TB infections, identified by burst lymph nodes; for this study I considered these individuals to have died in association with TB. To investigate whether different factors contributed to stochastic versus TB-related mortality I re-ran the competing fate models with mortality split into two absorbing fates (Appendix III Figure 3, Tables 2, 3).

Results

Duration of tenure

The pattern of dominance loss over time for meerkats was best captured by a Weibull distribution with a shape parameter <1 ($k = 0.79$; Figure 6.1), whereby the risk of a dominant losing their status decreased as tenure progressed (Appendix II Table 1). While there was no sex difference in the pattern of dominance loss across time (shape parameter: mean effect [95% CI] = -0.036 [-0.195 - 0.123]), male dominants did have shorter tenures than females (scale parameter: mean effect [95% CI] = -0.395 [-0.666 - -0.123], SE 2), with a mean tenure length of 12.4 months (sd = 14.7, range = 0.03 – 68.3) in contrast to 17.8 months (sd = 22.3, range 0.2 – 127.8) for females (Figure 6.1).

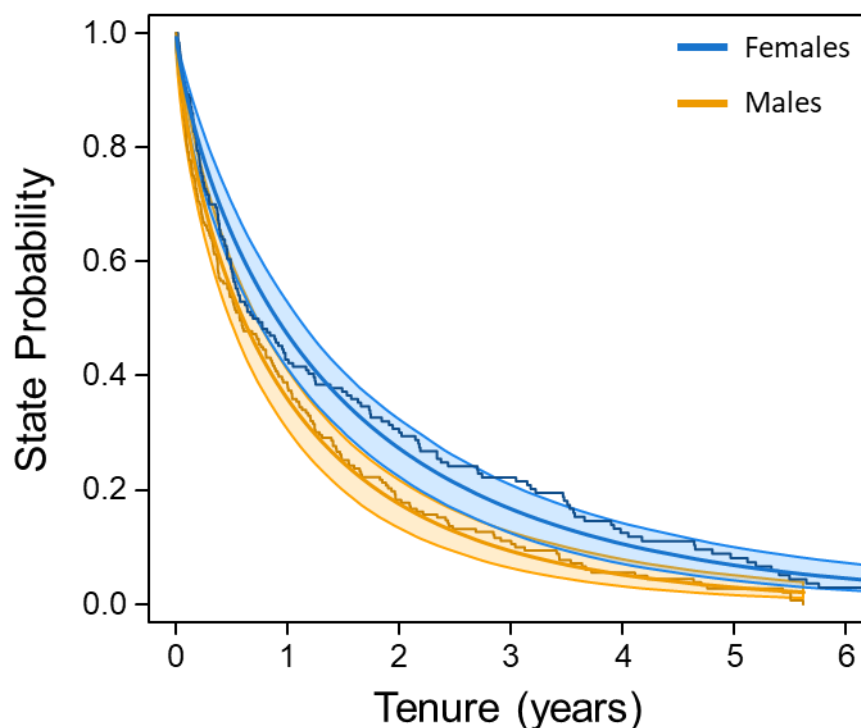


Figure 6.1: The probability of male (orange) and female (blue) dominants holding their position in relation to the length of their dominance tenure. Plotted survival curves (solid line) and accompanying confidence intervals (shaded ribbons) were predicted from parametric survival models fitted with a Weibull distribution and both the scale and shape parameters allowed to vary in relation to sex. Values were predicted for each sex only up until the maximum observed dominance tenure for the sex. The predictions are overlaid on raw Kaplan-Meier plots (darker lines) for each sex. The x-axis was restricted to 6 years to allow easier visual comparison between males and females, females held tenures over ten years, so their predictions extend beyond the limits of this plot.

Some individuals experienced multiple temporally distinct periods of dominance over their lifespan, either in the same group or in different groups. Males tended to hold more distinct positions of dominance than females during their lifespan. Only 8% of female dominant meerkats held multiple positions and none held more than two, while 20% of male dominants held multiple positions, with two individuals even holding a total of 4 different positions of dominance across multiple groups

during their lifespan. However, even with the males holding more positions of dominance within their lifespan, their total tenure as a dominant summed across their span still tended to be shorter than that of females (scale parameter: mean effect [95% CI] = -0.197 [-0.483 - 0.089]).

Causes of tenure loss in females

In females, 70% (116/164) of tenures ended with their death, while 24% (40/164) of tenures ended in displacement by another resident meerkat of the same sex (Figure 6.2a). Of females whose tenures ended due to mortality, 34% died in association with a disease, usually TB, while the remaining 66% died of other stochastic causes such as predation. The risk of mortality remained constant throughout a dominant's tenure (Figure 6.2b), as well as the different categories of mortality (Appendix II Figure 3). In contrast, the risk of displacement varied across tenure, being highest at the beginning of a female's tenure and declining as tenure progressed (Figure 6.2b).

Lighter females were more likely to die and were at a higher risk of displacement (Table 6.1). That lighter individuals were more likely to die was not just a product of terminal declines associated with disease as lighter individuals were also more likely to die from other causes such as predation (Appendix II Table 2). The effect of body mass on mortality and displacement followed a quadratic shape. However, only for mortality did individuals at the upper end of the body mass distribution begin to experience a considerable increase in risk relative to individuals of mean weight (Table 6.1). As the heaviest females are often those who are pregnant, this suggests a possible mortality risk/cost of pregnancy (Appendix II Figure 2). Females whose breeding partner, the dominant male, died were also more likely to die. Analyses of the causes of mortality, revealed this effect was associated with disease related mortality and not other stochastic causes, suggesting the simultaneous infection of both dominants.

Dominant females' resident in larger groups were less likely to lose tenure due to mortality (Table 6.1). In contrast, group size had no effect on displacement risk, although, after the effects of group size were accounted for, the likelihood of a dominant female being displaced tended to increase as the number of subordinate adult female group members increased (Table 6.1, Figure 6.4a). Dominant females were also significantly more likely to be displaced by subordinate females in the month following the immigration of new males into the group (Table 6.1), which suggests that the arrival of unrelated males influenced the motivation of subordinates to compete for dominance.

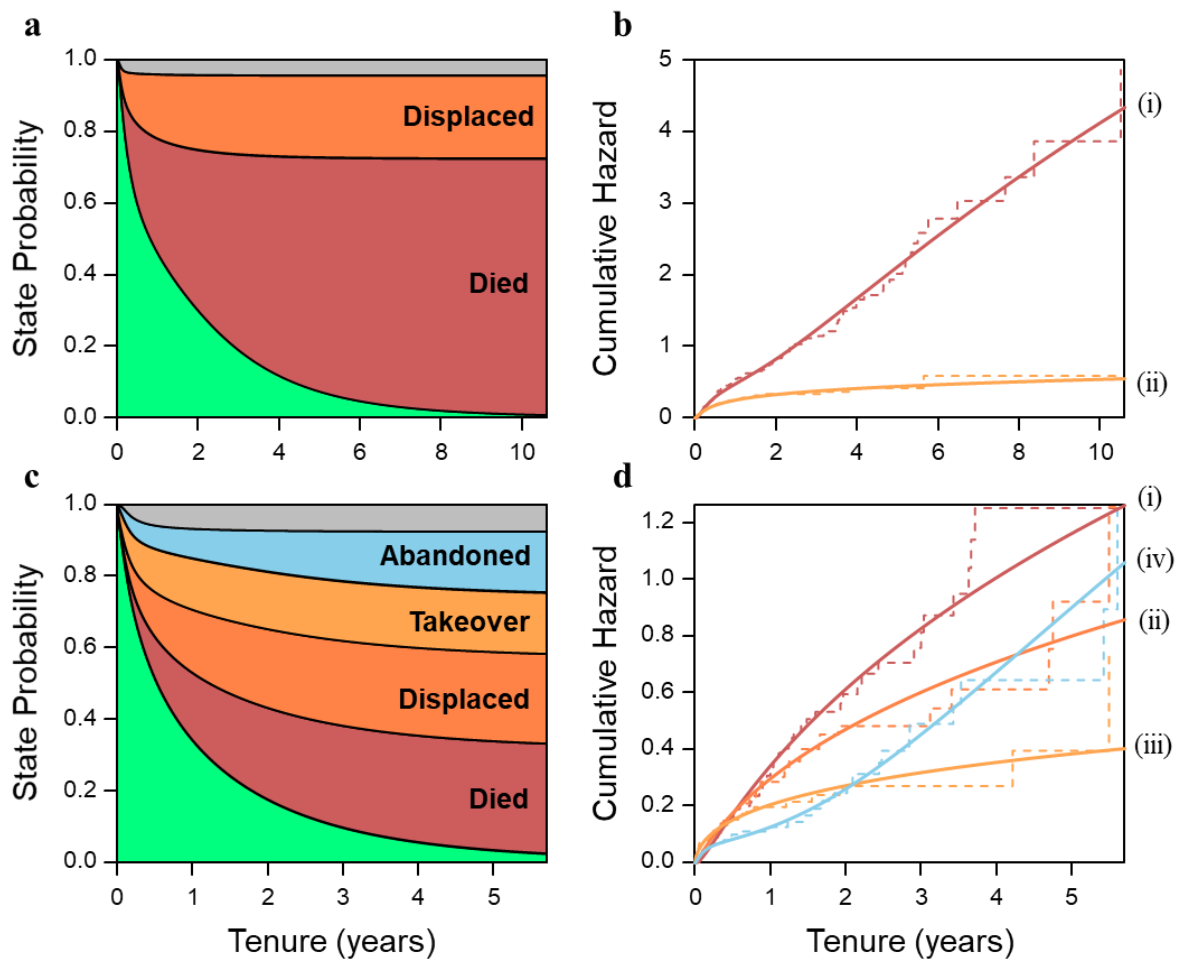


Figure 6.2: Routes to tenure loss in male and female meerkats. Stacked state probability (a,c) and cumulative hazard (b,d) plots for female (a,b) and male (c,d) dominants. Each individual starts in a position of dominance (green) and when their tenure ends will transition to a fate specific state representing death (i, red), displacement (ii, dark orange), takeovers (iii, light orange), abandonment (iv, blue) or group collapse (grey). The width of a band represents the predicted proportion of individuals who have lost their dominance via a specific fate at each time step. The cumulative hazard predictions (solid lines) are plotted over the raw data (dashed lines) and indicate the change in risk of a particular fate over time, with straight lines indicating constant risk and curvature indicating either increasing risk (exponential) or decreasing risk (asymptotes) respectively. All plots were produced with predictions from multistate models fitted with parametric Royston-Palmer spline models with the sexes modelled separately.

Causes of tenure loss in males

Male dominants could lose dominance in more ways than dominant females (Figure 6.2c). In addition to losing dominance by mortality or displacement from within the group, male tenures could also be ended by takeovers, or by the abandonment of position. In males, mortality represented an approximately constant risk across tenure and was responsible for most tenure ends (32%, 57/181). Displacement by resident subordinate males was responsible for 26% (47/181) of tenure ends, with the risk of displacement greatest at the start of tenure and declining across tenure. The risk of takeovers by extra-group males followed a similar pattern. However, as tenure progressed the risk of

a takeover declined to a greater extent than displacement (Figure 6.2d), and takeovers resulted in fewer tenure ends (18%, 32/181). The abandonment of dominance position was also responsible for several male tenure ends, with 17% (31/181) of tenures being abandoned. Except for a brief period of increased hazard at the start of tenure, the likelihood of abandonment was lower early in tenure and increased gradually as tenure progressed (Figure 6.2d)

While mortality represented a constant risk across time for both male and female dominants, mortality accounted for a smaller proportion of tenure ends in males (32%) than females (70%). Cox proportional hazard models indicated that the mortality hazard was lower for male dominants than females (Estimate \pm SE = -0.430 ± 0.164 , $P = 0.008$), with visualisations of cumulative incidence that accounted for competing risks supporting this (Figure 6.3a). The cause-specific nature of mortality also differed between the sexes (Appendix II Figure 2). In contrast to females, disease (TB) was responsible for most dominant male mortalities (63%) and mortalities via other stochastic causes were less prevalent (37%). In contrast, both male and female dominants experienced a similar proportion of tenures lost to displacement (Females = 24%, Males = 26%), and there was also no evidence of sex differences in the risk of internal displacement across time (Estimate \pm SE = 0.315 ± 0.217 , $P = 0.147$, Figure 6.3b).

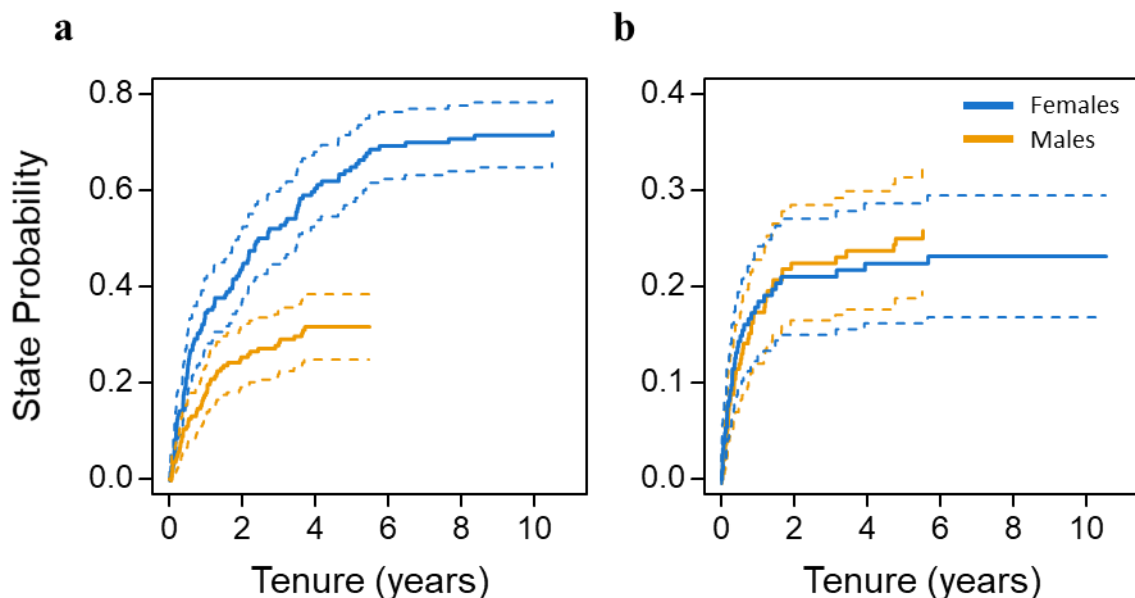


Figure 6.3: State probability plots for dominance loss caused by mortality (a) and internal displacement (b) with the data grouped by sex, males in orange and females in blue. In addition to the cumulative incidence (solid line), 95% confidence intervals were plotted as well (dashed line). These state probabilities were calculated from non-parametric cumulative incidence functions using the Cuminc function in the *mstate* package.

Like dominant females, heavier male dominants compared to lighter dominants were less likely to lose their status, with heavier males less likely to die, be displaced, or experience a takeover (Table 6.1). However, group size did not appear to have a clear effect on the likelihood of male tenures ending due to mortality. Males who experienced the death of their breeding partner were more likely to die, as seen in females. While not limited to disease-related mortality, partner loss had a stronger effect on disease-related mortality (Appendix II Table 2), and similarly for females, as TB generally spreads throughout the group, the effect of partner loss on mortality is likely a result of TB affecting the dominant male and female concurrently.

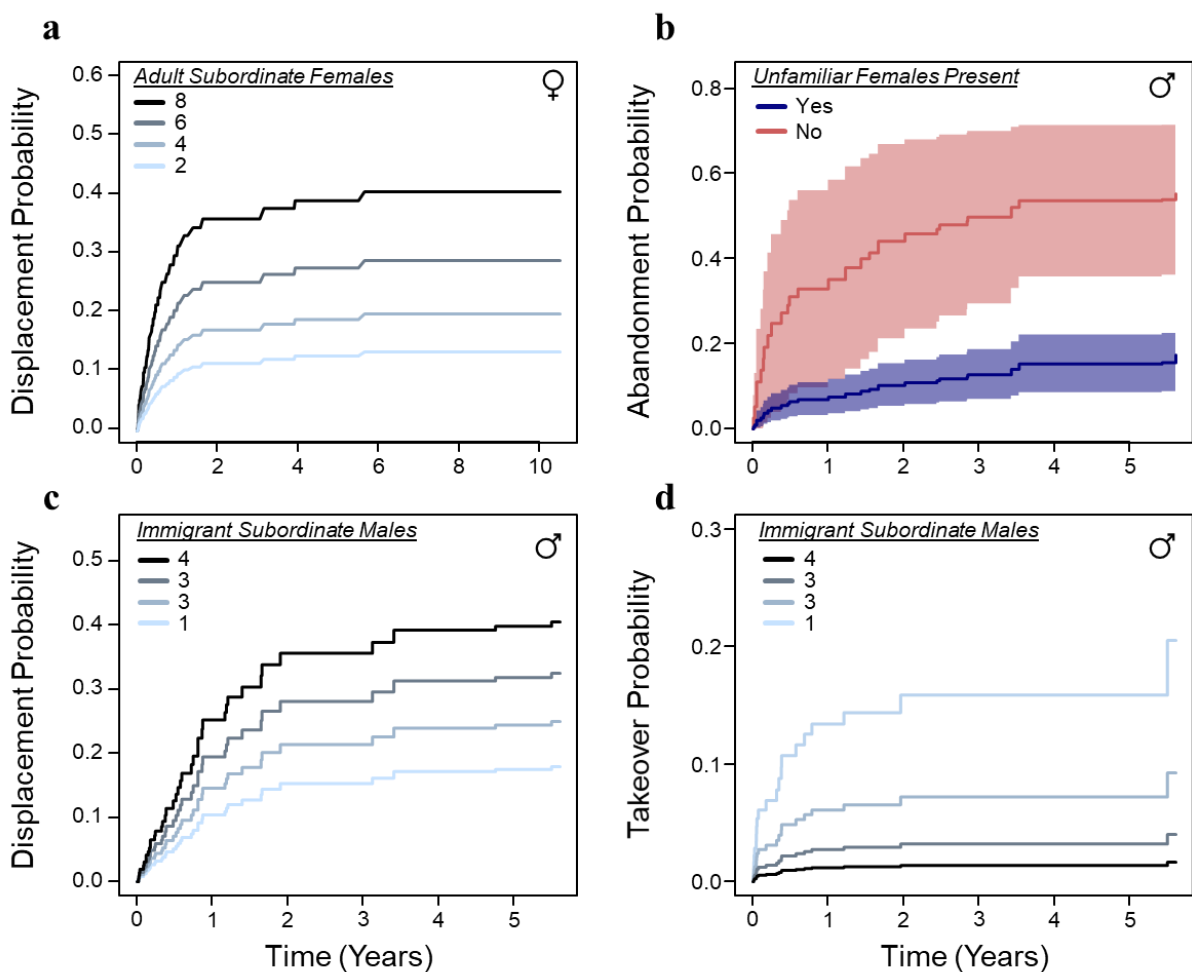


Figure 6.4: Predictions from semi-parametric multistate models showing (a) the effect of adult female subordinate number on dominant female displacement, (b) the effect of the absence of unfamiliar females on dominant male abandonment, (c) the effect of immigrant male subordinate number of dominant male displacement, and (d) the effect of immigrant male subordinate number on the probability of a dominant male experiencing a takeover. Solid lines represent model predictions and shaded areas represent 95% confidence intervals. For all prediction the other fixed effects in the model were held at their mean, except for the number of natal males which was set to zero for prediction of male displacement (c) and takeovers (d). The number of natal males was set to zero to better represent the beginning of a dominant male's tenure where immigrant subordinate male numbers are the highest and adult natal males tend to be absent (Figure 6.5b).

The likelihood that a dominant male was taken over by out-of-group males decreased as the numbers of subordinate immigrant males increased (Table 6.1, Figure 6.4d). There was also evidence that natal males contributed towards reducing takeover risk, although while this effect was strong the margin of error was considerable (Table 6.1). These effects are consistent with evidence that subordinate males play a leading role in chasing away intruding males. That both classes of subordinate male influenced takeover risk was further supported by the fact that a model with total adult male number included fitted better than the model with natal and immigrant subordinate males separated ($\Delta AIC > 2$). However, the apparent benefit to dominant males of having additional immigrant male group members in this context also carries an associated cost in the form of an increased risk of displacement (Figure 6.4c). The number of resident natal male subordinates, by contrast, did not make displacement any more or less likely (Table 6.1). Thus, for dominant males, having immigrant subordinates in their group trades off the benefits of group defence against the risk of displacement. These effects of resident males on displacement and takeovers could explain the decline in risk of these causes of dominance loss across tenure. As the numbers of immigrant males decreased as tenure progressed the risk of displacement was reduced, while the overall number of adult males increased reducing the risk of takeovers (Figure 6.5b). This suggests that the recruitment of natal subordinates was more than enough to compensate for the loss of immigrant males across tenure (Figure 6.5b).

The kinship structure of groups affected the probability that dominant males would leave their group by abandoning their position. Males that had no unfamiliar females present in their group were significantly more likely to abandon their position of dominance (Figure 6.4b; Table 6.1), as were males whose dominant female breeding partner had died (Table 6.1). An interaction between the presence of breeding females and partner death did not improve model fit, likely due to the small sample sizes. However, of the 8 abandonments following partner death, 7 were cases where the dominant female represented the last unfamiliar female to the dominant male. As the dominant male's tenure progresses, the number of unfamiliar females declined (Figure 6.5a), consequently, the likelihood of there being no unrelated females to replace the dominant female in the event of her death will increase across tenure, potentially explaining the gradual increase in abandonment risk across tenure (Figure 6.2d).

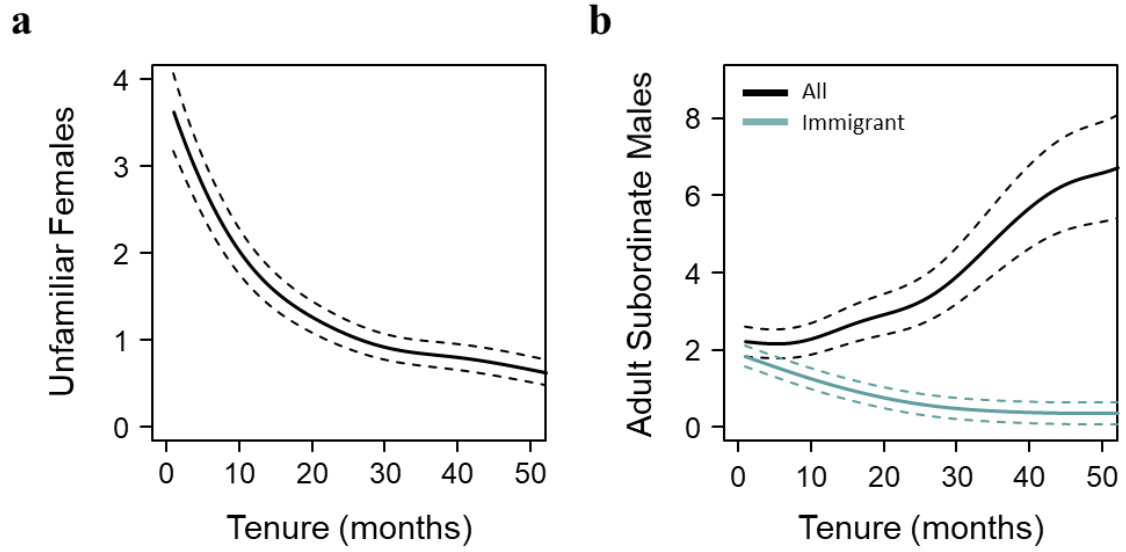


Figure 6.5: Estimated mean number of unfamiliar females (a) and adult subordinate males (b) within the group across the tenures of dominant males. Plot for adult males includes predictions for both the number of all adult subordinate males (black) and just immigrant subordinate males (grey). Predictions restricted to between 0 and 50 months to allow for clearer visualisation of changes in the first years of dominance.

Table 6.1: Model outputs for competing-fates models of tenure loss in male and female dominants.

	Males				Females			
	Estimate ± SE	HR	z-value	P	Estimate ± SE	HR	z-value	p
<u><i>Death (N=49)</i></u>								
Weight	-1.003 ± 0.266	0.36	3.88	<0.001	-0.581 ± 0.165	0.56	3.52	<0.001
Weight ²	NA	NA	NA	NA	0.954 ± 0.160	2.60	5.96	<0.001
Group Size	-0.564 ± 0.373	0.57	1.51	0.13	-0.828 ± 0.296	0.44	2.80	0.005
Partner Death	1.160 ± 0.336	3.19	3.46	<0.001	0.847 ± 0.307	2.33	2.76	0.006
<u><i>Internally Displaced (N=40)</i></u>								
Weight	-1.723 ± 0.453	0.18	3.81	<0.001	-0.458 ± 0.284	0.63	1.61	0.11
Immigrant Males	0.935 ± 0.166	2.55	5.63	<0.001	0.611 ± 0.259	1.84	2.36	0.018
Natal Males	0.563 ± 0.404	1.76	1.39	0.164	-0.763 ± 0.649	0.47	1.18	0.24
time:Body Mass	0.785 ± 0.368	2.19	2.14	0.033	1.164 ± 0.601	3.20	1.93	0.053
<u><i>Takeover (N=21)</i></u>					1.167 ± 0.389	3.21	2.99	0.003
Weight	-1.160 ± 0.428	0.32	2.70	0.007				
Immigrant Males	-2.628 ± 0.957	0.07	2.75	0.006				
Natal Males	-3.134 ± 1.741	0.04	1.80	0.072				
<u><i>Abandonment (N=26)</i></u>								
Partner Death	1.244 ± 0.494	3.46	2.52	0.012				
Unfamiliar Females	-1.720 ± 0.480	0.18	3.64	<0.001				

The effect *time:Body*:Mass represents an interaction between the fixed effect Body Mass and time (tenure) to account for the non-proportionality of this effect.

Discussion

In many social species the length of time an individual holds a position of dominance is an important determinant of fitness, and differences in tenure length can explain variation in lifetime reproductive success both within and between the sexes (Alberts 2012; Pusey 2012; Lukas & Clutton-Brock 2014). In meerkats dominant females experience longer tenures than dominant males, which results in greater variance in reproductive success among females and higher mean lifetime reproductive success (Clutton-Brock *et al.* 2006). In this chapter, I show that the shorter tenures of males compared to females in meerkats arises principally from the greater number of distinct processes driving dominance loss in males. While both male and female dominants can lose their position as a result of death or displacement from within the group, males are also uniquely exposed to threats of takeover from outside the group and situations that cause them to abandon their position. These additional causes of dominance loss in males are driven by sex differences in dispersal and mating strategies, which for males generate additional sources of intrasexual competition and cause the decline in available mating opportunities as their tenure progresses.

Intrasexual competition has clear effects on the maintenance of tenure in male and female dominant meerkats. Indeed, a quarter of tenures ended when dominant individuals were displaced by a same-sex competitor from within their group. These results suggest that internal displacement is a function of the limited control dominants exert over subordinates, as lighter dominants and those with high numbers of in-group competitors were most likely to be displaced. A lack of dominance control has also been invoked to explain loss of dominance in alpine marmots (Lardy *et al.* 2015), and in meerkats it is thought to prevent the complete reproductive monopoly of dominant females (Bell *et al.* 2014; Dubuc *et al.* 2017). However, these results emphasize that the realisation of the competition faced by dominants is contingent on the motivation of subordinates to compete for dominance, which itself is a function of the potential fitness benefits they stand to acquire by claiming the position. For males, the number of natal subordinates has no effect on the probability of internal displacement. This is likely a result of natal individuals being related to the incumbent dominant female and therefore stand to acquire no reproductive benefits by acquiring dominance due to inbreeding avoidance (O’Riain *et al.* 2000). In contrast, the number of immigrant males increases the probability of displacement as these immigrant males are typically unrelated to the dominant female and will be able to breed with her. Similarly, the immigration of males into a group leads to subordinate females being more likely to displace the dominant female, again suggesting a shift in the motivation of subordinates to compete when breeding opportunities present themselves.

The immigration of males into a group can have wide ranging effects on resident females in social mammals, including triggering abortions (Andreassen & Gundersen 2006), reproductive maturation (Cooney & Bennett 2000), and changes in hormonal profiles (Engh *et al.* 2006), as well as killing the young of resident females (Packer & Pusey 1983). In meerkats male immigration events have previously been shown to stimulate short-term increases in growth in female meerkats (Dubuc & Clutton-Brock, 2019) and is associated with broad-scale changes in the hormonal profile of subordinate females (Carlson *et al.*, 2004; Clutton-Brock *et al.*, 2001). These changes could be reflective of the heightened readiness of subordinate females to compete for reproduction and dominance in the presence of an unrelated male. These results add further support to this argument and indicate that the immigration of males into the group can have a destabilising effect on the social structure of meerkat groups and trigger competition for dominance among females.

Considering the threat subordinates pose to the maintenance of dominance tenures it might be expected that dominants would enact strategies to remove competitors from the group. The eviction of subordinates by dominant female meerkats could be such a strategy (Clutton-Brock *et al.* 2010). While eviction appears primarily to be a response to reproductive competition in social mammals (Kappeler & Fichtel 2012), occurring predominantly during the later stages of dominant females' pregnancies (Young *et al.* 2006; Cant *et al.* 2010), it still drives the dispersal of subordinate females (Maag *et al.* 2018). As a result, even though there is no direct evidence showing that dominant females evict in response to dominance challenges, eviction nevertheless serves to continually remove the eldest subordinates, which could explain the decline in displacement risk over tenure as the most competitive subordinates are evicted from the group.

Unlike females, males do not try to evict their competitors from the group despite also facing a risk of displacement. This apparent tolerance could be because subordinate immigrant males reduce a dominant male's risk of experiencing takeovers from invading out-of-group males. Similar trade-offs are seen for dominant males in a number of primate species where the defensive benefits conferred by subordinate male group members can extend a dominant's tenure length and outweigh the costs of increased competition and lost paternity (Henzi *et al.* 2010; Port *et al.* 2010; Snyder-Mackler *et al.* 2012). However, it appears that as subordinate immigrants' numbers increase their presence will become costly as the extent that they decrease takeover risk diminishes, while they continue to increase the likelihood of displacement. In addition, these results also suggest that natal subordinate meerkats also provide a defensive benefit, but do not impose any risk of displacement as they are related to all female group members. The same is not true for immigrant males, who present a viable breeding opportunity for in-group females, and in this context it could be predicted that it would be worthwhile for dominant males to evict subordinate immigrants in cases where enough natal males

are present to defend the group. However, even in the absence of eviction, the composition of groups changes markedly across the tenure of dominant males and these changes are associated with decreases in the risk of takeover or displacement. Notably, the number of immigrant males is highest at the beginning of tenure when the numbers of natal adult males are lowest. As the tenure of male dominants progress, demographic processes such as secondary dispersal and mortality lead to a decline in the number of immigrant males. However, these changes do not appear to compromise the defence of the group; this is because natal males are recruited at a higher rate, resulting in the total number of adult male group members increasing over time.

The dominant males' tolerance of resident subordinate immigrants might also be influenced by the fact that the cost of a takeover event is also likely to be greater than that of being displaced. In meerkats and other species where males takeovers occur (Jack & Fedigan 2004), the takeover events are usually followed by the expulsion of the previous dominant and other resident adult males. In contrast, when a dominant is displaced from their position from within their group, they can often remain resident and compete for extra-pair paternity, possibly reclaiming their position in the future. In addition, whereas out-of-group competitors are generally unrelated to the incumbent dominant, resident immigrant subordinate males are often their siblings (Griffin *et al.* 2003), having previously immigrated into the group together. Therefore, should dominants be displaced it is likely that they will still acquire indirect fitness from the new dominant's reproductive efforts, which is not the case following a takeover. Under these circumstances, the increased risk of internal displacement might be offset by the benefits of having additional group members to repel incursions of out-of-group males.

While the prospecting behaviour and active dispersal of males from established groups generates increased competition for incumbent dominant males, it provides dominant females with a constant supply of breeding opportunities across their tenure. Conversely, the absence of habitual dispersal behaviour in females prevents the steady influx of unfamiliar females to groups. As a result, as subordinate females die or are sequentially evicted from the group by the dominant female, her male breeding partner experiences a decline in the number of viable breeding options; as females born after his immigration are likely to be his close relatives, and meerkats avoid inbreeding where possible (Leclaire *et al.* 2013). Therefore, as a male's tenure progresses the likelihood that he will be left without mating opportunities following the death of his breeding partner increases, which could explain the increase in abandonment risk across tenure. This is supported by the fact that the probability of male abandonment increases when their partner dies and there are no unfamiliar females remaining to breed with.

The absence of viable in-group breeding partners is also suspected to drive abandonment of widowed 'dominant' females in some cooperatively breeding bird species (Hidalgo Aranzamendi *et al.* 2016; Walters & Garcia 2016), where females are the habitually dispersive sex, as well as the secondary dispersal of individuals in communally breeding spotted hyenas *Crocuta crocutta* (Höner *et al.* 2007). Similar processes might also explain observations of group collapse following the death of reproductive or 'alpha' individuals in grey wolves *Canis lupus* (Borg *et al.* 2015), African wild dogs *Lycaon pictus* (Woodroffe *et al.* 2020), and Damaraland mole-rats *Fukomys damarensis* (Jarvis & Bennett 1993), with the implication that partner loss compromises the ongoing reproductive viability of groups. By contrast, where breeders can maintain reproduction after partner loss, such as via the immigration of opposite-sex individuals or out-of-group reproductive opportunities, abandonment is rare (Nelson-Flower *et al.* 2012), and this is probably why female meerkats, unlike males, have not been found to abandon their position of dominance.

These results show that dominants can lose their tenure in multiple ways, and the ability of dominants to maintain long tenures is affected both by the intrinsic traits of the dominant, and by social factors related to the structure of the group in which they reside. In addition, my results highlight that the social environment can influence multiple causes of dominance loss simultaneously and can sometimes produce opposing effects that generate a trade-off for dominants. While these results focus on meerkats, the results are of broader relevance to other cooperative breeders and social taxa where dominance hierarchies and reproductive skew are present. Where the turnover of dominants is driven by multiple processes, identifying the causes of dominance loss and accounting for them in a cause specific analysis is crucial to understanding the differences in tenure length both within and between the sexes. More generally, the spatiotemporal distribution of mating opportunities is likely to have widespread consequences for intrasexual competition and tenure maintenance across social systems, and will also influence the strength of sexual selection and the expression of competitive traits in either sex.

Chapter 7: The drivers of group persistence in meerkats

This chapter was written for Ecology and Evolution

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Abstract

In many social vertebrates, variation in group persistence exerts an important effect on individual fitness and population demography. However, few studies have been able to investigate the failure of groups or the causes of the variation in their longevity. In this chapter data were used from a long-term study of cooperatively breeding meerkats, *Suricata suricatta*, to investigate the different causes of group failure and the factors that drive these processes. Many newly formed groups failed within a year of formation and smaller groups were more likely to fail. Groups that bred successfully and increased their size, could persist for several years, even decades. Long lived groups principally failed in association with the development of clinical tuberculosis, *Mycobacterium suricattae*, a disease that can spread throughout the group and be fatal for group members. Clinical tuberculosis was more likely to occur in groups that had smaller group sizes and that had experienced immigration.

Introduction

In social animals, the dynamics of groups can exert considerable influence on the fitness of their members (Riehl 2011; Woodroffe *et al.* 2020) and the demography of the population (Angulo *et al.* 2018). Groups often vary in productivity and persistence and can last for several decades or longer (Moss & Lee 2011; Alberts & Altmann 2012). Contrasts in the characteristics, persistence, and productivity of groups can influence the direct fitness of group members (Rood 1990; Lardy *et al.* 2015). Moreover, in many social mammals, subordinate females inherit breeding positions in their natal group from their mother. Therefore, successive breeding females are often closely related and matrilineal connections between successive breeding females can persist for several years (Pope 2000, Chapter 3). As a result, the persistence of breeding groups (group 'longevity') will also have important effects on the indirect fitness of individuals through the maintenance of their lineage (Akçay & Cleve 2016).

Currently, relatively few studies of social vertebrates have explored the variation in the persistence of groups, and we know little about the factors that influence their susceptibility to failure. This is especially the case in species with long persisting groups where research has been limited to describing the longevity (Woodroffe *et al.* 2020) or between season survival of groups (Pillay & Rymer 2017). Groups may fail for multiple different reasons. Sources of mortality including extreme climatic conditions, disease or predation can either kill all group members (McGuire *et al.* 2002; Hanya *et al.* 2004; Sillero-Zubiri *et al.* 2015), or reduce groups to a size where they are below the Allee threshold in the presence of strong group level Allee effects (Angulo *et al.* 2018). In addition, group conflict can also cause mortality (Wilson & Wrangham 2003), particularly in territorial species that display higher rates of interspecific killing (Gómez *et al.* 2016). The consequences of losing conflicts such as mortality, displacement from valuable territories and reductions in productivity can all contribute to a group's eventual failure, with smaller groups often being disadvantaged relative to larger groups (Mosser & Packer 2009). Alternatively, the end of a group as a distinct social unit can occur through fission, with a group splitting into smaller distinct groups or coalitions of dispersers (Moss & Lee 2011; Alberts & Altmann 2012). Fission can occur in response to changing ecological conditions (Daniel *et al.* 2009; Thaker *et al.* 2010) or due to social perturbations such as the mortality of individuals key to maintaining cohesion between group members (Borg *et al.* 2015).

Variation in group dynamics has important effects in species where reproductive skew is high, such as the cooperative breeders where either a single female (Rood 1990; Clutton-Brock *et al.* 2006) or a subset of females (Cant *et al.* 2016) are responsible for most reproduction within the group. Where reproductive skew is particularly high, recruitment at the population level will be more strongly

affected by the number of breeding groups than by the number of adult females. Moreover, where the characteristics of groups influence reproduction and survival, they will have considerable impacts on population trends. For example, in cooperatively breeding species, breeding females rely on assistance from other group members to raise their young successfully (Koenig & Dickinson 2016) and as group size increases, the frequency with which they breed and the survival of their offspring increases (Rood 1990; Creel & Creel 2015). This has led to demographic studies of cooperative breeders in recent years incorporating group dynamics and social structure to improve the accuracy with which they capture demographic trends (Zeigler & Walters 2014). Indeed, where reproductive skew is high, the number of groups rather than the number of adult females becomes the most realistic indicator of the breeding units within a population and can accurately model population demography (Chapron *et al.* 2016). Therefore, the rates of group failure and formation are likely to determine the recruitment rates and the subsequent trajectory of the population.

In this chapter, I explore variation in the persistence of groups in cooperatively breeding meerkats, *Suricata suricatta*, using long term data from a population in the Southern Kalahari that have been monitored for 26 years (Clutton-Brock & Manser 2016). Meerkats form stable, highly territorial social groups that can persist for many years, consisting of a dominant breeding pair and several subordinates who are usually the dominant's offspring. Dominant females reproductively suppress resident subordinates by killing their offspring and evicting them before they reach full adult weight at 3-4 years (Clutton-Brock *et al.* 2010), thus monopolising their group's reproduction (Clutton-Brock *et al.* 2006). Unlike subordinate females, subordinate males voluntarily leave their natal groups at 3 – 5 years of age to search for breeding opportunities elsewhere, either migrating into other groups or founding new groups with evicted subordinate females (Spong *et al.* 2008). Dispersing females rarely join established breeding groups and the probability of newly founded groups establishing themselves successfully increases with their coalition size (Maag *et al.* 2018). Once a group has formed, new females are not able to migrate into the group and when a dominant female dies, her position will most commonly be inherited by a resident daughter or sibling (Chapter 3). The tenure of dominant females can last many years and with multiple successive dominant females holding position, a group can persist for over a decade. Meerkat groups are exposed to multiple risks. In addition to mortality in the forms of predation and starvation (Clutton-Brock *et al.* 1999a), a fatal species-specific strain of tuberculosis (TB), *Mycobacterium suricattae*, is endemic within the population (Patterson *et al.* 2017).

Here I aim to characterise the persistence of meerkat groups, identifying the different causes of group failure and quantifying their prevalence over time. I also explore the environmental and sociodemographic factors influencing the rate of group failure. I predict that smaller groups will be

more likely to fail as they experience increased vulnerability to stochastic mortality (Courchamp *et al.* 1999), and have reduced helper numbers to mitigate the effects of adverse conditions (Groenewoud & Clutton-Brock 2021). However, larger group sizes are commonly associated with increased prevalence of pathogens due to a greater number of social contacts and therefore more opportunities for disease to spread (Altizer *et al.* 2003). Consequently, I suspect that larger groups of meerkats may be more likely to develop clinical TB which could increase their likelihood of failing. Finally, I test whether groups are more likely to fail in periods of adverse environmental conditions, where the severity of diseases can increase (Summers 2009) and where groups' vital rates often decrease (Groenewoud & Clutton-Brock 2021).

Methods

These analyses were conducted using the long-term dataset collected between October 1993 and May 2019. Over the course of the study 98 distinct groups were followed, of which 54 were followed until their failure, 14 were still present at the end of the study and 30 were lost therefore their final fates could not be determined. A group was defined as a continuous association of two or more individuals containing members of both sexes. In the rare occasion that all resident males were displaced following the immigration of new males, the group was considered to still exist with the group's identity following the dominant female. A group was considered failed when there were no longer individuals of both sexes present, which could result from either the mortality of all members of one sex within the group or fission between the sexes where the group splits into sex segregated dispersing coalitions (often following the death of the dominant female). To account for the role of TB in group failure, I classified group failure into two distinct categories to distinguish between groups that failed without clinical signs of TB and those that failed in association with an ongoing clinical TB infection. Following the development of clinical signs, TB could spread throughout the group, and individuals that developed clinical TB commonly died of natural causes or were euthanised within 6 months (Patterson *et al.* 2017), resulting in the group declining in size until failure. The exact failure event was observed for most groups in my sample that failed in association with clinical TB. However, due to the mortality of the radio-collared individual and the emaciated state of the rest of the group, two groups in the final stages of disease could not be followed to failure. There were no sightings of these groups more than two weeks after the loss of the radio collared individual and for my analyses, these groups were considered failed on the date the group ceased to be followed.

Assessment of Tuberculosis

Tuberculosis (TB) is believed to be endemic in the population and is caused by a species-specific strain, *Mycobacterium surricattae* (Parsons *et al.* 2013). The first reports of visual symptoms associated with TB were recorded in 1998 and were confirmed to be cases of TB by Alexander *et al.* (2002). Due to the absence of consistent diagnostic sampling for TB across the study, visual indicators of TB were utilised for the identification of clinical infections. The pathology of TB has been extensively investigated, with numerous clinical signs being described, including swollen lymph nodes that present as visible lumps and eventually burst to form lesions (Drewe *et al.* 2009). Early in the study, it was determined that individuals that developed clinical TB died within 6 months of developing signs (Patterson *et al.* 2017). Since the strain was initially identified as bovine TB and was thought to be a by-product of cattle ranching, a practice of euthanising animals whose lymph node swellings burst was

adopted to reduce the impact of the disease (Patterson *et al* 2017). This policy was maintained throughout the study period with 274 individuals euthanised since 1999.

To investigate the role of TB in the failure of groups, I needed to identify the frequency of clinical TB outbreaks in different groups and to separate temporal clusters of clinical TB in group members that were likely to have been the result of the same initial infection event from successive clusters in the same group. Since individuals can remain asymptomatic for many months, it is likely that groups were infected some time before clinical signs of TB were identified in their members (Drewe *et al.* 2011). To identify the start and end of a temporal cluster of clinical TB, I used individual-level health records to identify signs indicative of TB and combined them with data on TB related euthanasia. To distinguish whether consecutive appearances of clinical TB in a group were likely to have been the result of a single episode of infection or of successive separate infections, I used multi-state models to analyse the temporal distribution of successive periods of clinical disease (Figure 7.1a, b).

To merge periods of clinical TB that were likely part of the same underlying group infection, I utilised a multi-state model that transitioned groups that no longer displayed signs of clinical TB to a “recovered” state (Figure 7.1a). I then created datasets where distinct periods of clinical TB occurring within a certain time period of each other were merged and treated as a single continuous period of clinical TB. Datasets were created with cut-offs for merging periods of clinical TB ranging from 0 – 24 months at one-month increments (30 days). Beyond two years the data was too sparse for modelling the recurrence of clinical TB. These datasets were then fitted to parametric survival models and the survival curves for the transition to TB from a “recovered” state and a “stable” state (group with no prior clinical TB) were compared (Figure 7.2).

Fitting models with the raw data and all periods of clinical TB treated as separate I found that the probability of a recovered group returning to a TB state was highly likely (Figure 7.2a). This is to be expected if the disease was present in a latent state within the group. When TB periods <13 months apart were merged and the models were re-run, the groups that recovered from TB had a similar TB probability across time to stable groups (Figure 7.2c). While I cannot be sure that the TB infection disappeared from the group without molecular diagnostic monitoring, this suggested that clinical TB infections more than 13 months apart were likely two separate infections. Models ran with datasets where the merging cut-off was >13months gave similar results showing no increased likelihood of clinical TB reoccurring compared to groups with no prior history. For datasets where the merging cut-off was <13 months, the “recovered” groups were more likely to redevelop clinical TB than groups with no prior history of TB (Figure 7.2b), especially at lower cut-offs (<6 months).

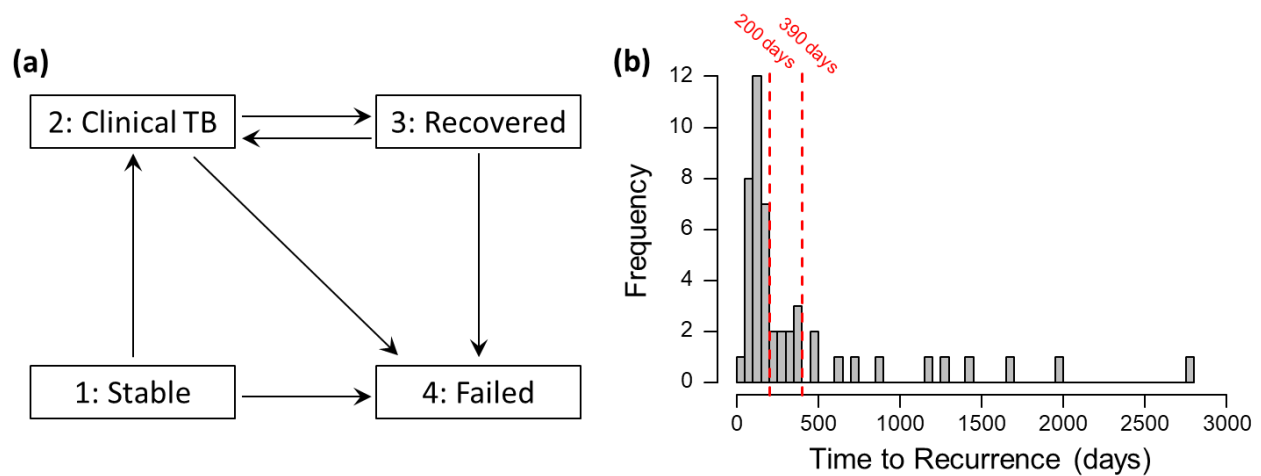


Figure 7.1 Multi-state model design, an expanded illness death model with an additional state for groups that stopped displaying clinical signs of TB (a). The distribution of time to recurrence of clinical TB plotted as a histogram (b).

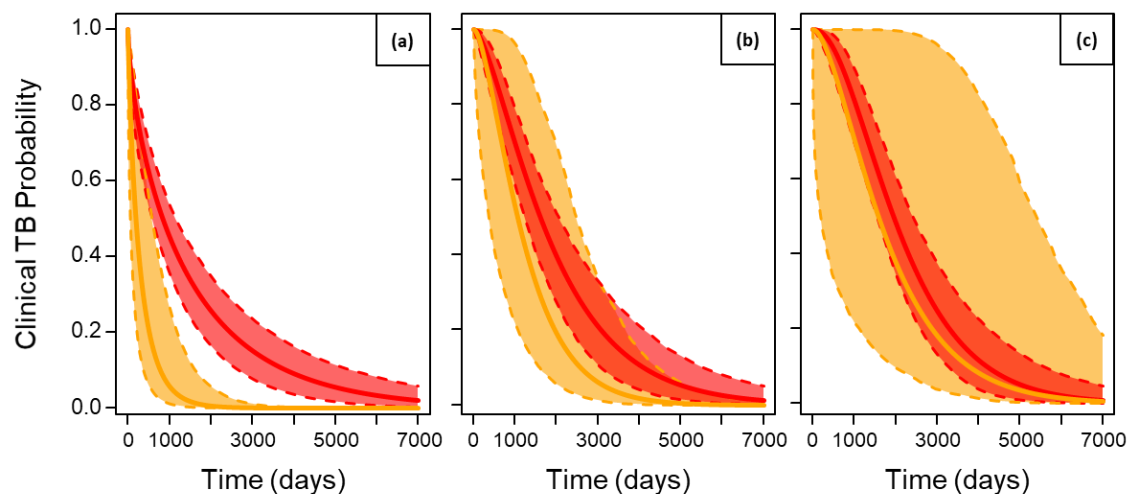


Figure 7.2: Parametric survival curves for the probability a group enters a clinical TB state, depending on whether the group had no prior history of clinical TB (red) or had returned to a recovered state after experiencing a period of clinical TB (orange). All models are accelerated time failure models fitted with a gamma distribution; goodness of fit was checked visually against Kaplan–Meier plots in all cases. The curve predicted by the model (solid line) along with 95% confidence intervals (translucent polygon with dashed borders) were plotted for all models. Plot (a) represents the raw data where groups with clinical TB infections that do not display visual signs of TB for a month are transitioned to a recovered state, for plot (b) groups that have clinical TB reoccur within 200 days are kept in the TB state between the clinical periods and for plot (c) groups that have clinical TB reoccur within 390 days are kept in the TB state between the clinical TB periods. As for plots (b) and (c), recovered groups had to have survived for a certain period without visual signs of TB, by definition, they were only compared against naïve groups that had survived at least that long without an infection

Based on these analyses, I treated periods of clinical TB occurring more than 13 months apart as distinct periods of clinical infection and periods occurring less than 13 months apart, as part of the same clinical infection. Once the data were analysed in this way, there were 25 cases in 22 groups where clinical signs of TB did not reoccur within 13 months. To account for the possibility the disappearance of clinical TB was caused by the euthanasia policy, I recalculated the measures of group longevity with groups that experienced the disappearance of clinical TB removed.

Modelling population level reproduction

To investigate the effect of group number on the reproductive output of the population the study period was divided into 3-month periods. The number of pups born within a period was counted and fitted as the response variable in a GLMM with a negative binomial error distribution and zero inflation parameter, to account for excess zeros and overdispersion. The quarter of the year the period started in was included as a fixed effect and the year was fitted as a random effect to account for both seasonal and longer-term environmental variations. Then the number of groups in the population and the number of adult females (older than a year) were fitted independently as fixed effects.

Group size trajectories

To investigate whether the early-life growth trajectories of groups correlated with their cause of failure I utilised LMMs with a Gaussian error distribution. The monthly mean group size for each group was calculated up until two years of age, the development of clinical TB or their failure, whichever came first. Mean group size was fitted as the response variable. The age of the group in months and whether its failure was associated with a clinical TB infection were included as fixed effects and interacted with each other. Additionally, both a random intercept and slope were included for age and group ID. This model consisted of 471 month periods from 36 groups. To investigate the early-life reproductive success of groups, the number of pups produced that emerged from the burrow in the first two years of a group's persistence was fitted as the response variable in a GLMM with a negative binomial error distribution. This analysis was restricted to groups that survived long enough to conceive and have pups emerge (3 months). In addition, to account for variation in the amount of time groups had to breed, due to differences in longevity, the number of months a group persisted in the two years following formation was included as an offset term in the model. Additionally, to quantify the rearing success of groups I fitted an additional GLMM with a binomial error distribution and the proportion of pups emerged that survived to nutritional independence (90 days) fitted as the

response. To compare groups that failed in association with TB and those that did not, a fixed effect was included in both models with the cause of group failure as a binary factor.

Multistate models of the causes and drivers of group failure in meerkats

To analyse group longevity, I restricted the sample to groups whose formation was observed to allow for accurate calculation of age at failure. This resulted in a sample of 62 groups, of which 15 failed without clinical TB, 25 failed in association with clinical TB and a further 22 that were either still alive or lost before their failure. To characterise the pattern of group failure across time, parametric survival models were fitted. The distributions of best fit were identified by selecting the models with the lowest AIC in combination with visual inspection of the parametric curves against Kaplan-Meier curves (Appendix III Table 1, 2). To investigate variation in patterns of failure relating to the presence or absence of clinical TB parametric survival models were fitted for each fate; I then fitted these cause specific models within a competing risk model, a form of multi-state model (Figure 7.3a). To account for the occurrence of clinical TB being an important precursor step to TB associated failure I also constructed an illness-death multi-state model, whereby all groups eventually transition to the same final absorbing state (failure), but groups can transition to an intermediary state representing clinical TB prior to transitioning to failure (Figure 7.3b). Groups that stopped showing signs of clinical TB transitioned back to a stable state. Groups that were alive at the end of the study or were lost during the study were censored.

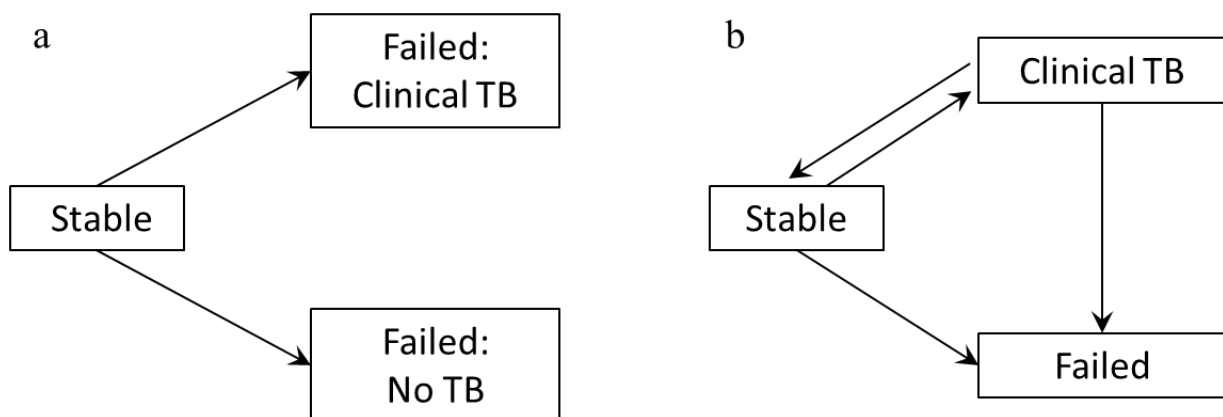


Figure 7.3: Visual representations of multi-state models where boxes represent states a group can occupy and arrows the possible transitions a group can make from one state to another. (a) A competing risk multi-state model where groups can transition from being in a stable state to one of either two absorbing states, failure with clinical TB or failure without TB. (b) A multi-state illness-death model with recovery groups can transition from a stable state to having clinical TB and recover again, with failure being the sole absorbing state.

To investigate how different factors influence a group's likelihood of failure via different causes I utilised the illness-death multi-state framework (Figure 7.3b). Semi-parametric Cox proportional hazard models were used, and group lifespans were split into month long periods to allow for the fitting of time-dependent effects that can vary across a group's lifespan. Transition specific survival models were used to allow different covariates to be fitted for each transition and to allow the baseline hazard to vary for each transition. As it is possible that the disappearance of clinical TB is influenced by the projects euthanasia policy, I did not test any fixed effects for this transition leaving it as a null model. Due to the relatively small sample sizes, I conducted univariate models to identify significant variables (Table 7.2). I then constructed models with the significant variables and the models of best fit were identified using AIC ($\Delta AIC < 2$) and all covariates were tested for violation of the proportional hazard's assumption. Once the best fitting models had been ascertained I refitted the insignificant variables from the univariate analysis to identify effects that became apparent with other sources of variance controlled for. All continuous variables were mean centred and scaled by two standard deviations to allow for comparisons of effect sizes (Gelman 2008). Excluding periods with missing data my sample consisted of 2148 months with groups in the stable state from which 41 transitions to a clinical TB state and 14 to a failed state were observed, and 466 months with groups in a clinical TB state from which 20 transitions to failure and 19 to a stable state were observed.

To test for the influence of climate on all transitions, I used standardised precipitation indices (SPI) calculated monthly with remotely-sensed rainfall estimates from the NOAA Global Precipitation Climatology Project (Adler *et al.* 2018). SPI is a drought index which quantifies how precipitation deviates from the monthly mean based on historical data (McKee *et al.* 1993). The period over which SPI can be calculated can be adjusted to test short- and long-term variations in precipitation. I tested a range of SPI measures from 1 to 12 months to see if climate had a direct effect on these processes and whether short- or long-term precipitation was more important. Further details on the calculation of this measure for the system can be found in Groenewoud & Clutton-Brock (2020). I also fitted season as a binary effect, with the months from October to March, where rainfall and reproduction are the highest, classified as the "high season" and April to September as the "low season".

The effect of sociodemographic factors on the different transitions was also investigated. For the transition of groups in a stable state to failure and clinical TB, I included mean group size and population density as time varying fixed effects. Density was calculated as the monthly population size divided by the total study area derived from 95% Kernel Density estimations using all burrows used by the population within the month (see Cozzi *et al.* 2018b; Paniw *et al.* 2019), using the R package *adehabitat* (Calenge 2006). Previous research suggests that TB is spread between meerkat groups via dispersal events (Drewe 2010). I therefore included variables representing whether new individuals

had immigrated into the group and the number of out-of-group excursions group members had made. The period over which immigration and excursions were calculated was back cast in time to account for the fact a group's infection event likely occurred prior to visual signs of TB becoming apparent. To avoid setting an arbitrary period to measure immigration and excursions I refitted the models with periods ranging from 1 to 16 months prior and selected the time period with the lowest AIC value (Appendix III Table 3). Taking this into account I fitted the final models with a binary term for whether immigration had occurred within the previous 7 months and a term for the number of excursions that occurred within the previous 6 months. For the transition from TB to failure, group size was fixed at the time clinical TB occurred, to avoid modelling the expected terminal decline as group members die from disease. Additionally, to test whether recruitment of new group members via reproduction allowed groups to postpone their failure, I included their reproductive rate (number of pups survived to 90 days/number of days in state) during the period of clinical TB as a time fixed variable.

To increase the power of the analysis investigating the progression of groups with clinical TB to failure, I constructed a separate Cox-proportional hazard model. The time from the development of clinical TB to failure was fitted as the response variable. This allowed sample size to be increased by including groups of unknown formation date for which the development of clinical TB was observed, as progression was relative to the onset of clinical TB not group formation. The model was fitted with the same covariates that were tested on the transition from TB to failure in the multi-state model. The sample for this analysis consisted of 580 months with groups in a clinical TB state from which 25 groups failed.

To test the robustness of the multistate illness-death model (Table 7.1) to the assumption that periods of clinical TB greater than 13 months apart were distinct, the multistate models were rerun on additional datasets. I fitted datasets with TB periods merged across greater time periods (2 - 5 years in yearly increments), which results in more conservative estimates of distinct infections. Furthermore, I ran a model where only the first occurrence of clinical TB was modelled, thereby making no assumptions about subsequent periods of clinical TB. These models largely yielded results in concordance with the model presented in the results (Table 7.1, Appendix III Table 6). The direction and strength of all the effects were conserved with periods of distinct clinical TB occurring within up to 5 years of each other being treated as the same clinical infection, with only negligible changes in statistical significance, which likely result from decreasing sample size (Appendix III Table 4). Only in the most conservative model, where groups were considered to have clinical TB from first occurrence irrespective of how long they returned to a non-clinical state for, was a non-negligible change in effect sizes observed (Appendix III Table 4). However, the directionality of the effects in this conservative

model was still consistent with previous models, and I suspect this treatment is overly conservative as it treats two sets of distinct clinical TB separated by 5.4 years and 7.4 years in which no clinical TB was observed as the same underlying infection. Therefore, I believe the results of the model to be robust and not a function of the way I have treated these data.

Results

Group number and recruitment

As a single female (virtually) monopolises reproduction in each group, the total productivity of the population was more closely related to changes in the number of groups in the population than to the numbers of adult females. With seasonal and between year variation in reproduction accounted for (Appendix III Table 5), the number of pups produced increased as the number of groups in the population increased (Figure 7.4a, GLMM: $\text{Est} \pm \text{SE} = 0.057 \pm 0.018$, $P = 0.001$), while the number of adult females present in the population had no effect (Figure 7.4b, GLMM: $\text{Est} \pm \text{SE} = 0.001 \pm 0.003$, $P = 0.807$).

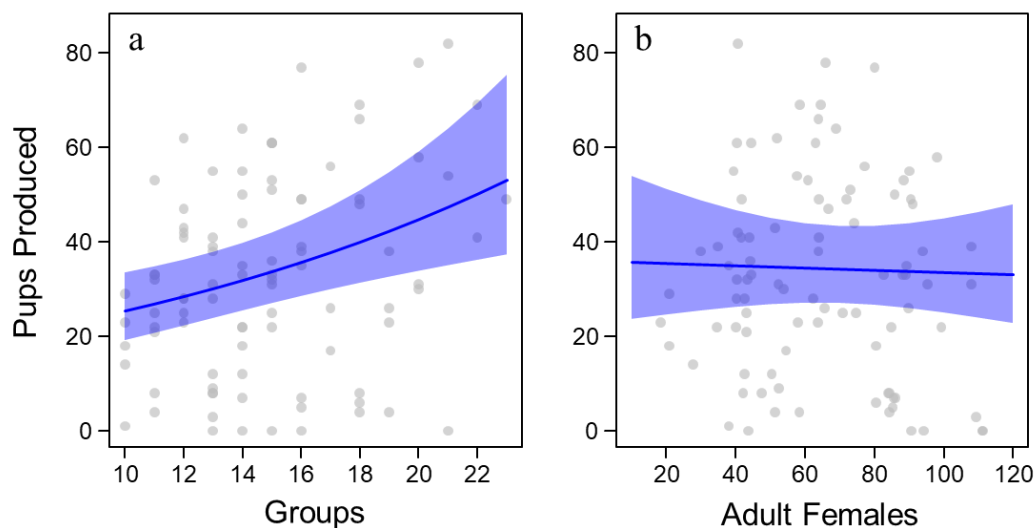


Figure 7.4: The relationship between the number of pups produced that emerged in the population during 3-month periods and the number of (a) groups and (b) adult females in the population. Raw data plotted as grey points and the model predictions plotted as solid blue lines with accompanying confidence intervals shaded in blue. All predictions derived at the population level with the time of year set to the third quarter (July-Sept), from GLMMs with a negative binomial error distribution and a zero-inflation term. The dataset included 92 periods from October 1996 to October 2019.

Group longevity and failure

Three groups have been observed to survive for longer than 20 years, of which two were still active at the end of this study. However, the distribution of group longevity for groups followed from formation to failure was left skewed with a median longevity of 1.17 years ($N = 40$, mean = 3.32 years, range = 0.08 - 18.66 years; Figure 7.5a). Excluding groups that had experienced a recovery from clinical TB, the median longevity was 0.97 years and groups could still persist for over a decade with a maximum observed longevity of 13.5 years ($N = 30$, mean = 2.18 years, range = 0.08 - 13.5). Of the 54 groups whose failure was observed, 37% failed with no signs of clinical TB; of these groups 13 failed because of fission between the sexes and 7 following a mortality event that killed all the members of

one sex. The risk of failure not associated with TB was highest in the first year after a group formed, with the rate of failure declining to negligible levels within five years (Figure 7.5b, c). These groups tended to show no growth following formation, remaining small in size, possibly explaining their subsequent failure and short persistence (Figure 7.5d, Appendix III Table 6). This was in contrast with the pronounced growth in size, groups that failed in association with TB displayed prior to the development of clinical disease (Figure 7.5d, Appendix III Table 6). The absence in growth appears to be due to the reduced rate of reproduction these groups experienced (GLMM: $n=32$, $\text{Est} \pm \text{SE} = -3.814 \pm 1.482$, $P = 0.01$, as they were not significantly smaller at formation (GLMM: $n=31$, $\text{Est} \pm \text{SE} = -0.207 \pm 0.186$, $P = 0.26$) and their offspring did not experience significantly reduced rates of survival to independence (LM: $n=28$, $\text{Est} \pm \text{SE} = -0.752 \pm 0.848$, $P = 0.40$).

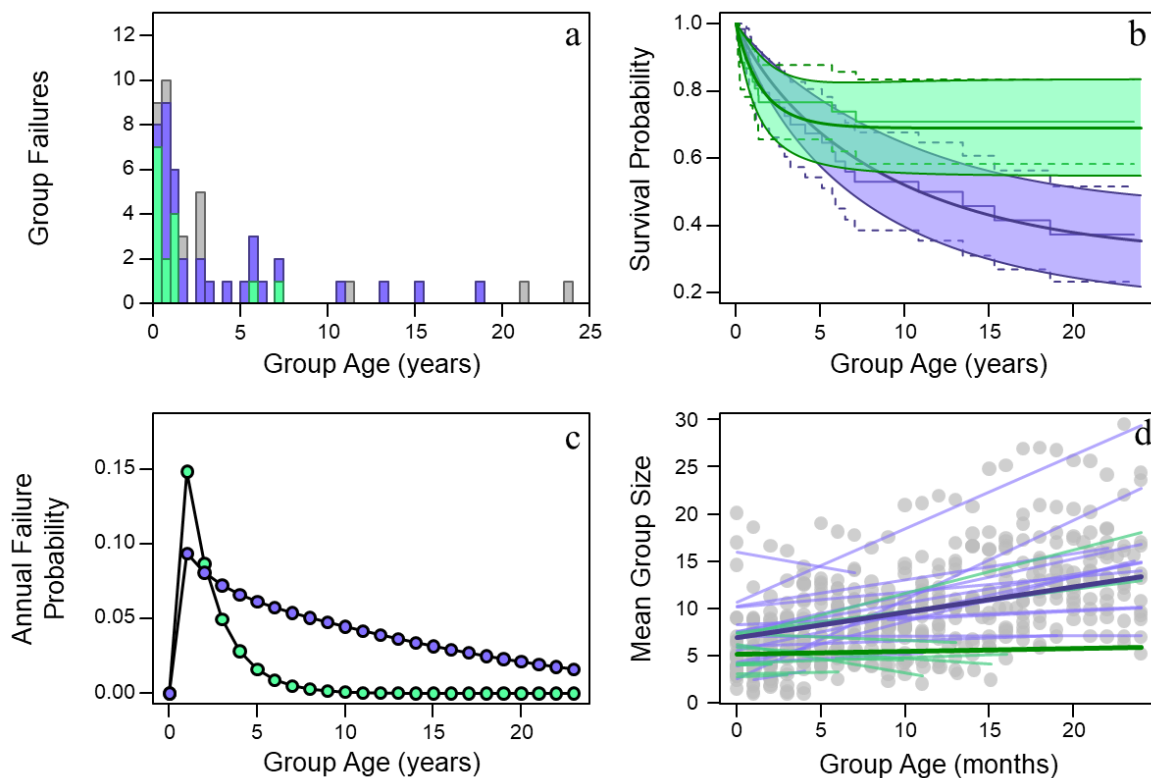


Figure 7.5: The variation in group characteristics across existence in relation to the group's cause of failure, with failures relating to TB (purple) and failures of groups with no TB (green) represented. (a) Stacked frequency plot of age at failure with groups still alive included with their age at study end (grey). (b) Survival probability across a group's existence with 95% confidence intervals (shaded area) predicted from parametric competing fate survival models overlaid on raw Kaplan-Meier plots with 95% confidence intervals (dashed lines). (c) The annual probability of a group failing across their existence derived from parametric survival models. (d) The mean monthly group size across the first 2 years of persistence with raw data (grey points), population level predictions (thick lines) and group level predictions (lighter thin lines) plotted.

The remaining 63% of groups failed in association with clinical TB and the risk of failure with clinical TB peaked after formation and gradually declined over time (Figure 7.5b). For groups that survived beyond a year, TB became the most probable cause of failure and of the 7 groups that failed with longevities greater than 10 years, all failed with clinical TB (Figure 7.5a, 7.5c). When modelled within an illness-death framework the probability of a group developing clinical TB was approximately stable across a group's lifespan following a peak early in life (Figure 7.6a). Once groups developed clinical TB, their survival probability decreased considerably compared to that of groups without visual signs (Figure 7.6b). For groups that failed with clinical TB their mean survival time after the development of visible signs was 10 months.

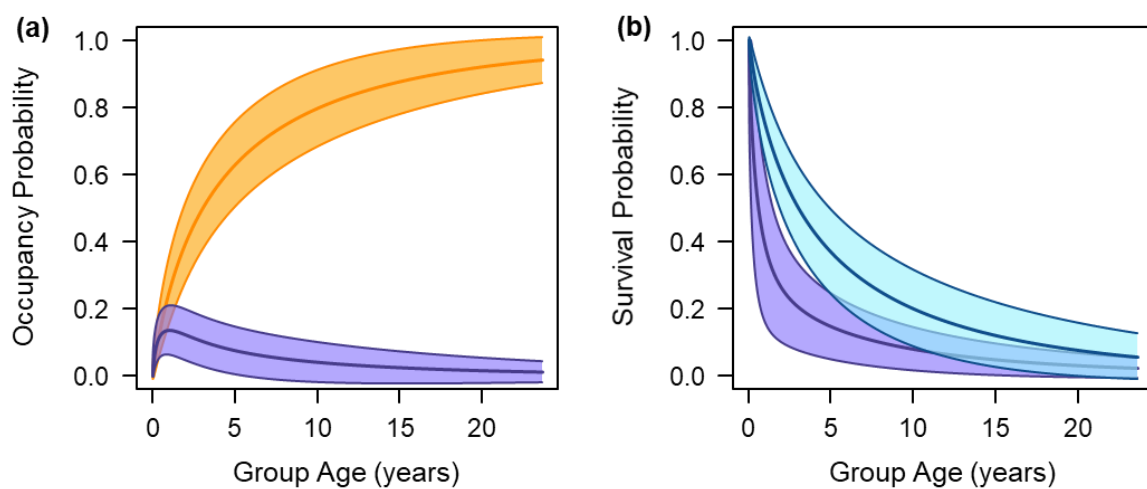


Figure 7.6: Model predictions from the parametric multi-state illness-death model. (a) Predicted occupancy probabilities for a group having clinical TB (purple) and a group having failed (orange) across their lifespan. (b) The survival probability across a group's lifespan depending on whether TB symptoms are absent (blue) or they have clinical TB (purple).

Causes of failure

For groups without clinical TB, smaller groups and those experiencing a higher population density were more likely to fail. Group size exerted a strong negative effect on the probability of group failure, whereas population density had a positive effect (Table 7.1). Smaller groups were also significantly more likely to develop clinical TB, along with groups that had increased exposure to out of group individuals (Table 7.1). Immigration events within the previous 7 months had a significant positive effect on the probability of developing clinical TB. In addition, the number of excursions individuals undertook outside the group within the previous 6 months also had a positive effect on the probability of developing TB, although this was not significant (Table 7.1). Most groups that developed clinical TB failed, however, groups that were larger at the onset of clinical TB and had a higher recruitment rate during the period of clinical infection survived for longer. The negative effects of group size and recruitment rate on the probability of failure of groups with clinical TB and of known

formation date, were not significant in both univariate models (Table 7.2) and when fitted together (Table 7.1). However, when this transition was modelled with a larger dataset including all observed bouts of clinical TB including groups of unknown formation date, both the negative effect of group size and recruitment rate were statistically significant (Table 7.1). There was evidence that groups that developed clinical TB were less likely to fail when precipitation was above average in the preceding 6 or 12 months (SPI6 & SPI12, Table 7.2). Although this effect remained statistically significant only for precipitation in the previous 12 months when the larger dataset including all TB bouts was modelled, yet this effect was relatively small compared to other covariates (Table 7.1). Beyond this, environmental factors had little impact on group failure and neither season nor the standardized precipitation index had a significant effect on any of the other transitions within the models (Table 7.2).

Table 7.1 Model outputs and forest plot for semi-parametric multistate illness–death model of meerkat group survival (black points and lines). In addition, the model outputs for the remodelled transition from clinical TB to failure on a larger dataset, including groups of unknown formation are also reported (italics) and included in the forest plot (blue points and lines)

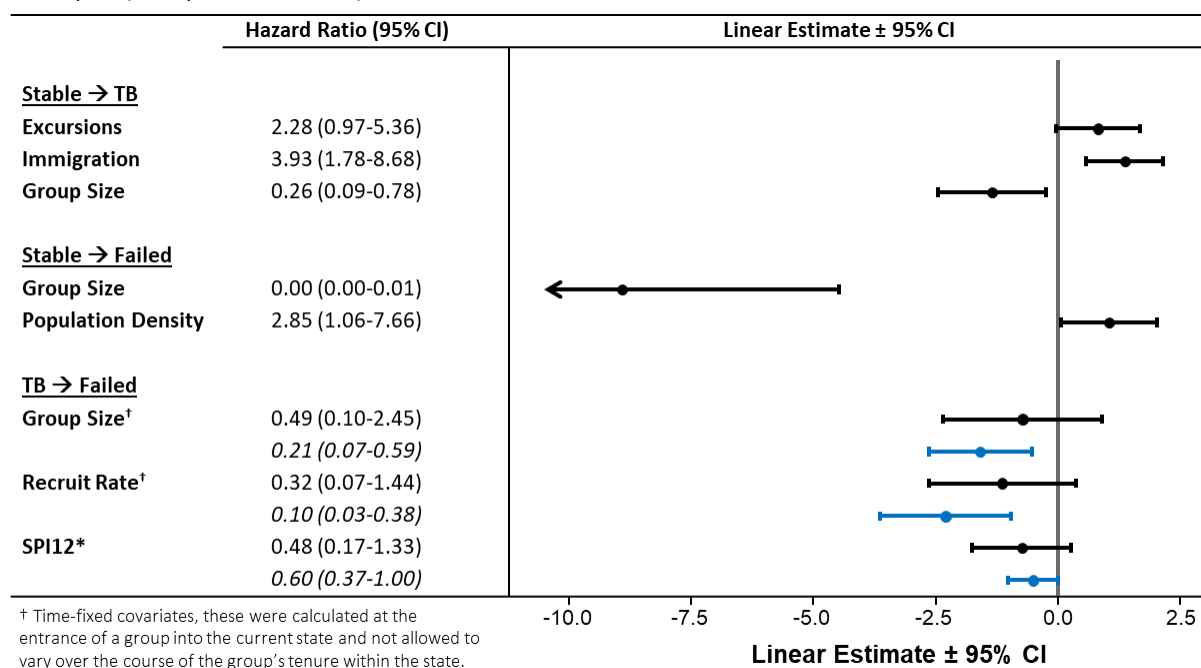


Table 7.2: Univariate model outputs for semi-parametric Cox proportional hazard models fitted within the multi-state illness-death model.

	Alive -> Dead		Alive -> TB		TB -> Dead	
	Est ± SE	P	Est ± SE	P	Est ± SE	P
Group Size	-7.215 ± 1.889	<0.001	-1.109 ± 0.484	0.022	-1.32 ± 0.768	0.086
Pop Density	0.175 ± 0.515	0.734	-0.558 ± 0.080	0.136	-0.106 ± 0.128	0.409
Immigrants	NA	NA	1.489 ± 0.395	<0.001	NA	NA
Excursions	NA	NA	0.195 ± 0.350*	0.578	NA	NA
Recruit Rate	NA	NA	NA	NA	-1690 ± 0.873	0.053
SPI1†	0.417 ± 0.297	0.166	-0.002 ± 0.198	0.992	-0.261 ± 0.309	0.397
SPI3†	0.056 ± 0.287	0.845	-0.190 ± 0.168	0.26	-0.533 ± 0.325	0.101
SPI6†	-0.081 ± 0.278	0.772	-0.228 ± 0.173	0.186	-1.214 ± 0.518	0.019‡
SPI12†	-0.218 ± 0.347	0.53	-0.074 ± 0.189	0.697	-1.029 ± 0.512	0.044
Season	0.350 ± 0.551	0.525	-0.313 ± 0.326	0.338	-0.397 ± 0.547	0.468

*This term was not significant when modelled with a univariate approach, however, when the terms were refitted with the significant terms it became apparent that these terms improved model fit once the effect of group size had been accounted for. Models fitted better with these terms included according to AIC values.

†SPI refers to the Standardised Precipitation Index

‡When modelled with a larger dataset including all transitions from TB to death, the significance of this effect no longer held (Haz [CI 95%] = 0.78 [0.50 - 0.23], Est ± SE = -0.24 ± 0.23, p = 0.29)

Discussion

Meerkat groups are exposed to a high risk of failure in the first few years of their life with many groups failing. However, groups that survive this period can experience longevities of over a decade. Long lived groups primarily failed in association with a clinical TB infection that increased their likelihood of failure. The persistence of groups is important for maintaining meerkat populations, as due to the high levels of reproductive skew, the number of groups rather than the number of breeding age females better predicts the reproductive output of the population. The survival and persistence of groups is strongly influenced by sociodemographic factors, particularly their group size which positively influences group survival. Larger groups are less likely to fail, develop clinical TB and will survive with clinical TB for longer. The influence of climate on the persistence of groups was also investigated, yet contrary to expectations this did not appear to influence the occurrence of clinical TB or the failure of groups without clinical signs of TB. There was evidence of groups with TB being less likely to fail when precipitation had been above average in the previous year, however this effect was relatively small.

The positive relationship between the persistence of groups and their size supported my prediction and has been previously described in several other vertebrates, including the African ice rat, *Otomys sloggetti robertsi* (Pillay & Rymer 2017), Arabian babblers, *Turdoides squamiceps* (Keynan & Ridley 2016), and cichlids, *Neolamprologus pulcher* (Jungwirth & Taborsky 2015). Smaller groups are often more vulnerable to mortality events (except see McGuire *et al.* 2002), experiencing mortality at a higher rate and with individuals key to maintaining group cohesion exposed to a greater mortality risk due to a reduction in the predator dilution effect (Courchamp *et al.* 1999). Smaller groups of meerkats have also been shown to experience higher per capita mortality (Bateman *et al.* 2012), as well as reduced dominant reproductive success (Hodge *et al.* 2008). The effect of these constraints were visible in the data as groups that were smaller at formation and reproduced less successfully experienced little growth, therefore remaining small in size and vulnerable to failure.

Group failure also occurred due to fission between the sexes. The failure of smaller groups in this way may be a result of the reduction in survival and reproduction that smaller groups experience, making residency costly with few fitness benefits. Individuals may therefore benefit by abandoning their group, triggering its failure, to undergo a secondary dispersal to found or migrate into a larger group with better fitness prospects. Possibly, even to return to their natal group, obtaining inclusive fitness by providing care for relatives' offspring. The same processes could also explain why groups were more likely to fail during periods of high population density. Increases in population density can lead to the saturation and overlap of territories (Ridley *et al.* 2004; López-Sepulcre & Kokko 2005),

resulting in increases in the rate and severity of intergroup conflict (Wilson *et al.* 2014). The consequences of increasing conflict including decreases in territory quality, productivity, and survival, may generate situations where it benefits individuals to abandon their group. These effects are also believed to operate on dispersing meerkats, explaining why as population density increases, emigration and settlement rates decline while the rates of dispersers returning to their previous groups increase. Although, it seems at the highest population densities these effects begin to reverse (Maag *et al.* 2018). I suspect that the negative effect of population density will be biased towards relatively smaller groups as they are more likely to lose inter-group interactions (Dyble *et al.* 2019) and therefore would disproportionately suffer the consequences of increased rates of competition. However, my sample sizes were too small to test for the existence of this effect.

The groups that avoided failure early in their lifespan displayed increased rates of successful reproduction and were able to grow their group size considerably during their first two years, going on to persist for many years. Of the groups that survived beyond a year, the majority failed following the development of clinical TB infections that greatly increased a group's risk of failure. By driving the failure of long persisting groups that play an important role in recruitment and emigration within the population, TB plays an important demographic role for meerkats. Much of the demographic variation in meerkats will be explained by the balance between groups failing from TB and the formation rate of new groups to replace lost breeding units.

Corroborating previous research on meerkats, I show that the levels of contact with outgroup individuals predicts the risk of groups developing observable signs of a TB infection (Drewe 2010). In addition to confirming the positive effect male immigration events have on TB developing (Patterson *et al.* 2017), I also found some evidence that the number of individual excursions away from the group, possibly interacting with infected individuals or groups, may also increase a group's likelihood of clinical TB. Mobile individuals, such as dispersers and prospectors, can be important drivers of pathogen transmission (see badgers *Meles meles* Vicente *et al.* 2007; lizards, *Tiliqua adelaidensis* Fenner *et al.* 2011), as they create infection pathways between groups and are often exposed to a diversity of individuals (Nunn *et al.* 2008). However, this is not universal. In lions, highly mobile "nomad" individuals have little impact on disease transmission, with transmission instead occurring between neighbouring groups (Craft *et al.* 2011).

With the levels of extra-group movement controlled for, I also found that smaller groups were more likely to develop clinical TB. This was in contrast to my expectations and the general perception that a cost of increasing group size and sociality is the increased exposure to pathogens (Altizer *et al.* 2003). While I cannot be sure that the effect of group size on the development of clinical disease

translates to the risk of infection, negative effects of group size on disease prevalence have been observed in other species (Woodroffe *et al.* 2009; Keiser *et al.* 2018). Moreover, it is hypothesised that the increasingly modular organisation of larger groups could reduce disease prevalence (Nunn *et al.* 2015), with social clustering that could limit disease transmission being reported in meerkats (Drewe *et al.* 2011). However, these mechanisms influence the prevalence rather than the presence of disease, largely explaining the patterns of spread within and not between groups. Therefore, while this could explain larger groups of meerkats persisting longer with clinical TB, it does not explain why larger groups are less likely initially to develop clinical TB. The increased probability of clinical TB occurring in smaller groups could be a function of how they interact with other groups and coalitions of dispersers. For example, in badgers it has been suggested that increased TB prevalence in smaller groups could result from smaller groups having higher contact with neighbouring group members (Woodroffe *et al.* 2009). Variation in the nature of these interactions could also influence the likelihood of transmission. If smaller groups are more likely to experience inter-group interactions that escalate to physical aggression, this could increase the risk of transmission, as aggressive behaviours such as biting are possible transmission pathways (Drewe 2010).

Though climatic factors can play an important role in disease dynamics (Summers 2009), influencing the prevalence and lethality of infections (Munson *et al.* 2008; Randall & Van Woesik 2015), I found no evidence of direct relationships between season and precipitation on the emergence of clinical TB in groups. This differed from my prediction and a previously reported weak effect indicating TB incidence was higher in drier periods (Patterson *et al.* 2017). However, as I was unable to measure the exact time of a group's infection with TB, only the development of clinical signs, this could have prevented the detection of climate effects on TB spread. I suspect that climatic variation will be involved in indirectly driving the process of TB infection. For both group size and the rates of extra-group movement, predictors of the development of clinical TB, have been shown to be influenced by seasonal and climatic variation (Bateman *et al.* 2013; Mares *et al.* 2014). Considering the importance TB has for the persistence of meerkat groups, understanding how climate operates through these parameters to influence disease prevalence, will be essential for predicting the future population trends in response to changing climatic conditions.

The practice of targeted euthanasia for individuals with clinical TB is likely to impact on the persistence of groups in the study population. For example, the premature removal of infectious individuals could prevent the spread of disease to other groups and possibly stem the further spread and development of TB within groups. While it is not known whether euthanasia prevented further development of TB within some groups, if it is the case, then the median and maximum observed longevity of groups would be artificially increased in the population. In contrast, euthanasia could also

accelerate a group's progression from developing clinical signs to failure. However, as individuals were euthanised in the later stages of what appears to be a terminal infection, I suspect euthanasia rarely curtails a group's persistence by more than a few months. More broadly, while euthanasia may influence the longevity of groups, I believe that the results describing the general patterns of group persistence and how they are affected by group characteristics will be largely unchanged and will still be relevant beyond the population of this study.

In conclusion, I characterise the longevity of meerkat groups and identify the causes of their failure, revealing the influence of TB on meerkat demography by driving the failure of the longest-lived groups. Additionally, I show the importance of large group sizes for reducing a group's risk of failure, with groups that grow quickly after formation and sustain a large group size persisting the longest. Research, as undertaken in this chapter, that investigates the processes of group survival and their eventual failure provides valuable information for understanding and modelling the demography of social species. As sample sizes continue to grow, I believe that extending this work to investigate how the composition of groups and the characteristics of their members influence group persistence will provide valuable results.

Chapter 8: General Discussion

Many group-living species across the animal kingdom have been observed to exhibit high levels of reproductive skew (Clutton-Brock 1988), with dominant individuals producing the majority of a group's offspring. Some of the most extreme examples of this are found among the singular cooperative breeders, where obtaining a position of dominance is critical to acquiring reproductive success (Koenig & Dickinson 2016). Consequently, there are often substantial differences in fitness dependant on whether an individual acquires dominance during their lifespan (Hauber & Lacey 2005). However, even among dominants there is often substantial variation in fitness (Stockley & Bro-Jørgensen 2011; Clutton-Brock & Huchard 2013). Due to the importance of acquiring dominance in many species, the traits associated with dominance have been the focus of much research. In contrast, we understand less about the differences in fitness among dominants, even though there is likely to be a similarly strong selection on the traits that maximise a dominant's reproductive success as there is on the traits associated with acquiring dominance.

In this thesis, I used long-term data collected on a population of cooperatively breeding meerkats, *Suricata suricatta*, to investigate the processes underlying the variation in fitness, with particular focus on the acquisition and maintenance of dominance status. My investigation can be broken down into four topics: (1) The impacts of different routes to acquiring dominance, (2) sex differences in the maintenance of dominance tenures, (3) the costs, and benefits of multi-male association for dominant males, and (4) the drivers of group persistence. In this chapter, I consider each of the four topics in turn discussing my findings, their implications, and avenues for future research.

The impact of different routes to dominance

There are multiple distinct routes to dominance; the presence of these routes varies across species, and in some species, individuals can have multiple dominance routes (Raihani *et al.* 2010; Walters & Garcia 2016). In Chapters 3 and 4, I characterised the distinct dominance routes available to both male and female meerkats; comparing the characteristics of dominance acquired via different routes. Of the individuals born in the population that reached adulthood a minority acquired dominance, with just 20% of females and 14% of males holding dominant breeding positions during their observed lifespans. Although, this is likely to be slightly underestimated due to individuals acquiring dominance outside the population, especially for males who are the more dispersive sex.

Female meerkats can acquire dominance in their natal groups or by dispersing and acquiring dominance in a newly founded group. From a subordinate position in either a natal or dispersed group, females can either inherit dominance when a vacancy arises or challenge and displace the incumbent dominant from their position. Males can similarly acquire dominance through inheritance or displacement, however, to acquire dominant breeding positions they must disperse. Following dispersal they may found a new group and acquire dominance, or unique to males, they may migrate into an established group taking over dominance.

Considering the diversity of dominance routes, some routes could potentially offer greater fitness (Walters & Garcia 2016), being optimal dominance routes compared with others that represent “best-of-a-bad-job” strategies. However, I find that in both sexes there are no differences in either tenure length or reproductive rate for dominants in relation to their dominance route (Chapter 3 & 4). This is likely to result from the long tenures dominants experience, averaging out any early tenure differences in reproductive success related to group characteristics at the start of a dominant’s tenure. In addition, the skewed tenure distributions suggest the presence of reasonably high levels of individual stochasticity which could mask all but strong effects (Tuljapurkar *et al.* 2009; Snyder & Ellner 2018). Furthermore, in both sexes I find that irrespective of the route to dominance pursued, the traits determining acquisition are the same, with older and heavier individuals often winning the competitions. Therefore, while males and females pursue differing routes to dominance, I suspect they will both employ flexible strategies for pursuing dominance as opposed to adopting specialised strategies that commit them to specific routes.

Future research should consider the importance of the sociodemographic environment under which individuals acquire dominance. The availability of certain routes to dominance are likely to be determined by sociodemographic factors such as the density of opposite sex dispersal coalitions and the size and composition of neighbouring groups. In addition, as an individual’s sociodemographic environment varies temporally, not only might the availability of certain routes to dominance change, but the requirements and fitness benefits of certain routes may vary (Davidian *et al.* 2016). This variation may generate differences between dominance routes that were averaged out in these analyses, and individuals may strategically respond to environmental variation to maximise their chances of successful dominance. Indeed, several mammalian and avian species have been found to show remarkable plasticity in their response to environmental and sociodemographic variation, pursuing breeding strategies that have the greatest prospective fitness returns under their current circumstances (Rood 1990; Davidian *et al.* 2016; Nelson-Flower *et al.* 2018).

Even in the absence of differences in fitness between dominance routes, for females natal dominance may still be preferred to dispersed dominance as it avoids costly dispersal (Young & Monfort 2009; Marty *et al.* 2017b). Consequently, subordinate female meerkats may employ strategies to reduce their likelihood of eviction and maintain residency. To maintain residence and maximise inheritance probability, subordinates in several cooperatively breeding fish employ behavioural and growth strategies to reduce their threat to the dominant and maximise their value (Buston 2003b; Wong *et al.* 2008; Zöttl *et al.* 2013). To investigate this in meerkats, I tested whether subordinates tried to sustain their natal residency by adjusting their growth to reduce the perceived risk to the dominant female and increase their cooperative efforts possibly “paying-to-stay”. However, in Chapter 3 I found no such evidence. In fact, rather than increasing cooperative expression, recent analyses of age-related changes in subordinate cooperative effort reveal that adult subordinate meerkats reduce their cooperative contributions as they age (Duncan *et al.* 2019; Thorley *et al.* unpublished). Therefore, eviction risk is negatively correlated with cooperative investment (Clutton-Brock *et al.* 2010), providing further evidence for the absence of pay-to-stay mechanisms in meerkats. Eviction in meerkats is strongly associated with dominant female reproductive suppression, rather than the policing of group membership as is seen in banded mongooses (Cant *et al.* 2010; Thompson *et al.* 2017). Indeed, subordinates commonly return to the group following the dominant female’s birth, and for those that do not it is likely due to mortality (Cram *et al.* 2018) or successful dispersal (Maag *et al.* 2018), as opposed to exclusion from the group.

Evidence for declines in cooperative effort with age and social rank have also been reported more widely in other cooperative breeders (Zöttl *et al.* 2016, 2018) and some primitively eusocial insects (Field *et al.* 2006). These changes in cooperative investment have been suggested as trade-offs in current indirect fitness against future direct fitness. For subordinate female meerkats, acquiring dominance is energetically costly and as the probability of dominance acquisition increases with social rank, it is therefore logical for them to divert investment from cooperation towards maximising their condition, thereby increasing their probability of acquiring dominance should an opportunity arise. Future work on the variation of cooperative effort in subordinate females should therefore consider the possible existence of these trade-offs. Furthermore, similar processes are present in males and warrant further investigation, as evidenced by declines in helping behaviour by male subordinates as they increase their rates of prospecting for mating opportunities, representing a trade-off in direct versus indirect fitness (Young *et al.* 2005).

Sex differences in the maintenance of dominance tenure

Following the acquisition of dominance individuals must maintain their status to maximise their breeding tenure, an important determinant of lifetime reproductive success in iteroparous species. Where individuals can hold breeding positions for substantial periods of time, variation in tenure length can drive substantial differences in individual fitness. Beyond individual differences in tenure length, many mammalian breeding systems also exhibit sex-differences in tenure length (Clutton-Brock & Isvaran 2007; Lukas & Clutton-Brock 2014). Sex-differences in tenure length have often been viewed in the context of intrasexual competition, with the sex exhibiting the higher levels of competition experiencing shorter tenures. For example, in many polygynous species where males compete intensely over harems, the breeding tenures of males are considerably shorter than females who will breed for many years (Toïgo & Gaillard 2003; Nussey *et al.* 2009). However, sex differences in tenure length are also likely to arise from other sources, including differences in the causes of tenure loss between the sexes. It is therefore important to account for the different causes of tenure loss to properly understand the processes that determine individual tenure lengths and potentially drive sex-differences.

In Chapter 6, I characterised the different causes of tenure loss in both male and female dominant meerkats, investigating the factors that influenced the propensity of dominants to lose tenure in a cause specific approach. Similar to other cooperative breeders, dominance in meerkats is synonymous with holding a breeding position and tenure lengths are generally longer in females (Clutton-Brock *et al.* 2006). I find that these sex differences are driven by males being exposed to a greater number of causes of tenure loss. The dominants of both sexes are at risk of mortality and my results indicate they both experience equivalent levels of within-group intrasexual competition with similar risk profiles for displacement. However, males are uniquely exposed to intrasexual competition from outside the group in the form of takeovers from extra-group males. Furthermore, as available breeding opportunities decline across male tenure, they are eventually forced to abandon their position and disperse in search of other reproductively viable positions of dominance. Consequently, these additional causes of tenure loss prematurely curtail the tenures of male dominants, while female dominants are generally able to hold tenure until their death, resulting in males experiencing shorter tenures relative to females.

That the tenures of dominant males are curtailed by the existence of intrasexual competition from extra-group males raises the question of why this is absent in females who have not been observed to invade established groups? This is a phenomenon widely observed in mammals where the takeover of groups is either absent or rare among females (Rood 1990; Thompson *et al.* 2017). It

is possible that females do not disperse in large enough coalitions to overcome the resident females in established groups. Additionally, dispersing females may never need to invade groups to acquire breeding positions; as males are the more dispersive sex it is likely that male coalitions are always in excess relative to female coalitions, allowing females to form new groups rather than invading established ones. It would therefore be interesting to see if this trend is reversed in birds, where dispersal is often biased towards females.

Overall, the work in Chapter 6 shows that sex differences in the breeding tenures of species can be driven by multiple complex process including variation in breeding strategies and dispersal patterns among the sexes. Key to uncovering these processes is the application of cause specific methods to investigate tenure loss. Sex specific differences in dispersal and breeding are widely reported across the animal kingdom and are thus likely to influence the variation in the breeding tenures of other species. Therefore, investigating differences in the causes of tenure loss in other species, especially those with different breeding systems, is likely to be fruitful.

The costs and benefits of subordinate immigrants for dominant males

The existence of multi-male groups in species where the presence of subordinate males inflicts costs upon dominants is unexpected, as dominant males should not tolerate their presence. It could simply be that dominant males are unable to exclude subordinates from the group, however, both theoretical and empirical research has shown that subordinate males can offset the costs they impose on dominants (Port & Cant 2014; Port *et al.* 2018). Most commonly it appears subordinate males offset their reproductive costs by aiding in group defence, causing dominants to experience longer tenures and experience net increases in lifetime reproductive success (Port *et al.* 2010). There is also evidence that subordinate males can increase dominant male reproduction through increasing the survival of their offspring and the number of breeding females they have access to (Feh 1999; Snyder-Mackler *et al.* 2012). In meerkats the presence of subordinate immigrant males appears to be costly; increasing numbers of subordinates reduce both a dominant's tenure length and their probability of fathering pups within the group (Spong *et al.* 2008). Consequently, dominant male meerkats should not tolerate the presence of subordinate immigrants, however, evidence of dominant males trying to exclude subordinates from groups is conspicuously absent.

The results in Chapters 5 and 6 reveal that the impact of subordinate immigrant males on the productivity and maintenance of dominant male tenures is more nuanced than expected. By deconstructing the different causes of tenure loss and sources of reproductive competition, my results confirm that the negative effects of subordinate immigrants are a function of direct competition.

Greater numbers of subordinate immigrants increase the likelihood of them siring young and displacing the incumbent dominant. However, these results also revealed that subordinate immigrants confer benefits by reducing the risk of takeovers and paternity from roving males. However, the overall negative effect of immigrant subordinates on male tenure length and paternity probability (Spong *et al.* 2008) suggests these benefits do not completely compensate the costs subordinates impose. My results suggest this could be due to the diminishing reductions in takeover risk and extra-group paternity that subordinate immigrants confer as their number increases while their cost continues to grow. Although these contrasts do not account for additional factors that could influence the magnitude of the cost imposed by subordinates, such as kinship and variation in the consequences of competition from different sources.

Group kinship structure is important for mediating the costs of competition. In species where intragroup kinship is high, as in meerkats and other cooperative breeders (Dyble & Clutton-Brock 2020), it is likely that dominant males are more highly related to resident competitors than extra-group competitors. This generates a difference in relatedness between sources of competition that can in turn generate differences in the costs of competition. Indeed, in Chapter 5 I show that because of high kinship between dominant males and immigrant subordinates, the offspring of within-group extra-pair paternity are more highly related to dominants than the offspring of extra-group paternity. This is strong evidence that the costs of losing paternity to resident competitors is lower than to extra-group competitors, when observed through the lens of inclusive fitness. Consequently, the required benefits subordinates need to confer to dominants for tolerance to be selected for are likely to be reduced where the kinship among resident males is high.

In summary, my results show that within the usual range of subordinate male numbers that dominant males experience, subordinate immigrant males are likely to offset their costs by reducing the likelihood of extra-group paternity and takeovers and may even benefit dominant males when relatedness is accounted for. However, as subordinate immigrant numbers increase along with their costs, the benefits provided by each additional subordinate will diminish and at high numbers (>3) the negative effects of subordinates will begin to outweigh their benefits, even accounting for relatedness. Subsequently, dominants will no longer benefit by tolerating these subordinates and should therefore enact strategies to reduce their numbers. However, with subordinates being present in such high numbers it is unlikely that the dominant will have the capacity to exclude subordinates from the group. This suggests that individual strategies to prevent the numbers of subordinate immigrants reaching costly levels are likely to occur prior to the acquisition of dominance.

In meerkats, the numbers of subordinate immigrants in a dominant male's group are largely determined by the size of coalition they disperse with. Therefore, it might be the case that dispersing

individuals will try to exert control over the composition of their dispersing coalitions to maximise their probability of acquiring dominance and reduce the future levels of intrasexual competition they will experience. However, such strategies will need to account for the benefits associated with larger coalitions, including reduced dispersal costs (Young & Monfort 2009) and increased probability of successful group formation and immigration (Young 2003). Therefore, there is likely to be an optimal dispersal coalition size that balances the benefits of increasing the likelihood of successfully dispersing against the future fitness costs of increased intrasexual competition. Similarly, in both Asiatic and African lions, there is an optimum coalition size over which the benefits of grouping decline, resulting in members abandoning their coalition and pursuing solitary dispersal (Packer *et al.* 1991; Chakrabarti *et al.* 2020). Consequently, I suspect that male meerkats will employ strategies to balance these factors, dispersing in coalitions of a size and composition that maximise their future fitness prospects, warranting further investigation.

The drivers of group persistence

In singular cooperative breeders and other species with high levels of reproductive skew, the group is essentially equivalent to a breeding unit. Subsequently, the frequency and longevity of groups have important effects on a population's vital rates, such as seen in Chapter 7 for recruitment in meerkats. Therefore, it is important to account for a species social organisation to accurately model their demography (Zeigler & Walters 2014). In Chapter 7, I investigate the causes of group failure in meerkats and the factors that increase a group's probability of extinction. My results revealed that groups were particularly vulnerable to failure via stochastic causes in their first few years of existence, especially when small in size, however groups that persisted could experience multi-decade longevities. In addition, clinical Tuberculosis (TB) was associated with the failure of many groups in the meerkat population, being responsible for the failure of all long-lived groups. This indicates that TB will have a strong influence on the demography of meerkats, and these results will be of relevance to a number of wild populations of social mammals where TB is present, ranging from European badgers (*Meles meles*, Woodroffe *et al.* 2009) to water buffalo in southern Africa (*Bubalus bubalus*, Corner 2006). In addition, to providing further support for larger groups being less vulnerable to stochastic causes of failure (Jungwirth & Taborsky 2015; Pillay & Rymer 2017), my results also show that with extra-group movements controlled for, larger groups appeared less likely to develop clinical signs of TB. This adds to a growing body of evidence suggesting that increased disease prevalence is not necessarily an ubiquitous cost of increasing socialisation, as has been commonly found (Altizer *et al.* 2003; Kappeler *et al.* 2015). Indeed, several benefits of group-living for countering pathogens have

been identified, that could potentially outweigh the pathogen related costs of sociality (Ezenwa *et al.* 2016). Overall, these results not only aid the incorporation of social organisation into demographic models of meerkats, but also describe several processes associated with group failure that will be relevant to many group-living species, not just cooperative breeders.

The persistence of groups also has important consequences for individual fitness. The failure of groups is responsible for a non-negligible number of individuals losing dominance (see Chapter 6), and the curtailment of their tenure will limit their life-time reproductive success. Furthermore, beyond ending the tenure of dominants, in species that form family groups, the failure of a group will represent the termination of a lineage branch, the “bearer” of fitness (Akçay & Cleve 2016). To prevent group failure ending a lineage’s representation within the population, it is critical for groups to propagate their lineage through the successful dispersal of their group members. The extent to which a lineage proliferates will be determined by the longevity of a group and the rate at which they produce successful dispersing units. My results indicate that to maximise longevity, groups must maintain large group sizes. In addition, larger groups are also likely to propagate at a higher rate, with larger groups producing larger dispersal units (Young 2003), that are more likely to successfully form new groups and invade established groups (Young 2003; Maag *et al.* 2018).

The magnitude of the impact of group failure on individual fitness will depend on the fates of individuals following group failure. Group failure does not necessarily mean the death of all group members, instead many individuals will likely become floaters and attempt to disperse. For dominant individuals, determining their post group failure fates will reveal whether group failure represents the end of their reproductive lifespan or just a reduction in breeding tenure, with dominants able to successfully disperse and resurrect their lineage. For subordinates, group failure may be less costly, with individuals able to return to their natal groups and gain inclusive fitness by becoming a helper or pursuing breeding positions by undergoing dispersal. Indeed, the fact that some groups fail due to fission, with members of one sex actively abandoning the group suggests that maintaining a group may not always be the optimal fitness strategy. I expect that the consequences of failure will also vary with the cause of group failure. While individuals that experience group fission may experience a productive future after dispersing, individuals that experience their group failing in association with TB are likely to carry the disease to whichever group they disperse to, consigning that group to future failure. To quantify the true costs of group failure for individuals, future studies should track individuals following group failure to accurately determine their fates.

Conclusion

Over the course of this thesis, I have characterised the ways in which meerkats of both sexes can acquire dominance and maintain their status. These results provide insights into the processes that drive variation in fitness both within and between the sexes. Beyond meerkats and cooperative breeders, the social processes described here are likely to be of relevance to any species where holding dominance is beneficial and sought after. Indeed, the dominant males' trade-offs in tolerating subordinate males that are described in this thesis are similarly observed across the animal kingdom. The last chapter on group persistence provides a foundation through which to extend our understanding of fitness in meerkats, by beginning to consider fitness through the wider lens of lineage maintenance and proliferation.

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Appendices

Appendix I – Chapter 4: pairwise contrast plots

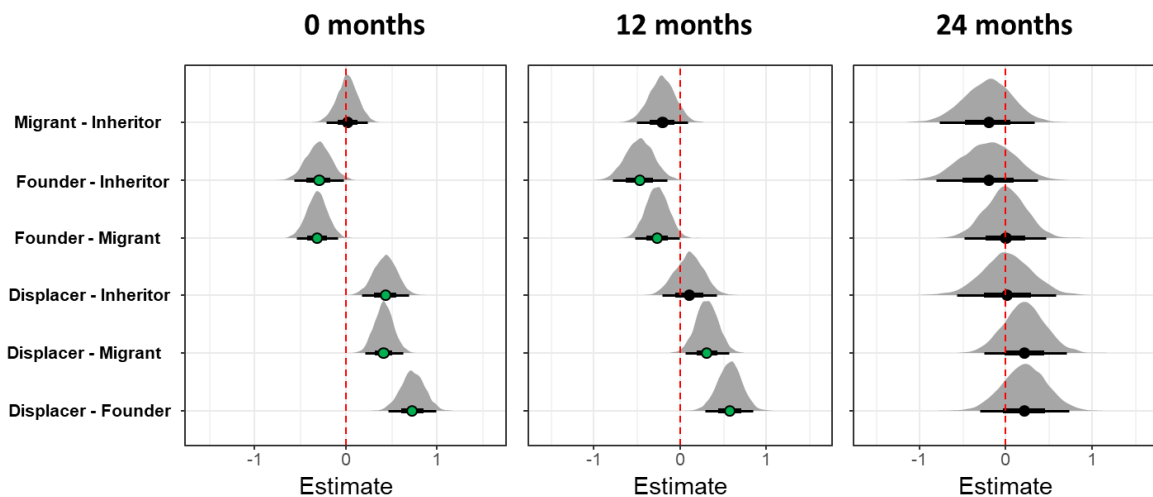


Figure 1: Pairwise contrast for the effect of dominance route on group size at different points in a dominant's tenure (0, 12 & 24 months). Contrasts where the credible intervals do not cross zero flagged with green points.

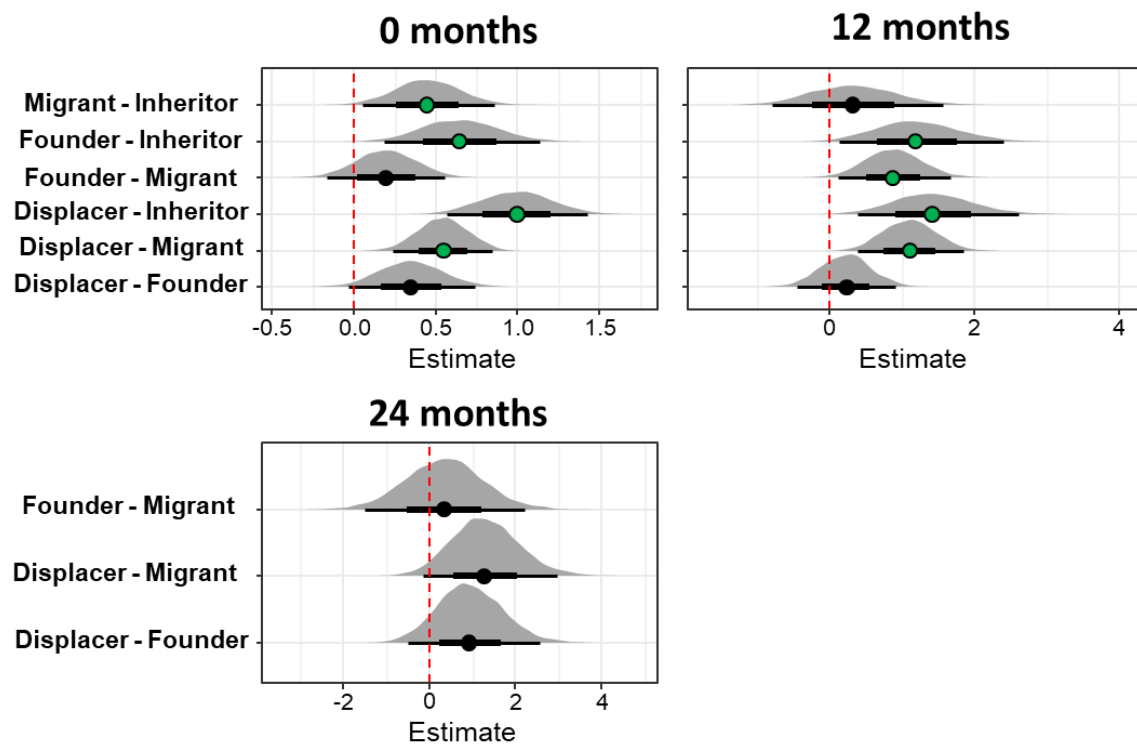


Figure 2: Pairwise contrast for the effect of dominance route on the number of immigrant subordinate males at different points in a dominant's tenure (0, 12 & 24 months). Contrasts where the credible intervals do not cross zero flagged with green points. As there were no inheritor dominants with resident subordinate immigrant males at 24 months, contrasts with inheritors could not be calculated.

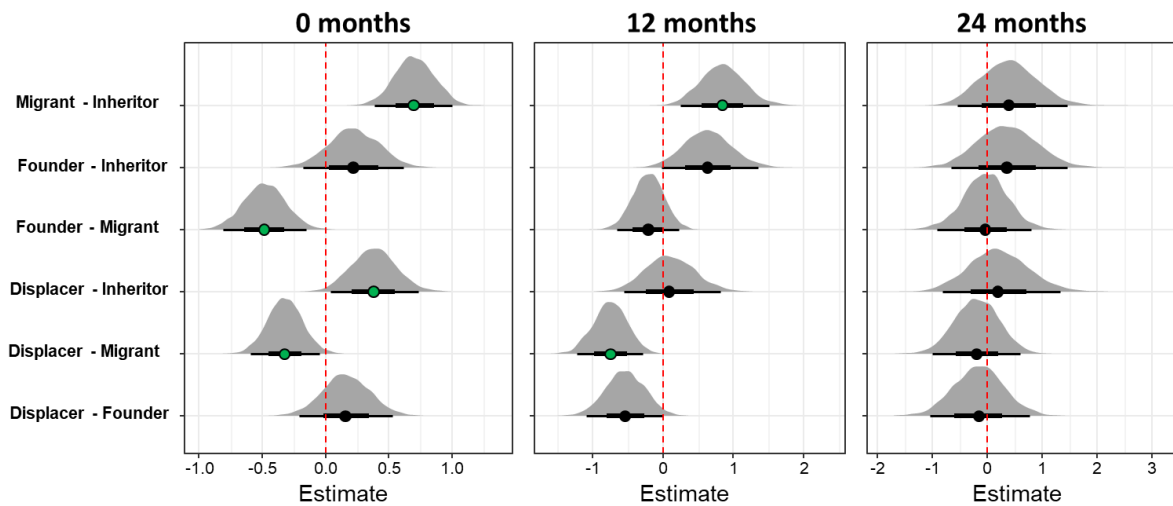


Figure 3: Pairwise contrast for the effect of dominance route on the number of females unfamiliar to the dominant male at different points during the dominant male's tenure (0, 12 & 24 months). Contrasts where the credible intervals do not cross zero flagged with green points.

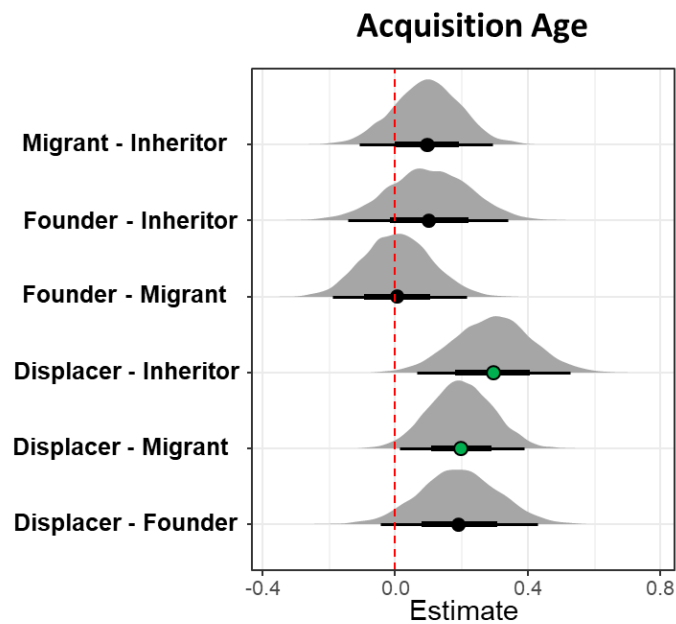


Figure 4: Pairwise contrast of dominant male's acquisition age in relation to their dominance route. Contrasts where the credible intervals do not cross zero flagged with green points.

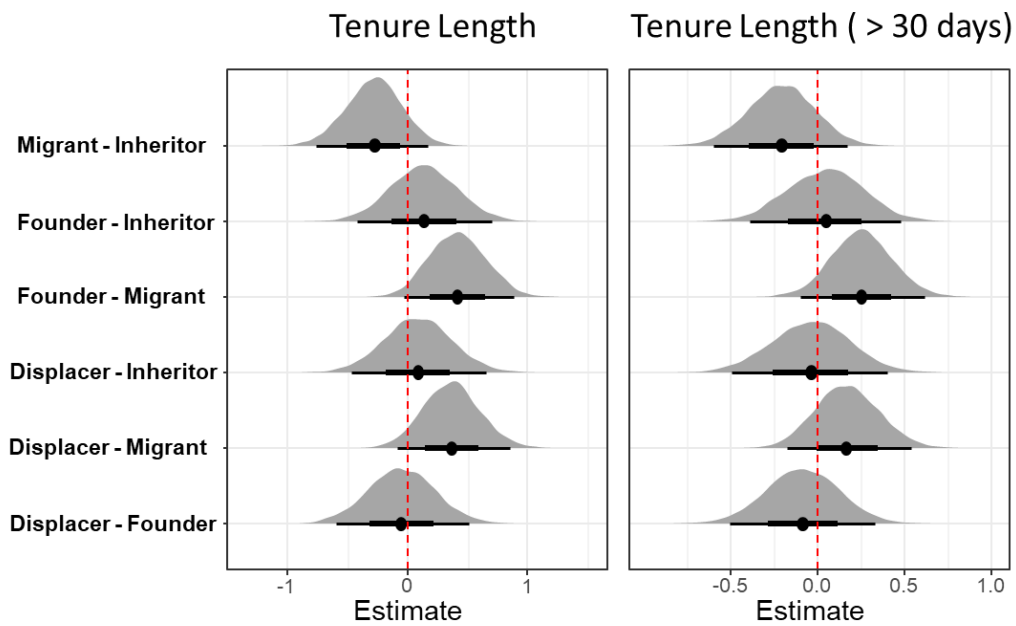


Figure 5: Pairwise contrast of dominant male's tenure length in relation to their dominance route. Contrasts where the credible intervals do not cross zero flagged with green points. Contrast present for a model with all dominance bouts included and for a model where only bouts longer than 30 days were included.

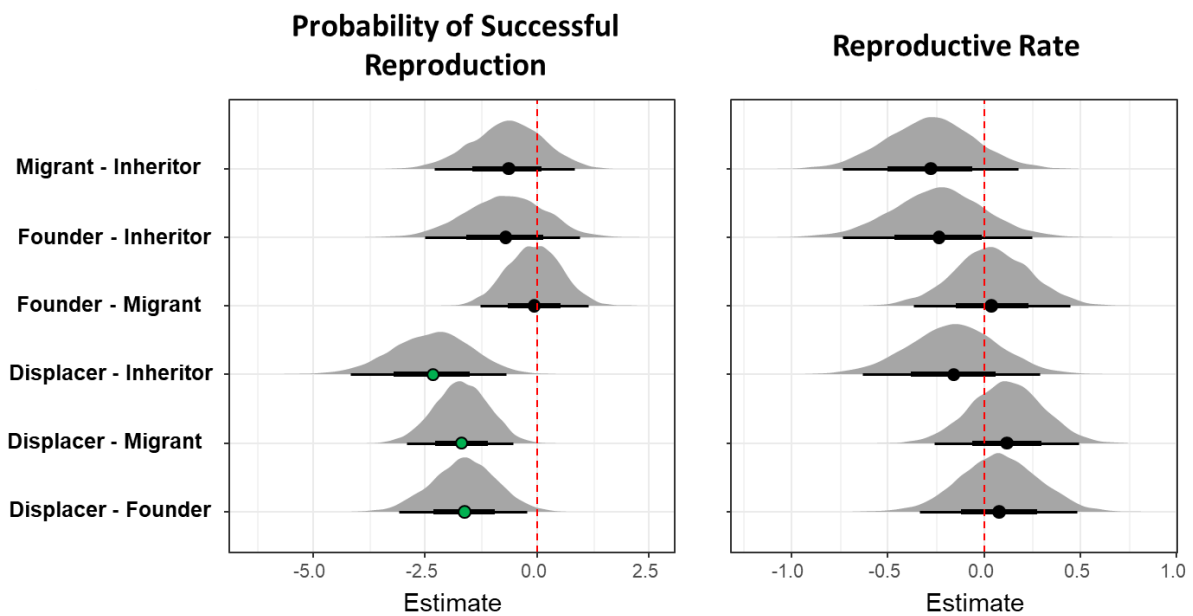


Figure 6: Pairwise contrast of dominant male's reproduction in relation to their dominance route. Contrasts where the credible intervals do not cross zero flagged with green points. Contrast presented for both the zero probability (probability of successful reproduction) and the zero-truncated (Reproductive Rate) components of the model.

Appendix II – Chapter 6: pregnancy and mortality analyses

Table 1: Model selection table for sex specific parametric survival models of dominance loss across tenure.

	Female		Male	
	AIC	Δ AIC	AIC	Δ AIC
Weibull	2418.75	0.00	2889.35	0.00
Gompertz	2428.14	9.40	2907.45	18.09
Log Normal	2419.00	0.26	2908.34	18.99
Log Logistic	2427.52	8.77	2912.82	23.46
Gamma	2421.34	2.60	2890.28	0.92
Exponential	2434.10	15.34	2915.17	25.82

Pregnancy driving mortality through increased body mass.

When the relative hazard of the quadratic weight effect on female mortality is plotted it can be seen that the effect of increased body mass buffering against mortality not only asymptotes, but reverses with the heaviest females experiencing greater mortality risk than a female of average mass (Figure 1a). As would be expected pregnancy has a considerable influence on female weight with the heaviest weights being achieved by females in pregnancy (Figure 1b). With visualisation indicating that the upper part of the quadratic trend where mortality increases is comprised primarily of pregnant females. Indeed, remodelling on a reduced dataset where pregnancy weights are removed from the mass calculations reveals the presence of an asymptotic effect but not a clear increase in mortality at the upper end of the mass distributions (Figure 1c).

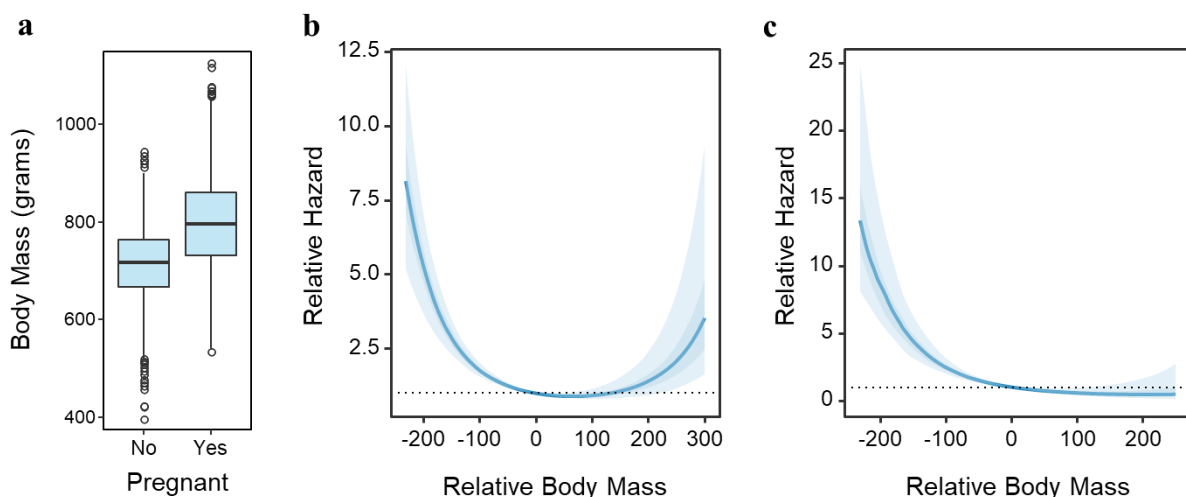


Figure 1: (a) Box plot of mean monthly female weights in relation to their pregnancy status and relative hazard plots for the effect of body mass on mortality risk for a model including all weights (b) and a model with pregnancy weights excised (c). Relative hazard plots were derived from cox-proportional hazard models with mean monthly body mass fitted as a quadratic effect using the simPH package (Gandrud 2015). The relative hazard plots were centered with zero representing the mean body mass for the sample (b = 763g, c = 727).

Contrasting causes of mortality

In addition to the levels of mortality differing between dominant males and females, the proportion of mortalities being associated with disease rather than stochastic processes also differs between the sexes. Most females who lose their position due to mortality are killed by stochastic processes such as predation (76/116; Figure 2a) rather than disease (40/116; Figure 2a). The opposite is true for male dominants where the numbers of dominants losing their position due to disease related mortality (36/57; Figure 2c) is higher than due to stochastic mortality (21/57; Figure 2c).

There is a step change in the hazard rate of mortality in female dominants that is present for both disease associated and stochastic mortality when they modelled as separate fates. The risk of both forms of mortality is higher during the first year before changing to a reduced and relatively constant risk across the rest of their tenures (Figure 2b), with the reduction in hazard being greater for disease. Disease related and stochastic mortality follow similar patterns in males, with a largely consistent hazard across time. The difference in male mortality causes appears to be due to a higher risk of disease associated mortality early in tenure that levels out (Figure 2d).

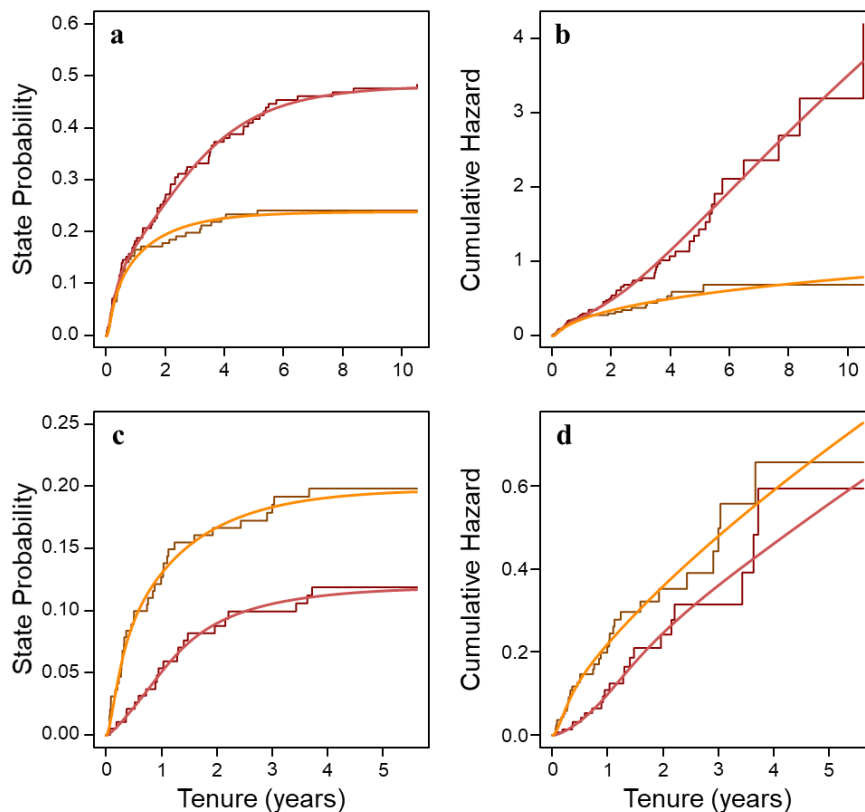


Figure 2: State probability (a,c) and cumulative hazard (b,d) plots for female (a,b) and male (c,d) dominants losing their tenure in relation to disease associated mortality (orange) and stochastic mortality. Curves predicted from parametric multistate state survival models fitted with Royston-Palmer spline models and overlaid on the outputs of non-parametric multistate models fitted with Kaplan-Meier curves.

Table 2: Model outputs for cause specific survival analysis of dominant female mortality causes.

	Females			
	Estimate \pm SE	HR	z-value	p
<u><i>Stochastic Mortality</i></u>				
Body Mass	-0.438 \pm 0.188	0.65	2.33	0.020
Body Mass ²	1.024 \pm 0.190	2.78	5.41	<0.001
Group Size	-0.846 \pm 0.351	0.43	2.41	0.016
Partner Loss	0.390 \pm 0.437	1.47	0.89	0.372
<u><i>Disease Mortality</i></u>				
Body Mass	-1.110 \pm 0.404	0.33	2.75	<0.006
Body Mass ²	0.641 \pm 0.345	1.90	1.86	0.063
Group Size	-1.183 \pm 0.306	0.31	2.24	0.025
Partner Loss	1.495 \pm 0.445	4.46	3.36	<0.001

Table 3: Model outputs for cause specific survival analysis of dominant male mortality causes.

	Males			
	Estimate \pm SE	HR	z-value	p
<u><i>Stochastic Mortality</i></u>				
Body Mass	-1.205 \pm 0.427	0.30	2.82	0.005
Group Size	-0.338 \pm 0.532	0.71	0.64	0.526
Partner Loss	0.966 \pm 0.599	2.63	1.61	0.107
<u><i>Disease Mortality</i></u>				
Body Mass	-0.933 \pm 0.338	0.39	2.76	0.006
Group Size	-0.815 \pm 0.523	0.44	1.56	0.120
Partner Loss	1.289 \pm 0.435	3.64	2.96	0.003

Appendix III – Chapter 7: additional model tables

Table 1: Model comparisons for competing risk survival analyses characterising the failure of groups accounting for two distinct fates (TB vs No TB) in addition to censoring. The models with the lowest ΔAIC value were considered the model of best fit.

	No TB			TB		
	AIC	LogLik	ΔAIC	AIC	LogLik	ΔAIC
Exponential	114.13	-56.06	14.94	163.34	-80.67	0
Weibull	102.47	-49.23	3.28	164.73	-80.36	1.39
Gamma	103.46	-49.73	4.28	164.97	-80.49	1.63
Log Normal	99.25	-47.62	0.06	163.36	-79.68	0.02
Gompertz	99.19	-47.6	0	164.21	-80.1	0.87
Log Logistic	101.25	-48.63	2.06	163.86	-79.93	0.52

Table 2: Model comparisons for parametric time homogeneous survival models for each transition in the multistate illness death model. The models with the lowest ΔAIC value were considered the model of best fit.

	Stable à TB			Stable à Failure		
	AIC	LogLik	ΔAIC	AIC	LogLik	ΔAIC
Exponential	810.89	-404.45	4.82	281.13	-141.57	9.85
Weibull	806.53	-401.3	0.46	274.8	-135.4	3.52
Gamma	806.07	-401.04	0	275.91	-135.95	4.63
Log Normal	817.59	-406.8	11.52	271.28	-133.64	0
Gompertz	NA	NA	NA	NA	NA	NA
Log Logistic	817.95	-407	11.88	273.34	-134.67	2.06

	TB à Stable			TB à Failure		
	AIC	LogLik	ΔAIC	AIC	LogLik	ΔAIC
Exponential	294.51	-146.25	0	373.16	-185.58	1.72
Weibull	295.93	-145.96	1.42	371.44	-183.72	0
Gamma	295.72	-145.86	1.21	372.63	-184.31	1.19
Log Normal	300.87	-148.44	6.36	371.55	-183.78	0.11
Gompertz	NA	NA	NA	NA	NA	NA
Log Logistic	304.2	-150.1	9.69	372.91	-184.46	1.47

For some transitions, models fitted with a Gompertz distribution could not be fitted due to convergence issues, these are represented by NAs.

Table 3: Model Comparison table for the effect of excursions and immigration on the likelihood of clinical TB developing calculated over different timeframes.

Months	Excursions		Immigration	
	AIC	Δ AIC	AIC	Δ AIC
1	201.31	2.90	207.41	6.16
2	201.69	3.29	206.88	5.63
3	201.51	3.10	210.08	8.83
4	200.23	1.83	208.13	6.87
5	199.12	0.71	206.21	4.96
6	198.40	0.00	207.99	6.74
7	198.99	0.59	201.25	0.00
8	199.96	1.56	203.59	2.33
9	200.22	1.81	204.11	2.86
10	200.24	1.83	206.60	5.35
11	200.48	2.08	205.33	4.07
12	200.12	1.72	205.63	4.38
13	200.33	1.93	206.70	5.45
14	200.36	1.96	206.92	5.66
15	200.09	1.69	207.97	6.71
16	199.95	1.55	209.34	8.09

Table 4: Multistate non-parametric survival model outputs for the transition from stable state to clinical TB, modelled with distinct periods of clinical TB that occurred within a set number of months of a previous clinical TB period merged and treated as a continuous clinical TB infection. Different timeframes for merging TB periods were modelled, ranging from 13 – 60 months in yearly intervals, with the results present here. 13 months is the timeframe over which clinical TB periods were merged in chapter. Full merge refers to a model where only the first occurrence of clinical TB was modelled, and all subsequent periods of clinical TB were treated as the same infection period.

Model	Events	EST	SE	Haz[95%CI]	p
<i><u>Immigration</u></i>					
13 months	41	1.369	0.404	3.93[1.78 - 8.68]	<0.001
24 months	38	1.405	0.425	4.07[1.77 - 9.38]	<0.001
36 months	38	1.405	0.425	4.07[1.77 - 9.38]	<0.001
48 months	35	1.485	0.44	4.41[1.86 - 10.45]	<0.001
60 months	34	1.441	0.445	4.22[1.76 - 10.12]	0.001
Full Merge	32	1.626	0.489	5.08[1.95 - 13.28]	<0.001
<i><u>Group Size</u></i>					
13 months	41	-1.346	0.563	0.26[0.08 - 0.78]	0.018
24 months	38	-1.251	0.584	0.28[0.09 - 0.90]	0.032
36 months	38	-1.251	0.584	0.28[0.09 - 0.90]	0.032
48 months	35	-1.163	0.616	0.31[0.09 - 1.04]	0.059
60 months	34	-1.107	0.627	0.33[0.10 - 1.13]	0.077
Full Merge	32	-0.904	0.637	0.41[0.12 - 1.41]	0.156
<i><u>Excursions</u></i>					
13 months	41	0.824	0.436	2.28[0.97 - 5.36]	0.059
24 months	38	0.941	0.47	2.56[1.02 - 6.44]	0.046
36 months	38	0.941	0.47	2.56[1.02 - 6.44]	0.046
48 months	35	0.89	0.526	2.41[0.86 - 6.74]	0.095
60 months	34	0.901	0.571	2.46[0.80 - 7.55]	0.11
Full Merge	32	0.512	0.541	1.67[0.58 - 4.83]	0.344

Table 5: Model outputs for GLMMs investigating the factors influencing the number of pups produced in the population during 3 month periods over the course of the study.

	Estimate \pm SE	z-value	P
<i><u>Group Model</u></i>			
Group Number	0.057 \pm 0.018	3.243	0.001
Quarter (Set to 1 st)			
2 nd Quarter	-1.115 \pm 0.163	6.861	<0.001
3 rd Quarter	-0.304 \pm 0.154	1.975	0.048
4 th Quarter	-0.154 \pm 0.150	1.029	0.303
Zero-Inflation Term	-2.870 \pm 0.474	6.160	<0.001
<i><u>Females Model</u></i>			
Adult Female Count	-0.000 \pm 0.003	0.244	0.807
Quarter (Set to 1 st)			
2 nd Quarter	-1.137 \pm 0.173	6.562	<0.001
3 rd Quarter	-0.295 \pm 0.166	1.774	0.076
4 th Quarter	-0.170 \pm 0.160	1.059	0.290
Zero-Inflation Term	-2.888 \pm 0.474	6.090	<0.001

Table 6: LMM model outputs for the effect of covariates on group size variation in the first 2 years of a group's longevity.

	Estimate \pm SE	z-value	P
Tenure*	-0.238 \pm 1.102	0.296	0.768
Failure Cause	4.234 \pm 1.333	3.176	0.002
Tenure:Failure Cause	1.691 \pm 0.945	1.790	0.074

*The tenure of a group is the time in months since the formation of the group.