

Dispersal Decreases Survival but Increases Reproductive Opportunities for Subordinates in a Cooperative Breeder

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ABSTRACT: In most socially structured populations, the formation of new groups depends on the survival and reproduction of dispersing individuals. Quantifying vital rates in dispersers, however, is difficult because of the logistic challenges of following wide-ranging animals. Here, using data from free-ranging meerkats (*Suricata suricatta*), we estimate survival and reproduction of dispersing females and compare these estimates to data for established residents. Meerkat groups consist of a dominant pair and several subordinate helpers. Female helpers are evicted from their resident groups by the dominant female, allowing her to monopolize reproduction, and evicted females may form small dispersing coalitions. We show that, as in established resident groups, one female is behaviorally dominant in parties of dispersing females. During dispersal and the first 4 months after new group formation, survival is lower for all females compared with established resident groups. At the same time, subordinates in disperser groups have higher birth rates than those in established groups, which rarely breed successfully. This may partly offset the survival costs of dispersal to subordinate females. Further studies of dispersal based on direct observation of dispersing animals are needed to explore the costs and benefits of dispersal in species with contrasting breeding systems.

Keywords: demography, dispersal distance, GPS tracking, settlement, transience.

Introduction

Natal dispersal plays a key role in the persistence of most natural populations, as dispersers ensure gene flow and recolonization of locally extinct territories (Bowler and Benton 2005). However, dispersal is often associated with high costs in species where individuals move through unfamiliar territories and have to compete for suitable breeding habitat during settlement (Bonte et al. 2012). In many birds and mammals, recruits delay dispersal for extended periods to avoid the high costs of dispersal (Bonte et al. 2012). During this delay, offspring of cooperative breeders can gain indirect fitness as subordinate helpers by helping raise close kin (Hamilton 1964; Koenig et al. 1992). In most cooperative mammals where females live in groups with relatives, subordinate females leave their natal group only when forcefully evicted (Cant et al. 2001; Clutton-Brock 2016). When evicted females eventually disperse, they form new groups and can attain direct reproductive output, although their breeding success may be low (Thompson et al. 2017; Duncan et al. 2018). As both costs and benefits of dispersing vary during transient and settlement stages of dispersal (Bowler and Benton 2005), stage-specific vital rates (i.e., survival and reproduction) need to be quantified to gain a comprehensive understanding of the fitness consequences of dispersal in cooperative breeder life history.

A variety of processes can be expected to influence survival and reproduction during transience and settlement (Bonte et al. 2012). For instance, unfamiliarity with a new area may result in reduced feeding efficiency (Pinter-Wollman et al. 2009) and decreased reproductive success (Part 1991). Unfamiliar and inhospitable territories also

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increase susceptibility to predators (Daniels and Walters 2000), and long-distance dispersers, which spend more time in such territories, have lower survival than short-distance dispersers (Murray 1967). There may also be additional anthropogenic dispersal costs, such as collision with wind turbines (Smallwood et al. 2009), power lines (Real and Mañosa 2001), roadkills (Klar et al. 2009), and killing by humans (Cozzi et al. 2020). Furthermore, dispersers are often exposed to aggression from resident conspecifics (Packer and Pusey 1982), and attacks may lead to critical wounds (Soulsbury et al. 2008) and increased stress (Young et al. 2006). An overall deterioration in body condition can in turn lead to a decrease in immune defense (Srygley et al. 2009). In cooperative species, the loss of social group benefits rendered by group members, such as antipredator vigilance and alloparental care, may further decrease survival and reproduction of dispersers (Brown et al. 1982).

Tracking free-ranging individuals over long distances can be difficult (Tomkiewicz et al. 2010), and most demographic studies of dispersal are therefore based on resightings (Daniels and Walters 2000; Germain et al. 2017; Martinig et al. 2020). Except for spatially closed populations (Nevoux et al. 2013; Kingma et al. 2016), such dispersal studies are inevitably biased toward short-distance movements within the study area, where disperser vital rates may be underestimated because individuals that leave the study area are often assumed dead (Lucas et al. 1994). In contrast, studies that rely on measurements of immigration rates may underestimate associated costs because individuals that immigrate are the ones that have survived dispersal (Koenig et al. 1996). Hence, to gain unbiased estimates of disperser vital rates, it is important to tag and track dispersers over all three dispersal stages, from emigration through transience to settlement. However, while several recent studies have used radio tracking to quantify energetic (Benoit et al. 2020) or endocrine (Maag et al. 2019) costs, no previous study of mammals has measured rates of survival and reproduction—and the biotic and abiotic correlates of changes in these rates—directly during the different stages of dispersal.

We worked with a population of wild but habituated meerkats (*Suricata suricatta*) in the Kalahari, where it was possible to systematically radio-tag and follow dispersing females and determine their fate during dispersal. Meerkats live in groups of up to 50 individuals that are composed of a dominant pair, which monopolizes reproduction, and several related subordinate helpers (Griffin et al. 2003). During her pregnancy, the dominant female often evicts one or multiple subordinate females (Young et al. 2006). Voluntary female emigration is not observed, and almost all dispersing females have been evicted from their natal group by the resident dominant female, who is

frequently their mother (Clutton-Brock et al. 1998). When two or more females are evicted simultaneously, they form coalitions (Clutton-Brock et al. 1998). Evicted females remain close to their natal group for a variable period, after which they are either accepted back to the natal group or permanently disperse in a coalition or alone (Maag et al. 2018). Dispersing females associate with unrelated males from other groups and attempt to establish their own new group (Maag et al. 2018). While males disperse voluntarily and can either group with evicted females to establish new groups or immigrate into existing groups (Mares et al. 2014), females are not usually allowed to immigrate into existing groups. Subordinate females can acquire dominance in their natal group either through inheritance after the previous dominant dies or through displacement (usually after a protracted fight), or they can acquire dominance through dispersal and establishment of dominance in a new group (Duncan et al. 2018; Morales-González et al. 2019). Hereafter, we refer to females that inherit dominance in their natal group or displace the dominant female there as “natal dominants” and to females that disperse and acquire a dominant position during group formation as “disperser dominants” (natal dominants very seldomly disperse).

Meerkats—like many other cooperative mammals (McNutt 1996; Cant et al. 2001) and some birds (Koenig et al. 2000)—disperse in coalitions, whereby increases in coalition size increase their chances of successful settlement and reduce the costs of dispersal (Young 2004; Maag et al. 2018). Dispersing in coalitions also guarantees the immediate presence of helpers, which may increase average survival and reproductive success in newly settled groups (Clutton-Brock et al. 2001*b*). When a new female assumes the dominant role in a meerkat group, either through inheritance in her natal group or through dispersing to form a new group, the likelihood of subordinate reproduction increases because the new dominant female is not immediately able to completely monopolize reproduction (Clutton-Brock et al. 2001*a*). With both dominant and subordinate individuals reproducing, groups may grow faster immediately after settlement, although when groups grow larger and multiple females are pregnant, reproductive competition and risk of infanticide increase as well (Young and Clutton-Brock 2006), which may offset the benefits of increases in group size. As newly formed groups grow, subordinate reproduction may decrease because established dominant females are better able to suppress subordinate females (Clutton-Brock et al. 2010; Harrison et al. 2021), and dominant reproduction and offspring survival increase as the number of helpers rises (Clutton-Brock et al. 2001*b*; Hodge et al. 2008).

Previous investigations of dispersal in meerkats have shown that evicted helpers do not persist in the population

as long as resident dominants and have attributed this to decreased rates of survival during extra-group prospecting trips (Cram et al. 2018), but none have been able to directly measure survival or reproduction rates during the different stages of dispersal (i.e., transience and settlement) or explore potential causes of variation in these rates. This is in contrast with the detailed information available on demographic rates in established meerkat groups (Clutton-Brock and Manser 2016).

In this study, we used radio tracking to collect vital rates of dispersing female meerkats (dominants and subordinates) from emigration through the transient stage of dispersal and for up to 2 years after settlement in a new territory. We compared vital rates of dispersing females to those of resident natal females while taking into account other environmental and social factors that have been shown to affect demographic rates and group dynamics in meerkats (e.g., temperature, rainfall, and population density; Ozgul et al. 2014; Maag et al. 2018; Paniw et al. 2019). We expected (1) that dispersers would have lower survival than residents based on results from meerkats (Cram et al. 2018) and other species (Bonte et al. 2012); (2) that rates of survival per unit time would be lowest during transience and would decrease with dispersal distance based on theoretical (Murray 1967) and empirical (Johnson et al. 2009) research; (3) that the probability of reproduction would be lower during transience and early settlement than in residents but that subordinates in disperser groups would have higher reproduction than those in established groups because subordinate breeding frequency increases when the identity of the dominant female changes (Clutton-Brock et al. 2001a); and (4) that both survival and reproduction would increase with dispersing coalition size (Clutton-Brock et al. 2001b; Young 2004).

Methods

Study Population

Our study was conducted between September 2013 and March 2018 at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26°59'S, 21°50'E), South Africa. We used a matched approach where we compared each dominant female in a dispersing coalition (and her subordinate coalition members) to the natal dominant female (and her subordinate group members) of the disperser's natal group. To make a meaningful comparison between natal and disperser dominants and their ability to monopolize reproduction, they had to be compared during the same life periods (i.e., similar ages). We therefore included dominant females from the start of their tenures (i.e., inheritance or displacement for natal individuals, eviction for dispersers) until they died or were no longer fol-

lowed (i.e., lost or alive at the end of the study). We selected natal dominant females by identifying those dominants that resided in dispersers' respective natal groups at the time of dispersers' eviction and then included backdated life history data on these natal dominants from the start of their tenures, resulting in a longer time series for resident females. We selected subordinate females present in the group or coalition (for dispersers) at the start of dominance tenure (i.e., eviction for dispersers) and included them until they died or were unfollowed.

Matched natal dominants attained their position on average at 9.6 months (interquartile range [IQR]: 7.8–27.1 months) prior to the eviction of dispersing coalitions. Therefore, some of the dispersing subordinates were followed as resident subordinates prior to their dispersal. As such, 26 out of a total of 55 resident females were followed before and after eviction. The remaining 29 resident females consisted of natal dominants and resident subordinates that died or were no longer followed before eviction (see below for more details). The 26 evictees that were followed prior to their eviction were joined by 37 younger evictees (individuals not yet born or of reproductive age at the start of their natal dominant's tenure) and dispersed as a total of 63 dispersing females. Hence, we worked with a total of 92 individual females (29 resident only; 26 before and after eviction; 37 disperser only) but pools of 55 (29 + 26) residents and 63 (26 + 37) dispersers, adding up to a total of 118 final events. A more detailed description of the selection process of study animals is included in the "Supplementary text" section of the supplemental PDF (available online), and we accounted for natal group and individual identity in all of our models (see below).

Captures and Tracking

We located dispersing coalitions and resident groups by means of radio tracking. One individual per resident group carried a radio collar (Biotrack, Wareham, United Kingdom; 23 g), and we fitted GPS radio collars (25 g; ~3.5% of meerkat body mass) to one female per dispersing coalition. As not all animals carried a collar, we used unique dye marks for individual identification within a group or coalition. The GPS collars were composed of a GPS module (CDD, Athens, Greece) and a VHF module (Holohil Systems, Ontario, Canada). Collars of the described size and weight do not compromise meerkat behavior and survival (Jordan et al. 2007). To mount the collars, we caught and sedated animals immediately after eviction using a mixture of isoflurane and oxygen, in compliance with the KMP protocol (Jordan et al. 2007). Eviction could be anticipated by a period of increasing aggression from the dominant female toward the subordinate prior to eviction. All necessary permits to handle and tag meerkats were granted to

the KMP by the Department of Environment and Nature Conservation of South Africa and the Animal Ethics Committee of the University of Pretoria (permit FAUNA 192/2014).

Dispersers

Dispersers included disperser dominants and their subordinate coalition members, which we visited every 2–7 days from eviction until they died ($n = 31$), were lost ($n = 20$), or were recorded as alive at the end of the study ($n = 12$). To identify the disperser dominants within each dispersing coalition, we observed the frequency and direction of aggressive behavior toward other coalition members, which is substantially higher in dominants than in subordinates (Thavarajah et al. 2014). In most cases, disperser dominants were identifiable in the first few days after eviction, and it is likely that the dominance hierarchy already existed prior to eviction, with the oldest and heaviest of subordinates taking the top position (Thavarajah et al. 2014). In addition, we recorded data on dispersing coalition size and number of associated unrelated males that remained with females for at least 4 days. After 4 days, most males permanently remained with the coalitions and were included in the analysis, whereas shorter, temporary associations with males were ignored.

To compare survival rates across dispersal distances and between transient and settlement stages, we used locations from the GPS collars. We calculated the Euclidean dispersal distance from the natal group for each dispersing coalition on any given day (fig. S1; figs. S1–S3 are available online). We defined the transition from transience to settlement based on visual investigation of the inflection point of the net squared displacement (NSD) plots (Cozzi et al. 2016). NSD measures the square of the Euclidean distance from the place of eviction to any given GPS location along the dispersal path and is commonly used to investigate different dispersal modes (Börger and Fryxell 2012).

Residents

Residents included natal dominants and their subordinates, which were visited on average five times per week by volunteers as part of the long-term research at the KMP (Clutton-Brock and Manser 2016) and were included until they died in their natal group ($n = 12$), were lost ($n = 8$), were evicted ($n = 29$), or were recorded as alive at the end of the study ($n = 6$). Twenty-six out of the 29 evictees were later followed as dispersers, and three could not be tagged. We excluded nonnatal dominant females that started a new group after dispersal in years prior to our study (i.e., earlier founder dominants) from this sample. Natal dominants were identified by the frequency and

direction of aggressive behavior toward their subordinate group members (Thavarajah et al. 2014). At each visit, volunteers recorded GPS locations of the groups with handheld GPS devices (Garmin, Olathe, Kansas) as well as information on individual age, number of males, total group size, reproduction, and mortality. The location of a group was defined by the location of its dominant female, such that the focus of observation was always with the dominant female even if she was temporarily separated from her group.

Collection of Vital Rates

We assessed two reproductive events: monthly probability of conceiving and giving birth and, conditional on successful birth, successful recruitment, that is, the number of pups that survived to at least 6 months of age (Ozgul et al. 2014). We identified pregnancies by abdominal swelling and associated weight increase. Females give birth to pups approximately 70 days after conception (generally occurring 4 weeks prior to initial weight gain). We assessed birth in the field by sudden weight loss and lactation marks (Sharp et al. 2013). Pups are weaned by the time they are 4–6 weeks old (Brotherton et al. 2001) and reach nutritional independence 2 months later. Three months after nutritional independence (i.e., 6 months of age), they become subadults (Brotherton et al. 2001). This also corresponds to the observed earliest age of dispersal. Information on individual age and relatedness to other individuals were available from the long-term KMP database.

After females had died, we located their collars and determined the cause of death. We assigned predation when the collar was found near a predator's nest or signs of predation were evident on the collar or on the meerkat's body; roadkills were evident when bodies were found on the road; and death following injury was usually preceded by a period of observed affliction. End-stage clinical tuberculosis, a prevalent cause of mortality in meerkats, could be identified by submandibular swellings, where individuals typically die within 6 months after swellings appear (Drewe 2010; Patterson et al. 2017).

Population Density

Population density has nonlinear effects on the probability of female emigration (Paniw et al. 2019) and the behavior of females during dispersal (Maag et al. 2018) and therefore was accounted for in our analyses. To estimate population density for each month (individuals/km²), we divided the number of all resident individuals present in the study population by the size of the population range. We obtained the population range by using GPS locations of meerkat sleeping burrows (collected

during group visits) to calculate 95% kernel utilization distributions (Calenge 2006). Detailed descriptions of the range estimation methods and smoothing parameter estimators can be found in Paniw et al. (2019).

Climatic Parameters

Temperature and rainfall variation are associated with changes in body mass, survival, and recruitment in the meerkats (Ozgul et al. 2014) as well as with changes in the size of groups (Groenewoud and Clutton-Brock 2020). To account for the effect of key climatic factors on vital rates, we obtained daily temperature estimates from the National Oceanic and Atmospheric Administration's (NOAA's) Climate Prediction Center (<https://psl.noaa.gov/data/gridded/data.cpc.globaltemp.html>) and monthly total rainfall data from NOAA's Global Precipitation Climatology Project (<https://psl.noaa.gov/data/gridded/data.gpcp.html>). We used the monthly average of maximum daily temperatures, which have been shown to reduce foraging time as meerkats avoid high midday temperatures by retreating into burrows or shaded areas (Doolan and Macdonald 1996). We used the sum of daily rainfall in the previous month because rainfall in the past 1 month is an indicator of ecological conditions such as food availability (Hodge et al. 2009).

Analysis

We tested for the effects of social status (dominant vs. subordinate vs. single dispersers), group size (coalition size for dispersers and group size for residents, including both sexes), and environmental factors on disperser and resident vital rates. To ensure that covariates were not correlated with each other, we calculated variance inflation factors for coefficients in the full models (Belsley et al. 2005). We standardized all continuous explanatory variables by subtracting their mean and dividing by their standard deviation. Model selection was based on Akaike's information criterion corrected for small sample sizes (AICc) and was performed using the library MuMin (Bartoń 2018) in R version 4.0.3 (R Core Team 2013). Where no single model was clearly the most parsimonious (i.e., $\Delta\text{AICc} < 2$), we chose the model with the fewer number of parameters, as it is reasonable to conclude that a covariate is not informative if it does not improve model fit by >2 AIC units (Arnold 2010). Details on candidate model list and model selection procedure can be found in tables S1–S4, available online. Data and code supporting this article have been archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.jm63xsj85>; Maag et al. 2022).

Survival. We used two Cox proportional hazard models with mixed effects implemented in the R library *coxme* (Therneau 2018) to analyze daily survival rates. We cal-

culated the daily likelihood of death—that is, hazard rate $h[t]$ —as a function of time-dependent covariates, where each day t is taken as a separate observation. To account for the unknown fate of individuals that were lost or un-followed (including females evicted from resident groups), we right censored these individuals, that is, labeled them as “not dead” on the day of last observation (75 out of 118 final events; Fox and Weisberg 2011). Right censoring is a common application in survival analysis and applied to incomplete fates to avoid biasing survival estimates toward dead individuals. In practice, one includes an event variable (i.e., death), which is coded as 1 if the event occurs or as 0 if the period of observation expires or an individual is lost before the event occurs.

In the first model, we tested for differences in survival between dispersers and residents (*pathway*) as well as between dominants and subordinates (*status*). As single dispersers could be categorized as neither dominant or subordinate, we included lone individuals as a third *status* category. We included age (*age*), group size (coalition size for dispersers, *coal*), whether males were present or not (*male*), population density (*pop*) and its quadratic effect (*pop*²; to account for known nonlinear associations between density and survival), rainfall (*rain*), and temperature (*temp*) as further covariates. We also tested for two-way interactions between *pathway* and *age*, to investigate whether older individuals had an advantage during dispersal (Maag et al. 2019), and between *pathway* and *coal*, to assess different effects of group size in dispersers and residents (Young 2004). Since lone females occurred only in dispersers, we first included only an additive *pathway* and *status* effect. We then performed an additional run of the model, where we excluded lone females and tested for interactions between *pathway* and *status* (tables S1a—additional run). To control for repeated sampling across time and individuals, we used month of the year (*month*) and individual identity nested in natal group identity (*group/ind*) as random terms in both survival models and in all reproduction models described below.

In the second model, we looked at dispersers only to investigate the survival difference between two dispersal stages (*stage*: transience vs. settlement) and how survival was influenced by dispersal distance from the natal group (*dist*). We used the covariates *age*, *status*, *coal*, *pop*, *pop*², *rain*, *temp*, and the interaction between *stage* and *coal* to assess different effects of coalition size during transience and settlement (table S1b).

In addition, we compared the causes of mortality between dispersers and residents (totally tuberculosis = 22 individuals; predation = 16; roadkill = 2; injury = 2; unknown = 1) with a multinomial logistic regression using the library *nnet* (Venables and Ripley 2002). As sample sizes were small, we pooled roadkills, injuries, and

unknown causes and performed regression with *pathway* as single predictor and no random effects (table S2). Here, we did not perform model selection but used hypothesis testing with *P* values.

Birth. We estimated birth rates at a monthly interval by generating discrete-time-step censuses (0 = no birth, 1 = birth) for each individual (Paniw et al. 2019). We used a generalized mixed effects model (GLMM) to investigate the monthly probability of birth as a binomial response variable (table S3). Here and for all models below, we used the R library lme4 (Bates et al. 2014) to perform GLMMs. We used the covariates *pathway*, *status*, *coal*, *male*, *pop*, *pop*², *rain*, *temp*, and two-way interactions *pathway* × *pop*. In addition, we tested whether subordinates had increased birth rates in the first few months after dominance takeovers (Clutton-Brock et al. 2001a) and whether this effect differed between dispersers and residents by using time elapsed since the start of dominance tenure (*time*) and its two-way interaction with *pathway*. As with survival, we performed an additional run of the model, where we excluded lone females and tested for interactions *pathway* × *status* and *pathway* × *status* × *time* (table S3—additional run) to assess differences in the relative frequencies of reproductive rates between subordinates and dominants in disperser and resident groups (Clutton-Brock et al. 2001a). This way, we account for the possible effect of limited control of novice dominant residents on subordinate conception rates. We excluded *age* from the model because of strong collinearity with *time*.

Recruitment. Conditional on birth, we investigated recruitment as the number of pups that survived to at least 6 months of age using a Poisson GLMM (after testing and finding no overdispersion; Ver Hoef and Boveng 2007). We included the covariates *age*, *coal*, *pathway*, *status*, *rain*, *temp*, and *pathway* × *coal* (table S4). As with birth, we first looked at additive *pathway* and *status* effects and then at their interaction (*pathway* × *status*) after removing lone dispersers from the data (table S4—additional run). As recruitment is conditional on birth, sample sizes (shown in tables S3, S4) decreased, and we dropped the covariates *male*, *pop*, and *pop*² from the recruitment models to avoid overfitting.

Results

Females that we followed from eviction to their new territory settled on average 2.2 km (minimum–maximum: 0.4–10.7 km) away from their natal sites, with 27% of dispersers settling outside the study area. We followed dispersers for a mean period of 5.6 months (IQR: 1.0–9.0 months), with the longest period being 2.3 years (834 days). Settlement occurred after a mean transient time of 50 days (IQR: 30–59 days). Female meerkats dispersed either alone or in dis-

persing coalitions that ranged from one to six females and later grouped with none or up to six unrelated males. Resident groups contained 1–13 females and 0–16 males, including adults and subadults.

Evicted females included 16 females that were clearly dominant to other members of their coalition (i.e., disperser dominants), 30 females that were subordinate in their coalition, and 17 females that were single dispersers. Fourteen of the original 30 subordinates (47%) inherited the dominant position in their coalition over the study period. Most single dispersers (13/17) were evicted as part of a coalition but became single after the death of coalition members. Of the resident females, 13 females acquired the dominant position during the study period (i.e., natal dominants), and 42 females were subordinates. Subordinate females in dispersing coalitions were therefore more likely to gain dominance (32% of all dispersers) than subordinate females in resident groups (23% of residents).

Mean age at the start of dominance tenure for dispersing animals was 2.5 years (IQR: 1.8–2.9 years), compared with 2.4 years (IQR: 1.9–2.7 years) for natal dominants; the corresponding age for disperser subordinates was 2.0 years (IQR: 1.3–2.7 years) and 2.1 years (IQR: 1.1–3.0 years) for resident subordinates. Mean dominance tenure length was 0.7 years (IQR: 0.1–1.0 years) in disperser dominants and 2.6 years (IQR: 1.1–3.7 years) in natal dominants.

Survival. The most parsimonious Cox proportional hazard model suggested that *pathway* (disperser vs. resident) accounted for a substantial amount of variation in daily survival rates (i.e., daily hazard of dying). Resident females' daily log odds of dying were 1.70 lower than those for dispersing females that either were in transience or had recently established a new group (table 1; fig. 1a). Neither dispersal distance (net squared displacement) nor dispersal stage (transience vs. settlement) were included in the most parsimonious model (table S1b). The increased mortality among the dispersers could be attributed to a higher probability, compared with residents, of dying from tuberculosis (log odds = 2.89, *P* = .020) and predation (log odds = 2.49, *P* = .048; fig. 1b; table S2). Among dispersing or resident individuals, female status (dominants, subordinates, or lone females in dispersers) did not account for much variation in daily survival (table S1a). In the most parsimonious model, daily log odds of dying were negatively correlated with population density, likely reflecting environmental conditions that positively affect the entire population (Paniw et al. 2019), and increasing age had a positive effect on daily odds of dying in both dispersers and residents (table 1). Coalition size, presence of males, rainfall, and temperature did not affect survival (table S1a).

Birth. The most parsimonious binomial GLMM that included lone dispersers suggested that female *status*

Table 1: Effects of individual, social, and environmental factors on survival and reproduction of female meerkats

Model	Estimate	SE
Daily hazard of dying:		
<i>pathwayRes</i>	-1.70	.49
<i>pop</i>	-.45	.16
<i>age</i>	.56	.01
Monthly birth probability:		
<i>statusSub</i>	-.42	.27
<i>pathwayRes</i>	.24	.21
<i>pathwayRes</i> × <i>statusSub</i>	-.98	.40
No. subadults recruited:		
<i>age</i>	.18	.07
<i>statusSub</i>	-.10	.18
<i>statusSingle</i>	-.89	.36

Note: The estimate and standard error from the most parsimonious model are reported for each explanatory variable (for details, see the tables in the supplemental PDF). The explanatory variables are as follows: *pathway* = disperser versus resident; *status* = dominant versus subordinate versus single; *age* = female age; *pop* = population density. The base levels for categorical variables *pathway* and *status* (i.e., intercept) are dispersers (*pathwayDis*) and dominant (*statusDom*), respectively.

accounted for a substantial amount of variation in birth rates. In this model, the log odds ratios of giving birth were 0.9 lower for subordinate females than for dominants, regardless of whether these females were in resident groups or dispersing (fig. S2; table S3). At the same time, the most parsimonious model that excluded lone dispersers to test for an interaction effect between female

pathway (disperser vs. resident) and social *status* (dominant vs. subordinate) on birth rates suggested that this interaction effect was an important predictor of birth rates (tables 1, S3—additional run). That is, in resident groups, the differences between dominant and subordinate birth rates were substantially more pronounced than in dispersing coalitions. Average birth probabilities were 0.20 and 0.04 on average for dominant and subordinate females in resident groups, respectively (fig. 2). Subordinate females in dispersing groups, on the other hand, had higher birth rates (0.14 on average) than their counterparts in resident groups, and, unlike in resident groups, these rates did not differ substantially between females that gained dominance or remained subordinate during dispersal (fig. 2). The most parsimonious model also suggested that no other covariate explained a substantial amount of variation in birth rates (table S3), and the lack of an effect of presence of males suggests that females effectively always have access to a mating partner (Mares et al. 2014).

Recruitment. The most parsimonious Poisson GLMM suggested that the recruitment of subadults was substantially lower for females that dispersed alone (i.e., lone females had 0.89 lower odds of recruiting than dominants). But recruitment did not differ among resident or dispersers or among dominants or subordinates (fig. 3). The most parsimonious model also indicated that recruitment was additionally strongly positively affected by the age of the female (the odds of recruiting increasing by 0.18 with every month of age; tables 1, S4; fig. 3).

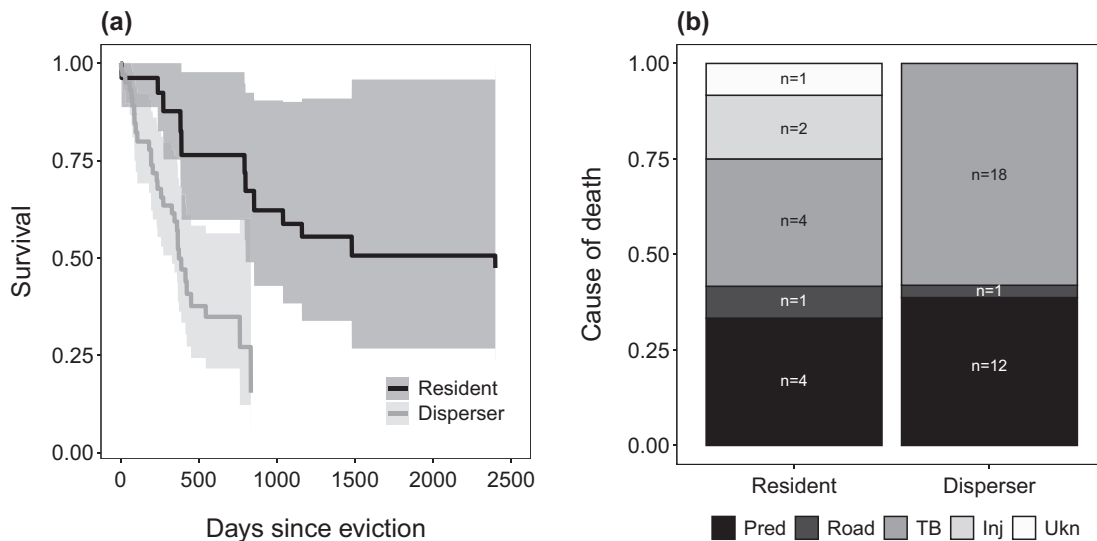


Figure 1: Differences in daily survival (a) and cause of mortality (b) between resident and dispersing female meerkats. In a, the survivorship curve and 95% confidence intervals are predicted by a Cox hazard model comparing female strategies. Age and population density were set to average values. In b, results are shown for predation (Pred), roadkill (Road), tuberculosis (TB), injury (Inj), and unknown (Ukn).

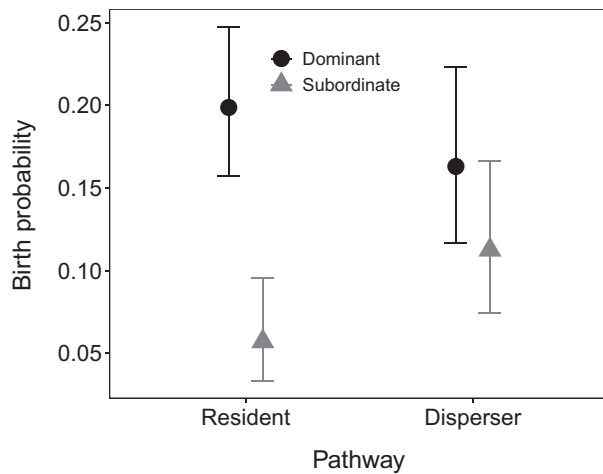


Figure 2: Birth probabilities in resident and dispersing female meerkats depending on their social status (dominant or subordinate). Mean probabilities (points) and 95% confidence intervals (error bars) show predictions from a binomial generalized mixed effects model.

Discussion

We monitored dispersing female meerkats from emigration to death or until they were no longer followed, which occurred on average 6 months after emigration, and compared daily survival rates and reproductive parameters to those of resident females. We found that during transient and settlement stages, dispersers had lower survival rates than residents. We also found that birth rates of subordinates in newly formed disperser groups were higher than those of subordinates in established resident groups. Our

study emphasizes the importance of following dispersers through transience and settlement to estimate and understand the costs of dispersal in natural populations.

By frequently assessing survival and reproduction during the entire dispersal event, we extend previous studies of the cost of dispersal in meerkats (Young et al. 2006; Cram et al. 2018; Duncan et al. 2018), other social species (Heg et al. 2004; Ridley et al. 2008), and animal species in general (Bonte et al. 2012). The lower survival of dispersers compared to residents in our study confirms that dispersal incurs high costs. These costs likely arise because dispersing groups move through unfamiliar territory, which can cause a reduction in feeding efficiency (Pinter-Wollman et al. 2009) or body mass (Maag et al. 2019). Dispersal may also exacerbate the consequences of infectious diseases. Evicted meerkat females are likely already infected with *Mycobacterium suricattae*, which causes tuberculosis, potentially as a result of frequent aggression received from dominants (Drewe 2010). However, increased physical stress during dispersal may contribute to outbreaks and rapid progression of clinical, end-stage tuberculosis (Dwyer et al. 2020). The potential costs of dispersal in terms of disease dynamics may be prevalent among mammals but have received relatively little attention (Bonte et al. 2012).

Higher mortality during dispersal probably explains why subordinate females do not leave their natal group unless they are forcefully evicted (Young et al. 2006). In addition, once dispersers gain dominance in a new group, their reproductive output does not differ substantially to resident dominants, and previous analyses that have compared survival and lifetime reproductive success of established dominants that obtained their position after dispersing with those of established breeders that inherited

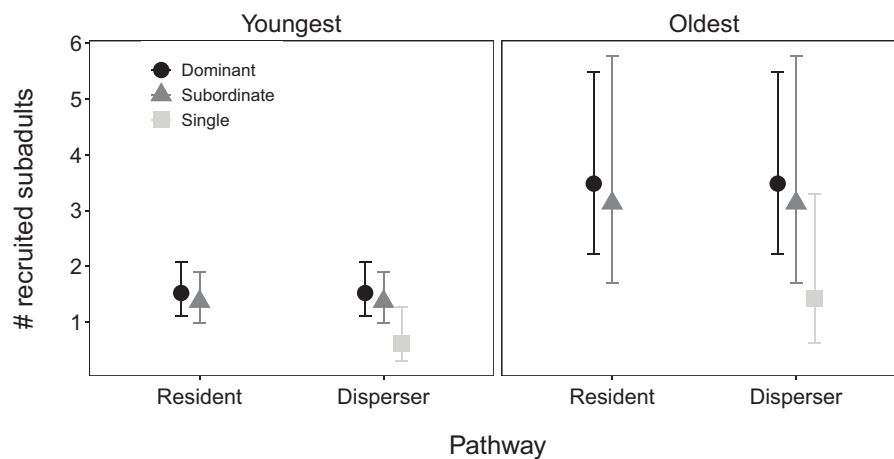


Figure 3: Number of recruited subadults (≥ 6 months of age) among resident and dispersing female meerkats depending on their social status (dominant, subordinate, or lone) and age (youngest = 12 months; oldest = 99 months). Mean recruitment (points) and 95% confidence intervals (error bars) show predictions from a Poisson generalized mixed effects model.

dominant status in their natal group found no differences between them (Duncan et al. 2018). This indicates that the lifetime reproductive success (i.e., survival and reproductive output) of females that remain in their natal groups and queue for and acquire the dominant position there is higher than that of dispersers. Therefore, direct fitness benefits alone—as opposed to indirect fitness benefits (Hamilton 1964)—may be sufficient to retain offspring (Koenig et al. 1992; Clutton-Brock and Manser 2016).

Although theoretical models have predicted that the survival of dispersers should decline with dispersal distance (Murray 1967) and there is some empirical evidence that this is the case in other species (Johnson et al. 2009), survival of meerkats did not vary with dispersal distance. We previously showed that glucocorticoid levels and body mass were also independent of dispersal distance (Maag et al. 2019). One possible explanation is that long-distance dispersers were more likely to locate better patches of habitat than animals that did not move so far and that the effects of differences in range quality offset the costs of long-distance dispersal (Koenig 1999; Stamps et al. 2005). However, it is also possible that there is substantial stochastic variation in survival that obscures any effect of dispersal distance or that we overestimated the survival of long-distance dispersers, since we were unable to determine the fates of a substantial proportion of animals in our sample (20 out of 63). Existing empirical studies of survival costs in relation to dispersal distance suggest that there is considerable variation across species (Johnson et al. 2009; Lowe 2010), and further empirical studies are needed to better understand the influence of dispersal distance on dispersal survival and the costs and benefits of long-distance dispersal.

Our work also shows that an increased reproductive output during dispersal and immediately after settlement may offset the high costs of dispersal to subordinate females. Limited control theory suggests that reproductive skew results from variation in the capacity of dominants to suppress subordinate reproduction (Clutton-Brock 1998) and can result in subordinates adversely affecting fitness components of dominants (Cant et al. 2001). Optimal skew theory, by contrast, suggests that reproductive skew results from dominants making reproductive concessions to retain subordinates as helpers (Vehrencamp 1983). By showing that dispersing meerkats incurred high survival costs, our findings support the limited control theory, as no reproductive concessions may be necessary to retain helpers in the group. The increase in birth rates in subordinate dispersers may indeed have been facilitated by the failure of novice disperser dominants to suppress subordinate reproduction, leading to reduced reproductive skew in the first months after settlement (Harrison et al. 2021). This conclusion is in line with Clutton-Brock et al. (2001a), who showed that the limited control of newly dominant

females leads to increased subordinate birth rates in the first 3 months after dominance inheritance. Subordinate females also appear more likely to gain dominance in a newly formed group compared with subordinates in resident groups, and such prospective reproductive monopoly once the group is established can further offset dispersal costs (Robbins et al. 2019).

Interpreting the relative benefits of philopatry versus dispersal is often challenging in longitudinal observational studies of social animals (Akçay et al. 2012), as differences in traits among individuals may confound such interpretations. Older individuals that are most experienced or ones that have superior phenotypes are both more likely to disperse successfully (Debeffe et al. 2012; Maag et al. 2019) and reproduce in their natal group after dominance change (Hoogland 1995; Buston 2003), which then obscures the benefits gained when dispersing. Age, however, did not explain differences among females in survival and birth rates in our models, indicating that our inferences on changes in reproductive skew are robust (Ross et al. 2020). In addition, our results show a relatively low contribution of individual variation to variation in survival and birth rates (see the supplemental PDF), which suggests that unobserved differences in individual quality did not substantially affect our interpretation of costs and benefits of dispersal for subordinate females.

A positive effect of increasing group size on breeding success has previously been shown in meerkats (Clutton-Brock et al. 2001b) and other social mammals (Malcolm and Marten 1982; Rood 1990; Clutton-Brock 2016). The reason that we did not observe this effect in our analyses may be due to our categorization of lone dispersers into a separate social status, obscuring the effect of group size. We chose to do this because lone dispersers could be assigned to neither dominants nor subordinates, as categorization of dominants and subordinates is by definition based on behavioral interactions. At the same time, while increased breeding success in larger groups has been shown for dominants, subordinates breed more frequently in smaller groups (Ozgul et al. 2014), so that groups can rapidly increase in size (Clutton-Brock and Manser 2016). This may explain why no positive association between group size and breeding success is evident in dispersal coalitions, which are generally smaller than established groups.

The costs of dispersal are likely to differ between species in relation to contrasts in their social organization (Clutton-Brock 2016). For example, they may be particularly high for females in species, like meerkats, where groups consist of related individuals that defend their territories against intruders and females are unable to join established breeding groups. The costs of dispersal may be much lower in other mammals where females habitually leave their natal groups after reaching breeding age

and without receiving aggression, like golden lion tamarins (Romano et al. 2019), and where groups consist of unrelated females and dispersing individuals are usually able to join established groups without harassment, as in social equids (Monard and Duncan 1996) and some primates, like mountain gorillas (Harcourt and Stewart 2007). Since dispersal has far-reaching consequences for the demography and genetic structure of populations, developing an understanding of the related costs and how these vary among different life histories is likely to be a necessary component of future studies. As our study shows, this will require further studies that follow dispersing individuals and monitor their survival and reproduction throughout their entire life spans.

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Statement of Authorship

N.M., G.C., and A.O. conceived the study. N.M. collected data on dispersing individuals and wrote the original manuscript, while M.P. wrote the first revised version of the manuscript. N.M. and M.P. performed statistical modeling and wrote the final version of the work. G.C. and A.O. consulted on statistical modeling and writing. T.C.-B. and M.M. led the collection of data on resident groups. All authors discussed the results and contributed to the manuscript.

Data and Code Availability

Data and code supporting the results of this article have been archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.jm63xsj85>).

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