

Cost of dispersal in a social mammal – body mass loss and increased stress

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Abstract

Dispersal is a key process influencing the dynamics of socially and spatially structured populations. Dispersal success is determined by the state of individuals at emigration and the costs incurred after emigration. However, quantification of such costs is often difficult, due to logistical constraints of following wide-ranging individuals. We investigated the effects of dispersal on individual body mass and stress hormone levels in a cooperative breeder, the meerkat (*Suricata suricatta*). We measured body mass and faecal glucocorticoid metabolite (fGCM) concentrations from 95 dispersing females in 65 coalitions through the entire dispersal process. Females that successfully settled lost body mass, while females that did not settle but returned to their natal group after a short period of time did not. Furthermore, dispersing females had higher fGCM levels than resident females, and this was especially pronounced during the later stages of dispersal. By adding information on the transient stage of dispersal and by comparing dispersers that successfully settled to dispersers that returned to their natal group, we expand on previous studies focusing on the earlier stages of dispersal. We propose that body mass and stress hormone levels are good indicators to investigate dispersal costs, as these traits often play an important role in mediating the effects of the environment on other life-history events and individual fitness.

Keywords: Dispersal stage, glucocorticoid metabolites, individual trait, life history, meerkat

Introduction

Dispersal is an important life-history process typically consisting of three stages: emigration from a natal territory, transience through an unfamiliar landscape, and settlement in a new area [1,2]. At each stage, dispersing individuals incur costs resulting from different individual, social, and environmental factors, and these costs influence the outcome of dispersal and consequently the associated population dynamics [1,3]. Costs of dispersal have been typically measured in the form of changes in survival and reproductive rates [3–5]. However, the effects of social and environmental factors on survival and reproduction are often mediated by morphological and physiological traits [6–8]. As such, a more mechanistic understanding of dispersal costs can be achieved by investigating traits such as body mass and stress hormone levels, which are known to correlate with individual fitness [9,10].

A variety of processes can be expected to influence body mass and stress hormone levels during dispersal [3]. For instance, unfamiliarity with a new area may result in reduced feeding efficiency [11], which may lead to loss in body mass and increased stress hormone levels. Unfamiliar territory often comes with higher susceptibility to predators, which might be reflected in further elevated stress levels [12]. Furthermore, dispersers are often exposed to aggression from resident conspecifics [13,14], and attacks may lead to wounds and increased stress [15–17]. An overall deterioration in body condition can in turn lead to a decrease in immune defence [18–20]. Social factors associated with dispersal, such as loss of social rank and loss of benefits rendered by group membership (e.g., secured foraging territory and anti-predator vigilance), may further exacerbate morphological and physiological costs of dispersal [21,22].

Due to the difficulties of following wide-ranging individuals in the wild, quantification of morphological and physiological costs of dispersal has proven challenging, and there have been only a few such studies on vertebrates. For example, in the red squirrel (*Tamiasciurus hudsonicus*), where juveniles make temporary forays outside the natal territory prior to emigration, no strong relationship between maximum foray distance and body mass was observed [23]. In the cooperatively breeding pied babbler (*Turdoides bicolor*), lone evicted individuals (“floaters”

without territory) lost more body mass than residents due to increased time allocated to vigilance and less efficient foraging [24]. In the cooperatively breeding meerkat (*Suricata suricatta*), where subordinate males undertake extraterritorial prospecting trips [25] and subordinate females are evicted from their natal group [26], both sexes experienced increased stress levels and body mass loss while outside their natal group [16,25,27]. In addition, female meerkats showed reproductive down-regulation [16] and males showed increased testosterone levels [27]. All the above-mentioned studies followed individuals during exploratory movements and early phases of dispersal. Such results are, however, not generalizable among dispersal stages, because disperser candidates are often young and inexperienced and exploratory movements are typically carried out close to the natal range [16,28].

Social species may be able to alleviate some of the costs of dispersal by forming multiple-member dispersing coalitions [29–31], and in many cooperative breeders, subordinate helpers disperse in multiple-member coalitions [13,32–34]. Larger coalitions are likely to experience reduced individual predation risk [30,35], have increased competitive ability [36–38], and faster group-size augmentation, as having more helpers increases reproductive success [31]. Dispersing in larger coalitions may also reduce deterioration in body condition. For example, meerkats that left their natal group in larger coalitions had higher hourly foraging mass gain and lower parasite loads and stress levels [38]. However, how body condition changes with varying coalition size during the entire dispersal event has not yet been formally tested.

Meerkats live in groups of 2–50 individuals and groups are characterized by the presence of a dominant pair that monopolises reproduction [26,39]. During her pregnancy, the dominant female often evicts one or multiple subordinate females [16,26]. When several females are evicted simultaneously, they usually form same-sex multiple-member dispersing coalitions [26]. After eviction, females remain within the territory of the natal group for a variable period (hereafter referred to as the “post-eviction stage”). At the end of this period, individuals are either accepted back to the natal group as “returners”, or permanently emigrate and enter transience as “emigrants”. Emigration is here defined as the time when emigrants leave the natal territory and enter transience. Returners do not leave the natal territory nor enter the transient stage [40]. Evicted females’ decision to return or emigrate is dependent on a

multitude of factors such as natal group size, age, rainfall, population density, coalition size, and availability of unrelated males from other groups [40,41].

In this study, we explore the morphological and physiological costs of dispersal throughout the entire dispersal process from the eviction of subordinate female meerkats until either establishment of a new group or return to the natal group. As such, we extend previous studies by comparing dispersers that successfully settled to dispersers that returned, and by formally assessing costs during the transient stage. We specifically investigate (1) how the loss in body mass and faecal glucocorticoid metabolite levels vary among emigrants, returners, and resident subordinates; and (2) how these measures change between emigration and transient stages. We further investigate (3) how these changes vary with the size of the dispersing coalition while controlling for additional individual and environmental factors.

Methods

We conducted our study between September 2013 and March 2017 at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26° 59' S, 21° 50' E), South Africa. The region is characterized by low seasonal rainfall between October and April and large daily and seasonal temperature variations [26]. Temperature data were collected hourly and precipitation data daily with an on-site weather station, allowing for accurate investigation of climatic conditions.

GPS data collection and definition of dispersal stages

We fitted lightweight GPS radio-collars (<25 g, ~3.5% of body mass) on subordinate females a few days prior to, or immediately after, eviction from their natal groups. The collars were composed of a VHF module (Holohil Systems Ltd., Canada) and a GPS module (CDD Ltd., Greece). Collars of this size and weight do not affect meerkat behaviour and survival [42], and we did not observe any sign of distress in animals carrying collars. Typically, only one individual in each dispersing coalition was fitted with a radio-collar. To mount the collars, we sedated individuals using a mixture of isoflurane and oxygen in compliance with the KMP protocol and in collaboration with trained project staff [42]. All necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of the Northern Cape, South Africa, and the Animal Ethics Committee

of the University of Pretoria (permit 'FAUNA 192/2014'). We set the collars to automatically record and store GPS locations at hourly intervals during daytime [43]. However, due to miniaturization of the GPS antenna, we observed a considerable amount of missing GPS fixes (i.e., on average 40 % of fixes were not recorded).

We used the net squared displacement (NSD) approach, which is stable against missing GPS fixes, to identify time of emigration and time of settlement. The NSD measures the square of the Euclidean distance from the place of eviction to any given GPS location along the dispersal path [44]. By visually investigating the NSD plots of each dispersal event, we identified the inflection points [45], which corresponded to time of emigration and time of settlement (Supplementary material: Figure S1). We further used field observations to validate the NSD approach.

Field observations

We located collared dispersing females by means of VHF radio-tracking every two to seven days. Study animals were part of the long-term research at the KMP and were habituated to the presence of humans [46]. At each visit, we recorded dispersing coalition size, number of associated unrelated males from other groups, and pregnancy status, and we measured individual body mass and collected faecal samples for stress hormone metabolite analysis (see below for more details). To compare dispersers (emigrants and returners) to resident females, we included data collected on same-age subordinate females that resided in the dispersers' respective natal groups (hereafter referred to as "residents").

Resident groups were located by means of VHF radio-tracking (one individual per group was carrying a radio-collar) several times each week by volunteers working at the KMP, and data on group size and composition, female pregnancy status, body mass, and faecal samples were collected. Information on birth date and relatedness of each individual (i.e., dispersers and resident) were available from the long-term database. We considered data on resident individuals for the exact period during which dispersers were absent from the group.

Determination of body mass

Individuals in our study population were trained to stand on an electronic balance [46]. We weighted dispersing females at each visit, either in the morning before foraging started or in the evening after foraging ended. To match mass measures collected in the evening and morning, we subtracted the average overnight mass loss (28 g for dispersers) from evening masses and treated them as morning masses on the following day. We calculated average overnight mass loss by subtracting evening and morning masses of dispersers for which consecutive measures were available. Morning measures for resident females were more abundant as resident groups were visited five times per week, and therefore, morning measures alone were sufficient for residents. We excluded from the analyses mass data from pregnant females between the day of conception and the day of parturition or abortion. We determined pregnancy onset by backdating 28 days from the first evidence of abdominal swelling [47,48]. We identified parturition and abortion from a sudden change in abdominal shape and mass loss. After filtering data, we had 192 mass measurements from 25 emigrants, 200 from 28 returners, and 504 from 49 resident subordinates.

Faecal glucocorticoid metabolite (fGCM) analysis

We opportunistically collected faecal samples for fGCM analysis immediately after defecation and assigned them to identified individuals. The average time lag between a perceived stressor and its reflection in altered meerkat fGCM concentrations is about 24 hours [49] and we therefore did not collect faecal samples within 2 days after collar deployment. We kept collected samples in insulated thermal bags filled with ice packs until the samples were frozen at -80°C within three hours from collection. Overall, we collected 125 samples from 32 emigrants, 113 samples from 25 returners, and 111 samples from 47 resident subordinates. For steroid extraction, we lyophilized and pulverized faecal samples, and subsequently extracted 0.10-0.11 g of faecal powder with 3 ml of 80 % watery methanol [50]. We subsequently analysed faecal extracts for immunoreactive glucocorticoid metabolite concentrations using a group-specific enzyme immunoassay (EIA) for the measurement of 11 β -hydroxyetiocholanolone [51]. The assay has previously been validated for assessing glucocorticoid output in captive meerkats [49] and has recently been applied successfully to study adrenocortical activity of wild meerkats [52]. Details on assay performance and characteristics, including full descriptions of the assay components

and cross-reactivities are provided elsewhere [51,53]. The sensitivity of the EIA at 90 % binding was 0.6 pg. Intra- and inter-assay coefficients of variation of high- and low-value quality controls were 6.2 % (high) and 8.1 % (low) and 7.3 % (high) and 8.7 % (low), respectively. All fGCM concentrations are expressed as hormone mass per dry faecal mass.

Statistical modelling

We used linear mixed effects models to analyse variation in (1a) body mass loss and (1b) fGCM concentration among emigrants, returners, and residents. We used two additional models to compare (2a) body mass loss and (2b) fGCM concentration between post-eviction (time between eviction and emigration) and transient (time between emigration and settlement) stages. For models 2a and 2b we only used data collected on emigrants. We conducted all statistical analyses using the library *lme4* [54] in the software R [55]. We used the library *MuMin* [56] to test different combinations of individual, social, and environmental variables using model selection based on Akaike's Information Criterion [57]. As we could not identify any single best model, we calculated the natural model average across all models with ΔAIC_c values within 2 units [58]. Details for full models, descriptions of model variables, and outcomes of model selection are given in the supplements (Tables S1-S4). To ensure that predictor variables were not correlated with each other, we calculated variance inflation factors [59] for coefficients in the full models. We standardised continuous variables across all data points used for a given model by subtracting their mean and then dividing by their standard deviation. We created residuals plots (Figure S2) and investigated them visually to ensure that model assumptions were met; we did not find any considerable departure from theoretical expectations. Additionally, for each female, we obtained autocorrelation function plots from model residuals to test for temporal autocorrelation [60]. Model residuals showed minor autocorrelation in 3.8 % of the cases and we therefore did not consider temporal autocorrelation as reason for concern.

1a) Body mass in emigrants, returners, and residents: We compared the daily proportional change in body mass of emigrants to those of returners and residents. We used a proportional rather than absolute mass change because a given mass loss (or gain) in a light individual would not be equivalent to the same mass loss (or gain) in a

heavy individual. Because mass data were collected opportunistically, time between mass measures varied considerably and ranged from 1–81 days (average: 3.21 days, interquartile range: 1–4 days). As we could not assume linearity in mass change across time, we could not reliably and consistently calculate a typically used daily growth rate. Instead, we used a net proportional daily growth rate since eviction $(m_t - m_0)/(m_0 * \Delta t)$, where m_0 is the mass at eviction and Δt is the number of days elapsed between eviction and a given mass measure m_t . Because we were interested in comparing emigrants, returners, and residents, we included a categorical variable (*strategy*) with these three levels. As larger individuals usually have higher metabolic rates and may lose proportionally more of their body mass [61], we added mass at eviction m_0 as an explanatory variable. We treated m_0 as a surrogate for body condition because we could not measure body size in the field. We also included the number of days since eviction (Δt) to investigate if time away from the group influenced mass loss. We included both *age* and $age^{1/2}$ to account for known nonlinearity in meerkat growth [62]. We included a continuous variable (*#female*) indicating the average number of females in a coalition. The reason for averaging being that only 29% of the coalitions changed in size and such changes were of only ± 1 individual in most cases. Without averaging, these coalitions would have had a disproportionate high weight in the model output. We added additional covariates, which are known to influence mass of meerkats: number of nutritionally dependent offspring younger than three months in the relevant group (*#pup*), maximum daily temperature (*temp*), and cumulative amount of rain during three months prior to mass measurements (*rain*, [62]). We assigned a unique coalition ID to each dispersal event, and resident individuals that were in dispersers' respective natal group during a given dispersal event.

We treated individual (*indID*) nested in coalition (*coalID*) as the random intercept terms, to account for consistency across repeated measures. Because *coalID* was specific to a given year and therefore partially captured the year effect, we did not include year as a random term to avoid overfitting. We assessed the variability within and between individuals and coalitions by calculating the within-individual and within-coalition repeatability [63]. We calculated repeatability for all models described below.

1b) *fGCM in emigrants, returners, and residents*: The distribution of *fGCM* levels was right-skewed, and we used $\log(fGCM)$ as response variable in order to assess differences in stress hormone levels between emigrants, returners, and residents. As described above, we included *strategy* as well as Δt , *age*, *temp*, *rain*, *#female*, and *male* as explanatory variables. Faecal GCM concentration can vary during the day [49] and between pregnant and non-pregnant females [64]. We accounted for this variation by incorporating two fixed binary variables: sample collected during morning hours (5-12:00) vs. sample collected in the afternoon (15-20:00, *collect*) and female pregnant vs. not pregnant (*preg*). As above, we treated *indID* nested in *coalID* as random intercept terms.

2a) *Emigrant body mass during dispersal stages*: In this analysis, we focused solely on emigrants, ignoring returners and residents, as we were interested in the effect of dispersal stage, which is not available for returners and residents. As above, we used $(m_t - m_0)/(m_0 * \Delta t)$ as response variable and incorporated m_0 as a fixed explanatory variable. To investigate the differences in mass loss between dispersal stages, we included a binary variable indicating post-eviction and transience stage (*stage*). Here, Δt was the time elapsed since the start of the respective dispersal stage. In contrast to the first model, we removed the variable *#pup* because no pups were present during dispersal. We further included a binary variable (*male*) indicating if at least one unrelated male had joined the coalition. For the rest, we included the same explanatory variables used in the first model: *age*, $age^{1/2}$, *temp*, *rain*, and *#female*. *IndID* was nested in *coalID* as random intercept terms.

2b) *Emigrant fGCM during dispersal stages*: As above, we only used data on emigrants. We used $\log(fGCM)$ as response variable and included the variables *stage*, *collect*, *preg*, Δt , *age*, *temp*, *rain*, and *#female*. We treated *indID* nested in *coalID* as random intercept terms.

Results

Females were evicted from their natal groups either alone ($n = 33$) or as several females at a time forming same-sex dispersing coalitions ($n = 32$) that varied in size from two to six related females (19 two-, 7 three-, 3 four-, 2 five-, and 1 six-member coalition). On the day of eviction, females were between nine months and five years

of age. After eviction, emigrants ($n = 26$) dispersed for an average period of 41 days (interquartile range: 13–65 days) before they settled, and returners ($n = 39$) spent an average period of 24 days (7–30 days) away from their natal group.

1a) Body mass in emigrants, returners, and residents: At eviction, emigrants were heavier ($716 \text{ g} \pm 21 \text{ SE}$) than returners ($672 \pm 26 \text{ g}$; ANOVA: Est = 43.4, SE = 8.3, $p < 0.001$) and resident subordinates ($585 \pm 15 \text{ g}$; ANOVA: Est = 129.9, SE = 6.8, $p < 0.001$). Based on model predictions, emigrants had an average negative daily growth rate (-0.09% of body mass = $-0.61 \pm 1.33 \text{ g}$), whereas resident subordinates (0.13% , $0.79 \pm 0.73 \text{ g}$) and returners (0.03% , $0.23 \pm 2.32 \text{ g}$) had a positive growth rate. Daily growth rates decreased with increasing initial body mass (Est = -0.003 , SE = 0.001 , $p = 0.002$; Table 1), and the effect of initial body mass was strongest in returners (Est = -0.002 , SE = 0.001 , $p = 0.006$; Figure 1A, Table 1). Young females gained body mass disproportionately faster than old females (nonlinear age effect: Est = 0.002 , SE = 0.001 , $p = 0.012$), and females lost body mass faster at high temperatures (Est = -0.001 , SE = 0.0002 , $p = 0.009$). Growth rates remained constant throughout the entire dispersal event and were not influenced by coalition size.

1b) fGCM in emigrants, returners, and residents: Faecal GCM levels varied among dispersal strategies. Emigrants and returners experienced overall similar fGCM levels (Est = -0.21 , SE = 0.17 , $p = 0.214$) that were on average higher than those of residents (emigrants: Est = 0.48 , SE = 0.18 , $p = 0.008$; returners: Est = 0.70 , SE = 0.21 , $p = 0.001$; Figure 1B, Table 1). Faecal GCM levels increased with time after eviction (Est = 0.18 , SE = 0.07 , $p = 0.009$) and decreased with increasing daily temperatures (Est = -0.23 , SE = 0.07 , $p < 0.001$). Faecal GCM levels did not change with changing coalition size.

2a) Emigrant body mass during dispersal stages: Mass loss of emigrants did not vary between post-eviction and transience, nor with coalition size or presence of unrelated males (Table 1). Mass at eviction had a negative effect on changes in emigrant body mass (Est = -0.003 , SE = 0.001 , $p = 0.022$). Time spent in a dispersal stage did not influence emigrant body mass (Table 1).

2b) Emigrant fGCM during dispersal stages: Faecal GCM levels of emigrants varied among dispersal stages (Figure 2) but did not depend on the time emigrants spent in a

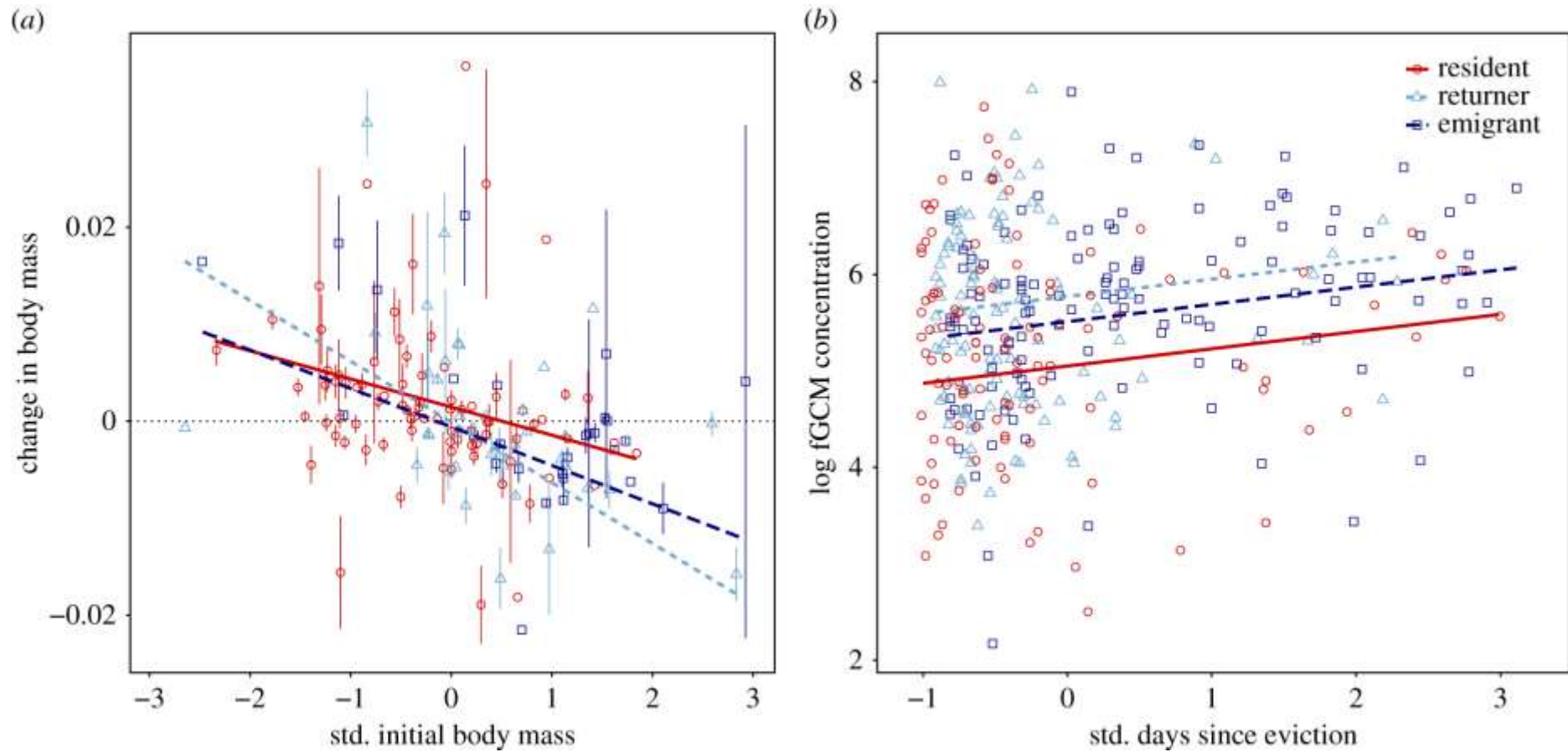


Figure 1. Effects of (a) initial body mass at eviction on net proportional daily change in body mass, and (b) dispersal time on fGCM concentration in female meerkats. (a) Points show average daily mass changes for each female with standard errors. The lines show model predictions for each female strategy (resident, returner, emigrant) when all other model predictors were set to their mean. (b) Points show observed fGCM concentrations and lines show model predictions for each female strategy when all other model predictors were set to their mean. The slopes capture the change in the response for a one standard deviation increase in the respective variable. Significance values are given in table 1.

Table 1. Effects of individual, social, and environmental factors on net proportional daily changes in body mass and faecal glucocorticoid metabolite (fGCM) concentrations of female meerkats. We report the estimate (Est), standard error (SE), significance (p, based in Wald statistics), and relative importance (RI) for each term based on the model average from models with $\Delta\text{AICc} < 2$. Marginal R^2 represents the variance explained by fixed factors (R^2_{m}), and conditional R^2 represents the variance explained by both fixed and random factors (R^2_{c}). The explanatory variables are m_0 = initial mass, $temp$ = max daily temperature, $\#female$ = average number of females, $strategy$ = emigrants vs. returners vs. residents, age = age in month, $age^{1/2}$ = sqrt of age to account for nonlinearity in growth, $rain$ = rain sum of previous 3 months, Δt = days since eviction, $\#pup$ = number of offspring < 3 months of age, $collect$ = sample collected am or pm, $preg$ = female pregnant or not, and $stage$ = post-eviction vs. transience.

Model	Est	SE	p	RI
1a) Body mass in emigrants, returners, and residents			$R^2_m=0.13, R^2_c=0.72$	
<i>intercept</i>	0.001	0.001	0.371	
<i>m₀</i>	-0.003	0.001	0.002	1.00
<i>temp</i>	-0.001	0.000	0.009	1.00
<i>#female</i>	-0.002	0.001	0.085	1.00
<i>strategyReturner</i>	0.000	0.002	0.842	
<i>strategyEmigrant</i>	0.000	0.002	0.857	0.70
<i>strategyReturner:m₀</i>	-0.003	0.001	0.006	
<i>strategyEmigrant:m₀</i>	-0.001	0.001	0.339	0.70
<i>age^{1/2}</i>	0.002	0.001	0.012	0.53
<i>age</i>	0.002	0.001	0.013	0.47
<i>rain</i>	0.001	0.001	0.201	0.42
<i>Δt</i>	0.000	0.000	0.243	0.31
<i>strategyReturner:#female</i>	-0.001	0.004	0.909	
<i>strategyEmigrant:#female</i>	-0.004	0.002	0.104	0.10
<i>#pup</i>	0.000	0.000	0.635	0.04
1b) fGCM in emigrants, returners, and residents			$R^2_m=0.15, R^2_c=0.29$	
<i>intercept</i>	5.180	0.150	<0.001	
<i>collectPM</i>	-0.405	0.111	< 0.001	fixed
<i>pregPregnant</i>	0.138	0.129	0.284	fixed
<i>temp</i>	-0.231	0.065	< 0.001	1.00
<i>strategyReturner</i>	0.697	0.205	0.001	
<i>strategyEmigrant</i>	0.482	0.180	0.008	1.00
<i>Δt</i>	0.180	0.068	0.009	1.00
<i>#female</i>	0.150	0.081	0.064	0.75
<i>age</i>	0.087	0.080	0.282	0.28
2a) Emigrant body mass during dispersal stages			$R^2_m=0.09, R^2_c=0.70$	
<i>intercept</i>	0.001	0.002	0.760	
<i>m₀</i>	-0.003	0.001	0.022	0.88
<i>stageTransience</i>	-0.001	0.001	0.293	0.18
<i>temp</i>	0.000	0.001	0.389	0.15
<i>rain</i>	0.001	0.001	0.550	0.12
<i>#female</i>	-0.001	0.002	0.544	0.12
2b) Emigrant fGCM during dispersal stages			$R^2_m=0.11, R^2_c=0.25$	
<i>intercept</i>	5.611	0.119	<0.001	
<i>collectPM</i>	-0.447	0.131	0.001	fixed
<i>pregPregnant</i>	0.054	0.148	0.717	fixed
<i>stageTransience</i>	0.366	0.163	0.026	1.00
<i>rain</i>	-0.106	0.073	0.148	0.44
<i>temp</i>	-0.094	0.071	0.189	0.41
<i>age</i>	0.058	0.083	0.488	0.11

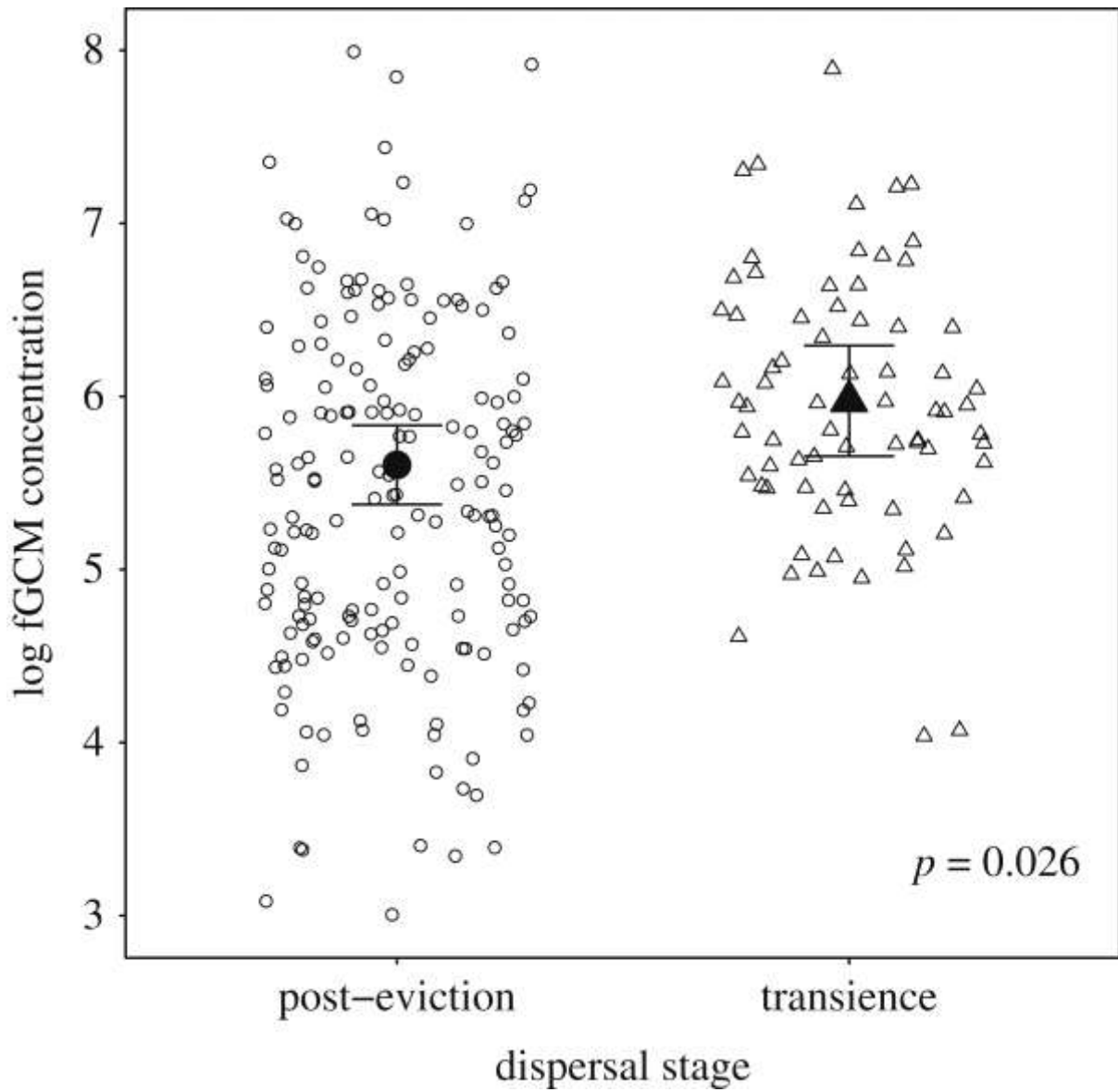


Figure 2. fGCM concentrations in female meerkat emigrants depending on whether they were in the post-eviction or transience stage. Empty symbols show observed fGCM concentrations and filled symbols show model estimates with 95% confidence intervals.

Table 2. Within-individual and within-coalition repeatability (R) for each model. $R < 0.40$ means low variability between individuals (coalitions, respectively,) and high variability within individuals (coalitions, respectively). $R > 0.60$ means high variability between individuals (coalitions, respectively) and low variability within individuals (coalitions, respectively) [63].

Model	Random factor	R
1a) Body mass in emigrants, returners, and residents	Individual	0.33
	Coalition	0.62
1b) fGCM in emigrants, returners, and residents	Individual	0.02
	Coalition	0.15
2a) Emigrant body mass during dispersal stages	Individual	0.10
	Coalition	0.65
2b) Emigrant fGCM during dispersal stages	Individual	0.00
	Coalition	0.16

stage (Table 1). Emigrant females had higher fGCM levels during transience than during post-eviction (Est = 0.37, SE = 0.16, $p = 0.026$). Dispersing coalition size and presence of males did not affect fGCM levels (Table 1).

In all models, much of the observed variation was explained by the random effects, which is shown by the difference between the conditional and marginal R squared (Table 1). This was mostly due to high variability in daily body mass changes within each individual and between coalitions (Table 2, models 1a and 2a), and due to high variability in fGCM levels within individuals and coalitions (Table 2, models 1b and 2b). In general, variability between individuals was low (Table 2).

Discussion

Our study emphasizes that dispersal is a costly process and that costs vary between dispersal strategies and dispersal stages. Dispersing females who successfully settled lost body mass, thus confirming the expectation that loss of body mass is associated with dispersal [3]. We further showed that the negative effect of mass at eviction on daily growth rates was more pronounced in dispersers that returned to their natal group than in dispersers that successfully settled in a new territory. Finally, we showed that dispersing females experienced higher faecal glucocorticoid metabolite (fGCM) levels than their resident counterparts, especially in the later stages of dispersal. Our findings thus provide empirical support for the prediction that dispersal is associated with increased stress hormone levels [3].

The fact that dispersers that successfully settled (i.e., emigrants) were on average heavier (also reported in [41]) and less affected by the negative effect of mass at eviction than dispersers that returned to their natal group (i.e., returners), suggests that heavier individuals cope better than lighter individuals when away from the natal group. In actively dispersing species (e.g., birds and mammals), heavier individuals or individuals in better condition often have an advantage during dispersal as they can move faster and further away from the natal territory [65,66]. This increases the likelihood of finding less-saturated territories to settle and to increase breeding opportunities [2,67]. In returners, we did not observe loss of body mass during the time they spent away from the group. This is in line with a study on red squirrels

showing that individuals experience only minor changes in body mass during temporary forays around the natal site [23]. While individuals roaming through familiar areas close to the natal territory are likely to maintain their condition, permanent dispersers may suffer from inefficient foraging in unknown areas [11]. Based on the observed differences in growth rates between emigrants and returners, conclusions regarding a successful dispersal process should be drawn very carefully when based only on prospecting individuals.

The stronger negative effect of body mass at eviction on growth rates of returners may be due to their inexperience of being outside of the group. Over the first years of their life, subordinate females are generally evicted several times before they finally emigrate and establish their own group [26]. During these early evictions, young females can gain information on their surroundings (N. Maag, *pers. obs.*). Similar pre-dispersal movements are common in many species as individuals can gain information on mate availability or quality of future breeding habitat [68,69]. Pre-dispersal forays can thus reduce the costs of dispersal and improve settlement success [28,70]. We propose that lighter and less experienced individuals may not be able to survive dispersal and settle successfully, but that they collect information essential for future dispersal.

Contrary to expectations [3,24], we did not observe a decrease in growth rate with increasing dispersal time nor with time spent in a dispersal stage [3,24]. Hence, the energetic costs of being away from the group may not be as high as previously thought [3,11]. However, to assess the influence of dispersal on body condition, an investigation of distance covered by each individual could be more informative [3]. While our main interest was to investigate the variation of costs among dispersal strategies and stages, we suggest that future studies should explore the influence of dispersal distance on changes in individual body mass and stress levels. This would increase our understanding of how costs vary between different movement strategies followed by each individual.

We could not confirm previous results showing that mass loss in dispersing meerkats can be alleviated in larger coalitions [38]. However, the coalition size effect was close to being significant (Table 1, model 1a) and more information on large coalitions may have improved the model fit. Since cooperative birds and mammals can partition

cooperative behaviour like vigilance among group members [71,72], dispersing in larger coalitions is likely to reduce the individual costs of such behaviour during dispersal. This allows individuals in larger coalitions to allocate more time to foraging [38,71,72]. If increased foraging time in larger coalitions buffers against daily individual mass loss, many cooperative species that disperse in multiple-member coalitions – such as lions (*Panthera leo*), wild dogs (*Lycaon pictus*), green woodhoopoes (*Phoeniculus purpureus*), or Arabian babblers (*Turdoides squamiceps*) [13,32–34] – may experience reduced mass loss during dispersal. In addition, individuals in larger coalitions may have an advantage as they can establish a new breeding unit with a larger initial group size. Starting a new group with several helpers will likely increase total group reproduction and survival of individuals due to improved group augmentation [73,74].

Aggression from the dominant female during eviction and the lack of protection offered by the group after eviction may be responsible for the higher fGCM levels during the post-eviction stage [16]. Aggressive attacks are used by dominants of several cooperative species to render their subordinates infertile through chronic stress [75,76] and are a likely explanation for increased fGCM concentrations in meerkats [16]. Changes in physical and social environment associated with dispersal, such as unfamiliarity with the landscape and aggression from unrelated residents, are likely to intensify during transience and offer an explanation for the increased stress hormone levels during this stage of the dispersal process [77,78]. Many species cope with unpredictable stimuli by exhibiting a stress response, which may lead to increased glucocorticoid levels [6]. Increased glucocorticoid levels as response to homeostatic challenges are at first place adaptive [79]. Only when stress hormones are elevated over prolonged periods (i.e., chronically) they have deleterious impacts on an individual's fitness [80]. As such, the observed change in fGCM concentrations may be an adaptive response to the challenge of dispersal rather than a real cost of affecting fitness negatively. However, if individuals are unable to find suitable territory for settlement in time, chronic stress may lead to decreased fitness later in life [78].

In contrast to previous work by Young [38], we did not observe a reduction of stress hormone levels in females of larger coalitions. This difference is possibly due to the fact that Young [38] focused mainly on the early phases of dispersal. We showed that stress hormone levels increased over time and when moving from the post-eviction to the transience stage. Hence, the increased stress response associated with the late stages of dispersal [3] may have masked the positive effect of coalition size. In addition, studies on other species have shown that glucocorticoid levels of reproductive competitors increase during times of social instability [81,82] and such instability is likely to occur during the late stages of dispersal, when individuals establish new breeding groups. As aggression and reproductive conflict increase with group size in social species [83,84], increased reproductive competition in larger coalitions may increase individual stress hormone levels and counteract the benefits of dispersing with several helpers. Our results suggest that environmental and social circumstances can change during the dispersal process and cause variation in fGCM concentrations.

In conclusion, we show that dispersing females who successfully settle experience greater mass loss than resident females and evicted females who return to the natal group. Both emigrants and returners have higher stress hormone output than residents, especially during the later stages of dispersal. We thereby confirm previous findings, but also extend those by showing how body condition varies between different female strategies and dispersal stages. Body mass and stress hormone output seem suitable parameters for monitoring the costs associated with dispersal, as these traits often play an important role in mediating the effects of the environment on other life-history events such as survival and breeding [7–9]. A better quantification of how such costs change in response to social and environmental conditions across different stages of dispersal can therefore help gain a better mechanistic understanding of this important life history event. As many vertebrate species are expected to experience condition loss during dispersal [2,3], our results – showing how body condition changes during the later stages of dispersal – should hold implications for a wide range of taxa. Quantification of the effects of dispersal on individual condition will permit a trait-based investigation of the associated demographic rates and how these affect population dynamics.

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References

1. Bowler DE, Benton TG. 2005 Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev. Camb. Philos. Soc.* **80**, 205–225.
2. Clobert J, Baguette M, Benton TG, Bullock JM. 2012 *Dispersal Ecology and Evolution*. Oxford University Press.
3. Bonte D *et al.* 2012 Costs of dispersal. *Biol. Rev. Camb. Philos. Soc.* **87**, 290–312.
4. Nevoux M, Arlt D, Nicoll M, Jones C, Norris K. 2013 The short-and long-term fitness consequences of natal dispersal in a wild bird population. *Ecol. Lett.* **16**, 438–445.
5. Kingma SA, Komdeur J, Burke T, Richardson DS. 2017 Differential dispersal costs and sex-biased dispersal distance in a cooperatively breeding bird. *Behav. Ecol.* **28**, 1113–1121.
6. Romero LM. 2004 Physiological stress in ecology: lessons from biomedical research. *Trends Ecol. Evol.* **19**, 249–255.
7. Crespi EJ, Williams TD, Jessop TS, Delehanty B. 2013 Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals? *Funct. Ecol.* **27**, 93–106.
8. Plard F, Gaillard J-M, Coulson T, Delorme D, Warnant C, Michallet J, Tuljapurkar S, Krishnakumar S, Bonenfant C. 2015 Quantifying the influence of measured and unmeasured individual differences on demography. *J. Anim. Ecol.* **84**, 1434–1445.
9. Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson LE, Tuljapurkar S, Coulson T. 2010 Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**, 482–485.
10. Pride ER. 2005 High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biol. Lett.* **1**, 60–63.
11. Pinter-Wollman N, Isbell LA, Hart LA. 2009 The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). *Proc. Biol. Sci.* **276**, 1009–1014.
12. Metzgab LH. 1967 An Experimental Comparison of Screech Owl Predation on Resident and Transient White-Footed Mice (*Peromyscus Leucopus*). *J. Mammal.* **48**, 387–391.
13. Packer C, Pusey AE. 1982 Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* **296**, 740.
14. Boydston EE, Morelli TL, Holekamp KE. 2001 Sex Differences in Territorial Behavior Exhibited by the Spotted Hyena (*Hyaenidae, Crocuta crocuta*). *Ethology* **107**, 369–385.
15. Solomon NG. 2003 A reexamination of factors influencing philopatry in rodents. *J. Mammal.* **84**, 1182–1197.
16. Young AJ, Carlson AA, Monfort SL, Russell AF, Bennett NC, Clutton-Brock T. 2006 Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proc. Natl. Acad. Sci. U. S. A.* **103**, 12005–12010.

17. Soulsbury CD, Baker PJ, Iossa G, Harris S. 2008 Fitness costs of dispersal in red foxes (*Vulpes vulpes*). *Behav. Ecol. Sociobiol.* **62**, 1289–1298.
18. Calleri DV, Rosengaus RB, Traniello JFA. 2006 Disease and colony establishment in the dampwood termite *Zootermopsis angusticollis*: survival and fitness consequences of infection in primary reproductives. *Insectes Soc.* **53**, 204–211.
19. Adamo SA, Roberts JL, Easy RH, Ross NW. 2008 Competition between immune function and lipid transport for the protein apolipoprotein III leads to stress-induced immunosuppression in crickets. *J. Exp. Biol.* **211**, 531–538.
20. Srygley RB, Lorch PD, Simpson SJ, Sword GA. 2009 Immediate protein dietary effects on movement and the generalised immunocompetence of migrating Mormon crickets *Anabrus simplex* (Orthoptera: Tettigoniidae). *Ecol. Entomol.* **34**, 663–668.
21. Cant MA, Otali E, Mwanguhya F. 2001 Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). *J. Zool.* **254**, 155–162.
22. Vanderwerf EA. 2008 Sources of Variation in Survival, Recruitment, and Natal Dispersal of the Hawai'i 'Elepaio. *Condor* **110**, 241–250.
23. Larsen KW, Boutin S. 1994 Movements, Survival, and Settlement of Red Squirrel (*Tamiasciurus Hudsonicus*) Offspring. *Ecology* **75**, 214–223.
24. Ridley AR, Raihani NJ, Nelson-Flower MJ. 2008 The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*. *J. Avian Biol.* **39**, 389–392.
25. Young AJ, Carlson AA, Clutton-Brock T. 2005 Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Anim. Behav.* **70**, 829–837.
26. Clutton-Brock TH, Brotherton PN, Smith R, McIlrath GM, Kansky R, Gaynor D, O'Riain MJ, Skinner JD. 1998 Infanticide and expulsion of females in a cooperative mammal. *Proc. Biol. Sci.* **265**, 2291–2295.
27. Young AJ, Monfort SL. 2009 Stress and the costs of extra-territorial movement in a social carnivore. *Biol. Lett.* **5**, 439–441.
28. Haughland DL, Larsen KW. 2004 Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. *J. Anim. Ecol.* **73**, 1024–1034.
29. Brown JL, Brown ER, Brown SD, Dow DD. 1982 Helpers: effects of experimental removal on reproductive success. *Science* **215**, 421–422.
30. Courchamp F, Grenfell BT, Clutton-Brock TH. 2000 Impact of natural enemies on obligately cooperative breeders. *Oikos* **91**, 311–322.
31. Clutton-Brock TH, Russell AF, Sharpe LL, Brotherton PN, McIlrath GM, White S, Cameron EZ. 2001 Effects of helpers on juvenile development and survival in meerkats. *Science* **293**, 2446–2449.
32. Ligon JD, Ligon SH. 1978 Communal breeding in green woodhoopoes as a case for reciprocity. *Nature* **276**, 496.
33. Lundy KJ, Parker PG, Zahavi A. 1998 Reproduction by subordinates in cooperatively breeding Arabian babblers is uncommon but predictable. *Behav. Ecol. Sociobiol.* **43**, 173–180.

34. McNutt JW. 1996 Sex-biased dispersal in African wild dogs, *Lycaon pictus*. *Anim. Behav.* **52**, 1067–1077.
35. Clutton-Brock TH, Gaynor D, McIlrath GM. 1999 Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* **68**, 103–111.
36. Packer C, Scheel D, Pusey AE. 1990 Why Lions Form Groups: Food is Not Enough. *Am. Nat.* **136**, 1–19.
37. Wilson ML, Britton NF, Franks NR. 2002 Chimpanzees and the mathematics of battle. *Proceedings of the Royal Society B: Biological Sciences* **269**, 1107–1112.
38. Young AJ. 2004 Subordinate tactics in cooperative meerkats: helping, breeding and dispersal. University of Cambridge.
39. Griffin AS, Pemberton JM, Brotherton PNM, McIlrath G, Gaynor D, Kansky R, O’Riain J, Clutton-Brock TH. 2003 A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav. Ecol.* **14**, 472–480.
40. Maag N, Cozzi G, Clutton-Brock T, Ozgul A. 2018 Density-dependent dispersal strategies in a cooperative breeder. *Ecology* (doi:10.1002/ecy.2433)
41. Ozgul A, Bateman AW, English S, Coulson T, Clutton-Brock TH. 2014 Linking body mass and group dynamics in an obligate cooperative breeder. *J. Anim. Ecol.* **83**, 1357–1366.
42. Jordan NR, Cherry MI, Manser MB. 2007 Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Anim. Behav.* **73**, 613–622.
43. Cozzi G, Maag N, Börger L, Clutton-Brock TH, Ozgul A. 2018 Socially informed dispersal in a territorial cooperative breeder. *J. Anim. Ecol.* **87**, 838–849.
44. Börger L, Fryxell JM. 2012 Quantifying individual differences in dispersal using net squared displacement. In *Dispersal Ecology and Evolution* (eds J Clobert, M Baguette, TG Benton, JM Bullock), pp. 222–230. Oxford University Press, Oxford, UK.
45. Cozzi G, Chynoweth M, Kusak J, Çoban E, Çoban A, Ozgul A, Şekercioğlu ÇH. 2016 Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears. *J. Zool.* **300**, 142–150.
46. Clutton-Brock TH *et al.* 1998 Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. Biol. Sci.* **265**, 185–190.
47. Doolan’ SP, Macdonald DW. 1997 Breeding and juvenile survival among slender-tailed meerkats (*Suricatu suricatta*) in the south-western Kalahari: ecological and social influences. *J. Zool., Lond.* **242**, 309–327.
48. Sharp SP, English S, Clutton-Brock TH. 2013 Maternal investment during pregnancy in wild meerkats. *Evol. Ecol.* **27**, 1033–1044.
49. Braga Goncalves I, Heistermann M, Santema P, Dantzer B, Mausbach J, Ganswindt A, Manser MB. 2016 Validation of a Fecal Glucocorticoid Assay to Assess Adrenocortical Activity in Meerkats Using Physiological and Biological Stimuli. *PLoS One* **11**, e0153161.
50. Heistermann M, Finke M, Hodges JK. 1995 Assessment of female reproductive status in captive-housed Hanuman langurs (*Presbytis entellus*) by measurement of urinary and

- fecal steroid excretion patterns. *Am. J. Primatol.* **37**, 275–284.
51. Ganswindt A, Palme R, Heistermann M, Borrigan S, Hodges JK. 2003 Non-invasive assessment of adrenocortical function in the male African elephant (*Loxodonta africana*) and its relation to musth. *Gen. Comp. Endocrinol.* **134**, 156–166.
 52. Mausbach J, Goncalves IB, Heistermann M, Ganswindt A, Manser MB. 2017 Meerkat close calling patterns are linked to sex, social category, season and wind, but not fecal glucocorticoid metabolite concentrations. *PLoS One* **12**, e0175371.
 53. Heistermann M, Ademmer C, Kaumanns W. 2004 Ovarian Cycle and Effect of Social Changes on Adrenal and Ovarian Function in *Pygathrix nemaeus*. *Int. J. Primatol.* **25**, 689–708.
 54. Bates D, Maechler M, Bolker B, Walker S, Others. 2014 lme4: Linear mixed-effects models using Eigen and S4. *R package version 1*, 1–23.
 55. R Core Team. 2013 R: A language and environment for statistical computing.
 56. Bartoń K. 2018 MuMIn: multi-model inference. R package version 1.40.4. <http://CRAN.R-project.org/package=MuMIn>
 57. Akaike H. 1998 Information Theory and an Extension of the Maximum Likelihood Principle. In *Selected Papers of Hirotugu Akaike* (eds E Parzen, K Tanabe, G Kitagawa), pp. 199–213. New York, NY: Springer New York.
 58. Burnham, K.P. & Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Berlin, Germany: Springer.
 59. Belsley DA, Kuh E, Welsch RE. 2005 *Regression Diagnostics: Identifying Influential Data and Sources of Collinearity*. John Wiley & Sons.
 60. Pinheiro JC, Bates DM, editors. 2000 Linear Mixed-Effects Models: Basic Concepts and Examples. In *Mixed-Effects Models in S and S-PLUS*, pp. 3–56. New York, NY: Springer New York.
 61. Calder WA. 1984 *Size, Function, and Life History*. Courier Corporation.
 62. English S, Bateman AW, Clutton-Brock TH. 2012 Lifetime growth in wild meerkats: incorporating life history and environmental factors into a standard growth model. *Oecologia* **169**, 143–153.
 63. Stoffel MA, Nakagawa S, Schielzeth H. 2017 rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* **8**, 1639–1644.
 64. Sheriff MJ, Dantzer B, Delehanty B, Palme R, Boonstra R. 2011 Measuring stress in wildlife: techniques for quantifying glucocorticoids. *Oecologia* **166**, 869–887.
 65. Delgado M del M, Penteriani V, Revilla E, Nams VO. 2010 The effect of phenotypic traits and external cues on natal dispersal movements. *J. Anim. Ecol.* **79**, 620–632.
 66. Debeffe L, Morellet N, Cargnelutti B, Lourtet B, Bon R, Gaillard J-M, Mark Hewison AJ. 2012 Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *J. Anim. Ecol.* **81**, 1327–1327.
 67. Gundersen G, Andreassen HP, Ims RA. 2002 Individual and population level

- determinants of immigration success on local habitat patches: an experimental approach. *Ecol. Lett.* **5**, 294–301.
68. Davidian E, Courtiol A, Wachter B, Hofer H, Höner OP. 2016 Why do some males choose to breed at home when most other males disperse? *Sci Adv* **2**, e1501236.
 69. Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M. 2009 Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**, 197–209.
 70. Stamps JA, Krishnan VV. 1999 A Learning-Based Model of Territory Establishment. *Q. Rev. Biol.* **74**, 291–318.
 71. Gaston AJ. 1977 Social behaviour within groups of jungle babblers (*Turdoides striatus*). *Anim. Behav.* **25**, 828–848.
 72. Elgar MA. 1989 Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* **64**, 13–33.
 73. Kokko H, Johnstone RA, Clutton-Brock TH. 2001 The evolution of cooperative breeding through group augmentation. *Proc. Biol. Sci.* **268**, 187–196.
 74. Clutton-Brock T. 2002 Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72.
 75. Wingfield JC, Hegner RE, Lewis DM. 1991 Circulating levels of luteinizing hormone and steroid hormones in relation to social status in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. *J. Zool.* **225**, 43–58.
 76. Schoech SJ, Mumme RL, Moore MC. 1991 Reproductive Endocrinology and Mechanisms of Breeding Inhibition in Cooperatively Breeding Florida Scrub Jays (*Aphelocoma c. coerulescens*). *Condor* **93**, 354–364.
 77. Rubenstein DR. 2007 Stress hormones and sociality: integrating social and environmental stressors. *Proc. Biol. Sci.* **274**, 967–975.
 78. Creel S, Dantzer B, Goymann W, Rubenstein DR. 2013 The ecology of stress: effects of the social environment. *Funct. Ecol.* **27**, 66–80.
 79. McEwen BS, Wingfield JC. 2003 The concept of allostasis in biology and biomedicine. *Horm. Behav.* **43**, 2–15.
 80. Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson R. 1998 Ecological Bases of Hormone—Behavior Interactions: The ‘Emergency Life History Stage’. *Integr. Comp. Biol.* **38**, 191–206.
 81. Sapolsky RM. 1993 The physiology of dominance in stable versus unstable social hierarchies. In *Primate social conflict* (eds WA Mason, SP Mendoza), pp. 171–204. State University of New York Press, Albany, New York, USA.
 82. Creel S. 2001 Social dominance and stress hormones. *Trends Ecol. Evol.* **16**, 491–497.
 83. Dantzer B, Bennett NC, Clutton-Brock TH. 2017 Social conflict and costs of cooperation in meerkats are reflected in measures of stress hormones. *Behav. Ecol.* **28**, 1131–1141.
 84. Clutton-Brock TH, Hodge SJ, Flower TP, Spong GF, Young AJ. 2010 Adaptive

suppression of subordinate reproduction in cooperative mammals. *Am. Nat.* **176**, 664–673.