# Matrix Models of Hierarchical Demography: Linking Group- and Population-Level Dynamics in Cooperative Breeders

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ABSTRACT: For highly social species, population dynamics depend on hierarchical demography that links local processes, group dynamics, and population growth. Here, we describe a stage-structured matrix model of hierarchical demography, which provides a framework for understanding social influences on population change. Our approach accounts for dispersal and affords insight into population dynamics at multiple scales. The method has close parallels to integral projection models but focuses on a discrete characteristic (group size). Using detailed long-term records for meerkats (*Suricata suricatta*), we apply our model to explore patterns of local density dependence and implications of group size for group and population growth. Taking into account dispersers, the model predicts a per capita growth rate for social groups that declines with group size. It predicts that larger social groups should produce a greater number of new breeding groups; thus, dominant breeding females (responsible for most reproduction) are likely to be more productive in larger groups. Considering the potential for future population growth, larger groups have the highest reproductive value, but per capita reproductive value is maximized for individuals in smaller groups. Across a plausible range of dispersal conditions, meerkats' long-run population growth rate is maximized when individuals form groups of intermediate size.

*Keywords:* matrix models, population dynamics, hierarchical demography, social species, cooperative breeders, Allee effects.

## Introduction

Populations are often structured into subunits either by features of the environment or by social organization (Levins 1969; Hanski 1999; Al-Khafaji et al. 2009), and variation in this structure may affect behavior, demography,

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and population dynamics. For example, a constrained relationship between social group size and new group production appears to stabilize the number of groups in populations of lions (*Panthera leo*; Packer et al. 2005), and group living stabilizes lions' predator-prey dynamics (Fryxell et al. 2007). To understand the population dynamics of social species (those that form stable social groups), we need to understand how demographic processes operating within and among groups combine to yield population-level dynamics in a multiscale process that has been termed hierarchical demography (Al-Khafaji et al. 2009).

Cooperative breeders—such as fire ants (*Solenopsis wagneri*), long-tailed tits (*Aegithalos caudatus*), and meerkats (*Suricata suricatta*)—in which nonbreeding group members help to rear young produced by one or more breeding individuals (Clutton-Brock 2002, 2016), present well-studied examples of populations that are socially organized into subunits. While there exist extensive behavioral and demographic data for cooperative breeders, however, it is not clear how group-level dynamics connect the behavior and demography of individuals to population-level dynamics.

Relevant in the context of cooperative breeders' hierarchical demography is the possibility for Allee effects (positive density dependence; Courchamp et al. 1999b; Angulo et al. 2018). The seemingly altruistic behaviors exhibited by cooperative breeders (Clutton-Brock 2002) have been shown in some cases to improve survival, breeding, or dispersal success in larger social groups (Courchamp et al. 1999b). These examples of positive density dependence, or component Allee effects (Stephens et al. 1999), operating at the group level have been hypothesized to influence overall patterns of group- and population-level dynamics (Clutton-Brock et al. 1999a; Courchamp et al. 1999b). In particular, there has been an expectation of demographic Allee effects (Courchamp et al. 1999b, 2000): per capita rates of group or population growth that increase with the size of the population unit in question

(Stephens et al. 1999). Empirical examples of demographic Allee effects in cooperative breeders' group and population dynamics, however, have been limited (Somers et al. 2008; Gregory et al. 2010; Woodroffe 2011; Bateman et al. 2012). This may be due, in part, to a lack of clarity surrounding how Allee effects should be integrated across levels of population structure. Positive group-level density dependence might, for example, cause large groups to grow faster or to produce additional daughter groups, with differing implications for population dynamics. Considering group size–dependent demographic rates in their population context is key to understanding the implications of local density dependence.

Only by connecting patterns of demography in social groups to patterns of population-level change is it possible to analyze how group-level processes contribute to population dynamics (Al-Khafaji et al. 2009). Here, we develop a stage-structured matrix model of hierarchical demography, a framework within which to explore the effect of social group dynamics on population-level change. Our aim is twofold: (1) to develop a tool for the study of demography in social species and (2) to explore the population-level implications of group-level demographic and dispersal processes in cooperative breeders.

We use our model with data from a long-term study of meerkats (*Suricata suricatta*) to analyze how demography within groups and, in particular, how emigration (one of the major drivers of meerkats' group-level dynamics; Bateman et al. 2013) contributes to population growth rates. Our modeling framework is similar to standard matrix models for age- or stage-structured populations (Caswell 2001), but instead of life-history stages, it follows the fate of groups of different sizes; in doing so, it provides insight into the relationship between group- and population-level dynamics. Although density independent at the population level, our model retains explicit density dependence at the social group level. This allows us to explore how patterns of density dependence—such as Allee effects—within groups affect population dynamics. Our analysis leads us to reexamine our expectation that selection for sociality should be manifest in a group-level demographic Allee effect, and we go on to show how intermediate emigration rates (and resultant intermediate group sizes) can maximize associated population growth rates, even in the absence of a group-level demographic Allee effect.

## A Matrix Model of Hierarchical Demography

We use stage-structured matrices (Caswell 2001) to model the dynamics of group sizes within a population. The model tracks the abundance of groups of different sizes, and individual groups can increase or decrease in size. Group size is therefore analogous to an individual's stage (e.g., vegetative/reproductive growth stages in plants) in conventional stage-structured matrix population models. Our method

has close parallels to integral projection models (IPMs; Easterling et al. 2000), which incorporate continuous (rather than discrete) traits into discrete-time population models but have not been used to explicitly model social group dynamics. Because social groups can attain any possible integer number of individuals, the model we describe is a discrete analog of an IPM. We provide a summary of the model here, with details in the appendix (available online).

*The group matrix model.* Matrix models are commonly used to analyze how population growth is affected by survival, reproduction, and maturation that change across a species' life history. Rather than a population of individuals, however, we consider a population made up of social groups of varying sizes. In this context, we let $g_{i,t}$ be the number of groups of size $i$ censused in a population in year $t$, and we assemble the counts of groups of all possible (nonzero) starting sizes into a column vector, $\mathbf{g}_t = (g_{1,t}, g_{2,t}, \ldots)^T$. The vector $\mathbf{g}_{t+1}$ gives the expected counts of group sizes after 1 year, the starting group sizes for the next iteration of the model. Below, we define group size transition and group formation matrices, $\mathbf{T}$ and $\mathbf{F}$, respectively, summing to give a group-focused population projection matrix, $\mathbf{A} = \mathbf{T} + \mathbf{F}$, with entries $a_{ij}$, which describes interannual changes in the number of groups of each size:

$$\mathbf{g}_{t+1} = \mathbf{A}\mathbf{g}_t = (\mathbf{T} + \mathbf{F})\mathbf{g}_t. \qquad (1)$$

Equation (1) represents a model for the expected dynamics of a population composed of social groups of different sizes. This model is identical in form to a standard stage-structured matrix model (Caswell 2001), except that the units of focus here are groups rather than individuals. As with standard stage-structured matrix models, a group can transition from one stage class (group size) to another, according to the probabilities in $\mathbf{T}$, or form a new group, according to expected group production rates given in $\mathbf{F}$. While the entries of $\mathbf{T}$ and $\mathbf{F}$ are correlated (e.g., groups that lose dispersers have a higher chance of producing a new group), we rely on the fact that the expected value of a sum is the sum of the expected values to ensure the validity of the identity, $\mathbf{A} = \mathbf{T} + \mathbf{F}$ (for details, see appendix).

To compose the group size transition matrix, $\mathbf{T}$, we consider the discrete-time dynamics of integer-valued female group size, $N_t$, measured for established breeding groups in year $t$. Every year, individuals may be born into, die in, immigrate to, or emigrate from a group of any given size. In reality, each of these demographic processes is stochastic, so that its outcome at the start of any given year is unknown, and we consider that there is some probability associated with any possible outcome. As a result of the contributing demographic processes, groups transition from one group size ($j$) to another group size ($i$) over the course of a year with probability $\tau_{ij}$. By appropriately parameterizing these $\tau_{ij}$ entries of matrix $\mathbf{T}$, it is possible to build group-level den-

sity dependence into the transition probabilities. For example, a very large group may have lower per capita survival and breeding success—resulting in lower probabilities of transition to larger group sizes—than a relatively smaller group.

Analogous to individual reproduction, existing social groups can generate new social groups when individuals disperse. The **F** matrix represents this process of new group formation, with entries ($\varphi_{ij}$) indicating the average number of new groups of size $i$ formed each year for each group of size $j$. To form a new group of a given size, an existing group must produce a sufficiently large dispersing coalition within which sufficient individuals survive, and that coalition must establish itself as a new breeding group. Again, by choosing appropriate functions with which to parameterize the elements of matrix **F**, it is possible to build group-level density dependence—for example, in disperser production or settlement success—into the model. While we do not explicitly incorporate population-level density dependence, the model can describe different rates (e.g., of group settlement), which we interpret to represent varying levels of habitat saturation.

Given **A**, we can model expected discrete-time population changes and apply standard matrix model theory (Caswell 2001). In particular, the dominant eigenvalue of **A** is the asymptotic rate of increase in the number of social groups in a population. Because both **T** and **F** can describe density dependence within groups, so too can **A**. In the same way that older or younger individuals in a standard population matrix model may be responsible for more or fewer individuals in the subsequent time step, larger or smaller groups may result in more or fewer future groups. In the model we describe here, however, we do not consider density dependence at the population level. That is, the entries of **A** do not depend on the total size of or the number of groups in the overall population being modeled.

By modeling changes to the number of groups of each size within a population, we indirectly model changes in population size. Other authors have shown that the long-run rate of increase in the number of social groups in a population is equivalent asymptotically to the long-run rate of population increase overall (Al-Khafaji et al. 2009). Using this result and other results from population-matrix theory (Caswell 2001), we can explore how group dynamics contribute to population change. We go on to use the model, parameterized with data on meerkat demography, to assess potential demographic implications of component Allee effects and patterns of group formation in meerkats.

## Application: Meerkats

Meerkats are social mongooses of family Herpestidae. They exhibit high reproductive skew, with one female in each so-cial group producing the vast majority of offspring raised in the group (Courchamp et al. 1999*b*; Ozgul et al. 2014). Nonbreeding group members—usually the dominant breeding pair's offspring—cooperate to raise young in the group through babysitting, allolactation, pup feeding, and predator vigilance (Clutton-Brock et al. 2002). Meerkat breeding is highly seasonal, dependent on wet season rainfall (Doolan and Macdonald 1996), but dominant females can breed multiple times per year, subject to prey availability (Clutton-Brock et al. 1999*b*; Bateman et al. 2013). At the end of the dry season, dominant females evict older subordinate females—which are the dominants' potential competitors—from their respective groups (Young et al. 2006). Around the same time, subordinate males disperse from their natal groups and attempt to establish new breeding groups with evicted females (Young et al. 2005; Mares et al. 2014). Although females can inherit dominant breeding positions in their natal groups, males must disperse to gain dominant breeding positions in nonnatal groups (Spong et al. 2008).

While meerkats have been suggested as a species that should be subject to substantial Allee effects (Clutton-Brock et al. 1999*a*; Courchamp et al. 1999*b*), empirical results are equivocal. Within-group rates of survival decline with group size, showing a component Allee effect (Clutton-Brock et al. 1999*a*; Bateman et al. 2012). Reproductive output increases with group size (Hodge et al. 2008), but per capita recruitment is conventionally density dependent, declining with group size (Bateman et al. 2012, 2013). Per capita emigration increases with group size (Bateman et al. 2012), and immigration rates are small overall but decline with group size (Bateman et al. 2012). Reproduction and emigration explain more of the observed variation in group dynamics than does within-group adult mortality, which occurs throughout the year but is usually below 25% (Bateman et al. 2012, 2013). Overall, established meerkat groups appear to be conventionally density dependent, in the sense that small groups grow more per capita from year to year than do larger groups (Bateman et al. 2012, 2013).

Here, Allee effect definitions become relevant. A demographic Allee effect is generally defined as a positive association between population size (or density) and either (1) per capita growth of the population or (2) mean evolutionary fitness of constituent individuals (Courchamp et al. 1999*a*, 1999*b*; Stephens et al. 1999). In the case of homogeneous populations, these definitions are equivalent and unambiguous, but when the population of interest is a social group, things are not so clear. In particular, emigration from a social group decreases that group's size, but it is likely critical for the long-term fitness of group members. Also, larger groups produce more emigrants (Bateman et al. 2012, 2013) in larger dispersing coalitions (Young 2004), and larger coalitions appear more likely to successfully establish new breeding groups (Young 2004). We must consider meerkat social groups in

the context of a broader population if we seek to apply an Allee effect definition or understand how group-level relationships contribute to population dynamics and, ultimately, fitness.

*Demographic parameterization.* To parameterize our model, we used data from a long-term study of meerkat behavior and life history on and around the Kuruman River Reserve (26.978°S, 21.832°E) in the Northern Cape Province of South Africa. Census counts and demographic data are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.r9k214r (Bateman et al. 2018). The same data have been used before to explore population and group dynamics of meerkats without integrating across levels of hierarchical demography (Bateman et al. 2011, 2012, 2013). To discretize annual meerkat group demography, we employed a census date of July 1 to correspond with the dry season lull in reproduction and dispersal and align with past studies (Bateman et al. 2011, 2012). In reality, demographic processes occur in continuous time rather than discrete time, but we accrued events into annual demographic rates, a common assumption in matrix models that aligns well with demographic timing for meerkats.

Informed by past study of meerkat demography (Bateman et al. 2012, 2013; Mares et al. 2014), we first constructed a probabilistic description of interannual dynamics of established meerkat groups of varying sizes. Our model explicitly accounts for emigration, mortality, and natality, similar to past descriptions (Bateman et al. 2012), but focuses exclusively on females to avoid complications associated with male immigration. Supporting this simplification, meerkat groups tend to have equal sex ratios, and reproduction is not male limited (most young within a group are the offspring of the dominant male; Spong et al. 2008). We provide details of model fitting in section A2, and below we give key functional forms that relate demographic rates to $N_t$, a group's size at time of census in year $t$. Using our group dynamics model to describe interannual transitions from one group size to another and making empirically informed assumptions about the fate of dispersers attempting to found new breeding groups (Young 2004), we parameterized a stage-structured matrix model for our focal population of meerkat groups.

To describe group transitions, we used the long-term monitoring data to parameterize models of the probabilities with which established groups incurred given rates of emigration, mortality, and recruitment. Each model combines a core functional form describing relevant average trends and a probabilistic component that associates a probability with any possible observation. We considered emigration to occur immediately after census, allowing the expected per capita emigration rate to increase with group size according to

$$p_{\mathrm{E}}(N_t) = p_{\mathrm{E\,max}}[1 - e^{(-k_{\mathrm{E}}N_t)}], \qquad (2)$$

with maximal emigration rate $p_{\mathrm{E\,max}}$ and saturation rate parameter $k_{\mathrm{E}}$. We assumed that reproduction and mortality follow emigration concurrently, dependent on the postemigration group size, $N_{t+0.5}$. We modeled per capita mortality rate as a modified logistic function of postemigration group size,

$$p_{\mathrm{M}}(N_{t+0.5}) = p_{\mathrm{M\,min}} + \frac{1 - p_{\mathrm{M\,min}}}{1 + e^{(-k_{\mathrm{M1}} - k_{\mathrm{M2}}N_{t+0.5})}}, \qquad (3)$$

with parameters $k_{\mathrm{M1}}$ and $k_{\mathrm{M2}}$ and minimum annual mortality of $p_{\mathrm{M\,min}}$. We modeled expected recruitment in a group as a saturating function of postemigration group size,

$$\mu_{\mathrm{R}}(N_{t+0.5}) = \frac{k_{\mathrm{R0}}N_{t+0.5}}{1 + k_{\mathrm{R0}}N_{t+0.5}/k_{\mathrm{R\,max}}}, \qquad (4)$$

with parameters $k_{\mathrm{R0}}$ and $k_{\mathrm{R\,max}}$. Recruitment refers to the total number of offspring born in a group that survive to be censused on July 1. To align with past work (Bateman et al. 2011, 2012, 2013), we included only individuals older than 2 months of age in the census, although census timing led to the inclusion of most surviving offspring produced over the previous year. Informed by past work, we sought to use the simplest appropriate probabilistic descriptions of demographic rates. While this might suggest that recruitment would be Poisson distributed and emigration and mortality binomially distributed, we knew that variation in annual rainfall—which we did not incorporate here—has a strong influence on recruitment and emigration rates and contributes substantially to variation in meerkat group dynamics (Bateman et al. 2012, 2013). We thus assumed emigration to be beta-binomially distributed and reproduction to be negative-binomially distributed to account for interannual variability in the mean values of these rates, and we assumed mortality to be binomially distributed (sec. A2). Using these models, we analytically composed a group size transition matrix, **T**, describing the probabilities with which a meerkat group of any given size was likely to become any size over the course of a year.

Making empirically informed assumptions about the rates at which emigrant coalitions of various sizes formed new breeding groups, we similarly formulated a new-group formation matrix, **F**. Since the elements of **F** involve dispersal success, associated parameters can be difficult to measure (Bowler and Benton 2005). We lacked detailed dispersal data for meerkats and therefore had to make several assumptions. Dispersal is risky (Bowler and Benton 2005), and meerkats in same-sex dispersal coalitions show evidence of elevated stress (Young and Monfort 2009). For each dispersing coalition (composed of the emigrants from an existing breeding group) of size $N'_{t+0.5}$, we modeled the per capita mortality rate for dispersers, $p'_{\mathrm{M}}(N'_{t+0.5})$, as equivalent to that in an established group a fraction of the size:

$$p'_M(N'_{t+0.5}) = p_M \left( \frac{N'_{t+0.5}}{k'_M} \right). \qquad (5)$$

Here, we use the prime symbol to denote a nascent group as opposed to an established group. The parameter $k'_M$ is a scaling quotient, in part accounting for the size of the dispersing coalition, composed of only females and therefore approximately half the size of a breeding group containing the same number of females. Values of $k'_M > 2$ also model an elevated mortality rate during the stressful emigration period (Young 2004; Young and Monfort 2009). We assumed $k'_M$ to be 3 and performed a sensitivity analysis for this parameter. To estimate settlement probability of dispersing coalitions (of size $N'_{t+0.75}$ following dispersal mortality), we made use of the observations that dispersing males refuse to form new breeding groups with lone females (T. H. Clutton-Brock, unpublished data) and that larger dispersing coalitions tend to enjoy greater success (Young 2004). We model settlement probability as a saturating function:

$$p_S(N'_{t+0.75}) = p_{S\,max}\{1 - e^{[-k_S(N'_{t+0.75}-1)]}\}, \qquad (6)$$

with $p_{S\,max}$ the settlement probability for large dispersing coalitions and $k_S$ a saturation constant, which we assume to be 0.5 for general correspondence with observed patterns (Young 2004). Once a group had settled, we counted it as an established breeding group in the subsequent year, but we assumed complete mortality for groups that failed to settle. We made the simplifying assumption (see sec. A2.3) that an established group could produce at most one new group over the course of a year.

Finally, we summed the group size transition matrix and new-group formation matrix into a group projection matrix, describing expected annual dynamics of a population of meerkat groups. With this parameterized version of our group matrix model, we could apply standard tools of matrix modeling (Caswell 2001) to gain insight into model behavior. A key piece of matrix model theory is that, under the majority of realistic conditions, we can calculate a population's asymptotic growth rate as the dominant eigenvalue of the relevant projection matrix. Important here is the result that the long-run rate of increase in the number of groups in a population is equivalent to the long-run rate of increase in the overall size of that population, provided that group sizes remain finite (Al-Khafaji et al. 2009; sec. A3). As a consequence, we can equate the asymptotic annual population growth rate $\lambda$ to the asymptotic annual rate of increase in the number of groups in the population: the dominant eigenvalue of the group size projection matrix.

The primary uncertainty in our parameterized model enters in the parameters relating to new-group formation. To provide a point of reference, we solved for the maxi-

mum settlement probability, $p^*_{S\,max}$, that produced an asymptotically stable population ($\lambda = 1$). To find this value, we numerically searched across possible $p_{S\,max}$ values to find the one that produced a population growth rate closest to 1. We bracketed results by considering $p_{S\,max}$ values of 0 (no new-group formation) and 1 (all dispersing coalitions form groups). This allowed us to consider model dynamics at points spanning the range of possible settlement rates, which we interpret to represent varying levels of population density or habitat saturation. We also assessed the effect on population growth of varying $k'_M$, the scaling coefficient for dispersal mortality, between 0.1 and 10 (allowing density-dependent mortality in a dispersing coalition to be equivalent to that in a much larger or much smaller established group), and we considered versions of the model for which settlement probability was consistent across dispersing-coalition size.

As one validation of our model against observations, we compared the stable group size distribution of the modeled meerkat population, $\nu$, to the empirical group size distribution. Calculated as the right eigenvector associated with the dominant eigenvalue (here, $\lambda = 1$, assuming stability) of the population projection matrix, $\nu$ gives the distribution of group sizes for a population of groups that has been growing according to $\mathbf{A}$ for many years (Caswell 2001).

While group size is potentially unbounded, it is limited in reality (sec. A3), and we considered group sizes of up to 80 individuals. A group size of 80 falls in the extreme tail of the stable group size distribution (see "Dynamics of the Parameterized Model"), and social groups containing 80 females have never been observed. We chose this high upper bound to minimize truncation-related errors in probability calculations at relevant group sizes.

We performed all calculations in R (R Development Core Team 2017). For probability calculations and matrix manipulation, we used the base package. We used the chisq.test function to perform Monte Carlo goodness-of-fit tests. We used the optim optimizer, with default convergence tolerances ($\approx 10^{-8}$) for numerical maximum likelihood model fitting. To solve for $p^*_{S\,max}$, we used methods from Brent (1973), as implemented in R's optimize function, for which we again used the default convergence tolerance ($\approx 10^{-4}$). Further details of model parameterization are provided in the appendix.

## Analysis and Results

### Dynamics of the Parameterized Model

The parameterized models for demographic rates and group transition were consistent with observations (fig. 1; sec. A2.2) and previous descriptions of the same processes (Bateman et al. 2012, 2013, their figs. B17, B18). Parameter estimates
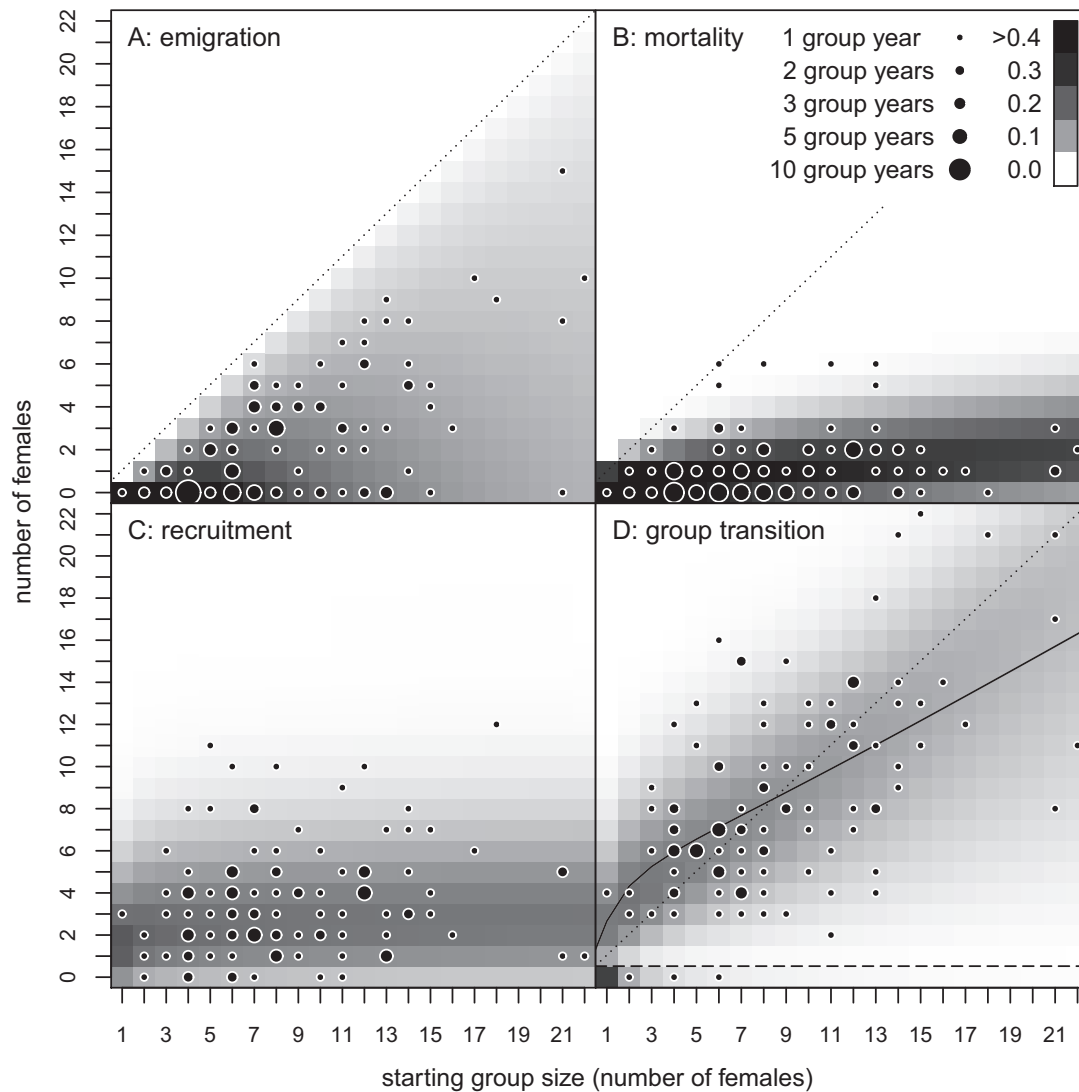
**Figure 1:** Total annual counts of emigrant (*A*), dead (*B*), and recruited (*C*) female meerkats in social groups of given starting sizes on July 1 of each year and resultant group sizes 1 year later (*D*). Observations (circles; area proportional to number of group/year observations) and predictions (shading) are for meerkats on and around the Kuruman River Reserve, South Africa, between 1998 and 2008. Models that describe component demographic rates (*A–C*) combine analytically to produce the annual group transition probabilities in *D*. Dotted line indicates 1 : 1, dashed line separates zeros (not explicitly part of projection matrix), and solid line shows mean final group sizes.

for all models are given in table 1. While absolute rates of emigration, mortality, and recruitment all increased with group size, per capita rates showed different trends. Per capita recruitment decreased with group size, per capita emigration increased with group size, and per capita mortality decreased with group size. Although this relationship between mortality and group size represents a component Allee effect, overall changes in focal group size were conventionally density dependent, with groups growing the fastest (per capita) when small and declining when large (fig. 1). From previous analysis, we know that the component Allee effect in mortality

does not translate to group dynamics in general, because within-group mortality is a minor contributor to changes in group size (Bateman et al. 2012).

The new-group formation matrix, **F**, synthesized empirical estimates of emigration with our assumptions about dispersal and settlement. Larger established groups were more likely to found new groups and tended to found larger groups, whereas small established groups were unlikely to found new breeding groups (fig. 2*A*). To achieve population equilibrium, new dispersing coalitions had to be relatively unlikely to form new breeding groups (we solved for $p^*_{S\,max}$

**Table 1:** Parameter estimates

| Symbol | Interpretation | MLE | 95% CI |
|---|---|---|---|
| Emigration: | | | |
| $p_{E\,max}$ | Maximal per capita emigration rate | .353 | .263 to .443 |
| $k_E$ | Emigration saturation rate | .347 | .020 to .674 |
| $\theta_E$ | Overdispersion in emigration | 2.871 | 1.603 to 4.139 |
| Recruitment: | | | |
| $k_{R\,max}$ | Maximal annual group recruitment rate | 4.227 | 3.051 to 5.402 |
| $k_{R0}$ | Initial increase in recruitment with group size | 6.964 | 0 to 20.387[a] |
| $\theta_R$ | Overdispersion in recruitment | 2.871 | 1.603 to 4.139 |
| Mortality: | | | |
| $k_{M1}$ | Logistic intercept for mortality | −.999 | −3.286 to 1.289 |
| $k_{M2}$ | Logistic effect of postemigration group size on mortality | −.044 | −.177 to .088 |

Note: 95% confidence interval (CI) calculated via the quadratic approximation method. MLE, maximum likelihood estimate.

[a] 0 is edge of allowable range; further approximation of CI.

[the maximal settling rate for large coalitions at population equilibrium] of 6.7%), and the equilibrium group size projection matrix closely resembled the group size transition matrix (figs. 2B, 1D). Because density dependence in mortality was relatively weak, varying the scaling coefficient for dispersal mortality ($k_M'$ in eq. [5]) between 0.1 and 10 had no effect (to two decimal places) on the population growth rate.

Observed meerkat group sizes corresponded to the long-run stable distribution of group sizes, as predicted by our equilibrium group projection model (fig. 3; $\chi^2 = 31.259$, simulated $P = .083$ based on $10^6$ pseudorandom draws from the stable group size distribution).

### Effects of Group Size

We next considered how the size with which a group starts the year influences two measures of that group's annual productivity: (1) group number growth rate, the average number of groups the group produces; and (2) per capita
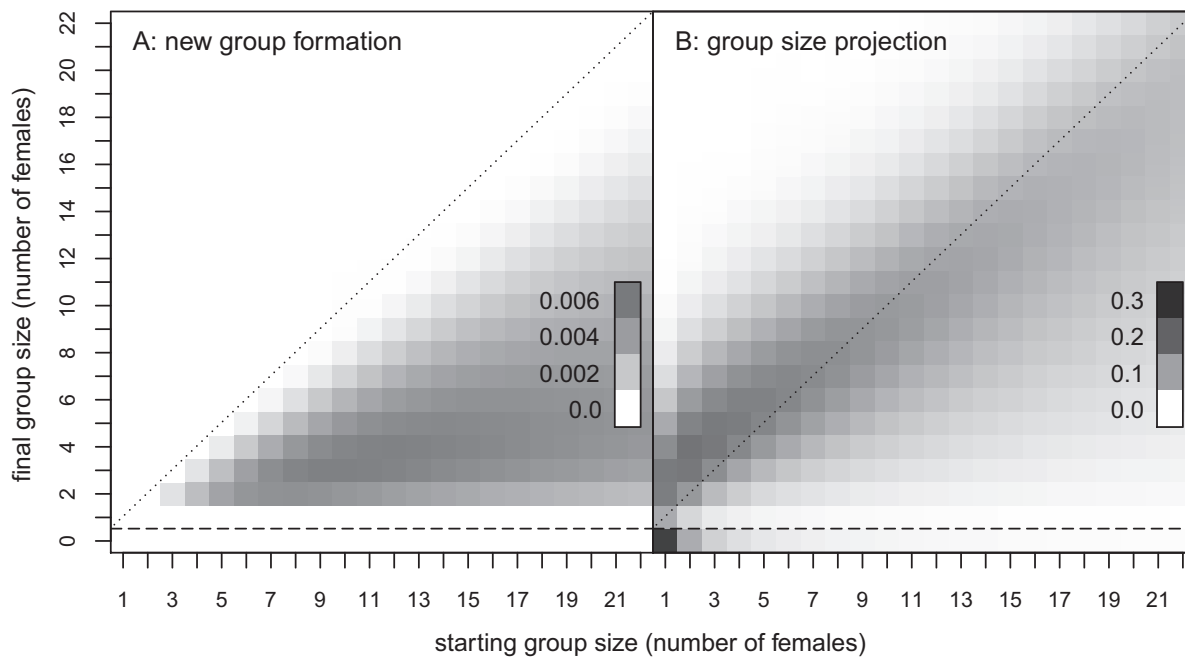


**Figure 2:** Annual group formation matrix **F** (*A*) and group size projection matrix **A** (*B*) for meerkat groups. **A** is the sum of **F** with an empirically parameterized group size transition matrix **T**. Values for **F** assume a maximal new-group settlement probability of 0.067, resulting in population equilibrium. Dotted line indicates 1:1, and dashed line separates zeros (not explicitly part of matrices). Note scale for shading and that new groups of size 0 are not indicated.
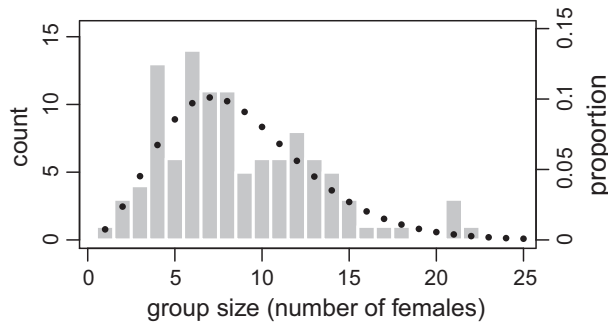
**Figure 3:** Observed group sizes (histogram) for meerkat groups on and around the Kuruman River Reserve, South Africa, between 1998 and 2008, and stable group size distribution (circles) from a group matrix model parameterized using data from those groups.

growth rate, the average number of individuals that a group member produces. We calculated group number growth rates from the entries of the group projection matrix, **A**, as $\sum_{i>0} a_{ij}$ for groups of different starting sizes ($j$) and for maximal settlement probabilities ($p_{S\,max}$) of 0, 0.067 (the equilibrium value, $p_{S\,max}^*$), and 1. We calculated per capita growth rates as $\sum_{i\geq 0} i a_{ij}/j$ for groups of different starting sizes, again considering $p_{S\,max}$ values of 0, 0.067, and 1. Both of these measures are inclusive of the original group or individual, so values of 1 indicate no change.

For a population overall, as noted previously, the rate of growth in the number of groups and the per capita growth rate converge over a long time period, but a given year's group number and per capita growth rates are not similarly related for individual groups. Both measures of group productivity incorporate dispersal, involving associated mortality, which may lead to a net reduction in the number of surviving individuals that originate from a group in a given year (per capita productivity <1), even if the group is expected to produce a new daughter group (group productivity >1).

We repeated all calculations, omitting component Allee effects in mortality and settling rate (see sec. A2.3) from the model, to assess the Allee effects' influence on overall dynamical patterns. In this case, we replaced group size–dependent per capita mortality with its overall demographic average, and we replaced coalition size–dependent settlement probability with a constant, $p_S = 0.017$, that maintained population equilibrium (we also considered bracketing settlement probabilities of 0 and 1).

The relationship between group size and a group's annual productivity differed depending on whether focus was on a group overall or on an average female within a group. The model-predicted group number growth rate ($\sum_{i\geq 0} a_{ij}$) increased with group size (toward a maximum of 2 because of model assumptions; sec. A2.3), while the per capita growth rate ($\sum_{i\geq 0} i a_{ij}/j$) declined with group size (fig. 4).

This pattern held true for each $p_{S\,max}$ value we considered and was qualitatively unchanged when we omitted component Allee effects in mortality and new-group settlement rate (fig. A2; figs. A1–A4 are available online).

To assess future population contributions by groups of different sizes, we calculated the set of reproductive values, *v*, for groups within the meerkat population. Here, reproductive value measures the relative long-term demographic contribution by groups of different starting sizes (Caswell and Werner 1978). Reproductive values depend on rates of both new-group formation and group persistence. The set of reproductive values is commonly calculated from matrix models as the left eigenvector associated with the dominant eigenvalue of the population projection matrix (Caswell 2001). To once again contrast group-level patterns with individual-level patterns, we also calculated average per capita reproductive value ($v_i/i$) for all mature females in each size of group.

Mirroring the trends for group number growth rate, reproductive value increased with group size while per capita reproductive value (each individual's proportional share of
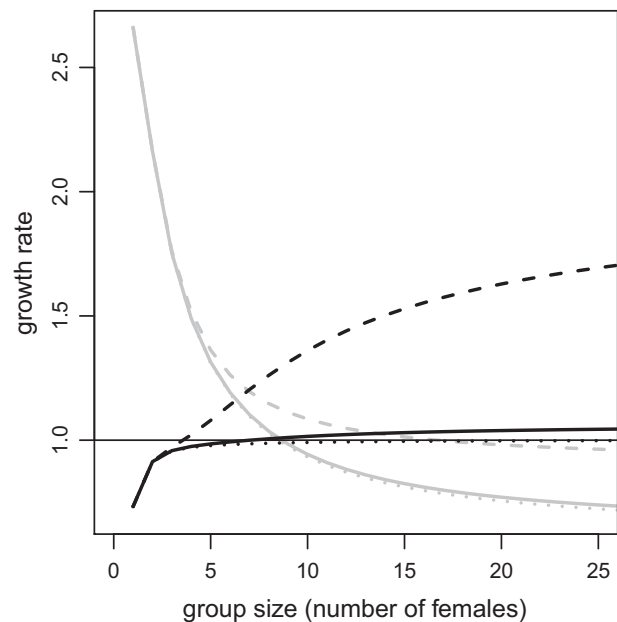


**Figure 4:** Annual per capita growth rate (gray) and group number growth rate (black) for meerkat groups growing and producing new daughter groups, as predicted by an empirically parameterized group size projection matrix model. Annual growth in group number corresponds to the number of new breeding females produced by a dominant breeder, responsible for the majority of reproduction within a group. Rates are shown for no new-group formation (dotted lines) and maximal new-group settlement probabilities of 0.067 (population equilibrium; solid lines) and 1 (dashed lines). This approximates the range of relationships possible under different environmental or population density conditions. Lines above the horizontal line at 1 represent net annual growth.

her group's future contribution) declined with group size (fig. 5). Qualitative patterns were unchanged when we omitted component Allee effects in mortality and new-group settlement rate (fig. A3).

These results present different perspectives on how group size affects short- and long-term demographic success in terms of annual growth rate and reproductive value. For an average individual, per capita growth rate and reproductive value appear to decline with group size (figs. 4, 5). In most groups, however, a single dominant female is responsible for the majority of successful breeding attempts (Clutton-Brock et al. 2008), and it is therefore relevant to consider how reproduction per dominant female (or per group) relates to group size. If we make the (largely correct) assumption that a group's reproductive output derives from the single dominant female, then her annual rate of production of new breeders and her reproductive value both appear to increase with group size (figs. 4, 5).

### Effects of Emigration Rate

Although we found that group size affected growth rates and reproductive values (see "Effects of Group Size"), our model considered a population of groups in which all indi-
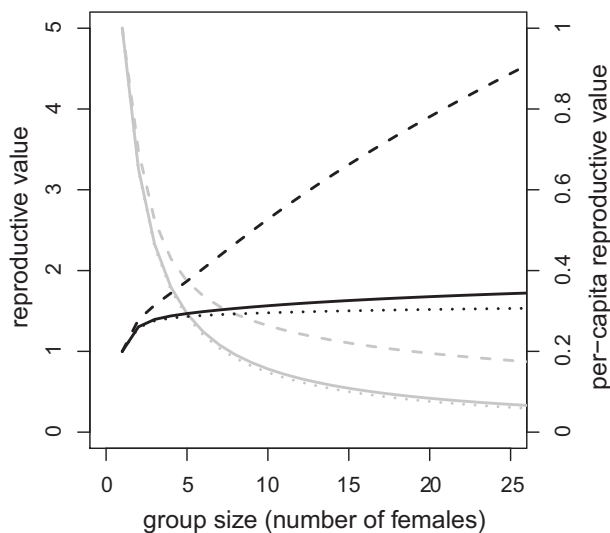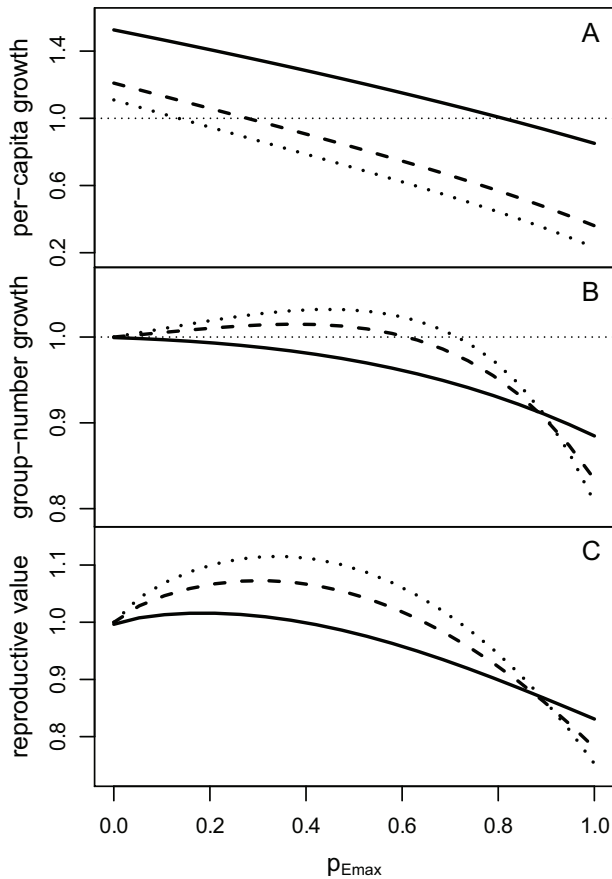


**Figure 5:** Reproductive values (black) and per capita reproductive values (gray) for meerkat groups of different sizes, as predicted by an empirically parameterized group size projection matrix model. Reproductive value indicates a group's overall contribution to future population growth, directly attributable mainly to a single dominant breeding female, while per capita reproductive value represents an average group member's share of that contribution. Values are shown relative to those for a group with a single female, assuming no new-group formation (dotted lines) and maximal new-group settlement probabilities of 0.067 (population equilibrium; solid lines) and 1 (dashed lines). This approximates the range of relationships possible under different environmental or population density conditions.

viduals exhibited the same relationships between group size and demographic rates, as determined by empirically parameterized functions. Consequently, the distribution of group sizes—as described by the stable group size distribution predicted by our model (fig. 3)—and the resultant distribution of annual group growth rates would be a natural consequence of group size/demography relationships and associated demographic stochasticity. On the basis of matrix model theory, under the assumption that relevant conditions remained constant, the descendant groups produced by any starting group would eventually conform to the stable group size distribution (fig. 3), and the resultant lineage would eventually grow at the same rate, regardless of starting group size. Thus, although groups of different sizes in a single year may fare differently, dynamical differences erode over time.

These insights from matrix theory led us to consider how different behavioral tendencies could result in different average group sizes and influence the associated growth rate of a lineage. That is, how might a tendency to form larger or smaller groups affect the fitness of a lineage? We view a group's emigration rate as an inverse measure of meerkats' tendency to maintain large groups, since higher emigration rates result in smaller social groups, on average (see "Effects of Emigration Rate"). In this light, we explored how changes in the model parameter controlling emigration rate in large groups, $p_{E\max}$, affected measures of group success. Note that the model form we used for per capita emigration (eq. [2]) means that increases in $p_{E\max}$ also increase emigration rates across group sizes.

First, we considered how varying emigration tendency, as determined by $p_{E\max}$, affected annual per capita growth rates, annual group-number growth rates, and long-term reproductive values for groups of initial sizes of five, ten, and fifteen (fig. 6). Because individuals cannot directly choose the size of group they inhabit, varying emigration tendency allowed us to consider a range of behavioral options, relevant to determining group size, that individuals might employ.

The three different measures of group success showed different patterns. For all group sizes, per capita growth rate was maximized when emigration ceased at $p_{E\max} = 0$ (fig. 6A); that is, any group appears to maximize its surviving descendents after 1 year by avoiding emigration altogether. Group number growth rate, however, displayed maxima at intermediate emigration rates for the two larger group sizes (fig. 6B). Together, these patterns illustrate the risks and benefits that emigration carries: emigrating individuals are likely to suffer mortality, but emigration is the only way to increase the number of daughter groups any group can produce over the course of a year. Note that group number growth rates for smaller groups exceed those for larger groups at high values of $p_{E\max} = 0$ because of the

**Figure 6:** Per capita group growth rates (*A*), group number growth rates (*B*), and reproductive values (*C*) across the range of maximal per capita emigration probabilities, $p_{E\,max}$, for meerkat groups of five (solid lines), 10 (dashed lines), and 15 (dotted lines) females, as predicted by an empirically parameterized group size projection matrix model. Reproductive values shown relative to that for a group size of 15 with $p_{E\,max} = 0$.

functional form of equation (2), whereby per capita emigration increases with group size toward the $p_{E\,max}$ asymptote. Patterns in reproductive value (fig. 6*C*) show that maximizing a group's future descendents invariably involves some level of emigration, with lineages that start out as larger groups displaying maximal reproductive value at higher emigration rates. Note that reproductive value is maximized when some emigration occurs for a group of size 5, even though zero emigration would maximize both per capita and group number growth rates. This occurs because reproductive value is a long-term measure, calculated for a fixed emigration/group size relationship, and a small group will eventually grow to the point that emigration will increase the growth rate of the lineage.

Next, we explored how changes in emigration tendency and the ability to found new groups affected the long-term population growth rate λ. Because our model ignores

population-scale density dependence in group establishment, we also calculated these $p_{E\,max}$-dependent λ values across the possible range of maximum settlement probabilities, $p_{S\,max}$. When habitat is saturated with established groups, we would expect group formation to be less probable, such that we consider different levels of $p_{S\,max}$ to stand in for different levels of density-dependent habitat saturation.

Finally, we assessed how component Allee effects in mortality and settlement influenced patterns in population growth rates. To do this, we recalculated λ values after omitting both Allee effects from the constituent submodels, as we did for the annual growth rate calculations above.

Across nonzero probabilities of new-group formation, $p_{S\,max}$, the population growth rate was maximized at intermediate asymptotic emigration rates, $p_{E\,max}$ (fig. 7). Results were qualitatively unchanged when component Allee effects were omitted from the model (see sec. A4).

To illustrate how population growth was maximized at intermediate levels of emigration for each level of settlement, we explored per capita group growth rates and group size distributions under three sets of example conditions. Specifically, we calculated groups' per capita growth rates across group sizes for three different values of the maximal emigration rate ($p_{E\,max}$ in {0.05, 0.15, 0.5}), with the maximum settlement probability, $p_{S\,max}$, set to our reference value of 0.067. Note that $p_{S\,max} = 0.067$ did not correspond to population
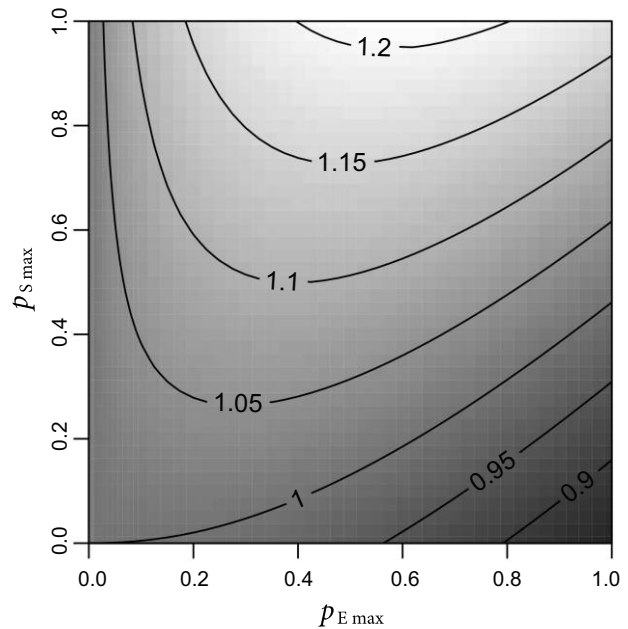


**Figure 7:** Contour plot of long-run population growth rates for populations of meerkat groups with specified maximal new-group settlement probabilities, $p_{S\,max}$, and maximal per capita emigration probabilities, $p_{E\,max}$. The maximal rates apply to large dispersing coalitions and large existing groups, respectively.

equilibrium for any of the example $p_{E\,max}$ values. As shown previously (fig. 4), per capita group growth rates decline with group size, and while lower emigration rates lead to faster per capita group growth, lower emigration rates also cause the stable group size distribution to shift toward larger and slower-growing groups (fig. 8). This relationship results in there being a certain $p_{E\,max}$ value that balances emigration's effects on the stable group size distribution and per capita group growth rates, maximizing long-term population growth for a given value of $p_{S\,max}$.

## Discussion

To analyze social influences on population dynamics in cooperative breeders, we adapted a linear stage-structured matrix model to describe discrete-time changes in social group size and abundance, capturing the hierarchical demography (Al-Khafaji et al. 2009) of a socially structured population. While our model is strictly density independent at the population level, the use of appropriate group transition and new-group formation rates allowed incorporation of explicit density dependence at the group level. Using data from a long-term study of cooperatively breeding meerkats, we parameterized the model (figs. 1, 2), offering in-

sight into the population dynamic implications of group-level density dependence and dispersal in this species. Although detailed dispersal data were unavailable, model results predicted patterns that were consistent across a range of dispersal scenarios.

Our approach allowed us to analyze intricacies of component and demographic Allee effects in meerkats. Taking dispersers into account, the model indicates that small groups exhibit higher annual growth rates per capita than do larger groups but that larger groups are responsible for faster increases in the number of groups. These results support the view that meerkat groups are locally conventionally density dependent from a per capita perspective and caused us to reconsider the dynamical consequences and fitness benefits of group formation. In a socially structured population, selection acts through dispersing individuals' abilities to found new groups that yield emigrants (Metz and Gyllenberg 2001). We note that group size is not a trait directly under selection but rather a result of other traits—such as those affecting dispersal—that may be under selection. As a result, we explored how emigration rates (which directly affect a population's apparent level of sociality, reflected in the group size distribution) affect a population's overall rate of growth.

### Allee Effects and Local Density Dependence

A demographic Allee effect is commonly defined as positive density dependence either in the per capita population growth rate or in average fitness (Courchamp et al. 1999a; Stephens et al. 1999). Although these two measures are equivalent for closed populations, since the annual growth rate of a lineage is a measure of its fitness (Metcalf and Pavard 2007), they differ when the population of interest is actually an open subpopulation, such as a social group. In particular, the ultimate fate of emigrating offspring is a critical component of fitness for members of social groups (Metz and Gyllenberg 2001; Lehmann et al. 2016), whereas emigration and mortality are indistinguishable in their effect on the size of a focal group.

Previous analyses of group-level demographic Allee effects in cooperative breeders have defined those Allee effects on the basis of per capita change in a focal group's size (e.g., Bateman et al. 2012; Angulo et al. 2013, 2018). Meerkat studies specifically have assumed a demographic Allee effect in group dynamics on the basis of trends in component demographic rates (Clutton-Brock et al. 1999a; Courchamp et al. 1999b). Although subsequent studies have found a group-level component Allee effect in survival, they have not found strong support for a group-level demographic Allee effect (Bateman et al. 2012, 2013). These past studies, however, did not consider the fate of emigrants.

Our hierarchical demographic model accounts for emigration and the formation of new groups and permits a
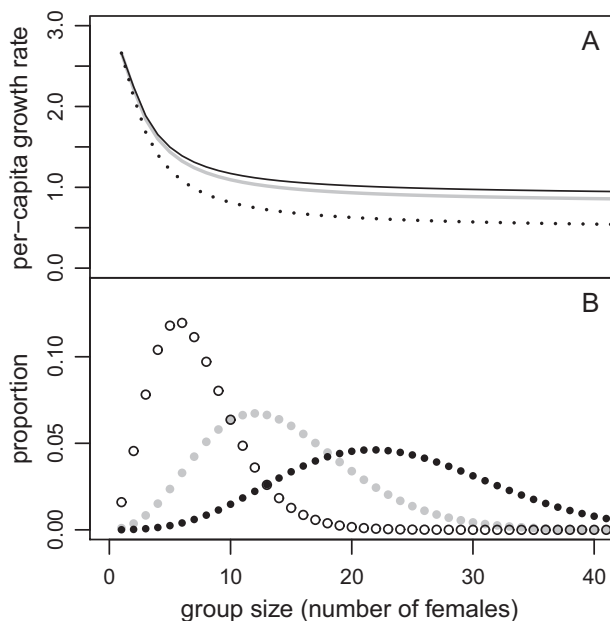


**Figure 8:** Annual per capita group growth rates (*A*) and stable group size distributions (*B*) for meerkat populations with maximal per capita group emigration probabilities, $p_{E\,max}$, of 0.05 (black), 0.15 (gray), and 0.5 (dotted line, open circles). Corresponding long-term population growth rates are 1.006, 1.010, and 0.981, respectively. In all cases, the maximal new-group settlement probability, $p_{S\,max}$, is set to 0.067. The maximal rates apply to large existing groups and large dispersing coalitions, respectively.

new analysis of group-level demographic Allee effects, defined to be a positive association between a group's size and its annual per capita growth rate, inclusive of dispersal. This definition considers the fate of all group members and recovers the link between per capita growth and average fitness over the short term. Given the previously identified positive associations between group size, dispersal group size, and new-group establishment (Young 2004), we expected that our model might reveal demographic Allee effects in meerkat groups. Our model instead revealed conventional per capita density dependence at the group level, predicting that short-term per capita growth—including dispersal—would be reduced in larger groups (figs. 4, A2) and that an average individual in a small group would be responsible for a greater proportion of the future population than an average individual in a large group (figs. 5, A3).

On the basis of our findings for meerkats, we suggest that conventional negative density dependence—in terms of the relationship between group size and estimates for per capita growth calculated across all individuals—may be a more common feature of cooperative breeder demography than previously acknowledged, at least for high-skew, singular cooperative breeders, in which a single breeding pair is responsible for most reproduction in each social group. African wild dogs (*Lycaon pictus*) have perhaps received the most attention in this regard (Courchamp et al. 2000; Courchamp and Macdonald 2001; Somers et al. 2008; Gusset and Macdonald 2010; Woodroffe 2011; Creel and Creel 2015). Although the theoretical implications of group-level Allee effects for wild dog population dynamics are striking (Courchamp et al. 1999b, 2000), studies have found little empirical support for group-scale demographic Allee effects, even in this archetypal case (e.g., Somers et al. 2008; Woodroffe 2011). Our study presents supporting evidence from another well-studied cooperative mammal, which originally sparked interest about Allee effects in cooperative breeders (Clutton-Brock et al. 1999a). Conclusions about other species might change if our revised concept of a group-level demographic Allee effect, taking dispersal success into account, were applied. Fruitful insights might also come from examining demographic patterns in plurally breeding species, such as banded mongooses (*Mungos mungo*), where reproductive output appears not to be constrained by reproductive suppression as group size increases (Cant et al. 2013). For such species, a component Allee effect in reproduction is more probable, and a group-level demographic Allee effect in terms of per capita growth rate may be more likely to arise. Further exploration of potential Allee effects in social species that exhibit little alloparental care, such as elephants (*Loxodonta* spp. and *Elephas maximus*) and red deer (*Cervus elaphus*), could help disentangle the influences of breeding system, cooperative rearing, and the survival benefits of group living.

Of course, the direction of the relationship between group size and short-term growth depends on which measure of growth we considered. While per capita growth declines with group size, the annual group number growth rate displays an increasing trend with respect to group size (fig. 4). This may seem to hint at the potential for conflict between breeders and average group members, but our model was not specifically formulated to explore this, and the two measures of growth are not directly comparable. Both growth rates contribute to group members' fitness over time, and the two rates converge over the long term. Small groups tend to exhibit relatively high per capita growth rates and low per capita emigration, and small groups tend to grow over the course of a year. Large groups appear to exhibit higher group formation rates and lower per capita growth, leading to smaller resulting groups over the course of a year. On average, over time, these processes lead to convergence in the group size distribution— and both growth rates—across lineages, regardless of starting group size. Behavior that maximizes one or the other growth rate for group members in the short term does not necessarily maximize representation of those individuals' descendants in the long term (fig. 6). Paradoxically, per capita growth is maximized in small groups, but reducing per capita emigration rates increases average per capita growth rate (fig. 6) while simultaneously increasing group size. We would argue that neither of the short-term measures of growth tell a complete story, and we should not restrict our thinking to the relationship between group size and short-term growth.

## Other Demographic Considerations of Sociality

Our finding of conventional per capita density dependence in meerkat groups seems to beg the question: If group size is not positively related to a group's per capita growth rate (or mean fitness over the short term; Metcalf and Pavard 2007), why form groups? Although we would expect persistent cooperation to afford fitness benefits, we argue that those benefits need not emerge as demographic Allee effects in social group dynamics. This may seem counterintuitive, but two points related to our analysis are relevant to consider.

First, the concept of a demographic Allee effect ignores important differences between dominant and subordinate group members. Our model predicted that the rate of new-group production and contributions to future population growth would increase for larger groups (figs. 4, 5, A2, A3). Interpreted from the perspective of dominant breeding females responsible for the bulk of reproduction, these relationships indicate that dominant breeders in large groups likely produce more new groups (with dominant breeders of their own) per year and contribute more to future breeding than do dominant breeders in small groups. This would seem to align with the view that the meerkat social system tends to

benefit dominant females, which control group membership by choosing when to evict their subordinates (Stephens et al. 2005; Ozgul et al. 2014). Such a positive association between group size and dominant breeders' success may hold relevance for the evolution of cooperation but fall outside the strict definition of Allee effects in terms of average fitness. The scenario for meerkats seems suited to interpretation in terms of inclusive fitness (Hamilton 1964); however, a detailed accounting of inclusive fitness is not empirically simple (Grafen 1982) and would likely require incorporating males explicitly into our model. In any case, kinship effects are implicitly taken into account when we average across all bearers of an allele (Grafen 1982), and theoretical equivalence has been established between the fitness of a lineage and average inclusive fitness in socially structured populations (Lehmann et al. 2016). Here, we have averaged across bearers of given functional relationships (e.g., the relationship between group size and emigration rate), thus accounting for net empirical kinship effects among group members. Our approach makes an implicit assumption that the population reproduces by selfing, making all individuals in a lineage identical by descent. We expect that a model of true diploid inheritance would reduce the correspondence of traits passed down a lineage, perhaps unless they are transmitted culturally (e.g., Thornton et al. 2010). An approach aiming to track inclusive fitness (similar to Stephens et al. 2005) might be better suited to explore any potential conflict between breeding females and average group members.

Second, considerations of short-term average fitness ignore long-term dynamics and the associated implications for group formation strategies. Forming groups of a certain size is not a strategy unto itself but rather the result of behavioral strategies and stochasticity within the system. In the matrix model we present, for any given fixed functional relationship between group size and expected demographic rates, a lineage arising from groups of any starting size will eventually be composed of the same distribution of group sizes and grow at the same rate (Caswell 2001). Individuals cannot directly select their group size, and some individuals will always end up in small groups, even if the species has evolved to produce large groups on average. As a result, searching for simple associations between a group's size at a given point in time and the short-term average fitness of the constituent group members may not offer insight (the approach would be similar to asking whether juveniles or adults are more fit). Rather, a tendency to form groups will be selected for if it elevates the growth rate of lineages exhibiting that tendency over the long term.

Using our model, we were able to assess long-term dynamics in the context of emigration strategies, predicting that meerkats' long-run population growth rate should be maximized at intermediate emigration rates (figs. 7, A4) across a plausible range of conditions. We interpret this as a trade-off between the risks of dispersal mortality (when emigration rates are high) and low per capita reproduction experienced in large groups (when emigration rates are low). All else being equal, the result suggests that a lineage with an appropriate, fixed group-forming strategy would grow faster—be more fit—than a lineage with a fixed emigration strategy. Although individuals do not appear to be fitter (measured on average over the short term) as members of larger groups within a given lineage, intermediate levels of emigration (and associated intermediate average group sizes; fig. 8) provide benefits over the long term.

## Conclusions

In developing a matrix modeling framework for hierarchical demography, we have necessarily left many avenues unexplored. Although we conceived our method to describe hierarchical demography in cooperative breeders, the approach could readily be applied to other stratified populations, be they socially structured groupings or spatially structured metapopulations. Such an application might complement existing approaches (e.g., matrix models of metapopulations; Hunter and Caswell 2005) or build on spatially explicit techniques (e.g., integrodifference equations; Kot et al. 1996; Neubert and Caswell 2000). The models used to parameterize a group projection matrix need not draw on detailed individual-based data, such as those available for meerkats, but could use basic subpopulation counts (e.g., Bateman et al. 2012). The approach simply requires information or assumptions about the dynamics of localized population subunits and about the way in which local dynamics interact to create new subunits. We considered models for which density dependence played a role only at the group level, and while we implicitly addressed the effects of varying levels of habitat saturation (see "Effects of Emigration Rate"), we did not explicitly consider population-wide density dependence (e.g., in the group formation process). The approach could be adapted, however, using techniques similar to those for density-dependent matrix models (Caswell 2001) or IPMs (Ellner and Rees 2006).

Empirical application and assessment of our model could follow at least two routes. First, the model could be applied to social species under intensive management or of conservation concern, such as wild dogs or killer whales (*Orcinus orca*), offering a tractable way to explore the implications of group-level and intergroup processes on population growth. Standard matrix population models often provide a useful first pass at modeling population dynamics in conventional species (Caswell 2001), and the model we present could serve a similar role for social species. The fact that our approach incorporates local density dependence means that it could offer improvement on classical model forms. The model form

we explored, lacking population-scale density dependence, may in fact be most useful for modeling the dynamics of imperilled species not subject to the negative density dependence seen in larger populations. Second, the model could be used to assess the importance of accounting for hierarchical structure in understanding population dynamics of social species. The form of density dependence exhibited in different demographic rates is likely to modify the mismatch between short-term measures of population growth (figs. 4, 6) and their relationship to long-term dynamics. For example, if increased recruitment were directly tied to increased emigration and group formation rates, group number and per capita growth rates would likely be closely aligned, and a simpler description of population dynamics might be possible. Parameterizing our model for species that exhibit different within-group patterns (such as banded mongooses) or particularly strong constraints on dispersal (such as lions) would improve our understanding of the dynamical processes at play in hierarchical populations and the relevance of hierarchical structure in population dynamics. Increasingly available high-quality dispersal data (e.g., Cozzi et al. 2018) will allow empirical assessment of the long-term implications of various dispersal strategies and patterns. Given that dispersal and new-group formation are key components of fitness in structured populations (Metz and Gyllenberg 2001), better dispersal data will allow for clearer assessment of how within- and between-group processes interact to influence long-term population growth and are likely to yield insight into the evolution of social species.

In the context of cooperative breeders, further elaborations of our model could incorporate additional environmental or demographic stochasticity, employing other techniques already available (e.g., Caswell 2001). Such approaches might help shed light on the high frequency of cooperative breeding species in arid environments (Lukas and Clutton-Brock 2017). If variation in extreme climatic conditions removes small social groups that fail to breed in particularly dry years, selection may favor large groups able to retain habitat in which they can recommence breeding when conditions improve. An exacerbation of Allee effects in extreme conditions could also contribute to this scenario (Clutton-Brock et al. 1999*a*; Bateman et al. 2012).

Our specific results provide context for the lack of evidence for group-level Allee effects in meerkats (Bateman et al. 2012, 2013) and other cooperative breeders, exemplified by African wild dogs (Somers et al. 2008; Woodroffe 2011). Social groups are inherently subject to extinction via environmental and demographic stochasticity, and it is perhaps not surprising that we fail to find obvious Allee effects, measured in terms of per capita group growth rates, in cooperative breeders. Over time, these species have likely evolved to overcome some of the drawbacks of group living (including genetic conflict; Lukas and Clutton-Brock 2012), and we might also expect selection to have resulted in traits that ameliorate potential Allee ef-

fects, leaving "ghosts of Allee effects past" (Courchamp et al. 2008, pp. 131, 159). Indeed, evidence for demographic Allee effects has been scarce across species (Myers et al. 1995; Kramer et al. 2009; Gregory et al. 2010). Here, we have shown evidence to suggest that such effects may not be required to explain aspects of sociality in a cooperative species.

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Meerkats (*Suricata suricatta*). Photo credit: Arpat Ozgul.