THEORY OF SOCIAL GROUP DYNAMICS

by

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Preface

Cooperative behavior is widespread. Organisms as varied as humans, ants, dogs, and microbes are reliant on conspecifics throughout their lives. But understanding cooperation from an ecological and evolutionary perspective is challenging. Cooperation is often associated with population structures that facilitate interactions between individuals (e.g. groups). Although helpful for the cooperators, group structure provides one of the biggest challenges in studying the ecological and evolutionary impacts of cooperation. Nevertheless, understanding the role of groups is vital as this is the environment in which many cooperative behaviors are carried out. This thesis is dedicated to understanding the influences of group structure and intergroup dynamics on the ecology of cooperative behavior.

When considering the ecology and evolution of cooperation, it is easy to immediately consider the expansive theory of social evolution that has been developed over the preceding decades. This, however, is not the perspective I aim to take here. Rather, I will attempt to clarify ecological impacts of cooperation. Surprisingly, questions on the ecology of cooperative behavior are often neglected compared to their evolutionary counterparts.

As an example, consider the population dynamics of cooperative breeders. Cooperative breeders such as African wild dogs, meerkats, and Arabian babblers live in discrete, permanent groups. A result of this is that each group is an entity which is fairly distinct from the rest of the population. What are the implications of this for population dynamics? This question was not explicitly considered until

the 1990s. Even then, much work simply assumes that population dynamics will be an obvious sum of the individual group dynamics. Empirical work in the early 2000s, however, failed to support this claim. Of particular interest is whether and how density dependence (e.g. Allee effects) scales up from the group level to the population level. In my first chapter (Why are demographic Allee effects so rarely seen in social species?), I develop and analyze a simple model of group-level density dependence to consider its role in population dynamics. I find that social structure typically acts as a buffer preventing within group dynamics from translating into population dynamics. I show that intergroup dynamics (e.g. dispersal, group formation, and group failure) mediate the relationship between group and population dynamics.

My first chapter shows the importance of group dynamics to the population as a whole, but it does not consider the mechanics of specific group decisions and behaviors. In my second chapter (Better baboon breakups: Collective decision theory of complex social network fissions), I zoom in to study individual decisions within a group. In particular, I consider the efficiency of various strategies at making the collective decision of a group fission. Cooperative behavior in groups often implies a social network. Individuals benefit from maintaining a strong social network. This leads to a challenge when a group must fission and split its social network. What strategies can individuals take to disturb their group's social network as little as possible during a fission? I apply collective decision theory to this question to show that democratic decisions are required to best maintain a social network through a fission. The computational

model developed is then applied to data from baboon group fissions and supports the claim that baboons democratically decide how to split up their groups.

As hinted at above, understanding the way in which cooperation and group structure influences a system's ecology is a challenging and grandiose goal. There exist many angles from which such questions may be considered. In this thesis, I specifically consider the role social population structures play in population dynamics and collective decisions. Despite the clear connection between these topics, further integration is necessary. In fact, this thesis may pose more questions than answers. Most notably, how do individual decisions influence group dynamics which ultimately produce population dynamics? Answering this question would truly provide a synthesis of the two chapters provided here. But there are many other exciting future directions to be considered. For example, how does the population dynamics of social structures feedback into the evolution of cooperation? Is group size heterogeneity necessary for the buffering nature of group structure? How can democratic decision making evolve? These are all questions I feel important to consider moving forward from what has been written here.

Theory of Social Group Dynamics

Abstract

by

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Group structure plays a vital role in understanding the ecology of cooperative behavior. Not only do groups provide the stage for cooperative behaviors to occur, but they also mediate the way in which these behaviors scale up to influence populations. In particular, intergroup dynamics are known to provide the means by which cooperation ultimately determines population dynamics. In this thesis, I consider intergroup dynamics from two perspectives. First, at the level of the population, I show that minimal intergroup interactions are sufficient to buffer the population against density dependence occurring at the group level. Second, I consider how individual decisions and various within group strategies can affect the efficiency of group fissions (a specific, important intergroup interaction). This thesis thus provides two perspectives on analyzing the importance and role of group structure in social species.

Why are demographic Allee effects so rarely seen in social animals?

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Keywords: component Allee effect, cooperative breeding, demographic Allee effect,

group Allee effect, group size, Lycaon pictus

Abstract

- 1. Allee effects in group-living species are common, but little is known about the way in which Allee effects at the group-level scale up to influence population dynamics. Most notably, it remains unclear whether component Allee effects within groups (where some component of fitness in small groups decreases with decreasing group size) will translate into a population-level demographic Allee effect (where per capita fitness in small populations decreases with decreasing overall population size).
- 2. The African wild dog (*Lycaon pictus*) is an obligate cooperative breeder that lives in packs and has a multitude of group-level component Allee effects. With the African wild dog as a case study, we use models to determine the effect that group structure has on the population dynamics of social animals and, specifically, whether Allee effects operating at the group level lead to a demographic Allee effect at the population level.
- We developed a suite of models to analyze the population dynamics of groupliving species, as well as comparable "packless" models lacking group structure. By comparing these models we can identify how Allee effects within groups influence population-level dynamics.
- 4. Our results show that group structure buffers populations against a demographic Allee effect, because mechanisms affecting birth and mortality are more strongly influenced by group size than population size. We find that interactions between groups is vital in determining the relationship between density-dependence within groups and density-dependence at the population level.
- Since sufficiently large groups provide protection against positive density dependence, even at low overall population sizes, our results have conservation

implications for group-living species, as they suggest group size is a necessary population feature to consider in efforts to manage population size. Furthermore, we provide novel insight regarding the role that dispersal and pack size variation plays in the buffering nature of social structure in groups subject to Allee effects.

Introduction

The Allee effect, in which the average fitness of individuals in a small population decreases with decreasing population size (Allee, 1931), is considered a driving force behind the population dynamics of many species. Allee effects are of ecological concern because they can doom small populations to extinction (Courchamp et al., 1999a; Stephens & Sutherland, 1999). Allee effects at the population level are broken into two categories: component and demographic (Box 1.1). A population-level component Allee effect is the reduction of any single aspect of an individual's fitness at low population sizes. Population-level component Allee effects can arise from the inability to find mates in small populations and beneficial conspecific interactions such as external fertilization and environmental conditioning (Courchamp et al., 1999a; Rinella et al., 2012). A population-level demographic Allee effect is the reduction in individuals' average total fitness at low population sizes. If this is detrimental enough to cause a negative population growth rate, it is called a "strong Allee effect" (Berec et al., 2007; the type we explore in this paper). A strong demographic Allee effect results in a heightened extinction risk below a population's Allee threshold – the population size below which the per capita population growth rate becomes negative (Courchamp et al., 1999a; Stephens & Sutherland, 1999; Berec et al., 2007). Importantly, population-level component Allee effects do not necessarily result in a population-level demographic Allee effect (Stephens et al., 1999). For example, decreased fecundity at low population sizes (a population-level component Allee effect) may be masked by decreased intraspecific competition, resulting in no net reduction in the growth of small populations and thus no population-level demographic Allee effect.

Group-living animals have long served as textbook examples for illustrating component Allee effects (Courchamp et al., 1999a; Stephens et al., 1999; Courchamp &

MacDonald, 2001). However, recent work has questioned the logic of framing Allee effects as purely population-level phenomena (Bateman et al., 2012; Angulo et al., 2013). Angulo et al. (2017) defined group-level component and group-level demographic Allee effects to make explicit the level at which an Allee effect occurs. These group-level effects are largely analogous to the population-level effects, with group size rather than population size as the driving variable (Box 1.1). However, to complete the analogy, we must take care in how we measure the fitness, and its components, of individuals within a group. First, groups (unlike many populations) are not approximately closed: dispersal is common and vital in many group-living species. Thus, defining group-level demographic Allee effects through group growth rate may be problematic, as a group could produce many surviving offspring (fitness is high within the group) that disperse, causing the group to shrink (Bateman et al., 2013). Clearly, this should not be considered a grouplevel demographic Allee effect. To avoid this problem, we define the group-level demographic Allee effect in terms of the group's reproductive success (Box 1.1) rather than the group's growth rate. We define a group-level demographic Allee effect, therefore, as a reduction in the average fitness of individuals in a group at low group sizes. Defining group-level Allee effects through average fitness of individuals within a group ensures that the definitions are consistent even if there is high reproductive skew within the group. It follows that a group-level component Allee effect is the reduction in a single aspect of average individual fitness at low group sizes (Box 1.1). Examples of group-level component Allee effects include beneficial social behaviors dependent upon group size, such as cooperative breeding, cooperative hunting, cooperative defense, etc. These definitions are broadly consistent with Angulo et al.'s (2017) definitions, but are more narrowly defined here to ensure that the effects are well-defined in open groups with non-breeding members.

While population-level demographic Allee effects are possible in group-living animals (supported by models (Courchamp et al., 2000) and seen in Arabian babblers (*Turdoides squamiceps*; Keynan & Ridley, 2016)), they appear to be rare. Most empirical studies have failed to detect population-level demographic Allee effects, including in social meerkats (*Suricata suricatta*; Bateman et al., 2011; Bateman et al., 2012) and other group-living species (Frank and Brickman, 2000; Gregory et al., 2010; Angulo et al., 2017). It is unclear whether this lack of evidence is surprising, or whether instead we ought not to expect population-level demographic Allee effects to result from group-level behaviors (Courchamp et al., 1999a; Stephens et al., 1999; Berec et al., 2007). The distinction between group-level and population-level component Allee effects is needed to resolve this issue (Bateman et al., 2012).

The African wild dog (*Lycaon pictus*), a well-studied species for Allee effects, is an obligate social carnivore that breeds, rears young, and hunts in packs varying in size from 2 to 30 individuals (e.g. Creel et al., 2004; Buettner et al., 2007; Somers et al., 2008). It is also a declining, endangered species with a badly fragmented habitat (IUCN/SSC, 2007; Woodroffe & Sillero-Zubiri, 2012; Tensen et al., 2016). There are numerous group-level component Allee effects affecting the African wild dog. For example, as pack size decreases, reproductive and hunting success decline while pup and yearling mortality increase (Malcolm & Marten, 1982; Creel & Creel, 1995; Courchamp & MacDonald, 2001). Due to the extent of preexisting research on their demography and the species' many Allee effects, we will use the African wild dog as a case study.

Empirical studies have consistently failed to detect a population-level demographic Allee effect in any population of African wild dog (Somers et al., 2008; Woodroffe, 2011; Angulo et al., 2013), possibly due to masking by competition in large groups (Bateman et al., 2011). However, Angulo et al. (2013) suggest intergroup

dynamics maintain healthy sized packs at low population sizes. Consequently, a population-level demographic Allee effect is not present despite group-level (component and demographic) Allee effects. Further, they suggest group size variation may be a key aspect mediating the relationship between group dynamics and population dynamics. In general, it is clear that group structure plays a vital role in shaping the population dynamics of social species (Bateman et al., 2012).

In this study, we examine the effect of group formation, failure, and intergroup dispersal (i.e. group structure) on the dynamics of the population as a whole. Although empirical work has been conducted (Bateman et al., 2011; Bateman et al., 2012; Bateman et al., 2013; Angulo et al., 2013; Keynan & Ridley, 2016), there exists no theoretical framework for how Allee effects at the group level affect population dynamics. It is therefore somewhat unclear whether and how population-level demographic Allee effects may arise in populations with group structure and group-level component Allee effects. Clarifying the link between within-group interactions and population dynamics is the central goal of this study. Using a suite of mathematical models, we find that group structure is often sufficient to buffer the population from population-level demographic Allee effects, as pack size becomes decoupled from population size at all population sizes. This prevents group-level Allee effects from scaling up to the population level, as proposed by Bateman et al. (2011) and Angulo et al. (2013). Furthermore, we find that this result is extremely robust to the presence or absence of variability in pack sizes, and to assumptions about age structure, sex structure, and how packs form and fail. This suggests that the protective effect of group structure may be quite general across groupliving species and that the lack of empirical evidence for population-level demographic Allee effects in social species is unsurprising.

Methods

Case Study

African wild dogs reproduce once per year (Malcolm & Marten, 1982; Creel & Creel, 2002), with only one dominant, breeding pair per pack and breeding ability suppressed in all other adults (Creel & Creel, 2002; Rasmussen et al., 2008; Somers et al., 2008). Although pack sizes vary, pack size is not correlated with population size (Woodroffe, 2011; Angulo et al., 2013). Group-level component Allee effects arise at several life stages. More pups are born and survive their first year in larger packs (Creel & Creel, 2002; Creel et al., 2004; McNutt & Silk, 2008; Woodroffe, 2011), because pups receive more protection and food with more adult helpers (Malcolm & Marten, 1982; Creel & Creel, 2002; Buettner et al., 2007; McNutt & Silk, 2008; Angulo et al., 2013). Yearlings also receive greater protection from larger packs, although they are not always given priority feeding at kills (Malcolm & Marten, 1982). As a result, yearling survival decreases in both small packs (due to loss of protection; a group-level component Allee effect) and in large packs (due to increased competition within the group). There are conflicting results about whether adult survival is density dependent (Somers et al., 2008; Woodroffe, 2011; Anuglo et al., 2013; Creel & Creel, 2015).

Yearlings typically disperse among packs before adulthood (McNutt, 1996; Creel & Creel, 2002). New packs typically form when two opposite-sex cohorts of dispersing yearlings fuse together into a pack (McNutt, 1996; Courchamp et al., 2000; Somers et al., 2008).

General approach

We use the terminology of the African wild dog (e.g. pack, yearling, pup) throughout the explanation of our models, but we believe our models to be general in their description of group-living populations (although they may require different parameter values or functional forms to be applied to other systems).

We formulated population-level models in pairs, where each model with pack structure was paired with a comparable model without pack structure (a "packless" model). We built three pairs of pack and packless models with varying levels of complexity: models lacking age and sex structure ("unstructured"), models with age structure, and models with both age and sex structure. Sex structure did not meaningfully extend our models' conclusions, so the age- and sex-structured model pair can be found in Appendix 1A. Studying multiple model pairs at different levels of complexity balances a desire for realism with a desire to isolate the effect of groups. Age and sex structure can affect population dynamics (Boukal & Berec, 2002), so models that omit these factors may provide limited insight into real world dynamics. However, we wish to ensure that any effects we attribute to group structure are truly due to groups, and unstructured models provide a straightforward way to assess this. We use the comparison between the age-structured pack model and the age-structured packless model as a baseline, then check whether our conclusions change when the models are simpler (unstructured) or more complex (age- and sex-structured).

In most pack models, pack structure is implicit: we write density dependence as a function of the average number of dogs per pack without modeling the individual packs themselves. To assess the importance of this simplifying assumption, we also built an age-structured model in which we explicitly tracked juveniles, yearlings, and adults in each individual pack.

This series of models (pack models with implicit pack structure and varying complexity, analogous packless models, and one model with explicit pack structure) are given in Table 1.1 and explained below. We model dynamics in discrete time with a time step of one year. All pack models have group-level component Allee effects in pup and yearling mortality rates. Packless models were built with comparable population-level component Allee effects. We iterated all models for 250 time steps using parameter values from Appendix 1B and a range of ten logarithmically spaced initial population sizes from 20 to 3000 and initial pack sizes 2 to 30 adults per pack (steps of 4). The initial number of packs in the implicit pack models was calculated as the population size divided by the number of adults per pack (and rounded to the nearest integer). The first four time points were dropped from our analyses to prevent initial-conditions from dominating our results.

To determine whether the populations displayed a population-level demographic Allee effect, the realized per capita population growth rate was plotted against the population size in each time step. A population-level demographic Allee effect is present if no small population sizes exhibit positive population growth.

<u>Models</u>

Age-structured models:

At the start of year *t*, the total number of juvenile pups (age 0) in the population is \mathbf{J}_t , the total number of yearlings (age 1) is \mathbf{Y}_t , and the total number of mature adults (ages ≥ 2) is \mathbf{M}_t . In models with pack structure, there are p_t packs during *t* and thus an average of $A_t = \mathbf{M}_t/p_t$ adults per pack.

In our models, R_t is the number of reproductive units in the population and C_t is the number of caregivers in the pack (pack models) or population (packless models). Caregivers are adult members of the pack or population, as these are the individuals known to contribute to group hunting, defense, and rearing of young (Malcolm & Marten, 1982; Creel & Creel, 2002; Buettner et al., 2007; McNutt & Silk, 2008; Angulo et al., 2013). R_t and C_t are functions of the other state variables. The form of these functions, and the state variables they depend on, are different for models with differing social and age structure, thus we can use equations 1-6 to build both pack and packless models. In models with pack structure, we use the number of packs as the number of reproductive units $(R_t = p_t)$, representing cooperative breeders with one breeding pair per pack. Care of juvenile pups and yearlings is provided by all adults in the pack, so in implicit pack models the number of caregivers is equal to the average number of adults per pack (C_t = A_i). In packless models, as we intend to illuminate the differences between Allee effects at the group and population levels, all adults may reproduce and provide care, so $R_t = C_t =$ \mathbf{M}_{t} . The packless models are not based on any particular population, and are rather a theoretical construct providing a basis of comparison to help discover the fundamental differences between Allee effects at the group and population levels.

The birth rate in our models increases with number of caregivers. Reproducing adults give birth to juveniles at per capita rate,

$$f(C_t) = \frac{rC_t}{L + C_t} \tag{1}$$

The maximum birth rate is *r*. When there are $C_t = L$ caregivers, reproducers achieve half this maximum (Fig. 1 A). Because $f(C_t)$ is a per capita rate, the population-level reproductive rate is $f(C_t)R_t$.

By the end of their first year, a fraction $d_J(C_t)$ of the pups die, where

$$d_J(C_t) = \frac{d c_1}{c_1 + C_t^2} + \mu_J$$
(2)

Density-dependent deaths decrease with the number of caregivers from a maximum of *d* to a minimum of 0 with an inflection point at $\sqrt{c_1/3}$ caregivers (Fig. 1 B). μ_J is the density-independent juvenile death rate. We do not consider cases where $d + \mu_J > 1$ to ensure juvenile mortality never exceeds 100%. The total juvenile population at the start of year *t*+1 is thus,

$$\mathbf{J}_{t+1} = f(C_t) R_t \left(1 - d_J(C_t) \right)$$
(3)

Accounting for the risks to yearlings of living in both under- and oversized groups, the fraction of individuals that die as yearlings is,

$$d_Y(C_t) = \left[c_y(C_t - s)^2 + c_4\right] + \mu_Y$$
(4a)

with

$$c_y = \begin{cases} c_2 & C_t \le s \\ c_3 & C_t > s \\ , \end{cases}$$
(4b)

where μ_Y is the density-independent death rate and the polynomial in square brackets in (4a) is a piecewise quadratic function with a minimum death rate of c_4 at $C_t = s$ caregivers (Fig. 1 C). We always take the minimum of (4a) and 1 to ensure the death rate does not exceed 1. If $c_2 > c_3$, having fewer than *s* caregivers is more detrimental than having greater than *s*. Year *t*+1 yearlings are the previous year's juveniles who have survived another year,

$$\mathbf{Y}_{t+1} = \mathbf{J}_t (1 - d_Y(C_t))$$
(5)

Finally, the population of mature adults in *t*+1 consists of surviving adults and remaining yearlings from the previous year's population. With a density-independent death rate of μ_M (see Appendix 1D for results with density dependence in adults), the mature adults at the start of *t*+1 are given by,

$$\mathbf{M}_{t+1} = (\mathbf{M}_t + \mathbf{Y}_t)(1 - \mu_M)$$
. (6)

We model new pack formation by allowing yearlings to form new packs. We assume that pack formation rates scale linearly with the number of dispersing yearlings (i.e., with more dispersers, opposite-sex cohorts are more likely to encounter each other and initiate a new pack). Using the parameter k to describe how pack formation is triggered, we assume that 1 new pack will form when the number of yearlings in the population rounds to k (that is, round $[\mathbf{Y}_t] = k$), and that n new packs will form when round $[\mathbf{Y}_t] = nk$. To ensure an integer number of packs our pack models add round $[\mathbf{Y}_t/k]$ packs after year t. Packs fail at a higher frequency if there are too few adults per pack. Using the parameter *j* to control pack failure we remove round $\left[\frac{j}{A_t}\right]$ packs after *t*. This means that 1 pack is lost if the average number of adults per pack rounds to j (round $[A_t]$ = *j*), and no packs are lost as long as $A_i > 2j$. In years with high pack failure, there is an increase in juvenile and yearling mortality due to the group-level component Allee effects (see equations 2 and 4). This can be interpreted as the effects of pack failure being distributed across all packs in the population (another assumption that we will relax when we model packs explicitly), since death and pack failure occur simultaneously in our models. The number of packs at the start of year t+1 is then,

$$p_{t+1} = p_t + \text{round} \left[\frac{\mathbf{Y}_t}{k}\right] - \text{round} \left[\frac{j}{A_t}\right].$$

(7)

However, we assume that the landscape can hold at most k_p packs, and that there is always at least 1 pack when the population size is greater than 0.

Unstructured models:

In our models with neither age nor sex structure, the we assume the equations simplify to,

$$\mathbf{N}_{t+1} = (\mathbf{N}_t + f(C_t)R_t)(1 - d_Y(C_t)) \quad , \tag{8}$$

where \mathbf{N}_t is the total population size (= $\mathbf{J}_t + \mathbf{Y}_t + \mathbf{M}_t$). Our use of the hump-shaped function $d_{\mathbf{Y}}(C_t)$ (Fig. 1 C), with density-independent death parameter μ in place of $\mu_{\mathbf{Y}}$ (Appendix 1B), allows us to consider detrimental effects of both small and large packs on survival. The number of reproductive units, R_t , is again p_t in the pack model and is now \mathbf{N}_t in the packless model. The number of caregivers is \mathbf{N}_t/p_t in the pack model and \mathbf{N}_t in the packless model. In the unstructured pack model,

$$p_{t+1} = p_t + \text{round} \left[\frac{\mathbf{N}_t}{k}\right] - \text{round} \left[\frac{jp_t}{N_t}\right],$$
(9)

where we constrain p_t to remain between 1 and k_p as above.

Modeling packs explicitly:

All pack models above include the simplifying assumption that the dynamics of the whole population are insensitive to variability among packs in their sizes. That is, we modeled reproduction and caregiving within each pack as a function of the average pack size without keeping track of the sizes of individual packs. In our final model, we relax this assumption. Within-pack dynamics are equivalent to the implicit-pack model with age structure, except that we use the individual pack sizes in place of average pack sizes (Table 1.1). We simulate the model with the same range of initial population and average pack sizes as before, but rather than initiate all packs at the exact same size, we draw initial pack sizes in this model from a normal distribution with variance 4 around the average.

Each year, the surviving yearlings in each pack form a dispersing cohort. When the total number of dispersing yearlings is low ($\mathbf{Y}_t <$ the pack formation parameter k), no new packs form. Instead, each dispersing cohort of yearlings is randomly assigned to another pack. If the conditions are met for pack formation ($\mathbf{Y}_t > k$), some cohorts become a new pack instead of joining existing packs. As in implicit pack models, we add \mathbf{Y}_t / k packs when the conditions for pack formation are met. We allow up to k_p packs.

As the number of adults in a pack decreases, pack reproductive success decreases and it becomes more likely to fail (defined as having fewer than 1 adult). Pack failure in the explicit pack model is thus contained to individual packs and has no effect on the rest of the population. This contrasts with the implicit pack models, where a pack failure implicitly increases the size of the remaining packs. The explicit pack model is more realistic for African wild dogs, so by considering both models, we can evaluate the implicit pack models' simplifying assumptions. Considering both models also allows us to assess the generality of our conclusions for other group-living species, which may have different modes of group formation and failure (see also *Sensitivity analysis*).

Parameter values

We drew on the results of many different studies to choose reasonable values for all parameters in the age-structured implicit pack model (Appendix 1B). Whenever possible, for consistency, parameter values were based on the African wild dog population in Selous Game Reserve, Tanzania (for a detailed account of this population, see Creel et al. (2004)).

Parameter values for all other models were chosen to make these models as comparable as possible to the age-structured implicit pack model. To illustrate why this is necessary, consider the maximum per capita birth rate, r: in pack models ($R_t = p_t$), this is the maximum litter size per pack whereas in the packless models ($R_t = \mathbf{M}_t$), it is a number per adult. Clearly, r should be adjusted to a lower value in the packless models to give comparable levels of overall population growth. In the same way, each parameter with units relating to the units of R_t or C_t must be rescaled to accommodate the addition or subtraction of pack or age structure.

The procedure for determining appropriate parameter adjustments in the packless models starts with a function for a group-level component of fitness (e.g. 3rd row of Table 1.1) and replaces group size on the x-axis with population size (e.g. 1st row of Table 1.1). Then, to determine the appropriate scaling of this new x-axis, we equated a pack size of 0 with a population size of 0, and the equilibrium pack size with the equilibrium population size observed in our age-structured pack model (13.25 adults per pack and 927.5 total adults). In the unstructured models, parameters were adjusted based on the equilibrium pack composition ratios observed in the age-structured pack model (24% juvenile pups, 18% yearlings, 58% adults; see results). All adjusted parameter values are shown in Appendix 1B.

Sensitivity analysis

To understand the range of situations for which we expect our qualitative conclusions to hold, we assessed the sensitivity of our models to three types of changes: different pack formation rules, different adult mortality functions, and changes to the parameter values.

First, we explored a large number of parameter combinations (Appendix 1B) and rechecked our results to test their generality. Sensitivity analysis for the unstructured models involved three values of each of the ten parameters (the 2 values shown in square brackets in Appendix 1B and their midpoint, for a total of $3^{10} = 59,049$ parameter combinations). Analysis for the age-structured models involved 2 values for each of fourteen parameters (the 2 values shown in square brackets in Appendix 1B, for $2^{14} = 32,768$ parameter combinations). These ranges are broad enough to capture a wide range of possibilities that may occur in nature.

For every parameter combination, we recorded the smallest pack and population size that achieved a positive growth rate from the pack models, and the smallest population size with a positive growth rate from the packless models. Pack models do not exhibit a population-level demographic Allee effect if positive growth occurs at small population sizes. To better understand the role of the pack formation and failure parameters (k and j, respectively), we determined what combinations of k and j resulted in group structure buffering against a population-level demographic Allee effect, using values of 1 to 30 for each parameter.

To understand the role dispersal and pack formation play in our models, we considered an alternative pack number equation (7), replacing \mathbf{Y}_t / k with $\mathbf{Y}_t / (p_t k)$ and adjusting the value of *k* accordingly (Appendix 1C). In this formulation, pack formation

is a function of the number of yearlings per pack (i.e. dispersing cohort size) rather than the total number of yearlings (related to the number of dispersing cohorts). Because this model is less prone to add new groups, analyzing it provides a means of sensitivity analysis of our pack formation function.

In the explicit pack model, we considered a version that distributed yearlings evenly amongst packs rather than keeping (different-sized) cohorts intact when assigning yearlings to new packs. Even distribution of yearlings homogenizes pack sizes. Comparing this model to the original explicit pack model allowed us to test the general importance of pack size variability. Lastly, we studied the sensitivity of our results to changes in the pack failure rule in the explicit pack model by allowing packs with fewer than *j* adults to attempt to fuse with another pack. Analyzing this model tests whether increasing connectedness between groups also increases the buffering nature of groups. Specific results from these models can be found in Appendix 1C.

Finally, we modified the adult number equation (6) to include both positive and negative density dependence in adult mortality to determine whether or not this change qualitatively affects our results (Appendix 1D). We also assessed the influence of demographic stochasticity on our model using lognormally distributed perturbations (Appendix 1E). All analyses were conducted using Mathematica (Wolfram Research, Inc., 2016).

Results

Effect of packs on population persistence

We iterated implicit pack and packless models through time using a range of parameters to determine which parameter values result in indefinite persistence. We found longer persistence in the pack model at any given parameter set (not shown), as well as persistence under a wider range of parameters when packs are present (Table 1.2). These conclusions held across all model pairs, with weaker protective effects from packs in models without age structure (Table 1.2).

We evaluated the presence of population-level demographic Allee effects directly by examining the realized per capita population growth rates in the simulations. The packless models display a strong population-level demographic Allee effect – that is, no observed positive population growth rates when population sizes were below the Allee threshold of approximately 950 adults (black curve, column I, Fig. 2; always negative at small population sizes). In contrast, the pack models lack a population-level demographic Allee effect, showing a positive per capita population growth rate in some years when population sizes were very low (red dots at small population sizes, column I, Fig. 2; positive population growth is possible in small populations). This suggests that pack structure prevents the group-level component Allee effects in our pack models from translating into a population-level demographic Allee effect. However, the implicit and explicit pack models do display a group-level demographic Allee effect (which we measure using per capita population growth rate as a proxy in the implicit pack models, since individual packs are not modeled), with a group Allee threshold of around 8 adults per pack (average pack size at which per capita population growth rate becomes negative, column II, Fig. 2) in models with age structure. These results hold for all pairs of models (and their variations; Appendices A; C-E), as well as the explicit pack model, meaning that neither age structure nor the rules of pack formation and failure qualitatively affected the buffering nature of groups. The similarity between our implicit and explicit pack models suggests that our models with implicit pack structure reliably capture the

protective effect of pack structure. Additional sensitivity analysis revealed that these results are robust across the range of parameters considered (Table 1.2).

These results raised the question of whether a population-level demographic Allee effect can ever arise from group-level component Allee effects. To answer this, we explored the effect of the pack failure parameter (j) and pack formation parameter (k) in our implicit pack models more broadly and found that a demographic Allee effect can result at low values of both j and k (Fig. 3). That is, when packs are either extremely robust against failure (small j) or form quite easily (small k), intergroup dynamics are no longer sufficient to protect against a population-level demographic Allee effect.

The ability of Allee effects to exist at the group level but not the population level can be understood by plotting average pack size against population size. Column III in Fig. 2 shows a lack of correlation between pack size and population size in the pack models; rather, a specific average pack size tends to be favored across population sizes. The result is that healthy, stable average pack sizes can exist even in small populations. Such conditions will allow the population to grow even with relatively few individuals, preventing a population-level demographic Allee effect.

We also found that if dispersal is a function of the number of yearlings per pack, this can lead to a rescue effect from which the population can recover even if its average pack size drops below the group Allee threshold (Appendix 1C). This occurs in the modified model but not the primary model, as groups form more slowly when dispersal is a function of the number of yearlings per pack. The result is the number of failing groups is more likely to overwhelm the number of forming groups, bringing the average group size in the population back above the group Allee threshold.

Characteristics of packs

Our models tend toward a pack size of 13.25 adults per pack with the parameters given in Appendix 1B. The pack size that maximizes growth in our model was just over 10 adults per pack. Further, our modeled packs have the age ratios of 24% pups, 18% yearlings, and 58% adults, again with the parameters from Appendix 1B. Although not central to our study question, we use these results as a way of assessing realism in our models' predictions.

Discussion

Our results show that a wide range of rules for group dynamics create more viable populations in social species by preventing group-level component Allee effects from translating into a population-level demographic Allee effect in most parameter combinations we explored. This occurs due to the independence of group size and population size that arises from dispersal and group failure allowing groups to approach the same size regardless of the population. Because per capita population growth is dependent upon average pack size, but not population size, the lack of correlation between average pack size and population size that arises in our models prevents the group-level component Allee effects from resulting in a population-level demographic Allee effect (Bateman et al., 2011; Angulo et al., 2013). That is, healthy-sized packs in a small population still result in positive population growth and thus no population-level demographic Allee effect. However, because group size and population size need not decouple, mechanisms that lead to a positive correlation between group size and population size would interfere with the buffering nature of group dynamics. Such a relationship between group structure and population dynamics is important for sustaining

small populations with healthy pack sizes, providing a plausible explanation for the unexpected recovery of the African wild dog population in Northern Kenya which persisted at very low numbers for a decade before expanding into a large population (Woodroffe, 2011).

Through our suite of models, we show that the way in which groups mediate the interaction between group Allee effects and population-level phenomena does not depend on age structure, sex structure, or pack size heterogeneity. Due to the robustness of our results to drastic changes in model structure and parameter values (Table 1.2; Appendices A; C-E), we believe them to be general to a wide range of social animals.

Our predictions about pack demography are consistent with naturally observed values. A pack size of 13.25 adults falls well within the range (2-30 adults) described by Creel et al. (2004), McNutt & Silk (2008), Angulo et al. (2013), and others. The pack size that maximizes group growth rate in our models (approximately 10) corresponds closely to the 10.25 adults per pack optimum found by Angulo et al. (2013). Additionally, our models predict packs to be 24% pups, with the census coming at the end of the pups' first year. Creel et al. (2004) observed packs with 33% pups at their emergence from the den (Creel et al., 2004; McNutt & Silk, 2008); pup mortality thereafter could explain our somewhat lower estimate. Our models' ability to predict realistic pack sizes and compositions (neither of which was considered in our choice of model equations or parameter values) demonstrates their consistency with known biology, and supports our use of these models to predict novel phenomena.

Variation in group size has been considered important for maintaining the lack of correlation between group dynamics and population dynamics that allows group structure to act as a buffer against detrimental dynamics at the population level (Bateman et al., 2011; Angulo et al., 2013). Interestingly, even in our implicit pack models that lack between-pack size variation, group dynamics create a strong buffer. In this way, we show just how fundamental the buffering nature of groups may be. Group size variation could lead to the rescue of populations whose average group size has dropped below the group Allee threshold (Appendix 1C), because when small groups fail, average group sizes rise; however, this is not a general requirement to prevent group Allee effects from scaling up to a demographic Allee effect. The key is not failure of small packs, but failure of some packs such that average group size can grow.

Dispersal between groups has been considered important for how group dynamics scale to population dynamics (Courchamp et al., 1999b; Bateman et al., 2011; Bateman et al., 2012; Bateman et al., 2013). Dispersal provides a way for group size to be maintained independent of population size. The movement of dispersing individuals throughout the population between generations can allow large groups to persist in small populations. Interestingly, the Arabian babbler is an example where dispersal was found to be insufficient to buffer group level Allee effects from becoming a demographic Allee effect (Keynan & Ridley 2016). This system has a much lower transfer of individuals among groups, implying that decreasing intergroup connectivity weakens the buffering nature of group structure. This conclusion is consistent with our implicit pack models producing a demographic Allee effect at very low values of the pack failure parameter (i), as small *j* indicates low transfer of individuals between groups. As an extreme example, the packless model is particularly prone to population extinction and population-level demographic Allee effects. Conversely, low pack formation parameter (k) also produces a population-level demographic Allee effect. This shows that low group fidelity and a propensity to form new groups can lead to a population-level demographic Allee effect, as it will create a population of many small groups that cannot reproduce successfully.

Such insight requires a theoretical approach to uncover and could help explain the evolution of dispersal rates in social species.

In addition to Allee effects, demographic stochasticity can make small groups prone to extinction. Our implicit pack models assume that when the average pack size is small, the frequency of pack extinction increases. Although we cited this as a manifestation of a group-level demographic Allee effect, demographic stochasticity could add to this pattern of pack failure (Lande, 1998; Dennis, 2002; Appendix 1E). In general, however, we do not include stochasticity in our models and consider only average pack size. This has drawbacks, as we are interested in instances where averages may not fully capture population dynamics (when packs are small making variability and noise increasingly important). In this way, the simplicity of our implicit pack models may cloud their interpretation with respect to fundamental biological mechanisms. Nevertheless, they capture phenomena seen empirically (Somers et al., 2008; Bateman et al., 2011; Woodroffe, 2011; Angulo et al., 2013; Angulo et al. 2017) and produced in our explicit pack model that includes both stochastic effects and variability in pack size. The way in which we can build such a simple model that still captures the protective effect of packs justifies that it contains the important aspects of the system.

In summary, our results indicate that many social species seemingly prone to a demographic Allee effect have protection against such population-level phenomena. While many of our specific modeling choices were motivated by African wild dog populations, our results are also consistent with past findings on Arabian babbler and meerkat populations. Our conclusions are relevant not only for these species, but also any social species with Allee effects at the group level, intergroup interactions, and a lack of correlation between group size and population size. Future research analyzing the strength of intergroup interactions required to prevent group Allee effects from

translating into a demographic Allee effect would help determine more completely the species to which our results apply. The robustness of our core results to changes in population structure, the way pack failure is modeled, the representation of packs as implicit or explicit, and parameter values together suggest broad generality. Our results therefore have the potential to demystify the widespread failure to find population-level demographic Allee effects in group-living species prone to component Allee effects (Gregory et al., 2010; Angulo et al., 2017), and also to better the understanding of the population dynamics of a wide range of social species. Further, our results suggest that populations of social species with group level Allee effects may respond best to management efforts that promote healthy group sizes, perhaps with less emphasis on the size of the population as a whole.

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References

- Allee, W. C. (1931). Animal Aggregations: A study in General Sociology. Chicago, IL: University of Chicago Press.
- Angulo, E., Luque, L. Q., Gregory, S. D., Wenzel, J. W., Bessa-Gomes, C., Berec, L., and Courchamp, F. (2017). Allee effects in social species. Journal of Animal Ecology, 87(1), 47-58. doi: 10.1111/1365-2656.12759

- Angulo, E., Rasmussen, G. S. A., Macdonald, D. W., & Courchamp, F. (2013). Do social groups prevent Allee effect related extinctions?: The case of wild dog. Frontiers in Zoology, 10. doi: 10.1186/1742-9994-10-11
- Bateman, A. W., Coulson, T., & Clutton-Brock, T. H. (2011). What do simple models reveal about the population dynamics of a cooperatively breeding species?.Oikos, 120(5), 787-794. doi: 10.1111/j.1600-0706.2010.18952.x
- Bateman, A. W., Ozgul, A., Coulson, T., & Clutton-Brock, T. H. (2012). Density dependence in group dynamics of a highly social mongoose, *Suricata suricatta*. Journal of Animal Ecology, 81(3), 628-639. doi: 10.1111/j.1365-2656.2011.01934.x
- Bateman, A. W., Ozgul, A., Nielsen, J. F., Coulson, T., & Clutton-Brock, T. H. (2013).
 Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*. Ecology, 94(3), 587-597. doi: 10.1890/11-2122.1
- Berec, L., Angulo, E., & Courchamp, F. (2007). Multiple Allee effects and conservation management. Trends in Ecology and Evolution, 22(4), 185-191. doi: 10.1016/j.tree.2006.12.002
- Boukal, D. S. & Berec, L. (2002). Single-species models of the Allee effect: Extinction boundaries, sex ratios and mate encounters. Journal of Theoretical Biology, 218(3), 375-394. doi: 10.1006/jtbi.2002.3084
- Buettner, U. K., Davies-Mostert, H. T., Du Toit, J. T., & Mills, M. G. L. (2007). Factors affecting juvenille survival in African wild dogs (*Lycaon pictus*) in Kruger National Park, South Africa. Journal of Zoology, 271(1), 10-19. doi: 10.1111/j.1469-7998.2006.00240.x

- Creel, S. & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour, 50(5), 1325-1339. doi: 10.1016/0003-3472(95)80048-4
- Creel, S. & Creel, N. M. (1996). Limitation of African Wild Dogs by Competition with Larger Carnivores. Conservation Biology, 10(2), 536-548. doi: 10.1046/j.1523-1739.1996.10020526.x
- Creel, S. & Creel, N. M. (2002). The African wild dog: behavior, ecology, and conservation. Princeton, NJ: Princeton University Press.
- Creel, S. & Creel, N. M. (2015). Opposing effects of group size on reproduction and survival in African wild dogs. Behavioral Ecology, 26(5), 1414-1422. doi: 10.1093/beheco/arv100
- Creel, S., Mills, M. G. L., & Mcnutt, J. W. (2004). Demography and population dynamics of African wild dogs in three critical populations. Biology and Conservation of Wild Canid, pp: 337-350.
- Courchamp, F., Clutton-Brock, T., & Grenfall, B. (1999a). Inverse density dependence and the Allee effect. Trends in Ecology and Evolution, 14(10), 405-410. doi: 10.1016/S0169-5347(99)01683-3
- Courchamp, F., Grenfall, B., & Clutton-Brock, T. (1999b). Population dynamics of obligate cooperators. Proceedings of the Royal Society B: Biological Sciences, 266(1419), 557-563.
- Courchamp, F., Clutton-Brock, T., & Grenfall, B. (2000). Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. Animal Conservation, 3(4), 277-285.
- Courchamp, F. & MacDonald, D. W. (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. Animal Conservation, 4(2), 169-174.
- Dennis, B. (2002). Allee effects in stochastic populations. Oikos, 96(3): 389-401. doi: 10.1034/j.1600-0706.2002.960301.x
- Frank, K. T. & Brickman, D. (2000). Allee effects and compensatory population dynamics within a stock complex. Canadian Journal of Fisheries and Aquatic Sciences, 57(3), 513-517. doi: 10.1139/f00-024
- Fuller, T. K., Kat, P. W., Bulger, J. B., Maddock, A. H., Ginsberg, J. R., Burrows, R.,
 McNutt, J. W., & Mills, M. G. L. (1992). Population dynamics of African wild
 dogs. Wildlife 2001: populations. McCullough, D. R. & Barrett, R. H. (Eds).
 London: Elsevier Applied Science.
- Ginsberg, J. R., Alexander, K. A., Creel, S., Kat, P. W., McNutt, J. W., & Mills, M. G. L. (1995). Handling and survivorship of African wild dog (*Lycaon pictus*) in five ecosystems. Conservation Biology, 9(3), 665-674. doi: 10.1046/j.1523-1739.1995.09030665.x
- Gregory, S. D., Bradshaw, C. J. A., Brook, B. W., & Courchamp, F. (2010). Limited evidence for the demographic Allee effect from numerous species across taxa. Ecology, 91(7), 2151-2161. doi: 10.1890/09-1128.1
- IUCN/SSC. 2007. Regional Conservation Strategy for the Cheetah and African Wild Dog in Southern Africa. IUCN Species Survival Commission, Gland, Switzerland.
- Keynan, O. & Ridley, A. R. (2016). Component, group and demographic Allee effects in a cooperatively breeding bird species, the Arabian babbler (*Turdoides squamiceps*). Oecologia, 182(1), 153-161.

- Lande, R. (1998). Demographic Stochasticity and Allee Effect on a Scale with Isotropic Noise. Oikos, 84(2), 353-358. doi: 10.2307/3546849
- Malcolm, J. R. & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). Behavioral Ecology and Sociobiology, 10(1), 1-13.
- McNutt, J. W. (1996). Sex-biased dispersal in African wild dogs, *Lycaon pictus*. Animal Behavior, 52(6), 1067-1077. doi: 10.1006/anbe.1996.0254
- McNutt, J. W. & Silk, J. B. (2008). Pup production, sex ratios, and survivorship in African wild dogs, *Lycaon pictus*. Behavioral Ecology and Sociobiology, 62(7), 1061-1067.
- Mills, M. G. L. & Gorman, M. L. (1997). Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology, 11(6), 1397-1406. doi: 10.1046/j.1523-1739.1997.96252.x
- Rasmussen, G., Gusset, M., Courchamp, F., & MacDonald D. W. (2008). Achilles' Heel of Sociality Revealed by Energetic Poverty Trap in Cursorial Hunters. The American Naturalist, 172(4), 508-518. doi: 10.1086/590965
- Rinella, D. J., Wipfli, M. S., Stricker, C. A., Heintz, R. A., & Rinella M. J. (2012).
 Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmononids increase with spawner density.
 Canadian Journal of Fisheries and Aquatic Sciences, 69(1), 73-84. doi: 10.1139/f2011-133
- Somers, M. J., Graf, J. A., Szykman, M., Slotow, R., & Gusset, M. (2008). Dynamics of a small reintroduced population of wild dogs over 25 years: Allee effects and the

implications of sociality for endangered species' recovery. Oecologia, 158(2), 239-247.

- Stephens, P. A. & Sutherland, W. J. (1999). Consequences of the Allee effect for behaviour, ecology, and conservation. Trends in Ecology and Evolution, 14(10), 401-405. doi: 10.1016/S0169-5347(99)01684-5
- Stephens, P. A., Sutherland, W. J., & Freckleton, R. P. (1999). What is the Allee effect?. Oikos, 87(1), 185-190.
- Tensen, L., Groom, R. J., van Belkom, J., Davies-Mostert, H. T., Marnewick, K., & van Vuuren, B. J. (2016). Genetic diversity and spatial genetic structure of African wild dogs (*Lycaon pictus*) in the Greater Limpopo transfrontier conservation area. Conservation Genetics, 17(4), 785-794.
- Wolfram Research, Inc. (2016). Mathematica Version 11.0. Wolfram Research, Inc., Champaigne, IL.
- Woodroffe, R. (2011). Demography of a recovering African wild dog (*Lycaon pictus*) population. Journal of Mammalogy, 92(2), 305-315. doi: 10.1644/10-MAMM-A-157.1
- Woodroffe, R., Davies-Mostert, H., Ginsberg, J., Graf, J., Leigh, K., McCreery, K.,
 Robbins, R., Mills, G., Pole, A., Rasmussen, G., Somers, M., & Szykman, M.
 (2007). Rates and causes of mortality in endangered African wild dogs *Lycaon pictus*: lessons for management and monitoring. Oryx, 41(2), 215-223. doi: 10.1017/S0030605307001809

Woodroffe, R. & Ginsberg, J. R. (1999). Conserving the African wild dog. I. Diagnosing and treating causes of decline. Oryx, 33(2), 132-142. doi: 10.1046/j.1365-3008.1999.00052.x

Woodroffe, R. & Sillero-Zubiri, C. (2012). *Lycaon pictus*. The IUCN Red List of Threatened Species 2012.

Box 1.1. Glossary of terms for Allee effects in social species. For consistency, we use the terminology put forth by Angulo et al. (2017); however, we have made some alterations for conceptual clarity (see second introduction paragraph). The rightmost column displays an example graph to illustrate the various Allee effects and relevant thresholds. Our use of fecundity on the y-axes of some graphs is merely an example of a fitness component.

Population- level component Allee effect	One aspect of an individual's fitness (e.g. survival, fecundity) is reduced at low population sizes. Commonly referred to simply as a "component Allee effect" in the literature (Stephens & Sutherland, 1999); "population- level" emphasizes that the driving variable is population size.	Fecundity	_	Population Size
Population- level Demographic Allee effect	A reduction in an <u>individual's</u> <u>overall fitness</u> at low <u>population</u> sizes. Possible but not inevitable outcome of population-level component Allee effects. Results in reduced population growth rate (in a closed population) and heightened extinction risk at low population sizes.	Per Capita	Population Growth Rate	Population Size Allee Threshold Demographic Allee effect Traditional density dependence
Group-level component Allee effect	One aspect of average fitness of individuals within a group (e.g. survival, fecundity) is reduced at low group sizes. Analogous to a population-level component Allee effect, except with group size rather than population size as the driving variable. This level of Allee effect adds clarity, since the level of component Allee effects is not usually specified in the literature.	Fecundity	/	Group Size
Group-level demographic Allee effect	A reduction in the <u>average</u> <u>fitness of individuals within a</u> <u>group at low group sizes.</u> Possible but not inevitable outcome of group-level component Allee effects. Can lead to reduced growth rate of the group and heightened risk of group failure at low group sizes.	Group Reproductive	Success	Group Size

 Table 1.1. Summary of variables and models.

VARIABLES USED IN MODELS							
Variable	Meaning	When used					
\mathbf{N}_t	total population size (sum over packs [*])	Unstructured models					
\mathbf{J}_t	total juveniles (sum over packs [*])	Age structured models					
\mathbf{Y}_t	total yearlings (sum over packs [*])	Age structured models					
\mathbf{M}_{t}	total mature adults (sum over packs [*])	Age structured models					
p_t	number of packs	Pack models, when					
		packs modeled					
		implicitly					
A_t	$= \mathbf{M}_{t}/p_{t}$, mature adults per pack	Pack models, when					
		packs modeled					
		implicitly					
$\mathbf{J}_{i,t}$	juveniles in pack <i>i</i>	Pack model, when packs					
		modeled explicitly					
$\mathbf{Y}_{i,t}$	yearlings in pack <i>i</i>	Pack model, when packs					
		modeled explicitly					
$\mathbf{M}_{i,t}$	mature adults in pack <i>i</i>	Pack model, when packs					
* 1 1		modeled explicitly					
noted) in the population	on.	as (summed over age/sex as					
	MODEL FOLLTIONS						
Madal	MODEL EQUATIONS	Dealslage model					
Model	Pack model	Packless model					
No nonulation st							
Reproducers	R = n	$P_{\rm c} - N_{\rm c}$					
Caregivers	$R_l = p_l$ $C_l = \mathbf{N}_l / p_l$	$R_l = R_l$ $C_l = \mathbf{N}_l$					
Equations	$\frac{\mathbf{r}_{l} - \mathbf{N}_{l}}{(\mathbf{r}_{l} - \mathbf{N}_{l})} \left(\frac{\mathbf{N}_{l}}{(\mathbf{N}_{l})^{2}} \right)$	$C_l = N_l$					
Equations	$\mathbf{N}_{t+1} = \left(\mathbf{N}_t + \frac{1}{p_t L + \mathbf{N}_t} p_t\right) \left(1 - c_y \left(\frac{1}{p_t} - s\right) - c_4 - \mu\right)$	$\mathbf{N}_{t+1} = \left(\mathbf{N}_t + \frac{\tau_1 \mathbf{N}_t}{L + \mathbf{N}_t} \mathbf{N}_t\right) \left(1\right)$					
	with $c_y = \begin{cases} c_2 & \frac{N_i}{p_i} \le s \\ N_i & N_i \end{cases}$	$\int c_2 \mathbf{N}_t \leq s$					
	$\left(C_3 \frac{1}{p_t} > s \right)$	with $c_y = \begin{cases} c_3 & \mathbf{N}_t > s \end{cases}$					
	$p' = p_t + \text{round} \left \frac{\mathbf{N}_t}{k} \right - \text{round} \left \frac{jp_t}{\mathbf{N}_t} \right $						
	$\begin{pmatrix} 1 & p' < 1 \end{pmatrix}$						
	$p_{t+1} = \begin{cases} k_p & p' > k_p \end{cases}$						
	p' otherwise						
Age structure	-						
Reproducers	$R_t = p_t$	$R_t = \mathbf{M}_t$					
Caregivers	$C_t = A_t$	$C_t = \mathbf{M}_t$					
Equations	$\mathbf{J}_{t+1} = \frac{rA_t}{L+A_t} p_t \left(1 - \frac{dc_1}{c_1 + A_t^2} - \mu_J \right)$	$\mathbf{J}_{t+1} = \frac{r\mathbf{M}_t}{I + \mathbf{M}} \mathbf{M}_t \left(1 - \frac{dc_1}{c_1 + 1} \right)$					
	$\mathbf{Y}_{t+1} = \mathbf{J}_t (1 - c_y (A_t - s)^2 - c_4 - \mu_Y)$	$\mathbf{Y}_{t+1} = \mathbf{J}_t (1 - c_y (\mathbf{M}_t - s)^2 - c_t)$					
	with $c_{t} = \int c_2 A_t \leq s$	$\int c_2 \mathbf{M}_t \leq s$					
	when $c_y = \begin{cases} c_3 & A_t > s \end{cases}$	with $c_y = \begin{cases} c_2 & \mathbf{M}_t \ge 0 \\ c_3 & \mathbf{M}_t > s \end{cases}$					
	$\mathbf{M}_{t+1} = (\mathbf{M}_t + \mathbf{Y}_t)(1 - \mu_M)$	$\mathbf{M}_{t+1} = (\mathbf{M}_t + \mathbf{Y}_t)(1 - \mu_M)$					
	$p' = p_t + \operatorname{round} \left[rac{\mathbf{Y}_t}{k} ight] - \operatorname{round} \left[rac{j}{A_t} ight]$						
	$\begin{pmatrix} 1 & p' < 1 \end{pmatrix}$						
	$p_{t+1} = \left\{ \begin{array}{ll} k_p & p' > k_p \end{array} ight.$						
	p' otherwise						
Age structure, packs modeled explicitly							

Reproducers	$R_{i,t} = \begin{cases} 1 & M_{i,t} \ge 1\\ 0 & \text{otherwise} \end{cases}$	n/a
Caregivers	$C_{i,t} = \mathbf{M}_{i,t}$	
Equations	$J_{i,t+1} = \begin{cases} 0 & M_{i,t} < 1\\ \frac{rM_{i,t}}{L+M_{i,t}} \left(1 - \frac{dc_1}{c_1 + M_{i,t}^2} - \mu_J\right) & M_{i,t} \ge 1\\ Y_{i,t+1} = J_{i,t} (1 - c_y (M_{i,t} - s)^2 - c_4 - \mu_Y)\\ \text{with } c_y = \begin{cases} c_2 & M_{i,t} \le s\\ c_3 & M_{i,t} > s \end{cases}\\ M_{i,t+1} = \left(M_{i,t} + \frac{\mathbf{Y}_{i,t}}{p_{t+1}}\right) (1 - \mu_M) \end{cases}$	
	see text for description of pack formation/failure	

Table 1.2. Summary of sensitivity analyses comparing implicit pack and packless model pairs. For each model, we report the percentage of parameter combinations, across all combinations used in the sensitivity analyses (see text): (*i*) that resulted in population growth at some time step in the simulation (after an initial four time points) and (*ii*) for which the pack model had a lower minimum population size capable of positive population growth, compared to its corresponding packless model.

	(i) % with gro	population wth	(<i>ii</i>) % with smallest growing population size		
Model type	Pack Packless		Pack models		
	models	models			
Unstructured	65.4 %	57.1 %	81.2 %		
Age-	74.1 %	29.0 %	99.4 %		
structured					



Figure 1.1. Density dependence in (A) birth rate (equation (1)), (B) pup survival (1 – the first term in equation (2)), and (C) yearling survival (1 – the bracketed term in equation (4)). The top x-axes show or adult population size, corresponding to density dependence in the packless models. The bottom x-axes are pack size, corresponding to density dependence in the pack models. (B) and (C) show the component Allee effects in our models. All functions were plotted using the parameter values in Appendix 1B.



Figure 1.2. Model results with rows showing: (i) the unstructured models, (ii) the agestructured models, (iii) the age and sex-structured models, and (iv) the explicit pack model. Column (I) shows per capita population growth rate in a single time step versus the number of adults in the population. All points are from models with packs, with positive growth rates colored red and negative growth rates colored light purple. Scatter in these points is due to differences not fully captured by the variate on the x-axis (e.g. in column (I), different mean pack sizes at the same total population size). The black line in column (I) shows the same relationship from the corresponding packless models; because population size fully determines growth rate in the packless models, there is no scatter in these points. These lines are never positive at small population sizes, showing the strong demographic Allee effect from packless models. Contrasting the packless models, the presence of positive growth rates at small population size (red points on the left of the figures in (I)) in the pack models show the lack of a demographic Allee effect: small populations do not necessarily shrink in our pack models. The column (II) shows the per capita population growth rate (population growth is analyzed in the explicit pack models simply for easier comparison with the implicit pack models) versus the average number of adults per pack for pack models, revealing the group-level demographic Allee effect (per capita population growth rate decreases when the average pack size is small). The column (III) plots average pack size versus population size during the course of the simulations, with points within each trajectory shifting from green (initial) to red (final) over time. This shows the lack of correlation between pack size and population size, and a strong trend toward a single pack size, appearing as a horizontal red stripe, across many population sizes.



Figure 1.3. *j-k* space and the occurrence of population-level demographic Allee effects. Red regions indicate that levels of group formation and failure are insufficient to buffer a population from population-level demographic Allee effects. Blue regions indicate the absence of a population-level demographic Allee effect.

Better baboon breakups: Collective decision theory of complex social network fissions

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Abstract

Many social groups are made up of a complex social network in which each individual has a unique and non-overlapping set of others with which they tend to associate. Frequently groups that have grown too large must decide how to fission in order to release themselves from competition. Complex social networks make fissions much harder as both a multidimensional optimization problem and a collective decision. This is because it is advantageous for each individual to remain with their closest allies post fission, but doing so for every individual is clearly impossible. Here, we develop computational algorithms for group fissions in a network theoretic framework. We analyze three algorithms (democracy, community, and despotism) that fall on a spectrum between a democratic collective decision to a dictatorial decision. We parameterize our social networks with data from baboons (*Papio cynocephalus*) and compare our algorithms with actual baboon fission events. We find that democratic decisions are much better at splitting the group while disturbing the network structure as little as possible. Even with high information skew amongst individuals, allowing a single individual to dictate fission does not appear capable of maintaining the social

network. Finally, we find evidence that actual baboon fissions are most similar to democratic algorithms.

Introduction

Across social species, an individual's social position is crucial for its ability to successfully reproduce. This is obvious in species in which a single, dominant individual monopolizes reproduction, but equally true in species with many reproductive individuals (Cameron et al 2009; Stanton & Mann 2012; Lehmann et al 2015; Cheney et al 2016). Thus, there is strong reason to believe individuals gain fitness benefits from attempting to maintain their social network position. However, even in cooperative species, intragroup competition can be strong (Barton et al 1996; Majer et al 2018; Sheppard et al 2018), so groups must occasionally fission to release themselves from competition when they become too large (Malik 1985; Dittus 1988; Dunbar 1992; Henzi et al 1997). Deciding how to fission presents a challenge, as each individual has a unique set of social bonds that it would benefit from maintaining through the fission. However, it is impossible for every individual to accomplish this. What strategies can groups take to achieve this complicated collective decision of splitting up a social network? How can individuals attempt to retain their social ties, even when networks are complex?

Primates provide excellent case studies for understanding group fissions from a network perspective. A critical reason for this is that many primate fissions

are permanent (Cords & Rowell 1986; Okamoto & Matsumura 2001; Van Horn et al 2007; in contrast to a fission-fusion society), so the decision of which postfission group to join will influence an individual for the duration of its life. Primate fissions are also well studied. In particular, it is often considered that fissions in matrilineal societies (such as baboons) will be characterized by an attempt to remain with matrilineal kin (Chepko-Sade & Oliver 1979; Dittus 1988; Holekamp et al 1993; Archie et al 2005; Widdig 2006). However, there are many examples in fissions of matrilineal societies wherein individual decisions appear not to be driven by matrilineal kinship (Chepko-Sade & Oliver 1979; Armitage 1987; Widdig 2006; Van Horn 2007). Decisions of how to fission may be influenced by individuals trying to improve their rank (abandon-your-superior hypothesis; Ron et al 1994), but again other fissions do not follow this pattern (Van Horn 2007). Thus, at the level of which bonds to maintain and which to break during a fission, there is much individual variation. However, at the level of the whole network, do group fissions follow a common pattern? We believe that taking a global view of the social network is a simple and powerful means of understanding the way in which a fission proceeds. This is the first study to our knowledge to apply a global network theoretic approach to understand the collective decision of permanent fissions.

Network theoretic approaches have become a vital part of studying animal sociality (Krause et al 2009), and group fissions have been viewed through this lens. Network theoretic models have sought to understand how nutritional needs can interact with sociality to lead to both permanent fissions and fission-fusion

societies (Sueur & Maine 2014). Relatedly, empirical studies have shown fissionfusion societies are shaped by resource availability (Sundaresan et al 2007; Sueur et al 2014). Network approaches have also been extended to understand how grooming relationships in primates influence group cohesion and ultimately whether a fission will be necessary (Sueur et al 2011). Still, such work tends to focus on the benefits of a fission-fusion society as well as the reasons for fission. Here, we intend to ask a different, albeit related, question: *how* does the fission proceed?

As mentioned above, group fissions are, by definition, a collective decision. As such, collective decision theory provides a means by which to understand fission dynamics. Much of collective decision theory focuses heavily on animal movement and considers democratic versus despotic decisions as well as information asymmetry (Conradt & Roper 2003; Conradt & Roper 2005; Couzin et al 2005; Miller et al 2013; Strandburg-Peshkin et al 2015). Once again, syntheses of fissions with collective decision theory have focused heavily on fission-fusion societies. For example, various authors discuss the ways in which groups may temporarily fission, so individuals in a given group may have options without abandoning their group (Kerth et al 2006; Sueur et al 2011; Merkle et al 2015). But, because group fissions in fission-fusion societies are not permanent, individuals suffer less from separating from their allies. Further, permanent fissions are less likely the result of an immediate response to the spatial distribution of resources, which drives many temporary fission events (Sundaresan et al 2007; Sueur et al 2014). This means that existing theory on

fission-fusion dynamics cannot readily inform an understanding of permanent fissions. As such, we will extend a collective decision approach specifically to understanding permanent fissions.

Here, we provide a novel synthesis of network approaches with collective decision theory to understand possible outcomes of permanent fissions resulting from different collective decision strategies. We consider the question of why fissions occur (which has been addressed elsewhere) to be outside the scope of this study. We find that democratic decision making is necessary to disturb social networks as little as possible during a fission. We apply our model to observed savannah baboon (*Papio cynocephalus*) fissions and find evidence that fissions proceed democratically.

Methods

Case Study: Amboseli Baboons

Baboon groups are subject to strong intragroup competition and must split when they have become too large (Dunbar 1992; Henzi et al 1997). Since its inception 1971, the Amboseli Baboon Research Project has observed and recorded data for seven events during which one group split into two daughter groups. We used grooming data from two years prior to the start of the fission event to parameterize social networks for each of these seven baboon groups. To do so, we tallied the number of grooming events between all pairs of individuals in the group. We then normalized the number of grooming events to be between 0 and 1, removing bonds from pairs that had groomed less than ten times as these were less reliable measures of a bond between individuals. The resulting value was used as the bond strength (edge weight) between individuals on the network.

Our ultimate goal is to understand differences in fission strategies that collectively decide how to split up a group with a complex social network. To ensure that we are using realistic social networks, we will apply various strategies to the actual pre-fission baboon networks described above. We have developed five hypothetical algorithms for fission strategies (figure 2.1). Note that the first four algorithms are stochastic, as described below.

Random Algorithm

We first developed the random algorithm as a null expectation for how fissions would proceed if they were random with respect to global network structure. The random algorithm assigns each individual from the pre-fission group into daughter group 1 or daughter group 2 randomly and with equal probability. Any individuals in the same daughter group who were bonded before the fission retain their original bond strength; all other bonds are severed.

Democracy Algorithm

For the purposes of this study, a democratic decision is one in which each individual influences the outcome of the fission. The democracy algorithm treats the fission as a collective decision wherein each individual in the group controls which daughter group they will join. First, two individuals are randomly selected from the pre-fission group and assigned as the first members of daughter group 1 and daughter group 2. Then, individuals that have yet to be assigned a daughter group are successively and randomly selected from the pre-fission group and assigned to the daughter group in which they have the highest average bond strength to individuals already in that group. If a selected individual has no bonds with any individual in either daughter group, they are not yet assigned a group and returned to the pool of individuals needing assignment. Since our networks are connected, these individuals will eventually have connections to members of one or both daughter groups, so this procedure will assign every individual a daughter group for each simulated fission.

Despotism Algorithm

To contrast with a democratic decision, we developed the despotism algorithm, which allows the individual with the greatest sum of bond weights (the despot; also, the individual with the most information about the network structure) to dictate the fission. Bond strengths used for the despotism algorithm were logtransformed prior to normalization, as this produced daughter groups of more realistic size. First, individuals of distance one from the despot (i.e. those with

direct social bonds to the despot) were selected and their bond strengths to the despot were used as the probability they joined the despot's daughter group (daughter group 1). Bonds between the despot and individuals not selected to join daughter group 1 were then severed. Next, all individuals from the revised network (with some removed bonds) of distance 2 from the despot were considered. The probability that these individuals were selected to join daughter group 1 was taken to be the product of bond strengths between the individual in question and the despot. Again, individuals not selected to join the despot's group had their bonds to individuals in daughter group 1 removed. This procedure continued until the network was no longer connected. At that point, all individuals not chosen for daughter group 1 were assigned to daughter group 2.

Community Algorithm

We next developed the community algorithm, which is intermediate between democracy and despotism on the collective decision making spectrum. First, we detected network communities using Mathematica's centrality-based community detection method. This method uses bonds with high betweenness centrality to find tightly-bonded regions (communities) in the network. We then assigned entire, intact communities to daughter groups in a procedure analogous to the democracy algorithm. That is, first we selected two communities at random; then we successively and randomly assigned the remaining communities to the daughter group with the highest average number of bonds per individual for all bonded pairs between the two communities. Although this is still a collective decision rather than a despotic one, it greatly reduces the number of independent entities involved in making the decision relative to the democracy algorithm.

Sparsest Cut

The sparsity of a fission is a measure of how little it disturbs the original network, with respect to the strength and number of bonds broken. It is quantified as the sum of bond weights broken divided by the number of individuals in the smallest resulting post-fission group. Then, the "sparsest cut" is the fission with minimum sparsity. This fission is characterized by breaking few bonds while producing approximately equally-sized daughter groups, both desirable characteristics. We use the sparsest cut as another basis of comparison (along with the random algorithm) for our collective decision algorithms.

Analysis of Resulting Post-fission Groups

The random, democracy, despotism, and community algorithms can each produce variable results even when applied to the same starting network, due to stochasticity in the order that individuals are selected for daughter group assignment and/or stochasticity in the assignment process itself. Therefore, we applied the four stochastic algorithms 100 times to each of the seven baboon social networks, simulating 100 fission events in each network for each algorithm. Various tests were carried out to determine the extent to which the algorithms disturbed the social network in each simulated fission event. In particular, we recorded for each simulation the percent of bonds broken, the average weight of broken bonds, the average weight of maintained bonds, the average betweenness centrality (see glossary, Table 2.1) of broken bonds, the average betweenness centrality of maintained bonds, and the sparsity of the fission. To characterize the nature of the groups, we also recorded the clustering coefficient, diameter, and density of each pre- and post-fission groups (Table 2.1).

Finally, we compared the simulated fissions to the actual observed fission event in each social network. To do so, we calculated the average percentage of bonds that each algorithm correctly assigned as either broken or maintained. All analyses were performed using Wolfram Mathematica.

Results

A complete summary of results can be found in tables 2 and 3.

Bonds broken during fission

All other algorithms disturb the networks less than random, as measured by percent of bonds broken and mean weight of broken bonds. Across groups, a lower percentage of bonds were broken in the democracy and community algorithms than the despotism algorithm (figure 2.2). In addition to breaking fewer bonds, both the democracy and community algorithms have a tendency to break weaker bonds than the despotism algorithm. The community algorithm even appears to outperform the democracy algorithm by breaking weaker bonds on average (figure 2.3). None of the algorithms differed in the weights of maintained bonds. The democracy and community collective decision algorithms disturbed the networks similarly to their sparsest cut.

In addition to breaking weak bonds, the algorithms tended to break bonds with high betweenness centrality. Although true for all of the algorithms (except for random), the democracy and community algorithms produce a much greater difference in the centrality of broken and maintained bonds than does the despotism algorithm. Here, the algorithms often differ from the actual fissions. Only three out of seven observed fissions were such that broken bonds had a markedly higher centrality that maintained bonds. A complete summary of these metrics can be found in table 2.2.

Post-fission network properties

All algorithms except for random increased the groups' density and clustering coefficient. The predicted post-fission groups tended to have approximately equal clustering coefficients for each algorithm, even despotism. Post-fission groups from the democracy and community algorithms also tended to have approximately equal densities. Notably, the despotism algorithm tended to produce one post-fission group with very high density and one post-fission group

with density equal to or lower than that of the pre-fission group. Actual fissions increased the density of groups at a level comparable to the democracy and community algorithms. Actual fissions increased the clustering coefficient of the groups at a level comparable to all of the algorithms except for random. The random algorithm tended to decrease both the density and clustering coefficient of the groups. A complete summary of these metrics can be found in table 2.3.

Are any of the algorithms correct?

Although correctly predicting network metrics is valuable, this is very different than accurately assigning membership to the post-fission groups. In each fission except for Hook's, all algorithms outperformed random with respect to predicting the observed fission. Excluding Hook's fission, despotism was the second least accurate algorithm in each group except for Viola's. In some of the remaining five fissions, the community algorithm outperforms the democracy algorithm, however these appear equal in others (figure 2.4).

Discussion

In summary, we find that more democratic decisions (both the democracy and community algorithms) outperform other means of splitting the social network. That is, more democratic decisions break fewer and weaker bonds. Given the importance of the social network for baboons, we should then expect that actual fissions appear to be democratic. Indeed, we find evidence that in most

cases the democracy and community algorithms more accurately predict actual fissions than other means of splitting the network.

The network theoretic approach that we have taken here highlights the complexity of group fissions. First, a fission is a high-dimensional, discrete optimization. Each individual in the group has a different and often conflicting view of the fission from others. As such, it is interesting to ask how such a collective decision occurs from the basis of an individual's behavior. This is the second major source of complexity: a fission is a complex collective decision. Individuals need to coordinate and cooperate in their actions to form post-fission groups that still have strong social bonds. In our case study, we showed that they are most often able to do so. Notably, we believe this to be the first study of how permanent fissions of social networks unfold from a collective decision perspective.

Collective decision theory often considers asymmetric information between individuals. Democratic decisions have been shown to typically outperform despotic decisions, even when the despot is the most experienced group member (Conradt and Roper 2003). In our study, information asymmetry can be thought of as a knowledge of the topology of the social network. If individuals with the most social bonds have the best information on network topology, then the despot has more information than most members of the group. Still, the despotism algorithm does much worse than either the democracy or community algorithms, aligning with Conradt and Roper's (2003) result.

Our results make clear that both the democracy and community algorithms best predict how real baboon fissions proceed. There even appears to be a weak trend of the community algorithm performing the best at predicting actual fission events (figure 2.4). Perhaps the community algorithm is a way to simplify the collective decision. That is, it collapses the network into 5-10 vertices representing the group's communities. These few communities then split up the social network as opposed to the 30-50 individuals. Anecdotal evidence supports the idea that the community algorithm may be the closest to actual fission events in baboons as well. Ron (1996) observed that group fissions were preceded by increased subgrouping. That is, individuals first collapsed themselves into subgroups before completing the fission. Van Horn et al (2007) hypothesized that their inability to explain the dynamics of one fission was due to a subset of individuals with shared interests joining forces. These examples provide support that our community algorithm mirrors the way baboon fissions proceed in nature. Of course, it may also be the case that baboons are using a combination of strategies (i.e., democracy with the despot having unequal power in the fission).

An interesting result that can be seen from figures 2 and 3 is that the baboons consistently break more bonds than either the democracy or community algorithms and consistently break stronger bonds. We believe this is the first study equipped to test the efficiency of group fissions (defined here as the ability to fission the group while disturbing the social network as little as possible). Our results indicate that baboon fissions are not nearly as efficient as they could be. We believe there are three, non-mutually exclusive possibilities for why this is the

case: 1) the baboons are unable to be as efficient as the algorithms, 2) the baboons are not trying to maintain their social network, or 3) there is "another network" that the baboons are using to inform the fission.

The first possibility is that the baboons simply cannot split their social network as well as our computational algorithms. As we point out above, it is an extremely complicated collective decision to fission a complex social network. Supporting this possibility is the observation that actual baboon fission events can take many months to complete. Further, baboons are limited in their communication, which could exacerbate the challenge of deciding and coordinating the fission. Finally, individuals may make mistakes and ultimately end up in post-fission groups with which they are not as bonded, while our democratic algorithms do not include such sources of error. If these factors play a large role in group fissions, perhaps baboons are unable to reach the higher efficiency obtained by the algorithms.

A second possibility is that the baboons are not attempting to maintain their social network (that is, our definition of efficiency is flawed). Although this would certainly explain why baboons are more disruptive to the social network than our algorithms, there are reasons to believe this is unlikely. First, social bonds have been shown to predict lifetime reproductive success (Cameron et al 2009; Stanton & Mann 2012; Lehmann et al 2015; Cheney et al 2016), so it seems likely that selection would lead to fission strategies that maintain social networks. Unfortunately, it is often not possible to compare the success of our algorithms with other strategies that have been proposed. Here, we report the percent of

bonds that our algorithms successfully predict as either broken or maintained. Such information simply does not exist from most studies (see e.g. Van Horn et al 2007). As such, despite the discordance in efficiency from our algorithms and actual fissions, we believe this study provides evidence that baboon fissions can be viewed as a democratic collective decision.

Of course, this is not to say that previous hypotheses for fission strategies are entirely inaccurate. The final possibility is that there is other information that should be included in a social network. For example, many authors (Chepko-Sade & Oliver 1979; Dittus 1988; Holekamp et al 1993; Archie et al 2005; Widdig 2006) claim there is evidence that fissions often follow a pattern of remaining with matrilineal kin. It is possible that by increasing edge weights based on relatedness, we would have better predicted baboon fission events, but there is limited support for the extent to which relatedness matters (Van Horn et al 2007). We believe this to be a more likely possibility than baboons simply not caring about maintaining their social network.

From a theoretical perspective, we find that democratic decisions are better at maintaining complex social bond structure through a group fission than despotic decisions, despite information asymmetry which favors the despot. Methodologically, our study provides a unification of network theoretic approaches with collective decision theory to analyze permanent group fissions. Our results demonstrate the promise of continuing to use network theory to better understand collective decisions. More concretely, we take advantage of multiple baboon group fissions that have been observed in the wild to show that animals

with complex social bond structure also consider their social network during a fission. Furthermore, we find support for baboon fissions proceeding democratically. Previously, only baboon movement has been shown to be democratic (Strandberg-Peshkin et al 2015).

References

- Archie, E. A., Moss, C. J. & Alberts, S. C. (2005) The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B*, **273**, 513–522.
- Armitage, K.B. (1987) Social dynamics of mammals: Reproductive success, kinship and individual fitness. *Trends in Ecology & Evolution*, 2, 279– 284.
- Barton, R.A., Byrne, R.W. & Whiten, A. (1996) Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, 38, 321–329.
- Cameron, E.Z., Setsaas, T.H. & Linklater, W.L. (2009) Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, **106**, 13850–13853.
- Cheney, D.L., Silk, J.B. & Seyfarth, R.M. (2016) Network connections, dyadic bonds and fitness in wild female baboons. *Royal Society Open Science*, 3, 1–7.
- Chepko-Sade, B.D. & Olivier, T.J. (1979) Coefficient of genetic relationship and the probability of intragenealogical fission in Macaca mulatta. *Behavioral Ecology and Sociobiology*, 5, 263–278.
- Conradt, L. & Roper, T. J. (2003) Group decision-making in animals. *Nature*, **421**, 156–158.
- Conradt, L. & Roper, T. J. (2005) Consensus decision making in animals. *Trends in Ecology and Evolution*, **20**, 449–456.

- Cords, M. & Rowell, T. (1986) Group Fission in Blue Monkeys of the Kakamega Forest, Kenya. *Folia Primatologica*, **46**, 70–82.
- Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. (2005) Effective leadership and decision-making in animal groups on the move. *Nature*, **433**, 513– 516.
- Dittus, W.P. (1988) Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Animal Behaviour*, 36, 1626–1645.
- Dunbar, R.I.M. (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, **31**, 35–49.
- Henzi, S.P., Lycett, J.E. & Piper, S.E. (1997) Fission and troop size in a mountain baboon population. *Animal Behaviour*, **53**, 525–535.
- Holekamp, K.E., Ogutu, J.O., Dublin, H.T., Frank, L.G. & Smale, L. (2010)Fission of a Spotted Hyena Clan: Consequences of Prolonged FemaleAbsenteeism and Causes of Female Emigration. *Ethology*, **93**, 285–299.
- Kerth, G., Ebert, C. & Schmidtke, C. (2006) Group decision making in fissionfusion societies: evidence from two field experiments in Bechstein's bats. *Proceedings of the Royal Society B*, **273**, 2785–2790.
- Krause, J., Lusseau, D. & James, R. (2009) Animal social networks: an introduction. *Behavioral Ecology and Sociobiology*, **63**, 967–973.
- Lehmann, J., Majolo, B. & Mcfarland, R. (2015) The effects of social network position on the survival of wild Barbary macaques, Macaca sylvanus. *Behavioral Ecology*, 27, 20–28.

- Majer, M., Holm, C., Lubin, Y. & Bilde, T. (2018) Cooperative foraging expands dietary niche but does not offset intra-group competition for resources in social spiders. *Scientific Reports*, 8, 1–13.
- Malik, I., Seth, P.K. & Southwick, C.H. (1985) Group fission in free-ranging rhesus monkeys of Tughlaqabad, Northern India. *International Journal of Primatology*, 6, 411–422.
- Merkle, J. A., Sigaud, M. & Fortin, D. (2015) To follow or not? How animals in fusion-fission societies hand conflicting information during group decision-making. *Ecology Letters*, **18**, 799–806.
- Miller, N., Garnier, S., Hartnett, A. T. & Couzin, I. D. (2013) Both information and social cohesion determine collective decisions in animal groups. *PNAS*, **110**, 5263–5268.
- Okamota K. & Matsumura S. (2001) Group Fission in Moor Macaques (Macaca maurus). *International Journal of Primatology*, **22**, 481–493.
- Ron, T. (1996) Who is responsible for fission in a free-ranging troop of baboons. *Ethology*, **102**, 128–133.
- Ron, T., Henzi, S. & Motro, U. (1994) A new model of fission in primate troops. *Animal Behaviour*, **47**, 223–226.
- Sheppard, C.E., Inger, R., Mcdonald, R.A., Barker, S., Jackson, A.L., Thompson, F.J., Vitikainen, E.I.K., Cant, M.A. & Marshall, H.H. (2018) Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecology Letters*, **21**, 665–673.

- Stanton, M.A. & Mann, J. (2012) Early Social Networks Predict Survival in Wild Bottlenose Dolphins. *PLoS ONE*, 7, 1–6.
- Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D. & Crofoot, M. C. (2015) Shared decision-making drives collective movement in wild baboons. *Science*, 348, 1358–1361.
- Sueur, C, Deneubourg, J., Petit, O. & Couzin, I. D. (2011) Group size, grooming and fission in primates: A modeling approach based on group structure. *Journal of Theoretical Biology*, 273, 156–166.
- Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C. M., Williams, L., Zinner, D. & Aureli, F. (2011) Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos*, **120**, 1608–1617.
- Sueur, C. & Maire, A. (2014). Modelling Animal Group Fission Using Social Network Dynamics. *PLoS ONE*, 9, 1–10.
- Sueur, C., Petit, O. & Deneubourg, J.L. (2010) Short-term group fission processes in macaques: a social networking approach. *Journal of Experimental Biology*, 213, 1338–1346.
- Sundaresan, S. R., Fischhoff, I. R., Dushoff, J. & Rubenstein, D. I. (2007) Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. *Oecologia*, **151**, 140– 149.

- Van Horn, R.C., Buchan, J.C., Altmann, J. & Alberts, S.C. (2007) Divided destinies: group choice by female savannah baboons during social group fission. *Behavioral Ecology and Sociobiology*, **61**, 1823–1837.
- Widdig, A., Nürnberg, P., Bercovitch, F.B., Trefilov, A., Berard, J.B., Kessler,
 M.J., Schmidtke, J., Streich, W.J. & Krawczak, M. (2006) Consequences
 of group fission for the patterns of relatedness among rhesus macaques. *Molecular Ecology*, 15, 3825–3832.

Term	Definition	Purpose		
Betweenness	The sum of weights of shortest	A measure of how		
centrality	paths between any two individuals	much one bond is in		
	that passes through a given edge.	the middle of the		
		network.		
Clustering	The number of closed triplets	A measure of the		
coefficient	divided by the total number of	strength of		
	triplets.	cliquishness in a		
		network.		
Density	The number of bonds divided by	A measure of how		
	the total possible number of bonds.	well connected a		
		network is.		
Diameter	The longest of all shortest paths	A measure of how		
	between any two individuals.	tightly connected a		
		network is.		
Sparsity	The sum of bond weights broken to	A measure of how		
	the number of vertices in the	evenly a fission		
	smallest resulting post-fission	occurred while		
	group.	minimizing broken		
		bonds.		

 Table 2.1. Glossary of network theoretic terms used here.

Table 2.2. Summary of bond metrics from the actual fissions (bold next to group name) and the algorithms for each group. % broken: percentage of bonds broken during fission. Mean broken and maintained: average weight of broken and maintained bonds during fission. Broken and maintained bw: average centrality of broken and maintained bonds during fission. Broken, maintained, total correct: percent of bonds correctly broken or maintained by the algorithms.

	% broken	mean broken	mean maintained	sparsity	broken bw	maintained bw	broken correct	maintained correct	total correct
Dotty	44	0.11	0.20	0.44	0.30	0.19			
Despotism	40	0.14	0.17	0.53	0.26	0.24	43	63	54
Community	14	0.08	0.18	0.11	0.34	0.23	23	92	61
Democracy	18	0.10	0.18	0.16	0.30	0.23	24	87	60
Random	51	0.16	0.16	0.75	0.24	0.24	52	50	51
Sparsest Cut	25	0.09	0.19	0.21	0.30	0.22	35	82	62
Hook	76	0.21	0.37	0.97	0.89	0.47			
Despotism	32	0.22	0.27	0.43	0.87	0.74	34	72	43
Community	15	0.13	0.27	0.12	1.13	0.73	16	88	33
Democracy	18	0.20	0.27	0.21	0.96	0.74	19	85	34
Random	50	0.24	0.26	0.72	0.81	0.79	50	52	50
Sparsest Cut	20	0.16	0.28	0.19	0.97	0.74	24	93	41
Linda	28	0.29	0.33	0.31	0.76	0.83			
Despotism	32	0.29	0.35	0.35	0.84	0.80	32	67	59
Community	17	0.17	0.36	0.11	1.31	0.72	24	86	71
Democracy	19	0.27	0.33	0.19	1.01	0.76	25	84	70
Random	49	0.32	0.32	0.59	0.80	0.81	50	51	52
Sparsest Cut	23	0.20	0.36	0.17	0.95	0.77	35	81	70
Lodge	23	0.41	0.30	0.35	3.22	3.87			
Despotism	9	0.26	0.33	0.09	3.87	3.63	13	91	75
Community	3	0.20	0.33	0.02	8.87	3.50	6	98	80
Democracy	4	0.26	0.33	0.04	6.65	3.56	2	95	76
Random	51	0.33	0.31	0.65	3.59	3.69	48	48	49
Sparsest Cut	5	0.20	0.33	0.04	7.67	3.43	11	97	79
Nyayo	36	0.16	0.16	0.33	0.45	0.61			
Despotism	36	0.14	0.17	0.29	0.58	0.55	34	64	53
Community	19	0.11	0.17	0.12	0.69	0.52	23	83	62
Democracy	20	0.13	0.17	0.15	0.62	0.54	21	81	60
Random	50	0.16	0.16	0.45	0.55	0.55	49	49	49
Sparsest Cut	22	0.10	0.17	0.12	0.77	0.50	23	79	59
Viola	35	0.37	0.37	0.38	1.48	1.21			
Despotism	31	0.35	0.37	0.33	1.37	1.27	33	70	57
Community	14	0.23	0.38	0.10	1.96	1.21	15	87	62
Democracy	15	0.31	0.37	0.13	1.63	1.25	14	85	61
Random	51	0.37	0.37	0.56	1.31	1.29	51	49	50
Sparsest Cut	13	0.23	0.38	0.10	2.02	1.19	17	88	63
Vogue	36	0.23	0.24	0.53	0.68	0.68			
Despotism	34	0.23	0.24	0.52	0.71	0.66	38	68	57
Community	15	0.14	0.24	0.16	0.96	0.62	17	86	62
Democracy	17	0.19	0.26	0.20	0.86	0.64	15	82	58
Random	51	0.24	0.24	0.80	0.67	0.69	51	49	50
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Sparsest Cut	19	0.16	0.27	0.19	0.92	0.62	14	79	56

Table 2.3. Summary of connectedness metrics from the fissions. Bold group names give pre-fission metrics, with post-fission information listed for the two groups in the two columns underneath. Red "Obs" are the metrics for how the fission actually proceeded. n: group size. % correct: percent of pairs correctly placed together by the algorithms.

		1	bond ind	ls per ivid	Clusteri	ng Coeff	Dian	neter	Der	nsity	% Correct
Dotty	5	0	19	98	0.	.3	20	50	0.	11	
Obs	17	43	109	115	0.35	0.4	5	4	0.23	0.17	
Despotism	21	29	193	77	0.37	0.2	4	8	0.23	0.08	53
Community	39	11	194	105	0.32	0.22	4	3	0.13	0.17	81
Democracy	38	12	186	114	0.31	0.23	4	3	0.13	0.23	76
Random	25	25	69	61	0.26	0.28	8	8	0.1	0.11	50
Sparsest	27	23	214	120	0.35	0.23	4	5	0.16	0.16	65
Hook	3	6	7	4	0.	.1	14	14	0.	09	
Obs	17	22	34	9	0.21	0	∞	∞	0.18	0.13	
Despotism	15	21	72	37	0.16	0.08	5	~	0.21	0.09	57
Community	27	9	72	48	0.12	0.1	5.97	4.28	0.12	0.28	76
Democracy	25	11	66	50	0.11	0.09	5.87	4.76	0.12	0.3	67
Random	19	17	26	20	0.09	0.1	8	8	0.09	0.1	50
Sparsest	19	17	59	71	0.12	0.08	5	7	0.16	0.15	64
Linda	3	7	9	2	0.	.2	13	39	0.11		
Obs	20	19	23	34	0.13	0.43	5	~	0.14	0.15	
Despotism	21	16	89	31	0.24	0.13	5	~	0.18	0.07	49
Community	27	10	92	60	0.24	0.04	6	4	0.13	0.23	60
Democracy	25	13	82	65	0.25	0.20	5.8	4.8	0.14	0.26	57
Random	19	18	28	22	0.18	0.17	8	8	0.11	0.11	47
Sparsest Cut	19	18	105	51	0.27	0.00	5	8	0.22	0.11	54
Lodge	3	6	38		0.	09	29	96	0.	06	
Obs	30	16	18	11	0.19	0	8	4	0.08	0.22	
Despotism	5	32	33	36	0	0.12	2	8	0.5	0.07	84
Community	26	10	36	37	0.04	0.13	12	5	0.09	0.28	67
Democracy	26	10	36	35	0.04	0.13	12	5	0.08	0.33	65
Random	18	18	13	10	0.07	0.03	8	8	0.06	0.06	50
Sparsest Cut	18	18	39	35	0.19	0.00	8	7	0.12	0.12	62
Nyayo	4	4	7	5	0.	11	1:	10	0.09		
Obs	28	15	22	22	0.12	0.23	8	8	0.1	0.17	
Despotism	16	28	62	44	0.09	0.12	5	∞	0.19	0.09	53
Community	29	15	68	57	0.13	0.15	5	5	0.12	0.2	56
Democracy	30	14	65	50	0.13	0.13	6	5	0.12	0.21	58
Random	22	22	24	20	0.10	0.10	8	8	0.09	0.09	48
Sparsest Cut	23	21	71	57	0.17	0.12	6	6	0.14	0.15	53
Viola	3	3	5	9	0.	18	13	35	0.1		
Obs	17	19	10	13	0.18	0.26	8	8	0.1	0.12	
Despotism	14	19	45	39	0.09	0.26	5	8	0.19	0.11	50
Community	21	12	55	49	0.19	0.21	7	6	0.14	0.29	51
Democracy	23	10	55	43	0.20	0.16	7	5	0.13	0.31	56
Random	17	16	21	14	0.17	0.14	8	8	0.1	0.1	47

Sparsest Cut	17	16	53	56	0.07	0.38	6	8	0.15	0.2	46
Vogue	3	4	7	5	0.	15	1	77	0.	11	
Obs	18	9	40	24	0.2	0	4	∞	0.2	0.19	
Despotism	13	21	60	42	0.22	0.15	4	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	0.23	0.1	53
Community	23	11	72	55	0.20	0.17	6	5	0.14	0.23	67
Democracy	24	11	70	52	0.16	0.11	5.7	4.9	0.14	0.26	69
Random	18	16	27	21	0.14	0.12	8	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	0.1	0.11	50
Sparsest Cut	18	16	64	69	0.20	0.18	5	6	0.18	0.18	49



Figure 2.1. Walkthrough of the group fission algorithms on simplified, example networks.



Figure 2.2. Box plots showing the percent of bonds broken from the various algorithms across groups. Boxes are clustered by algorithm, with different colors indicating the seven different baboon social groups. Solid lines going across the plot are the actual percent of bonds broken observed from the fissions in nature. The democracy and community algorithms break the lowest percentage of bonds, while the random algorithm breaks the highest percentage.



Figure 2.3. Box plots showing the relative difference in average weight of broken bonds for the various algorithms from the observed weights of broken bonds across groups. Thus, values below 0 (the black line) indicate the algorithm broke weaker bonds on average than was observed and values above 0 indicate the algorithm broke stronger bonds on average than was observed. The community algorithm breaks the weakest bonds on average, followed by democracy, then despotism.



Figure 2.4. Box plots showing the percent of bonds accurately assigned as either broken or maintained for the various groups across algorithms.

Appendix 1A: Sex-structured model

Sex structure can have important consequences in populations, so we built this into an alternate version of our implicit pack model. In models with sex structure, we introduce additional state variables so that $\mathbf{J}_t = J_{m,t} + J_{f,t}$, $\mathbf{Y}_t = Y_{m,t} + Y_{f,t}$, and $\mathbf{M}_t = M_{m,t} +$ $M_{f,t}$ with subscripts *m* and *f* referring to males and females, respectively. Births and deaths from equation (3) are split as $J_{m,t} = m\mathbf{J}_t$ and $J_{f,t} = (1-m)\mathbf{J}_t$ where *m* is the proportion of males at birth (we use 0.56; Creel & Creel, 2002; McNutt & Silk, 2008; Somers et al., 2008; Woodroffe, 2011). We do not model differences in male and female survivorship (in accordance with Woodroffe (2011)), so the sex-structured yearling model is the same except for maintaining the sex of juveniles who aged: $Y_{m,t+1} = J_{m,t}(1-d_Y(C_t))$ and $Y_{f,t+1} = J_{f,t}$ $(1-d_Y(C_t))$. Dimorphic male and female survivorship could be added to apply this model to another system. Again, the sex-structured model maintains the sex of surviving individuals: $M_{m,t+1} = (M_{m,t} + Y_{m,t})(1-\mu_M)$ and $M_{f,t+1} = (M_{f,t} + Y_{f,t})(1-\mu_M)$. In the models with sex structure, we use females as the reproductive population. In the sex-structured pack model, if the average number of mature females per pack is <1, only packs with adult females can reproduce. This means using $R_t = M_{f,t}$ instead of $R_t = p_t$ when $M_{f,t} < p_t$.

Unsurprisingly, given the similarity of the models, the results from our sexstructured model align very closely with the age-structured model (Fig. 1A.1).
 Table 1A.1. Equations from the sex-structured model.

Model characteristics	Pack model	Packless model
Age and sex st	tructure	
Reproducers	$R_t = \begin{cases} p_t & M_{f,t}/p_t \ge 1\\ M_{f,t} & \text{otherwise} \end{cases}$	$R_t = M_{f,t}$
Caregivers	$C_t = A_t$	$C_t = \mathbf{M}_t = M_{m,t} + M_{f,t}$
Equations	$\begin{split} J_{m,t+1} &= m \frac{rA_t}{L+A_t} \min(p_t, M_{f,t}) \left(1 - \frac{dc_1}{c_1 + A_t^2} - \mu_J\right) \\ J_{f,t+1} &= (1-m) \frac{rA_t}{L+A_t} \min(p_t, M_{f,t}) \left(1 - \frac{dc_1}{c_1 + A_t^2} - \mu_J\right) \\ \text{for } g &= m, f: \\ Y_{g,t+1} &= J_{g,t}(1 - c_y(A_t - s)^2 - c_4 - \mu_Y) \\ & \text{with } c_y &= \begin{cases} c_2 & A_t \leq s \\ c_3 & A_t > s \end{cases} \\ M_{g,t+1} &= (M_{g,t} + Y_{g,t})(1 - \mu_M) \\ p' &= p_t + \text{round} \left[\frac{Y_t}{k}\right] - \text{round} \left[\frac{j}{A_t}\right] \\ p_{t+1} &= \begin{cases} 1 & p' < 1 \\ k_p & p' > k_p \\ p' & \text{otherwise} \end{cases} \end{split}$	$\begin{aligned} J_{m,t+1} &= m \frac{r \mathbf{M}_t}{L + \mathbf{M}_t} M_{f,t} \left(1 - \frac{dc_1}{c_1 + \mathbf{M}_t^2} - \mu_J \right) \\ J_{f,t+1} &= (1 - m) \frac{r \mathbf{M}_t}{L + \mathbf{M}_t} M_{f,t} \left(1 - \frac{dc_1}{c_1 + \mathbf{M}_t^2} - \mu_J \right) \\ \text{for } g &= m, f : \\ Y_{g,t+1} &= J_{g,t} (1 - c_y (\mathbf{M}_t - s)^2 - c_4 - \mu_Y) \\ &\text{with } c_y &= \begin{cases} c_2 & \mathbf{M}_t \le s \\ c_3 & \mathbf{M}_t > s \end{cases} \\ M_{g,t+1} &= (M_{g,t} + Y_{g,t}) (1 - \mu_M) \end{aligned}$

MODEL EQUATIONS



Figure 1A.1. The sex-structured models. Graphs and parameter values are the same as in figure 1.2, with (a) the per capita population growth rate vs the population size (with black line from packless model), (b) the per capita population growth rate vs the average pack size, and (c) the average pack size vs the population size.

Appendix 1B: Summary of parameter values

Parameters, their values, and the references on which the values were based. In many cases these parameters were extrapolated from more basic demographic data in the cited sources. For all parameters except for those marked with "*," data were from Selous Game Reserve. References were used to obtain parameter values for the age-structured pack models (third column). These estimates were then adjusted to get comparable values for other the models (see text). The top value shown is the value used to obtain our main results; square brackets show the smallest and largest value used in the sensitivity analyses. Abbreviations: DD = density dependent, DI = density independent, individ = individual, IP = inflection point.

Par a- met er	Description	Value in age- structured pack models	Pack model's value based on:	Value in age- structured packless model	Value in unstructu red pack model	Value in unstructur ed packless model
r	Maximum # pups born per reproducing unit	15 pups/pack [10, 20]	Creel et al. 2004	1.13 pups/adul t [0.755, 1.509]	15 pups/ pack [10, 20]	0.655 pups/ individ [0.437, 0.873]
L	Pack size (pack models) or population size (pack-less models) that produces r/2 pups	8.9 adults/pack [5, 15]	Creel et al. 2004	630 adults [354, 1062]	18.9 individs /pack [12, 26]	1086 individs [690, 1494]
d	Maximum pup mortality fraction due to DD causes	0.6 [0.5, 0.65]	Buettner et al. 2007; Creel et al. 2004	0.6 [0.5, 0.65]	-	-
<i>c</i> ₁	Sets inflection point in pup DD mortality curve	75 (IP at 5 adults/pack) [IP at 3, 8]	Fuller et al. 1992; Creel et al. 2004	3.675x10 ⁻ ³ (IP at 350 adults) [IP at 210, 560]	-	-
μ	Pup mortality fraction due to DI causes	0.22* [0.15, 0.3]	Woodroffe & Ginsberg 1999; Buettner et al. 2007; Woodroffe et al. 2007	0.22 [0.15, 0.3]	-	-
<i>C</i> ₂	Controls steepness of yearling DD mortality fraction with suboptimal pack sizes	9.6x10 ⁻³ * (adults/pac k) ⁻² [8x10 ⁻³ , 1.1x10 ⁻²]	Results in all yearlings dying if no adults present	2x10 ⁻⁶ adults ⁻² [1.7x10 ⁻⁶ , 2.3x10 ⁻⁶]	2.54x10 ⁻ 3 (individs /pack) ⁻² [2x10 ⁻³ , 3x10 ⁻³]	1.26x10 ⁻ 6 individ ⁻² [9.9x10 ⁻ 7, 1.5x10 ⁻⁶]

<i>C</i> ₃	Controls steepness	2.4x10 ⁻³ *	Results in	5x10 ⁻⁷	5.4x10 ⁻⁴	7.6x10 ⁻⁸
_	of yearling DD	(adults/pac	total	adults-2	(individs	individ ⁻²
	mortality fraction	k) ⁻²	mortality at	$[4.2 \times 10^{-7}]$	/pack) ⁻²	$[7x10^{-8}]$
	with above-optimal	$[2x10^{-3},$	pack sizes	5.8x10 ⁻⁷]	[5x10 ⁻⁴ ,	8.4x10 ⁻⁸]
	pack sizes (must be	7x10 ⁻³]	nearing 30		6x10 ⁻⁴]	
	$< c_2$)		(Malcolm &			
			Marten 1982)			
c_4	Minimum DD	0.1	Woodroffe &	0.1	0.1	0.1
	yearling mortality	[0.075,	Ginsberg	[0.075,	[0.075,	[0.075,
	fraction	0.125]	1999; Creel	0.125]	0.125]	0.125]
			et al. 2004			
S	Pack size (pack	10	Creel &	700	20	1207
	models) or	adults/pack	Creel 1995;	adults	individs	individs
	population size	[5, 15]	Creel et al.	[350,	/pack	[905,
	(packless models)		2004;	1050]	[15, 25]	1509]
	that minimizes		Angulo et al.			
	yearling mortality		2013			
μ_Y	Yearling mortality	0.14	Creel et al.	0.14	-	-
	fraction due to DI	[0.1, 0.2]	2004 with	[0.1, 0.2]		
	causes		Woodroffe et			
			al. 2007			
μ_M	Adult mortality	0.23*	Ginsberg et	0.23	-	-
	fraction due to DI	[0.12, 0.32]	al. 1995;	[0.12,		
	causes		Woodroffe &	0.32]		
			Ginsberg			
			1999;			
			Woodroffe et			
	DL and all's from		al. 2007		0.165	0.165
μ	DI mortality for	-	weighted	-	0.165	0.165
	modele		average of μ_J ,		[0.123, 0.175]	[0.123, 0.175]
1-	Movimum number	120 paala	μ_Y, μ_M		120	0.1/3]
κ_p	of pools in the	120 packs	arourary for	-	120	-
	population	[00, 100]	bunothatical			
	population		landscape		1801	
	# wearlings that	10	lanuscape		20	
Ŀ	# yearnings mai	10 vearlings/n		-	20 individe	-
ĸ	neek forming	yearings/p	Resod on		/pack	
	pack forming		stable		/pack	
		[2, 0]	nonulations		[0, 10]	
i	# adults per pack	80	described in		18.9	
J	that results in 1	o.z adults/pack	Creel et al	_	individe	-
	nack failing	[5 15]	2004		/nack	
	pack lanning	[3, 13]	2004		[12 26]	
1	1	1	1	1	[12,20]	1

Appendix 1C: Model sensitivity to dispersal function

The first modification we made to intergroup interactions was making pack formation a function of the number of yearlings per pack by replacing \mathbf{Y}_t with (\mathbf{Y}_t/p_t) in the second term of equation (7). Now, *k* has the interpretation of the number of yearlings per pack that results in one new pack forming. We used k = 4 primarily (again based on stable populations described in Creel et al. (2004)) and tested values from 2 through 10. Overall, our results hold in this model. There is no population-level demographic Allee effect, there is a group-level demographic Allee effect, and pack size is strongly decoupled from population size (Fig. 1C.1). However, in this model, it is not possible to create a population-level demographic Allee effect by reducing *k* (contrast with Fig. 3 in the main text). Here, pack formation halts when packs become too small (because \mathbf{Y}_t/p_t is then small). This explains why packs are a stronger buffer in this model. This also shows that when intergroup dynamics are more responsive to pack size than population size, social populations have greater protection.

In the implicit pack models with pack formation as a function of the number of yearlings per pack, social structure provides additional buffering against population extinction. When the age-structured pack and packless models start below their respective group and demographic Allee thresholds, only the packless model inevitably goes extinct. The dynamic nature of pack formation and failure prevents pack failures below the group Allee threshold from generating a positive feedback to cause population failure. When some packs fail, the average pack size can recover due to a reduction in the number of packs even if the population is declining (Fig. 1C.2). Thus, social structure can lead to a "rescue effect" when average pack size drops below the group Allee threshold.

Despite the ability of packs to support the population, this rescue effect does have its limits. It is possible for the pack model to be far enough below its group Allee

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threshold that packs are unable to buffer against extinction. We found that packs are unable to save the population from extinction once the average pack size in the population becomes approximately two-thirds of the group level Allee threshold pack size (not shown). This will occur for certain initial conditions when pack formation and failure rates are not adjusted quickly enough to bring average pack size into a viable range prior to extinction.

We also added multiple dispersal/pack formation forms to our explicit pack model. First, we built a version in which each pack received an equal number of yearlings each year. Again, our results were not qualitatively affected (Fig. 1C.3).

Finally, we allowed packs in the explicit pack model to fuse upon dropping below a threshold size in our explicit pack model. In this version of the model, if the pack in territory *i* drops below *j* adults, all adults from *i* disperse into territory *i*-1, whether or not that territory is occupied by a pack. Because the indexing is arbitrary (not assumed to contain any geographic or other information) this is similar to allowing the adults from pack *i* to move to a randomly chosen territory and join any pack that is present there. Dispersing adults move at most once per time step, regardless of whether their new pack exceeds *j* adults. Yearlings disperse separately, as described above, and we assume that juvenile pups from failed packs will die, due to the high risk associated with dispersal (Courchamp et al. 2000; Somers et al. 2008). In this model, packs are an extremely strong buffer against population-level demographic Allee effects (Fig. 1C.4). This is unsurprising, as packs now include an extremely strong mechanism against becoming too small, regardless of their size or the population size. This approach highlights that strong intergroup dynamics lead to groups providing populations with a cushion against population-level demographic effects.

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Figure 1C.1. The implicit pack model with pack formation as the number of yearlings per pack. Graphs and parameter values are the same as in figure 1.2 except where noted in the text, with (a) the per capita population growth rate vs the population size, (b) the per capita population growth rate vs the average pack size, and (c) the average pack size vs the population size. Making pack formation a function of the number of yearlings per pack also had no qualitative effect on the explicit pack model.





(a)

Figure 1C.2. Example time series, showing (a) the age-structured implicit pack model with pack formation as a function of the number of yearlings per pack and (b) the age-structured packless model, with initial conditions of 6.25 adults per pack and 900 adults, respectively. The initial conditions are below the pack model's group Allee threshold (at 8 adults/pack) and the packless model's traditional Allee threshold (at 950 adults), in order to highlight the differences in the population level consequences between group Allee effects and demographic Allee effects. Small average pack size in the model creates a negative feedback loop with packs failing (the bottom, red line), resulting in an increase in the average pack size and a recovery of the population. In the packless model, small population sizes further lower the per capita population growth rate, which creates a positive feedback loop from which the population cannot recover – a strong demographic Allee effect.



Figure 1C.3. The explicit pack model with homogeneous yearling dispersal. Graphs and parameter values are the same as in figure 1.2, with (a) the per capita population growth rate vs the population size, (b) the per capita population growth rate vs the average pack size, and (c) the average pack size vs the population size.



Figure 1C.4. The explicit pack model with adult dispersal/pack fusion. Graphs and parameter values are the same as in figure 1.2, with (a) the per capita population growth rate vs the population size, (b) the per capita population growth rate vs the average pack size, and (c) the average pack size vs the population size.

Appendix 1D: Adult density dependence in the age-structured implicit pack model

As there is debate about whether adult mortality is density dependent (Somers et al 2008; Woodroffe 2011; Anuglo et al. 2013; Creel & Creel 2015), we explored a component Allee effect in adult mortality with

$$M_{t+1} = (M_t + Y_t)(1 - \frac{d_m c_n}{c_n + A_t^2} - \mu_M)$$
(D1)

or

$$M_{t+1} = (M_t + Y_t)(1 - c_m(A_t - s)^2 - \mu_M).$$
 (D2)

Furthermore, we modeled negative density dependence in adult mortality using

$$M_{t+1} = (M_t + Y_t)(\frac{d_m c_n}{c_n + A_t^2} - \mu_M)$$
(D3)

or

$$M_{t+1} = (M_t + Y_t)(1 - c_p A_t - \mu_M).$$
(D4)

In general, we found that the group-level component Allee effects do not scale to a population-level demographic Allee effect regardless of density-dependent adult mortality (Fig. 1D.1), unless positive density dependence in adult mortality is extremely strong (i.e., approximately twice as strong as used for Fig. 1D.1). Although this is certainly of theoretical interest, we know of no evidence that suggests this is the case in any population that our model captures.



Figure 1D.1. Plots of per capita population growth rate vs population size with adult mortality following (a) equation (D1) with $c_n = 6.75$ and $d_m = 0.6$, (b) equation (D2) with $c_m = 0.0025$ and $\mu_m = 0.28$, (c) equation (D3) with $d_m = 0.9$ and $c_n = 350$, and (d) equation (D4) with $\mu_m = 0.33$ and $c_p = 0.01$. All other parameters are as in Appendix 1A.

Appendix 1E: Demographic stochasticity in the age-structured implicit pack model

We added demographic stochasticity to our age-structured implicit pack model by multiplying each of equations (3), (5), and (7) by a value drawn from a lognormal distribution (i.e. by multiplying equation (*x*) by $\exp[\varepsilon_x(t)]$, $\varepsilon_x(t) \sim i.i.d$. Normal(0, σ)). We found our results were not qualitatively affected by this change (figure 1E.1).



Figure 1E.1. Age-structured implicit pack model with demographic stochasticity. These graphs were produced with $\sigma = 0.1$; however, our results are insensitive to values of σ up to 0.5. Graphs and other parameter values are the same as in figure 1.2, with (a) the per capita population growth rate vs the population size, (b) the per capita population growth rate vs the average pack size, and (c) the average pack size vs the population size.

Bibliography

- Allee, W. C. (1931). Animal Aggregations: A study in General Sociology. Chicago, IL: University of Chicago Press.
- Angulo, E., Luque, L. Q., Gregory, S. D., Wenzel, J. W., Bessa-Gomes, C., Berec, L., and Courchamp, F. (2017). Allee effects in social species. Journal of Animal Ecology, 87(1), 47-58. doi: 10.1111/1365-2656.12759
- Angulo, E., Rasmussen, G. S. A., Macdonald, D. W., & Courchamp, F. (2013). Do social groups prevent Allee effect related extinctions?: The case of wild dog. Frontiers in Zoology, 10. doi: 10.1186/1742-9994-10-11
- Archie, E. A., Moss, C. J. & Alberts, S. C. (2005) The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B*, **273**, 513–522.
- Armitage, K.B. (1987) Social dynamics of mammals: Reproductive success,
 kinship and individual fitness. *Trends in Ecology & Evolution*, 2, 279–284.
- Barton, R.A., Byrne, R.W. & Whiten, A. (1996) Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, 38, 321–329.
- Bateman, A. W., Coulson, T., & Clutton-Brock, T. H. (2011). What do simple models reveal about the population dynamics of a cooperatively breeding species?.Oikos, 120(5), 787-794. doi: 10.1111/j.1600-0706.2010.18952.x
- Bateman, A. W., Ozgul, A., Coulson, T., & Clutton-Brock, T. H. (2012). Density dependence in group dynamics of a highly social mongoose, *Suricata suricatta*.

Journal of Animal Ecology, 81(3), 628-639. doi: 10.1111/j.1365-2656.2011.01934.x

- Bateman, A. W., Ozgul, A., Nielsen, J. F., Coulson, T., & Clutton-Brock, T. H. (2013).
 Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*. Ecology, 94(3), 587-597. doi: 10.1890/11-2122.1
- Berec, L., Angulo, E., & Courchamp, F. (2007). Multiple Allee effects and conservation management. Trends in Ecology and Evolution, 22(4), 185-191. doi: 10.1016/j.tree.2006.12.002
- Boukal, D. S. & Berec, L. (2002). Single-species models of the Allee effect: Extinction boundaries, sex ratios and mate encounters. Journal of Theoretical Biology, 218(3), 375-394. doi: 10.1006/jtbi.2002.3084
- Buettner, U. K., Davies-Mostert, H. T., Du Toit, J. T., & Mills, M. G. L. (2007). Factors affecting juvenille survival in African wild dogs (*Lycaon pictus*) in Kruger National Park, South Africa. Journal of Zoology, 271(1), 10-19. doi: 10.1111/j.1469-7998.2006.00240.x
- Cameron, E.Z., Setsaas, T.H. & Linklater, W.L. (2009) Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, **106**, 13850–13853.
- Cheney, D.L., Silk, J.B. & Seyfarth, R.M. (2016) Network connections, dyadic bonds and fitness in wild female baboons. *Royal Society Open Science*, 3, 1–7.

- Chepko-Sade, B.D. & Olivier, T.J. (1979) Coefficient of genetic relationship and the probability of intragenealogical fission in Macaca mulatta. *Behavioral Ecology and Sociobiology*, **5**, 263–278.
- Conradt, L. & Roper, T. J. (2003) Group decision-making in animals. *Nature*, **421**, 156–158.
- Conradt, L. & Roper, T. J. (2005) Consensus decision making in animals. *Trends in Ecology and Evolution*, **20**, 449–456.
- Cords, M. & Rowell, T. (1986) Group Fission in Blue Monkeys of the Kakamega Forest, Kenya. *Folia Primatologica*, **46**, 70–82.
- Courchamp, F. & MacDonald, D. W. (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. Animal Conservation, 4(2), 169-174.
- Courchamp, F., Clutton-Brock, T., & Grenfall, B. (1999a). Inverse density dependence and the Allee effect. Trends in Ecology and Evolution, 14(10), 405-410. doi: 10.1016/S0169-5347(99)01683-3
- Courchamp, F., Clutton-Brock, T., & Grenfall, B. (2000). Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. Animal Conservation, 3(4), 277-285.
- Courchamp, F., Grenfall, B., & Clutton-Brock, T. (1999b). Population dynamics of obligate cooperators. Proceedings of the Royal Society B: Biological Sciences, 266(1419), 557-563.
- Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. (2005) Effective leadership and decision-making in animal groups on the move. *Nature*, **433**, 513– 516.

- Creel, S. & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour, 50(5), 1325-1339. doi: 10.1016/0003-3472(95)80048-4
- Creel, S. & Creel, N. M. (1996). Limitation of African Wild Dogs by Competition with Larger Carnivores. Conservation Biology, 10(2), 536-548. doi: 10.1046/j.1523-1739.1996.10020526.x
- Creel, S. & Creel, N. M. (2002). The African wild dog: behavior, ecology, and conservation. Princeton, NJ: Princeton University Press.
- Creel, S. & Creel, N. M. (2015). Opposing effects of group size on reproduction and survival in African wild dogs. Behavioral Ecology, 26(5), 1414-1422. doi: 10.1093/beheco/arv100
- Creel, S., Mills, M. G. L., & Mcnutt, J. W. (2004). Demography and population dynamics of African wild dogs in three critical populations. Biology and Conservation of Wild Canid, pp: 337-350.
- Dennis, B. (2002). Allee effects in stochastic populations. Oikos, 96(3): 389-401. doi: 10.1034/j.1600-0706.2002.960301.x
- Dittus, W.P. (1988) Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Animal Behaviour*, **36**, 1626–1645.
- Dunbar, R.I.M. (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, **31**, 35–49.

- Frank, K. T. & Brickman, D. (2000). Allee effects and compensatory population dynamics within a stock complex. Canadian Journal of Fisheries and Aquatic Sciences, 57(3), 513-517. doi: 10.1139/f00-024
- Fuller, T. K., Kat, P. W., Bulger, J. B., Maddock, A. H., Ginsberg, J. R., Burrows, R.,
 McNutt, J. W., & Mills, M. G. L. (1992). Population dynamics of African wild
 dogs. Wildlife 2001: populations. McCullough, D. R. & Barrett, R. H. (Eds).
 London: Elsevier Applied Science.
- Ginsberg, J. R., Alexander, K. A., Creel, S., Kat, P. W., McNutt, J. W., & Mills, M. G. L. (1995). Handling and survivorship of African wild dog (*Lycaon pictus*) in five ecosystems. Conservation Biology, 9(3), 665-674. doi: 10.1046/j.1523-1739.1995.09030665.x
- Gregory, S. D., Bradshaw, C. J. A., Brook, B. W., & Courchamp, F. (2010). Limited evidence for the demographic Allee effect from numerous species across taxa. Ecology, 91(7), 2151-2161. doi: 10.1890/09-1128.1
- Henzi, S.P., Lycett, J.E. & Piper, S.E. (1997) Fission and troop size in a mountain baboon population. *Animal Behaviour*, **53**, 525–535.
- Holekamp, K.E., Ogutu, J.O., Dublin, H.T., Frank, L.G. & Smale, L. (2010)Fission of a Spotted Hyena Clan: Consequences of Prolonged FemaleAbsenteeism and Causes of Female Emigration. *Ethology*, 93, 285–299.
- IUCN/SSC. 2007. Regional Conservation Strategy for the Cheetah and African Wild Dog in Southern Africa. IUCN Species Survival Commission, Gland, Switzerland.
- Kerth, G., Ebert, C. & Schmidtke, C. (2006) Group decision making in fissionfusion societies: evidence from two field experiments in Bechstein's bats. *Proceedings of the Royal Society B*, **273**, 2785–2790.

- Keynan, O. & Ridley, A. R. (2016). Component, group and demographic Allee effects in a cooperatively breeding bird species, the Arabian babbler (*Turdoides squamiceps*). Oecologia, 182(1), 153-161.
- Krause, J., Lusseau, D. & James, R. (2009) Animal social networks: an introduction. *Behavioral Ecology and Sociobiology*, **63**, 967–973.
- Lande, R. (1998). Demographic Stochasticity and Allee Effect on a Scale with Isotropic Noise. Oikos, 84(2), 353-358. doi: 10.2307/3546849
- Lehmann, J., Majolo, B. & Mcfarland, R. (2015) The effects of social network position on the survival of wild Barbary macaques, Macaca sylvanus. *Behavioral Ecology*, 27, 20–28.
- Majer, M., Holm, C., Lubin, Y. & Bilde, T. (2018) Cooperative foraging expands dietary niche but does not offset intra-group competition for resources in social spiders. *Scientific Reports*, 8, 1–13.
- Malcolm, J. R. & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). Behavioral Ecology and Sociobiology, 10(1), 1-13.
- Malik, I., Seth, P.K. & Southwick, C.H. (1985) Group fission in free-ranging rhesus monkeys of Tughlaqabad, Northern India. *International Journal of Primatology*, 6, 411–422.
- McNutt, J. W. & Silk, J. B. (2008). Pup production, sex ratios, and survivorship in African wild dogs, *Lycaon pictus*. Behavioral Ecology and Sociobiology, 62(7), 1061-1067.

- McNutt, J. W. (1996). Sex-biased dispersal in African wild dogs, *Lycaon pictus*. Animal Behavior, 52(6), 1067-1077. doi: 10.1006/anbe.1996.0254
- Merkle, J. A., Sigaud, M. & Fortin, D. (2015) To follow or not? How animals in fusion-fission societies hand conflicting information during group decision-making. *Ecology Letters*, **18**, 799–806.
- Miller, N., Garnier, S., Hartnett, A. T. & Couzin, I. D. (2013) Both information and social cohesion determine collective decisions in animal groups. *PNAS*, **110**, 5263–5268.
- Mills, M. G. L. & Gorman, M. L. (1997). Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology, 11(6), 1397-1406.
 doi: 10.1046/j.1523-1739.1997.96252.x
- Okamota K. & Matsumura S. (2001) Group Fission in Moor Macaques (Macaca maurus). *International Journal of Primatology*, **22**, 481–493.
- Rasmussen, G., Gusset, M., Courchamp, F., & MacDonald D. W. (2008). Achilles' Heel of Sociality Revealed by Energetic Poverty Trap in Cursorial Hunters. The American Naturalist, 172(4), 508-518. doi: 10.1086/590965
- Rinella, D. J., Wipfli, M. S., Stricker, C. A., Heintz, R. A., & Rinella M. J. (2012).
 Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmononids increase with spawner density.
 Canadian Journal of Fisheries and Aquatic Sciences, 69(1), 73-84. doi: 10.1139/f2011-133
- Ron, T. (1996) Who is responsible for fission in a free-ranging troop of baboons. *Ethology*, **102**, 128–133.

- Ron, T., Henzi, S. & Motro, U. (1994) A new model of fission in primate troops. *Animal Behaviour*, **47**, 223–226.
- Sheppard, C.E., Inger, R., Mcdonald, R.A., Barker, S., Jackson, A.L., Thompson, F.J., Vitikainen, E.I.K., Cant, M.A. & Marshall, H.H. (2018) Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecology Letters*, **21**, 665–673.
- Somers, M. J., Graf, J. A., Szykman, M., Slotow, R., & Gusset, M. (2008). Dynamics of a small reintroduced population of wild dogs over 25 years: Allee effects and the implications of sociality for endangered species' recovery. Oecologia, 158(2), 239-247.
- Stanton, M.A. & Mann, J. (2012) Early Social Networks Predict Survival in Wild Bottlenose Dolphins. *PLoS ONE*, 7, 1–6.
- Stephens, P. A. & Sutherland, W. J. (1999). Consequences of the Allee effect for behaviour, ecology, and conservation. Trends in Ecology and Evolution, 14(10), 401-405. doi: 10.1016/S0169-5347(99)01684-5
- Stephens, P. A., Sutherland, W. J., & Freckleton, R. P. (1999). What is the Allee effect?. Oikos, 87(1), 185-190.
- Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D. & Crofoot, M. C. (2015) Shared decision-making drives collective movement in wild baboons. *Science*, 348, 1358–1361.
- Sueur, C, Deneubourg, J., Petit, O. & Couzin, I. D. (2011) Group size, grooming and fission in primates: A modeling approach based on group structure. *Journal of Theoretical Biology*, 273, 156–166.

- Sueur, C. & Maire, A. (2014). Modelling Animal Group Fission Using Social Network Dynamics. *PLoS ONE*, 9, 1–10.
- Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C. M., Williams, L., Zinner, D. & Aureli, F. (2011) Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos*, **120**, 1608–1617.
- Sueur, C., Petit, O. & Deneubourg, J.L. (2010) Short-term group fission processes in macaques: a social networking approach. *Journal of Experimental Biology*, 213, 1338–1346.
- Sundaresan, S. R., Fischhoff, I. R., Dushoff, J. & Rubenstein, D. I. (2007) Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. *Oecologia*, **151**, 140– 149.
- Tensen, L., Groom, R. J., van Belkom, J., Davies-Mostert, H. T., Marnewick, K., & van Vuuren, B. J. (2016). Genetic diversity and spatial genetic structure of African wild dogs (*Lycaon pictus*) in the Greater Limpopo transfrontier conservation area. Conservation Genetics, 17(4), 785-794.
- Van Horn, R.C., Buchan, J.C., Altmann, J. & Alberts, S.C. (2007) Divided destinies: group choice by female savannah baboons during social group fission. *Behavioral Ecology and Sociobiology*, **61**, 1823–1837.
- Widdig, A., Nürnberg, P., Bercovitch, F.B., Trefilov, A., Berard, J.B., Kessler,
 M.J., Schmidtke, J., Streich, W.J. & Krawczak, M. (2006) Consequences of group fission for the patterns of relatedness among rhesus macaques. *Molecular Ecology*, 15, 3825–3832.

- Wolfram Research, Inc. (2016). Mathematica Version 11.0. Wolfram Research, Inc., Champaigne, IL.
- Woodroffe, R. & Ginsberg, J. R. (1999). Conserving the African wild dog. I. Diagnosing and treating causes of decline. Oryx, 33(2), 132-142. doi: 10.1046/j.1365-3008.1999.00052.x
- Woodroffe, R. & Sillero-Zubiri, C. (2012). *Lycaon pictus*. The IUCN Red List of Threatened Species 2012.
- Woodroffe, R. (2011). Demography of a recovering African wild dog (*Lycaon pictus*) population. Journal of Mammalogy, 92(2), 305-315. doi: 10.1644/10-MAMM-A-157.1
- Woodroffe, R., Davies-Mostert, H., Ginsberg, J., Graf, J., Leigh, K., McCreery, K.,
 Robbins, R., Mills, G., Pole, A., Rasmussen, G., Somers, M., & Szykman, M.
 (2007). Rates and causes of mortality in endangered African wild dogs *Lycaon pictus*: lessons for management and monitoring. Oryx, 41(2), 215-223. doi: 10.1017/S0030605307001809