Population dynamics in meerkats, Suricata suricatta

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This dissertation is the result of my own work and includes work done in collaboration only where specifically indicated in the text. The total length of the text does not exceed 60,000 words. No part of this dissertation has been submitted to any other university in application for a higher degree.

Andrew Bateman January 4th, 2013

SUMMARY

Research on cooperatively breeding species has shown that their population dynamics can differ from those of conventional breeders. Populations of obligate cooperators are structured into social groups, the link between individual behaviour and population dynamics is mediated by group-level demography, and population dynamics can be strongly affected both by features of sociality *per se* and by resultant population structure. Notably, groups may be subject to inverse density dependence (Allee effects) that result from a dependence on conspecific helpers, but evidence for population-wide Allee effects is rare. To develop a mechanistic understanding of population dynamics in highly social species, we need to investigate how processes within groups, processes linking groups, and external drivers act and interact in space and time to produce observed patterns.

Here, I consider these issues as they relate to meerkats, *Suricata suricatta*, obligate cooperative breeders that inhabit southern Africa. I use mathematical and statistical models, in conjunction with long-term data from a wild meerkat population, to explore population dynamics, group dynamics, group demography, Allee effects, and territory dynamics in this species. I start out by examining broad-scale patterns, and then examine some of the constituent processes.

In Chapter Two, I assess the ability of phenomenological models, lacking explicit group structure, to describe population dynamics in meerkats, and I assess potential population-level Allee effects. I detect no Allee effect and conclude that explicit consideration of population structure will be key to understanding the mechanisms behind population dynamics in cooperatively breeding species.

In Chapter Three, I focus on annual group-level dynamics. Using phenomenological population models, modified to incorporate environmental conditions and potential Allee effects, I first investigate overall patterns of group dynamics and find support for only conventional density dependence that increases after years of low rainfall. To explain the patterns, I examine demographic rates and assess their contributions to overall group dynamics. While per-capita meerkat mortality is subject to an Allee effect, it contributes relatively little to observed variation, and other (conventionally density dependent) demographic rates – especially emigration – govern group dynamics.

In Chapter Four, I investigate group dynamics in more detail. I model demographic rates in different sex, age, and dominance classes on short timescales. Using these to build predictive and individual-based simulation models of group dynamics, I examine the demographic mechanisms responsible for declines in group size after dry years. Results reveal the delayed effect of environmental conditions, partially mediated by group structure.

In Chapter Five, I explore meerkat territorial patterns. Using mechanistic home-range models, I examine group interactions, habitat selection, territory formation, and territory movement. I use meerkat data to test proposed improvements to these models, and I use the model results to start building a picture of spatial processes in meerkat population dynamics, laying the groundwork for future research.

This thesis highlights the role of environment and social structure in characterizing population dynamics. I discuss the implications of my findings for the population dynamics of cooperative breeders and for population dynamics generally, noting the importance of sub-populations in drawing conclusions about socially complex systems.

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General Introduction

1.1 Overview

The study of population dynamics aims to explain temporal changes in population size, density, and composition. Understanding the patterns involved is one of the fundamental aims of ecology, and work has long been devoted to this end.

Interpreting patterns of population change is, in fact, relevant across disciplines: fisheries and forestry managers attempt to maximise the benefits derived from natural populations; conservationists work to minimise the negative ecological impacts of an ever-expanding human population, and to promote recovery where possible; public health workers labour to stop the spread of disease. All of these rely on understanding how populations behave, and how they respond to internal and external pressures.

Natural selection is, itself, a population process. Genotypes are favoured when their frequencies increase relative to competing genotypes, so that evolution occurs as a result of differential rates of natality and mortality, relative to rates within and across species. Thus, population dynamics function as the backdrop against which selection must act (Coulson et al. 2006).

Cooperative breeders, in which non-breeding individuals help reproductive individuals raise offspring in stable social groups, have received a great deal of attention and generated controversy in the context of both evolution (*e*, *g*, Nowak et al. 2010, Abbot et al. 2011) and conservation (*e*. *g*. Courchamp et al. 1999b, Courchamp et al. 2000, Courchamp and Macdonald 2001). Given the level of interest in these aspects of cooperative breeders' biology, their population dynamics - relevant to other study - have received relatively little attention. Population characteristics of cooperative breeders do, though, create the potential for complex dynamics. Populations are divided into groups, generating attendant spatial structure and the potential for territorial interactions; groups are divided into breeding and non-breeding demographic classes, with likely effects on patterns of change; and cooperation itself has the potential to influence dynamics by imposing minimum group-size thresholds.

Here, I present work to improve our understanding of population dynamics in cooperatively breeding meerkats, *Suricata suricatta*. This species has been the focus of much behavioural research, examining evolutionary causes and ecological consequences of cooperation, but meerkat population dynamics, *per se*, have not been modelled empirically. Detailed behavioural and life-history data, collected from more than a decade of field studies on this species, afford the opportunity to investigate dynamical patterns associated with cooperation, spatial structure, environmental variation, and age structure in a stochastic environment. By improving our understanding in these areas, I aim to answer important basic questions, help place existing work in context, and lay the groundwork for future research.

Throughout this thesis, I combine mathematical and statistical models with data to investigate meerkat population dynamics in gradually increasing complexity. I start by using relatively simple models to describe patterns of population-level dynamics. I then consider group-level dynamics, starting with simple models and eventually decomposing patterns into contributions from individual demographic rates in different social classes of individuals. Finally, I model territorial patterns, as an initial step towards combining findings relating to group-level patterns into a coherent description of overall population-level dynamics.

In the rest of this chapter, I introduce relevant underlying concepts and relevant sources of variation. I also provide general background about modelling and a brief description of pertinent meerkat biology. Further background and examples relevant to each analysis follow in the respective chapters.

1.2 Population Processes

Fundamentally, only four processes: birth, death, immigration, and emigration, add individuals to or remove individuals from any population. Details of these four demographic rates can vary considerably from one population to another, but several underlying relationships consistently play important roles (Berryman 1999). These relationships involve exogenous (*e.g.* resource-dependent) and endogenous (density-dependent) regulating and de-regulating processes. The specific combination of processes at play for a given population determines the pattern of dynamics observed.

1.2.1 Resources, Environment, and Predation

Resources are central to population and community dynamics, as without sufficient water, nutrients, and space, organisms cannot survive and reproduce. Patterns of primary productivity underlie all food webs, with each trophic level providing food for the next. The resulting patterns of resource distribution help determine the distribution of dependent species (Fretwell and Lucas 1969), and these patterns, in turn, have exerted crucial influence on species' evolution (*e.g.* Clutton-Brock and Harvey 1978).

In part through their influence on resource patterns, environmental conditions also play an important role in population dynamics. Climate and conditions influence primary productivity, but also make the physical environment more or less hospitable, with effects on body condition, reproduction, survival, and dispersal throughout food webs (*e.g.* Cumming and Bernard 1997, Coulson et al. 2001, Hallett et al. 2004, Ozgul et al. 2010, Packer et al. 2005).

While all populations are ultimately resource-*dependent*, resource availability is not the proximate driver of dynamical patterns in all populations (*i.e.* not all populations are resource-*limited*). As recent catastrophic human impacts clearly show (e.g. Worm et al. 2006), population-dynamic patterns can also be influenced by higher trophic levels. The numerical effects of predation directly affect population dynamics, and the associated risks and benefits have wide-ranging effects on relevant patterns of behaviour and space use (Lima and Dill 1990).

1.2.2 Negative Density Dependence

Many of the external factors that influence population dynamics are only relevant in the context of population density. Resource availability, for example, depends on the resources accessible to each individual within a population, and, on average, declines as more individuals fill an area. In addition, some processes are directly dependent on population density. For example, many predators vary their rate of predation on a given species out of proportion to its abundance (Holling 1965). As a result, rates of birth, death, and dispersal, as well as overall rates of change in population size and density, are likely to be density-dependent (*e.g.* Coulson et al. 2008).

The idea that population size is regulated by density-dependent processes is one of the most fundamental concepts in population biology (Berryman 1999).

Without some form of density dependence in the rate of population change, population size would follow a "random walk," with the potential to grow without bound (but invariably declining to zero; Murdoch 1994). In reality, competition among individuals increases with population density (Berryman 1999). Population sizes tend to fluctuate about stable equilibria, above which population size declines and below which it increases. This pattern is termed "negative" (or conventional) density dependence. Whether density-dependent regulation acts locally, on birth and death rates, or at larger scales, on rates of dispersal and colonisation, the pattern persists (Murdoch 1994).

1.2.3 Allee Effects

While increasing population density is most commonly thought to inhibit population growth, the opposite can also be true. Negatively density-dependent processes, such as competition for food or nesting sites, are likely to dominate at high densities, but other, positively density-dependent processes may have more influence at low densities (Allee 1931). These "Allee effects" can result from disadvantages associated with small or sparse populations, such as an inability to find mates, or from advantages associated with larger or denser populations, such as improved thermoregulation or anti-predator defence (Courchamp et al. 1999a).

Two classes of Allee effects exist: "component" Allee effects are positive associations between population size or density and components of fitness; "demographic" Allee effects are positive associations between population size or density and overall mean fitness (Stephens et al. 1999). While component Allee effects have the potential to result in demographic Allee effects, the connection is not guaranteed. Conventionally density-dependent demographic rates can swamp component Allee effects, resulting in conventional dynamics overall (Stephens et al. 1999).

Allee effects, and especially demographic Allee effects, have implications for ecology, evolution, and conservation, and findings have been extensively reviewed elsewhere (*e.g.* Courchamp et al. 1999, Stephens and Sutherland 1999 Stephens et al. 1999, Courchamp et al. 2008). The implications for conservation are of particular concern: low - or negative - rates of population growth in small or sparse populations present an added pressure for threatened species and can hamper reintroduction or conservation efforts (Stephens and Sutherland 1999). Given the increasing number of

species placed at risk by anthropogenic threats, the causes and consequences of Allee effects are relevant areas of study.

1.3 Modelling the Processes

Population dynamics involve complex interactions among individuals and between trophic levels, and the resultant patterns are rarely simple. In addition, population characteristics and interactions must often be measured by proxy, and comprehensive information is elusive. As a result, mathematical models that can describe underlying processes and draw necessary links between data are a cornerstone of population-dynamics research. While all models are ultimately wrong, well-placed and well-designed models can be useful, helping to interpret complex data and pointing out where our understanding falls short (Box 1976).

Mathematical models are often classed as either "phenomenological" or "mechanistic." The former provide descriptions of observed patterns, and can be used to identify relationships between variables (such as population size and population growth rate), while the latter combine mathematical descriptions of underlying processes, generating descriptions of resultant relationships that can be interpreted in the context of those processes. Both types of model can be useful in identifying and understanding biological processes, and in making predictions for conservation or management.

Models provide formal descriptions of hypothesised relationships or patterngenerating processes (both deterministic and stochastic) and help to hone scientific understanding. In the context of population dynamics, models relate patterns of demography, spatial distribution, or other population changes to underlying drivers, such as resource density, predator abundance, climatic factors, and features of the focal population itself. By critically confronting models with data (Hilborn and Mangel 1997), we can identify those descriptions of reality which are inadequate. Discarding inadequate descriptions and retaining good descriptions for further improvement, we correct misconceptions and refine ideas in an iterative pursuit of knowledge (Box 1976).

1.4 Structure in Populations

Simple models, treating populations as homogenous entities, and incorporating simple density dependence, have a long history in studies of population

dynamics. Primarily, such modelling represents a reasonable way to initially approach a problem: simple models are easiest to understand and have the potential to describe relevant processes in relatively accurate - if coarse - ways. In addition, even simple models can produce interesting mathematical results (e.g. chaos; May 1974) that occupy theoreticians. All models simplify reality to some extent, but much can be learned from investigating how violations of simple models' assumptions lead to deviations from their predicted patterns.

Information about wild populations can be difficult to obtain, and may often be limited to estimates of a species' abundance (*e.g.* Frank and Brickman 2000). In this case, commonly used, simple methods of modelling population dynamics can seem (and may be) appropriate. Real populations are not homogeneous, however, and incorporate some degree of structure: individuals differ in size and age, and population density can vary from location to location. These features can have important impacts on population processes. Evidence suggests that elucidation of process details and consideration of population structure are critical for accurate descriptions of population dynamics (Frank and Brickman 2000, Clutton-Brock and Coulson 2002, Packer et al. 2005).

1.4.1 Demographic Structure

Within any population, each demographic rate can manifest differently in different sexes or ages of individuals. Demographic models decompose population fluctuations into contributions from different sex-, stage-, or age-classes (Coulson et al. 2008). Classical approaches (Leslie 1945) considered average rates of mortality and fecundity across age or stage classes, and yielded the conclusion that every population should inherently approach a stable age distribution based on those rates (Schoen and Kim 1991).

The state of any population and specifics of each system are, in reality, important determinants of dynamical behaviour. Two populations of the same size but different age structures can behave very differently under otherwise identical conditions (Coulson et al. 2001, Clutton-Brock and Coulson 2002). Demographic structure can alter the dynamics of disease, invasion, and at-risk populations, and drawing conclusions about any population based on properties of its asymptotic dynamics may be of limited use (Fulford et al. 2002, Koons et al. 2005, Ozgul et al. 2009, Miller and Tenhumberg 2010).

1.4.2 Spatial Structure

Just as populations are not homogeneous with respect to age, sex, and stage, they are rarely homogeneously distributed in space. This is important, as how animals use space in their quest to extract resources, avoid predators, and gain access to mates has consequences for population and community dynamics (Fagan et al. 2007, Wang and Grimm 2007, Morales et al. 2010).

One of the simplest concepts used to describe spatially structured populations is that of a classical metapopulation (Levins 1970), in which localised populations suffer stochastic extinction and are recolonised by dispersers. The metapopulation approach focuses on the role of dispersal in population dynamics. Other approaches tend to focus on births and deaths (Hanski 1999), even though dispersal plays a crucial role in population dynamics (Bowler and Benton 2005). Metapopulation models also highlight that overall population persistence is a dynamic equilibrium of local extinction and colonisation. Absent from the classical formulation is the role of localised sub-population regulation, though more modern studies have included this feature (Hanski 1999).

Ignoring local dynamics can be confusing, and even misleading. In the same way that equally sized populations with different age structure can behave differently, superficially similar, but differentially structured, populations can behave differently. For example, when local dynamics involve Allee effects, ignoring sub-populations can lead to the false conclusion that the population is conventionally densitydependent overall (Frank and Brickman 2000). The Allee effects may not manifest at the population level until too many sub-populations have collapsed to retain a viable population overall. This scenario, drawn from fisheries science, shows the potential for inappropriate management decisions when a population's spatial structure is overlooked.

1.4.3 Social Structure

The patchy distribution of resources across landscapes determines the grouping of animals and strongly influences their social systems (Brown and Orians 1970, Clutton-Brock and Harvey 1978), and social structure within populations can have its own effects on dynamics. Species that form social groups often defend territories against other groups (Macdonald 1983), and males commonly defend resources or females (Clutton-Brock and Harvey 1978). In each case, social

interactions restrict the free movement of individuals - and acquisition of resources (Fretwell and Lucas 1969) - within the landscape.

Social interactions at least partially drive patterns of local density-dependence. Direct intraspecific competition can determine the form of density dependence (Brännström and Sumpter 2005), and hierarchies within social groups can directly restrict access to resources or mates (*e.g.* Clutton-Brock et al. 2008).

Social interactions also affect dispersal decisions (Bowler and Benton 2005) critical to overall population dynamics and persistence (Hanski 1999). In group-forming species, coordinating dispersal with other individuals can be important for its success (Young 2003), and even in solitary species, social cues can alter dispersal decisions (Cote and Clobert 2007). Dispersal decisions influence spatial (and social) dynamics, but can also affect the patterns of birth and death (*e.g.* Haydon et al. 2008, Young 2003) traditionally considered to be the core of population dynamics.

1.5 Population Dynamics of Cooperators

A number of species have evolved to breed cooperatively, most likely facilitated by monogamous breeding systems and the closely related social groups that result from delaying dispersal (Lukas and Clutton-Brock 2012). In some cases, cooperation has become obligate, so that helpers are required for successful breeding or survival (Courchamp et al. 1999b).

As cooperators form stable social groups of breeders and non-breeders, their population dynamics are affected by demographic, spatial, and social structure. Here, the link between individual behaviour and population dynamics is mediated by group-level demography. Breeders and non-breeders contribute differently to demographic rates within groups, which function as local populations, with inherent potential for local density dependence. Population dynamics can be strongly affected both by features of sociality *per se* and by resultant population structure (*e.g.* Hanski 1999, López-Sepulcre and Kokko 2005, Packer et al. 2005). Groups interact with each other socially, often aggressively. In addition, dispersal - important for inbreeding avoidance - ties the subpopulations together and provides the opportunity for vacated habitat to be filled.

Because of the reliance on conspecific helpers, especially in obligate cooperative breeders, Allee effects may play an important role in the population dynamics of cooperative species (Courchamp et al. 1999b). This could have worrying

implications for vulnerable populations of cooperatively breeding species, such as in the high-profile case of African wild dogs, *Lycaon pictus* (Courchamp et al. 2000, Courchamp and Macdonald 2001). Although component Allee effects might seem to be guaranteed for groups of cooperators (Courchamp et al. 1999b), few studies have assessed the potential for demographic Allee effects. Wild dogs have perhaps received the most study in this regard (Courchamp et al. 2000, Courchamp and Macdonald 2001, Somers et al. 2008, Gusset and Macdonald 2010, Woodroffe 2011), but some studies find little support for Allee effects, even in this archetypal case (Somers et al. 2008, Woodroffe 2011). Clearly, more work is required.

1.6 Meerkats

In the following chapters, I use behavioural and life-history data, collected over more than a decade of intensive research at the Kuruman River Reserve in the South African Kalahari (Figure 1.1), to investigate population dynamics in this highly social species. Given the structured nature of meerkat populations, and their situation within a highly stochastic environment, investigation of population-dynamic processes will benefit from the detailed data available. These data provide the potential to understand components of meerkat population, group, dispersal, and spatial dynamics, and start to piece the various aspects together into an overall picture.

Meerkats are cooperatively breeding mongooses (family Herpestidae) that inhabit arid regions of southern Africa. They form groups of up to 50 individuals, within each of which a long-lived, behaviourally dominant pair largely monopolises reproduction (Clutton-Brock et al. 2008, Hodge et al. 2008, Sharp and Clutton-Brock 2010). Subordinates of both sexes help to care for dependent offspring, accruing inclusive fitness benefits (Doolan and Macdonald 1996b, Clutton-Brock et al. 1999b). Helpers provision pups, "babysit" at the natal sleeping burrow, and take turns on sentinel duty, and non-breeding females also allolactate (Clutton-Brock et al. 1999b, Clutton-Brock et al. 2002).



Figure 1.1: Satellite images showing (A) the location of the Kuruman River Reserve (black star) within South Africa (source: www.maplibrary.org) and (B) detail of the study site, showing the dry bed of the Kuruman river running northeast to southwest (source: maps.google.com).

Though meerkats are desert-adapted, stochastic seasonal rainfall strongly affects regional ecology and, consequently, prey availability and meerkat demography (Doolan and Macdonald 1997, Clutton-Brock et al. 1999a, Clutton-Brock et al. 1999b, Hodge et al. 2008). Females usually produce multiple litters per year, but reproduction peaks in January, at the height of the rainy season, and is all but absent by July, in the depths of the dry season (Clutton-Brock et al. 1999b).

Seasonal patterns also drive dispersal. When pregnant, dominant females commonly evict subordinate females, in an effort to avoid infanticide (Clutton-Brock et al. 1998a). Around the same time, subordinate males engage in reproductive prospecting forays and sometimes form "roving coalitions" in an attempt to disperse (R. Mares, in preparation). Many evicted females return to their social groups, but can form new groups with unrelated coalitions of males (Doolan and Macdonald 1996b, Young 2003). Female immigration into established groups is extremely rare (Stephens et al. 2005), and those that cannot return from eviction or establish a new group die.

Past work has identified group-level patterns relevant to meerkat population dynamics. Density dependence at the level of the group affects birth, death, and dispersal processes (Clutton-Brock et al. 1999a, Young 2003, Clutton-Brock et al. 2008, Hodge et al. 2008), and evidence suggests component Allee effects at the group level: the probabilities of breeding, individual and litter survival, and group persistence in bad years all seem to increase with group size (Clutton-Brock et al. 1999a, Hodge et al. 2008). Authors have argued that each additional group member

improves survival and reproductive prospects for the group, and it has been tempting to extend this argument, assuming that meerkat groups experience Allee effects in their overall dynamics (Clutton-Brock et al. 1999a, Courchamp et al. 1999b), but the assertion remains untested. Meerkat population-level dynamics remain entirely unexplored.

Social groups give structure to meerkat populations, and patterns of social dominance create structure within groups. Social groups defend territories against their neighbours (Young 2003, Jordan et al. 2007, Mares et al. 2012), and dispersal creates a dynamic pattern, as new groups form and others die out. Additionally, stochastic environmental conditions are likely to cause fluctuations in groups' demographic structure, leading to varying patterns of dispersal and overall population dynamics. These processes, and the spatially structured population context in which they operate, remain largely unexplored.

1.7 Thesis Outline

Building mathematical and statistical models, and confronting them with detailed data, I aim to elucidate patterns of meerkat population dynamics, and provide mechanistic explanations for some of the observed patterns. I describe patterns of change in population density and then consider how processes within groups, processes linking groups, external drivers, and spatial patterns contribute to these broad-scale dynamics.

In Chapter Two, I use phenomenological population-dynamics models to investigate patterns of inter-annual change in meerkat population density. I assess different functional forms lacking explicit consideration of group structure and incorporate an effect of annual rainfall. I also assess potential Allee effects at the population level, as might be expected if component Allee effects produce group-level Allee effects and group dynamics are synchronised.

In Chapter Three, I consider inter-annual group-level dynamics. Again, I use phenomenological population models, modified to incorporate environmental conditions and potential Allee effects, to investigate overall patterns of group dynamics. I then examine patterns of environmental and density dependence in constituent demographic rates - birth, death, immigration, and emigration - and assess their contributions to overall group dynamics. By decomposing group dynamics in this way, I describe the basic mechanisms behind observed patterns. In Chapter Four, I investigate group dynamics in more detail. I again model demographic rates, but here consider more detailed responses of different sex, age, and dominance classes over short timescales. Using the resulting models to build predictive and individual-based simulation models of group dynamics, I examine the demographic mechanisms responsible for dispersal-related declines in group size after dry years, identified in the previous chapter.

In Chapter Five, I explore meerkat territorial patterns. While chapters Two and Three describe patterns within groups, they do not explicitly consider group interactions or the specific spatial context. The goal of Chapter Five is to start building an understanding of the spatial processes that influence meerkat dynamics and of how group-level and inter-group patterns combine to produce the patterns of dynamics described in Chapter Two. At the same time, the detailed data available for meerkats provide an excellent opportunity to test potential improvements to relevant models. Using mechanistic home-range models, I examine group interactions, habitat selection, territory formation, and territory movement. I use meerkat data to test proposed improvements to these models, and I use the model results to start building a picture of spatial processes in meerkat population dynamics, laying the groundwork for future research.

In Chapter Six, the general discussion, I discuss some of the implications of my findings for meerkats, the population dynamics of cooperative breeders, and for population dynamics generally, noting the importance of sub-populations in drawing conclusions about socially complex systems. I highlight the importance of spatial processes in population dynamics, especially for territorial species like meerkats, and I propose related future work that will help bridge the gap between our knowledge of group dynamics and population dynamics overall.

What do simple models reveal about the population dynamics of a cooperatively breeding species?

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I designed the study, with input from T. Coulson; T. Coulson and T. H. Clutton-Brock contributed to discussion; T. H. Clutton-Brock provided access to data; and I analysed the data and wrote the paper.

2.1 Abstract

Research on cooperatively breeding species has shown that their population dynamics differ from those of conventional breeders. Populations of cooperators are structured into groups, and group-level Allee effects are likely common. We assess the ability of phenomenological models, lacking explicit group structure, to describe population dynamics in cooperative meerkats (*Suricata suricatta*), and we assess potential Allee effects at the population level. Using maximum likelihood model fitting and information theoretic model selection, applied to time series data from a wild meerkat population, we find simple models that incorporate rainfall and conventional density dependence to be the most parsimonious of the models considered. Detecting no population-level Allee effect, we conclude that explicit consideration of population structure will be key to understanding the mechanisms behind population dynamics in cooperatively breeding species.

2.2 Introduction

The population dynamics of cooperatively breeding species – species in which breeders receive help from other individuals when raising offspring – are likely to differ from those of conventional breeders (Courchamp et al. 2000, Packer et al. 2005). The association of breeders and their helpers structures populations into groups, creating the potential for unusual local dynamics that interact to produce overall population dynamics. Here, we examine population dynamics in meerkats (*Suricata suricatta*), a cooperatively breeding mongoose from southern Africa, asking

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whether standard, simple modelling techniques are appropriate and whether characteristic group-level dynamics produce similar population-level dynamics.

Across species, population structure can affect population dynamics. For example, in Soay sheep (*Ovis aries*) age structure, population density, and environmental effects interact to produce observed dynamics (Coulson et al. 2001). Group-living species are no exception. In marmotine rodents, environmental variation can interact with group structure: food availability affects dynamics largely through changes to fertility rate and age at maturity, but social suppression within groups can delay reproduction in young individuals (Dobson and Oli 2001, Oli and Armitage 2003). Many Serengeti species can respond gradually to environmental change, but regional populations of lions (*Panthera leo*) remain stable for years and shift to new equilibria in sudden bursts as a result of group structure (Packer et al. 2005).

For cooperative species, theoretical and empirical studies suggest that groups commonly display depressed growth rates and increased extinction risk at low group sizes (Clutton-Brock et al. 1999a, Courchamp et al. 1999b) – positive (or inverse) density dependencies referred to as Allee effects (reviewed in Courchamp et al. 1999a, Stephens and Sutherland 1999, Courchamp et al. 2008). It has been suggested (Courchamp et al. 2000) that cooperators in nature are subject to population-wide Allee effects – that the group-level Allee effects "scale up" to the population level – but empirical evidence is lacking. In one case, that of cooperative African wild dogs (*Lycaon pictus*), group-level Allee effects are apparent (Courchamp and Macdonald 2001) and have been predicted to generate a population-level Allee effect (Courchamp et al. 2000), but such an effect appears to be absent (Creel and Creel 2002, Somers et al. 2008).

Dynamical synchrony among groups is likely to be important for Allee effects to translate from groups to populations. If group growth rates are not synchronized, patterns of population growth are likely to differ from patterns of group growth. Simulations show that unsynchronized sub-populations, each with Allee dynamics, can combine to form a population displaying conventional density dependence (Frank and Brickman 2000). If groups are synchronized, either by broad-scale environmental effects or by inter-group migration (Bjørnstad et al. 1999), population dynamics are more likely to match group dynamics.

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Studies of population dynamics use a variety of mathematical models to describe fluctuations in population sizes or densities. The models range from simple "phenomenological" forms, describing population changes without explicitly considering births and deaths, to more complicated "demographic" models, specifying birth and death parameters and often incorporating aspects of a population's structure (Coulson et al. 2008). Although they lack explicit consideration of population structure, simple phenomenological models based on measures of size or density have long been central to studies of population dynamics. These models sometimes fail to capture dynamics (e.g. Clutton-Brock and Coulson 2002), and there is disagreement about how to interpret some model parameters (e.g. Royama 1992, Lande et al. 2002), but the models can describe population time series well (e.g. Lande et al. 2002). Specific phenomenological models have been developed to capture various processes, including Allee effects (Courchamp et al. 2008) and the dynamics of, stage- and agestructured populations (Lande et al. 2002). In Soay sheep, an early phenomenological model that ignored population structure (Grenfell et al. 1998) fitted data poorly ($r^2 =$ 0.21) compared to structured models (structured Markov model $r^2=0.92$: Coulson et al. 2001), but a simplified phenomenological approximation of a structured demographic model has since been relatively successful at approximating dynamics $(r^2=0.69$: Coulson et al. 2008). Phenomenological models have also succeeded in describing the dynamics of certain cooperative species (e.g. Octodon degus $r^2=0.94$: Previtali et al. 2009).

Meerkat populations involve structure at multiple levels, and groups display Allee effects (Clutton-Brock et al. 1999a, Hodge et al. 2008), but meerkat population dynamics have not previously been modelled empirically. As singular cooperative breeders (Clutton-Brock et al. 2001b), meerkats form groups of 3 to 50 individuals in which a long-lived (Sharp and Clutton-Brock 2010) dominant pair largely monopolises breeding attempts (Clutton-Brock et al. 2008, Hodge et al. 2008) and subordinate individuals of both sexes help to care for young (Clutton-Brock et al. 2001a). The existence of groups gives structure to the meerkat population, and division into dominant and subordinate classes provides structure within the groups. Group size affects meerkat survival and reproduction, and evidence demonstrates Allee effects in components of fitness, and suggests Allee effects on overall fitness, at the group level: the probabilities of breeding, individual and litter survival, and group persistence in bad years all increase with group size (Clutton-Brock et al. 1999a, Hodge et al. 2008).

We use phenomenological models to describe the dynamics of a wild meerkat population in the South African Kalahari and look for an Allee effect at the population level. Given the past success of simple models at describing dynamics in structured populations (Lande et al. 2002, Coulson et al. 2008, Previtali et al. 2009), we expect to be able to describe meerkat population dynamics using phenomenological models that do not explicitly consider population structure. If phenomenological models lacking explicit structure succeed in describing the dynamics of a meerkat population, we can examine how group interactions allow this. If phenomenological models are inadequate, we can proceed to more complex approaches (that consider group structure) to describe overall population dynamics. For a localised meerkat population, there is good reason to believe that group dynamics will be synchronized, since dispersal occurs between nearby groups (Clutton-Brock et al. 1998a) and environmental conditions will be closely correlated. We thus expect that group level Allee effects will result in an Allee effect detectable at the population level. To investigate, we compile a candidate set of discrete-time phenomenological population dynamics models, some of which are designed to capture Allee effects, and evaluate the models using eleven years of meerkat census data. We also assess group synchrony and the statistical power of our approach to detect an Allee effect.

2.3 Methods

2.3.1 Data Collection

We collected meerkat data from a study population of habituated, wild meerkats on and near the Kuruman River Reserve (26°58'S, 21°49'E), an area of ranchland near Van Zylsrus in the Northern Cape province of South Africa. A detailed description of the site and local conditions can be found elsewhere (Russell et al. 2002). The study population was open to immigration from and emigration to the surrounding area, and the number of social groups in the population fluctuated between eight and sixteen (mean 13.18). Throughout the study period, groups formed, disbanded, and died out; previously unknown groups were habituated, thus entering the study population; and the study of other groups was discontinued, for example, if they moved out of the general study area. Also, individual groups' ranges

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changed over the course of the study. We therefore used measures of population size and range to estimate population density (size/range) for analysis.

We "censused" individuals older than two months on July 1st each year, in the height of the dry season between annual pulses of reproduction (Clutton-Brock et al. 1999b). During weekly (and often daily) visits to meerkat social groups, volunteers collect life history data (Clutton-Brock et al. 1998a, Clutton-Brock et al. 2008). From these detailed records of each individual's birth, death, and dispersal events, we generated accurate population counts for the period from 1998 to 2008, inclusive.

To estimate the population's range, we used burrow location data (meerkats spend the night in subterranean sleeping burrows), collected during group visits in the two months following each census date, and a bivariate normal kernel with a fixed smoothing parameter to calculate a 95% kernel utilization distribution (Worton 1989) for the entire population. Initially, we used spatial "track" data collected with handheld GPS units at fifteen-minute intervals during group visits (for details see Jordan et al. 2007) to estimate 95% kernel utilization distributions for individual groups, using a common smoothing parameter that approximately resulted in contact without overlap for ranges of adjacent groups. Track data have been used previously to estimate meerkat group range (Jordan et al. 2007), and we considered the track data to be more representative than burrow location data of group ranges, but track data were not available for the entire study period. We thus chose a smoothing parameter for use with burrow location data so that, in the years when both datasets were available, the population range (as estimated using burrow location data) approximated, upon inspection, the combined ranges (as estimated using track data) of all the component groups. While this approach might not be appropriate to formally investigate the population's range, it produced a consistent estimate of the area occupied by the meerkat population.

Rainfall data were acquired using NASA's GES-DISC (Goddard Earth Sciences Data and Information Services Center) Interactive Online Visualization ANd aNalysis Infrastructure (Giovanni: NASA 2009). Giovanni provides monthly rainfall estimates based on 2.5° x 2.5° (latitude x longitude) gridded rainfall data from the Global Precipitation Climatology Project Version 2.1 Combined Precipitation Dataset (an update of the version 2 dataset from Adler et al. 2003).

2.3.2 Candidate Models

We initially identified a set of plausible discrete-time phenomenological models (Tables 2.1,2.2) to describe the meerkat population's changes in density from year to year (its population dynamics). We used discrete time models because meerkat reproduction is highly seasonal; births peak in the height of the rainy season and decline to nearly zero during the height of the dry season (Clutton-Brock et al. 1999b).

Table 2.1: explanation of variables and parameters in models (Table 2.2) used to describe meerkat population dynamics

variable/ parameter	Interpretation		
Dt	meerkat density at the beginning of year t		
λ_0	maximal growth rate, attained at zero population density in models with standard (negative)		
	density dependence		
Κ	carrying capacity		
δ	Allee effect parameter for the modified Beverton-Holt model		
α	parameter derived from λ_0 after Allee effect modification of the Beverton-Holt model – no		
	longer maximal model growth rate, but with a similar effect		
d	Allee effect parameter for model modification suggested by Barrowman et al. (2003)		
l	parameter derived from λ_0 after Allee effect modification suggested by Barrowman <i>et al</i> .		
	(2003) - no longer maximal model growth rate, but with a similar effect		
κ	parameter derived from K after Allee effect modification suggested by Barrowman et al.		
	(2003) - no longer carrying capacity, but with a similar effect		
\mathbf{X}_{t}	ln(D _t)		
β	autoregression parameter for the stage-structured life history model ^{\dagger}		
R _t	total rainfall in year t		
γ_{i}	coefficients relating rainfall to carrying capacity (or κ , see above)		
֥ .	$\left[1 + \frac{1}{2} \left(\ln(\overline{\phi}/\overline{\mu}) \right) \right]$		

[†] interpreted as $\left\lfloor 1+\overline{\mu}\left(\frac{\ln(\phi)\mu}{\ln D}\right) \right\rfloor$ evaluated at K, where $\overline{\mu}$ is the annual adult mortality rate, $\overline{\phi}$ is the annual adult recruitment rate, and D is density (Lande *et al.* 2002)

Our initial candidate model set consisted of simple phenomenological models that use one year's density to predict the next. The Beverton-Holt (Beverton and Holt 1957) and Ricker (Ricker 1954) models (Table 2.2 eqs. 1,3) are standard, widely used discrete-time population models (Brännström and Sumpter 2005). The stagestructured life history model (Table 2.2 eq. 5) of Lande et al. (2002) was designed to describe dynamics for species – like meerkats – with populations divided into breeding and non-breeding stage classes. It was derived by linearising a stagestructured demographic model about its carrying capacity equilibrium point, allowing model parameters to be interpreted based on their constituent demographic rates. The linear form of the model is an approximation that relies on small to moderate departures from equilibrium, and although the model was formulated as an autoregressive time series model, which could have incorporated multiple years of density for prediction (Lande et al. 2002), we used the first-order version, because meerkats reach sexual maturity at one year of age.

model	equation	reference
(1) Beverton-Holt model	$\mathbf{D}_{t} = \frac{\lambda_0 \mathbf{D}_{t-1}}{1 + \mathbf{D}_{t-1} \left(\frac{\lambda_0 - 1}{K}\right)}$	(Beverton and Holt 1957)
(2) modified Beverton- Holt model	$\mathbf{D}_{t} = \frac{\alpha \mathbf{D}_{t-1}^{\delta}}{1 + \left(\frac{\alpha}{K} - \frac{1}{K^{\delta}}\right) \mathbf{D}_{t-1}^{\delta}}$	(Beverton and Holt 1957)
(3) Ricker model	$D_t = D_{t-1} \lambda_0^{(1-D_{t-1}/K)}$	(Ricker 1954)
(4) modified Ricker model	$\mathbf{D}_{t} = \frac{\mathbf{D}_{t-1}}{\mathbf{D}_{t-1} + d} \mathbf{D}_{t-1} \ell^{(1 - \mathbf{D}_{t-1} / \kappa)}$	(Ricker 1954, Barrowman <i>et al.</i> 2003)
(5) stage-structured life history model	$^{\dagger}X_{t} = \ln(K) + \beta \left(X_{t-1} - \ln(K)\right)$	(Lande et al. 2002)
(6) modified stage- structured life history model	^{†‡} $X_t = ln(\frac{D_{t-1}}{D_{t-1}+d}) + ln(\kappa) + \beta(X_{t-1}-ln(\kappa))$	(Lande <i>et al.</i> 2002, Barrowman <i>et al.</i> 2003)

Table 2.2: discrete-time population dynamics models used to describe meerkat population density

NOTE: When we consider one and two years prior rainfall, K is replaced by $\gamma_1 R_{t-1}$ and $\gamma_1 R_{t-1} + \gamma_1 R_{t-1}$, respectively (similarly for κ).

[†]models (5) and (6) are formulated in $X_t = \ln(D_t)$

[‡]to generate model (6), we transformed model (5) to the linear scale, modified it to incorporate an Allee effect, and then converted it back to the log scale

We also considered modified forms of our initial models able to describe positive density dependence at low population densities (an Allee effect). The modified Beverton-Holt model (Table 2.2 eq. 2) was proposed by the parent model's authors to capture inverse density dependence (Beverton and Holt 1957). We modified the Ricker and stage-structured life history models (Table 2.2 eqs. 4, 6) using an adaptation suggested by Barrowman *et al.* (2003) to capture Allee effect dynamics: we multiplied the population growth function by a factor of D/(D+d), where D is density and d is an Allee effect parameter. Under this phenomenological modification, d is the density at which a population in the next timestep would be half as dense as predicted by the same model without the Allee parameter. Although meerkats are desert adapted (Clutton-Brock et al. 1999b), they benefit from rain. Increased rainfall affects aspects of meerkat demography such as litter production (Doolan and Macdonald 1997, Clutton-Brock et al. 1999b) and pup growth and survival (Russell et al. 2002). To improve the initial models, based solely on density, we extended each model to incorporate measures of annual rainfall as predictors. Because rainfall influences the abundance of prey (largely invertebrates) available to meerkats (Doolan and Macdonald 1997), and therefore the number of individuals the environment can support, we incorporated rainfall into models as a predictor of carrying capacity. Most models included an explicit carrying capacity term, K, or a term, κ , derived from carrying capacity in the parent model (Table 2.2 eqs. 4, 6). In these cases we assumed K (or κ) to be directly proportional to rainfall, R, in previous years: $K_t = \gamma_1 R_{t-1} + \gamma_2 R_{t-2} + \dots$ We took R_t to be the total rainfall from the census date (July 1st) at the start of model year t until the end of that model year (June 30th of the following calendar year). Each rain period captured one entire rainy season.

We considered models that incorporated rainfall from one year into the past and those that incorporated rainfall from two years into the past, because rainfall affects food availability (and thereby the meerkat population) in the year it falls but could also affect food availability in subsequent years. For example, when a rainy season brings particularly heavy rainfall, remains of the abundant annual vegetation that results can persist well into the following year, potentially maintaining high levels of prey available to meerkats.

Thus, our final candidate set was composed of 12 models: three initial phenomenological forms and their respective Allee effect modifications, each with a version incorporating one year's rainfall and a version incorporating two years' rainfall.

2.3.3 Model Fitting and Selection

We fit all models using maximum likelihood techniques, assuming process error to be normally distributed on the log scale (Myers et al. 1995, Hilborn and Mangel 1997). Because of the frequency of meerkat group observation, we were almost always aware of the presence or absence of each meerkat on any given day, and GPS-recorded burrow locations were highly accurate. We therefore assumed measurement error to be negligible. For each model fitted, we calculated the small-

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sample-corrected version of Akaike's information criterion (AIC_c: Sugiura 1978), r^2 , and adjusted r^2 values. We used each model's Δ AIC_c (the model's AIC_c minus the minimum AIC_c observed for any model in the set) to assess the models (Hurvich and Tsai 1989, Burnham and Anderson 2002). The most parsimonious model has, by definition, a Δ AIC_c of zero, but we considered all models with Δ AIC_c less than two to be "best" models (Burnham and Anderson 2002). We used the r^2 values to evaluate the absolute amount of variation explained by different models and to compare the model fits to those found elsewhere. We report adjusted r^2 for completeness; it allows assessment of the amount of variation explained by different models, accounting for the inherent ability of more complicated models to explain additional variation.

The data series we used (ten annual changes in population density) is short for model fitting and comparison. Hurvich and Tsai (1989) evaluated AICc, showing it to perform well with sample sizes as low as ten, and studies of other species have evaluated models based on data sets of a similar size (*e.g.* Hilborn and Mangel 1997, Angulo et al. 2007, Previtali et al. 2009); however, our short time series still raises issues of parameter identifiability and model overfitting. With so few data, it may be impossible to accurately estimate model parameters, and fitting a relatively large number of models may generate at least one good fit by chance alone. We chose to use a small candidate model set in an effort to avoid overfitting and look closely at the information available about parameters related to a possible Allee effect.

We investigated the likelihood profiles (see Hilborn and Mangel 1997) of the Allee effect parameters in the modified Beverton-Holt, modified Ricker, and modified stage-structured life history models ($\delta \ge 1$], d ≥ 0], and d ≥ 0] in eqs. 2, 4, and 6, respectively, from Table 2.2). To generate a parameter's likelihood profile in a given model, we fixed the parameter at regular intervals and calculated the corresponding negative log likelihood, with all other parameters free to vary. Often, a 95% χ^2 confidence interval is presented in this situation (Hilborn and Mangel 1997, Bolker 2008), but since such an interval relies on a large sample size, we take the slightly more conservative approach of presenting the 2-unit support region (Edwards 1992, Bolker 2008). The 2-unit support region is the parameter range over which the negative log likelihood differs by at most two from the minimum value (associated with the best-fit model). We present this region to qualify the precision of the parameter estimates – less precise estimates have wider 2-unit support regions – while avoiding the use of a strict confidence interval. If an Allee effect were detected (via

model selection), the likelihood profiles and support regions of the Allee parameters would give an estimate of its strength and reliability. If an Allee effect were not detected, the likelihood profiles could clarify its absence: do even the best-fit Allee effect models fail to show an Allee effect, or do the models show an Allee effect and simply lack parsimony?

2.3.4 Power Analysis

We followed a similar approach to Myers *et al.* (1995) for assessing the statistical power of our attempt to detect an Allee effect using the stage-structured life history model incorporating one year's rainfall. We first found the best-fit modified stage-structured life history model with d set equal to 5 - near the data in the range of observations but with a moderate Alee effect – for use as a simulation model. Then, in 1000 simulations, we used that model to generate pseudorandom Monte Carlo data corresponding to the observed initial densities, drawing simulated data from a lognormal distribution with mean determined by the simulation model and shape parameter matching that of the best-fit standard stage-structured life history model. Using AIC_c values, we compared the fit of modified and standard stage-structured life history models to the Monte Carlo data generated in each simulation.

2.3.5 Group Synchrony

We calculated the Pearson moment cross-correlation between changes in loggroup sizes (Bjørnstad et al. 1999) as a measure of group synchrony. First, for each group, we calculated the changes in log-group size, $\Delta_t = \ln(N_{t+1}) - \ln(N_t)$, over the course of the study. Then, for each pair of groups, if both groups were present for at least two concurrent periods of growth or decline, we calculated the correlation between their Δ_t series – their cross-correlation coefficient. Finally, we calculated the population mean cross-correlation coefficient and generated a 95% bootstrap confidence interval for this mean value (Bjørnstad et al. 1999). The confidence interval was based on 1000 calculations of mean sample synchrony, for which we drew, with replacement, samples of complete time series from the set of group time series. We excluded correlations between any time series and itself (arising when time series were resampled multiple times and equal to one by definition) from all calculations of mean synchrony.
2.3.6 Software

We used R 2.8.2 (R Development Core Team 2008) for all analyses and simulation. We used the *optim* function for model fitting and the *kernelUD* function in the *adehabitat* package (Calenge 2006) for kernel home range estimation.

2.4 Results

2.4.1 Data Series

Over the course of our study, meerkat population density ranged between 7.5 and 17.1 individuals per square kilometre (mean 11.7). The population went through two periods of density increase and subsequent decline, peaking in 2001 and 2006 (Figure 2.1A). Annual rainfall ranged between 178.6 and 473.4 millimetres (mean 296.6), and followed a similar trend to density but with peaks in 1999 and 2005 (Figure 2.1B).



Figure 2.1: Population density (A) of meerkats and total annual rainfall (B) on and near the Kuruman River Reserve, Northern Cape province, South Africa. Population censuses occurred on July 1st, and rainfall measurements are for the twelve months following that date each year.

2.4.2 Model Fitting

According to our information-theoretic approach, the Beverton-Holt, Ricker, and stage-structured life history models incorporating one year's rainfall and the stage-structured life history model incorporating two years' rainfall performed best (Δ AIC_c less than two), with the stage-structured model incorporating one year's rainfall having the lowest AIC_c value overall. Table 2.3 gives a complete model fitting summary. We present the best fit predictions and estimated carrying capacities for the stage-structured life history model (Figure 2.2).

2.4.3 Allee Effects

In all models incorporating a possible Allee effect, the Allee parameter estimates we did obtain were those that reduced the modified (Allee effect) models to their parent (Allee effect-lacking) forms: $\delta = 1$, d = 0, and d = 0 in equations 2, 4, and 6, respectively. We were able to generate upper 2-unit support region limits for Allee effect parameters in all models except the modified Beverton-Holt model with two years' rainfall (Figure 2.3). The Allee parameter estimates necessarily formed the lower support region limits, given that the estimates were all on the edges of their allowable ranges.

	Model	AIC _c	ΔAIC_{c}	model df	r ²	adjusted r ²
Models incorporating one previous year's rainfall	Beverton-Holt	-24.26	0.19	3	0.51	0.37
	modified Beverton-Holt	-18.27	6.19	4	0.51	0.27
	Ricker	-23.78	0.67	3	0.49	0.35
	modified Ricker	-17.78	6.67	4	0.49	0.24
	stage-structured life history	-24.45	0.00	3	0.51	0.37
	modified stage-structured life history	-18.45	6.00	4	0.51	0.27
Models incorporating two previous years' rainfall	Beverton-Holt	-22.30	2.15	4	0.66	0.49
	modified Beverton-Holt	-12.92	11.53	5	0.66	0.39
	Ricker	-21.19	3.26	4	0.61	0.42
	modified Ricker	-11.84	12.61	5	0.61	0.29
	stage-structured life history	-22.59	1.87	4	0.67	0.51
	modified stage-structured life history	-13.59	10.86	5	0.67	0.41

 Table 2.3: results of fitting candidate population-dynamics models, incorporating density and annual rainfall, to describe meerkat density dynamics



Figure 2.2: Stage-structured life history model (solid line) fit to population density (points) of meerkats on and near the Kuruman River Reserve, Northern Cape province, South Africa. The modelestimated carrying capacity (dashed line) is a linear combination of 1 (A) or 2 (B) years' annual rainfall. Overall, the version of the model incorporating one year's rainfall (A) was the most parsimonious.



Figure 2.3: Likelihood profiles of the Allee effect parameters, *d* and δ , for modified Beverton-Holt, modified Ricker, and modified stage-structured life history models. Models were used to describe density dynamics of meerkats, on and near the Kuruman River Reserve, incorporating 1 (A) and 2 (B) years of prior rainfall data. d > 0 and $\delta > 1$ indicate the presence of an Allee effect. ***** indicates the upper boundary of the 2-unit support region (see text). Note different scales.

Our estimated statistical power to detect an Allee effect was 0.238: in 1000 power analysis iterations, AIC_c for the modified (Allee effect) model was less than AIC_c for the standard model 114 times and exceeded AIC_c for the standard model by less than two 124 times (for a combined total of 238 out of 1000).

2.4.4 Group Synchrony

We calculated a total of 77 pairwise correlations between changes in log group size. The average population-wide synchrony was 0.22, with a 95% bootstrap confidence interval of -0.01 to 0.46.

2.5 Discussion

We explored the ability of phenomenological, discrete-time population dynamics models to describe the dynamics of a meerkat population, and we looked for an Allee effect in that population. The most parsimonious models from our candidate set describe meerkat dynamics moderately well (r^2 0.51 to 0.67) at observed population densities, but none of these models indicate a population-level Allee effect.

Although we did not consider groups explicitly, we expected group-level Allee effects, combined with group synchrony, to produce a population-level Allee effect. The Allee effect models in our candidate set lacked parsimony, providing limited evidence of conventional density dependence in the meerkat population. Our estimated Allee effect detection power was, however, not high (slightly under 0.24). We were hampered by the short time series at our disposal, and thus cannot draw firm conclusions about Allee effects in our study population.

When an Allee effect does exist in a population, demographic and environmental variability can make it difficult to detect, so an inability to detect an Allee effect does not mean it is unimportant in the population's dynamics (Liermann and Hilborn 2001). Clutton-Brock *et al.* (1999b) noted that all small meerkat groups went extinct in the 1994-1995 season of exceptionally low rainfall; while survival was relatively constant in good and bad years, observed reproduction dropped to nil during the 1994-1995 season (Clutton-Brock *et al.* 1999a), hinting at an Allee effect mediated by an interaction between environmental conditions and demographic rates. Our models indicate that meerkat population densities are heavily influenced by rainfall (Figure 2.2), and it could take an exceptionally poor year, and perhaps some inopportune demographic stochasticity, to reveal such an Allee effect at the population level.

On the other hand, a population can exhibit conventional density dependence even when its component sub-populations exhibit inverse density dependence (Frank and Brickman 2000). The lack of synchrony among meerkat groups could produce this pattern: any Allee effects that affected small groups may have been masked by conventional density dependence in large groups, and the existence of some large groups might serve, through dispersal, to rescue smaller groups from collapse (Courchamp et al. 2008). Alternatively, conventional density dependence in

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dispersal, disperser mortality, or group establishment could mask inverse density dependence in within-group survival and reproductive success. It is, however, impossible to quantify group-level Allee effects, or how synchrony and rate-specific density dependence affect them, using only population time series. Bjørnstad *et al.* (1999) note that synchrony-generating mechanisms are best studied by examining dispersal and the demographic rates affected by extrinsic synchronizing agents, and similar examinations could identify conventional density dependence in contributions to overall dynamics.

Though our models broadly show how density and environment affect the meerkat population, we would ultimately like to know how population density relates to individual-level processes of birth and death and how those relationships are mediated by groups. If our aim is to understand the mechanisms behind population dynamic processes, it will be important to understand demography (Coulson et al. 2001, Dobson and Oli 2001). For example, we now know that increased rainfall leads to increased meerkat population density, but even if we can identify weather-dependent dynamics and describe dynamics as a whole through phenomenological modelling, we must examine environmental effects on demographic parameters such as survival, reproduction, and dispersal to understand the mechanisms by which environment and observed dynamics are linked in structured populations (Coulson et al. 2001).

As an example, dominance structure influences reproduction within meerkat groups, which could in turn affect population growth differently when different numbers or sizes of groups are present. In marmotine rodents, environment and social structure can affect dynamics through their effects on age at maturity (Dobson and Oli 2001, Oli and Armitage 2003). Our best model implicitly considered the population's stage structure by incorporating age at maturity, which we took to be one year. In meerkats, dominants control reproduction in subordinates (Clutton-Brock et al. 2008); dominants are much more fecund than subordinates (Hodge et al. 2008, Sharp and Clutton-Brock 2010); and, while meerkats are sexually mature by one year, individuals are rarely dominant by one year of age. Our best model thus simplifies an important aspect of meerkat biology that we know to affect dynamics in other cooperative species. Models that ignore stage structure within groups cannot shed light on processes that involve aspects of that structure and will be unable to explain resulting variation.

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Our results demonstrate that it is important to consider population dynamics and Allee effects at the appropriate scale (Frank and Brickman 2000). Consideration of meerkats at the population level only would have failed to detect inverse density dependence we know to be present from long-term behavioural studies. The relevance of this density dependence to meerkat dynamics overall remains to be seen, and further work will focus on this. As the number of species that may fall victim to Allee effects increases (Courchamp et al. 2008), the in-depth understanding that can be afforded by long-term demographic studies will become ever more important. Only through the investigation of group dynamics and their interaction with population-level dynamics will we be able to understand how the density dependence observed in groups of cooperators translates into observations at larger scales.

Density dependence in group dynamics of a highly social mongoose, *Suricata suricatta*

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I designed the study; A, Ozgul, T. Coulson, and T. H. Clutton-Brock contributed to discussion; T. H. Clutton-Brock provided access to data; and I analysed the data and wrote the paper.

3.1 Abstract

For social species, the link between individual behaviour and population dynamics is mediated by group-level demography. Populations of obligate cooperative breeders are structured into social groups, which may be subject to inverse density dependence (Allee effects) that result from a dependence on conspecific helpers, but evidence for population-wide Allee effects is rare. We use field data from a long-term study of cooperative meerkats (Suricata suricatta) - a species where local Allee effects are not reflected in population-level dynamics – to empirically model inter-annual group dynamics. Using phenomenological population models, modified to incorporate environmental conditions and potential Allee effects, we first investigate overall patterns of group dynamics and only find support for conventional density dependence that increases after years of low rainfall. In order to explain the observed patterns, we examine specific demographic rates and assess their contributions to overall group dynamics. Although we find that per-capita meerkat mortality is subject to an Allee effect, it contributes relatively little to observed variation in group dynamics, and other (conventionally density dependent) demographic rates – especially emigration – govern group dynamics. Our findings highlight the need to consider demographic processes and density dependence in subpopulations before drawing conclusions about how behaviour affects population processes in socially complex systems.

3.2 Introduction

Across species, populations are often subdivided into smaller units, such as social groups, among which local dynamics interact and combine to produce population-wide patterns. Regardless of the level of organisation, observed dynamics are a consequence of local birth, death, immigration, and emigration processes. To understand a population's dynamics, we therefore need to understand the dynamics of its sub-units and the demographic components that contribute to those dynamics (Coulson et al. 2001, Ozgul et al. 2009).

For populations of group-living species, social structure likely has important demographic consequences, and can lead to dynamics that are qualitatively different from those of homogeneous populations. In Serengeti lions (*Panthera leo*), for example, periods of population equilibrium were punctuated by periods of abrupt increase while environmental conditions improved gradually (Packer et al. 2005), and models that ignore lions' social structure fail to reproduce the observed population dynamics. This is likely true for other highly social species.

Obligate cooperative breeders – species characterised by the presence of nonbreeding individuals that help to raise offspring in social groups – are notable in this context for two reasons. First, they present good opportunities to study the relationships among demography, group-level dynamics, and population-level dynamics. Second, they can be subject to Allee effects (positive, or inverse, density dependence in individual demographic rates or per-capita growth rates; Clutton-Brock et al. 1999a, Courchamp et al. 1999b) acting at the group level but potentially inconspicuous at the population level (Bateman et al. 2011a). While Allee effects have been widely studied before, the full implications of such effects in obligate cooperators are unclear, and empirical investigation would contribute to what has been a largely theoretical discussion.

Allee effects can act at two levels. Initially, increasing group or population size may positively affect one or more components of individual fitness, such as the probabilities of survival or successfully raising offspring; Stephens, Sutherland, and Freckleton (1999) define such relationships as "component" Allee effects. These component effects may or may not combine to produce overall "demographic" Allee effects at the group or population level (Stephens et al. 1999). Overall population- or group-level Allee effects (we avoid the term "demographic" Allee effect to avoid

confusion when discussing component demographic rates) are most often measured as negative per-capita growth rates of the appropriate unit (Courchamp et al. 2008). As one of the potential proximate causes of population decline, these effects are of ultimate relevance for conservation and management and are more easily monitored than component-level effects. To understand when and how component-level effects may translate into population-level effects, we need to investigate the link between the two levels.

Allee effects of one form or another may be common in obligate cooperators (Courchamp et al. 1999a), because when group members work together (e.g. in hunting, thermoregulation, or alloparental care) they can initially overcome conventional negative density dependence (Allee 1931). The downside for some species may be negative per-capita growth rates in small groups due to their reliance on conspecific helpers, leading to increased risks of group extinction (Courchamp et al. 1999b). We might thus expect some signature of Allee effects at the population or group level, but current empirical evidence in obligate cooperators is sparse and somewhat ambiguous. In African wild dogs (Lycaon pictus) there is evidence for Allee effects in specific demographic rates (Courchamp et al. 1999b, Courchamp and Macdonald 2001), but recent empirical studies offer limited support and no evidence for group- or population-level effects (Somers et al. 2008, Gusset and Macdonald 2010, Mebane Jr and Sekhon 2011). In meerkats (Suricata suricatta) there is evidence of an Allee effect in survival and circumstantial evidence of an Allee effect in overall group dynamics (Clutton-Brock et al. 1999a), but it is unlikely that all demographic rates are affected (Stephens et al. 2005), and the only empirical study of meerkats' population-level dynamics found no evidence for an Allee effect (Bateman et al. 2011a). According to theory, Allee effects in individual demographic rates should not necessarily generate population- or group-level effects, and Allee effects in sub-populations should not necessarily scale up to populations overall (Frank and Brickman 2000), but further empirical work is required to identify the level at which Allee effects break down in populations of obligate cooperators.

A starting point in understanding the population dynamics of obligate cooperators is to understand their group dynamics. We propose a combination of simple group dynamics models and models of constituent demographic rates to link patterns of life history and behaviour with patterns of group dynamics. Phenomenological discrete-time models provide a well-supported basis to describe

the dynamics of populations and sub-populations (Brännström and Sumpter 2005, Coulson et al. 2008), but they do not account for contributions from underlying demographic rates. To investigate contributions to group dynamics from birth, death, and dispersal, we can combine simple descriptive models that capture density or environmental dependence in each rate (Coulson et al. 2008). Assessing contributions from each rate under different conditions can illuminate how various factors affect group dynamics and may provide clues as to how Allee effects shape the dynamics of obligate cooperators.

Here, we report an empirical investigation of group dynamics in meerkats. Past work has focused on meerkat population-level dynamics, and discussions of Allee effects in cooperative breeders have paid special attention to group-level processes. We therefore chose to focus on group-level dynamics to bridge the gap between behavioural and population-dynamics work. Because they are well-studied behaviourally, and individual-based demographic data exist from more than a decade of field-study in a wild population, meerkats provide an excellent opportunity to investigate the dynamics of obligate cooperative breeders. Employing an information-theoretic approach, we use well-established phenomenological discretetime models to describe group dynamics and then use simpler models to examine contributions from individual demographic rates to group dynamics. We aim to clarify the importance of Allee effects for meerkats, thereby illustrating the importance of considering the appropriate scale in population dynamics studies more broadly.

3.3 Methods

3.3.1 Study Species

Meerkats – social mongooses that inhabit semi-arid regions of southern Africa – form groups of 3 to 50 individuals at approximate population densities of 7-17 individuals/km² (Bateman et al. 2011a). Within groups, reproduction is largely monopolised by a long-lived, behaviourally dominant pair (Clutton-Brock et al. 2008, Sharp and Clutton-Brock 2010), and subordinate individuals help to care for dependent offspring (Clutton-Brock et al. 1999b). Females produce multiple litters per year, but reproduction peaks in January, at the height of the rainy season, and falls to almost nil in July, at the height of the dry season (Clutton-Brock et al. 1999b).

Before giving birth, dominant females commonly evict subordinate females, sometimes permanently but often temporarily, in an effort to avoid infanticide (Clutton-Brock et al. 1998a). Each year, peaking early in the breeding season, some subordinate males and females disperse to join existing groups or form new groups (Doolan and Macdonald 1996b), but female immigration is extremely rare (Stephens et al. 2005). Although meerkats are arid-adapted, inter-annual variation in rainfall strongly affects their reproduction, survival, and overall population dynamics (Doolan and Macdonald 1997, Clutton-Brock et al. 1999a, Bateman et al. 2011a).

3.3.2 Data Collection

We used individual-based demographic data from a population of habituated, wild meerkats on and near the Kuruman River Reserve (26°58'S, 21°49'E), an area of ranchland near Van Zylsrus in the Northern Cape province of South Africa. A detailed description of the site and local conditions can be found elsewhere (Russell et al. 2002).

During weekly (and often daily) visits to meerkat social groups, researchers collected detailed birth, death, immigration, and emigration records for individually marked meerkats (Clutton-Brock et al. 1998a, Clutton-Brock et al. 2008). Following Bateman *et al.* (2011), we generated from these data group censuses of individuals older than two months on July 1^{st} (in the height of the dry season between annual pulses of reproduction; Clutton-Brock et al. 1999b) for each year between 1998 and 2008.

We often had complete and accurate death and dispersal information for individual meerkats (emigrants recorded in neighbouring groups, carcasses found, or predation observed). For cases of unknown fate, we used knowledge of meerkat behaviour (Clutton-Brock et al. 1998a, Clutton-Brock et al. 1998b, Clutton-Brock et al. 2002, Stephens et al. 2005, Russell et al. 2007) to assign disappearances as either apparent emigration or apparent death. We deemed individuals that had shown signs of pre-dispersal (*i.e.* spent time outside the group) in the month before disappearance to have emigrated, disappearances of a dominant individual to be deaths, multiple simultaneous same-sex disappearances to be group emigration, and all other disappearances to be deaths. All further references to death and emigration thus refer to apparent death and apparent emigration, respectively.

To estimate population density, we divided population census counts by estimates of the population's range. During group visits, researchers recorded the GPS coordinates of sleeping burrows, which we used to estimate a 95% utilization distribution from an empirical kernel utilisation distribution (Worton 1989) generated with a bivariate normal kernel and fixed smoothing parameter. Further details of GPS data collection and our estimation of population range can be found elsewhere (Jordan et al. 2007, Bateman et al. 2011a).

We acquired rainfall data using NASA's GIOVANNI (Goddard Earth Sciences Data and Information Services Center Interactive Online Visualization ANd aNalysis Infrastructure) data system (NASA 2009). GIOVANNI provides monthly rainfall estimates based on $2.5^{\circ} \times 2.5^{\circ}$ (latitude x longitude) gridded rainfall data from the Global Precipitation Climatology Project Version 2.1 Combined Precipitation Dataset (an update of the version 2 dataset described in Adler et al. 2003).

3.3.3 Modeling Approach

We used an information-theoretic approach (Akaike 1973, Burnham and Anderson 2002) to compare models, which represented competing hypotheses, describing meerkat group dynamics and demographic rates. In each instance, we first generated a candidate set of discrete-time models. Next, we used maximumlikelihood techniques to fit each model to annual meerkat group size data, estimating best-fit model parameters in the process (for a detailed description see Hilborn and Mangel 1997 or Bolker 2008). With the resulting negative log-likelihoods, we calculated Akaike's Information Criterion (AIC;Akaike 1973), ΔAIC relative to the minimum AIC model, and Akaike model weights for each model (see Burnham and Anderson 2002 for details). Lower AIC values represent "better" (more parsimonious) models; $\Delta AIC \leq 2$ indicates a model with substantial support, while $\Delta AIC \ge 10$ indicates a model with essentially no support; and each Akaike model weight (w) is interpreted as the probability that the associated model is the "best" (most parsimonious) model, given the candidate model set (Burnham and Anderson 2002).

3.3.4 Phenomenological Group Dynamics Models

The core models for our overall analysis of group dynamics were standard discrete-time population dynamics models. We used these to predict group dynamics

in year-long intervals, or time steps, between annual group size observations. At their simplest, these models take the form

$$N_{t+1} = N_t \cdot \lambda(N_t) , \qquad (3.1)$$

where N_t is group size at the beginning of year t and λ is a density-dependent function defining per-capita group growth rate ($\lambda_t = N_{t+1}/N_t$). Note that t enumerates a model timestep and not a calendar year; each year t spans two calendar years, from July 1st of one to June 30th of the next.

Many possible models exist in the literature, but most fall into two categories describing different types of competition among individuals: contest and scramble (Brännström and Sumpter 2005). In both cases λ declines as N_t increases, but under contest competition a number of individuals, as determined by habitat quality, are always able to secure sufficient resources, and N_{t+1} is an increasing function of N_t , whereas under scramble competition each additional competitor reduces the resources secured by its conspecifics, and N_{t+1} initially increases but then peaks and declines to zero for large N_t . Classic models of contest and scramble competition are the Beverton-Holt (Beverton and Holt 1957) and Ricker (Ricker 1954) models, respectively. The Beverton-Holt model takes the form

$$N_{t+1} = N_t \cdot \frac{\lambda_0}{1 + N_t \left(\frac{\lambda_0 - 1}{K}\right)}, \qquad (3.2)$$

where λ_0 is the theoretical per-capita growth rate at $N_t = 0$, and *K* is the population (group) carrying capacity. The Ricker model takes the form

$$N_{t+1} = N_t \cdot \lambda_0^{\left(1 - \frac{N_t}{K}\right)}.$$
(3.3)

While refinements to these models and different functional forms might capture other subtleties in dynamics, for our purposes, models (3.2) and (3.3) were sufficient to describe relevant patterns.

3.3.5 Incorporating Rainfall and Density

Previous research has shown that rainfall in year t, and possibly in year t-1, affects population dynamics in year t (Bateman et al. 2011a), and we wanted to consider the possibility that population density (meerkats/km² across the study site) affects group-level dynamics. We therefore extended the Beverton-Holt and Ricker models above to incorporate effects of rainfall and population density such that

$$N_{t+1} = N_t \cdot \lambda \left(N_t, R_t, R_{t-1}, D_t \right).$$
(3.4)

To do this, we assumed that λ_0 and *K* are functions of total rainfall in year *t*-1 and *t* (R_{t-1} and R_t , respectively) and density at the beginning of year *t* (D_t). As first-order approximations of what may be the "true" nonlinear relationships, we used linear functions:

$$\lambda_0 = a_0 + a_1 D_t + a_2 R_t + a_3 R_{t-1} \text{ and} K = b_0 + b_1 D_t + b_2 R_t + b_3 R_{t-1}$$
(3.5)

within the phenomenological models, considering a set of models that included different combinations of the individual effects of R_t , R_{t-1} , and D_t (see next section for incorporation of Allee effects). Models that included R_{t-1} also included R_t for biological realism. For model fitting, we centred (subtracted the sample mean value) and normalized (divided by the sample standard deviation) annual rainfall measures. Our initial set included twelve group dynamics models, six variants for each of the Beverton-Holt and Ricker basic forms (Table 3.1).

Making the assumption that errors were negative binomially distributed, we fit each candidate model to our set of group time series, estimating one set of parameters across all groups in the study population. Given the nature of our data collection regime, observation error is negligible, and we assumed that group dynamics were subject to process error only (Hilborn and Mangel 1997). In practice, this meant that the likelihood we calculated for each group size observation, given a model, came from a negative binomial distribution with mean predicted by the model (incorporating the group's size in the previous year as well as the appropriate rainfall and population density information) and shape parameter fit as an additional free parameter.

3.3.6 Allee Effects in Group Dynamics

After fitting the initial candidate models, we assessed the presence of a grouplevel Allee effect, taking as a starting point the group dynamics models from the initial candidate set with greater than 10% support based on Akaike model weights. We modified the form of the per-capita growth rate in these models by raising $\lambda(N_t, R_t, R_{t-1}, D_t)$ to an Allee exponent term:

$$N_{t+1} = N_t \cdot \lambda_{\text{mod}} = N_t \cdot \lambda \left(N_t, R_t, R_{t-1}, D_t \right)^{\left(\frac{N_t - d}{N_t}\right)}.$$
(3.6)

This modification represents a strong Allee effect, where *d* is the (positive) Allee parameter, or threshold, indicating the group size below which group size declines in year *t*. *K* remains unchanged (since $\lambda = 1$ at *K*, and $1^a = 1$ for all *a*), but λ_0 no longer represents initial per-capita growth rate, but rather the theoretical initial per-capita growth rate in the absence of an Allee effect.

Although strong Allee effects are a specific sub-class of Allee effects in general, they do not have special properties above their Allee threshold, and more general models use an additional degree of freedom. Given that our data were sparse at low initial group sizes (Figure 3.2), our ability to distinguish between strong and weak Allee effects was minimal, so we considered only the modification in (3.6).

Adopting the approach of Bolker (2008) to estimate confidence intervals for parameters on the edge of their allowable ranges, we used the likelihood surface approach to calculate 95% confidence intervals for d in each modified model to assess precision of the estimated Allee effects.

3.3.7 Demographic Rates

To explain the results of phenomenological modelling, we decomposed group dynamics into contributions from constituent demographic rates. For any social group (and indeed for any unit of population generally) changes in group size must obey

$$N_{t+1} = N_t + B_t - M_t + I_t - E_t, (3.7)$$

where B_t , M_t , I_t , and E_t enumerate recruitment (here at two months of age), mortality, immigration, and emigration, respectively, in year *t*. Rearranging (3.7), we can write

$$N_{t+1} = N_t + B_t + I_t - (N_t + B_t + I_t) \left(\frac{E_t + M_t}{N_t + B_t + I_t}\right)$$

= $(N_t + B_t + I_t) \left(1 - \frac{E_t}{N_t + B_t + I_t} - \frac{M_t}{N_t + B_t + I_t}\right)$
= $N_t \left(1 + \overline{B}_t + \overline{I}_t\right) \left(1 - \overline{E}_t - \overline{M}_t\right),$ (3.8)

where \overline{B}_t , \overline{M}_t , \overline{I}_t , and \overline{E}_t are the per-capita versions of B_t , M_t , I_t , and E_t , respectively. Note that (3.8) makes the implicit assumption that mortality and emigration are preceded by recruitment and immigration and that the rates of influx, \overline{B}_t and \overline{I}_t , are relative to initial group size (N_t) and are bounded below by zero, while the rates of efflux, \overline{M}_t and \overline{E}_t , are relative to the total number of individuals present in the associated group at some point in year $t (N_t+B_t+I_t)$ and lie between zero and one (inclusive).

The different properties of each influx and efflux rate, as described above, necessitated different modeling approaches. We used a linear function of N_t , R_t , and R_{t-1} (the model terms from the most parsimonious group-dynamics model – see results section), plus interactions, to predict each log-transformed mean per-capita rate of influx, $\overline{r_{influx i,t}}$, so that

$$\overline{r}_{influx \ i,t} = e^{\left(c_0 + c_1 N_t + c_2 R_t + \dots\right)}.$$
(3.9)

Because B_t and I_t take integer values, we fit models to observed values of these influx rates, $r_{influx i,t}$, assuming negative binomial error distributions:

$$r_{influx \ i,t} \sim \text{negative binomial} \Big(\mu = N_t \cdot \overline{r_{influx \ i,t}}, \eta \Big),$$
 (3.10)

where η is the negative binomial shape parameter, which we fit as a free parameter for each rate. We assumed that each logit-transformed mean per-capita rate of efflux was a linear function of N_t , R_t , R_{t-1} , plus interactions, so that

$$\overline{r}_{efflux \ i,t} = \left(1 + e^{-\left(c_0 + c_1 N_t + c_2 R_t + \dots\right)}\right)^{-1}.$$
(3.11)

For an individual, present in a given group in year t, (3.11) represents the probability of death or the probability of emigration by the start of year t+1. We modeled observed values of M_t and E_t assuming a binomial distribution:

$$r_{efflux \ i,t} \sim \text{binomial} \left(p = \overline{r}_{efflux \ i,t}, n = N_t + B_t + I_t \right). \tag{3.12}$$

While we did not include interaction terms in the linear functions for λ_0 and K in the group dynamics models, λ_0 is the initial value and K controls the steepness of the per-capita group growth rate in those models. By including interaction terms in the per-capita demographic rate models, we allowed the predictor variables to have potentially similar control over each predicted demographic rate.

Our candidate model set for the demographic rates consisted of the models described above with distinct c_i coefficients for each rate (Table 3.2). We found the most parsimonious model for each rate independently and then combined those models to generate predictions of N_{t+1} as follows.

Let $\theta_t = \{N_t, R_t, R_{t-1}\}$, the set of conditions in year *t*. Using $P(B_t = x | \theta_t)$ and $P(I_t = x | \theta_t)$, given by (3.9) and (3.10), the distribution for total influx, $(\Phi_t = B_t + I_t)$, becomes

$$\mathbf{P}(\Phi_t = x \mid \theta_t) = \sum_{j=0}^{\infty} \mathbf{P}(B_t = j \mid \theta_t) \cdot \mathbf{P}(I_t = x - j \mid \theta_t).$$
(3.13)

Now, \overline{M}_t and \overline{E}_t , given by (11), are the probabilities of mortality and emigration, respectively, for an individual present in a given group in year *t*. $\overline{S}_t = 1 - \overline{M}_t - \overline{E}_t$ is, therefore, the probability that an individual present in year *t* is present at the start of year *t*+1. The conditional group size distribution for year *t*+1 becomes

$$\mathbf{P}(N_{t+1} = x \mid \theta_t, \Phi_t) = \mathbf{P}_{binomial}(p = \overline{S}_t, n = N_t + \Phi_t).$$
(3.14)

Summing over all possible values of Φ_t , we get the unconditional distribution for N_{t+1} :

$$P(N_{t+1} = x | \theta_t) = \sum_{j=0}^{\infty} P(\Phi_t = j | \theta_t) \cdot P(N_{t+1} = x | \theta_t, \Phi_t = j), \quad (3.15)$$

from which we calculated the expected values of N_{t+1} :

$$\mu(N_{t+1})\Big|_{\theta_{t}} = \sum_{x=0}^{\infty} \Big[x \cdot P(N_{t+1} = x \mid \theta_{t}) \Big] = \sum_{x=0}^{\infty} \Big[x \cdot \sum_{j=0}^{\infty} P(\Phi_{t} = j \mid \theta_{t}) \cdot P(N_{t+1} = x \mid \theta_{t}, \Phi_{t} = j) \Big]$$
$$= \sum_{j=0}^{\infty} \Big[P(\Phi_{t} = j \mid \theta_{t}) \cdot \sum_{x=0}^{N_{t}+j} x \cdot P(N_{t+1} = x \mid \theta_{t}, \Phi_{t} = j) \Big]$$
$$= \sum_{j=0}^{\infty} P(\Phi_{t} = j \mid \theta_{t}) \cdot (\overline{S}_{t}) \cdot (N_{t} + j), \qquad (3.16)$$

using the fact that the expected value of a binomial random variable with parameters n and p is $n \cdot p$.

3.3.8 Assessing Model Contributions

To estimate the explanatory power of the most parsimonious models, as selected by AIC, and of different model components, we used R^2 , which gives the proportion of total variation in data explained by a model fit to those data. As a measure of goodness of fit, standard R^2 has its limitations, but it provides a reasonable sense of how well a model describes data (Kvålseth 1985).

Because a random walk is the appropriate null model for population dynamics with pure process error, we would not expect each group's size to fluctuate about some mean value, but rather about $N_t \cdot \lambda$, where λ is a constant value (typically one, not dependent on θ_t) for all t. We used $\hat{\lambda}$, the maximum-likelihood constant estimate for $\lambda(N_t)$ in (3.1), to estimate λ and calculated R² based on predicted and observed group sizes, taking total sum of squares to be $\sum_{\text{all groups } t} (N_{t+1} - N_t \cdot \hat{\lambda})^2$.

We also used R^2 to assess the explanatory power of different model components. The difference between the R^2 value of a maximally parsimonious model and the R^2 value of the same model without a component of interest gives an estimate of that component's contribution to the model fit (Coulson et al. 2008). We assessed the contributions of R_t , R_{t-1} , and density dependence in λ_t (by using the mean value of N_t in estimation of λ_t) for the phenomenological dynamics models, and we assessed the contributions of R_t , R_{t-1} , and N_t overall and through their contributions to individual demographic rates, as well as the contribution from each demographic rate model (by fixing the predicted rate at its observed mean), in the combined model of demographic rates in (3.15).

3.3.9 Statistical Software

We carried out analyses in R (R Development Core Team 2011). To minimize model negative log-likelihoods, we used the *optim* optimiser for models of demographic rates and the *genoud* optimiser from the *rgenoud* package for group dynamics models (*genoud* combines *optim*'s quasi-Newton optimization algorithm with a genetic optimization algorithm in an effort to avoid "getting stuck" at local optima; Mebane Jr and Sekhon 2011). For kernel home range estimation we used the *kernelUD* function in the *adehabitat* package (Calenge 2006).

3.4 Results

3.4.1 Data

We recorded a total of 104 group-years over the ten years of the study. Group sizes on July 1^{st} ranged from 4 to 47 individuals, with a mean of 17.7; population density on July 1^{st} ranged from 7.5 to 17.1 individuals per km², with a mean of 11.7; and annual rainfall ranged from 178.6 to 473.4 mm, with a mean of 294.4.

3.4.2 Phenomenological Models

The best models from our candidate set were those that incorporated both annual rainfall in year t and annual rainfall in year t-1. Overall, the Ricker model of this form was the most parsimonious, but the corresponding Beverton-Holt model had

a \triangle AIC of less than two. Together, these models shared more than 85% of model support, while no other model had more than 10% support (Table 3.1).

model	predictors for λ_0 , K df		$-ln(\mathcal{L})$	ΔΑΙϹ	model weight (w)
Ricker	_	3	350.5	13.5	0.001
	D_t	5	347.6	11.8	0.002
	R_t	5	349.9	16.5	0.000
	R_t, R_{t-1}	7	339.7	0	0.601
	D_t, R_t	7	346.2	13.0	0.001
	D_t, R_t, R_{t-1}	9	339.5	3.6	0.099
Beverton-Holt	_	3	350.1	12.7	0.001
	D_t	5	348.0	12.5	0.001
	R_t	5	349.6	15.8	0.000
	R_t, R_{t-1}	7	340.5	1.7	0.258
	D_t, R_t	7	346.7	14.0	0.001
	D_t, R_t, R_{t-1}	9	340.5	5.7	0.035

Table 3.1: results of model fitting for phenomenological group dynamics models, with most parsimonious ("best") models shown in bold

The parameter estimates in the best Ricker model gave $\lambda_0 = 1.45 + 0.16 \cdot R_t - 0.21 \cdot R_{t-1}$, and $K = 27.34 - 0.62 \cdot R_t + 14.06 \cdot R_{t-1}$, with a negative binomial shape parameter of 15.71. The parameter estimates in the best Beverton-Holt model gave $\lambda_0 = 1.72 + 0.23 \cdot R_t - 0.34 \cdot R_{t-1}$, and $K = 24.47 - 0.20 \cdot R_t + 12.32 \cdot R_{t-1}$, with a negative binomial shape parameter of 15.02. This meant that in both best models the main effects of rainfall were those associated with R_{t-1} ; the best models both describe group dynamics in which per-capita group growth rates decline in large groups after years of low rainfall (Figure 3.1).



Figure 3.1: Phenomenological group-dynamics model predictions and observed group sizes (circles), after years of higher-than-median rainfall (black) and lower-than-median rainfall (grey), for meerkats on and near the Kuruman River Reserve, South Africa, between 1998 and 2008. Ricker (solid lines) and Beverton-Holt (dashed lines) models use group size in a given year (N_t) to predict group size in the next year (N_{t+1}). Curves show average model predictions, weighted by the number of observations in appropriate years. Dotted 1:1 line represents no year-on-year change.

3.4.3 Allee Effects

We fit Allee effect-modified versions of the best-fitting Ricker and Beverton-Holt models (which we refer to as "Allee-Ricker" and "Allee-Beverton-Holt" models, respectively). In both cases, the maximum-likelihood Allee parameter estimates were zero, reproducing the dynamics of the non-Allee effect parent model forms. AIC values for the Allee models were simply two units higher due to one additional parameter but the same negative log-likelihood as their non-Allee counterparts.

95% confidence intervals for the Allee parameters were [0, 4.3] for the Allee-Ricker model and [0, 4.0] for the Allee-Beverton-Holt model. Comparing the maximum-likelihood fit of the Allee-Ricker model with Allee parameter 4.3 to the maximum-likelihood fit overall (Figure 3.2), we see that the two models give almost identical predictions across the range of observed group sizes and that very few observations exist for small groups which might arbitrate between the two model forms.



Figure 3.2: Allee-Ricker models relating group size in a given year (N_t) to group size in the next year (N_{t+1}) for meerkats. The black curve shows the best-fit model (with no apparent Allee effect due to an Allee parameter estimate of zero); the grey curve shows the model refit with its Allee parameter fixed at 4.3 (on the edge of the 95% confidence interval as estimated for the best-fit model). Curves present average model predictions, weighted by the number of observations in each year. Dotted 1:1 line represents no year-on-year change. Rug shows observations of initial group size (plus a small amount of random noise to illustrate distribution).

3.4.4 Demographic Rates

Different per-capita rates were best predicted by different combinations of variables (Table 2). Of the models considered, the most parsimonious model for mean per-capita recruitment was $\exp(-0.11 - 0.04 \cdot N_t + 0.1 \cdot R_t)$, with a negative binomial shape parameter of 5.52; the most parsimonious model for mean per-capita immigration was $\exp(-0.19 - 0.03 \cdot N_t)$, with a negative binomial shape parameter of 0.16; the most parsimonious model for per-capita mortality rate was $[1+\exp(1.39 + 0.03 \cdot N_t - 0.76 \cdot R_{t-1} - 0.22 \cdot R_t + 0.03 \cdot N_t \cdot R_{t-1} + 0.02 \cdot N_t \cdot R_t)]^{-1}$; and the most parsimonious model for per-capita emigration rate was $[1+\exp(1.83 - 0.03 \cdot N_t + 0.10 \cdot R_{t-1} + 0.01 \cdot N_t \cdot R_{t-1})]^{-1}$.

Annual per-capita recruitment declined with increasing initial group size and increased with annual rainfall (Figure 3.3A). Per-capita immigration declined with increasing initial group size (Figure 3.3B). Per-capita mortality tended to decline with increasing initial group size (the only rate-specific Allee effect), with the trend more pronounced after years of high rainfall (Figure 3.3C). Per-capita emigration increased with increasing initial group size and was lower, especially in large groups, after years of high rainfall (Figure 3.3D).

Combining all the demographic rates together into a "combined demographic" model yielded group dynamics predictions (Figure 3.4) similar to those from the best phenomenological models. While the effect of past rainfall was not as strong as in the phenomenological models, it was still clearly present.

demographic rate	model predictors	df	$-\ln(\mathcal{L})$	ΔΑΙΟ	model weight (w)
	N _t	3	301.3	5.7	0.022
	N_t , R_{t-1}	4	301.3	7.5	0.009
	N_t , R_t	4	297.5	0	0.381
	N_t , R_{t-1} , N_t · R_{t-1}	5	300.1	7.2	0.011
recruitment	N_t , R_t , N_t · R_t	5	297.4	1.8	0.153
	N_t , R_{t-1} , R_t	5	297.5	2.0	0.143
	N_t , R_{t-1} , R_t , N_t : R_{t-1}	6	296.3	1.7	0.164
	N_t , R_{t-1} , R_t , $N_t \cdot R_t$	6	297.4	3.8	0.057
	N_t , R_{t-1} , R_t , N_t : R_{t-1} , N_t : R_t	7	296.3	3.7	0.061
	N _t	3	141.7	0	0.252
	N_t , R_{t-1}	4	141.4	1.5	0.116
	N_t , R_t	4	141.5	1.7	0.110
	N_t , R_{t-1} , N_t : R_{t-1}	5	141.4	3.5	0.043
immigration	N_t , R_t , N_t : R_t	5	141.4	3.5	0.043
	N_t , R_{t-1} , R_t	5	141.4	3.4	0.045
	N_t , R_{t-1} , R_t , N_t : R_{t-1}	6	141.4	5.4	0.017
	N_t , R_{t-1} , R_t , N_t : R_t	6	141.3	5.3	0.018
	N_t , R_{t-1} , R_t , N_t : R_{t-1} , N_t : R_t	7	141.2	7.2	0.007
	N _t	2	281.1	21.0	< 0.001
	N_t , R_{t-1}	3	280.0	20.8	< 0.001
	N_t , R_t	3	278.1	17.0	< 0.001
	N_t , R_{t-1} , N_t : R_{t-1}	4	271.9	6.6	0.032
mortality	N_t , R_t , N_t : R_t	4	277.0	16.8	< 0.001
	N_t , R_{t-1} , R_t	4	277.4	17.6	< 0.001
	N_t , R_{t-1} , R_t , N_t : R_{t-1}	5	269.8	4.4	0.094
	N_t , R_{t-1} , R_t , N_t · R_t	5	276.1	17.1	< 0.001
	N_t , R_{t-1} , R_t , N_t · R_{t-1} , N_t · R_t	6	266.6	0	0.873
	N_t	2	376.5	52.5	< 0.001
	N_t , R_{t-1}	3	349.9	1.3	0.138
	N_t , R_t	3	374.2	49.9	0.000
	N_t , R_{t-1} , N_t · R_{t-1}	4	348.3	0	0.267
emigration	N_t , R_t , N_t : R_t	4	373.5	50.5	< 0.001
	N_t , R_{t-1} , R_t	4	349.1	1.6	0.117
	N_t , R_{t-1} , R_t , N_t : R_{t-1}	5	347.4	0.4	0.222
	N_t , R_{t-1} , R_t , $N_t \cdot R_t$	5	348.0	1.5	0.123
	N_t , R_{t-1} , R_t , N_t : R_{t-1} , N_t : R_t	6	347.0	1.4	0.132

Table 3.2: results of model fitting for component demographic rates, with maximum parsimony models used in further analyses shown in bold



Figure 3.3: Annual per-capita demographic rates across the observed range of initial group sizes (N_t) for meerkat groups on and near the Kuruman River Reserve, South Africa, between 1998 and 2008. Curves show average model predictions, weighted by the number of observations in appropriate years. Circles show corresponding observations. A: recruitment rate (recruits/ N_t ; note different scale) *in* years of higher-than-median (black) and lower-than-median (grey) annual rainfall; **B**: immigration rate (immigrants/ N_t); **C**: mortality rate (deaths/ $[N_t + \text{recruits} + \text{immigrants}])$ *after*years of higher-than-median (black) and lower-than-median (grey) annual rainfall;**D** $: emigration rate (emigrants/<math>[N_t + \text{recruits} + \text{immigrants}])$ *after*years of higher-than-median (black) and lower-than-median (grey) annual rainfall.

The combined demographic model, unlike the best-fitting phenomenological models, can describe a group-level Allee effect if Allee effects of sufficient magnitude exist in individual demographic rates. In two years, 2000 and 2006, the Allee effect present in the mortality model was strong enough to produce an overall group-level Allee effect in the combined demographic model (Figure 3.5).



Figure 3.4: Predictions from "combined demographic" group-dynamics model (solid lines) and observed group sizes (circles), after years of higher-than-median rainfall (black) and lower-thanmedian rainfall (grey), for meerkats on and near the Kuruman River Reserve, South Africa, between 1998 and 2008. The model combines sub-models of component demographic rates to predict change between group size in a given year (N_t) and group size in the next year (N_{t+1}). Curves show average model predictions, weighted by the number of observations in appropriate years. Dotted 1:1 line represents no year-on-year change.



Figure 3.5: Annual per-capita changes in group size (λ_t) for meerkats on and near the Kuruman River Reserve, South Africa, for years 2000 (grey) and 2006 (black). Circles show observations and solid lines show predictions from a model combining sub-models for component demographic rates to predict change between group size in a given year (N_t) and group size in the next year. Dotted line represents no year-on-year change.

3.4.5 Model Contributions

The best group dynamics models explained between 32% and 39% of the observed variation in group size, with the Ricker model explaining the most variation (Table 3.3). In all three models (Ricker, Beverton-Holt, and combined demographic), rainfall in year *t*-1 was responsible for far more of the explanatory power than rainfall in year *t* (43-49% compared with 2-7%, respectively). Within the component demographic model, the sub-model describing per-capita emigration explained more variation than did any other per-capita rate model. The majority of the explanatory power of the emigration model resulted from the inclusion of R_{t-1} terms, and inclusion

of R_{t-1} in the emigration model accounted for the majority of the explanatory power of R_{t-1} in the combined demographic model overall.

model	model form †		$R^{2 \ddagger}$	ΔR^2	% of explanatory power attributed to model component
	maximum parsimony model		0.39	_	_
Ricker	(R_{t-1})		0.20	0.19	49
	(\mathbf{R}_t)		0.37	0.02	6
	λ_t density-independent		0.29	0.10	27
	maximum	0.38	_	_	
Beverton-	(R_{t-1})		0.20	0.18	47
Holt	(R_t)		0.35	0.02	7
	λ_t density-independent		0.29	0.08	22
	maximum	parsimony model	0.32	—	-
	(all R_{t-1} term	ms)	0.19	0.13	43
	("	in recruitment)	N/A	_	_
	("	in immigration)	N/A	_	_
	("	in mortality)	0.31	0.01	5
	("	in emigration)	0.22	0.10	32
	(all R_t terms)		0.32	0.01	2
	("	in recruitment)	0.32	0.01	2
	("	in immigration)	N/A	_	-
combined	("	in mortality)	0.33	-0.01	-4
demographic	("	in emigration)	N/A	_	-
	(all N_t terms)		0.17	0.15	47
	("	in recruitment)	0.29	0.04	12
	("	in immigration)	0.32	0.00	0
	("	in mortality)	0.29	0.03	10
	("	in emigration)	0.28	0.05	15
	recruitment set to mean value		0.27	0.05	17
	immigration set to mean value		0.32	0.00	0
	mortality set to mean value		0.30	0.03	8
	emigration set to mean value		0.20	0.12	38

Table 3.3: explanatory power of group dynamics models and contributions from model components.

[†] Parentheses indicate omission of specified term(s) from the associated maximum parsimony model to assess explanatory power.

[‡]R² values were calculated based on expected and observed group sizes, assuming a null model with constant λ_t (a random walk model).

3.5 Discussion

We investigated the relationship between demographic processes and group dynamics in meerkats, obligate cooperative breeders for which group dynamics have been assumed to exhibit Allee affects. Although we found a component Allee effect in rates of mortality, all other demographic rates were conventionally density dependent. Combination of component rate models successfully reproduced group dynamics, as described by phenomenological models. Mortality rates contributed relatively little to group dynamics, however, and the associated component Allee effect failed to produce an overall (demographic) Allee effect at the group level.

3.5.1 Overall Group Dynamics

Using field data from a long-term study, we compared competing models of inter-annual meerkat group-size dynamics, assessing support for models describing contest and scramble competition, effects of rainfall and population density, and a group-level Allee effect. Because neither the Ricker nor the Beverton-Holt model form was clearly better at describing group dynamics, we were unable to distinguish between contest and scramble competition. We found good support for effects of two years' past rainfall but little support for an effect of population density. The best model explained almost 40% of the observed variation in group size but did not include an Allee effect. Observations for groups smaller than five individuals were limited (Figure 3.2), and uncertainty in the Allee parameters reflected this. Still, the most parsimonious descriptions of meerkat group dynamics within the range of observations, and even the best-fitting Allee effect models themselves, did not include an Allee effect. Instead, conventional density dependence was evident and increased after years of relatively low rainfall (Figure 3.1), an effect that accounted for nearly half of the best model's ability to explain group dynamics (Table 3.3).

The lack of an obvious Allee effect, and stronger conventional density dependence after low-rainfall years, is somewhat surprising, given that past studies have suggested that meerkats derive considerable benefits from living in larger groups (Clutton-Brock et al. 2001c, Hodge et al. 2008) and that small groups suffer disproportionate negative effects in bad years (Clutton-Brock et al. 1999a). There are two potential explanations for this inability to detect an Allee effect: we may have missed an Allee effect present in small groups, or Allee effects in component demographic rates may not translate to the group level.

3.5.2 Constituent Demography

To assess contributions to group dynamics from different demographic components, we constructed a group dynamics model from models of individual demographic rates. First, we used simple models to describe the effects of rainfall and group size on recruitment, immigration, mortality, and emigration. Next, we assembled the models of individual rates into a combined demographic model of group dynamics. The resulting model predictions matched those of our earlier phenomenological models well (Figures 3.1, 3.4) and explained a similar amount of variation (Table 3.3), lending support to our subsequent assessment of each model term's explanatory power.

Our treatment of individual demographic rates illuminates the observed patterns of group dynamics. As previously described (Clutton-Brock et al. 1999a), meerkat mortality tends to decrease with increasing group size (Figure 3.3C). Recruitment, immigration, and emigration, however, are conventionally density dependent (Figures 3.3A,B,D). Emigration accounted for the largest proportion of variation explained by the combined demographic model. Mortality – the only demographic rate subject to an Allee effect – accounted for relatively little (Table 3.3). This explains why overall group dynamics, as described by the best phenomenological models, did not exhibit an Allee effect.

The combined demographic model did exhibit a demographic Allee effect in two out of ten years, but this is likely a case of overfitting: the combined demographic model has more parameters and actually exhibits a poorer fit to the data than the best phenomenological models (Table 3.3), and the apparent Allee effect is not wellsupported by the data (Figure 3.5).

3.5.3 Interpretation

The existence of inverse density dependence in meerkat mortality rates – the feature of meerkat biology that initially sparked interest in potential Allee effects (Clutton-Brock et al. 1999a) – has at least two possible interpretations. First, meerkat sentinel behaviour may help individuals in larger groups to avoid predation, and second, small groups may suffer from an inability to compete for hospitable territories (Clutton-Brock et al. 1999a). Because reduced mortality in small groups after years of low rainfall coincides with reductions in population density (Bateman et al. 2011a), which likely reduces intergroup competition, our results offer support for the latter.

Conventional density dependence in recruitment seems at first paradoxical, since dominant female reproductive output, which constitutes the majority of reproductive success for any group (Clutton-Brock et al. 1999b, Clutton-Brock et al. 2008), increases with group size (Hodge et al. 2008). The simple explanation is that recruitment increases do not keep pace with increasing group size, leading to reduced per-capita recruitment in larger groups (Figure 3.3A). A similar result is likely to explain patterns observed in wild dogs, in which breeding females produce more offspring in larger groups but population dynamics show conventional density dependence (Mebane Jr and Sekhon 2011).

Dispersal patterns are consistent with a pattern of dominant control over female group membership and almost exclusive male immigration. Subordinate females jeopardize dominant reproductive success through infanticide (Young and Clutton-Brock 2006, Hodge et al. 2008), which dominants avoid by evicting potential same sex rivals (Stephens et al. 2005, Young et al. 2006), leading to increased eviction rates in larger groups (Clutton-Brock et al. 2008). There is some indication that dominant reproductive output levels-off at group sizes of 20 to 25 (Hodge et al. 2008) – the approximate stable group size (Figures 3.1, 3.4) – and female emigration is predicted to be under dominant control over most of the range of group size we observed (Stephens et al. 2005). Taken together, these suggest that dominant females use eviction to regulate group size in order to maximize their own reproductive success. Males, on the other hand, tend to emigrate of their own accord, but we would also expect male emigration to increase with group size, since larger groups can produce larger, more successful multi-male "coalitions" (Young et al. 2007) to seize dominance at neighbouring, typically small (Figure 3.3B) groups.

Dispersal processes have the ability to affect population dynamics beyond their direct contributions to group dynamics. Dispersers may join existing groups, form their own groups, or die before joining new groups. Over large spatial scales, the surrounding population may be heterogeneous, with group formation and augmentation rates varying accordingly. The average emigration rates that we observe are substantially higher than those of immigration (Figure 3.3). Combined with the fact that patterns of local population density closely correspond to group size dynamics (Lehmann and Rousset 2010, Bateman et al. in press) this suggests that group formation and extinction have reached an equilibrium, locally at least, and dispersers either die or leave the area. More work will be required to elucidate further consequences of dispersal.

The importance of rainfall in meerkat group dynamics is not surprising, but our results help clarify the effects. A number of studies have shown the positive effect of rainfall on breeding success (Doolan and Macdonald 1997, Clutton-Brock et al. 1999b, Hodge et al. 2008), likely mediated by rain's effect on food availability (Doolan and Macdonald 1997) and physical condition (English et al. 2011) and physical condition's effect on reproductive success (Doolan and Macdonald 1997, Hodge et al. 2008). The increase in apparent emigration after years of low rainfall (Figure 3.3D) is, however, the single aspect of demography with the largest effect on group dynamics (Table 3.3). This increase may be due to increased extra-group mortality rates that result from reduced physical condition in temporary female evictees and male prospectors. Alternatively, changes to group age structure may play a more important role. In a year of low rainfall, reproduction is limited (Figure 3.3A), increasing the proportion of subordinates above one year of age in the subsequent year. Because older subordinates are more likely to disperse and suffer eviction (Clutton-Brock et al. 2002, Clutton-Brock et al. 2008), such an effect could result in an increase in emigration rates after dry years. More detailed, age-specific analyses will be required to differentiate between these two scenarios.

3.5.4 Conclusions

In addition to the birth and death processes that regulate any population, group size in social species is regulated by immigration and emigration decisions on the part of individuals. The factors affecting these decisions vary: dominant female meerkats may control group sizes through eviction of subordinates at a cost to subordinate fitness (Stephens et al. 2005), while female lions remain in prides of a size that maximizes territory defensibility and reproductive success at the cost of foraging success (Packer et al. 1990, Mosser and Packer 2009, VanderWaal et al. 2009). Regardless, these behavioural decisions combine with birth and death processes to produce a stable group size and can lead to density dependence in groups similar to that observed in many non-social populations. Classic phenomenological population models, designed with birth and death in mind, were thus able to describe average meerkat group dynamics.

Our results modify our view of meerkat group dynamics. Past work has invoked an Allee effect to explain observed patterns of group dynamics, particularly the high rates of group extinction, especially of small groups, in bad years (Clutton-Brock et al. 1999b, Courchamp et al. 1999b). As previously noted (Clutton-Brock et al. 1999b), group growth rates are low (group size predictions are never far from the 1:1 lines in Figures 3.1 and 3.4), but the conventional density dependence we describe here likely explains past results. Given the stochastic nature of group dynamics and meerkats' susceptibility to environmental fluctuations, we would expect small groups to be prone to extinction, even if changes in mean group size are conventionally density dependent.

We have highlighted the importance of sub-population processes and the idea that those processes can display conflicting patterns, leading to non-intuitive dynamics. Allee effects may represent a case study for such dynamical complexity across species. Past evidence for an Allee effect in one aspect of meerkat demography lead to the assumption that group dynamics were inversely density dependent, but this now seems inaccurate. Given that meerkat group-level dynamics appear conventionally density dependent, it is unsurprising that an Allee effect has not been found in meerkat population-level dynamics (Bateman et al. 2011a). Although Allee effects have broad theoretical support (Courchamp et al. 2008) and have been sought across taxa, there are relatively few convincing population-wide examples (Myers et al. 1995, Gregory et al. 2010). In such a situation, with obvious implications for conservation and management decisions, it would be prudent to consider population dynamics in the context of population structure (Frank and Brickman 2000) and demographic sub-processes before drawing firm conclusions.

Our analysis of meerkat demography suggests that different drivers affect different demographic rates, but we ignored inter-individual variation in those rates. Because meerkats live in groups made up of multiple age and dominance classes, demographic rates (such as dispersal) differ among classes, and different drivers within each class could increase the impact of this class structure on dynamics (Coulson et al. 2008), future work will focus on incorporating class structure into our model

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Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*

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I designed the study, with input from A. Ozgul and T. Coulson; A, Ozgul, T. Coulson, and T. H. Clutton-Brock contributed to discussion; T. H. Clutton-Brock provided access to behavioural and life-history data; J. F. Nielsen performed genotyping and conducted genetic analyses; and I analysed all other data and wrote the paper.

4.1 Abstract

Population dynamics in group-living species can be strongly affected both by features of sociality per se and by resultant population structure. To develop a mechanistic understanding of population dynamics in highly social species, we need to investigate how processes within groups, processes linking groups, and external drivers act and interact to produce observed patterns. We model social group dynamics in cooperatively breeding meerkats, Suricata suricatta, paying attention to local demographic as well as dispersal processes. We use generalised additive models to describe the influence of group size, population density, and environmental conditions on demographic rates for each sex and stage, and we combine these models into predictive and individual-based simulation models of group dynamics. Shortterm predictions of expected group size and simulated group trajectories over the longer term agree well with observations. Group dynamics are characterized by slow increases during the breeding season and relatively sharp declines during the prebreeding season, particularly after dry years. We examine the demographic mechanisms responsible for environmental dependence. While individuals appear more prone to emigrate after dry years, seasons of low rainfall also cause reductions in reproductive output that produce adult-biased age distributions in the following dispersal season. Adult subordinates are much more likely to disperse or be evicted than immature individuals, and demographic structure thus contributes to crashes in group size. Our results demonstrate the role of social structure in characterizing a population's response to environmental variation. We discuss the implications of our findings for the population dynamics of cooperative breeders and population dynamics generally.

4.2 Introduction

Population dynamics of social, group-living species can differ markedly from those of solitary species comprising relatively homogeneous populations. Social structure *per se* can have dynamical consequences, such as thresholds for successful emigration or group persistence (Packer et al. 2005, Courchamp et al. 1999b), and group living also implies spatial structure, with associated complications relating to dispersal, regional synchrony, and population persistence (*e.g.* Hanski 1999). Although such structure does not guarantee atypical dynamics (Frank and Brickman 2000, Bateman et al. 2011a), the potential needs to be considered when examining the population dynamics of social species. Local processes, such as social interactions; broad-scale processes, such as dispersal; and external drivers, such as environmental conditions, can all play a role (Bjørnstad et al. 1999, Packer et al. 2005, Ozgul et al. 2009). To develop a mechanistic understanding of dynamics in a given population, we must ask how these processes act and interact to produce broader patterns.

Whereas studies of uniform populations can afford to focus, implicitly or explicitly, on changing population-wide rates of birth and death (*e.g.* Coulson et al. 2008), studies of socially structured populations must also consider local (group-level) dynamics and dispersal processes. Even the simplest metapopulation models reveal the potential importance of dispersal among habitat patches (Hanski 1999), and recent work has highlighted the important role that local dynamics play in the overall dynamics of group-living species (Packer et al. 2005, Ozgul et al. 2009).

Group dynamics and dispersal are, in fact, closely related. We can describe dispersal in three phases: emigration, transience, and immigration, of which two (emigration and immigration) are directly tied to groups where individuals must weigh information relating to resource availability, survival prospects, and reproductive potential (Bowler and Benton 2005). Immigration and emigration directly contribute to dynamics within groups, and within-group processes likely play a particularly important role in the dispersal of social species. Group conditions, through their influence on the costs and benefits associated with remaining in or leaving any group, are major determinants of dispersal – when and how individuals

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Chapter Four — Stage-structured Group Dynamics

emigrate from their natal group and where, or if, they join a new group – are affected by the social environments within those groups (Bowler and Benton 2005, Clutton Brock and Lukas 2011). Changes in group composition alter the social landscape, and thus the incentives surrounding dispersal. One sex is often philopatric, remaining in the natal group to breed, while the other sex emigrates to seek mating opportunities elsewhere (Clutton Brock and Lukas 2011), but the presence of kin may lead to kin competition or inclusive fitness benefits that select for or against different dispersal strategies in different situations (Bowler and Benton 2005).

Linked by emigration and subsequent immigration, or group formation, group dynamics combine to produce population dynamics. Thus, if we aim to understand what drives population-level patterns, we must first understand group-level patterns. Within groups, how do intrinsic demographic processes combine and interact with extrinsic drivers, such as fluctuations in environmental conditions, to produce group dynamics? Relative to other demographic rates, how does dispersal contribute to group dynamics, and how do group dynamics, in turn, affect dispersal? How do social structure and social interactions influence these processes?

Here, we report a detailed investigation of group dynamics in highly social meerkats, *Suricata suricatta*. Meerkats provide an excellent system in which to investigate social group dynamics: they are well-studied behaviourally, and detailed life history data, at fine temporal-resolution, exist for multiple groups over more than a decade of field study in a wild population. We use these data to construct an empirical model, with the aim of better understanding meerkats' group-level demography, the patterns of emigration and immigration linking groups, and how these processes influence each other and are influenced by highly stochastic environmental conditions.

Past work has shown that dispersal plays an important role in regulating meerkat group size and that sharp declines after dry years result from increased rates of emigration (Bateman et al. 2011b). It remains unclear, however, whether elevated rates of apparent emigration are due to an effect on per-capita rates after dry years (potentially including biases in detection, e.g. undetected mortality that mimics emigration resulting from reduced body condition) or whether they result from shifts in the age structure of groups (Bateman et al. 2011b). The model we describe here has been motivated in part by these observations.

Our model is spatially implicit, considering groups in a descriptive context of

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environmental and population conditions, and demographically explicit, modeling mortality, recruitment, immigration, and emigration in two-month timesteps as functions of intrinsic and extrinsic predictors. We treat different sex-, age-, and dominance-classes separately, allowing for different patterns in each component demographic rate. By incorporating finer temporal and demographic structure than used in previous models, we show how different processes are related seasonally and over the course of our study and clarify the relationships among environment, dispersal, and demographic structure in this social species. Specifically, we investigate the causes of declines in group size after dry years, assessing the contributions of elevated emigration rates *per se* and those that result from shifts in age structure within groups.

4.3 Study Species

Meerkats are arid-adapted social mongooses native to southern Africa. Living at approximate population densities of 7-17 individuals/km² (Bateman et al. 2011a), they form groups of up to 50 individuals. Seasonal rainfall strongly affects the regional ecology and thereby meerkat reproduction, survival, and overall population dynamics (Clutton-Brock et al. 1999a, Bateman et al. 2011a). Long-term rainfall (over the previous nine to ten months) is also a good predictor of meerkat body condition (English et al. 2011).

Dispersal shapes meerkat social structure and group dynamics. Females are considered philopatric, but in each social group a long-lived dominant pair produces the majority of offspring (Clutton-Brock et al. 2008, Sharp and Clutton-Brock 2010), and the dominant female, when pregnant, often evicts subordinate females – sometimes permanently – to suppress their reproduction and avoid infanticide (Clutton-Brock et al. 1998a, Clutton-Brock et al. 2008). Subordinate males engage in reproductive prospecting forays, and occasionally form "roving coalitions" that can seize dominance at other groups, often displacing resident males, or form new groups with unrelated female evictees (Doolan and Macdonald 1996b, Young 2003). As obligate cooperative breeders, subordinates of both sexes nonetheless assist in raising the closely related dominants' dependent offspring, thus accruing inclusive fitness benefits (Doolan and Macdonald 1996b, Clutton-Brock et al. 1999b). Although dispersal may lead to direct fitness benefits, the individual risks are high (Stephens et al. 2005), and it reduces group size and thereby the survival prospects of non-

dispersing kin (Clutton-Brock et al. 1999a, Bateman et al. 2011b).

Dominant females come into oestrus soon after giving birth and produce multiple litters, usually of one to seven pups, per year (Hodge et al. 2008). The breeding season peaks in January, to coincide with seasonal rains, and reaches a low in July (Clutton-Brock et al. 1999b). Gestation lasts for about 70 days (Young et al. 2006). Pups remain at the natal burrow for about 25 days after birth, attended by one or more older individuals while the rest of the group forages (Clutton-Brock et al. 2002). Females suckle pups for up to two months, but pups are nutritionally dependent on other group members until almost three months of age (Clutton-Brock et al. 1999b, Clutton-Brock et al. 2002). Individuals contribute little to cooperative activities until about six months, and are not sexually mature until about a year (Clutton-Brock et al. 2002).

As might be expected in the semi-arid regions of southern Africa, seasonal rainfall has a strong effect on meerkat population and group dynamics (Clutton-Brock et al. 1999a, Bateman et al. 2011a, Bateman et al. 2011b), a relationship that, at the group level, appears to be mediated largely by environment-dependent dispersal (Bateman et al. 2011b). Annual emigration rates increase markedly in large groups after years of low rainfall, but the mechanism remains unclear; individuals may fail to return from eviction or prospecting when they are in poor physical condition, or group composition may become biased towards mature individuals ready to disperse in the year after a poor reproductive season (Bateman et al. 2011b). Rainfall also appears to affect reproduction, reportedly by increasing the frequency of breeding and rate of pup survival rather than the size of litters (Doolan and Macdonald 1997, Clutton-Brock et al. 1999b, Hodge et al. 2008).

Group- and population-level density dependence affect meerkat demography (Clutton-Brock et al. 1999a, Clutton-Brock et al. 2008, Hodge et al. 2008, Bateman et al. 2011a, Bateman et al. 2011b). Evidence suggests that annual population-level dynamics, at least, are affected by population density (Bateman et al. 2011a), and group size has an effect on group-level dynamics as well as many life-history traits, including recruitment, survival, and dispersal rates (Clutton-Brock et al. 1999a, Clutton-Brock et al. 2008, Hodge et al. 2008, Bateman et al. 2011b).

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4.4 Methods

4.4.1 Data Collection

We used individual-based demographic data from a population of habituated, wild meerkats on and near the Kuruman River Reserve (26°58'S, 21°49'E), an area of ranchland near Van Zylsrus in the Northern Cape province of South Africa. Details pertaining to the site are available elsewhere (*e.g.* Clutton-Brock et al. 1999a). During weekly (and often daily) visits to meerkat social groups between January 1998 and December 2008, researchers collected detailed life-history records for individually marked meerkats (Clutton-Brock et al. 1998a, Clutton-Brock et al. 2008). These records detailed group composition and individual reproduction (including pup birth and survival), mortality, immigration, and emigration.

When multiple females are pregnant simultaneously in a group, usually only the last female to give birth produces a surviving litter, because she kills the pups of females that give birth earlier (hence dominant females' tendency to evict subordinates before reproduction; see Clutton-Brock et al. 1998a, Clutton-Brock et al. 2008). As a result, pups could usually be attributed to a specific female using behavioural data. In some instances, however, multiple females produced litters almost simultaneously, and pups could not be reliably attributed to one of them. In these cases, we relied on genetic maternity assignment. Tissue samples, taken from pups upon emergence and other individuals after anaesthetisation or death, were genotyped at up to 18 variable microsatellite loci (Nielsen et al. 2012). А combination of behavioural records and genetic data were used with two programs, Colony2 2.0.1.1 (Wang 2004) and MasterBayes 2.47 (Hadfield et al. 2006), to infer parentage for as many members of the population as possible. When assigning maternity for individual births, any females known to have given birth in the appropriate group at the appropriate time were considered candidate mothers, and the gestational status of females, dominance status, and group membership were used as phenotypic predictors in MasterBayes. Only assignments with at least 80% individual-level confidence were considered when combining the parentage inferences from both programs to generate a categorical pedigree (Nielsen et al. 2012). If genetic information was unavailable or ambiguous for a litter, we randomly assigned pups to the candidate mothers.
We often had reliable information regarding death and dispersal; emigrants were recorded in nearby groups, carcasses were found, and predation was observed. When an individual's fate was unclear, we used knowledge of meerkat behaviour (*e.g.* Clutton-Brock et al. 1998a, Clutton-Brock et al. 2002, Stephens et al. 2005) to assign the disappearance as either apparent emigration or apparent death. We deemed any disappearance in which an individual had shown signs of pre-dispersal in the month prior to be emigration, disappearance of a dominant individual to be death, multiple simultaneous same-sex disappearances to be group emigration, and all other disappearances to be deaths (Bateman et al. 2011b). Further references to death and emigration therefore refer to apparent death and apparent emigration, respectively.

To estimate population densities, we divided population-wide census counts by estimates of the population's geographic range. We estimated population range as the 95% confidence region from an empirical kernel utilization distribution (Worton 1989) fit to GPS sleeping burrow location data (collected by researchers during group visits) using a bivariate normal kernel and fixed smoothing parameter. Further details of GPS data collection and our estimation of population range are available elsewhere (see Bateman et al. 2011a).

We used rainfall data from the Global Precipitation Climatology Project Version 2.1 Combined Precipitation Dataset (an update of the version 2 dataset described in Adler et al. 2003). Raw data were monthly rainfall estimates on a 2.5° x 2.5° (latitude x longitude) grid, which we accessed from NASA's GES-DISC (the National Aeronautics and Space Administration's Goddard Earth Sciences Data and Information Services Center) Interactive Online Visualization ANd aNalysis Infrastructure (Giovanni; NASA 2009).

4.4.2 Model Overview

We extended the methods of Coulson *et al.* (2008), incorporating immigration and emigration in addition to natality and mortality, to model meerkat group dynamics. Broadly, this meant fitting functions to describe rates of immigration, emigration, juvenile recruitment, and mortality in discrete time windows and then combining these functions to predict group dynamics one timestep, or period, at a time. Because meerkats of different age, sex, or dominance status can exhibit extreme differences in relevant demographic rates (*e.g.* dominant females produce almost all pups), we fit separate demographic functions for different "classes" of meerkats, considering six classes in total: dominants, immature subordinates (<one year old), and adult subordinates (\geq one year old) for each of males and females.

We used two month observation periods, dividing the year into six sequential pairs of consecutive calendar months (January/February, March/April, May/June, July/August, September/October, and November/December). Two months is the approximate minimum interbirth interval for meerkats, and a longer window would have introduced the potential complication of single females producing multiple litters in one timestep, while too short a window would have resulted in extremely low demographic rate estimates.

For a detailed explanation of out modelling approach, see Appendix A. In short, we used generalised additive models (GAMS; Wood 2006) and informationtheoretic model selection to developed maximum-parsimony descriptions of recruitment (broken into the probability of litter production, litter size, and pup survival to recruitment), mortality, immigration, and emigration rates for each stage class in relation to time of year, group size, population density, current rainfall, and rainfall in the past ten months. We then combined the component rate models into an overall model of group dynamics to predict each group's expected size two months ahead.

4.4.3 Model Assessment

We used R^2 , the proportion of total variation in data explained by a model fit to those data, as an estimate of the explanatory ability of our final model (Coulson et al. 2008). We are aware that R^2 has its limitations, but with appropriate care R^2 provides a good measure of goodness of fit (Kvålseth 1985). See Appendix A for a detailed description of our R^2 calculations, relative to a trendless random walk model.

We also used R^2 to assess the explanatory ability of various aspects of the final model (Coulson et al. 2008). To do this, we used the relative decrease in R^2 from the full model to a reduced model, not including an aspect of interest, as an estimate of that aspects's contribution to the overall fit. In this way, we assessed contributions from the five predictor variables (by refitting the model without each variable in turn); age, sex, and dominance structure (for example, to assess the effect of including sexspecific models, we estimated demographic rates for each age-by-dominance class as the weighted mean of the appropriate sex-specific rates); and each demographic rate (by fixing the predicted rate at its observed mean). To investigate potential explanations for emigration-induced declines in group size following dry years (Bateman et al. 2011b), we also assessed the contributions of current rainfall, past rainfall, and age-structure through emigration alone.

4.4.4 Simulations

To place the final model's goodness of fit estimate in context and to visualise overall model behaviour, we adapted the predictive model into an individual-based simulation model and generated a set of 10,000 Monte Carlo simulated group trajectories. See Appendix A for further details.

4.4.5 Statistical Software

We performed all statistical analyses and simulations in R version 2.13.1 (R Development Core Team 2011). We used the *kernelUD* function from the *adehabitat* package (Calenge 2006) to estimate kernel utilization distributions, the *gam* function from the *mgcv* package (Wood 2006) to fit GAMs, and the *optim* function (from the *stats* package) for numerical optimisation.

4.5 Results

4.5.1 Data Series

We had data from a total of 32 groups, with between 5 and 15 (mean 11.8) groups under study at any one time. Group size ranged between 2 and 47 (mean 15.5) individuals, with periodic changes in group size somewhat synchronous, especially during major crashes in 2003 and 2007 and an apparent minor crash in 2001 (Figure 4.1A). Population density ranged between 5.2 and 17.1 (mean 10.7) individuals/km², following the same general trends as the observed group sizes (Figure 4.1A). Group density ranged between 0.5 and 0.9 (mean 0.7) groups/km².

The data included records for a total of 1205 individuals. There were 406 apparent deaths. 766 individuals apparently emigrated, compared to 155 individuals that joined existing groups and 105 individuals that founded new groups (including immigrants from outside the study population). 638 pregnancies resulted in 343 emergent litters with a total of 1256 pups, 1010 of which survived to recruitment age.



Figure 4.1: Observed initial meerkat group sizes (**A**, grey lines), meerkat study population density (**A**, black line), and rainfall (**B**) for two-month periods between January 1st 1998 and January 1st 2009 at the Kuruman River Reserve, South Africa. (**C**) shows 150 group trajectories simulated from the individual-based stochastic version of a meerkat group dynamics model. The model pseudorandomly simulated reproduction, mortality, immigration, and emigration in two-month timesteps based on generalized additive model characterizations of meerkat demographic rates, parameterized using field data. Each trajectory was seeded with one of five observed group compositions from the first half of 1998. *In reference to population density, "individuals" refers to individuals/km².

Rainfall was 90.4 \pm 49.5 (mean \pm standard deviation), 90.2 \pm 54.4, 14.7 \pm 14.0, 2.3 \pm 2.3, 29.3 \pm 13.4, and 70.2 \pm 37.6 in January/February, March/April, May/June, July/August, September/October, and November/December, respectively (Figure 4.1B), and ten-month rainfall averaged 203.2 \pm 74.2, 202.3 \pm 76.6, 279.7 \pm 96.8, 292.0 \pm 100.7, 264.1 \pm 101.4, and 227.0 \pm 83.3 for the same periods. Rainfall reached lows in the 2002/2003 and 2006/2007 rainy seasons, just before major reductions in group-size (Figure 4.1B).

4.5.2 Component Rate Models

As with any modelling exercise, the design and selection of our component rate models involved trade-offs. Our aim was not to provide definitive descriptions of our system, but to identify key relationships - the most parsimonious descriptions at our disposal. We do not attempt to draw specific conclusions about the precision of individual parameter estimates; instead we discuss strong trends and take a relatively holistic view of the "best" models.

Reproduction showed two main trends: subordinate females reproduced far less than dominants (Table 4.B1, Figure 4.2), mainly due to a lack of litter production rather than reduced litter size or pup survival, and reproduction was severely reduced

in dry years (Figures 4.3, 4.B7-4.B10), again due to reductions in litter production. Litter production generally peaked in January and reached a low in July but increased with short-term rainfall and occurred throughout the year if conditions were wet (Figures 4.B7-4.B10); litter production all but ceased in off-peak months when conditions were dry, but dominants tended to produce January litters regardless of rain (Figure 4.B7). Extremes in ten months' total rainfall reduced the probability of litter production, with dry conditions in the ten months prior to July particularly detrimental (Figures 4.B7, 4.B8). Dominant females produced more litters in large groups, while the reverse was true (per capita) for subordinates (Figures 4.B7, 4.B8). The mean litter sizes (for litters of at least one emergent pup) were 3.82 for dominants and 3.29 for subordinates. Pup survival for dominant female litters peaked around January in slightly wetter than average conditions (both just after birth and in the preceding ten months), while pup survival for subordinate litters benefited from increased rainfall in the relevant period and varied little with season. All pups were most likely to reach recruitment age in groups of slightly more than twenty individuals (Figures 4.B9, 4.B10).



Figure 4.2: Factors effecting crashes in meerkat group sizes. Reduced rates of reproduction (A) in dominant females (solid line) after relatively dry rainy seasons (reproduction in subordinates – dashed line – is consistently low) contribute to adult-biased age structure (B) in subordinate females (solid line) and males (dashed line). This combines with patterns of emigration in subordinate females (C) and males (D) – emigration rates are much higher in adults (solid lines) than in immature individuals (dashed lines) and increase following dry conditions – to bring about large emigration events. Hatched and solid grey regions show the ranges, across observed group sizes, of mean model predictions corresponding to solid and dashed population-mean observations, respectively.



Figure 4.3: Demography of a single meerkat group between January 1st 1998 and January 1st 2009. Lines show observations (grey) and generalized additive model expectations (black) for recruitment (A), mortality (B), immigration (C), and emigration (D) during two-month periods. The resultant changes in group size (E) relate group size at the start of each period (F) to group size at the start of the next period (the model relates each group size observation to a single subsequent prediction).

Rates of within-group mortality were very low (Figure 4.3). For most classes, mortality was highest in the dry season, but dominant males also tended to die in the wet season if conditions in the previous ten months had been dry, and seasonal effects were less apparent in females (Figures 4.B1-4.B6). The effects of rain and population density varied across demographic classes, but individuals in larger groups consistently enjoyed reduced mortality (Figures 4.B1-4.B6).

Rates of emigration generally peaked between July and September, and were much higher for subordinate adults than for other meerkat classes (Table 4.B1, Figures 4.2, 4.B11-4.B15). For adult subordinates, emigration was similar for both sexes, tending to occur most in September from large groups when conditions had been dry in the past ten months or when conditions were relatively wet (Figures 4.B13, 4.B15). For adult subordinate females, however, emigration was rare in wet conditions after the past ten months had been dry and at high population densities.

Male-only immigration into established groups also peaked between July and September, but increased with rain in a given period and was highest when rain in the previous ten months was slightly above average Figure 4.B16). Absolute rates of immigration declined initially with group size, reaching a minimum for groups of just over twenty, and increasing thereafter; however, the equivalent per-capita rates of immigration were maximised in small groups and remained consistently low for groups of more than ten individuals (Figure 4.B16). The negative binomial shape parameter for the distribution of immigration in a given period was 0.086, producing a heavily right-skewed distribution with mode at zero.

Rates of recruitment and immigration showed higher levels of stochastic noise, relative to mean model predictions, than did rates of mortality and, in particular, emigration. For immigration, this was due to the considerable aggregation, but rarity, of the process. For recruitment, it was due to the fact that a single dominant female, either breeding or not breeding, was responsible for most reproduction within each group; reproductive models combined to predict intermediate but sustained levels of recruitment throughout the breeding season, but large litters produced an abundance of pups while failures to breed produced none, and both were common (Figure 4.3). On the other hand, emigration tended to occur in more concentrated bursts across more individuals, leading to less stochasticity on average (Figure 4.3).

4.5.3 Crash Dynamics

The abrupt decreases in group size seen in "crash" years (Figure 4.1A,C) were due to a combination of recruitment and emigration processes, partially mediated by changes in group composition. Three factors - current rainfall, past rainfall, and changes in age structure - contributed substantially to the model's ability to describe these environment-dependent patterns of emigration (10%, 14%, and 9%, respectively, overall contributions to the models explanatory ability; Table 4.B2). Litter production all but ceased in dry conditions (except at the peak of the breeding season; Figure 4.B7), and recruitment, especially in the periods surrounding the usual July/August low season, therefore suffered after dry years (Figure 4.2A). Emigration also fell during the usual season in dry years (Figures 4.B13, 4.B15). These effects led to an increase in the ratio of adult to immature subordinates in the following emigration season (Figure 4.2B). Per-capita emigration rates were elevated after low-rainfall years, and the emigration rates of adult subordinates were much higher than those of immature subordinates (Figure 4.2C,D). When paired with the changes in subordinate age structure, this led to sharp declines in group size.

4.5.4 Predictive Model

Combining the component rate models into an overall model to predict each group's expected size two months ahead explained about 40% of the observed variation in group size (Table 4.B2). Of the explanatory variables considered, seasonality accounted for 60% of the model's overall explanatory ability, current and past rain each accounted for 15%, and group size, followed by population density, accounted for most of the rest (Table 4.B2). Taken together, demographic structure (allowing for different demographic rates across meerkat classes) accounted for almost 30% of the model's explanatory ability, with dominance structure responsible for the most (Table 4.B2). Of the various demographic rate models, those of emigration accounted for two thirds of the explanatory ability of litter production) accounting for almost a fifth of the overall explanatory ability; immigration and mortality models accounted for relatively little (Table 4.B2).

4.5.5 Individual-based Simulations

As a set, the individual-based simulations of group dynamics captured observed patterns well (Figure 4.1C). Simulated dynamics corresponded with observed annual patterns and past models of annual dynamics; in particular, the simulations reproduced the major crashes in 2003 and 2007, as well as the minor crash in 2001, and the intervening periods of growth and relative stability (Figures 4.1C, 4.B17, 4.B18, Bateman et al. 2011b). Simulated groups also generally displayed appropriate patterns of seasonal growth and decline, tending to grow moderately from January through June and crash or remain relatively static (depending on year) from July through December (Figure 4.B17). Model fits for empirical group trajectories were statistically similar to model fits for model-simulated trajectories (Figure 4.B19).

4.6 Discussion

Our model shows that meerkat group size dynamics are governed primarily by reproduction and emigration. On average, groups increase moderately between January and July (Figure 4.B17A) due mainly to production of recruits by the dominant female. From July to January recruits are produced at lower numbers, and group size tends to decrease (Figure 4.B17B) as a result of emigration, especially in

large groups if the past rainy season was relatively dry. This model provides detail at a much finer temporal resolution than past models (Bateman et al. 2011b) and allows us to investigate the role of social structure on group dynamics.

In particular, our model provides detail surrounding the social and environmental mechanisms behind declines in group size following low-rainfall years. Sharp declines in the size of large groups after dry rainy seasons are due partially to the effect of rain on stage-specific dispersal rates, but also to rainfall's effects on reproduction, subsequent shifts towards older age-structure, and differences in agedependent dispersal rates. Reduced rates of reproduction in dry years lead to relative declines of non-dispersive immature individuals within groups, and, as a result, group-wide per-capita rates of emigration increase in the following dispersal seasons. Thus, although we can attribute less of our model's short-term explanatory ability to recruitment than to emigration (Table 4.B2), we see that the former is integral in explaining trends in group dynamics, and the model's realistic simulated dynamics over the longer term support this.

Past work was only able to identify elevated average emigration rates after dry years (Bateman et al. 2011b), leaving the question of mechanism entirely unanswered. Rather than ruling out one of the potential explanations for group-size declines following dry years (Bateman et al. 2011b), our model reveals a system in which demographic shifts and rain-related changes in behaviour both appear to be important.

4.6.1 Model Performance

The model provided a good description of dynamics in a socially complex and environmentally variable system. The component rate models described the major contributing rates (recruitment and emigration) well at the population level (Figure 4.2), and emigration predictions closely matched observations at the group level, but recruitment within each group proved more difficult to capture (Figure 4.3). Because most reproductive events produced multiple recruits, small errors in predicting litter production led to larger errors in predicting the number of recruits in any period. Nevertheless, the overall model's predictions matched observed patterns of change (e.g. Figure 4.3E) and explained more than 40% of the observed variation in group size.

Individual-based simulation confirmed the ability of the model to match observed patterns over longer timescales. Simulated group dynamics qualitatively matched observed group dynamics (Figures 4.1C, 4.B17, 4.B18), with year-by-year patterns in the set of simulated trajectories matching those from the set of real groups, including group-size crashes after particularly low-rainfall years (compare Figure 4.1A and 4.1C). The simulations also provided a description of average annual dynamics in relation to past rainfall that is very similar to that provided by classical phenomenological population dynamics models (compare Figure 4.B18 to Figures 1 and 4 in Bateman et al. 2011b).

We note that, because of our constrained definition of a group (at least one female present), we were forced to abandon simulated groups that became all-male. This mirrors practice in the field, but does not explicitly account for the formation of what are, in effect, large cohorts of male dispersers. Something similar holds for all-female groups, which we did follow in our simulations, but which effectively represent large cohorts of female dispersers.

4.6.2 Group-level Implications

Group size plays an important role in the frequency with which dominant females evict subordinates and the frequency with which subordinates disperse. Though the likelihood that a dominant female reproduces increases with group size, it increases little once her group surpasses thirty individuals, and the survival prospects of her pups appear to suffer in large groups (Figure 4.B7, Hodge et al. 2008). Large groups are also more likely to produce large cohorts of emigrant females, which are better able to form new groups (Young 2003). Thus, although female group membership is thought to be largely under dominant control, it appears to be in the interests of both dominants and subordinates that emigration should increase in larger groups (Young 2003, Stephens et al. 2005), and the propensity of subordinate females to emigrate could explain paradoxically low rates of challenges to the status of dominant females (Sharp and Clutton-Brock 2011).

High rainfall in a given period and low rainfall in the preceding ten months are both associated with relatively high rates of subordinate emigration in both sexes. The former corresponds to favourable current conditions while the latter is associated with poor physical condition in meerkats (English et al. 2011). Females disperse either to establish new groups or because they fail to return to their group after being forced out by the dominant female, in her effort to avoid reproductive conflict and infanticide (Clutton-Brock et al. 1998a, Stephens et al. 2005, Clutton-Brock et al.

2008). Notably, female emigration is reduced in dry years, at precisely the same time that dominant litter production suffers and reproductive conflict is thus at a minimum (Clutton-Brock et al. 1998a, Clutton-Brock et al. 2010). Males disperse to establish new groups and to find extra-group mating opportunities (Doolan and Macdonald 1996b, Young 2003). Both eviction for females and prospecting for males are physiologically costly, stressful events (Young 2003, Young et al. 2006, Young and Monfort 2009). While favourable environmental conditions are likely to give rise to group formation attempts, poor physical condition, combined with high levels of physiological stress, is likely to be associated with elevated extra-group mortality rates that show up here as increased rates of apparent emigration. The lack of apparent adult subordinate female emigration in wet conditions after dry periods could be due to those females being in too poor a condition to emigrate successfully but having access to sufficient resources to avoid eviction-related mortality.

Our approach was good at predicting the timing and population-wide mean levels of male-only immigration but unable to accurately predict group-specific immigration. Occasionally, when immigrant males expelled resident males, this led to errors in the prediction of emigration as well (*e.g.* Figure 4.3C,D). Our inability to precisely predict immigration was largely due to the fact that male immigration is rare and clustered (*i.e.* males tend to immigrate in groups). Future attempts to investigate the effects of immigration may, therefore, be best served by simulation-based approaches in place of assessment of mean rates.

4.6.3 Population-level Implications

Although we did not explicitly consider population-level dynamics in our model, they appear to be closely tied to group dynamics (Figure 4.1A), and population density closely parallels median group size. If this pattern persists beyond our study population, it would suggest that group territories, in size at least, are relatively stable, and that the population-level response to favourable conditions is largely an increase in density through group augmentation. Aggressive interactions between meerkat groups are common, with large groups often chasing smaller groups out of their range (Young 2003), and this probably hinders new group formation under otherwise favourable conditions. High population density does appear to inhibit adult subordinate female emigration; in a saturated local environment, group-establishment prospects would be limited, and dispersal would provide little benefit at high cost.

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Group turnover does occur, however, and few of the groups we followed were present for the duration of the study. Some moved out of the study area, but others disbanded or died out. Not surprisingly, the few groups we observed to collapse entirely were small (although this appears to be due to stochasticity rather than inverse density dependence – Allee effects; Bateman et al. 2011b), and their collapses generally coincided with low-rainfall years or emigration-mediated declines in group size (Figures 4.1, 4.B18).

As large emigration events directly precede the rainy season, group formation resulting from dispersal would be well-timed to take advantage of favourable conditions. After crash years, newly formed groups might be better able to compete with reduced existing groups or take over territory from groups that perished, and this might contribute to increased rates of apparent emigration after dry years. It also suggests that dispersal in poor years, even if it puts some groups at risk, may facilitate population recovery after periods of decline.

Although not strictly equivalent, the meerkat system resembles a metapopulation and, given the patterns of demography and dispersal, presents the potential for source-sink dynamics (Hanski 1999). Large groups appear to act as sources, their emigrants able to augment other groups and colonise empty habitat patches or regions of marginal habitat (collectively sinks). These sinks, in turn, could have an important stabilising effect on the population of source groups, which are both intrinsically stochastic and susceptible to extrinsic environmental stochasticity (Hanski 1999). Given the location of our study population, in what seems to be meerkats' preferred territory (along a dry riverbed; Clutton-Brock et al. 1999b) surrounded by marginal habitat, the potential for interesting local and regional source-sink dynamics certainly exists.

Male dispersal behaviour has the potential to strongly affect population dynamics. Because resident males are sometimes forced to emigrate when foreigngroup males move in, single dispersal events potentially have knock-on effects population-wide. Immigration events appear to be able to spur even larger, otherwise unpredicted emigration events (*e.g.* Figure 4.3C,D). Groups thus reduced in size might be less able to defend territories, shifting otherwise stable patterns (see above). Pre-dispersal behaviour may also affect population dynamics: past work indicates that group interactions may drive male prospecting behaviour and affect disease transmission (Doolan and Macdonald 1996b, Drewe et al. 2009b).

4.6.4 Broader Implications

For meerkats, environmental fluctuations alter stage structure across groups, contributing to observed dynamical patterns. Past work has shown that differentially stage-structured populations of the same size can respond differently under identical conditions (Coulson et al. 2001) and that stage structure has implications for the dynamics of disease, invasion, and at-risk populations (Fulford et al. 2002, Koons et al. 2005, Miller and Tenhumberg 2010). There is growing consensus that investigations of stage-structured populations relying on characterizations of asymptotic dynamics provide limited insight into the behaviour of those populations under conditions of interest (Koons et al. 2005, Ozgul et al. 2009, Miller and Tenhumberg 2010).

Spatial and social structure add complexity to the investigation of population dynamics and can affect population responses to given sets of conditions (Packer et al. 2005, Ozgul et al. 2009). Local processes combine to produce population-wide patterns, but the relationships are not always simple, and when local conditions affect per-capita demography, observed dynamics can differ markedly from population mean predictions (Morales et al. 2010). Even in relatively simple systems, large-scale dynamics can be difficult to explain based on local dynamics (Hanski and Meyke 2005). Here, however, we have a socially complex species for which observed group dynamics, though exhibiting stochastic noise, are closely correlated and match patterns of change in local population density (although population density seems to decline slightly just before sharp declines in group size; Figure 4.1A).

4.6.5 Conclusion

By considering the effects of social and environmental factors on contributions to group dynamics at fine temporal resolution, we were able to describe the mechanisms by which environmental conditions control group size in meerkats. Climatic variation influences dispersal behaviour and leads to changes in groups' demographic structure, producing lagged changes in group size. Our detection of this mechanism relied on an integrated modeling approach that considered stagestructured demography at a fine timescale.

Population dynamics in socially structured populations are the result of both within-group and among-group processes. In reality, the two processes are intimately tied to one another, and in order to improve our understanding of spatially structured

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population dynamics, we must work towards integrated models that consider both in concert (Bowler and Benton 2005). The dispersal-related processes that we identified as important to meerkat group dynamics are also the processes that have the largest potential effect on population-level dynamics, and future work will focus on the connections among group dynamics, inter-group movement, group formation, and population-level dynamics.

4.A Appendix A: Details of model formulation and assessment

4.A.1 Combining Demographic Rates

For a group of size n_t at the beginning of any observation period, t, we can calculate the group's size at the beginning of the next period by accounting for observed recruitment of juveniles, r_t ; mortality, m_t ; immigration, i_t ; and emigration, e_t , in period t:

$$n_{t+1} = n_t + r_t - m_t + i_t - e_t.$$
(4.A1)

Allowing for different rates in each class, c, we get

$$n_{t+1} = n_t + \sum_{all \ c} \left(r_{c,t} - m_{c,t} + i_{c,t} - e_{c,t} \right).$$
(4.A2)

Now, if we treat n_{t+1} as the value of a random variable, N_{t+1} , that has yet to be observed by the beginning of period *t* (and do similar for each demographic rate in period *t*), we can take the expectation across all possible values of N_{t+1} to get

$$\mathbf{E}(N_{t+1}) = n_t + \sum_{all c} \left[\mathbf{E}(R_{c,t}) - \mathbf{E}(M_{c,t}) + \mathbf{E}(I_{c,t}) - \mathbf{E}(E_{c,t}) \right].$$
(4.A3)

In this context, we use the convention that an uppercase Latin character represents a random variable, while the corresponding lowercase character represents an observed value of that random variable.

We assumed it possible to describe the expected value of each component rate from (4.A3) using a smooth function of local conditions (usually) in period *t*:

$$\mathbf{E}(RATE_{c,t}) = f_{RATE_c}(\mathbf{X}_t), \qquad (4.A4)$$

where $\mathbf{X}_{t} = \{x_{1,t}, x_{2,t}, ..., x_{k,t}\}$ is the set of relevant conditions in period *t*. To estimate functions for the expected demographic rates, we used generalized additive models (GAMs) fit to demographic data corresponding to the appropriate two-month windows. A GAM fits additive combinations of linear and nonlinear functions of given predictor variables to achieve a parsimonious description, via a link function, of

a univariate response variable (see Wood 2006). We fit each GAM using data available from all groups throughout the course of our study.

The predictors we considered for each demographic rate included both intrinsic and extrinsic variables. We included group size, measured as the number of group members older than two months (recruitment age – see below), to assess grouplevel density dependence, and we included population density, measured as meerkats per square kilometre across the study population, to assess population-level density dependence. To assess annual patterns in demographic rates we included season, as indicated by the two-month time period, which, though technically a discrete-valued measure, we considered as a continuous variable to avoid overly flexible models. Finally, we included rainfall in a given two-month period and, separately, rainfall in the preceding ten months, both measured as deviations (standardised by the seasonspecific standard deviations) from the appropriate seasonal averages taken over the course of the study.

Given the potentially important predictor variables, we used an informationtheoretic approach to select the most parsimonious model from a candidate set of plausible models. We developed the candidate model set (Table A1) to include models that incorporated reasonable combinations of smooths of the predictor variables and their two-way interactions (fit as tensor product smooths; Wood 2006). After fitting each GAM, we used Akaike's Information Criterion (for AIC in the context of GAMs, see Wood 2006) to compare the models and adopted the minimum-AIC model for future use. In fitting the models, we used a cyclic cubic spline basis for season and a standard cubic spline basis for all other predictors; three knot locations for each predictor except season, for which we used four knot locations to allow more reasonable cyclic smooths; and a degrees-of-freedom inflation factor (the gamma argument of the fitting function – see *Statistical Software*) of 1.4, to avoid overly flexible smooths (Wood 2006).

We used a similar generalized additive modelling approach for part or all of each component demographic rate. Unless otherwise specified, we fit GAMs to percapita demographic rates (see below), using a binomial error structure with a logit link function. Because each component demographic rate has slightly different properties, however, the details of our approach differed slightly for each.

4.A.2 Recruitment

We treated the number of juveniles recruited as the result of a multi-step process dependant on litter production (by dominant or adult subordinate females only), the size of any litter produced, and pup survival to recruitment age (Kendall and Wittmann 2010). We assumed that each female of class c gave birth to an emergent litter in period t-1 with probability $E(B_{c,t-1})$, that litter size for mothers of class c followed a zero-truncated generalized Poisson distribution (Kendall and Wittmann 2010) with expectation $E(L_c)$, and that pups born to a mother of class c in period t-1 survived to at least recruitment age to be counted at the start of period t+1with probability $E(S_{ct})$. The generalized Poisson distribution has been proposed for modelling litter sizes, because it avoids attributing likelihood to excessively large litters, and truncating (and rescaling) the distribution to omit zero allowed the probability of a litter of size zero to be incorporated into the litter-production stage (Kendall and Wittmann 2010). We set recruitment age to two months, which meant that pups born in period t-1 reached recruitment age in period t and were counted as group members at the beginning of period t+1 at between two and four months of age (three months – the midpoint of this range – is the approximate age of nutritional independence for meerkats; Clutton-Brock et al. 2002). Under the above conditions, the expected per-capita recruitment attributable to a female of class c in period tbecomes (Kendall and Wittmann 2010)

$$\mathbf{E}\left(\overline{R}_{c,t}\right) = \mathbf{E}\left(B_{c,t-1}\right) \cdot \mathbf{E}\left(L_{c}\right) \cdot \mathbf{E}\left(S_{c,t}\right)$$
(4.A5)

for dominant and adult subordinate females and zero otherwise. Expected recruit production for a class of size $n_{c,t}$ at the beginning of period *t* is therefore

$$\mathbf{E}(\boldsymbol{R}_{c,t}) = \boldsymbol{n}_{c,t} \cdot \mathbf{E}(\boldsymbol{B}_{c,t-1}) \cdot \mathbf{E}(\boldsymbol{L}_{c}) \cdot \mathbf{E}(\boldsymbol{S}_{c,t}).$$
(4.A6)

We modelled expected pup survival, $E(S_{c,t})$, according to the standard approach described above, using a GAM incorporating smooths of local conditions in period *t*, but we treated expected litter production, $E(B_{c,t-1})$, and expected litter size, $E(L_c)$, differently. We assumed that expected litter production depended on local conditions in period *t*-2 rather than period *t*-1, because gestation in meerkats is approximately 70 days (Clutton-Brock et al. 2008), and pups born in period *t*-1 were, therefore, most commonly conceived in period *t*-2. The model forms we fit for litter production were identical to the standard GAM model forms, except that they incorporated predictor variable from period *t*-2 rather than period *t*. For expected litter size, we fit one truncated generalized Poisson distribution to the observed litter sizes for each reproductive class of females. To do this, we used numerical optimisation to find the distribution parameter values that maximised the total log likelihood of the appropriate observed litter sizes across time periods. This allowed us to use the appropriate distribution, at the cost of excluding covariate predictors.

4.A.3 Mortality and Emigration

We used our standard GAM approach to model expected per-capita rates of emigration and mortality, $E(\overline{E}_{c,t})$ and $E(\overline{M}_{c,t})$, respectively, so that the expected rates of class-specific emigration and mortality took similar forms:

$$E(E_{c,t}) = n_{c,t} \cdot E(\overline{E}_{c,t}), \text{ and}$$

$$E(M_{c,t}) = n_{c,t} \cdot E(\overline{M}_{c,t}).$$
(4.A7)

Dominant female emigration is almost never observed, so we made the assumption that it does not occur and did not include it in our models. Although resident males may disperse when immigrants arrive (Doolan and Macdonald 1996b, Young 2003), the associated close temporal correlation meant we were unable to include the effect in our models.

4.A.4 Immigration

Unlike the other rates, immigration in period t is not readily attributable to any individuals present at the beginning of the period, and we observe immigration almost exclusively in adult males. We therefore modelled expected immigration not as a percapita rate but as the mean of a count variable. Because immigration commonly occurs when "coalitions" of males join a group (Doolan and Macdonald 1996b, Young 2003), we assumed the number of immigrants to be distributed negative-binomially, to allow for aggregation (overdispersion relative to a Poisson random variable). We used the standard candidate model set, but with a negative binomial error structure and natural log link, and fit the negative binomial shape parameter using outer iteration (Wood 2006).

4.A.5 Final Model

The final model took the form:

$$\mathbf{E}(N_{t+1}) = n_t + \sum_{all \ c} n_{c,t} \cdot \left[\mathbf{E}(B_{c,t-1}) \cdot \mathbf{E}(L_c) \cdot \mathbf{E}(S_{c,t}) - \mathbf{E}(M_{c,t}) - \mathbf{E}(E_{c,t}) \right] + \mathbf{E}(I_t)$$

$$= n_t + \sum_{all \ c} n_{c,t} \cdot \left[f_{B_{c,t-1}}(\mathbf{X}_{t-2}) \cdot \mathbf{E}(L_c) \cdot f_{S_{c,t}}(\mathbf{X}_t) - f_{M_{c,t}}(\mathbf{X}_t) - f_{E_{c,t}}(\mathbf{X}_t) \right] + f_I(\mathbf{X}_t).$$

$$(4.A8)$$

Within this final model, each function, f, was the maximum-parsimony GAM from the appropriate candidate model set.

4.A.6 Calculation of R^2

We calculated \mathbb{R}^2 based on predicted and observed group sizes, taking total sum of squares to be $\sum_{\text{all groups},t} [n_{t+1} - \mathbb{E}_{null}(N_{t+1})]^2$, where $\mathbb{E}_{null}(N_{t+1})$ is the expected value of N_{t+1} under the null model. In (4), we implicitly treated each observed demographic rate in (2) as the value of a function, *f*, plus error, ε :

$$rate_{c,t} = f_{RATE_c}\left(\mathbf{X}_t\right) + \varepsilon_{rate_{c,t}}, \qquad (4.A9)$$

so that

$$n_{t+1} = \mathbf{E}(N_{t+1}) + \sum_{all \ rates, c} \varepsilon_{rate_{c,t}} .$$
(4.A10)

Given the high quality of the data involved (in each two-month timestep we have near-perfect knowledge of each group's composition), we make the simplifying assumption that deviations of n_{t+1} from $E(N_{t+1})$ represent process error only. For a population dynamics model with pure process error, the appropriate null model is a random walk, so that $E_{null}(N_{t+1}) = n_t$ and total sum of squares $= \sum_{\text{all groups}, t} [n_{t+1} - n_t]^2$.

4.A.7 Monte Carlo Simulations

We initially seeded 2,000 trajectories with the conditions from the first three timesteps for each of five groups present at the beginning of the study. To attain each group trajectory, we used the final models for each component demographic rate, with their associated error distributions, to simulate individual recruitment, mortality, immigration, and emigration within a group, and thereby group dynamics, in twomonth timesteps over the course of the study period. To simulate any individual demographic rate for a given timestep, we made a pseudorandom draw from the distribution defined by the appropriate model's predicted mean and error structure, taking group sizes from the simulation data but all other predictor variables from the true population values for the given timestep.

While the demographic rate models defined the probabilities associated with rates in each timestep, we needed additional rules and assumptions to produce a functional individual-based model. As we defined them, the probabilities of mortality and emigration were mutually exclusive; therefore we determined whether each individual of class *c* remained in its group in timestep *t* by drawing from a single binomial distribution with P(death or emigration) = P(death) + P(emigration) = $E(\overline{M}_{c,t}) + E(\overline{E}_{c,t})$. We drew the ages of immigrants from the distribution of immigrant ages observed across all groups in the field data. We kept track of each simulated individual's age throughout the course of the simulations, advancing its age class as appropriate. When a dominant individual died (or a dominant male emigrated), we "promoted" the oldest same-sex individual within the group. We assigned pup sex stochastically, with a 50% chance of each sex. We stopped simulating a group's trajectory when its group size fell below two or it contained only males (since our assumptions about demography did not allow for female influx in such a situation).

Once simulation was complete for a group trajectory, we used the predictive model to calculate the expected group size for each period, given the simulated conditions for the previous periods. With this information, we calculated 10,000 R^2 values (one for each trajectory), representing the distribution of goodness of fit when the model was used to predict the individual-based stochastic version of itself.

Table 4.A1: Candidate model set for generalized additive models. S = two-month "season" of period t^* , R2 = normalized rainfall in period t (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period t (relative to the long-term seasonal mean), GS = group size at the start of period t, PD = estimated population density for period t; s() indicates a cubic regression spline smooth of a single variable, while te() indicates a tensor product smooth of two variables using cubic regression spline bases[†].

model ID	model form for $f_{RATE_{et}}^{\ddagger}$		
1	s(S)		
2	te(S,R2)		
3	te(S,R10)		
4	te(S,R2) + te(S,R10)		
5	te(S,R2) + te(S,R10) + te(R2,R10)		
6	s(S) + s(GS)		
7	te(S,R2) + s(GS)		
8	te(S,R10) + s(GS)		
9	te(S,R2) + te(S,R10) + s(GS)		
10	te(S,R2) + te(S,R10) + te(R2,R10) + s(GS)		
11	te(S,GS)		
12	te(S,R2) + te(S,GS)		
13	te(S,R10) + te(S,GS)		
14	te(S,R2) + te(S,R10) + te(S,GS)		
15	te(S,R2) + te(S,R10) + te(R2,R10) + te(S,GS)		
16	te(S,GS) + te(R2,GS)		
17	te(S,R2) + te(S,GS) + te(R2,GS)		
18	te(S,R2) + te(S,R10) + te(S,GS) + te(R2,GS)		
19	te(S,R2) + te(S,R10) + te(R2,R10) + te(S,GS) + te(R2,GS)		
20	s(S) + te(GS,PD)		
21	te(S,R2) + te(GS,PD)		
22	te(S,R10) + te(GS,PD)		
23	te(S,R2) + te(S,R10) + te(GS,PD)		
24	te(S,R2) + te(S,R10) + te(R2,R10) + te(GS,PD)		
25	te(GS,PD) + te(S,GS)		
26	te(S,R2) + te(GS,PD) + te(S,GS)		
27	te(S,R10) + te(GS,PD) + te(S,GS)		
28	te(S,R2) + te(S,R10) + te(GS,PD) + te(S,GS)		
29	te(S,R2) + te(S,R10) + te(R2,R10) + te(GS,PD) + te(S,GS)		
30	te(GS,PD) + te(S,GS) + te(R2,GS)		
31	te(S,R2) + te(GS,PD) + te(S,GS) + te(R2,GS)		
32	te(S,R2) + te(S,R10) + te(GS,PD) + te(S,GS) + te(R2,GS)		
33	te(S,R2) + te(S,R10) + te(R2,R10) + te(GS,PD) + te(S,GS) + te(R2,GS)		

*Models for litter production incorporated conditions from period *t*-2 instead of period *t* (see text). † All smooths of season used cyclic cubic regression spline bases.

[‡]As the smooth components of GAMs are, by default, centred, each model also includes a constant parameter, omitted here for brevity.

4.B Appendix B: Details of final model, submodels, and simulations

Table 4.B1: Maximum parsimony generalised additive model forms used to describe demographic rates for different meerkat classes. The forms given describe the linear predictor of each generalised model. S = two-month "season" of period *t*, R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*, PD = estimated population density for period *t*.

demographic rate	meerkat class	maximum parsimony model form
	dominant females	$-3.02 + f(S,R10)_{df=1.3} + f(GS)_{df=1.0}$
	adult subordinate females	$-3.59 + f(S,R2)_{df=2.3} + f(S,GS)_{df=0.8} +$
		$f(R2,GS)_{df=1.6}$
moutolity	immature subordinate females	$-3.48 + f(S,R2)_{df=1.7} + f(S,R10)_{df=0.1} +$
		$f(R2,R10)_{df=0.0} + f(S,GS)_{df=0.0} +$
		$f(R2,GS)_{df=0.7}$
	dominant males	$-3.39 + f(S,R2)_{df=1.0} + f(S,R10)_{df=2.8} +$
mortanty		$f(GS,PD)_{df=4.0} + f(S,GS)_{df=0.6} +$
		$f(\mathbf{R2,GS})_{df=0.7}$
	adult subordinate males	$-3.97 + f(S,R2)_{df=3.2} + f(S,R10)_{df=0.6} +$
		$f(GS,PD)_{df=3.8} + f(S,GS)_{df=0.5}$
	immature subordinate males	$-3.63 + f(S,R2)_{df=3.9} + f(S,R10)_{df=0.8} +$
		$f(R2,R10)_{df=0.6} + f(GS,PD)_{df=3.0} +$
		$f(S,GS)_{df=0.0} + f(R2,GS)_{df=1.5}$
	dominant females	$-0.93 + f(S,R2)_{df=4.8} + f(S,R10)_{df=5.4} +$
litter		$f(R2,R10)_{df=2.8} + f(GS,PD)_{df=3.0} +$
production [†]		$f(S,GS)_{df=0.0} + f(R2,GS)_{df=1.8}$
production	adult subordinate females	$-3.90 + f(S,R2)_{df=3.7} + f(S,R10)_{df=4.4} +$
		$f(GS,PD)_{df=3.5} + f(S,GS)_{df=0.0}$
	dominant females	$1.60 + f(S,R2)_{df=4.1} + f(S,R10)_{df=0.1} + f(S,R10)_{df=0.1}$
		$f(R2,R10)_{df=3.2} + f(GS,PD)_{df=6.1} +$
pup survival		$f(\mathbf{S},\mathbf{GS})_{df=2.3}$
	adult subordinate females	$1.28 + f(GS,PD)_{df=6.8} + f(S,GS)_{df=0.0} +$
		$f(R2,GS)_{df=1.0}$
	adult subordinate females	$-3.06 + f(S,R2)_{df=5.8} + f(S,R10)_{df=6.0} +$
		$f(R2,R10)_{df=4.0} + f(GS,PD)_{df=4.7}$
	immature subordinate females	$-7.11 + f(GS,PD)_{df=7.7} + f(S,GS)_{df=2.3} +$
		$f(\mathbf{R2},\mathbf{GS})_{df=1.0}$
emigration	dominant males	$-3.15 + f(S,R2)_{df=3.1} + f(S,GS)_{df=0.6}$
emgration	adult subordinate males	$-3.06 + f(S,R2)_{df=5.0} + f(S,R10)_{df=6.0} +$
		$f(R2,R10)_{df=2.8} + f(S,GS)_{df=1.0} +$
		$f(\mathbf{R2},\mathbf{GS})_{df=3.3}$
	immature subordinate males	$-5.08 + f(S,R2)_{df=4.5} + f(S,GS)_{df=0.0} +$
		$f(\mathbf{R}2,\mathbf{GS})_{df=0.8}$
immigration	males	$-2.24 + f(\mathbf{S},\mathbf{R}2)_{df=4.2} + f(\mathbf{S},\mathbf{R}10)_{df=0.0} +$
		$f(R2,R10)_{df=0.9} + f(GS)_{df=1.7}$

[†]Models for litter production incorporated conditions from period t-2 instead of period t (see text).

model form [†]	R ^{2‡}	ΔR^2	fraction of explanatory power attributed to model component
full model	0.414	_	-
(Season)	0.165	0.249	0.60
(Rperiod)	0.349	0.064	0.15
(R10months)	0.350	0.063	0.15
(GroupSize)	0.393	0.021	0.05
(PopDensity)	0.408	0.005	0.01
(age structure)	0.376	0.038	0.09
(dom structure)	0.340	0.074	0.18
(sex structure)	0.403	0.011	0.03
mean immigration	0.414	0.000	0.00
mean mortality	0.408	0.005	0.01
mean litter production	0.346	0.068	0.16
mean pup survival	0.414	-0.001	0.00
mean reproduction	0.338	0.075	0.18
mean emigration	0.149	0.264	0.64
(Rperiod in emigration)	0.371	0.042	0.10
(R10months in emigration)	0.356	0.058	0.14
(age structure in emigration)	0.378	0.035	0.09

Table 4.B2: Explanatory power of group dynamics model and model components

[†]Parentheses indicate omission of specified predictor or aspect from the full predictive model in order to assess explanatory ability. ${}^{*}R^{2}$ values were calculated based on expected and observed group sizes, assuming a trendless random

walk null model.



Figure 4.B1: Generalised additive model terms from maximum-parsimony model used to predict percapita **mortality in dominant male meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*, PD = estimated population density for period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B2: Generalised additive model terms from maximum-parsimony model used to predict percapita **mortality in immature subordinate male meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period t (0 and 6 represent May/June), R2 = normalized rainfall in period t (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period t (relative to the long-term seasonal mean), GS = group size at the start of period t, PD = estimated population density for period t. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B3: Generalised additive model terms from maximum-parsimony model used to predict percapita **mortality in adult subordinate male meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*, PD = estimated population density for period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B4: Generalised additive model terms from maximum-parsimony model used to predict percapita **mortality in dominant female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support. Shaded region in **B** represents approximate 95% confidence region and "rug" shows observed predictor values.



Figure 4.B5: Generalised additive model terms from maximum-parsimony model used to predict percapita **mortality in immature subordinate female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B6: Generalised additive model terms from maximum-parsimony model used to predict percapita **mortality in adult subordinate female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B7: Generalised additive model terms from maximum-parsimony model used to predict percapita **litter production in dominant female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period t(0 and 6 represent May/June), R2 = normalized rainfall in period t-2 (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period t-2 (relative to the long-term seasonal mean), GS = group size at the start of period t-2, PD = estimated population density for period t-2. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B8: Generalised additive model terms from maximum-parsimony model used to predict percapita **litter production in adult subordinate female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period t (0 and 6 represent May/June), R2 = normalized rainfall in period t-2 (relative to the longterm seasonal mean), R10 = normalized rainfall in the ten months prior to period t-2 (relative to the long-term seasonal mean), GS = group size at the start of period t-2, PD = estimated population density for period t-2. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B9: Generalised additive model terms from maximum-parsimony model used to predict percapita **survival in pups of dominant female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*, PD = estimated population density for period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B10: Generalised additive model terms from maximum-parsimony model used to predict percapita **survival in pups of adult subordinate female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*, PD = estimated population density for period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B11: Generalised additive model terms from maximum-parsimony model used to predict percapita **emigration in dominant male meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B12: Generalised additive model terms from maximum-parsimony model used to predict percapita **emigration in immature subordinate male meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B13: Generalised additive model terms from maximum-parsimony model used to predict percapita **emigration in adult subordinate male meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.



Figure 4.B14: Generalised additive model terms from maximum-parsimony model used to predict percapita **emigration in immature subordinate female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*, PD = estimated population density for period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support.
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Figure 4.B15: Generalised additive model terms from maximum-parsimony model used to predict percapita **emigration in adult subordinate female meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*, PD = estimated population density for period *t*. Lighter grey represents higher predictions. Gaps in the surface epresent regions of parameter space without empirical support.

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Figure 4.B16: Generalised additive model predictions from maximum-parsimony model used to predict per-group **immigration of male meerkats** at two-month intervals. For each component, all predictive variables not shown were set at their median level. S = two-month "season" of period *t* (0 and 6 represent May/June), R2 = normalized rainfall in period *t* (relative to the long-term seasonal mean), R10 = normalized rainfall in the ten months prior to period *t* (relative to the long-term seasonal mean), GS = group size at the start of period *t*. Lighter grey represents higher predictions. Gaps in the surface represent regions of parameter space without empirical support. **D** shows immigrants per existing group member; shaded region represents approximate 95% confidence region and "rug" shows observed predictor values.



Figure 4.B17: Ricker plot of observed (circles; area proportional to number of observations) and simulated (shaded squares) meerkat group size (*N*) dynamics over three two-month observation periods (*t*) from January 1st to July 1st (**A**) and July 1st to January 1st (**B**) for the period January 1st 1998 to January 1st 2009. Simulated dynamics were based on generalized additive model characterizations of meerkat demographic rates, parameterized using data from the Kuruman River Reserve, South Africa. 2 000 simulations were seeded with each of five sets of observed group compositions from the first half of 1998 and run until the earlier of group disappearance and January 1st 2009. Final group sizes indicated as zero represent simulation-ending group sizes of both zero and one. *legend indicates rates of observation out of 100 000 simulated group-years.



Figure 4.B18: Ricker plot of observed (circles; area proportional to number of observations) and simulated (shaded squares) meerkat group size (*N*) dynamics over six two-month observation periods (*t*) from July 1st to the following July 1st between 1998 and 2008 after years with higher-than-median (**A**) and lower-than-median (**B**) annual rainfall. Simulated dynamics were based on generalized additive model characterizations of meerkat demographic rates, parameterized using data from the Kuruman River Reserve, South Africa. 2 000 simulations were seeded with each of five sets of observed group compositions from the first half of 1998 and run until the earlier of group disappearance and July 1st 2008. Final group sizes indicated as zero represent simulation-ending group sizes of both zero and one. *legend indicates rates of observation out of 100 000 simulated group-years.



Figure 4.B19: R^2 values for the stage-structured demographic model of group dynamics (described in the main text) used to predict simulated (**A**) and observed (**B**) meerkat group trajectories, assuming a trendless random walk null model. The vertical dashed line shows the overall estimated R^2 of the model used to predict all observations.

Territoriality and home-range dynamics in meerkats, Suricata suricatta

Aspects of this chapter are the result of collaboration with M. A. Lewis and G. Gall. M. A. Lewis contributed through discussions concerning mathematical models, and G. Gall collected sand-type data on the Kuruman River Reserve, South Africa.

5.1 Abstract

Multiple approaches have been used to study patterns of space use across species, among them resource selection analysis, mechanistic movement modelling, and statistical home range modelling. Mechanistic home-range models combine the benefits of these approaches, describing emergent territorial patterns based on finescale individual- or group-movement rules, incorporating interactions with neighbours and the environment. Using mechanistic home-range models, we explore meerkat territorial patterns. We consider scent marking, direct group interactions, and habitat selection. Notably, larger groups do not seem to enjoy an advantage in controlling larger territories, and groups appear to prefer dune edges along a dry riverbed. We also extend models to accommodate descriptions of territory formation and territory movement. We use meerkat data to test the proposed improvements to these models, and We use the model results to start building a picture of spatial processes in meerkat population dynamics.

5.2 Introduction

In order to survive and procreate, individuals must perform a suit of relevant activities - avoid predators, forage, compete with conspecifics, and search for mates - all within a limited spatial context. Individuals' space-use decisions, and the resulting spatial patterns, mediate among these activities (*e.g.* Clutton-Brock and Harvey 1978, Davies 1980, Lima and Dill 1990). Territorial patterns, specifically, can have important impacts on population dynamics (López-Sepulcre and Kokko 2005, Packer et al. 2005, Wang and Grimm 2007), and answering related questions - what drives patterns? how are environmental and social factors involved? how do patterns change over time? - is critical to understanding the dynamics of territorial species.

Through radio telemetry and, more recently, the global positioning system (GPS), empirical space-use data have become widely available, presenting valuable opportunities to ask questions and test theory concerning space-use patterns. Common approaches to data analysis (such as kernel home-range estimation and resource selection analysis; Worton 1989, Boyce and McDonald 1999, Getz et al. 2007) are, however, phenomenological in nature, lacking a theoretical basis in the movement processes that generate associated patterns (Moorcroft and Lewis 2006). Mechanistic home-range models (Lewis and Murray 1993, Moorcroft and Lewis 2006) provide an alternate approach to studying patterns of space-use in social carnivores. These models link fine-scale behaviour to resultant territorial patterns, and offer direct links to telemetry data (Moorcroft and Lewis 2006).

In general, spatial patterns arise from animals moving in (and interacting with) their environment (Börger et al. 2008). For many species, each individual's movement is ultimately restricted in space and comes to define a home range: habitat of which the individual makes regular use, without reference to specific types of behaviour (Burt 1943, Brown and Orians 1970). In some species, a subset of each individual's home range forms its territory: a region of near-exclusive use associated with some form of defence or display behaviour (Burt 1943, Fretwell and Lucas 1969, Brown and Orians 1970). Territoriality constrains how animals distribute themselves in the environment, for example, by altering access to available resources, with important consequences for species and their communities (Brown and Orians 1970, Lewis and Murray 1993, Wang and Grimm 2007, Börger et al. 2008).

In many of the carnivora, individuals form stable social groups that jointly defend shared territories (Macdonald 1983). Here, the distinction between home range and territory can break down, and the pattern of space use often becomes that of a "defended home range" (Börger et al. 2008). Defence may take the form of physical violence, but interactions can also be mediated by nonviolent cues that carry information about implied threats (Gosling and Roberts 2001). In many cases, carnivores use scent marks to indicate territory ownership (Peters and Mech 1975, Bowen and McTaggart Cowan 1980, Wells and Bekoff 1981, Kruuk et al. 1984, Gese and Ruff 1997, Boydston et al. 2001, Sillero-Zubiri and Macdonald 2006, Jordan et al. 2007), and individuals often avoid (Peters and Mech 1975, Wells and Bekoff 1981, Sillero-Zubiri and Macdonald 2006, Jordan 2007) in response to foreign scent marks.

As a result, scent marking and its related behaviours can reinforce territorial patterns without recourse to direct aggression.

Lewis and Murray (1993) incorporated scent-marking, over-marking, and scent-mark avoidance behaviours into random walk models of animal movement to develop mechanistic home-range models of carnivore territoriality. Further improvements have used terrain- and resource-sensitive movement rules to capture stable patterns in spatially variable environments (Moorcroft et al. 1999, 2006).

Here, we modify the Lewis-Murray model and apply it to a population of wild meerkats, *Suricata suricatta*. Our primary aim is to understand the spatial distribution of meerkat groups in their habitat, paying attention to interactions with other groups, the effects of group size, and the influence of habitat features. Ultimately, we would like to use the knowledge gained here to inform models that link descriptions of group-level and intergroup processes to offer insight into population-level dynamics. Such an approach will benefit from an understanding of dynamical aspects of territoriality, such as the formation of new groups and movement of existing groups. We therefore extend the Lewis-Murray model to examine processes of home-range formation and movement. This simultaneously offers relevant insight into meerkat territoriality and goes some of the way towards addressing concerns, discussed below, raised about mechanistic home-range models as they have been used in the past.

5.3 Study Species and Site

Meerkats are highly social carnivores that inhabit the Kalahari region of southern Africa. They live at approximate population densities of 7-17 individuals/km² and form groups of up to 50 individuals (Bateman et al. 2011a, Bateman et al. 2011b). Within each group, a socially dominant pair largely monopolises breeding, and socially subordinate individuals (typically the offspring of the breeding pair) assist in pup rearing, predator vigilance, and territory defence (Doolan and Macdonald 1997, Clutton-Brock et al. 2008).

Group members defend shared home ranges against other groups (Young 2003, Jordan et al. 2007), and resident males invest in repulsion of prospecting males (Mares et al. 2012). Direct interactions take multiple forms: stereotyped "war dance" threat displays, chases, physical fights, and violent burrow excavations that sometimes result in deaths (in order of increasing severity; Jordan et al. 2007, Drewe et al. 2009b). Group size confers benefits in these instances; in any aggressive

interaction greater group-size disparity increases the chances that the smaller group will flee, and decreases the chances of a physical fight (Young 2003).

Meerkats scent mark their territories using urine, feces, and anal gland secretions (Decker et al. 1992, Jordan 2007). Overmarking is common, and defecation often occurs at shared latrine sites (Jordan 2007, Jordan et al. 2007, Mares et al. 2011). While shared latrines occur at boundaries between group home ranges, they are more dense within territory cores and are used most heavily in the breeding season, and they have therefore been implicated in mate defence, rather than territory defence *per se* (Jordan et al. 2007; but see Mares et al. 2011).

Females are considered philopatric, almost never joining established groups, but both sexes periodically disperse in same-sex coalitions and attempt to found new groups (Young 2003, Bateman et al. in press). Larger dispersal groups are more successful at establishing new breeding groups (Young 2003), but the groupformation process has otherwise been little-studied. The process by which new groups establish their own home ranges remains unexplored.

Newly established breeding groups must often carve out home ranges from already populated habitat. Before forming new groups, dispersers can go through a period of "floating" (Peters and Mech 1975, Young 2003), and newly formed meerkat groups often make wider use of space than established groups. Groups regularly form from dispersing coalitions of nearby origin, so that newly formed groups are at times situated next to the natal groups of their founders (T. Clutton-Brock, unpublished results). Though "parent" and "daughter" groups do engage in violent direct interactions (Drewe et al. 2009b), other behavioural evidence suggests how each group's avoidance of the other's territory may build up gradually over time. Meerkats often fail to recognise group members by sight; when individuals return to their group after being separated while foraging they are liable to be greeted with an aggressive war dance (usually reserved for hostile inter-group interactions) until the two factions are in close proximity and individuals can use scent or other cues to aid recognition. Based on this observation, it is conceivable that direct interactions between a new group and its parent group could become aggressive before scent cues or mental maps associated with home-range behaviour adapt to the realities of local group compositions. A new group's territory would emerge over time in such a context, because its members would not initially recognise the territory or scent marks of the other group as foreign.

Established group home ranges are often relatively stable (sometimes over a period of years; T. Clutton-Brock, unpublished data), but shifts do occur. Moorcroft et al. (1999, 2006) showed how removal of a social group could alter the space use of neighbouring groups. With meerkats, however, territories at times appear to shift longer distances than could reasonably be explained by this reconfiguration process. This may happen because groups move their territories in response to a changing "landscape" of aggressive interactions or scent marks that results from group formations and extinctions.

Patterns may also shift in response to habitat features, such as periodically dense sour grass, *Schmidtia kalahariensis*, growing in previously over-grazed riverbed habitat on the Kuruman River Reserve (personal communication, T. P. Flower, field site manager, 2004-2007). Sour grass can impede movement, likely reducing meerkat foraging efficiency, and meerkats seem to avoid it.

The arid Kalahari environment is characterised by a cold, dry winter (approximately May to September) and a hot, wet summer (approximately October to April; Doolan and Macdonald 1996). Prey availability shows strongly seasonal trends (Doolan and Macdonald 1996a, 1997), and although meerkats can breed year-round, most reproduction occurs in the summer to take advantage of seasonal prey abundance (Doolan and Macdonald 1997, Bateman et al. in press).

Throughout the year, groups forage together in close association, mainly consuming arthropods and small vertebrate prey (Doolan and Macdonald 1996a). Groups forage during the day, returning to a sleeping burrow each night. Most groups make use of several burrows within their home ranges, switching every few days (Young 2003, Manser and Bell 2004). Until pups are three or four weeks old, they do not forage with the group and are babysat at their natal burrow (Clutton-Brock et al. 1999b), though adults may move them between burrows during this time (Jordan et al. 2007).

Our study site consists of ranchland on and near the Kuruman River Reserve (26°58'S, 21°49'E), near Van Zylsrus in the Northern Cape province of South Africa. The site includes a regionally typical mix of habitats: a stretch of the dry Kuruman river, nearby herbaceous "flats," and sparsely grassed dunes. Details pertaining to the site are available elsewhere (Clutton-Brock et al. 1999a, Russell et al. 2002).

5.4 Mathematical Models

Mechanistic home-range models are derived from mathematical descriptions of fine-scale movement, assuming an underlying spatially biased random walk process, and take the form of systems of partial differential equations (see Moorcroft and Lewis 2006 for derivations). Early random walk models (Holgate 1971, Okubo 1980) generated stable home-range patterns with simple balances between spatial diffusion and attraction to a "localising centre" (*i.e.* a den site or core foraging area: Moorcroft et al. 1999). Lewis and Murray (1993) incorporated territorial scentmarking behaviours to produce realistic territorial patterns (see Moorcroft et al. 1999), and Moorcroft and Lewis incorporated habitat selection behaviours (see Moorcroft et al. 2006). Because the models describe spatial probability ("utilisation") distributions, representing the probability of finding a focal group at any point in space at a given time, they can be directly tied to data. Thus, mechanistic home-range models connect underlying movement processes, territorial behaviour, resource selection, and spatial utilisation patterns (Moorcroft and Lewis 2006, Moorcroft and Barnett 2008), making important progress towards a general understanding of home-range behaviour (Börger et al. 2008).

Börger *et al.* (2008) comment that a truly mechanistic model should be able to recreate observed patterns without fixing an aspect of the associated process (*i.e.* a localising centre) *a priori*, also noting that applications of Lewis-Murray-type models have been largely restricted to stable patterns in territorial carnivores. While our models remain targeted to territorial carnivores, we attempt to address some concerns about fixed localising centres and exclusively stable patterns.

5.4.1 General Model

To model meerkat home ranges, we developed a set of competing mechanistic home-range models that describe how groups' expected locations, i.e. their home-range utilisation distributions, change over time within the study area. The general form of these models relates temporal change in utilisation distributions to random and directed movement using a system of partial differential equations (PDEs). For each group, i:

$$\frac{\partial u_i(\mathbf{x},t)}{\partial t} = \underbrace{\nabla^2 \left[u_i(\mathbf{x},t) D(\mathbf{x},t) \right]}_{\text{diffusive (random) movement}} - \underbrace{\nabla \cdot \left[u_i(\mathbf{x},t) \mathbf{C}_i(\mathbf{x},t) \right]}_{\text{advective (directed) movement}},$$
(5.1)

where variables and parameters are as described in Table 5.1. ∇ indicates spatial derivatives, $(\partial/\partial x, \partial/\partial y)$.

Table 5.1: symbols used in the text. Where applicable, variables and parameters are nondimensionalised as in Lewis and Murray (1993) and Moorcroft *et al.* (2006).

symbol [†]	interpretation
X	spatial location, (<i>x</i> , <i>y</i>), rescaled so that $x, y \in [0, 1]$
t	time
$u_i(\mathbf{x},t)$	two-dimensional utilisation distribution (a probability density function) for
	group <i>i</i> at location $\mathbf{x} = (x, y)$ and time <i>t</i>
$D(\mathbf{x},t)$	spatial diffusion rate, describing the tendency for a group's location to
	become less and less certain, if movement were left unchecked
$\mathbf{C}_{i}(\mathbf{x},t)$	velocity of group <i>i</i> 's advective flux (directed movement), which in practice
	serves to check diffusive group movement
$\mathbf{J}_{D,i}$	diffusive flux
$\mathbf{J}_{C,i}$	advective flux
d	diffusion constant
С	advection constant
$p_i(\mathbf{x},t)$	intensity of group <i>i</i> 's scent marks at \mathbf{x} and <i>t</i>
п	number of groups in the spatial region under consideration
$\hat{\mathbf{v}}_i(\mathbf{x})$	unit vector directed from \mathbf{x} toward group <i>i</i> 's localising centre
$\chi_i(t)$	location of group <i>i</i> 's localising centre at time <i>t</i>
N_i	number of individuals, over two months of age, in group <i>i</i>
т	rate of overmarking, relative to the base scent marking rate
α_h	sensitivity to habitat features, $h(\mathbf{x})$
$h(\mathbf{x})$	habitat features: elevation, sand type, or change in sand type (see text)
κ	exponential coefficient determining rate at which interaction strength of
	parent and daughter groups approaches normal level (see text)
k	discrete analogue of κ
γ	rate of localising-centre movement, down aversion gradient (see text)
g	discrete analogue of γ
α_r	strength of movement down "grass gradient," associated with riverbed
	habitat (see text)
$r(\mathbf{x})$	riverbed habitat on the Kuruman River Reserve (used as a proxy for
de la	growth of sour grass during late 2007 and early 2008; see text)

[†]Note that symbols in bold face represent vectors

We can re-write (1) in terms of diffusive and advective flux ($\mathbf{J}_{D,i}$ and $\mathbf{J}_{C,i}$, respectively):

$$\frac{\partial u_i(\mathbf{x},t)}{\partial t} = -\left(\nabla \cdot \nabla \left[-u_i(\mathbf{x},t)D(\mathbf{x},t)\right] + \nabla \cdot \left[u_i(\mathbf{x},t)\mathbf{C}_i(\mathbf{x},t)\right]\right)$$
$$= -\nabla \cdot \left[\mathbf{J}_{D,i}(\mathbf{x},t) + \mathbf{J}_{C,i}(\mathbf{x},t)\right], \tag{5.2}$$

Diffusive flux reflects a tendency for the location of an unhindered group to become less certain over time (a passive, random process), and advective flux arises, in our case, from the tendency of each group to retreat towards a localising centre (an active, responsive process).

Much of the time, meerkat home ranges are relatively stable, year-to-year. Given appropriate forms of $D(\mathbf{x},t)$ and $\mathbf{C}_i(\mathbf{x},t)$, (5.2) can produce stable patterns at equilibrium (*i.e.* when $\partial u_i(\mathbf{x},t)/\partial t = 0$), maintained by a balance between diffusion and advection. We modelled these stable home-range patterns.

5.4.2 Boundary Conditions

We model interactions in a self-contained domain of interest, Ω , with (5.2) subject to zero-flux boundary conditions. Mathematically, this is written:

$$0 = \mathbf{n} \cdot \left[\mathbf{J}_{D,i}(\mathbf{x},t) + \mathbf{J}_{C,i}(\mathbf{x},t) \right],$$
(5.3)

where **n** is the unit vector, directed out of Ω at the boundary.

5.4.3 scent marking

The Lewis-Murray model describes diffusive group movement, scentmarking, overmarking, scent-mark avoidance, and scent-mark decay:

$$\frac{\partial u_i(\mathbf{x},t)}{\partial t} = d\nabla^2 \left[u_i(\mathbf{x},t) \right] - \nabla \cdot \left[u_i(\mathbf{x},t)c\hat{\mathbf{v}}_i(\mathbf{x})\sum_{\substack{j\neq i}}^n p_j(\mathbf{x},t) \right], \quad (5.4A)$$

$$\underbrace{\frac{\partial p_i(\mathbf{x},t)}{\partial t}}_{\text{ot}} = \underbrace{u_i(\mathbf{x},t) \left[1 + mN_i\sum_{\substack{j\neq i}}^n p_j(\mathbf{x},t) \right]}_{\text{scent mark deposition}} - \underbrace{p_i(\mathbf{x},t)}_{\text{scent mark deposition}} \right]. \quad (5.4B)$$

Here, in addition to the basic model with constant diffusion rate, we have included the potential for scent marking to occur in proportion to group size, as noted by Moorcroft and Lewis (2006). This occurs through the inclusion of N_i in the scentmark deposition term (fixing $N_i = 1$, for all *i*, recovers the size-insensitive model). We refer to this model as the scent-mark (SM) model.

When a group encounters foreign scent marks, it biases its movement towards its localising centre. While this pattern may be most applicable for central-place foragers, it corresponds broadly to the behaviour observed in multiple social carnivores (Moorcroft and Lewis 2006). This represents a less-than-mechanistic aspect of our models, and others have explicitly modelled other processes, such as memory, that can produce similar behaviour (*e.g.* Van Moorter et al. 2009). For our purposes, we consider the assumption of a localising centre to be a phenomenological description of attraction to a territory core.

5.4.4 Direct Group Interactions

As an alternative to the Lewis-Murray model, we considered the possibility that home ranges are restricted in size by direct interactions with neighbouring groups. In this case, instead of retracting in response to scent marks, groups retract in response to interactions, assumed to occur according to the law of mass action (i.e. in proportion to the product of two groups' expected density at a given location) so that:

$$\mathbf{C}_{i} = \underbrace{c \hat{\mathbf{v}}_{i} \sum_{j \neq i}^{n} \frac{N_{j}}{N_{i} + N_{j}} u_{i} u_{j}}_{\text{velocity of movement directed}} \qquad (5.5)$$

Here, there is no need to keep track of scent marks, and we have suppressed dependence on space and time for convenience. Once again, we include group size in the model, assuming that groups avoid regions of space in proportion to the size advantage of competing groups with which they interact there. We measure a group's size advantage in a given interaction as the proportion of interacting meerkats it represents, which strongly correlates with the propensity for groups to win interactions (unpublished results; see Young 2003).

In initial numerical approximations (see Methods) using (5.5) in (5.1), the resulting $(u_i)^2$ factor produced unrealistic, "pointy" home ranges, *i.e.* probability density functions declined quickly from maxima at localising centres. We therefore modified (5.5) so that:

$$\frac{\partial u_i}{\partial t} = d\nabla^2 u_i - \underbrace{\nabla \cdot \left[u_i c \hat{\mathbf{v}}_i \sum_{\substack{j \neq i}}^n \frac{N_j}{N_i + N_j} u_j \right]}_{\text{advection, directed away from space}} \qquad (5.6)$$

Such a modification can be interpreted to mean that groups integrate their experience of group interactions in the context of knowledge of their own pattern of space use, so as to avoid regions used by other groups (not just regions in which they interact with other groups). We refer to this model as the "direct-interaction" (DI) model, and note that in the absence of group-size dependence, the DI model is equivalent to the SM model with an overmarking rate, m, of zero (Moorcroft and Lewis 2006).

5.4.5 Habitat Selection

To account for habitat-specific patterns of space use, we employed additions to the model introduced by Moorcroft *et al.* (2006). Group diffusion and advection rates come to depend on features of the habitat at each location, such that:

$$D = \left(e^{\alpha_h h(\mathbf{x})}\right) d , \qquad (5.7A)$$

$$\mathbf{C}_{i} = \left(e^{\alpha_{h}h(\mathbf{x})}\right)c\hat{\mathbf{v}}_{i}\sum_{j\neq i}^{n}u_{j}, \qquad (5.7B)$$

for the DI model without group-size dependence (similarly for the other models). Mechanistically, this relies on changes to group's underlying movement behaviour that lead to more time being spent in favourable habitat, where $\alpha_h h(\mathbf{x})$ is small. Such a model seems reasonable, as meerkats have been reported to move quickly between profitable foraging patches, in which they move more slowly (Doolan and Macdonald 1996a).

By considering several candidates for $h(\mathbf{x})$, we could compare related hypotheses concerning habitat selection. We did not have direct estimates of prey availability or risk across the study site, so we chose plausible correlates. We chose to consider elevation, sand type (red "ferrous" versus light-coloured "clay" sand), and a measure of sand-type "edges" as candidates for $h(\mathbf{x})$. The first two correlate with regions of dunes and riverbed/flats. For the last, we considered local spatial variance in sand type, as an indicator of the interface between ferrous and clay sands. See Methods for details. In the interest of full model-selection honesty, we note that we did not identify the potential importance of edge habitat until after fitting the territoryformation models, but there is *a priori* reason in the literature (Turbé 2006) to consider this habitat type.

We used the equilibrium conditions of PDE systems (5.4) and (5.6), with the modifications described in (5.7), to model stable meerkat home ranges. At other times, home-range patterns change in time, and we developed models (below) to describe two of these scenarios: group formation and home-range shifts.

5.4.6 Territory Formation

We suggest a model in which the strength of interaction between parent and daughter groups is time dependent, approaching the population-wide value from an initial value of zero. For the groups involved:

$$\mathbf{C}_{i} = e^{\alpha_{h}h(\mathbf{x})} c \hat{\mathbf{v}}_{i} \left[\sum_{j \notin \{i, K_{i}\}} u_{j} + \sum_{j \in K_{i}} u_{j} (1 - e^{-\kappa(t - t_{D})}) \right],$$
(5.8)

for the DI model without group-size dependence (similarly for the other models). Here, K_i is the set of relevant "kin" groups (*i.e.* the parent or daughter groups), and t_D is the time at which the daughter group forms.

5.4.7 Group Movement

We propose a mechanism for home range movement whereby a group's idealised localising centre moves in relation to the same stimuli that generate advection. Groups experience varying advection speed, $|C_i(\mathbf{x},t)|$, in different areas of habitat, as produced by social factors (scent marks, group interactions) and modulated by habitat features. For simplicity we term the advection speed "aversion," because it is the average rate of movement from less desirable to more desirable habitat. Groups should be drawn to areas with low aversion, where there is little motivation to avoid nearby regions. We therefore propose that a group's localising centre moves down the aversion gradient, averaged across the group's home-range,

$$\overline{\nabla} \overline{\mathbf{A}}_{i}(t) = \iint_{\Omega} u_{i} \nabla \left(\left| \mathbf{C}_{i}(\mathbf{x}, t) \right| \right) dx dy , \qquad (5.9)$$

to areas of habitat with lower advection speeds, such that:

$$\frac{d\mathbf{x}_{i}(t)}{dt} = -\gamma \overline{\nabla} \mathbf{A}_{i}(t) \,. \tag{5.10}$$

5.4.8 Terrain Avoidance

In the period during which we fit the group-movement model, meerkat groups seemed to completely avoid a relevant region of the riverbed within the Kuruman River Reserve (T. P. Flower, personal communication). This may have been due to extensive sour grass growth in the area, while sour grass was kept in check by high grazing pressure on the adjoining ranches.

To accommodate this feature of meerkat space use, we adapted the terrainavoidance model modification used by Moorcroft *et al.* (2006). Here, groups move down a "grass gradient," included, by proxy, as sand type in the reserve-specific area of riverbed:

$$\mathbf{C}_{i} = e^{\alpha_{h}h(\mathbf{x})} \left[c \hat{\mathbf{v}}_{i} \sum_{j \neq i}^{n} u_{j} - \alpha_{r} \nabla r(\mathbf{x}) \right], \qquad (5.11)$$

for the DI model without group-size dependence (similarly for the other models).

5.5 Methods

We modelled meerkat home ranges during three distinct periods. Currently, our models are not sufficiently developed to capture the full detail of meerkat territorial dynamics over the long term (and the associated model fitting would have been prohibitive, in any case). In an attempt to gain preliminary insight, we chose the specific periods to examine stable territorial patterns, territory formation, and territory movement such that the processes were plausibly tractable within an often complex and dynamic context. During period one (P₁: January 1st, 2003 to December 31st, 2003) groups were relatively stable. During period two (P₂: July 1st, 2004 to December 31st, 2005) a new group formed from dispersing propagules of two adjacent groups. During period three (P₃: June 15th, 2007 to February 14th, 2008) an existing group's home range shifted in space.

5.5.1 Data Collection and Processing

During the relevant periods, researchers made weekly (and often daily) visits to habituated groups of individually marked meerkats. Visits occurred while meerkats were foraging, either before or after their mid-day period of inactivity. During these visits, researchers collected detailed life-history information and recorded spatial locations of the groups using handheld GPS units. We used life-history data to generate group-size measurements (number of individuals older than two months, averaged over census counts made every two months) and group pedigrees. To manage spatial autocorrelation, we resampled one GPS point from each morning and afternoon group observation session.

We acquired elevation data for the study site from the Advanced Spaceborne Thermal Emission and Reflection Radiometer Global Digital Elevation Model, (ASTER GDEM) Version 2 (Abrams 2000). ASTER GDEM is a product of Japan's Ministry of Economy, Trade, and Industry and the United States' National Aeronautics and Space Administration (NASA). We standardised elevation data to fall between zero and one in the region of interest.

To generate sand-type data, we combined ground-based point observations of clay and ferrous sand (Gall 2012) with imagery from NASA's Landsat 7 satellite, provided courtesy of the United States Geological Survey. Using logistic regression, we classified sand-type observations based on at-sensor reflectance of Landsat bands one and five (and their interaction) from October 18th 2002. We then used predictions

from the regression model to give each Landsat image pixel a score ranging from zero (clay sand) to one (ferrous sand).

We resampled elevation and sand-type data (using a weighted mean algorithm) to correspond with the resolution of our spatial discretisation of the home range models (see below). Then, to identify locations at the interface between clay and ferrous sand, we calculated the standard deviation of sand-type values for each pixel and its set of four orthogonally adjacent pixels. We standardised this edge measurement to fall between zero (when the standard deviation was maximised) and one (when the standard deviation was minimised), so that regions of assumed habitat preference were represented consistently across $h(\mathbf{x})$ candidates.

We refer to the three standardised candidates for $h(\mathbf{x})$ as DEM, SAND, and EDGE, respectively (see Figure 5.B1 for versions used in P₁ models).

5.5.2 Model Discretisation, Fitting, and Comparison

Because no simple analytical solutions exist for the PDE home-range models above, we implemented them using finite-difference methods to approximate equilibrium states (Smith et al. 2012). This involved discretising equations in space and time and using central difference formulae to approximate derivatives (see Appendix A for details of SM model discretisation). For a given model and set of parameters, we simulated the time-dependent model to find approximate equilibrium solutions for the relevant systems of PDEs. At equilibrium, u_i depends on ratio of c_i and α_g to d (Moorcroft et al. 1999), so we fixed d at 0.1 in all simulations. For modelling stable home ranges in period one, we used this implementation directly.

For a given model form, parameter combination, and set of localising centres, we used the discretisations, described above, to model meerkat home-range distributions. Conveniently, these distributions are probability density functions and can be used directly to calculate the likelihood of empirical observations, given the model. By model-fitting convention, we use the negative log likelihood, summed across all relocations for all appropriate groups in all relevant timesteps:

$$-\sum \ln(\mathcal{L}) = \sum_{T \in \mathbf{T}_{p}} \sum_{i \in \mathbf{G}_{p}} \sum_{l \in \mathbf{L}_{p,i}^{T}} \left[-\ln\left(u_{i}^{T}(\mathbf{x}_{l})\right) \right],$$
(5.12)

where \mathbf{T}_P and \mathbf{G}_P are the sets of timesteps and groups used for fitting, respectively, in the period of interest; $\mathbf{L}_{P_i}^{T}$ is the set of GPS relocations for group *i*, during timestep *T* in the period of interest; u_i^T is the home-range distribution for group *i* in timestep *T*; and \mathbf{x}_i is the position of the l^{th} relocation for group *i* in timestep *T*. We fit each model to data by numerically optimising model parameter combinations to minimise (5.12).

In P₁, we modelled stable home range patterns over twelve months (*i.e.* we considered only one timestep during this period). We fit sixteen candidate models, as described above and outlined in Table 5.2. We fit models in a square region (Ω_1), oriented north-south and defined by universal transverse mercator (UTM) coordinates 34J 579125 7011500 in the southwest and 34J 586875 7019250 in the northeast. Within Ω_1 , we employed a 100 by 100 point grid for discretisation. Ω_1 captured all well-documented groups (identified as B, D, E, F, GG, L, MM, RR, W, V, XX, Y, and ZZ) on and near the Kuruman River Reserve during P₁. Because of potential edge-effects, however, we only considered non-edge groups (E, F, GG, L, W, V, and Y) in likelihood calculations. We used the centroid of each group's relocation data as the group's localising centre (Moorcroft et al. 1999), and fit *c*, *m*, and α_h , as appropriate, as free parameters.

When implementing the territory-formation and group-movement models (in P_2 and P_3), we made a quasi-equilibrium assumption that home range patterns equilibriate quickly relative to the dynamic processes that alter home ranges (territory formation and movement). Biologically, this translates to the assumption that groups make use of their territories, thereby generating patterns of space use, on a shorter time scale than that at which underlying determinants of space use change. Mathematically, we approximate continuous change by allowing stable homeranges to change step-wise, according to discretised changes in group interaction strength or localising centre location.

When temporally discretising the models, we chose timestep lengths to allow efficient model fitting, while offering reasonably fine-scale descriptions of processes that actually occur in continuous time. We assumed that relevant function values applied throughout entire timesteps, so that each set of equilibriated home-range patterns was associated with a set of empirical observations over several weeks (see below).

We discretised exponentially increasing interaction strength in (5.9) with:

$$1 - e^{-\kappa(t - t_D)} \approx 1 - e^{-k \cdot T},$$
 (5.13)

where $T \in \{0, 1, 2, ...\}$ numerates the timestep under consideration, and the replacement of ρ with *r* highlights the lack of direct equivalency between the two exponents. In discretising (5.9), we made the approximation:

$$\frac{d\boldsymbol{\chi}_{i}(t)}{dt} = -\gamma \overline{\nabla \mathbf{A}}_{i}(t) \quad \rightarrow \quad \frac{\Delta \boldsymbol{\chi}_{i}^{T}}{\Delta T} \approx -g \overline{\nabla \mathbf{A}}_{i}^{T}, \quad (5.14)$$

where ΔT is equal to one (*i.e.* a single timestep) and $\Delta \chi_i^T$ is the change in localising centre position from one timestep to the next (here, *T* is an index, rather than an exponent). Then the localising centre location at *T*+1 is

$$\boldsymbol{\chi}_{i}^{T+1} \approx \boldsymbol{\chi}_{i}^{T} - g \,\overline{\nabla \mathbf{A}}_{i}^{T}.$$
(5.15)

Although the SM model provided the best fit to data in P_1 (see Results), the DI model fit was similar (Figure 5.B3). The DI model was also much faster to fit, since scent marks in the discretised SM model take considerable computation time to equilibriate. We therefore used the DI model to investigate group formation and territory movement, as the inclusion of multiple timesteps itself increased the time required for each model fit. Because of their poor performance in P_1 , we did not include group size or elevation in the candidate model sets for P_2 and P_3 .

To model group formation, we focused on three groups during P₂: initially adjacent groups GG and Y and their daughter group, CD (formed at the beginning of October, 2004). In order to minimise edge effects, we chose the model domain (Ω_2 : north-south square from 34J 580500 7014250 in the southwest to 34J 585750 7019500 in the northeast) to include surrounding groups (B, E, L, RR, V, and W), but we based likelihood calculations on the three focal groups only. We used a 68 by 68 spatial grid, to match the spatial scale in P₁, and divided the eighteen-month period into six timesteps of three months. Our candidate model set (see Table 5.3) included models with the group-formation modfication, (5.8), and models in which all groups interacted at full strength throughout . For each timestep in P₂, we simulated models as in P₁, except when interactions between parent and daughter groups increased according to (5.8), with the exponential term discretised as in (5.12) and *k* fit as a free parameter.

To model territory movement in P₃ we focused on group CD's range shift to the northeast of the study site. We based likelihood calculations on the single group, but again chose the model domain (Ω_2 : north-south square from 34J 582500 7013500 in the southwest to 34J 588500 7019500 in the northeast) to include, where possible,

peripheral groups (GG, KU, RR, V, and W). We used a 77 by 77 spatial grid, again to match the scale in P₁, and divided P₃ into eight one-month timesteps (since groups have a tendency to move relatively quickly). We started timesteps halfway through each month to correspond with the extinction of groups GG and V (at the end of timesteps two and six, respectively) and the formation of group KU (at the start of timestep four). Our candidate model set (Table 5.4) included models with and without the territory-movement, (5.10), and terrain-avoidance, (5.11), modifications. We determined localising centres empirically, as in P₁, for CD in the first timestep and for peripheral groups, where possible. Subsequently, we allowed χ^{T}_{CD} to move according to (5.15), with g fit as a free parameter. For models without territory movement, $\chi^{\rm \scriptscriptstyle T}_{\rm \scriptscriptstyle CD}$ remained fixed at its initial location. For RR and V after timestep four, and for KU after timestep six, relocation data were extremely sparse or missing, and we based each group's localising centre on it's relocation data in all previous timesteps combined. Given that RR and KU remained in the same approximate positions subsequently (T. Clutton-Brock, unpublished data), this would seem to be a reasonable solution to the problem of missing data. We fit α_r as a free parameter.

To compare models in each period of interest, we used Akaike's information criterion (AIC; Akaike 1973) and the Bayesian information criterion (BIC; Schwarz 1978). AIC has been criticised in the past for favouring overly complex models, especially when used with large datasets (Kass and Raftery 1995). BIC penalizes model complexity while taking dataset size into account, and Bayesian derivations of both AIC and BIC are possible, indicating that the associated prior assumptions are strongest for AIC (Kass and Raftery 1995, Bolker 2008). BIC may, therefore, be a good criterion for model comparison with large datasets, though opinion is divided (*e.g.* Burnham and Anderson 2002). Given the size of our dataset, we present both criteria, which are minimised for "best" models. Between models, AIC and BIC differences of less than two provide weak evidence that the minimum-information-criterion model is better, while differences of more than ten provide strong evidence (Burnham and Anderson 2002, Bolker 2008).

5.5.3 Statistical Software

We performed model optimisation and spatial data manipulation using R 2.15.0 (R 2011). We used the *landsat* (Goslee 2011), *raster* (Hijmans and van Etten 2012), and *rgdal* (Keitt et al. 2012) packages for spatial data manipulation. We used Google Earth (Google Inc. 2012) to generate and export reserve-extent data to calculate grass cover in 2007-2008 (riverbed portion of SAND data within the confines of the study site: Figure 5.B2). For improved speed, we implemented PDE discretisations in the C programming language and interfaced the compiled code with R. We could then easily incorporate spatial information and other model features, fitting parameter values with R's *optim* optimiser.

5.6 Results

We fit mechanistic home-range models, describing territorial patterns in meerkat social groups that form as a balance between random diffusion and advection directed towards a home-range core. In modelling stable patterns, we compared model formulations in which advection resulted from contact with other groups' scent marks (the SM model) to those in which advection resulted from direct interactions with other groups (the DI model). We also considered modifications that incorporate group size and habitat selection based on elevation, sand type, and sand-type interface.

We then extended the direct-interaction model to investigate territory formation and territory movement. First, we considered increasing effective interaction strengths between parent and newly-formed daughter groups. Next, we considered movement of a group's attracting core area, towards regions of low advection speed.

5.6.1 General Model

The model that best described stable meerkat home-range patterns was the SM model, (5.4), without dependence on group size (N_i set to one, for all i) and with $h(\mathbf{x}) = \text{EDGE}$ (Table 5.2). The model describes space use that adapts to neighbouring groups and is concentrated along the edges of the riverbed and flats habitats (Figure 5.1).



Figure 5.1: Stable meerkat home-range distributions on the Kuruman River Reserve, South Africa, between January 1st, 2003 and December 31st, 2003. Contour lines represent individual groups' utilisation distributions, produced by the Lewis-Murray scent-marking model (see text), without group-size dependence and incorporating movement in relation to sand-type edge habitat. Points represent GPS relocations of actual meerkat groups. Group identifiers (black text) show the location of groups' relocation centroids, used as localising centres in the model.

AIC and BIC gave similar results. In general, models without group size performed better than those including group size, and sand-type edge was a better predictor of space use than was sand type itself, which was in turn better than elevation (and all habitat types were better than nothing; Table 5.2). While models that included scent marking performed better than the direct-interaction models, the best SM model and the best DI model produce very similar results (Figure 5.B3). SM models described utilisation distributions that were slightly more flat-topped and steep-sided.

Though all models captured the general pattern of space use where groups were tightly packed in the riverbed, and group spacing is determined empirically in the model, habitat features greatly improve the fit within groups' home ranges (Figure 5.B4).

model	terrain	group [†]	c/d^{\ddagger}	т	α_h	$-\Sigma \ln(\mathcal{L})$	number of	ΔΑΙϹ	ΔBIC
SM	_	-	2 40	0.0253	_	-4220.88	2	111.0	105.7
SM	_	+	2.40 0.12	0.0233	_	-4170.76	$\frac{2}{2}$	211.0	206.0
SM	DEM	_	2 50	0.0025	0 770	-4170.70	2	100 5	100.5
SM	DEM	1	2.30	0.0190	0.770 0.421	-4227.13	3	205.0	205.0
SIVI	DEM	+	0.11	0.0022	0.421	-41/4.90	5	205.0	205.0
SM	SAND	-	2.47	0.0118	0.522	-4253.22	3	48.4	48.4
SM	SAND	+	0.12	0.0017	0.587	-4211.88	3	131.0	131.0
SM	EDGE	_	2.47	0.0169	0.946	-4277.40	3	0.0	0.0
SM	EDGE	+	0.13	0.0013	0.945	-4226.04	3	102.7	102.7
DI	_	_	5.87	_	_	-4206.14	1	138.5	127.9
DI	_	+	6.18	_	_	-4123.51	1	303.8	293.1
DI	DEM	_	6.87	_	0.970	-4218.44	2	115.9	110.6
DI	DEM	+	6.07	_	0.762	-4130.23	2	292.3	287.0
DI	SAND	—	5.44	_	0.556	-4248.11	2	56.6	51.3
DI	SAND	+	5.64	_	0.627	-4173.07	2	206.7	201.3
DI	EDGE	—	5.74	_	0.944	-4267.75	2	17.3	12.0
DI	EDGE	+	6.02	_	0.945	-4190.95	2	170.9	165.6

Table 5.2: Model-fitting summary for mechanistic home-range models. Model fit to 1504 meerkat group relocations recorded in 2003, when patterns were stable.

[†] Observed mean group sizes were: 19.14 (B), 14.71 (D), 28.43 (E), 30.86 (F), 9.43 (GG), 13.86 (L), 8.14 (MM), 21.86 (RR), 26.57 (V), 16.86 (W), 4.80 (XX), 18.14 (Y), and 15.71 (ZZ).
 [‡] Equilibrium home range patterns depend on the ratio of advection to diffusion constants

5.6.2 group-formation model

Territorial patterns in the fifteen months after group CD formed were best captured by a model in which interactions between GG and CD and between Y and CD (parent and daughter groups) increased over time (Table 5.3). Again, EDGE performed better than SAND in predicting space use (Table 5.3). The model produced a pattern whereby CD's use of space initially overlapped that of Y and GG (Figure 5.2) - a pattern clearly present in the data but absent from the model without a gradual increase in interaction strength (compare Figure 5.2 to Figure 5.B5).

Table 5.3: Model-fitting summary for direct-interaction mechanistic home-range models incorporating a group-formation submodel, which allows for increasing interaction strength between parent and daughter groups (see text). Models fit to 908 meerkat group relocations across six three-month timesteps between July 1^{st} , 2004 and December 31^{st} , 2005. A dash ("–") indicates that the associated term was not included in the model.

terrain	c/d^\dagger	$lpha_h$	k	$-\Sigma \ln(\mathcal{L})$	number of parameters	ΔΑΙϹ	ΔBIC
SAND	0.556	-0.453	_	-1775.42	2	194.4	189.6
SAND	0.976	-0.584	0.300	-1871.79	3	3.6	3.6
EDGE	0.516	0.740	—	-1784.51	2	176.2	171.4
EDGE	0.936	1.197	0.311	-1873.61	3	0.0	0.0
*	1		1 1	1	11.00		

[†] Equilibrium home range patterns depend on the ratio of advection to diffusion constants



Figure 5.2: Territory formation in group CD. Contour lines show utilisation distributions, as described by a direct-interaction home-range model (see text) in which interaction strength of CD with Y and GG (its parent groups) starts at zero in timestep 1 and increases through timestep 5. Groups spend more time at interfaces between sand types (white background). Timesteps are three months each, starting July 1st, 2004 and ending December 31st, 2005. Points represent GPS relocations of actual meerkat groups. Group identifiers (black text) show the location of groups' relocation centroids, used as localising centres in the model.

5.6.3 territory-movement model

The territory-movement model including terrain (as a proxy for sour grass) avoidance best described changes in group CD's space use, performing better than models with a static localising centre (Table 5.4). While $h(\mathbf{x}) = \text{EDGE}$ generated the absolute minimum AIC and BIC values, $h(\mathbf{x}) = \text{SAND}$ generated a fit that is statistically as good (Table 5.3).

The best model (incorporating EDGE) captures many features of CD's space use, presenting a description whereby patterns change as a result of both changes in the set of surrounding groups and shifts in CD's localising centre (Figure 5.3). The disappearance of GG and V, and the appearance of KU, shifted CD's space use about its localising centre, and the localising centre tended to move away from neighbouring groups into less crowded habitat. The model incorporating SAND provides a broadly similar description (Figure 5.B6).

Table 5.4: Model-fitting summary for direct-interaction mechanistic home-range models incorporating the territory-movement submodel (see text). Models fit to 187 relocations of the "CD" meerkat group across eight one-month timesteps between June 15th, 2007 and February 14th, 2008. A dash ("-") indicates that the associated term was not included in the model.

terrain	c/d^\dagger	α_h	α_r	g/d^\dagger	$-\Sigma \ln(\mathcal{L})$	number of parameters	ΔΑΙϹ	ΔBIC
SAND	0.524	0.73	_	_	-221.891	2	115.5	109.1
SAND	0.528	0.74	_	-4.94 x10 ⁻⁴	-222.053	3	117.2	114.0
SAND	0.958	1.30	0.301	_	-268.697	3	23.9	20.7
SAND	0.733	1.30	0.173	1.91 x10 ⁻³	-281.215	4	0.9	0.9
EDGE	0.577	1.30	_	-	-241.958	2	75.4	68.9
EDGE	0.572	1.30	_	$1.06 \text{ x} 10^{-3}$	-242.994	3	75.3	72.1
EDGE	0.644	1.30	0.098	_	-247.986	3	65.3	62.1
EDGE	0.660	1.26	0.107	3.31×10^{-3}	-281.658	4	0.0	0.0
† F • • • • •	• •			1 .1 .1	C 1	11.00 1		

Equilibrium home range patterns depend on the ratio of advection to diffusion constants



Figure 5.3: Territory movement in group CD. Contour lines show utilisation distributions, as described by a direct-interaction home-range model, in which CD's localising centre moves down the average advection-speed gradient (see text for details) from one timestep to the next. Timesteps are one month, starting June 15th, 2007 and ending February 14th, 2008. Groups spend more time at interfaces between sand types (white background). Points represent group GPS relocations. Group codes (black text) show the location of localising centres, determined (except for CD) by the centroid of each group's GPS data in the corresponding timestep. Grey "CD"s show the location of group CD's empirically determined localising centre in timestep 0.

5.7 Discussion

Mechanistic home-range models, fit to meerkat space-use data, successfully described meerkat home ranges based on interactions with neighbouring groups and habitat selection patterns. These models provided particularly good descriptions of stable space-use patterns for groups from the core of the study area (to which models were fit; Figure 5.1), and modifications to the basic models captured features of dynamic patterns in periods of group establishment and movement (Figures 5.2, 5.3).

5.7.1 Scent Marking

Our results suggest that meerkat groups use scent-marking to reinforce spaceuse patterns. Caution would be prudent in drawing conclusions, however, since untested model formulations, involving memory or other feedback patterns, could generate similar stable patterns. That said, scent cues are clearly important in meerkat behaviour, and scent marking has been implicated in meerkat mate guarding and territory defence (Jordan 2007, Jordan et al. 2007, Mares et al. 2011). For dominant males, which must guard against cuckolding and complete group takeovers by foreign males (Spong et al. 2008, Mares et al. 2012), scent marking related to mate guarding and to territory defence may manifest in very similar ways (Mares et al. 2011). With respect to fecal marking in meerkat groups, dominant males engage in the most mark deposition and mark inspection (Jordan 2007, Mares et al. 2011), and groups' responses may be strongly influenced by dominant males' behaviour (Mares et al. 2011).

Observed patterns of scent marking are consistent with those we would expect if our best models are accurate. In a timeframe that largely overlapped with the one we used to fit our model of stable territorial patterns (period P_1), Jordan *et al.* (2007) found that latrine use was not concentrated in home-range borders, consistent with our best model's prediction of a low overmarking rate (consider Figure 5.B3). Also, while all individuals scent mark to some extent, group size and composition seem to have little effect on overall rates of fecal marking (Jordan 2007), an observation consistent with the lack of group-size dependence in our best-fitting models.

5.7.2 Group Size and Establishment

The lack of evidence for a direct group-size effect was somewhat surprising, given the benefits associated with group size in meerkats' inter-group interactions (Young 2003). It arguably offers circumstantial evidence that scent marking, performed disproportionately by a single dominant male in each group, mediates territorial interactions.

On the other hand, territorial group-size independence is wholly consistent with the observation that meerkat mean group size closely tracks population density (Bateman et al. in press), which changes in response to environmental conditions (Bateman et al. 2011a). It would seem that group size fluctuates over time within relatively consistent territories. Data from foxes, *Vulpes vulpes*, suggest a close

analogue; fox pairs calibrate territory size to resource availability in bad years, with group size increasing, rather than territory size shrinking, in years of plenty (Lindström 1989). In fact, establishment of territories based on food availability in poor conditions, and maintenance of those territories even in good conditions, may be a common pattern in the carnivora (Bertram 1975, Macdonald 1983).

Although group size does not seem to influence home-range size directly, our model of group establishment suggests a mechanism whereby large, productive groups could benefit. Larger meerkat groups tend to produce more numerous large dispersing coalitions, and therefore have the potential to establish more new groups (Young 2003, Bateman et al. in press). If our model is correct, it proposes a mechanism by which related groups could "carve out" territory. Even if parent and daughter groups do not actually tolerate each other *per se* (violent interactions certainly occur; Drewe et al. 2009b), the resulting influence on surrounding groups may be the same. Elevated density of overlapping breeding groups (Figure 5.2) would effectively push neighbouring groups out of an area, helping to avail habitat for the newly formed group. In this way, breeders might help to ensure that their progeny gained access to adequate habitat.

5.7.3 Habitat Selection and Seasonal Patterns

From our models, habitat type is clearly an important factor in determining meerkat space use. At a local scale, evidence suggests that meerkats prefer regions at the interface between clay-sand flats and ferrous-sand dunes (Figures 5.1-5.3). Notably, the inclusion of sand type (the next best predictor of space use; Table 5.2) produced ambiguous results: in the stable-territory models, groups showed a preference for clay sand, but in territory-formation models, groups showed the opposite preference (Tables 5.2, 5.3; territory-movement models must balance habitat preference with movement preference, so do not allow such clear interpretation). This has at least two potential explanations. First, annual conditions could have affected patterns; 2003 was a particularly dry year, while 2004/2005 was wet, and sour grass growth (as in 2007/2008) or prey availability in the riverbed may have played a role. Second, different choices of modelling domain may have forced apparent sand-type preference to switch between the model periods, when true preference is for edge habitat. In fact, this observation is what led to our consideration of edge habitat in the first place (as reported in section 5.4, Mathematical Models).

At a broad scale, meerkats seem to prefer the riverbed region to surrounding habitat (Clutton-Brock et al. 1999b), though at a finer scale they may seasonally prefer dune edges to the riverbed itself (Turbé 2006). Levels of both foraging success and predation risk are likely to affect this pattern. In nearby Botswana, substrates with a high clay content (like the riverbed and flats) appear to exhibit greater primary productivity, per unit rainfall, than low-clay substrates (Nicholson and Farrar 1994). The riverbed and flats also offer more "bolt hole" refuges than do the dunes (Manser and Bell 2004) and may offer lower levels of predation risk (Turbé 2006). Meerkats seem to prefer less productive, but less risky, flats habitat during the dry season, when foraging necessitates risk-prone digging, but they move to dune edges in the wet season, when an abundance of surface prey facilitates less risky, and highly profitable, foraging behaviour there (Turbé 2006)

We did not assess seasonal changes in interaction patterns or habitat preferences. Given the computational cost in fitting our models, even with only a few parameters, we deemed this infeasible for the current study. As a result, a preference for edge habitat in our models may represent an average across seasons, though seasonal trends are not immediately apparent from GPS data (Figures 5.2, 5.3). Future work should focus on this aspect of space use. Specifically, seasonal and interannual fluctuations in the rain-limited environment of the Kalahari, as well as seasonal breeding-related behaviours (see below), may play important roles in patterns. Analysis of prey availability and risk across habitat types and climatic conditions would be valuable (*e.g.* see Moorcroft et al. 2006).

Notably, breeding status can change territorial patterns (*e.g.* jackals, *Canis mesomelas* and *C. adustus*: Loveridge and Macdonald 2001; shrews, *Sorex araneus*: Wang and Grimm 2007). For meerkats, babysitting of pups at the natal burrow necessitates central-place foraging, while more fluid movement patterns are possible at other times (Turbé 2006). Also, when males prospect for extra-group matings, often during peak female fertility (Young et al. 2007, Mares et al. in preparation), they sometimes seem to draw their groups with them towards neighbouring groups (Mares et al. in preparation, T. H. Clutton-Brock unpublished data). As prospecting is related to male dispersal (Young 2003), such a process may also be able to explain some range shifts, if groups are drawn by dispersing male coalitions.

5.7.4 Territory Movement

From our model of territory movement, it appears that factors affecting movement patterns within a territory can also partly explain shifts in territory location. Our approach partially addresses one of the major criticisms of many mechanistic home-range models - that territorial patterns rely on a focal point chosen *a priori* (even if it is estimated from the data; Börger et al. 2008). Our models were, however, unable to capture dramatic shifts in localising centre, and much of the change in home range patterns resulted from altered local interactions as surrounding groups formed and disappeared, a process that has been noted previously (Moorcroft et al. 2006).

Other factors, which we did not consider, could easily influence group movement. For example, the availability of sleeping burrows, which are most dense in the riverbed, flats, and low dunes (Turbé 2006), could influence large-scale habitat selection. Also, even if group size does not obviously affect stable territorial patterns, large groups do enjoy advantages in group interactions (Young 2003) and seem to have more scope to position or reposition their home ranges by forcing other groups out of desirable habitat (T. P. Flower, personal communication).

5.7.5 Modelling Considerations

Due to dependence on initial conditions, any mechanistic model used with real data must be anchored in empirical observation. Because a model's localising centre and the centroid of its resulting home-range distribution do not necessarily coincide, the centroid of relocation data is not, inherently, the most representative choice of localising centre (*e.g.* locating the localising centre for group ZZ further to the northeast would have likely produced more realistic results: Figure 5.1). The use of the relocation centroid represents, however, a convenient and robust simplifying assumption that has produced good empirical results (Moorcroft et al. 1999, 2006, Smith et al. 2012, this study).

The concept of a localising centre is, itself, a simplification. Except perhaps when young pups remain at their natal burrow (Turbé 2006), meerkats do not have a clear single point of attraction in their home ranges. The idea of a core foraging area (Moorcroft et al. 1999) may apply, but, in reality, the multiple burrows within each meerkat group's home range may serve as multiple attraction points (Don and Rennolls 1983).

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Memory processes likely play an important role in space-use patterns. Van Moorter *et al.* (2009) propose a home-range model in which movement from any given location relies on a "dynamic attractor field" incorporating the "utility" of multiple surrounding locations and both working and reference memory of already-visited locations. Their model can produce stable home ranges without the need for territorial interactions, a characteristic that may be necessary for studying meerkat space use in sparsely populated habitat (e.g. group CD in the latter timesteps of P₃: Figure 5.3, and peripheral groups generally). More broadly, individual (and group) movement decisions depend on state, phenotype, and experience, but our current understanding of how animals integrate multiple sources of information is rudimentary (Morales et al. 2010). The use of memory in movement models has, so far, been a largely theoretical exercise, but its addition to mechanistic home-range models for use with empirical data is plausible (Morales et al. 2010). This might be a fruitful avenue for future research.

5.7.6 Further Implications and Future Work

Beyond the inherent relevance to spatial patterns themselves, territorial patterns are highly relevant to population dynamics more generally. Indeed, the dynamics of populations are inherently spatial processes, and even the simplest mass-action models are based on underlying simplifications of space-dependent models (Morales et al. 2010). Spatial structure can strongly influence population dynamics (Frank and Brickman 2000, Fagan et al. 2007), and group living and territoriality, specifically, can have important impacts on demography, dispersal, and community structure (Packer et al. 2005, Fagan et al. 2007, Wang and Grimm 2007). If we aim to develop mechanistic understanding of population processes, we therefore need to develop mechanistic understanding of the associated spatial processes. Whether we aim to understand the biology of a given species, or patterns across species, understanding spatial patterns is crucial.

Dispersal is one aspect of population dynamics for which spatial patterns are of utmost importance, and which has yet to be empirically explored in detail for meerkats. Improving knowledge of how groups select habitat, locally and at the landscape level, will be critical to understanding dispersal patterns. Emigration, in particular, plays a strong role in meerkat group dynamics (Bateman et al. 2011b, Bateman et al. in press), and dispersal is an important (and sometimes under-

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emphasized) aspect of population dynamics generally (Bowler and Benton 2005, Clobert et al. 2009). Territorial patterns directly affect groups' access to resources, with implications for individual condition that may impact dispersal decisions, and patterns of group movement and space use are likely to alter the movement and settlement decisions of dispersers (Clobert et al. 2009). Thus, understanding determinants of home-range behaviour is likely key to understanding all three phases of dispersal: emigration, transience, and settlement (Bowler and Benton 2005).

Multiple approaches have been used in the past to study spatial patterns, among them resource selection analysis, mechanistic movement models, and statistical home range models. Our approach has incorporated aspects of each, informed by behvaioural knowledge, to take advantage of a rich empirical dataset and extend existing models. In the future, the potential to unify behavioural, spatial, demographic, and evolutionary aspects of population dynamics into coherent models (*e.g.* Lewis and Moorcroft 2001, Haydon et al. 2008) presents exciting possibilities (Börger et al. 2008).

Future work will aim to explore further details of meerkat territoriality, such as seasonal patterns and group movement. Ultimately, we hope to link knowledge of spatial patterns with work on group dynamics and dispersal to gain further insight into the ecological and evolutionary processes at play for this cooperative breeder.

5.A Appendix A: Details of Partial Differential Equation Discretisation

We present the discretisation for the SM model without habitat selection or terrain avoidance. Implementation of these modifications, and of the DI model, is trivial, given the steps outlined below.

Let $u_i^{a,b,n}$ and $p_i^{a,b,n}$ be discrete analogues of $u_i(\mathbf{x},t)$ and $p_i(\mathbf{x},t)$, respectively, for space indices $a \in [1, A]$ and $b \in [1, B]$ (the region Ω) and time index $n \ge 1$. The associated discrete space- and time-steps were $\Delta x = 1/(A-1)$, $\Delta y = 1/(B-1)$ and Δt on the order of 0.0002 (adjusted downwards if error propagation became a problem). We used discretised bivariate normal distributions, centred at each group's localising centre, as initial conditions for $u_i^{a,b,n}$ and $p_i^{a,b,n}$. Starting at timestep n=1, we iterated the following discretised equations over all a,b in Ω until $\Delta u/\Delta t$ was less than 0.1 for all a, b, and i (in initial testing, this produced results that were extremely close to those attained when we allowed the simulation to run to machine tolerance, a much slower process).

5.A.1 Scent-mark Distribution

We discretised

$$\frac{\partial p_i}{\partial t} = u_i \left[1 + m \sum_{j \neq i} \left(p_j \right) \right] - p_i$$
(5.A1)

as:

$$\frac{p_{i}^{a,b,n+1} - p_{i}^{a,b,n}}{\Delta t} = u_{i}^{a,b,n} \left[1 + m \sum_{j \neq i} \left(p_{j}^{a,b,n} \right) \right] - p_{i}^{a,b,n}$$

$$\Rightarrow p_{i}^{a,b,n+1} = p_{i}^{a,b,n} + \Delta t \left[u_{i}^{a,b,n} \left[1 + m \sum_{j \neq i} \left(p_{j}^{a,b,n} \right) \right] - p_{i}^{a,b,n} \right].$$
(5.A2)

5.A.2 Space Use (Interior)

Letting $\hat{\mathbf{v}}_{i}^{a,b} = (v_{x,i}^{a,b}, v_{y,i}^{a,b})$ be the discrete analogue of $\hat{\mathbf{v}}_{i}(\mathbf{x})$, we discretised

$$\frac{\partial u_i}{\partial t} = d\nabla^2 u_i - c\nabla \cdot \left[u_i \hat{\mathbf{v}}_i \sum_{j \neq i} \left(p_j \right) \right]$$
(5.A3)

as:

$$u_{i}^{a,b,n+1} = u_{i}^{a,b,n} + \Delta t \left[d \left[\frac{u_{i}^{a+1,b,n} - 2u_{i}^{a,b,n} + u_{i}^{a-1,b,n}}{(\Delta x)^{2}} + \frac{u_{i}^{a,b+1,n} - 2u_{i}^{a,b,n} + u_{i}^{a,b-1,n}}{(\Delta y)^{2}} \right] - c \left[\frac{u_{i}^{a+1,b,n} v_{x,i}^{a+1,b} \sum_{j \neq i} \left(p_{j}^{a+1,b,n} \right) - u_{i}^{a-1,b,n} v_{x,i}^{a-1,b} \sum_{j \neq i} \left(p_{j}^{a-1,b,n} \right)}{2\Delta x} + \frac{u_{i}^{a,b+1,n} v_{y,i}^{a,b+1} \sum_{j \neq i} \left(p_{j}^{a,b+1,n} \right) - u_{i}^{a,b-1,n} v_{y,i}^{a,b-1} \sum_{j \neq i} \left(p_{j}^{a,b-1,n} \right)}{2\Delta y} \right] \right]$$
(5.A4)

for all a, b in the interior of Ω .

5.A.3 Space Use (Boundary)

The zero-flux boundary condition is:

$$0 = \left[d\nabla u_i - c u_i \hat{\mathbf{v}}_i \sum_{j \neq i} \left(p_j \right) \right] \cdot \mathbf{n} .$$
 (5.A5)

On the *x*-boundaries of Ω , **n** is (-1,0) at x = 0 (a = 1) and (1,0) at x = 1 (a = A), and in either case, (5.A5) becomes

$$0 = d \frac{\partial u_i}{\partial x} - c u_i \hat{\mathbf{v}}_i \sum_{j \neq i} (p_j).$$
(5.A6)

Using a first-order approximation of $\partial u_i / \partial x$, the discretisations for a=1 and a=A are:

$$\frac{u_{i}^{2,b,n+1} - u_{i}^{1,b,n+1}}{\Delta x} = cu_{g}^{1,b,n+1}v_{x,i}^{1,b}\sum_{j\neq i} \left(p_{j}^{1,b,n+1}\right)$$

$$\Rightarrow u_{i}^{2,b,n+1} = u_{i}^{1,b,n+1} \left[1 + \Delta x cv_{x,i}^{1,j}\sum_{j\neq i} \left(p_{j}^{1,b,n+1}\right)\right] \qquad (5.A7)$$

$$\Rightarrow u_{i}^{1,b,n+1} = u_{i}^{2,b,n+1} / \left[1 + \Delta x cv_{x,i}^{1,j}\sum_{j\neq i} \left(p_{j}^{1,b,n+1}\right)\right], \text{ and}$$

$$\frac{u_{i}^{A,b,n+1} - u_{i}^{A-1,b,n+1}}{\Delta x} = cu_{i}^{A,b,n+1}v_{x,i}^{N,b}\sum_{j\neq i} \left(p_{j}^{A,b,n+1}\right)$$

$$\Rightarrow u_{i}^{A-1,b,n+1} = u_{i}^{A,b,n+1} \left[1 - \Delta x cv_{x,i}^{A,b}\sum_{j\neq i} \left(p_{j}^{A,b,n+1}\right)\right]$$

$$\Rightarrow u_{i}^{A,b,n+1} = u_{i}^{A-1,b,n+1} / \left[1 - \Delta x cv_{x,i}^{A,j}\sum_{j\neq i} \left(p_{j}^{A,j,n+1}\right)\right]$$

(similarly for the *y*-boundaries).

5.A.4 Error Management

To deal with small errors that arose, we used two additional updating rules: 1) if any $u_i^{a,b,n+1}$ is less than zero, set it to zero, and 2) divide all $u_i^{a,b,n+1}$ by $\sum_{a=1}^{A-1} \sum_{b=1}^{B-1} \left[\frac{u_i^{a,b,n+1} + u_i^{a+1,b,n+1} + u_i^{a+1,b+1,n+1}}{4} \Delta x \Delta y \right]$ (used to approximate $\iint_{\Omega} u_i dx dy$).

5.B Appendix B: Additional figures



Figure 5.B1: Candidates for $h(\mathbf{x})$: DEM (a) - elevation data from a digital elevation model, with lighter grey indicating higher elevations; SAND (b) - sand type, with white indicating clay and grey indicating ferrous sand; and EDGE (d) - sand-type edge, with white indicating high standard deviation in SAND values across a pixel and its four orthogonally adjacent neighbours. DEM and SAND are average values for a 100 by 100 grid, with extreme locations centred on the coordinates shown, and EDGE was derived directly from SAND.



Figure 5.B2: Riverbed habitat on the Kuruman River Reserve (derived from SAND data in Figure B1), relevant to territory-movement model (see text). White regions used as proxy for presence of sour grass between July 1^{st} , 2004 and December 31^{st} , 2005.



Figure 5.B3: Stable meerkat home-range distributions produced by the Lewis-Murray scent-marking model (a) and the direct-interaction model (b), on and near the Kuruman River Reserve, South Africa, between January 1st, 2003 and December 31st, 2003. Contour lines represent individual groups' utilisation distributions, points represent GPS relocations of actual meerkat groups, and group identifiers (black text) show the location of groups' relocation centroids, used as localising centres in the model.



Figure 5.B4: Stable meerkat home-range distributions produced by the Lewis-Murray scent-marking model, on and near the Kuruman River Reserve, South Africa, between January 1st, 2003 and December 31st, 2003. Contour lines represent individual groups' utilisation distributions without habitat selection (a); where groups prefer low elevation habitat (b); where groups prefer clay sand, in white, over ferrous sand (c); and where groups prefer sand-type edges and scent marking rate depends on group size (d). Points represent GPS relocations of actual meerkat groups, and group identifiers (black text) show the location of groups' relocation centroids, used as localising centres in the model.



Figure 5.B5: Territory formation in group CD. Contour lines show utilisation distributions, as described by a direct-interaction home-range model (see text) in which interaction strength between all groups is consistent throughout. Groups spend more time at interfaces between sand types (white background). Timesteps are three months each, starting July 1st, 2004 and ending December 31st, 2005. Points represent GPS relocations of actual meerkat groups. Group identifiers (black text) show the location of groups' relocation centroids, used as localising centres in the model.



Figure 5.B6: Territory movement in group CD, where groups spend more time on clay sand (white background) than ferrous sand (grey background). Contour lines show utilisation distributions, as described by a direct-interaction home-range model, in which the localising centre of group CD moves down the group's average advection speed gradient (see text for details) from one timestep to the next. Timesteps are one month each, starting June 15th, 2007 and ending February 14th, 2008. Points represent GPS relocations of actual meerkat groups. Group identifiers (black text) show the location of groups' localising centres in the model, determined (except for CD) by the centroid of each group's relocation data in the corresponding timestep. Grey "CD"s show the location of group CD's empirically determined localising centre in timestep 0.
General Discussion

6.1 Overview

The population dynamics of cooperative breeders are likely to differ from those of conventional breeders. Population structure, resulting from social grouping within populations and distinct breeding roles within groups, and Allee effects, resulting from cooperation, both play potentially important roles. Understanding observed patterns of population and group dynamics and the resulting implications for individual and inclusive fitness, requires elucidation of the underlying mechanisms. In this thesis, I used mathematical and statistical models to analyse detailed meerkat (*Suricata suricatta*) data from over a decade of field study in the Kalahari. I initially examined broad-scale patterns, and then considered details of two constituent processes: group dynamics and territorial dynamics.

In Chapter Two, I used simple population-dynamics models to identify conventional density-dependence and an effect of rainfall in inter-annual populationlevel dynamics. I did not detect a population-level Allee effect, although statistical power was low due to the short time series available. Potential conclusions were limited, since models were blind to the underlying processes.

In Chapter Three, I went on to consider group-level dynamics at the same inter-annual timescale, where dynamics again appeared conventionally densitydependent, and group size declined sharply after (not during) years of low rainfall. Breaking group dynamics into constituent demographic rates, I showed that conventional density dependence resulted because only survival (a relatively minor contributor to group dynamics) exhibited an Allee effect, and that crashes in group size after dry years resulted from spikes in emigration.

In Chapter Four, I examined in more detail the patterns identified in the previous chapter by considering contributions from individuals of different age, sex, and dominance classes on a shorter timescale. Dynamical patterns are, in part, a result of stage structure within groups: breeding is reduced and mature subordinates do not emigrate as frequently in dry years, but emigration resumes in immediately subsequent years, by which time age structure has shifted towards the older age classes more likely to disperse.

In Chapter Five, I modelled the territorial processes by which established social groups interact, as well as some of the dynamics of group formation and movement. Intriguingly, larger groups did not seem to enjoy an advantage in controlling larger established territories. While this chapter was, in part, an exercise in further developing mechanistic home-range models, it will also help tie knowledge of group dynamics and future work on dispersal into a coherent model of overall population dynamics.

6.2 Density Dependence and the Allee Effect

I found support for only conventional density dependence in population-level meerkat dynamics. Given the short time series used in Chapter Two, detection of a population-level Allee effect would have been unlikely, even if one exists. Still, given past evidence for component Allee effects in survival and reproduction (Clutton-Brock et al. 1999a, Courchamp et al. 1999b, Hodge et al. 2008), and what previously appeared to be rain-induced demographic Allee effects in another meerkat population (Clutton-Brock et al. 1999a), a population-level effect would not have been surprising.

Work on other species, across taxa, suggests that Allee effects may actually be less common than some authors have supposed (Myers et al. 1995, Gregory et al. 2010). One explanation is that species prone to low population sizes or densities would be subject to strong selection pressure against Allee effects, and we should perhaps expect to see behavioural "ghosts of Allee effects past," rather than Allee effects themselves (Courchamp et al. 2008). Still, some Allee effect mechanisms, such as a reduced ability to find mates, may be ubiquitous at very low densities. More study will be required to determine if, or at what density, meerkat populations are subject to an Allee effect.

The lack of a demographic Allee effect at the group level (Chapters Three and Four) was surprising. Past studies have shown positive associations between group size and survival (Clutton-Brock et al. 1999a) and group size and reproduction (Hodge et al. 2008). My findings support the pattern for survival, but not for reproduction. The reason for the lack of effect in reproduction seems to lie in the distinction (often not made explicitly) between individual reproductive success and average per-capita reproductive success. Because of the inherent relationship between the two, what appear to be component Allee effects for a dominant breeder

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can often produce entirely conventional density dependence, when viewed from an average group member's perspective (Figure 6.1), *i.e.* as a component of the relevant per-capita group growth rate (Stephens et al. 1999).



Figure 6.1: Illustration of relationship between hypothetical component Allee effects in reproductive success (recruitment) of the focal breeder in a social group (A) and the equivalent per-capita patterns when reproductive success is averaged across all members of the social group (B). All curves, *y*, in B are transformations of the correspondingly patterned curves in A, such that $y_B = y_A/(\text{group size})$. Curves i and ii both show strong positive associations between group size and recruitment for the individual breeder (A), but only ii retains a positive association in average per-capita recruitment (B). In general, a *group-level* component Allee effect only persists if the slope of a line, passing through the origin and a point on the relevant *individual-level* recruitment curve, increases as that point moves along the curve away from the origin (as for the lower portion of ii in A). Example curves i and ii in A are defined by conventional and Allee-effect Beverton-Holt functions (Beverton and Holt 1957), respectively. Note that curves in B are undefined at zero group size, and are shown as smooth functions for the purposes of illustration only. Grey curves are shown for reference.

This distinction may help to reconcile other, seemingly conflicting reports, notably in wild dogs. A number of studies have found positive relationships between group size and breeding success in wild dogs (Courchamp and Macdonald 2001 and references therein, Gusset and Macdonald 2010, Woodroffe 2011), but others have failed to find population-level density dependence in reproduction (Creel and Creel 2002) or have found overall negative density dependence (Somers et al. 2008). Reproductive output per group (comparable to individual recruitment in Figure 6.1A) resembles curves i and ii in Figure 6.1A (Creel and Creel 2002, Woodroffe 2011), which may or may not produce Allee effects in per-capita reproductive success. As with meerkats (Chapters Three, Four), data are sparse for small groups, making the relevant form of any recruitment function difficult to identify. In stochastic environments, however, extinction of small groups is common, regardless of potential Allee effect (Chapter Four, Dennis 2002). Also, population-level patterns depend on

the dispersal processes that link groups and potentially fill vacant habitat, in addition to group-level density dependence (Hanski 1999).

Density-dependent patterns are potentially also habitat- and environmentdependent (wild dogs are, for example, affected by heterospecific competitor density; Creel and Creel 2002). An Allee effect in meerkats was first discussed after extremely low rainfall in the Kgalagadi Transfrontier Park (straddling the border between South Africa and Botswana) led to reproductive failure and reduced survival there (Clutton-Brock et al. 1999a). Evidence for an Allee effect was based on limited data, however, and the patterns were not inconsistent with the dependence of meerkat group dynamics on rainfall, paired with the high degree of observed demographic stochasticity, that I have described in the previous chapters.

While I did not identify a clear demographic Allee effect in meerkat group dynamics, demographic rates may combine to produce a demographic Allee effect under certain conditions. For example, during periods of extremely low rainfall, within-group mortality (which is inversely density-dependent; Chapters Three, Four) might play a more important role in determining local dynamics. Alternatively, recruitment might come to resemble curve ii from Figure 6.1. In Chapter Three, the combined demographic model did describe an Allee effect in two years (Figure 3.5), though this may have been an artefact of overfitting. Again, more work will be required to elucidate the patterns in small groups.

6.3 **Population/Group Similarity**

The evidence I have presented suggests that both group-level and populationlevel dynamics in meerkats are largely conventionally density-dependent, and that patterns at the two levels are synchronised (Chapters Two-Four). At the group level, patterns of density dependence change with environmental conditions, with groups experiencing stronger conventional density dependence after low-rainfall years, and this appears to translate into corresponding changes in population density.

Given the close correspondence between mean group size and population density (Figure 4.1A), it would seem that the short population time series made identification of one-year lag in the effect of rainfall - as seen in group dynamics - difficult to detect. The second chapter's population model including two years' rainfall did, after all, offer the best, though not most parsimonious, fit.

That population-level patterns so closely match group-level patterns is slightly surprising, given the potential for inter-group processes (*e.g.* dispersal, recolonisation, and source-sink dynamics) to cause patterns at the group and population levels to diverge. There is a chance that the correlation is, at least in part, an artefact of sampling from groups in the population. The vast majority of groups in the core of the study area are, however, under study at any one time. It seems likely that consistent responses to environmental conditions produce consistent patterns across the population.

6.4 Stage-structured Response to Environmental Conditions

The strong effect of rain on meerkat demography is consistent with past work on meerkats and the Kalahari system (Doolan and Macdonald 1996a, Clutton-Brock et al. 1999a, Clutton-Brock et al. 1999b), and the demographic patterns I identified (Chapter Four) fit with the existing picture of meerkat reproduction, developed through behavioural studies. That social factors influence group-size regulation is of fundamental importance to population dynamics across social carnivores (Macdonald 1983), and this certainly holds for meerkats, where the interaction between dominants and subordinates mediates environmental effects, especially for females. Past work has shown that rain increases the number of litters produced in a given year (Clutton-Brock et al. 1999b) and that pregnant dominant females tend to evict mature subordinate females (Clutton-Brock et al. 1998a). Essentially, rain drives food availability, improving body condition (English et al. 2011) and facilitating reproduction, and reproduction drives conflict between dominant and subordinate females, leading to dispersal of subordinates (Stephens et al. 2005, Clutton-Brock et al. 2010). Less work has focused on male emigration behaviour, but males tend to prospect according to female fertility and dispersal cues (R. Mares, in preparation), which may result in the synchronised patterns of male and female emigration I described (Chapter Four).

Dominant females breed less, and therefore evict fewer subordinates in a dry year. In the year immediately following, groups contain proportionately more mature females, and eviction (and resultant emigration) increase, on average, across groups. Group sizes decline dramatically as a result (Chapter Four).

This stage-structure-dependent mechanism behind changes in group size highlights the importance of transience in population dynamics. For any population with a given pattern of age-dependent demographic rates, the age distribution should become stable over time (Schoen and Kim 1991). In stage-structured populations, however, we must do more than characterise asymptotic dynamics to gain insight into patterns of interest (Koons et al. 2005, Ozgul et al. 2009, Miller and Tenhumberg 2010). In a changing environment, patterns of demography are likely to change. Ungulates, like meerkats, exhibit stage-specific patterns that respond differently to changes in environmental conditions and density (Coulson et al. 2001, Clutton-Brock and Coulson 2002). As a result, a population in a stochastic environment could remain in constant transience towards ever-changing, theoretically "stable" stage structures.

6.5 Dispersal

While classical approaches to population demography (Leslie 1945) tend to focus on birth and death, more recent approaches have integrated dispersal into analyses (Hunter and Caswell 2005, Ozgul et al. 2009). Here, I have shown how (apparent) emigration is one of the key drivers of meerkat group dynamics. This provides an interesting contrast to classical demography, and highlights the important role played by dispersal processes in local dynamics, in addition to their role at a meta-population scale (Hanski 1999, Bowler and Benton 2005).

In stochastic environments, where local extinction is common, recolonisation is important for population persistence (Hanski 1999). Patterns of meerkat grouplevel demography, while consistent with the view that dominants control group composition to avoid reproductive conflict (Stephens et al. 2005, Clutton-Brock et al. 2010), could also facilitate recolonisation of empty habitat. Dispersal is a highly stressful process (Young and Monfort 2009), and the improved body condition associated with rainfall (English et al. 2011) is likely to improve dispersal success. By retaining potential dispersers during poor conditions (dry years), and expelling them en masse when conditions improve, dominant females may maximise the potential to seed new breeding groups formed of their progeny.

Dispersal and regionally correlated environmental conditions can synchronise local dynamics (Bjørnstad et al. 1999). Here, climate plays an extremely important role in group dynamics, and while groups tend to diverge in size somewhat when conditions are good, crashes after years of low rainfall have a synchronizing effect (see Figure 4.1A). This happens via the effects, described above, of reduced rain on emigration rates. Population synchrony is generally thought to be detrimental to population persistence (Earn et al. 1998), but synchronising crashes in meerkat group size are a result of dispersal. As a result, the very process that synchronizes meerkat dynamics may also protect the population from extinction risk that might otherwise be associated with synchronised small groups.

The risk associated with apparent local synchrony in meerkat group dynamics might not bear out for other reasons. Firstly, spatial variation in weather patterns could preclude large-scale population synchrony (Hanski and Meyke 2005). Secondly, the patterns of immigration and emigration found here (negatively density-dependent immigration and positively density-dependent emigration) have been shown to stabilise dynamics in other systems (Bowler and Benton 2005). Alternatively, immigration - though relatively rare - may reduce synchrony if immigrant males primarily come from large groups and disproportionately reduce their destination group's size by expelling residents (see e.g. Figure 4.3).

More than just a link between groups, dispersal is of critical importance to fitness in cooperative breeders. The extremely limited prospects for reproductive success within the small, localised sub-populations that social groups comprise, combined with the inevitable extinction of each such group in a stochastic environment, make dispersal a necessity. Dispersal can also offer substantial genetic benefits by reducing the chance of inbreeding (Clutton-Brock and Lukas 2012). Ultimately, only offspring that survive, disperse, and breed successfully themselves contribute to the genetic makeup of future generations. For meerkats, high reproductive skew means that dominant individuals are responsible for the vast majority of breeding success, and while females can inherit dominant breeding positions in their natal groups, males depend on dispersal to gain dominance (Spong et al. 2008).

Many studies use lifetime reproductive success as a proxy for fitness. This can be misleading in changing environments, where population growth - and therefore average fitness - fluctuate (Coulson et al. 2006). In meerkats, environmental conditions influence dispersal rates as well as reproduction. In order for reproductive output to be interpretable with respect to evolutionary implications for group-living species, it should be placed in the context of group structure and dispersal; studying "fitness" in cooperative breeders without understanding dispersal may be misleading.

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Though viewing groups as population units indicates conventionally densitydependent demography, taking dispersal into account paints a potentially different picture. While average within-group per-capita reproductive success is maximised in small groups (Chapters Three, Four), larger groups produce more emigrants (Chapters Three, Four) in larger coalitions (Young 2003), and larger dispersing coalitions appear more likely to successfully establish new breeding groups (Young 2003). Depending on the specific rates of reproduction, emigration, and group establishment in relation to group and coalition size, large groups might actually produce more *effective* offspring per capita (i.e. those contributing to future reproduction in the population). Thus, meerkats may still be subject to a group-level Allee effect, in terms of average fitness within groups (Stephens et al. 1999), when all relevant demographic rates are considered in a population context.

6.6 Beyond the Group

In Chapters Three and Four, I focused on processes within groups. A good deal of what goes on in the meerkat population, however, happens between groups or outside of the group context. Dispersal is actually a multi-step process, made up of emigration, transience, and settlement phases (Bowler and Benton 2005). With respect to meerkats, I have considered the emigration phase, but the specifics of transience and settlement have not been explored in adequate detail (but see Young 2003). Once dispersers have emigrated from their original social groups, they function outside of a breeding group until they can successfully form a new group or immigrate into an existing one, though they must interact with other groups during this time. Territorial patterns, and thus their implications for population dynamics, are also heavily influenced by interactions between groups.

For social species, the transience phase of dispersal involves finding other groups of individuals to establish or join a social group. This relies on dispersers' abilities to survive and search. As previously discussed, increased group size is associated with increased coalition size and success in meerkats (Young 2003), and population density may also influence dispersal ability by affecting body condition or hormone levels (Cote et al. 2010). The availability of other dispersing groups is also of critical importance. Mate-finding Allee effects can be associated with sparse populations (Courchamp et al. 2008), and the problem may be exacerbated for social species where each dispersing unit takes up multiple individuals. A mate-finding

Allee effect has been found in at least one population of wild dogs (Somers et al. 2008), and it seems reasonable that this could be the most important Allee-effect mechanism for this species, given other, somewhat ambiguous results (see above). A similar mate-finding Allee effect could be relevant for meerkats, in which new groups commonly form from dispersing male and female coalitions. Behavioural observations also suggest that male coalitions of meerkats may refuse to establish new groups with female coalitions that are too small (T. H. Clutton-Brock, personal communication). Whether such an observation affects meerkat dynamics at the densities I have considered, or whether effects are apparent in poorer conditions, like those observed in the Kgalagadi, remains to be investigated.

During the settlement phase of dispersal in territorial species, individuals must either find empty habitat to colonise or take over occupied habitat. For group-living territorial species, this means that individuals or coalitions must invade established social groups or form social groups of their own and successfully claim empty habitat or gain habitat from another group. The details of this process depend on territorial behaviours and the patterns they generate. Our lack of understanding of how territorial behaviour and territorial patterns relate for meerkats motivated my preliminary modelling of territory formation and dynamics in Chapter Five.

Territories arise from intra-specific interactions in the context of resource availability and predation risk. The resultant patterns have the potential to affect processes ranging from individuals' ability to find mates and disperse to the interaction between predators and prey (Lewis and Moorcroft 2001, López-Sepulcre and Kokko 2005, Packer et al. 2005, Wang and Grimm 2007, Haydon et al. 2008), and they affect population dynamics in both asocial and social species. In asocial species, for example, territoriality seems likely to reduce the carrying capacity of a system, because territorial defence that is optimal for individual success is not optimal for the population as a whole (López-Sepulcre and Kokko 2005). In lions, *Panthera leo*, territoriality seems to preclude smooth population increases in response to gradually improving conditions, because new prides must be of a minimum size to be viable (Packer et al. 2005).

Contrary to expectation, I found no evidence that group size influences a group's territorial interactions over a given period. If this pattern persists over time, it would help to explain the apparently close relationship between group sizes and population density. Whether group size is tied to population density over larger spatial scales will depend on how dispersers and established groups respond to available habitat (see Chapter Five), and on the regional consistency of environmental conditions.

Spatial patterns of resource availability can strongly affect population patterns (Brown and Orians 1970, Clutton-Brock and Harvey 1978) but results can be complicated. Meerkats show preferences for different habitat types (Chapter Five), and under different conditions, these preferences may change depending, for example, on food availability and predation risk (Turbé 2006). In wet conditions, that might otherwise be considered beneficial, dense vegetation may impede foraging (Chapter Five). Perhaps partially as a result, meerkat demographic rates can respond nonlinearly to patterns of rainfall (Chapter Four). Territoriality also interferes with the tendency for animals to distribute themselves according to resource patterns (Brown and Orians 1970), and may affect responses to environmental conditions. The patterns are not simple, and more work is required.

Animal movement patterns, and features such as territoriality that modify those patterns, help to determine how individuals interact within populations and communities. The degree to which individuals mix dictates the modelling detail required to tie animals' behaviour with features of the environment to describe and predict population-dynamic patterns (Morales et al. 2010). Cooperative breeders living in stable social groups present a challenge for standard models. As techniques develop to integrate previously separate aspects of theory and make use of increasingly available spatial data (*e.g.*, optimality of home-range patterns in the context of predator-prey dynamics: Lewis and Moorcroft 2001; demographic patterns in relation to spatial movement: Haydon et al. 2008), the prospect of coherently modelling interacting demographic and spatial processes becomes ever more plausible (Morales et al. 2010).

6.7 Conclusion

I have presented the first empirical consideration of population- and groupdynamics in meerkats. I described environment-dependent patterns of group-level demography and dynamics consistent with meerkat behaviour. Also, I began to describe spatial patterns that appear consistent with a close link between group- and population-level dynamics. Surprisingly, I found that group size did not offer considerable benefit demographically or territorially. Initial work in relation to dispersal behaviour indicates benefits of increased group size (Young 2003), but further work is required to establish the effects of dispersal (and related spatial processes) in the system.

For meerkats, future study should focus on processes that link groups together in a population and on how intra- and inter-group dynamics combine to produce population-level dynamics. Central to this are dispersal patterns, the fate of emigrants, and the process of group establishment in the context of changing population density, territorial patterns, and environmental conditions. Spatial patterns: how groups move and interact, how dispersing coalitions find each other to form new groups, what makes habitat available for newly formed groups, how conditions affect spatial processes, and how these processes feed back on demography, are all important. Elaboration of the basic patterns I describe, explicitly considering disease (see Drewe et al. 2009a), predation risk (discussed in Clutton-Brock et al. 1999a), and additional demographic complexity (e.g. natal and immigrant dominant males do not behave consistently; Spong et al. 2008) could also prove fruitful.

The meerkat system presents an excellent opportunity to study population dynamics in a structured population, with the possibility of inverse density dependence without the immediately pressing conservation concerns associated with many other species. Ultimately, understanding how individuals function within groups within a population will help place observed behaviour in accurate evolutionary context and may help us understand the dynamics of other cooperative species. Combining models with data, the potential exists to elucidate the links from behaviour to local patterns to population-wide patterns to selection pressure that modifies behaviour (Morales et al. 2010).

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