DEPARTMENT OF ZOOLOGY

THE DYNAMICS AND DEMOGRAPHY OF SOCIALLY STRUCTURED CARNIVORES

BADGERS, LIONS AND WOLVES

A thesis submitted for degree of Doctor of Philosophy

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Abstract

Sociality in carnivores is theoretically expected to produce quantitatively different dynamics compared to solitary species, exhibiting Allee effects, increasing extinction risk and limiting population growth. There is also evidence in social species that demographic stochasticity can impact the population when densities are high. Empirical support for these processes is lacking and the effects of socio-spatial structure on population dynamics is now widely debated. The roles of social structure, reproductive suppression, communal predator vigilance, communal hunting and babysitting on population responses to perturbations away from carrying capacity have important implications for species management. Social systems also possess inherent spatial structure. Such structure is known to influence dynamics in solitary species. This thesis investigates the relative contributions of spatial and social structure on population dynamics in three contrasting carnivores, from three different families; badgers (*Meles meles*), lions (*Panthera leo*) and grey wolves (*Canis lupus*), that each demonstrate comparable and different life history strategies with one another. Simple and complex structured population models are used to demonstrate how intra-group processes interact within inter-group process and habitat features to produce population wide dynamics. The models are used to investigate whether general rules governing the dynamics of social species can be drawn across species.

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Author Contributions

Chapter 1

Author: Jack Massey

Chapter 2

Authors: Jack Massey, Tim Coulson, and Doug Smith

Doug Smith proposed the research question to develop on previous work that focused on the early stages of wolf reintroduction. Tim Coulson proposed using Mark-Recapture methods. The structural design of the survival model, implementation in the program E-SURGE, interpretation of results and manuscript writing were all performed by Jack Massey. Data collection was performed by United States government departments, and the Yellowstone Wolf Project. The article was submitted as an internal report for the United States Department of the Interior and was not permitted to be submitted to an academic journal by the government bodies.

Chapter 3

Authors: Jack Massey, Doug Smith and Tim Coulson

Tim Coulson proposed the general question with data provided by Doug Smith for the analysis. Jack Massey developed the research question, derived the simple models, implemented the analysis in R and wrote the manuscript.

Chapter 4

Authors: Jack Massey, Christina Beusching, Geetha Annavi, David Macdonald, Chris Newman and Tim Coulson

Tim Coulson and Jack Massey proposed the general question with mark-recaptur data provided by Chris Newman, Christina Beasuching and David Macdonald, with genotype data provided be Geetha Annavi. Jack Massey and Tim Coulson identified the modelling technique to be used, with Jack Massey implementing all statistical analyses and simulations in R, U-CARE and E-SURGE. Jack Massey wrote the manuscript under the useful guidance of Chris Newman and Tim Coulson.

Chapter 5

Authors: Jack Massey, Tim Coulson and Craig Packer

Craig Packer proposed the question and provided the long-term data. Jack Massey and Tim Coulson identified the modelling technique to be used, with Jack Massey implementing all statistical analyses and simulations in R. Jack Massey wrote the manuscript.

Chapter 6

Author: Jack Massey

Contents

Chapter 1

General Introduction

1.1 Motivation

Social structure exists in many vertebrate species, from birds to fish to mammals, with many different social structures [Tinbergen, 1953, Eisenberg, 1983, Brown and Laland, 2003]. Inherent to many socially structured species is spatial structure, the dynamics of which are well understood [Hanski, 1999, Clobert et al., 2012]. In many social carnivores, individuals receive fitness benefits from conspecifics from increased predator vigilance, increased hunting efficiency and partitioning of the costs of rearing offspring [Malcolm and Marten, 1982, Harrington et al., 1983, Macdonald, 1983, Packer et al., 1990, Heinsohn and Legge, 1999, Clutton-Brock et al., 1999b, Courchamp et al., 2002]. This thesis focuses on three different social carnivores, each of which share similarities and differences in their ecology. If patterns can be drawn across these species, a natural extension will be to try and draw general rules that socially imposes on population dynamics with other social mammals (e.g. yellow bellied marmots, *Marmota flaviventris*, and red deer, *Cervus elaphus* , [Svendsen, 1974, Lowe, 1969]) and across different classes (e.g social woodpeckers such as the acorn, *Melanerpes formicivorus*, and the red-cockaded, *Leuconotopicus borealis* [MacRoberts and MacRoberts, 1976, Ligon, 1970], or the social cichlid fish such as the african, *Haplochromis burtoni*, the princess *Neolamprologus brichardi* and the convict, *Archocentrus nigrofasciatus* [Fernald and Hirata, 1979, Taborsky, 1984, Mackereth and Keenleyside, 1993], among many others).

Both simple and complex models are used to address different aspects of population dynamics. By comparing the two, the pros and cons of each approach can be compared, providing insight for population modellers of any social species. Simple models have previously been used to test for Allee effects in meerkats [Bateman et al., 2011, 2012] with more complex individual based models often used to predict population viability and disease dynamics in socially structured populations [Letcher et al., 1998, Shirley et al., 2003, Pitt et al., 2003, Bateman et al., 2013, Ozgul et al., 2014]. Two of the species analysed here consist of breeding and non-breeding individuals (badgers, *Meles meles*, and gray wolves, *Canis lupus*)

[Woodroffe and Macdonald, 1995, Harrington et al., 1983] and two that partake in communal hunting and rearing of offspring (lions, *Panthera leo* and wolves) [Mech, 1970, Packer et al., 1990, Schmidt and Mech, 1997]. Comparing the results from each model enables the contribution of reproductive suppression and communal hunting on group and population level dynamics to be identified.

Many studies, across both social and non-social species, identify statistically significant predictors of demographic rates, but few simulate these to identify their relative contribution, accounting for interactions, to population dynamics. Chapters 4 and 5 parameterise each demographic function, survival, recruitment and dispersal, including trait based functions in chapter 5, and simulate the dynamics produced by their interactions, accounting for feedback loops. This demonstrates how statistically significant parameters from retrospective analyses, may not influence group and population dynamics to a large extent, and has important consequences for the debate of whether social species an increased propensity to exhibit Allee effects [Courchamp et al., 1999b,a, Angulo et al., 2013]. These results are not exclusive to social carnivores, with many other species exhibiting reproductive suppression and communal rearing of offspring [Riedman, 1982, Wasser and Barash, 1983, Wisenden, 1999]. Here I investigate whether comparisons and general patterns can be found across three social carnivores. If successful, then comparisons across a more diverse set of species may also be possible, that may results in a better understanding of the general rules governing social species dynamics, that has been of interest for many decades [Calhoun, 1952].

Sociality has evolved in many carnivores, across a range of families, through a diverse set of selective pressures, including: increased hunting efficiency and predator vigilance, reduced costs of territory defence, benefits of alloparental care and the potential for information transfer and social learning [Macdonald, 1983]. Given the diverse set of mechanisms that promote sociality, it is of interest to ask whether general patterns and rules governing population dynamics can be drawn across species with different social structures. Identifying general patterns will both further our knowledge of social evolution and aid in generating sustainable management plans, of great importance given many large carnivores have suffered years of anthropogenic persecution and are at risk of extinction [Purvis et al., 2000].

Population dynamics are understood by identifying the levels of structure that significantly influence individual fitness, and how regulatory mechanisms act through this structure [Coulson et al., 2001]. Therefore, identifying common structures across species will enable general patterns to be understood. Sociality imposes spatial structure on populations, where each social group can be viewed as a sub-population of a larger meta-population. General rules governing the dynamics of meta-populations in solitary species are well understood and are known to produce qualitatively different dynamics to non-spatial populations [Lande et al., 1999, Hanski, 1999]. Socio-structure imposes costs to small groups, otherwise sociality would not evolve, and an upper limit on group size above which fitness is reduced, without which a single group would eventually colonise the population. The dynamics of social carnivores can therefore be viewed in terms of three regulatory processes:

- Competition between groups (inter-group).
- Competition within groups (intra-group)
- Fitness costs associated with small groups (component Allee effects).

In non-spatial systems, dynamics can be regulated by density dependence, the equivalent of inter-group competition when group size is 1, and by Allee effects, that can restrict growth in low density populations [Allee, 1931, Allee et al., 1949]. In spatially structured populations regulation can act at the local scale, with density dependence occurring when a patch reaches carrying capacity, independent of global densities, and can also experience Allee effects when local densities are low, even when global population size is high [Hanski, 1999, Lande et al., 1999]. This can also result in demographic stochasticity influencing dynamics when population size is high, with low density patches susceptible to extinction through demographic stochasticity [Lande, 1993, Lande et al., 1999]. Social structure is an extension of meta-population spatial structure in that groups can actively attack other patches and expand territory range, producing a non-rigid spatial structure. The social structure differs from local density regulation in that dominance ranks might exist that result in fitness differences between individuals, due to processes such as reproductive suppression, that may also amplify the effects of demographic stochasticity through breeder loss [Wolff, 1997, Creel, 2001]. If dynamics of social species are to be captured by predictive models they must account for these differences.

The development of models incorporating this structure is important, as social-structure has been proposed to increase extinction risk, by introducing a threshold group size below which groups go extinct. These effects have been documented in African wild dogs (*Lycaon pictus*), meerkats (*Suricata suricatta*) and dwarf mongooses (*Helogale parvula*) [Rood, 1990, Courchamp and Macdonald, 2001, Courchamp et al., 2002, Creel and Creel, 1998, Clutton-Brock et al., 2001] although more recent work has contested whether this is due to socio-spatial structure or external anthropogenic pressures [Woodroffe, 2011, Gusset and Macdonald, 2010, Bateman et al., 2012].

1.2 Regulatory Mechanism Definition

In this thesis a regulatory mechanism is defined as a process that reduces a demographic rate from its maximum potential value, based on individual and spatial covariates. These are defined as density dependence, that may at act at the global level, or at the group level. Global level density dependence is viewed as competition between groups and is often referred to as inter-group competition. It may occur through competition for denning sites, resources and territories [Calhoun, 1952, Crook, 1970, Macdonald, 1983]. Group level density dependence, referred to as intra-group competition, is defined as a reduction in a demographic rate that correlates with increasing group size. This may occur through increased competition for dominance and breeding rights and access to resources [Calhoun, 1952, Crook, 1970, Macdonald, 1983]. A

third mechanism considered as regulatory in this thesis are Allee effects, explained in further detail in the following paragraph. I focus on Allee effects at the group level, where demographic rates are decreased in small groups. This could be through reduced hunting efficiency and increased per capita input to allo-parental care and territory maintenance [Sanderson et al., 2014, Rood, 1990, Courchamp and Macdonald, 2001, Clutton-Brock et al., 2001].

1.3 Allee effects

An Allee effect is a positive correlation between any component of individual fitness and the number, or density of conspecifics [Allee, 1931, Allee et al., 1949]. Traditionally, it is viewed as a positive correlation between population growth and density, where benefits of intra-specific cooperation can lead to negative density dependence, reviewed by Courchamp et al. [1999a] and Stephens et al. [1999]. It can be driven by genetic inbreeding and loss of heterozygosity, effects of demographic stochasticity and a reduction in cooperative interactions [Courchamp et al., 1999a]. Stephens et al. [1999] highlight the importance of distinguishing between effects that reduce a component of fitness (Component Allee effects), and those that reduce total fitness (Demographic Allee effects). Decreasing negative density dependence in one component may be offset by increasing density dependence in another component, such as increased hunting efficiency and reduced per capita resource at kills in cooperative hunters, as seen in african wild dogs, lions and grey wolves [Caraco and Wolf, 1975, Packer et al., 1990, Creel and Creel, 1995] . It is therefore essential to account for all fitness components to demonstrate whether demographic Allee effects are present.

The social systems studied in this thesis focus on high density populations. References to Allee effects in this thesis refer to decreases in fitness components associated with decreasing group size.

1.4 Social Species Dynamics: Examples

Grey wolves (*Canis lupus*) experienced slow recolonisation of the Northern Rocky Mountains due to difficulties of dispersing individuals in finding mates [Hurford et al., 2006]. In grey wolves, young males disperse great distances to find mates when population densities are low, as they are suppressed from breeding in their natal pack [Mech and Boitani, 2003]. Therefore, population growth can only occur when new packs form, as intra-group competition reduces per capita recruitment when pre-existing packs increase in size. In this case the demographic Allee effect is due to low population densities and not a group level effect. Whether component Allee effects at the group level reduce population growth has hitherto not been explored.

Ethiopian wolves (*Canis simensis*) experienced reduced population growth after an epizootic outbreak caused a population crash. Surviving packs chose to increase pack size and territory range above levels seen prior to the crash, inhibiting new immigrant packs from forming, by increasing the strength of inter-group

competition on small packs [Marino et al., 2013]. As packs increased in size the ratio of breeding to non breeding individuals decreased, decreasing per capita recruitment rates, reducing population growth. This highlights the inter-play between intra- and inter-group processes. Adding individuals to a pack produces different dynamics to forming a new pack with the same individuals.

Badger (*Meles meles*) population densities remained constant during a period of improving ecological conditions in the south-west of the United Kingdom in the late eighties before rapidly increasing up to a new equilibrium. In this case territories decreased in size as ecological conditions improved but new groups could not form until territories contracted significantly [Macdonald and Newman, 2002]. In this case all social groups experienced intra-group regulation inhibiting new individuals from joining pre-existing groups but could not form groups of their own, most likely due to inter-group pressure.

Similar dynamics were observed in lions (*Panthera leo*) with population densities remaining constant during periods of improving ecological conditions and after a canine distemper outbreak, before rapidly converging on a new equilibrium [Packer et al., 2005]. In this case it was the inability of new prides to form due to their susceptibility to extinction through demographic stochasticity and strong intra-pride regulation restricting individuals from joining pre-existing prides.

African wild dogs (*Lycaon pictus*) have struggled to recover after years of anthropogenic persecution as recruitment levels are decreased in small packs. In this case small groups experience a trade-off between hunting and pup-guarding, reducing survival and recruitment rates to levels that produce a strong demographic Allee effect at the group level, resulting in a threshold size below which groups cannot recover [Courchamp et al., 2002, Courchamp and Macdonald, 2001]

Each of the species outlined above have both similarities and differences in their ecology and exhibit population growth that is distinct from non-social species. Here I investigate three contrasting social species from three different families: grey wolves in Yellowstone National Park, USA, eurasian badgers in Wytham Woods, UK and lions in the Serengeti National Park, Tanzania. In each study population regulation is partitioned into costs to small groups, intra-group competition and inter-group competition such that the relative contributions of regulation at each structural level can be compared across species. Below I give a brief description of the motivation behind and the methods used in each chapter.

1.5 Grey wolves

Grey wolves were reintroduced into the Northern Rocky Mountains in 1995 to supplement the natural recolonisation of north western Montana by dispersing individuals from Canada. The original recovery plan partitioned the States of Idaho, Montana and Wyoming into three recovery areas managed by the federal government. Management goals were met in 2003 and grey wolves were removed from the endangered species list in 2009, before being relisted in 2010 and delisted subsequently in 2012 [Jimenez and Becker,

2012]. Grey wolves polarise public opinion, with local ranchers who incur the costs, vehemently against their presence, and environmentalists, who often live far away, very pro their reintroduction. Wildlife managers therefore have to strike a balance between appeasing ranchers and ensuring population persistence. Nuisance individuals can be removed as the population is classified as experimental (it was reintroduced) as opposed to endangered, where removal would be illegal. A second method for appeasing ranchers and stabilising population densities is through licensed hunting. This occurred in 2009 and from 2012 onwards in Idaho and Montana and between 2012 and 2014 in Wyoming. I was asked by the United States department of the Interior to investigate how survival rates had changed across the Northern Rocky Mountains since the previous analysis, that ended in 2004, and the level of anthropogenic caused mortality required to stabilise population growth.

Producing sustainable hunting quotas requires knowledge of the correlation between the rates of natural and anthropogenic caused mortality. The logic is, that at carrying capacity demographic rates are reduced through resource scarcity. Removing an individual from the population, increases the resource available to the remaining individuals, increasing their demographic rates. In this scenario the anthropogenic caused mortality is not realised in reduced population growth as the remaining individuals experience increased fitness. This is known as compensatory dynamics. Conversely, removing an individual may: disrupt group cohesion, result in failure to breed, increase the likelihood of territory takeovers or drive groups to levels where Allee effects are realised. This is known as additive mortality [Lebreton, 2005]. Three previous attempts to quantify the extent to which anthropogenic caused mortality is compensated in natural mortality have failed to reach an agreement, with some finding partial compensation and others super additivity [Murray et al., 2010, Creel and Rotella, 2010, Gude et al., 2012].

One fundamental problem with the previous analyses is their to failure account for imperfect detection of cause specific mortality. Imperfect detection is common in species with large home-ranges that often rely on radio-collaring for tracking and many methods exist to account for this [Gimenez et al., 2012]. In the Northern Rocky Mountains a main mortality cause is government control actions against wolves that depredate livestock. This mortality source is known with certainty as governments always record when an individual is removed. Natural mortality however, is usually detected from a plane using radio frequency tracking that can be expected to have reporting rates lower than 1. Therefore failure to account for this under-reporting has the potential to bias results and may be why the previous analyses have reached no firm conclusion [Gimenez et al., 2008]. A second reason may be that they do not account for socio-spatial structure such that removal of an individual may produce different responses in the remaining population depending on the pack it was removed from. This will depend on whether demographic Allee effects are present in the population, whether packs experience intra-group regulation and the extent to which packs regulate each other.

The analysis is partitioned across two chapters, the first (chapter 2) demonstrates how survival rates have

changed since 2005 in the new State (as opposed to federal) management areas. The method used partitions the observation process from the underlying survival process to remove the bias' incurred when detection is less than 1. The survival process is partitioned into a transition process between management areas and a mortality process where individuals can die from either government controlled sources or all other sources pooled. This decomposition has the benefit of understanding connectivity between management areas, a key management objective, and partitioning mortality into that which policy makers can manipulate against the sources where compensation will occur. The second analysis (chapter 3) demonstrates the fitness costs incurred by small and large packs and how they vary with population density and across ecosystems. This analysis demonstrates that the regulatory mechanisms affecting an individuals' fitness will depend on its own pack size relative to the size and abundance of other packs. It follows, that whether removal of an individual produces additive or compensatory dynamics will depending on the pack it is being removed from. Unfortunately these two chapters could not be used to definitively answer the compensatory Vs additive debate as survival rates in the absence of anthropogenic mortality are not known [see Lebreton, 2005, Péron, 2013, for details as to why]. Combined they do however demonstrate that mortality rates can be accurately estimated even in the presence of imperfect detection and that socio-spatial structure needs to be incorporated for the additive-compensatory models to be valid.

1.6 Eurasian badgers

The fourth chapter moves to a smaller, non-obligate cooperator, the Eurasian badger (*Meles meles*) a social mustelid where all individuals in the study population are tracked throughout their lives, enabling movement dynamics to be incorporated into models. Badgers are at an early stage of social evolution that live in pairs across the majority of their range [Kruuk, 1978b,a]. In the south west of the United Kingdom, where habitats are favourable, they live in groups of up to 30 individuals, making them an interesting case study of a species in an early stage of social evolution [Kruuk and Parish, 1982, Kruuk, 1989]. They are solitary foragers, with few notable fitness benefits of group living and costs including reduced fecundity and body condition in over-crowded groups [da Silva et al., 1994]. Even though they are at an early stage of social evolution their responses to harvest have been markedly different to that of a homogenous solitary population. In the United Kingdom culling has been trialled as a method to reduce transmission of bovine terburculosis to cattle. Post culling the population underwent a vast spatial reorganisation, known as the perturbation effect [Donnelly et al., 2006]. Whether this is similar to extinction-recolonization dynamics of meta-population models or whether their social structure also plays a role has hitherto not been explored.

The Wytham Woods population, Oxfordshire, UK, has not been culled but does exhibit dynamics typical of social species, in that populations can be trapped at densities below carrying capacity, with growth occurring in step jumps [Macdonald and Newman, 2002, Packer et al., 2005]. Improving ecological condi-

tions did not correlate with increases in population size, remaining relatively stable until a threshold limit was passed, above which the population rapidly converged on a new equilibrium [Macdonald and Newman, 2002]. Badgers provide an interesting case study in how simple social structure influences population dynamics in the absence of obvious Allee effects. Partitioning the roles of intra- and inter-group regulatory mechanisms in amplifying (or dampening) local and population wide fluctuations around carrying capacity, the differences of socio-spatial and spatial structure alone are compared, with implications for understanding the perturbation effect discussed.

1.7 Serengeti lions

Serengeti National Park lion (*Panthera leo*) populations experienced similar buffers against population growth to that seen in badger populations in the south west of England, remaining relatively stable through periods of improving ecological conditions until rapidly increasing to a new equilibrium [Packer et al., 2005]. Packer et al. [2005] demonstrated that this buffer was due to limitations on new pride formation, but the restrictive mechanisms were not identified. Mosser et al. [2009] demonstrated that the park contains areas of high value real estate that provide prides with fitness benefits and Cooper [1991] showed a small window of pride size within which fitness is maximised. In this chapter I investigate the mechanisms that impose upper bounds on pride size, restrict new pride formation and therefore the mechanisms which generate step jumps in population size. The average pride size on the Serengeti plains (5 adult females) correlates closely with group sizes of other large carnivores [Mech and Boitani, 2003, Courchamp and Macdonald, 2001, Marino et al., 2013] and is small enough to investigate whether Allee effects and demographic stochasticity at the group level leave a detectable signature at the population level [Lande et al., 1999, Stephens et al., 1999, Lande, 1993]. Given a similar group size to other large carnivores, the relative contributions of stochastic and deterministic effects will most likely hold true across species. The analysis demonstrates that demographic stochasticity can leave a distinct mark on population dynamics even when densities are high, with important implications for the conservation of social carnivores.

1.8 Closing remarks

The continual theme across each chapter is investigating the extent to which socio-spatial structure produces dynamics that differ (if at all) from spatially structured and solitary populations and whether sociality imposes a threshold groups size, below which groups go extinct (strong demographic Allee effects). Each chapter investigates the stability of the system and how socio-spatial structure may reduce stability and increase extinction risk relative to non-social species. Using three study species, each from a different social evolutionary path, comparisons and general impacts on the stability of populations due to socio-spatial structure are drawn.

Chapter 2

Movement and mortality dynamics in the Northern Rocky Mountains grey wolf

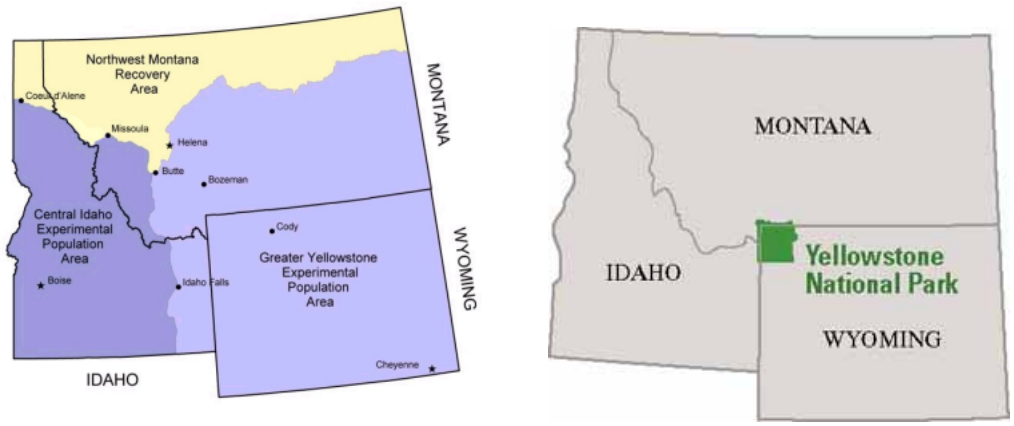
Abstract

The recolonisation of grey wolves (*Canis lupus*) to the Northern Rocky Mountains has been a resounding success. Population sizes (>1500) now greatly exceed the original management objective minimum number of 300 and licensed hunting has been introduced to control population numbers in Idaho, Montana and Wyoming. Given results of a previous survival analysis, and tests of connectivity between management areas, concentrated on the original recovery areas governed at the federal level, it is of interest to understand the underlying dynamics and connectivity in the new State level management areas and Yellowstone National Park. Utilising a mark-recapture-recovery framework, I model rates of mortality and movement between management areas, finding connectivity to be high, with each management area experiencing immigration and sending emigrants to at least one other area. Montana remained a sink population with Idaho and Yellowstone source populations. No evidence of different dynamics were found between Idaho and Montana producing a system with three distinct dynamical zones, Idaho and Montana, Yellowstone, and Wyoming. Pooled survival among adults and across years was 0.68 (95% CI 0.65, 0.71) a decrease from 0.75 from 1982 to 2004 (0.72,0.77), in line with increased density dependence as the population approaches carrying capacity. Allowing survival rates to vary temporally in each management area demonstrated high correlation between population growth rates and survival estimates. Mortality was partitioned into sources controlled by management agencies (control actions and licensed hunting) and all other sources pooled together. In Montana 41% of mortality (33%, 51%) was of management agency controlled sources whereas only 27% (19,36) and 25% (19, 32) were in Wyoming and Idaho respectively, demonstrating a system that experiences high levels of anthropogenic pressure outside of the protected Yellowstone National Park.

KEYWORDS. Grey wolf, *Canis lupus*, cause specific mortality, Northern Rocky Mountains, Survival, migration

2.1 Introduction

The reintroduction of grey wolves (*Canis lupus*) to the Northern Rocky Mountains is one of conservations great successes. Originally reintroduced in the States of Idaho and Wyoming to complement the natural recolonisation of Montana through dispersal from Canada, ranges have expanded into Oregon and Washington with populations exceeding 1500 individuals in 2011 [Jimenez and Becker, 2012]. Management objectives set out in the 1980's aimed for a population exceeding 300 individuals with at least 30 breeding pairs spread evenly across the three recovery areas of Central Idaho, North Western Montana and the Greater Yellowstone Ecosystem [U.S. Fish and Wildlife Service, 1987].



(a) (b)

Figure 2.1: Maps describing the original Federal management areas (a) and the current State controlled areas (b) along with Yellowstone National Park. Yellowstone National Park is under the control of the National Park Service. Maps are taken from the National Park Service and United States Geological Survey websites.

Dispersing wolves from Canada began naturally colonising North Western Montana in 1982 and reintroductions in the Central Idaho and Greater Yellowstone Ecosystem Recovery Areas occurred in 1995 and 1996. In 2002, grey wolves (*C. lupus*) met management objectives, resulting in removal from the endangered species list (delisting) in Idaho and Montana in 2009. This was contested in the supreme court and the species was placed back on the endangered species list (relisting) in 2010, followed by a second delisting in Idaho, Montana and Wyoming in 2012, ceding management from Federal to State agencies, permitting licensed hunting to stabilise population growth rates. Controversy surrounding the delisting still exists and relisting reoccured in 2014 in Wyoming. Given the polarised opinion on the benefits of large carnivore conservation in the Northern Rocky Mountains it is essential that managers understand the drivers of population dynamics in order to maintain a viable population. Changing management areas necessitate understanding the dynamics of each new area and their connectivity in order to predict how management plans designed in one State will affect dynamics in others. Previous work by Vonholdt et al. [2010] demonstrated high connectivity between original recovery areas but noted the need for continued management policies to 'promote natural dispersal and minimise anthropogenic factors that reduce connectivity'. The extent

to which connectivity persists and the direction of movement between the new areas will demonstrate the level of interdependence between management areas. Smith et al. [2010] found survival to be high across all areas (0.75, 95% CI = 0.73, 0.77) from 1982 to 2004, with the Central Idaho and Greater Yellowstone Recovery Areas providing source dynamics for North West Montana Recovery Areas sink. They similarly highlighted the necessity of continued monitoring of survival rates given that source-sink dynamics rely on high survival in certain areas. With new management structures and boundaries, increased population densities [Jimenez and Becker, 2012] and declining resource densities since the previous analysis [Ripple and Beschta, 2004, Vucetich et al., 2005], an updated picture of the Northern Rocky Mountain populations are essential if sustainable management plans, that are accepted by both sides of the wolf lobby, are to be derived.

Using a multi-site-multi-state mark-recapture-recovery analysis [Duriez et al., 2009, Gimenez et al., 2012, Pradel and Sanz-Aguilar, 2012, Tavecchia et al., 2012] I investigate the dynamics of the Northern Rocky Mountain grey wolf, the level of independence in dynamics between management areas and their connectivity, providing unbiased estimates of the rates of government sanctioned mortality and mortality outside of management agencies control (natural, accidental, unknown and illegal). Given management agencies wish to control population growth, they must understand how natural mortality rates respond to anthropogenic caused mortality and the contribution of survival to population growth.

Lebreton [2005] and Péron [2013] both provide reviews of additive and compensatory mortality. Compensation is defined as a negative correlation between two mortality sources. Increasing one mortality source decreases another. Complete compensation occurs when total mortality remains constant, when a mortality source is increased. This is represented by a correlation of -1. Additive mortality occurs when the two mortality sources are independent (zero correlation). Increasing one mortality source does not influence the other. Super-additivity occurs when a positive correlation is detected. Increasing one mortality source increases another, increasing total mortality by more than the affect of the direct killing alone.

Understanding the correlation between mortality sources is extremely useful for management agencies that wish to reduce population growth rates. The two mortality rates that management agencies can influence are licensed hunting and government sanctioned control actions. These sources of mortality are pooled together in the following analysis, with all other sources; natural, illegal and accidental, pooled together and defined as uncontrollable mortality. This partition has the added benefit that hunting and control actions are always reported whereas all the other sources can experience under-reporting. This is potentially where Murray et al. [2010] and Smith et al. [2010] may have introduced unknown biases into their results [see Gimenez et al., 2008, for details]. It is also potentially why the debate around the impact of anthropogenic induced mortality, and the extent to which it is compensated in natural mortality rates, has produced no clear answer. Murray et al. [2010] found partial compensation, Creel and Rotella [2010] super-additivity and Gude et al. [2012] somewhere in between. None of these account for imperfect and

management area specific detection of either live recaptures or dead recoveries. Gude et al. [2012] and Creel and Rotella [2010] also failed to estimate survival independently of mortality rates, essential when analysing additive-compensatory dynamics [see Lebreton, 2005, Péron, 2013, for detailed explanations as to why]. To understand compensation one must know:

1. Natural survival in the absence of anthropogenic pressure (S_0).
2. Survival rates in the presence of anthropogenic pressure.
3. Estimates of anthropogenic caused mortality estimated independently of (2).

Here I demonstrate that both (2) and (3) can be estimated (although not independently) which is the first step in understanding why the previous methods have reached no firm conclusion. I investigate the extent to which natural mortality is under-reported and identify the potential for compensation to occur. I identify the structured survival differences that have important implications for population stability, viability and where compensation can occur. Utilising mark-recapture-recovery timeseries data collected between 2005 and 2010 in Idaho, Montana, Wyoming and Yellowstone National Park, I test for temporal trends in migration, survival and cause specific mortality rates, accounting for detection and reporting heterogeneity while testing for independence of dynamics between the management zones.

2.2 Methods

2.2.1 Data Collection

Datasets were compiled on radio-collared wolf sightings from state-wide wolf studies outside of the federally managed Yellowstone National Park in Idaho, Montana and Wyoming. Inside of Yellowstone National Park data was collected from the Yellowstone Wolf Project study. Cause specific mortality was recorded when identifiable and individual covariates were recorded upon collaring. I use data collected between 2005 and 2010 and the results focus on patterns of wolf survival rates over this period. Survival rates have previously been published for wolf survival between 1982 and 2004. This study used a different method to estimate survival rates compared to the approach presented here. Smith et al. [2010] used Cox proportional hazard models, while I use an additive mark-recapture-recovery modelling framework that accounts for hidden processes and unobservable, or partially observable states [Gimenez et al., 2012]. The major difference between the two approaches is how individuals of unknown fate (never seen after a given time step) are handled. Cox proportional hazard models censor the individual back to its last sighting, whereas mark-recapture recovery models do not censor individuals, accounting for imperfect detection as a dynamic process, parameterised using maximum likelihood. If live recapture rates differ from dead recovery rates hazard models produce biased estimates [Catchpole et al., 2004].

In Idaho, data were collected by the US Fish and Wildlife Service, the Nez Perce Tribe (who are responsible for wolf management on the Nez Perce Reservation) and USDA Wildlife Services. The US Fish and Wildlife Service was responsible for data collection in Wyoming and Montana. In Yellowstone National Park data were collected by the Yellowstone Wolf Project, which is funded by the Department of the Interior, National Science Foundation grants and through private donations to the Yellowstone Foundation.

Data were collected from collared wolves containing individuals of all ages that are collared throughout the summer in Idaho, Montana and Wyoming and from November through March in Yellowstone National Park. Both GPS collars and VHF collars that increase signal pulse upon mortality were used. In Yellowstone National Park individuals were tracked via aircraft approximately every 14 days, and via vehicle and foot daily during winter studies in March and December. Tracking frequencies outside the park were lower, but aerial surveys occurred at least four times a year. A detailed summary of tracking methods and data collection in the original recovery areas can be found in Smith et al. [2010].

I define recapture as the detection of a telemetry signal or direct observation and recovery as observation of a dead individual or through the retrieval of a mortality signal transmission. A recapture is consequently confirmation that an individual is alive during a certain time interval, while recovery confirms death. Collaring of pups occurs from July onwards in Idaho, Montana and Wyoming and from November to April in Yellowstone National Park. For Idaho, Wyoming and Montana, no information on pup survival from birth through the denning season exists [Smith et al., 2010]. Age is defined from 10 months of age, the earliest common month pups enter the data set across all management areas, and increments of 1 year from this age. Given population counts occur in December of each year, I model survival from January to December such that the estimated survival rates correlated directly with population growth rates taken from minimum number alive counts [Krebs, 1966, Jimenez and Becker, 2012].

2.2.2 Model structure and selection

Mark-Recapture-Recovery methods handle state uncertainty and detection heterogeneity [Lebreton et al., 1992, Lebreton and Pradel, 2002, Pradel, 2005, Gimenez et al., 2012]. In the Northern Rocky Mountains individuals move between management areas (sites), although detection may be delayed or never occur in the new site. Similarly individuals that die are not always recovered and may depend on the mortality cause. Utilising known information on recaptures and recoveries one can estimate the underlying transitions between sites and states, including unrecorded states, avoiding flawed inference when detection probability is less than one [Gimenez et al., 2008]. The underlying survival process is therefore partitioned from the observation process. The survival process is partitioned into a movement process where individuals migrate between management areas and a mortality process, consisting of two mortality causes, one that government agencies control and all other sources pooled. Each rate is permitted to vary depending on the management area. The observation process is partitioned among individuals that were seen the previous time step and

those that were not to account for collar failures [Pradel and Sanz-Aguilar, 2012], explained in more detail below. A flow chart representation of the process is given in Figure 2.2. The observation processes are then constrained to each management area to account for different tracking methods that alter the observation process, but not the underlying survival process. Smith et al. [2010] did not remove the observation process from the survival process, that could have biased results to an unknown degree [Gimenez et al., 2012].

Due to the differing management structures and tracking regimes, each management area is treated as a site using a multi-site model similar to Duriez et al. [2009]. This partitions the survival process into a transition (migration) process whereby individuals move between sites, followed by the survival process where survival rates are based conditional on the arrival site. Given an individual is dead, the mortality is then allocated to sources governments can manipulate (denoted Gov in Table 2.1) and all other sources pooled [See Tavecchia et al., 2012, for methods]. Transitions into the source which governments can manipulate is known with probability 1 thus recovery rates determine the probability of recovering an individual given that it did not die of a control action or licensed hunting. This is the first analysis to correctly account for heterogeneity in reporting rates of mortality sources.

Goodness of fit tests of the data to model assumptions currently do not exist for mark-recapture-recovery data. Removing recoveries from the data set I test the assumptions of the Jolly-Move model using programme UCARE [Pradel et al., 2005]. These test for the effect of 'transient individuals', 'trap happiness' and independence of migration patterns. Transient individuals move through and leave the study area. They bias results through decreasing recapture rates below true levels. They are detected as individuals captured but never recaptured. Trap dependence tests for whether an individual has a different recapture probability when it was trapped the previous time step. This may be 'happiness' when the process is favourable to the individual, or 'shyness' when the process is unfavourable. Failure to account for this can bias recapture rates, feeding back through the other process, biasing all results. The independence of migration tests whether an individual that moved previously is more likely to move again. If this is true then movement rates need to be partitioned between individuals that have moved and those that have not.

Goodness of fit tests found no evidence of transient individuals or a memory effect on transitions between sites (Global Test 3G P = 0.979; 3G.Sm = 0.930, 3GS.R = 0.824, WBWA = 1) however trap dependence was found (Test M.ITEC = 0.00). Partitioning the data set into individual sites and utilising the single site goodness of fit tests found trap dependence in Idaho (P = 0.00) and Montana (P= 0.01). Therefore recapture rates inside Idaho and Montana are partitioned into an observed and unobserved at the previous time step states, following the methods of Pradel and Sanz-Aguilar [2012] whereas in Wyoming and Yellowstone there is only a single state 'alive'.

This generates 15 states, alive and dead in each site, recapture status at previous time step in Idaho and Montana, cause of death in each site along with an absorbing dead state although this state is omitted from the design matrices given in Appendix A.1. Models were fitted using the program E-Surge [Choquet et al.,

2009].

Model selection is performed using the Akaike Information Criterion (AIC) taking a ΔAIC value of greater than two to infer a significantly better model fit. As methods for estimating over dispersion coefficients from mark-recapture-recovery models currently do not exist [Pradel et al., 2005], the sensitivity of model selection to increases in the over dispersion coefficient ($\hat{c}$) using the Quasi-Akaike Information Criterion (QAIC), demonstrated the robustness of model fit. This avoids selecting over-parameterised models. This involves comparing the best fits models in the absence of over-dispersion ($\hat{c} = 1$) and in the presence of over-dispersion ($\hat{c} = 2$). If significance changes then the variable is not viewed as being robustly significant.

Temporal variation and site dependence are tested in migration, survival, mortality cause, recapture and recovery rates. Individual based covariates; sex, age and capture reason, defined as whether an individual is collared as part of a representative sample or targeted usually due livestock depredation are tested on survival. Smith et al. [2010] identified that individuals collared due to livestock depredation experienced increased risk of mortality. This is not surprising given the high rate of government induced mortality such that an individual collared due to it being a nuisance to ranchers will most likely be removed by a government control action. Therefore capture reason is fitted to remove the bias of collaring wolves that are nearly certain to be killed by control actions in the near future. The survival rates of interest are those in the general population and not nuisance individuals.

To maintain sample size, individuals of unknown age were pooled together as a single age class with survival rates in this age class not reported if age class is a significant predictor. They are used to model fluctuations in dynamics and differences between sexes, not age structured effects. Individuals of unknown age were maintained at the request of State management agencies.

Migration rates may depend on the management area an individual leaves, the area it moves to or both. Individuals may disperse out of an area in any direction with equal probability, but may also disperse in a given direction more frequently than others. This is denoted in as being dependent on the site FROM which it leaves (F in Appendix Table A1), the site it goes TO (T) or both which is represented as F.T.

I note here that migration is not analogous to dispersal. It is defined as an individual transitioning from being captured in a given site to being captured in a second site. This could be an individual disperser or a pack moving into another management area. Individuals whose territory is on the boundary of a management area may therefore appear to have dispersed but instead moved only a short distance. Individuals captured in two sites during a given year were randomly allocated to a site.

2.3 Results

A total of 822 individuals were included in the study with 1711 captures and 356 recorded mortalities. The numbers seen alive and recovered dead in each recovery area are given in Table 2.1. Over 60 different

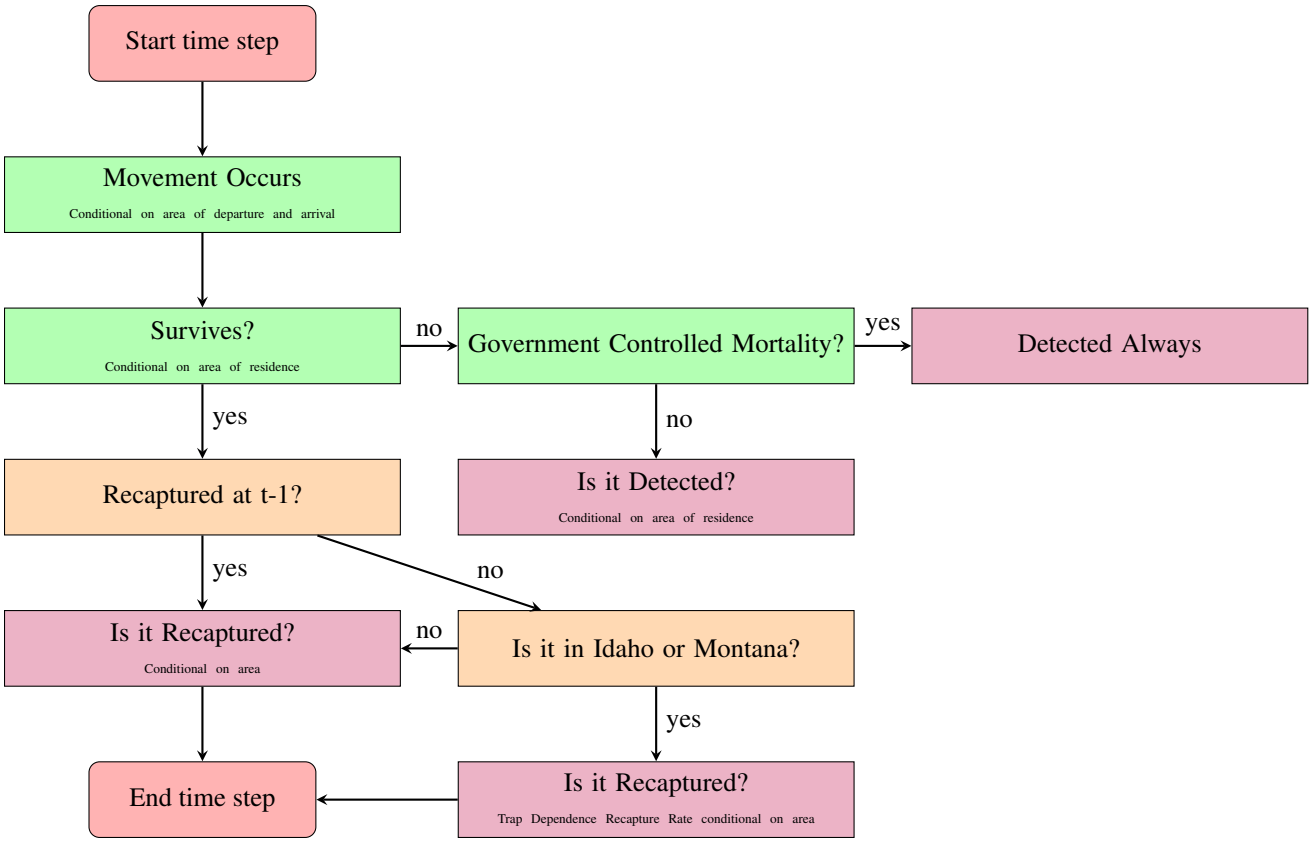


Figure 2.2: A flow-chart representation of the maximal mark-recapture model. Green represents part of the survival process, purple the observation process and orange how the model partitions the observation process between the two states; observed at the previous time step and unobserved the previous time step that account for trap dependence effects in Idaho and Montana.

models were fitted testing for temporal variation and individual level covariates, given in Appendix A1, on survival, temporal variation in recapture and recovery rates and whether migration rates varied between sexes and whether they depended on the departure site (F in Appendix A1), site of arrival (T) or both (F.T). Time is only fitted as varying every year or with all years pooled together. I do not pool a subset of years and test against other years. A selection of best-fit models are given in Appendix A4. Models containing temporal variation in migration did not converge and ages of seven and older were pooled together to enable convergence.

2.3.1 Best fit models

Different dynamics were identified in three ares; Yellowstone National Park, Wyoming and the areas of Idaho and Montana pooled together (Figures 2.3 and 2.4). No temporal variation was found inside Yellowstone National Park with mean survival 0.68 (95% CI 0.61, 0.74), the only management area where survival did not vary significantly between years. No evidence for differing temporal variation in annual intercept values were found between Idaho and Montana with survival rates decreasing from 0.79 (0.71, 0.85) in 2005 to 0.61 (0.51, 0.70) in 2009. Survival rates remained around 0.8 in 2006 and 2007 decreasing in 2008

	YNP			Idaho			Wyoming			Montana		
	Seen	Non-Gov	Gov	Seen	Non-Gov	Gov	Seen	Non-Gov	Gov	Seen	Non-Gov	Gov
2005	66	18	0	93	7	7	36	3	6	50	10	6
2006	53	7	0	104	11	4	39	7	5	63	8	4
2007	57	7	0	108	10	5	50	4	5	82	11	9
2008	60	16	1	119	27	12	55	14	7	93	12	19
2009	47	10	0	129	27	15	54	4	2	86	12	24
2010	41	10	0	87	27	2	63	4	24	76	12	24

Table 2.1: Number of collared individuals seen alive and dead from government controllable (Gov) and uncontrollable (Non-Gov) sources in the four management areas between 2005 and 2009.

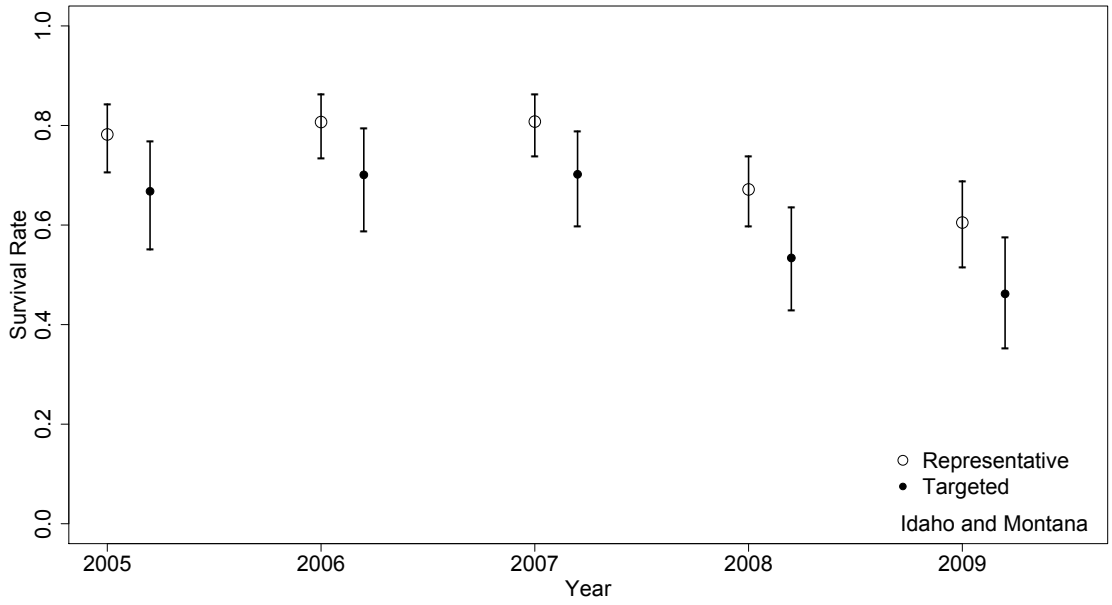


Figure 2.3: Annual survival estimates in Idaho and Montana pooled together, partitioned between individuals targeted for collaring and those that were part of a representative sample.

to 0.68 (0.60, 0.75) and continuing down in 2009 (Figure 2.3). A two age-class structure was found to be significant in Wyoming with young individuals (10-33 months) experiencing increased survival relative to older individuals (34 months and older, $\beta_{10:33\text{ months}}$= 0.88; 0.22, 1.54). Differences between sexes found reduced survival in females ($\beta_{female} = -0.27; -0.51, -0.02$) when fit as an additive effect across all sites although significance was not stable under small increases in $\hat{c}$ ($\hat{c} = 2$). Individuals targeted for sampling, usually due to livestock depredation (See Methods) experienced reduced survival ($\beta_{targeted}$= -0.16; -0.63, 0.32), fitted as an additive intercept across all areas. All individuals are collared as part of a representative sample in Yellowstone National Park and collaring information was not provided in Wyoming. Therefore this additive effect is from individuals collared in Idaho and Montana, although members of the representative sample did transition into the other management areas during the study. Pooling survival across management areas and across years yielded an estimate of 0.68 (0.65, 0.71) a decrease of 7% from the analysis of Smith et al. [2010], indicative of a population reaching carrying capacity experiencing increased

density dependence. Pooling years produced survival estimates of 0.74 (0.69, 0.79) in Idaho, 0.61 (0.55, 0.67) in Wyoming and 0.70 (0.63, 0.77) in Montana. Given low adult survival in Wyoming this indicates a younger age structure that may be less robust to harvest than in Idaho and Montana.

2.3.2 Correlations between survival and population growth

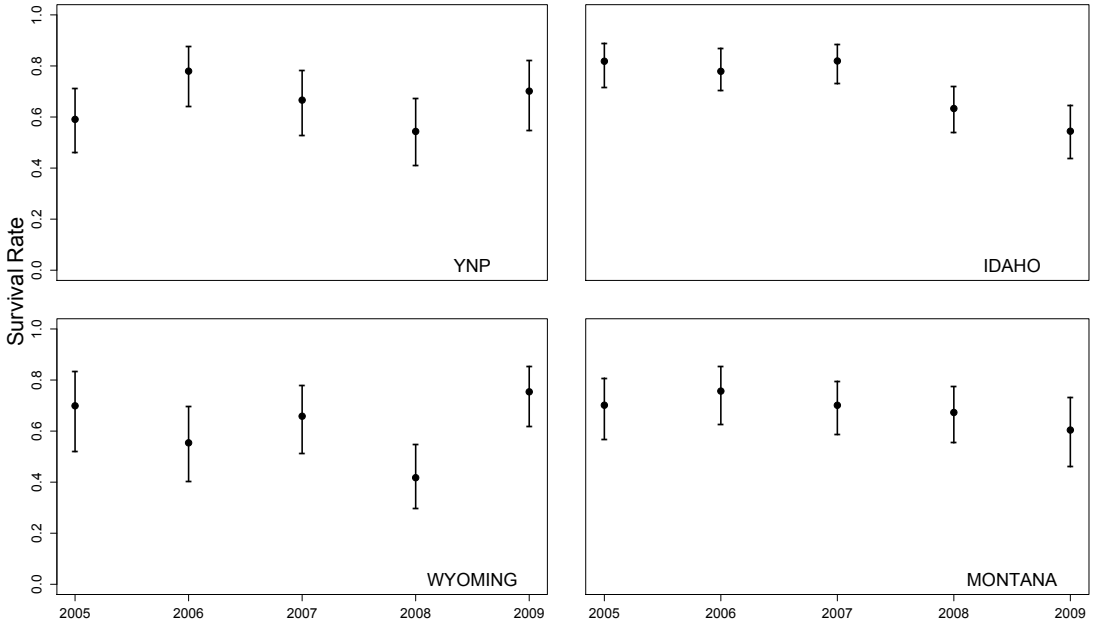


Figure 2.4: Annual survival rates of individuals of 10 months and older in the four management areas.

	YNP	Idaho	Wyoming	Montana
2005	0.69	1.21	1.33	1.68
2006	1.15	1.31	1.31	1.23
2007	1.26	1.09	1.07	1.34
2008	0.73	1.17	0.95	1.18
2009	0.77	1.02	1.26	1.05
2010	1.01	0.89	1.10	1.08

Table 2.2: Population growth rates in the four management areas.

To understand how survival correlates with population growth rates, models were fitted with cause specific mortality and survival varying temporally (Appendix A3). Population growth rates are given in Table 2.2.

Populations decreased in Yellowstone in 2005, 2008 and 2009 correlating with the drop in survival rates in 2005 and 2008 (Figure 2.4). Survival rates were good in 2009 and did not explain the decrease in population size (Table 2.2). Population growth rates decreased in Montana as the study progressed in line with decreases in population growth rates. Population counts predicted an increase of 68% in 2005 although this may be due to changing monitoring protocols between 2004 and 2005 inflating population

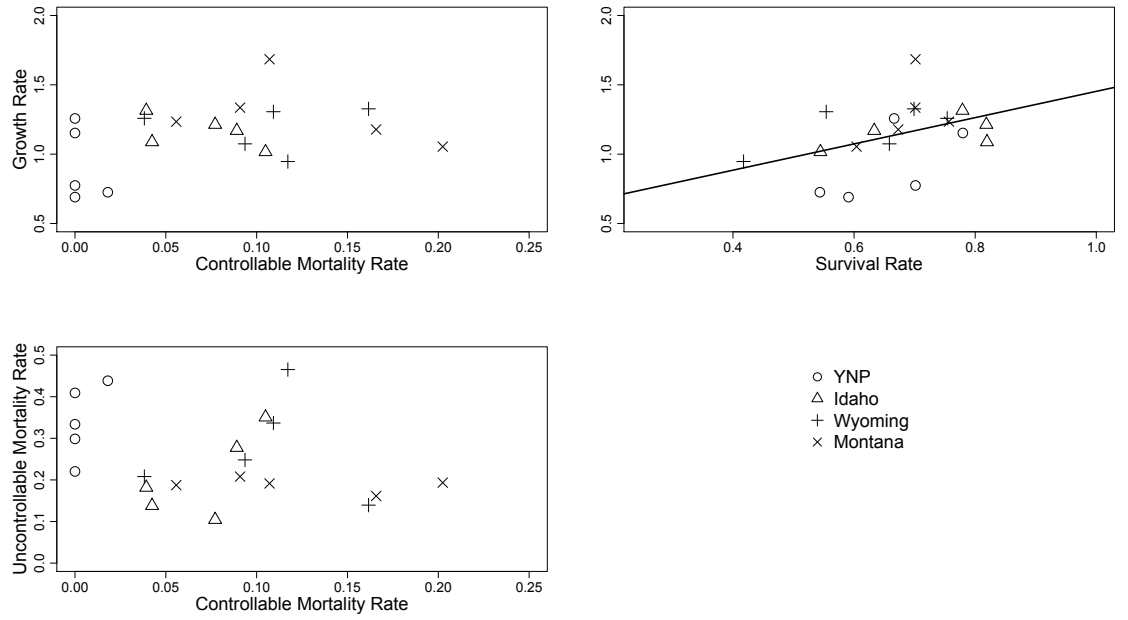


Figure 2.5: The effect of survival rates and government controlled mortality rates on growth rates (top row) and the correlation between government controlled and uncontrollable mortality sources (bottom).

counts in 2005. Population growth rates decreased similarly in Idaho with populations declining in 2009. Patterns of population growth rates in Wyoming follow similar trends to survival estimates. Given the correlation between survival trends and population growth rates it is clear that survival is driving population trends in these areas. Regressing growth rates against survival rates gives a positive correlation of 0.95 which, although marginally insignificant (p = 0.06, r^2=0.22), implies that survival and recruitment rates are independent, i.e. an increase in survival sees a direct and almost identical response in growth rate (an increase of 1% results in an increase of 0.95% in population growth rate).

2.3.3 Source Sink Dynamics

		time = t+1			
		YNP	Idaho	Wyoming	Montana
time = t	YNP	0.897	0	0.032	0.071
	Idaho	0.002	0.970	0.002	0.026
	Wyoming	0.019	0	0.971	0.010
	Montana	0	0.008	0	0.992

Table 2.3: Movement rates between the four management areas.

Movement between sites was dependent on both the site of departure and the site of arrival. Nearly ten percent of individuals in Yellowstone were predicted to migrate out of the park annually, mostly to Montana (rate = 0.071; 0.045, 0.112) with 3% moving to Wyoming (Table 2.3) and 1.9% moving in the

opposite direction (Wyoming to YNP). No individuals were predicted to have moved from Montana to either Wyoming or Yellowstone, making Yellowstone a source population for Montana. Wyoming was a source, although to a lesser extent than Yellowstone, with only 1% of individuals predicted to transition across into Montana, although net migration depends on population size in the site of departure so caution must be taken when interpreting the bigger source from per capita rates. Transition rates out of Idaho into both Yellowstone (0.002; 0, 0.013) and Wyoming (0.002; 0, 0.014) were identical, and higher into Montana (0.026; 0.015, 0.044). Transition rates from Montana to Idaho were 0.008 (0.003, 0.025) making Idaho a net source for Montana given a larger population size in Idaho [Jimenez and Becker, 2012]. Overall transitions occurred in at least one direction between each management area demonstrating high connectivity within the entire system.

2.3.4 Cause Specific Mortality Rates

	Est	LCI	UCI
Y	0.99	0.93	1.00
I	0.75	0.68	0.81
W	0.73	0.64	0.81
M	0.59	0.49	0.67

Table 2.4: Percentage of total mortality that is from non-government controlled sources in the four management areas.

Inside Yellowstone National Park nearly all mortality was of non-government controlled sources (99%, 95% CI: 93%, 100%), Table 2.4). In Idaho and Wyoming this decreased to around 75% (75% Idaho, 68%, 81%, and 73% Wyoming, 64%, 81%) and decreased further to 59% in Montana (49%, 67%).

2.3.5 Recapture Rates

Perfect recapture rates were reported inside Yellowstone and were high in Wyoming (0.91; 95% CI 0.83, 0.95). Confidence intervals around Yellowstone recapture rates did not converge due to being on the boundary of the parameter space. Recapture rates of individuals in the observed state were also high in Idaho 0.88 (0.82, 0.92) and lower in Montana (0.78; 0.70, 0.84). Recapture rates of individuals in the unobserved state were decreased at 0.24 (0.12, 0.42) in Idaho and 0.14 (0.06, 0.29) in Montana. Recovery rates were highest in Montana (0.71; 0.44, 0.88), similar in Yellowstone (0.65; 0.53, 0.74) and Idaho (0.63; 0.51, 0.73) and lowest in Wyoming (0.46; 0.34, 0.58).

2.4 Discussion

Given decreasing wolf population growth rates in Idaho, Wyoming and Montana and decreasing population size in Yellowstone National Park through the study (Table 2.2), coupled with the introduction of licensed

hunting in the State managed areas, understanding the contribution of changing survival rates to these declines, and whether marking and monitoring individuals provides useful insight of population trends for managers, is essential. In order for the recovery to be sustainable and for wolves to remain off of the endangered species list, connectivity between management sites is critical in maintaining source-sink dynamics and genetic diversity. Using a mark-recapture-recovery framework migration rates and survival rates between areas were estimated.

The analysis identified three distinct dynamic areas, Yellowstone National Park, Wyoming, and Idaho and Montana pooled together. Survival rates were constant throughout in Yellowstone, fluctuated in Wyoming with no general trend, but declined in the later part of the study in Idaho and Montana (Figure 2.3). The movement process found all areas to be connected with each area experiencing two way migration. A two age-class structure was identified in Wyoming, with an additive temporal effect decreasing survival greatly in 2008 but recovering after. This should result in a younger age structure in Wyoming, with population growth potentially driven by recruitment, producing a population more susceptible to crashes through harvest. Decreasing survival correlated closely with declining population growth in Idaho and Montana.

Movement rates between areas found Montana to remain a sink population with movement rates between Yellowstone particularly high (Table 2.3). Migrations were predicted to occur in at least one direction between any two management areas and all areas had immigration predicted from at least one area. This demonstrates a highly connected system and although it cannot be inferred whether this maintains genetic connectivity, it meets the basic criteria (movement of individuals) required for genetic connectivity to persist [Bergstrom et al., 2009, Vonholdt et al., 2010]. Whether these migration patterns decrease as populations are harvested requires future monitoring of collared individuals. Given the sink dynamics inside Montana [Smith et al., 2010], reduced number of migrants due to decreased source population sizes, decreased benefit of migrating due to reduced density dependence in the source area etc, could pose problems in decreasing genetic diversity and reducing population growth rates.

Survival rates of collared wolves correlate very closely with population growth rates (Figure 2.5) demonstrating that collaring of wolves can be used effectively to inform managers of population trends. No significant temporal variation was found inside Yellowstone although decreasing survival rates in Idaho and Montana should be closely monitored especially given decreasing populations in 2010 suggest survival continued to decline after this study (Table 2.2). Inside Wyoming survival rates for adults over 34 months of age were lower than individuals of 10-33 months. This demonstrates a high turnover in wolf numbers and potentially a younger age structured population than in the other management areas, potentially reducing the proportion of breeding age individuals. This could be a sign of a population that is less robust to harvest than in Idaho and Montana. Wolves were relisted in Wyoming in 2014 due to concerns over the sustainability of management protocols, and it is a shame that concerns raised in this analysis were not acted upon. Overall survival rates across the Northern Rocky Mountain have decreased since 2004 coinciding

with increasing population densities, reflected in decreasing population growth rate across the entire range (Table 2.2).

The ratio of cause-specific mortality (government control actions and hunting pooled against all other sources) was similar in Idaho and Wyoming where a quarter of mortality was from government controlled sources. Inside Montana this rate was 41% indicating a highly manipulated population (Table 2.4). After the introduction of hunting it is likely that the majority of mortality inside Montana will be government controlled. Such high levels of anthropogenic mortality will be almost certainly additive. Lower levels in Idaho and Wyoming (25% and 27% respectively) represent two heavily manipulated populations. Inside Yellowstone nearly all mortality was of non-government sources (99%) and the majority of this was through disease and other natural causes. It is not reasonable to assume that this is independent of anthropogenic pressure as the highly connected nature of the Northern Rocky Mountain system may result in anthropogenic pressure outside Yellowstone affecting dynamics inside. Survival rates inside Yellowstone can not therefore be used as survival in the absence of anthropogenic pressure in an analysis of compensatory mortality analysis.

The rates of anthropogenic mortality identified here are in stark contrast to those identified by Murray et al. [2010] who identified anthropogenic mortality to make up 80% of total mortality. Here I use a different metric, using government controlled mortality in place of all anthropogenic causes. The difference however is striking and raises the potential for compensatory dynamics to occur to a greater extent than previously identified [Murray et al., 2010, Creel and Rotella, 2010, Gude et al., 2012]. The decreases in survival, as populations have reached carrying capacity, however, indicate that compensation may be minimal and in line with many previously studied populations, discussed by Lebreton [2005] and Burham and Anderson [1984]. As populations reach carrying capacity removal of individuals can reduce density dependent regulation, potentially increasing survival, and recruitment rates of others. The increases in government controlled mortalities listed in Table 2.1 correlate closely with declines in survival and population growth identified in Figure 2.4 and Table 2.2, such that government sanctioned removal appears additive, although this is not a rigorous proof. Annual predictions of cause specific mortality contain both sampling and competition bias [see Péron, 2013, for details] and correlations between the two cannot be used to estimate levels of compensation unless these are accounted for. Given that survival in the absence of anthropogenic mortality is not known, in this system these biases cannot be removed. The analysis here, and the three previous studies, have ignored density dependent regulation that occurs at the group level [Harrington et al., 1983, Schmidt and Mech, 1997, MacNulty et al., 2012, Stahler et al., 2013]. This structural level may introduce additional areas for compensation to occur. The following chapter investigates how group structure further complicates the question, and whether the question can be answered over vast spatial scales such as a State or National Park.

In summary, survival rates decreased in Idaho and Montana and whether these trends continue down,

recover, or stabilise, will be of importance in maintaining sustainable harvest quotas. Low survival rates inside Wyoming of adults over 34 months of age could be of concern as young populations may not be able to respond to harvest through high recruitment rates, the primary mechanism through which wolf populations increase population growth [Fuller, 1989], due to fewer breeding age individuals than other populations. Decreased survival rates inside Yellowstone compared to the previous analysis [Smith et al., 2010] and decreasing trends in Idaho should be closely monitored as density dependence appears to be naturally regulating population growth. If density is regulating population growth initial harvest may be compensated by reducing density dependent regulation. At a certain density this regulation will disappear and harvest may shift to becoming additive, generating a dynamic where initially no change in population growth occurs, followed by a sudden and sharp decrease [Lebreton, 2005]. Yellowstone and Idaho are source populations for Montana. Decreasing survival rates further through licensed hunting could impact population growth rates inside Montana amplifying the effects of removal in Montana. The analysis here demonstrates the benefit of future monitoring and collaring of individuals, with analyses focusing on the entire inter-connected system, as opposed to small scale analyses within a given management zone.

Chapter 3

A simple model of the regulatory mechanisms acting in socially structured populations

Abstract

Understanding the relative contributions of inter and intra-group drivers on key demographic rates is essential for accurately predicting population level trends of social species. Derived here is a simple mechanistic model that clearly partitions demographic rates into Allee, inter and intra-group components. Using identical functions to parameterise survival and recruitment rates permits direct comparisons of the presence and strength of regulatory mechanisms and through which demographic rates they act. It is hypothesised that resource regulated populations will have greater intra-group limiters whereas space regulated systems should exhibit higher coefficients of inter-group competition. Parameterised for the Yellowstone National Park grey wolf (*Canis lupus*) across two distinct, well studied areas (Northern Range and Interior of the park) the model tests these hypotheses and demonstrate a complex interplay between within and between group drivers in determining population level growth rates. Utilising a novel descriptor of the relative contributions of inter and intra-group drivers to group specific growth rates, results clearly demonstrate the necessity to consider the distribution and abundance of group sizes when considering population level trends.

keywords: Group dynamics, *Canis lupus*, grey wolf, intra-group competition, inter-group competition, Allee effects.

3.1 Introduction

Population growth and return rates to carrying capacity in density dependent systems, can be explained through understanding how demographic rates are regulated [Sæther et al., 1996, Caswell, 2001]. This requires identification of the relevant population structure and the strength of regulatory mechanisms acting through each structural level. Group living promotes a two-tiered competition structure, whereby individu-

als compete as a unit alongside the same individuals with whom they also compete against. Within a group individuals compete for resources and breeding rights, while also competing alongside those same individuals against other social groups, for territories and access to resources [Calhoun, 1952, Crook, 1970, King, 1973, Macdonald, 1983].

Sociality imposes spatial structure on populations, that is known to produce qualitatively different dynamics to homogenous populations [Hanski, 1999]. Spatial structure can increase extinction risk and restrict population growth. In meta-populations this is known as extinction-recolonisation dynamics, with extinction risk dependent on the underlying dispersal mechanisms [Lande et al., 1999, Hanski, 1999]. In social species population growth can occur through new individuals joining pre-exisiting groups or through the formation of new groups. When fitness is reduced in both small and large groups, formation of new groups is difficult and individuals may be forced out of large groups. In this scenario populations can struggle to recover after population crashes, as individuals cannot join pre-existing groups and cannot establish new groups [Roelke-Parker et al., 1996, Courchamp et al., 2002, Packer et al., 2005]. When individuals experience reduced fitness in large groups, expanding group size through increased territory range instead of forming new groups can also inhibit population growth [Marino et al., 2006, 2013]. The mechanisms inhibiting group expansion, independently of population density, will strongly influence population growth.

In this article, regulation is defined as a mechanism that reduces a component of fitness. Allee effects are considered to be a regulatory mechanism [Allee, 1931, Allee et al., 1949]. These are partitioned into component and demographic Allee effects, reviewed by Stephens et al. [1999]. A component Allee effect is a reduction in a component of fitness due to a low number or density of conspecifics. Here Allee effects at the group level are modelled, such that a lack of group members reduces reduces a component of fitness. If this component reduces total fitness, resulting in negative density dependence it is termed a demographic Allee effect, the common interpretation reviewed by Courchamp et al. [1999a]. An example of a component Allee effect is decreased hunting efficiency in small groups. This may be offset by increased per capita intake at a kill, as seen in african wild dogs, *Lycaon pictus*, lions, *Panthera leo* and grey wolves, *Canis lupus* [Caraco and Wolf, 1975, Packer et al., 1990, Creel and Creel, 1995]. If it is compensated, reduced hunting efficiency is a component Allee effect, if it is not the component manifests in a demographic Allee effect.

Sociality also imposes a codependence between group members, such that components of individual fitness are expected to be reduced in small groups, with certain species failing to rear offspring below a certain group size [see Courchamp et al., 1999b, for multiple examples]. Whether this reduction in individual fitness in social carnivores translates into a reduction in population growth rate, differs within species in different environments [see Rood, 1990, Courchamp and Macdonald, 2001, Clutton-Brock et al., 2001, Sanderson et al., 2014, for evidence of demographic Allee effects] and [Gusset and Macdonald, 2010, Woodroffe, 2011, Bateman et al., 2012, Angulo et al., 2013, for the contrary]. In the presence of

demographic Allee effects, population growth will depend on the distribution of group sizes as well as population size. An abundance of small groups may still experience reduced fitness due to demographic Allee effects. If mean group size is small, demographic stochasticity may cause group size to drop to levels where strong demographic Allee effects drive them to extinction [Lande, 1993]. Thus, in social species, Allee effects and demographic stochasticity have the potential to influence population dynamics at high densities.

Groups also compete as a unit against other groups to obtain optimal territories that infer fitness benefits on their occupants [Mosser et al., 2009]. When competing as a unit, bigger means better, in that a single individual often increases the success of direct conflict events dramatically [Mech, 1994, Whitman et al., 2004]. Larger groups may experience stronger intra-group regulation but this may be offset by reduced inter-group competition. This has important implications for species regulated by anthropogenic methods. Population responses to harvest will depend on the changes in regulatory mechanisms alleviated through removal of individuals [Lebreton, 2005].

Using a simple mechanistic model, I decompose a generic demographic rate into three components, regulation that acts on small groups (component Allee effects), regulation that affects large groups independently of population size (intra-group competition) and regulation that acts across groups (inter-group competition). Parameterised to a long-term study of Yellowstone National Park (YNP hereafter) grey wolves the model demonstrates the dependence of the distribution and abundance of groups in regulating group-specific growth rates. Partitioning YNP into the resource-dense Northern Range, and the resource-scarcer Interior [see Metz et al., 2012, Cubaynes et al., 2014, for more details], the results provide comparisons of the presence and strength of regulatory mechanisms across each area.

In space limiting systems encounter rates between groups should occur more frequently than in resource limiting systems as territory size is expected to be smaller and overlap greater. In this scenario individuals should compete more as a unit defending their territory against others than against fellow group members for access to resources. Cubaynes et al. [2014] demonstrated this on the Northern Range with increasing intra-specific strife as densities increased. When a system is resource limiting, it is expected that territory ranges should increase, decreasing encounter rates with other groups but increasing competition between group members at kills, that may be acquired less frequently. Therefore it is expected that the regulatory mechanisms acting on a population will differ between areas when resource type or density differ.

This work was motivated by the ongoing debate around the sustainability of harvest in the Northern Rocky Mountain grey wolf population [Bergstrom et al., 2009]. Grey wolves have recently been removed from the endangered species list (delisting) and legal harvest is the proposed method to regulate population growth. Three studies have aired competing views onto the impact of anthropogenic induced mortality on natural mortality rates [Creel and Rotella, 2010, Murray et al., 2010, Gude et al., 2012]. Each aimed to investigate whether removal of individuals through government control actions and licensed hunting increases

natural mortality rates (additive mortality) or reduces natural mortality rates (compensatory dynamics).

Lebreton [2005] discusses the impacts of structure on compensatory dynamics, and sociality imposes both spatial structure and social structure onto populations. The issue with the debate surrounding sustainable hunting on the Northern Rocky Mountain wolf, is that previous studies have ignored the socio-spatial structure. Compensation occurs when a regulatory mechanism is removed or dampened through reductions in competition [Burham and Anderson, 1984, Schaub et al., 2004, Lebreton, 2005]. The models used by Murray et al. [2010], Péron [2013] and Gude et al. [2012] were derived on homogenous solitary populations and as such may fail in the presence of spatial and social structure. Here I aim to demonstrate that mechanisms regulating individual fitness depend on the size of the focal group, the level of inter-group pressure but also the habitat within which the group exists. Partitioned across the resource dense Northern Range and the lower resource density Interior of the park the model tests the extent to which all groups experience identical regulation. The model identifies the required structure for models of compensatory-additive dynamics to contribute meaningfully to the debate on sustainable hunting. Given wolves exhibit reproductive suppression and inter-group strife [Mech, 1970, Kleiman and Eisenberg, 1973, Van Ballenberghe, 1983, Peterson, 1977], combined with reduced hunting efficiency and reproductive output in large packs [Schmidt and Mech, 1997, MacNulty et al., 2012], they have the potential to produce an interesting interaction between intra-group, inter-group and component Allee regulatory mechanisms.

3.2 Methods

3.2.1 Study Species

Grey wolf group sizes range from 1 to 26 individuals consisting of a dominant breeding pair and their offspring that remain in their natal pack [Mech, 1970, Kleiman and Eisenberg, 1973] although packs consisting of multiple breeding pairs and unrelated individuals has been documented [Murie, 1944, Harrington et al., 1982, Mech, 2000]. Wolves are cooperative hunters that prey primarily on elk and to a lesser extent bison in YNP [Mech, 1970, Metz et al., 2012], with hunting success reduced in large and small packs [Schmidt and Mech, 1997, MacNulty et al., 2012]. Female fecundity has been shown to act non-linearly with group size [Harrington et al., 1983, Stahler et al., 2013] which combined with decreased hunting success has the potential to exhibit demographic Allee effects. Packs directly compete for optimal territories with inter-pack strife regulating survival and infanticide regulating recruitment in high density populations [Mech, 1970, Van Ballenberghe, 1983, McLeod, 1990, Cubaynes et al., 2014].

3.2.2 Study Site

Data was analysed from the initial 14 years (1996 to 2009) of a long-term study in Yellowstone National Park, a 8991 km^2 protected area in north-western Wyoming, USA. Each winter (January to February), 20-

30 individuals are captured and radio-marked, including between 30 and 50% of pups born in the previous year. Capture, collaring and handling protocols were approved by the National Park Service and are in accordance with recommendations from the American Society of Mammalogists. An in-depth description of Yellowstone National Park, its flora and fauna, details of the wolf reintroduction programme and the Yellowstone study can be found in Smith et al. [2004].

3.2.3 Data

Datasets were compiled from the Yellowstone National Park wolf study. The data is partitioned between the Northern Range and Interior areas. The Northern Range comprises some of the highest wolf densities in the world, due to the large abundance of elk (*Cervus elaphus*) and the wolves' protected status against anthropogenic pressures, contrasting that of the Interior of the park, where both wolf and elk densities are lower due to increased elevation changing the habitat. Wolves also experience protected status in the Interior of the park. Ground and air tracking established the number of pups at emergence and surviving to yearlings from 1995-2009. In depth ground tracking in March on the Northern Range combined with air tracking established March group size and status of collared individuals, either survived, died, missing or censored having left the population. Years experiencing outbreaks of canine distemper virus (1999 and 2006) were removed from the recruitment analysis [Almberg et al., 2010].

A previous survival analysis found no significant age structured effects on adult group residents survival inside the Greater Yellowstone Ecosystem, the original wolf recovery area containing Yellowstone National Park and areas of the surrounding states [Smith et al., 2010]. The model derived below does not account for age structure effects and all individuals are assumed to carry equal utility in rearing pups.

A total of 260 unique individuals were monitored throughout the study. Of these, 153 were recorded on the Northern Range and 120 in the Interior of the park. A total of 585 recaptures, of which 255 were on the Northern Range and 209 in the Interior, occurred during the study. In total, 93 mortalities were reported, 64 on the Northern Range and 29 in the Interior. Adult group sizes varied from 1 to 11 on the Northern Range and 1 to 15 in the Interior. April adult population sizes varied from 30 to 87 on the Northern Range and from 2 to 78 in the Interior. April population size does not include newly born pups and represents the number of individuals of 1 year of age and older.

3.2.4 The Model

The demographic rate (survival, recruitment, dispersal) is partitioned into three components: a cost to small groups, large groups and large population sizes. These drivers are defined as group level Allee effects, intra-group and inter-group competition. The model assumes a single breeder, identical survival between sexes and dispersal to act through adults (> 1 year) as this is the most common structure in grey wolves [Mech, 1970, Kleiman and Eisenberg, 1973, Macdonald and Moehlman, 1982].

Allee effects reduce demographic rates inversely to group size. A Michaelis-Menton function is used to model this cost (A full list of parameter definitions are given in Table 3.1):

Parameter	Definition
F_{max}	Maximum of a vital rate (used in the derivation of the model).
$F_{\frac{1}{2}}$	Half saturation of a vital rate (used in the derivation of the model). The number of group members required to obtain half of maximum rate. In the absence of inter-group competition and ignoring the intra-group limiter (α).
$\mathbf{x}$	Vector of groups. Each entry is the size of a group.
$\mathbf{x}_\mathrm{i}$	The ith group size (used in the derivation of the model).
S_{max}	Maximum survival rate.
L_{max}	Maximum litter size at Emergence.
$S_{\frac{1}{2}}$	Half saturation rate of survival (see $F_{\frac{1}{2}}$).
$L_{\frac{1}{2}}$	Half saturation rate of recruitment (see $F_{\frac{1}{2}}$).
α_s	The strength of intra-group competition on survival.
α_r	The strength of intra-group competition on recruitment.
β_s	Inter-group competition on survival.
β_r	Inter-group competition on recruitment.
δ	Dispersal rate.

Table 3.1: Definition of parameters.

$$\frac{f_{max}.x}{f_{\frac{1}{2}} + x}$$

Where x is the focal group size, f_{max} the maximum value of the rate and $f_{\frac{1}{2}} > 0$ the half saturation rate, the group size at which half of f_{max} is obtained. As group size increases the function converges on f_{max} (maximum survival, dispersal rate or litter size at emergence). A larger value of $f_{\frac{1}{2}}$ represents a stronger Allee effect and a larger group size is required for the function to converge on f_{max}. It may be the case that this value is never reached in nature as groups may always experience either Allee, inter and intra-group limiters.

Above some threshold size, survival and recruitment may decrease, a local Ricker density dependence term ($e^{-\alpha.\mathbf{x}_\mathrm{i}}$) acts on this function [Ricker, 1954]. The intra-group competition coefficient (α>0), determines the strength of competition and limits the maximum group size that can be obtained in the absence of inter-group competition. Combined this gives the intra-group functions of survival and recruitment.

$$\frac{f_{max}.x}{f_{\frac{1}{2}} + x} e^{-\alpha.x}$$

The three parameters determine the presence and strength of Allee effects ($f_{\frac{1}{2}}$), intra-group limiters (α) and the maximum value of the demographic rate that can theoretically be realised (f_{max}). It imposes no conditions on the presence or absence of either driver, and if they are not present then the parameter estimates will be zero.

Inter-group competition similarly, is a form of density dependence that may act non-uniformly across survival and recruitment. Creating a vector of group sizes $\mathbf{x}$ one can write population size as $\sum \mathbf{x}$. As a

group does not experience inter-group competition with itself, inter-group competition is modelled as being density dependent, removing the focal group ($e^{-\beta(\sum(\mathbf{x})-\mathrm{x_i})}, \beta > 0$). This form of inter and intra-group limiters is used by Leticia et al. [2002]. The difference between the two models is that it incorporates Allee effects whereas Leticia et al. [2002] incorporate a cooperation term, focusing on the evolution of cooperation. Here the aim is to understand the relative contributions of Allee effects, inter and intra-group competition on demographic rates and local dynamics as opposed to the marginal benefit of cooperation at the group level required for the trait to invade the population. The decomposed demographic rate, experienced by group i, in a population consisting of groups with sizes given by the vector $\mathbf{x}$, is defined as:

$$\frac{f_{max}.\mathbf{x_i}}{f_{\frac{1}{2}} + \mathbf{x_i}} e^{-\alpha.\mathbf{x_i}} e^{-\beta(\sum(\mathbf{x})-\mathbf{x_i})} \tag{3.1}$$

This clearly partitions the Allee effects and intra-group coefficients ($f_{\frac{1}{2}}, \alpha$; respectively) from inter-group competition (β). The survival estimate produced using this decomposition is per capita survival whereas on recruitment it is at the group level; the number of individuals recruited to 1 year of age. Utilising this decomposition to model group specific growth rates requires dividing the recruitment term below by $\mathbf{x}$ to obtain per capita and not group level rates. Assuming constant adult dispersal rate δ, the group size vector can be predicted across a single time step using the discrete time equation:

$$\mathbf{x}^{t+1} = \lambda(\mathbf{x}|\theta).\mathbf{x}^t$$

$$\mathbf{x}^{t+1} = \left[(1 - \text{dispersal rate}).(\text{survival rate}) + \text{recruitment rate}\right].\mathbf{x}^t$$

$$\mathbf{x}^{t+1} = \left[(1-\delta).\frac{\mathrm{S_{max}}.\mathbf{x}^t}{\mathrm{S}_{\frac{1}{2}} + \mathbf{x}^t}.\mathrm{e}^{-\alpha_s.\mathbf{x}^t}.\mathrm{e}^{-\beta_s.(\sum(\mathbf{x}^t)-\mathbf{x}^t)} + \frac{\mathrm{L_{max}}}{\mathrm{L}_{\frac{1}{2}} + \mathbf{x}^t}.\mathrm{e}^{-\alpha_r.\mathbf{x}^t}.\mathrm{e}^{-\beta_r.(\sum(\mathbf{x}^t)-\mathbf{x}^t)}\right].\mathbf{x}^t \tag{3.2}$$

The terms inside the brackets are the group specific growth rate. δ represents adult dispersal rates. Individuals in the YNP grey wolf system disperse near their second birthday and afterwards [Boyd and Pletscher, 1999], therefore dispersal acts on adults and not recruits. This term can be on recruitment or both depending on species specific dispersal strategies and can be partitioned into intra- and inter-group components in a similar manner given sufficient dispersal data. The flexibility of this model permits any of the coefficients to be zero, removing that form of competition from the model. If survival or recruitment do not increase with group size then $S_{\frac{1}{2}}$ or $L_{\frac{1}{2}}$ are zero and the equations reduce down to those which are limited by only inter and intra-group competition. If there is no intra-group competition on survival and recruitment then α_s or α_r are zero. If inter-group competition does not influence survival or recruitment then β_s or β_r are zero. It is clear from this decomposition that the population level growth rate is a combination of all drivers

$$\lambda_{pop} = \frac{\sum \mathbf{x^{t+1}}}{\sum \mathbf{x^t}} = \frac{\sum \lambda(\mathbf{x}|\theta).\mathbf{x}^t}{\sum \mathbf{x^t}}$$

and that larger variance in the distribution of groups increases the complexity of population growth rate by increasing the variance in $\lambda(\mathbf{x}|\theta)$.

3.2.5 Defining: Relative Contributions

The relative contribution of a regulatory mechanism, $g_i(\mathbf{x}|\theta)$ of a demographic rate in dampening group specific growth rates (λ_j) is measured using the following procedure. Each demographic rate is partitioned into three drivers:

1. Allee effects $\frac{\mathbf{x_i}}{f_{\frac{1}{2}}+\mathbf{x_i}}$
2. Intra-group competition $e^{-\alpha_{s,r}.\mathbf{x_i}}$
3. Inter-group competition $e^{-\beta_{s,r}.\left(\sum_i(\mathbf{x_i})-\mathbf{x_i}\right)}$

Denoting these drivers as $g_i(\mathbf{x}|\theta)$, where θ is the set of parameters and $i = 1:6$ represents the i^{th} driver (three on survival,1:3, and three on recruitment, 4:6). The contribution of regulatory mechanism i in regulating the demographic rate is defined as its weighted departure from unity, weighted such that the contribution of all three drivers sum to one. The departure from unity can be viewed as the strength of the limiter, such that the identity gives contribution zero and that it is inversely proportional to $g_i(\mathbf{x}|\theta)$ (A stronger limiter gives a greater contribution). The relative contribution , $C_i(\mathbf{x}|\theta)$, to group specific growth rates is this value, weighted against the ratio of the demographic rate to group specific growth rate (λ_j). Put simply, group specific growth rates are the sum of apparent survival and recruitment rates. To measure the relative contribution of recruitment to growth, the recruitment rate is divided by the group specific growth rate. The relative contribution metric derived here measures the relative contribution of each mechanism in regulating the demographic rate and scales it by the contribution of the demographic rate to the growth rate. The focus is on regulatory mechanisms, the stronger the mechanism, the closer to zero it will be.

Defining the survival (including dispersal here) and recruitment rates of group j as $S_j(\mathbf{x}|\theta)$ and $R_j(\mathbf{x}|\theta)$ respectively, given by the two terms in brackets in equation 3.2, the relative contributions of each driver to group specific growth rates are:

$$C_{i,j}(\mathbf{x}|\theta) = \begin{cases} \frac{1-g_i(\mathbf{x}|\theta)}{\sum_{i=1}^{3}(1-g_i(\mathbf{x}|\theta))}.\frac{S_j(\mathbf{x}|\theta)}{\lambda_j} & \text{for } i = 1:3 \\ \frac{1-g_i(\mathbf{x}|\theta)}{\sum_{i=4}^{6}(1-g_i(\mathbf{x}|\theta))}.\frac{R_j(\mathbf{x}|\theta)}{\lambda_j} & \text{for } i = 4:6 \end{cases}$$

Consider the case when there is no Allee effect, $f_{\frac{1}{2}} = 0$, therefore $\frac{\mathbf{x_i}}{f_{\frac{1}{2}}+\mathbf{x_i}} = 1$. From the definition above $1 - g_i(\mathbf{x}|\theta) = 0$ and the contribution is zero. Similarly for inter and intra-group limiters if $\alpha, \beta = 0$ then the contribution is zero. Conversely if there is a strong Allee effect and no intra- or inter-group regulation ($\alpha = \beta = 0$), then $\frac{\mathbf{x_i}}{f_{\frac{1}{2}}+\mathbf{x_i}} \approx 0$ when $\mathbf{x_i}$ is small and $1 - g_i(\mathbf{x}|\theta) \approx 1$. All other contributions are zero such that

$\sum_{i=1}^{3}(1 - g_i(\mathbf{x}|\theta)) = 1 + 0 + 0$ and the contribution of the Allee effect becomes the ratio of the demographic rate to the group specific growth rates $\frac{S_j(\mathbf{x}|\theta)}{\lambda_j}$ or $\frac{R_j(\mathbf{x}|\theta)}{\lambda_j}$ depending on the demographic rate. As it is the only mechanism regulating the demographic rate, its contribution to regulating the group growth rate is the the contribution of the demographic rate to the group growth rate.

3.2.6 Model Fit and Data Series

Survival rates were estimated at the individual level whereas recruitment was estimated at the pack level. In april of each year the pack affiliation of each individual, whether it survived or died and the area it inhabited in was recorded. A second data file was used for the recruitment analysis that recorded the april pack size of each pack, the area it inhabited and the number of pups surviving to april the following year. Least squares regression of pups survived and survival, against the decomposed demographic rate outlined in equation 3.1 was implemented using the 'nls' function in the statistical program R [R Core Team, 2015].

3.3 Results

	Survival				Recruitment			
	Northern Range		Interior		Northern Range		Interior	
	Est	Std. Er	Est	Std. Er	Est	Std. Er	Est	Std. Er
F_{max}	1.000	0.237	1.000	0.172	4.398	5.406	7.959	5.319
$F_{\frac{1}{2}}$	0.050	0.396	0.000	0.252	0.671	3.314	1.231	1.924
α	0.011	0.027	0.020	0.015	0.000	0.112	0.023	0.044
β	0.005	0.002	0.002	0.003	0.004	0.006	0.009	0.006
δ	0.271	0.085	0.242	0.090	-	-	-	-

Table 3.2: Parameter estimates across the two areas with standard errors.

3.3.1 Survival

Maximum survival was estimated at 1 in both areas (Table 3.2) and adult dispersal rates were similar at 0.27 ± 0.085 (mean ± S.E) on the Northern Range and 0.24 ± 0.090 in the Interior of the park. The only driver not detected was a component Allee effect in the Interior. Intra-group competition was almost twice as strong in the Interior ($\alpha_s^{Int} = 0.020, \alpha_s^{NR} = 0.011$) with the converse being true for inter-group competition ($\beta_s^{Int} = 0.002 \pm 0.003, \beta_s^{NR} = 0.005 \pm 0.002$).

3.3.2 Recruitment

112 recruitment events were included in our study (not during disease years See Methods), of which 65 were on the Northern Range and 47 in the Interior. Maximum litter size at emergence in the Interior (7.96 ± 5.32) was predicted to be almost double that on the Northern Range (4.40 ± 5.41, See Table 3.2).

No intra-group cost to recruitment was found on the Northern Range ($\alpha_r^{NR} = 0 \pm 0.112$) and both inter and intra-group competition were greater in the Interior than on the Northern Range ($\alpha_r^{Int} = 0.023 \pm 0.044; \beta_r^{Int} = 0.009 \pm 0.006, \beta_r^{NR} = 0.004 \pm 0.006$).

Corresponding survival and recruitment curves as functions of focal group size are given in Figure 3.1. The top row describes survival and recruitment when the focal group constitutes the population, i.e. in the absence of inter-group competition (solid lines represent the Northern Range, dashed the Interior). In this scenario small packs experience increased survival relative to larger packs with the effect being more pronounced in the Interior. An absence of component Allee effects produces a linear survival curve, whereas a weak component Allee effect on the Northern Range produces an initial increase that decreases linearly above a group size of 4 adults. As population size increases, stronger density dependence on the Northern Range causes the curves to converge. At population sizes above the highest observed (observed = 87, modelled = 100), survival rates on the Northern Range decrease below levels seen in the Interior (bottom row Figure 3.1). As larger packs experience reduced inter-group competition (inter-group competition does not include the focal pack size) the survival benefits observed in smaller packs are reduced on both ranges, cancelling out on the Northern Range.

Intra-group competition was similar across survival and recruitment in the Interior of the park although inter-group competition and Allee effects acted primarily through recruitment (Table 3.2). On the Northern Range intra-group competition acted to a greater extent through survival, Allee effects through recruitment and inter-group competition through both.

Component Allee effects do not produce in a minimum viable group size (strong demographic Allee effect) as smaller groups experience increased per capita recruitment relative to larger groups.

3.3.3 Relative Contributions

The relative contributions of component Allee, inter and intra-group competition across survival and recruitment, under low (29 solid) and high (100 dashed) population densities on the Northern Range (black) and Interior of the park (red) are given in Figure 3.3. To understand this plot consider a small group on the Northern Range, at high density (dashed black line). Cell (A) identifies the relative contribution of the Allee effect on survival. When the group is extremely small (2 individuals) it experiences a small cost and contributes around 4% to the total regulation of the group specific growth rate. This effect quickly disappears as the group increases in size. A group of two individuals in this scenario experiences no intra-group regulation (Cell (B)) on survival, but as the group increases in size intra-group regulation quickly dominates, increasing to more than 50% for a group of 14 adults. The effect of inter-group competition on survival is non-linear. As the group increases in size it no longer experiences reduced recruitment due to Allee effects (cell D) and begins to be regulated primarily by inter-group competition on survival. This does not mean that the small group was not experiencing inter-group competition before, just that the main

Figure 3.1

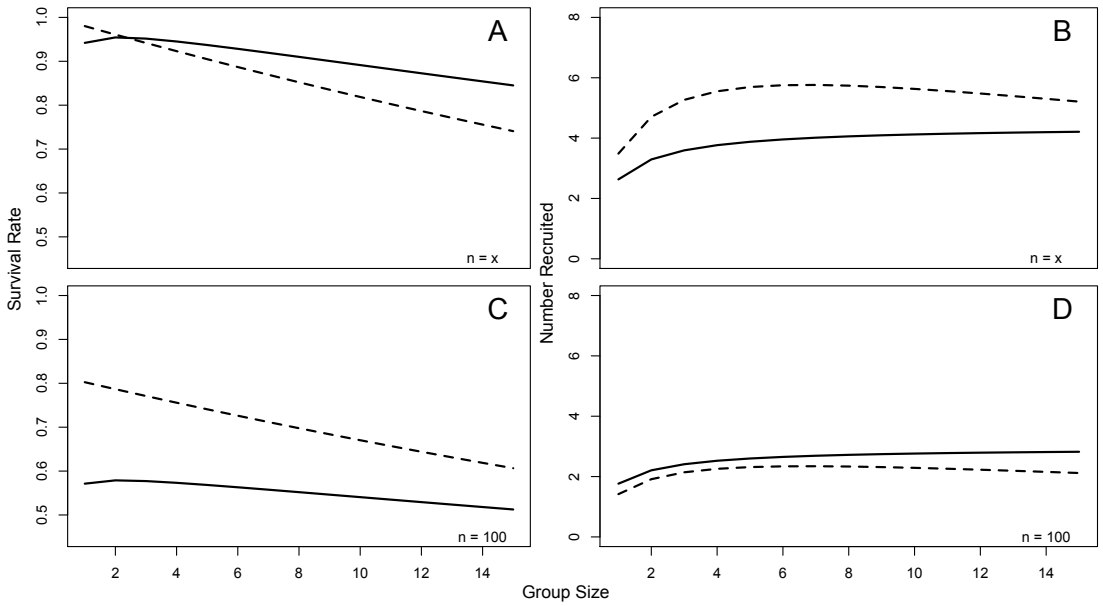


Figure 3.2: Survival and recruitment rates as a function of group size in the absence of inter-group competition (top row, focal group x is population size) and at population size n = 100 (bottom row). The Yellowstone National Park Northern Range are the solid and Interior the dashed lines.

limiter of demographic rates acted through reduced recruitment. As the group increases in size it begins to experience reduced inter-group competition (Cell D) due to competition between groups being focal group size specific (modelled as population size with focal group size removed See Methods). At large group sizes, it is the competition among members that dominates (Cell B).

3.4 Discussion

The simple model derived here partitions a generic demographic rate into mechanisms that reduce fitness in small and large wolf groups independently of population size, and those that act at high densities. Parameterised to two different grey wolf areas within Yellowstone National Park, the model demonstrates, that only upon consideration of the focal groups size, the population density, and the habitat the group resides in, can the mechanisms regulating individual fitness be identified. Competition between groups regulates adult survival to a greater extent on the resource rich Northern Range than in the Interior of the park, with the intra-group competition stronger in the Interior (Table 3.2). Component Allee effects close to zero on adult survival but reduced recruitment on both ranges to a similar extent (Figure 3.1). Recruitment was independent of group size on the Northern Range but decreased in the Interior, with groups in the Interior experiencing stronger inter-group competition than on the Northern Range.

Figure 3.3

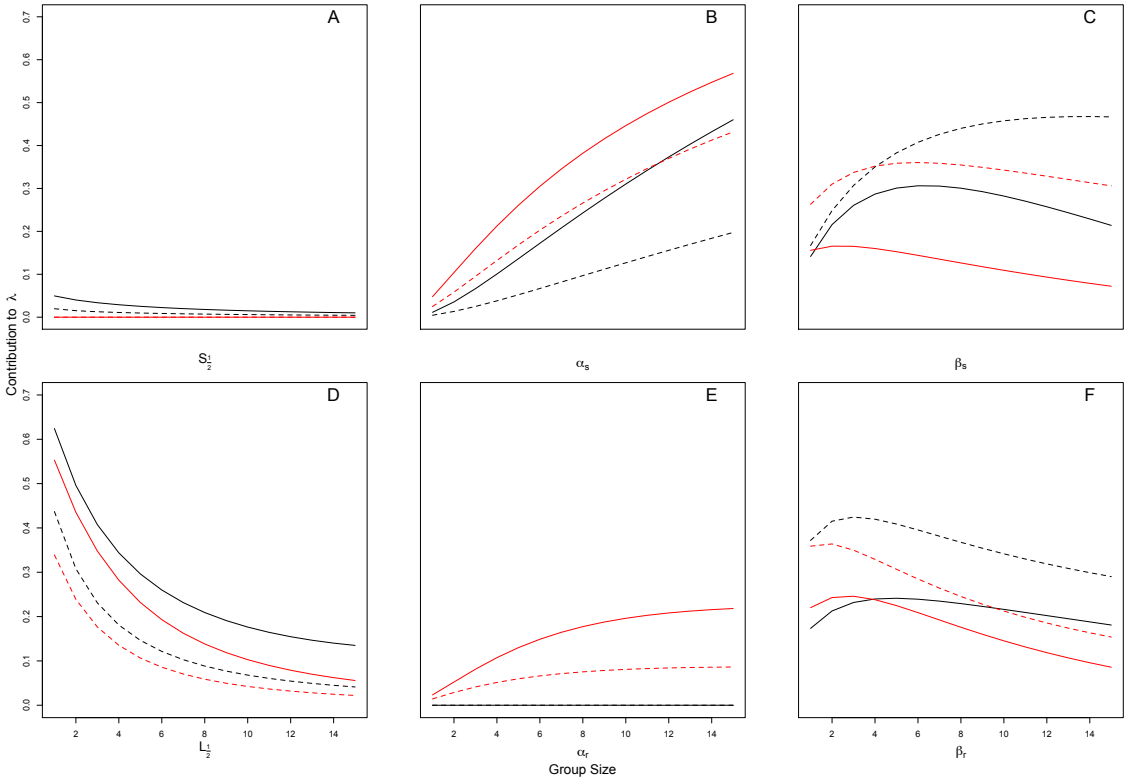


Figure 3.4: Relative contributions of parameters to group specific growth rates as a function of group size, on the Northern (black lines) and Interior (red) of Yellowstone National park at extremely low and high population sizes (solid = 100, dashed =29).

The work was motivated by understanding the extent to which socio-spatial structure generates variance in the regulatory mechanisms individuals in the population experience, relative to spatial and homogeneous populations. The discussion focuses first on the spatial aspects, followed by the social. Cubaynes et al. [2014] identified survival rates on the Northern Range to be regulated predominantly by inter-group conflict and by resource limitations in the Interior of the park. Therefore the argument is not for the drivers of regulation, instead the consequences that resource vs space limitation has on the regulatory mechanisms groups of different size experience, and whether it produces greater intra- or inter-group pressure. When resource densities are high and space is limiting, territory range is expected to contract, with overlap between territories increasing. Groups should spend less time defending a large territory as they can acquire all the necessary resources in a smaller area. They will most likely only defend the minimum area required for denning. In this scenario encounter rates between packs are expected to increase and this should be seen in increased inter-group competition. In systems regulated by resource densities, territory ranges should be larger, decreasing encounter rates with both prey and other packs. Reduced access to prey is expected to increase competition at kills and intra-group competition is expected to be the dominant regulatory

mechanism.

Comparisons of the mechanisms regulating survival identify clear differences between the resource rich Northern Range and the lower density Interior of the park (Table 3.2). The resource rich Northern Range produces inter-group competition 2.5 times stronger than in the interior and intra-group competition nearly half as weak. This is in line with our hypothesis that intra-group competition will be determined by access to resource, with competition between group members increasing when prey is difficult to acquire. Where resources are dense, competition switches to that for territory and inter-group competition dominates. As resources increase carrying capacity will increase up to a threshold limit, as packs require a minimum territory for denning and rearing pups, to prevent infanticide from competitors, eventually space will become limiting [Mech, 1970, McLeod, 1990, Mech, 1994].

This has important consequences for wildlife management, given the proposed method of licensed hunting to control populations. If populations experience stronger intra-group regulation, as in the Interior, removal of individuals in larger groups will increase the survival rates of conspecifics but will have a weaker effect on members of other groups. If, however, the population experiences regulation similar to the Northern Range it may alter the balance of power between groups, encouraging territory takeovers [Mech, 1970, Van Ballenberghe, 1983, Cassidy, 2013].

Considering the mechanisms regulating recruitment, the mechanisms acting on the Northern Range were either absent (no intra-group regulation) or weak in comparison to the Interior (0.004 against 0.009, inter-group), seen in Figure 3.1 where the difference in recruitment between high (top right) and low (bottom right) densities is marginal in comparison to the Interior (dotted line). This is contrary to the hypothesis that the resource limiting areas would exhibit weaker inter-group regulation than space limited areas and may represent the difficulty groups in the Interior have in acquiring enough resource to feed pups. Even at lower densities, as the number of competitors increases, resources decrease, exhibiting indirect pressure on other packs.

As for the impact of social structure in regulating dynamics, the component Allee effects generated a slight curvature in the number of individuals recruited in both areas and a small cost to adult survival on the Northern Range (Figure 3.1). Considering per capita recruitment in place of number of individuals recruited and it is in fact small groups that experience the highest rates, along with high survival relative to other groups. Therefore it is small groups that have the greatest potential to contribute to population growth. as they are not experiencing intra-group regulation. Similar dynamics were observed by Marino et al. [2006, 2013] where decisions by wolf groups to increase territory range instead of fissioning into smaller groups inhibited population growth after an epizootic outbreak due to reduced per capita recruitment in the presence of reproductive suppression. The model here demonstrates that at low densities, growth would be maximised if mean adult group size was minimised. Large litter size relative to adult group size enables this to occur and is in line with wolf population growth occurring primarily through changes in recruitment

[Fuller, 1989, Fuller et al., 2003]. This is not to say that decreasing mean group size in a population is a sustainable management strategy, due to increased risk of group extinction through demographic stochasticity [Lande, 1993], which has been shown to inhibit population growth by limiting new pride formation in lions [Packer et al., 2005]. It does however explain the exponential growth observed for many years in Yellowstone National Park post the reintroduction [Jimenez and Becker, 2012]. At low densities, dispersing groups, usually of small size, experience rapid growth through high recruitment, especially when inter-group competition is low due to densities below carrying capacity.

A secondary motivation for this work was to understand how various analyses of compensatory and additive dynamics have arrived at contradictory conclusion [Murray et al., 2010, Creel and Rotella, 2010, Gude et al., 2012]. The simple model demonstrates how removing an individual from a group will alter different regulatory mechanisms that the remaining members experience, some that increase demographic rates, some that decrease (Allee effects). Even within Yellowstone National Park there exists differences in the strength of regulatory mechanisms experienced across each habitat, with differences in the mechanisms experienced by each group in a given habitat. Therefore analysing compensatory dynamics across Idaho, Montana and Wyoming may be a futile task, without even considering the effect of breeder loss and increased susceptibility to territory takeovers [Mech, 1970, Van Ballenberghe, 1983, Brainerd et al., 2008, Cassidy, 2013]. Figure 3.3 demonstrates how the dominant regulatory mechanism a group experiences varies with density, group size and habitat such that at any given time there will be an array of regulatory mechanisms acting across a habitat and from one group to the next they may be very different.

Removal of a wolf from the North of a State may produce very different responses than removing an individual from the South. Even within a local area removal from a large pack may produce a different response from a small pack. Trying to generalise how population growth will respond to harvest when hunters can remove any wolf from any pack may be a fruitless task. This is most likely why investigations into the effect of hunting on lions *Panthera leo* took an individual based modelling approach and focused on a relatively small geographic area in comparison to the management areas of the Northern Rocky Mountains [Whitman et al., 2004]. This modelling approach however required detailed knowledge of all demographic processes. The underlying drivers of dispersal have hitherto not been explored in the Northern Rocky Mountain system and may prohibit this approach from being implemented. The long distances individuals disperse [Boyd and Pletscher, 1999] and the potential difficulties in tracking individuals across management areas that encompass vast geographic areas may prevent a similar analyses being performed on this system.

The model derived here provides a useful tool to provide comparisons of the strength of regulatory mechanisms and the demographic rates through which they act. Presented here are comparisons within a species, across two separate areas in the Northern Rocky Mountains. Parameterisation of the model to the same species in other locations may provide insights into the different group sizes seen across the grey wolf range [Zimen, 1976, Thurber and Peterson, 1993, Harrington et al., 1983]. As the model is parameterised

using only two variables, number of surviving adults and pups reared to 1 year of age, data should not be limiting and the model could therefore be easily parameterised to multiple species. This would present the similarities and differences in regulatory mechanisms acting across species, enabling comparisons to be drawn, and general rules governing the dynamics of social-carnivore dynamics, and potentially social species in general, to be better understood [Nudds, 1978].

Chapter 4

Identifying regulatory mechanisms in socially structured populations: An analysis of Eurasian badger population dynamics

Abstract

Sociality imposes both spatial structure on populations, known to produce qualitatively different dynamics to non-spatial, homogeneous populations, and social structure, that can reduce individual fitness in small groups, known as Allee effects. Restricted population growth in social species relative to non-spatial, homogenous populations has been documented in many social carnivore populations and as such, sociality has been proposed to increase extinction risk. However, the relative contributions of social and spatial structure that inhibit population growth are widely debated in the literature. An individual-based model is used to identify the relative contributions of deterministic and stochastic processes that determine population size, and fluctuations in population and group size in a high density, medium sized, non-obligate cooperative social carnivore, the Eurasian badger (*Meles meles*). The analysis identifies a system consisting of a small set of breeding females, around which, additional individuals queue for breeding rights, unable to form new social groups due to habitat saturation. Weak group-level density dependence (intra-group regulation) on adult survival, and weak environmental stochasticity, produce small between year fluctuations in local and population wide adult numbers, that are dampened by strong group-level density dependence on cub survival.

Keywords: Badgers, *Meles meles*, intra-group competition, inter-group competition.

4.1 Introduction

Should social species be expected to experience increased extinction risk and large fluctuations in population size? Social species are fundamentally different to non-social species because their dynamics can be influenced by intra- and inter-group processes, as well as by population level processes including intra- and

interspecific interactions and abiotic variation [Calhoun, 1952, Crook, 1970, King, 1973, Macdonald, 1983]. In general, group living species may experience increased extinction risk and larger fluctuations in population size when average group size is small [Rood, 1990, Walters, 1991, Courchamp et al., 1999a, O'Riain et al., 2000, Courchamp and Macdonald, 2001] although there are exceptions to this pattern [Fryxell et al., 2007]. Small groups are vulnerable to extinction because they are susceptible to inter-group strife and demographic stochasticity [King, 1973, Lande, 1993] but the manner in which localised dynamics impact population level dynamics can be complex [Hanski, 1998, Lande et al., 1999]. In addition many cooperative breeders have been predicted to exhibit group level Allee effects (reductions in fitness associated with decreasing group size) [Allee et al., 1949, Courchamp et al., 1999b] because it can be difficult for dispersing individuals to find mates, establish new territories and successfully rear offspring (e.g. dwarf mongooses, *Helogale parvula* [Rood, 1990], Florida scrub jays *Aphelocoma coerulescens* [Mumme, 1992],white fronted bee-eaters, *Merops bullockoides* [Emlen and Wrege, 1991], African wild dogs *Lycoan pictus* [Creel and Creel, 1998], meerkats *Suricata suricatta* [Clutton-Brock et al., 1999a], lions *Panthera leo* [Packer et al., 1988]). Here the findings of a modelling exercise investigating the extent to which social and spatial structure generate patterns at the group and population level, in a high density Eurasian badger (*Meles meles*) population in the southwest of the United Kingdom are reported [Kruuk, 1978a,b].

Fluctuations in population size are driven by environmental variation, migration, intra-specific regulation and species interactions [Sæther, 1997, Engen et al., 1998, Lande et al., 1999]. Modifying any of these drivers generates simultaneous responses in population dynamics, life history and the distribution of phenotypic characters, the latter introducing lag effects into the system [Childs et al., 2003, Ellner and Rees, 2006, Kuss et al., 2008, Coulson et al., 2010]. Changes in multiple demographic rates generate pronounced changes at the population level, but change in one rate may also counter changes in another depending upon the structure of the life history [Tuljapurkar et al., 2009]. Although there has been considerable research examining the consequences of altering environmental determinants of demographic rates on life history, population dynamics and quantitative traits in non-social species [Childs et al., 2003, Kuss et al., 2008, Childs et al., 2011, Traill et al., 2014], there has been relatively little research in social species, with interest growning in recent years, focusing solely on social mammals to the authors knowledge, with social structure often ignored [see Ozgul et al., 2010, Coulson et al., 2011, Traill et al., 2014, for examples without social structure] and [Bateman et al., 2013, Ozgul et al., 2014, for examples with social structure]. Part of the reason for this is that sociality introduces additional structural complexity into populations that can produce regulatory mechanisms at the local level, independently of population size [Courchamp et al., 1999b, Lande et al., 1999]. Consequently group living species in variable environments should have a higher propensity for fluctuations in local densities, creating large population crashes when vital rates fluctuate in synchrony, decreasing population viability [Stephens et al., 1999, Lande et al., 1999, Cassini, 2011].

Social structure may impose thresholds for group viability and successful emigration [Courchamp et al.,

1999b]. Spatial structure introduces localised regulation as patchy resources are depleted with additional complications arising from dispersal and site-specific synchrony in demographic rates [Hanski, 1999, Lande et al., 1999]. Demographic stochasticity can produce asynchronous fluctuations in group size, shifting the competitive ability of groups between years and rendering them susceptible to inter-group strife and territory takeovers, such as male takeover events in lions [Packer et al., 1988, Whitman et al., 2004], territory defence by helpers in the Red-Cockaded Woodpecker (*Picoides borealis*)[Walters et al., 1988] and direct conflict in grey wolves [Van Ballenberghe, 1983, Cubaynes et al., 2014]. Low-density regulation (including Allee effects) and potential for population level effects of demographic stochasticity at high densities are the two mechanisms that could make social species dynamics differ from solitary species, although whether this dampens or amplifies fluctuations around carrying capacity, and whether general trends exist across species, has not yet been investigated.

Social structure can restrict population growth, restricting recolonisation of African wild dogs (*Lycoan pictus*) [Courchamp et al., 2000a, Creel and Creel, 1998], grey and Ethiopian wolves (*Canis lupus* and *simensis*) [Hurford et al., 2006, Marino et al., 2006, 2013] and buffering against improving ecological conditions in lions (*Panthera leo*) [Packer et al., 2005] and Eurasian badgers [Macdonald and Newman, 2002]. Wild dogs and wolves experienced costs associated with small population size, whereas lions and badgers experienced restricted population growth at densities where Allee effects would not be expected to act. Therefore social-structure may not only increase extinction risk but maintain populations at densities lower than resources can support. Statistical analyses of demographic rates can identify potential mechanisms restricting population growth, but predictive modelling accounting for interactions between trait distributions and demographic rates, enables the whole process to be captured.

Individual-based models track individuals through time, with models able to explicitly capture individual, intra- and inter-group level processes. They have been used to model population responses to harvesting in lions (Whitman et al., 2004), the impact of environmental variation, reproductive suppression and forced dispersal in meerkats (*Suricata suricatta*) [Bateman et al., 2013, Ozgul et al., 2014], the effects of sociality on grey wolf dynamics [Pitt et al., 2003] and disease dynamics in badgers [Shirley et al., 2003], among many others [Grimm, 1999b].

Here an individual-based framework is used to account for heterogeneity in territory (or patch) quality while tracking social group affiliation, mating patterns and plastic ontogenetic development. The model is parameterised using generalised linear mixed effects models [Bolker et al., 2009] and long-term individual-level badger data from Wytham Woods, Oxfordshire, United Kingdom [Kruuk, 1978b,a, Macdonald and Newman, 2002, Macdonald et al., 2009]. Sensitivity analyses of population and group level processes to model parameters identify the extent to which parameters associated with social and spatial structure influence local and global dynamics. The system exhibited restricted population growth during a prolonged period of improving ecological conditions, suddenly experiencing rapid population growth, as seen in lions

and grey wolves [Macdonald and Newman, 2002, Packer et al., 2005, Hurford et al., 2006]. In contrast to these social systems badgers are not obligate cooperators and pre-increase densities were high enough that difficulties in finding mates can be excluded in a way they can not in grey wolves. Badgers therefore present an interesting case study in the effects of socio-spatial structure on population dynamics in the absence of obvious Allee effects.

Constructing a spatially implicit (incorporating intra-group and inter-group competition and territory quality) and demographically explicit (incorporating age, sex, body condition and social group size) individual-based model the extent to which model parameters associated with socio-spatial structure influence dynamics are investigated. Partitioning population growth into individual contributions of survival and fecundity, modelling movement between groups and the impact of individual traits on demographic rates, the model identifies the regulatory mechanisms at a finer scale than previously demonstrated by Macdonald and Newman [2002], while extending their results to the determinants of population fluctuations around carrying capacity.

4.2 Methods

4.2.1 Study Species

Eurasian badgers are solitary foragers that live in groups, with group sizes varying from two to more than 25 individuals [Kruuk, 1989, Rodríguez et al., 1996, Kowalczyk et al., 2000, Revilla and Palomares, 2002, Kowalczyk et al., 2003]. Large groups occur when densities exceed 10 km^{-}2, with groups composed primarily of a parental pair and offspring remaining post maturity [Kruuk and Parish, 1982, Cheeseman et al., 1987, Fell et al., 2006, Macdonald et al., 2008, Dugdale et al., 2008]. Benefits of communal living are small [da Silva et al., 1994] although there is evidence of nascent sociality, including occasional allo-maternal care [Dugdale et al., 2010, Fell et al., 2006], allo-grooming [Stewart and Macdonald, 2003, Macdonald et al., 2004], and communal sett maintenance [Stewart et al., 1999], with associated benefits for neo-natal cub survival [Kaneko et al., 2010] with body weight and fecundity decreasing in over-crowded groups [Macdonald and Newman, 2002].

Density independent, permanent dispersal between groups is infrequent, although temporary movement between groups is more common, with two thirds of individuals trapped at more than one social group during their lifetime in Wytham [Macdonald et al., 2008]. This is part of a complex mating system where nearly half of all paternities occur outside of the social group [Dugdale et al., 2008, Annavi et al., 2014b].

Survival and fecundity fluctuate with quantifiable climatic metrics, rainfall and winter frosts. Both determine the abundance of and accessibility to earthworms, their primary food source [Macdonald and Newman, 2002, Macdonald et al., 2010, Nouvellet et al., 2013].

Models focusing on population level trends identified adult survival and fecundity to be the predominant

drivers of population growth rate, with juvenile survival identified as an important mechanism through which regulation acts [Macdonald et al., 2009]. Macdonald and Newman [2002] also demonstrated that population growth could be captured by a simple two-age class Leslie matrix (cubs and adults) although this analysis focused on an expanding population, that has since stabilised.

4.2.2 Data Collection and Study Site

This study focuses on a high-density population of badgers inhabiting Wytham Woods, Oxfordshire, UK; a 424 ha site situated 5 km West of Oxford, England (51:46:26N; 1:19:19W), which has been studied intensively since the 1970s [Kruuk, 1978b,a]. A detailed description of the study site (e.g., soil, microclimates and vegetation) is provided elsewhere [Morecroft et al., 1998, Savill et al., 2010]. At this study site, there was a mean of 19 (95% CI = 17, 21; range = 14 to 26) [Dugdale et al., 2008] mixed-sex, social groups [Johnson et al., 2002, Newman et al., 2011], with a mean of 13 (95% CI = 12, 14; range: 2 to 51) individuals (including cubs) per social-group per year.

Since 1987, researchers have aimed to mark all individuals within the population, following a systematic capture-mark-recapture regime [Macdonald and Newman, 2002, Macdonald et al., 2009]. Live-trapping was conducted three to four times per year; generally over two weeks in June, September and November, with one week of trapping in January of some years [Macdonald et al., 2009]. Badgers were caught in mesh-traps, baited with peanuts [Macdonald and Newman, 2002, Macdonald et al., 2009], placed near the entrances of active communal badger dens, termed setts [Noonan et al., 2014]. Captured badgers were then transferred to holding cages and transported to a central handling facility, and sedated with an intramuscular injection of ketamine hydrochloride, at 0.2-ml/kg body weight [McLaren et al., 2005]. Upon their first capture all badgers were tattooed with a unique number on the left inguinal region for permanent individual identification. The sex, age-class (cub or adult, based on body size and previous trapping history) and capture location (social group name) of each badger were recorded. For genetic analysis, hair samples and/or blood from the jugular vein (ca 3 ml) were collected from all individuals, with parentage assigned using the methods of Annavi et al. [2014b]. Social group ranges were established using a 'bait-marking' technique approximately every two years [Kilshaw et al., 2009]. The number of social group ranges within this study site has increased steadily [Macdonald et al., 2004] with population density [Macdonald and Newman, 2002, Macdonald et al., 2009].

Population and social group sizes were estimated using minimum number alive estimates [Krebs, 1966]. Individuals were assigned a social group affiliation based on a given years trapping record alone. If an individual was trapped at a single location it was assigned to this social group. If it was trapped at more than one social group, it was assigned the social group most frequently trapped. Individuals trapped at more than one location an equal number times were randomly assigned a social group out of the social groups the individual was trapped at. Movement is defined as a transition to a new social group affiliation

between years. The period 1990 to 2012 was analysed, using the data from 1987 to 1989 in the minimum number alive estimates to account for individuals present in the population, not trapped in 1990 but trapped previously.

The next section describes the structure of the individual-based model and the dynamics its aims to capture. This is followed by the statistical methods used to parameterise the demographic functions and how sensitivity analyses are used to interpret the relative contributions of model parameters to population dynamics.

4.2.3 Model Overview

The methods of Coulson et al. [2011] are used to map the badger population over a breeding interval (12 months) extended into an individual-based framework. It maps individual survival, fecundity and movement between years while tracking the development and transmission of parent to offspring of individual traits (body mass and length). The iterative cycle is given in Figure 4.1.

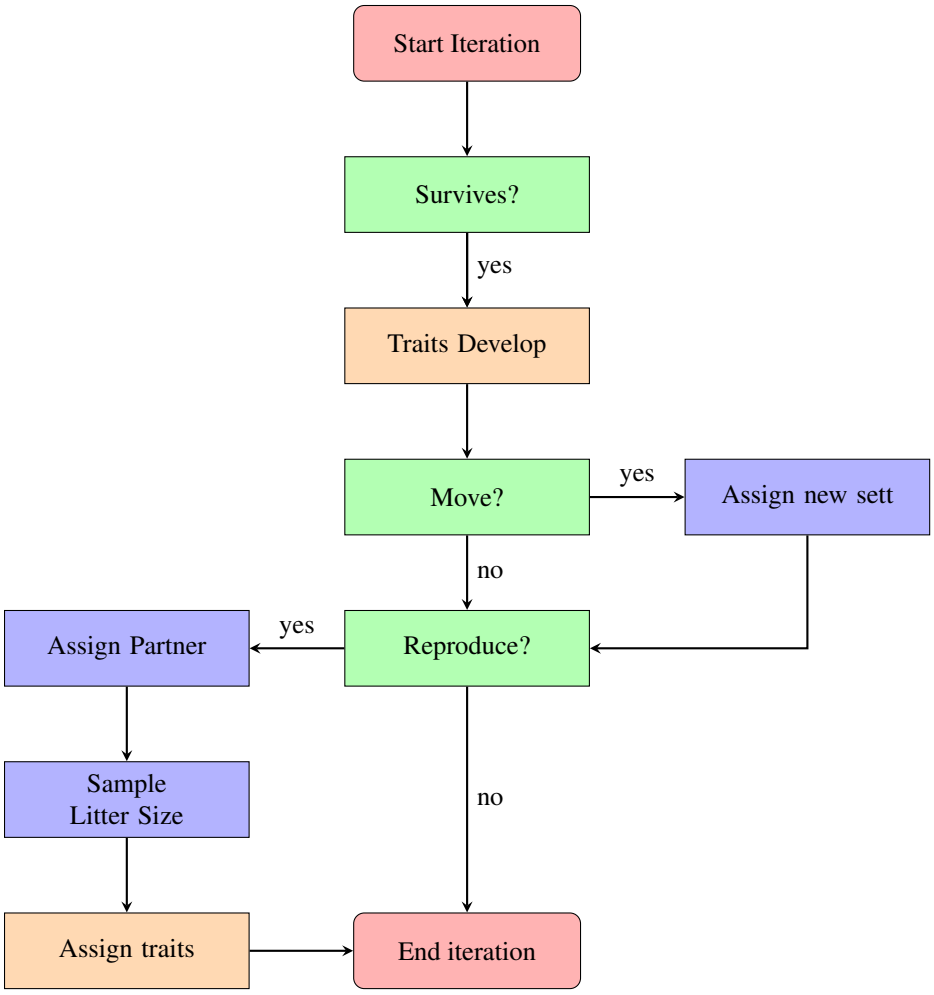


Figure 4.1: Flow diagram representation of the individual-based model.

The model simulates the observed population by generating 26 patches each with their own local carry-

ing capacity (or patch richness), with the fitness benefits of each patch for each demographic rate extracted from the statistical model. Individuals can move between patches independently of whether they are occupied, but no new patches can be colonised outside of the 26. The simulation commences by randomly generating a population of individuals based on observed densities, sex ratio, age structure and trait distributions.

At each time step an expectation is calculated for each individual's demographic function. This expectation includes environmental stochasticity, as intercepts of each function vary at each time step of the simulation. They vary because at each time step a random number from the relevant distribution defined by the variance components of the random effect, year, is drawn.

Demographic stochasticity is then incorporated by drawing random numbers from uniform distributions and comparing these random numbers with the expectation. If the random number is less than the expectation then the expectation is realised (i.e. the animal survives, reproduces, disperses). If the random number is greater than the expectation then the opposite outcome occurs.

Parameterisation

The model contains demographic functions relating traits to rates. Trait based functions include development and transmission from parents to offspring with transition probabilities modelled by normal distributions. The probability of developing from trait value x to x', or an offspring inheriting trait value x' from parents with average trait x is given by:

$$\frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x'-\bar{x})^2}{2\sigma^2}} \tag{4.1}$$

The expected trait value at time t+1, $\bar{x}$, for an individual with trait x at time t, is predicted by a linear mixed effects model (LMER). The variance term σ^2, represents plasticity in development and is estimated by regressing the squared residuals of the linear mixed effects model against explanatory variables. The variance represents how dispersed the development (or parent-offspring transmission) of traits is. The model predicts the probability distribution of possible trait values using the LMER and randomly samples a value from that distribution.

The demographic rates; movement, female fecundity and survival are modelled as binomial processes with means given by $\frac{1}{1+e^{-\bar{x}}}$, where $\bar{x}$ is estimated from a generalized linear mixed effects model (GLMM) with $\bar{x} = f(a + \beta_1.\gamma_1 + \beta_2.\gamma_2 + \dots)$.

The mixed effects models fit local competition, inter-group competition (number of individuals outside the focal group), age, sex, body condition and costs of reproduction as explanatory variables, using likelihood ratio tests to remove terms insignificant at the 5% level. A detailed definition of each variable is given in Appendix Section B.1. Year and social group affiliation are fitted as random effects in all functions to

account for environmental stochasticity (year effect) and patch quality (social group effect).

Body condition, defined as body mass divided by length, is used as the trait based explanatory variable to predict demographic rates (fecundity, movement, survival). This requires two traits to be modelled in the system, body mass and body length. Therefore two traits are tracked for each individual and two separate development (and parent-offspring transmission functions) are parameterised. The model maps the ontogenetic development of body mass and length between time steps, from which a body condition index is calculated and used to predict fecundity, survival and movement. Model selection is not performed on body condition (or body mass/length in the trait functions) as the focus of the model is on how trait distributions influence demographic rates. i.e. they are always retained in the models.

Only female fecundity, not male fertility, is analysed in the statistical model. Paternities are randomly sampled from the pool of available fathers constrained either to within or outside the focal group. With the probability of paternity occuring inside the focal group equal to 0.5, in line with the findings of Annavi et al. [2014b].

Tracking marked individuals that spend the majority of their lives underground results in low reporting rates of mortalities. A mark-recapture model was fitted to the time series data and annual recapture rates of 0.78 were taken to be high enough that using trapping session after last capture to signify mortality was sufficient to capture trends using GLMM's following a similar methodology to Catchpole et al. [2004]. The direction and effect sizes from the GLMM method were compared with mark-recapture methods and are reported in the Appendix Section B.2. Using GLMM's enabled annual variation to be captured using random effects that is then used to simulate environmental stochasticity. Current mark-recapture software can only handle individual random effects [Choquet et al., 2009] and the purpose of this study is to understand how group structure influences fluctuations in population size. Given variation in environmental conditions has been shown to influence survival rates it is necessary to capture this variation [Macdonald et al., 2010, Nouvellet et al., 2013].

Recapture rates of less than 1 resulted in under-reporting of pregnancies and of the number of individuals surviving. For a pregnancy to be recorded the female is required to be trapped the following year in a lactational state. Therefore individuals not recaptured cannot be assigned pregnancies. Similarly individuals that are not trapped but seen alive at a later time step are not included in the survival analysis but every individual is assigned a mortality unless they survive until the end of the study. Therefore survival events are also under-reported by the recapture rate. The intercept terms on fecundity and survival are increased by the proportion not captured (0.22) to account for this bias [See Catchpole et al., 2004, for similar methods].

4.2.4 Population Vs Social Structure Regulation

Macdonald et al. [2009] demonstrated population growth to be captured by population level density dependence without accounting for social or spatial structure. To demonstrate the differences in population

regulation dynamics from within (intra-group) and between group competition (inter-group) dynamics, a second individual-based model is also parameterised, performing model selection again, that uses population size instead of intra-group (group size) and inter-group (number of individuals outside focal group) regulatory mechanisms. Both models contain spatial structure with individuals moving between groups. The difference is that one contains local regulation with global density dependence modelled as the number of adult individuals outside the focal group, whereas the other no local regulation and global regulation is modelled as total adult population size.

4.2.5 Relative Contributions of Parameters to Population Fluctuations

Sensitivity analyses of parameter estimates to:

1. Population size

2. Coefficient of variation in population size

3. Coefficient of variation in group size averaged across groups

indicate the relative contribution of each parameter in comparison to each other, in producing the metric of interest. Sensitivities involve upward perturbing (increasing) parameter coefficients by 0.1 and calculating the change in statistical values from the original model. Comparisons are drawn across functions that are parameterised with the same error structure. Thus sensitivities of development and transmission of traits from parents to offspring can be compared (linear) but not with survival, fecundity or movement, which are compared separately as they are binomial processes. The sensitivity of population metrics to litter size was estimated by increasing the probability of twins from logit(β) to logit(β+0.1), where β determines the probability of twins. All age classes are perturbed when the intercept is increased. Sensitivity of the age class 'cub' is analysed by removing all other age classes from the sensitivity of the intercept.

4.2.6 Statistical Software

All analyses and simulations are implemented in the statistical software R with GLMM's and likelihood ratio tests implemented using the package lme4 [R Core Team, 2015]. Parentage was obtained using Master Bayes 2.47 [Hadfield, 2012] and Colony 2.0 [Jones and Wang, 2010]. Simulations were run for 1.5 million iterations with the first 1000 rejected as burn-ins. This achieved convergence of adult population size to 0.1 individuals and the coefficient of variation to $1e^{-3}$.

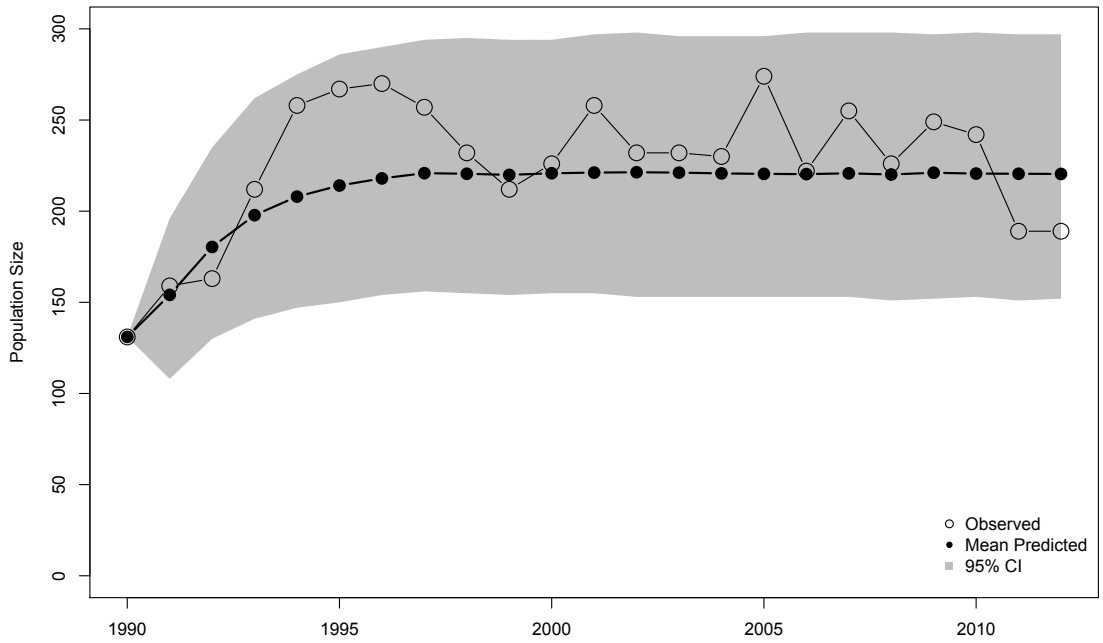


Figure 4.2: Comparison of model predictions to observed population sizes. 10,000 simulations were run with 95% confidence intervals given around the mean trajectory. The difference between captured population size and the minimum number alive estimate was accounted for, by sampling the missed individuals from the captured population, with replacement, at the beginning of each iteration.

4.3 Results

4.3.1 Data Series

The number of active social groups varied from 11 to 26 with a mean of 21 (95% CI 20, 22). Population size ranged from 131 to 274 individuals, averaging 225 (95% CI 218, 233). The coefficient of variation of group size was 0.88 (95% CI 0.13, 1.63).

The data included records of 3826 unique events (maximum of 1 per individual per year) of 1322 individuals (637 male, 685 female). 254 pregnancies were detected and 868 individuals were first trapped as cubs. 104 individuals included in the transmission of parent to offspring trait values analyses, satisfying

the conditions of being trapped as cubs with both parents trapped the previous year.

$$\begin{aligned} logit\left(S_{i,j,t}\right) = N_j^{surv} + 0.89 + 0.02.BC_t + 0.37.A^{1:9} - 0.96.A^{10^+} + 1.24.G_{i,t} - 1.00.G_{i,t}^2 - 0.27.S_{male} \\ -0.10.\left(P_t - G_{i,t}\right) - 0.72.G_{i,t}.A^{1:9} + 0.66.G_{i,t}^2.A^{1:9} - 2.13.G_{i,t}.A^{10^+} \\ +1.86.G_{i,t}^2.A^{10^+} + 0.26.G_{i,t}.\left(P_t - G_{i,t}\right) + \epsilon_t^1 \\ \epsilon_t^1 \sim \mathcal{N}_t(0, 0.45^2) \end{aligned} \tag{4.2}$$

$$\begin{aligned} logit\left(F_{i,j,t}\right) = N_j^{fec} - 2.88 + 0.80.BC_t + 1.43.R_{t-1} + 1.47.A^{1:9} \\ +0.37.A^{10^+} - 0.86.\left(P_t - G_{i,t}\right) + \epsilon_t^2 \\ \epsilon_t^2 \sim \mathcal{N}_t(0, 1.14^2) \end{aligned}$$

$$\begin{aligned} logit\left(D_{i,j,t}\right) = N_j^{move} - 2.72 + 0.07.BC_t - 0.28.A^{1:9} + 0.6.A^{10^+} - 0.16.\left(P_t - G_{i,t}\right) + \epsilon_t^3 \\ \epsilon_t^3 \sim \mathcal{N}_t(0, 0.38^2) \end{aligned} \tag{4.3}$$

The linearised demographic rates (Survival S, female fecundity F, movement D) are given in equations 4.2:4.3 and are functions of; body condition (BC), age class (cub, adult $A^{1:9}$, old adult A^{10^+}), group size ($G_{i,t}$), inter-group competition (population size, P_t, minus group size), whether a female reproduced the previous time step (R_{t-1}) with a neighbourhood specific intercept (N_j) Functions are modelled for group i in neighbourhood j at time t. Age dependencies were tested on survival with the optimal age class found; 0, 1 to 9 and 10+ years, fitted across all other demographic rates in place of the variable age.

The variables $A^{1:9}$ and A^{10^+} are binary variables that are 1 if the individual is in the age class (adult 1-9 years, old adult $\geq$ 10 years), zero otherwise. The cub age class is incorporated into the intercept term with the factor 'female' (when significant). To obtain survival for males and other age classes the reported coefficient in Table 4.2 is added to the intercept. Multiple age classes were tested on the survival function and the optimal age class on survival described above was fitted across all other demographic rates.

The survival process (Equation 4.2) appears complex due to local regulation acting differently through each age class although only age class, group size and sex were significant predictors (L-R tests of significance given in the Appendix Section B.1), with inter-group competition significant when interacting with group size. Females experienced higher survival rates than males (β_{male}= -0.27; s.e =0.08), with adults experiencing highest survival (β_{adult}= 0.37; s.e =0.09), followed by cubs ($\beta_{intercept}$ = 0.89; s.e =0.16) and old adults ($\beta_{old\ adult}$ = -0.96; s.e =0.21). Survival rates decreased with local over-crowding (β_{G^2} = -1.00; s.e =0.24) but also when group size was small (β_G= 1.24; s.e =0.25). Fitting an interaction of group size and inter-group competition determined that this cost was more pronounced at high levels of inter-group competition ($\beta_{G.(P-G)}$ = -0.26; s.e =0.07) indicating that small groups experience increased inter-group competition at high densities than the levels predicted from the inter-group competition variable alone. This could signify an inability of small groups to maintain or establish a territory at high densities, poten-

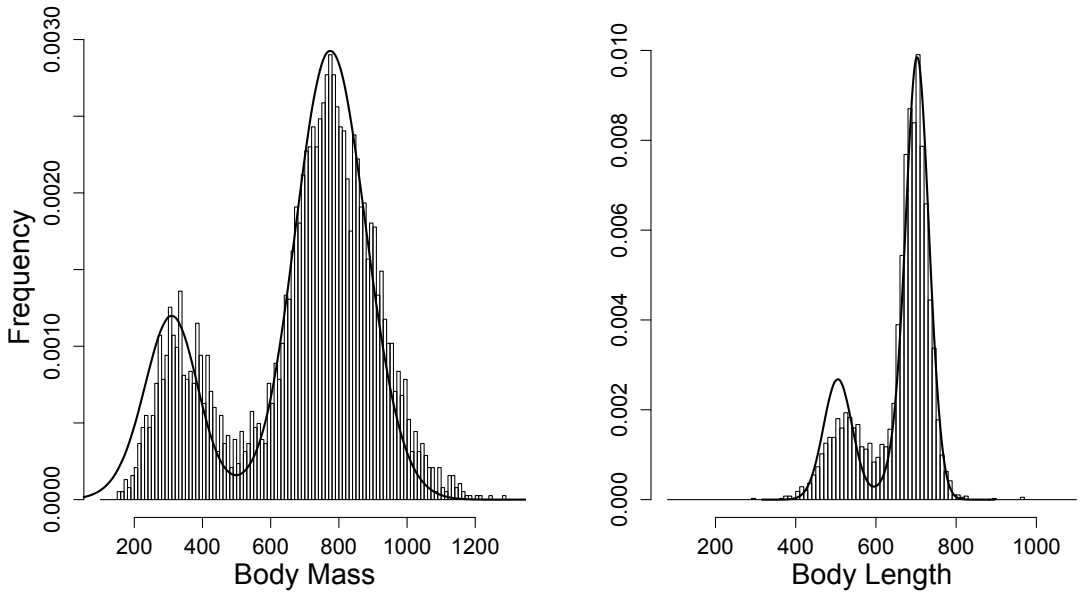


Figure 4.3: Observed and individual-based model predictions of trait distributions

tially restricting population growth. Inter-group competition was not a significant predictor outside of this interaction but was maintained due to the principles of marginality. Both the costs to small groups and local density regulation were weaker on adults ($\beta_{G_{adult}}$= -0.72; s.e =0.27, $\beta_{G_{adult^2}}$= 0.66; s.e =0.27) and old adults ($\beta_{G_{old\ adult}}$= -2.13.; s.e =0.84,$\beta_{G_{old\ adult^2}}$= 1.86; s.e =0.83) than cubs.

To account for this bias incurred by imperfect detection of individuals, the survival intercept was increased by the average proportion not trapped each year (22% See Methods). This increased the survival intercept by 0.2. The value reported in Table 4.2 is the value returned by the GLMM with the increase written additively alongside. The fecundity intercept was increased by 0.8.

A correlation between years of breeding individuals was detected with individuals breeding the previous year experiencing increased fecundity ($\beta_{R_{t-1}}$= 1.43; s.e =0.29). This implies a hierarchy of breeding and non-breeding individuals. Body condition was a significant predictor of fecundity such that non-breeding individuals must achieve high condition in order to reproduce relative to those with breeding positions (β_{BC}= 0.80; s.e =0.19). Cubs do not reproduce and old adults experienced reduced fecundity relative to adults (difference in β values = -1.10) with fecundity decreasing with increasing levels of inter-group competition (β_{P-G} = -0.86; s.e =0.29).

Movement rates decreased at higher levels of inter-group competition (β_{P-G}= -0.16; s.e =0.37) and interestingly, replacing inter-group competition with total adult population size lost significance at the 5% level (see following section). Adults moved most frequently (β = 0.60) with old adults moving more frequently than cubs but less than adults (β = 0.16).

$$
\begin{aligned}
E(M_{i,j,t+1}) = N_j^{mass} + 628.96 + 0.28.M_t - 31.42.(P_t - G_{i,t}) + 55.70.S_{male} \\
-63.95.A^{1:9} - 124.95.A^{10^+} - 12.34.G_t - 33.90.A^{1:9}.(P_t - G_{i,t}) \\
-12.81.A^{10^+}.(P_t - G_{i,t}) + \epsilon_t^4
\end{aligned} \tag{4.4}
$$

$$
\epsilon_t^4 \sim \mathcal{N}_t(0, 36.07^2)
$$

$$
\begin{aligned}
E(L_{i,j,t+1}) = N_j^{length} + 516.23 + 0.30.L_t - 10.60.(P_t - G_{i,t}) + 18.13.S_{male} - 29.78.A^{1:9} \\
-36.02.A^{10^+} - 8.83.A^{1:9}.(P_t - G_{i,t}) - 11.37.A^{10^+}.(P_t - G_{i,t}) + \epsilon_t^5
\end{aligned} \tag{4.5}
$$

$$
\epsilon_t^5 \sim \mathcal{N}_t(0, 10.75^2)
$$

$$
E(M_{i,j,t+1}^{off}) = N_j^{mass\ off} + 264.90 + 0.08\bar{M}_t^{parent} - 23.5.G_i + \epsilon_t^6 \tag{4.6}
$$

$$
\epsilon_t^6 \sim \mathcal{N}_t(0, 12.48^2)
$$

$$
E(L_{i,j,t+1}^{off}) = N_j^{length\ off} + 375.80 + 0.19\bar{L}_t^{parent} + \epsilon_t^7 \tag{4.7}
$$

$$
\epsilon_t^7 \sim \mathcal{N}_t(0, 5.77^2)
$$

Equations 4.4 and 4.5 describe the expected trait value of an individual at time t+1 given their trait values the previous time step. Equations 4.6 and 4.7 describe the offspring trait values given the average parental trait the previous time step.

Males were both heavier (β_{male}=55.70; s.e = 4.25) and longer (β_{male}=18.13; s.e = 1.33) than females with both sexes experiencing reduced development with increased inter-group competition ($\beta_{(P-G).M}$=-31.42; s.e = 11.77, $\beta_{(P-G).L}$=-10.60; s.e = 2.83) although this acted primarily through cubs, with adults experiencing no reduced development of body mass and small reductions in length ($\beta_{A^{1:9}.(P-G).M}$ = 33.90; s.e = 8.65, $\beta_{A^{1:9}.(P-G).L}$ =-8.83; s.e = 2.68) and old adults experiencing reduced mass development only ($\beta_{A^{10+}.(P-G).M}$=11.94; s.e = 29.44, $\beta_{A^{10+}.(P-G).L}$=-11.37; s.e =9.24). Individuals were lighter in larger social groups (β_G = -12.34, s.e = 3.63) with no significanct differences in length detected between different social group sizes.

Model	$\mu\,(log(\lambda))$	$\mu(N^{adult})$	$CV\left(N^{adult}\right)$	$CV\left(G^{adult}\right)$
Observed	0.02	183	0.18	0.88
Population Structure	0.00	242	0.40	0.64
Inter-Intra-Decomposition	0.00	167	0.19	0.79

Table 4.1: Population indices from; the population regulation, the inter-intra-group regulation simulations and observed values.

Population Regulation Model Vs Inter-Intra-Decomposition Model

Population size was not a significant predictor in any function where inter-group competition was insignificant. The only difference in significance occurred in the movement function, where population size was not a significant predictor in contrast to inter-group competition. The inter-intra model captured adult population size and its coefficient of variation well whereas the population density model over predicted population size and its coefficient of variation (Observed $\bar{N}$ = 183, Pop model = 242, Inter-Intra = 167; Observed $CV(N)$ = 0.18, Pop model = 0.40, Inter-Intra = 0.19). The population regulation model under-predicted the coefficient of variation in group size averaged across groups as opposed to the inter-intra-regulation that captured observed fluctuations well (Observed = 0.88, Pop model = 0.64, Inter-Intra = 0.79). This implies that local regulatory mechanisms reduce population size but increase local fluctuations that are asynchronous. If group sizes fluctuated in synchrony the larger fluctuations produced in the population regulation model at the population level would also be seen at the group level, but this is not the case.

The inter-intra model captured the observed trait distributions well (Figure 4.3) as well as population size and its variance. The sensitivity analyses therefore focuses on this model alone.

4.3.2 Sensitivity Analysis

Logit Link Functions

Population size was most sensitive to increases in parameters of the survival function (Table 4.2). The intercept on survival, that acts through all age classes, was the most sensitive ($\Delta\mu(N^{adult})$ = 6.73), although this was primarily driven by the age classes adult ($\Delta\mu(N^{adult})$ = 4.65) and cubs ($\Delta\mu(N^{adult})$ = 1.87). Decreasing inter-group competition decreased population size ($\Delta\mu(N^{adult})$ = −2.50) and was the strongest driver of its coefficient of variation ($\Delta CV(N^{adult})$ = 0.031). Increasing the standard deviation of the environmental stochasticity term, decreased population size but increased its coefficient of variation ($\Delta\mu(N^{adult})$ = $-1.80, CV(N^{adult})$ = 0.023), with decreased intra-group regulation acting through cub survival, increasing population size and its coefficient of variation ($\Delta\mu(N^{adult})$ = $0.86, CV(N^{adult}$ = 0.008).

Increased adult female fecundity and a stronger correlation between years of breeding females, increased population size ($\Delta\mu(N^{adult})$ = 1.84 and 0.73, respectively) but did not greatly influence its coefficient of variation ($CV(N^{adult}$ = 0.004 and 0.002, respectively). The coefficient of variation in group size, averaged across groups, was driven by mechanisms that reduce survival in small groups, ($\Delta CV\left(G^{adult}\right)$ = 0.075) and those that reduce survival in densely populated groups, acting through cubs and adults, ($\Delta CV(G^{adult})$ = 0.032 and 0.046, respectively). Increased adult female fecundity also increased the coefficient of variation in group size ($\Delta CV\left(G^{adult}\right)$ = 0.017).

Function	Variable	Coefficient	Standard Error	$\Delta\mu(N^{adult})$	$\Delta CV\left(N^{adult}\right)$	$\Delta CV\left(G^{adult}\right)$
	Intercept	0.89+0.2	0.16	6.73	-0.001	0.014
	Body Condition	0.02	0.04	-0.68	-0.002	0.00
	Adult	0.37	0.09	4.65	-0.002	0.00
	Old Adult	-0.96	0.21	0.21	0.000	0.00
	Inter-Group Competition	-0.10	0.13	-2.50	0.031	0.00
	Group Size	1.24	0.25	0.59	0.011	0.10
Survival	Group Size^2	-1.00	0.24	0.92	0.015	0.15
	Male	-0.27	0.08	1.49	0.003	0.00
	Adult:Group Size	-0.72	0.27	-0.05	0.005	0.10
	Old Adult:Group Size	-2.13	0.84	-0.06	0.001	0.00
	Adult:Group Size^2	0.66	0.27	0.04	0.006	0.10
	Old Adult:Group Size^2	1.86	0.83	0.02	0.001	0.00
	Inter-Group Competition:Group Size	0.26	0.07	-0.25	0.010	0.00
	Intercept	-3.68+0.8	0.38	2.07	0.004	0.011
	Body Condition	0.80	0.19	0.42	0.000	0.021
	Recruited t-1	1.43	0.29	0.73	0.002	0.008
Fecundity	Adult	1.47	0.30	1.84	0.003	0.017
	Old Adult	0.37	0.49	0.15	0.000	0.001
	Inter-group competition	-0.86	0.29	-0.69	0.003	-0.005
	Litter Size	1.50	-	0.66	0.002	0.008
	Intercept	-2.71	0.29	-0.17	0.002	-0.028
	Body Condition	0.07	0.11	-0.04	0.000	0.000
Movement	Adult	0.60	0.13	-0.06	-0.002	-0.023
	Old Adult	0.16	0.18	-0.02	0.000	-0.001
	Inter-group competition	-0.28	0.37	-0.46	0.002	0.021
	Intercept	628.96	13.36	-0.03	0.000	0.000
	Group Size	-12.34	3.63	0.05	0.000	0.000
Development	Inter-group competition	-31.42	11.77	0.00	0.000	0.000
Body	Adult	-63.95	8.21	0.03	0.000	0.000
Mass	Old Adult	-124.95	17.38	0.05	0.000	0.000
	Weight	0.28	0.02	6.55	0.010	0.052
	Male	55.70	4.25	0.06	0.000	0.001
	Inter-group competition:Adult	33.90	8.65	0.04	0.000	0.001
	Inter-group competition:Old Adult	12.81	29.37	0.00	0.000	0.000
	Intercept	516.23	7.87	-0.02	0.000	0.000
	Length	0.30	0.01	-5.95	-0.008	-0.041
Development	Adult	-29.78	2.54	0.04	0.000	0.000
Body	Old Adult	-36.02	5.50	0.04	0.000	0.000
Length	Inter-group competition	-10.60	2.83	-0.02	0.000	0.000
	Male	18.13	1.33	0.02	0.000	0.000
	Inter-group competition:Adult	8.83	2.68	0.10	0.000	0.000
	Inter-group competition:Old Adult	11.37	9.24	0.12	0.000	0.000
Transmission	Intercept	264.9	78.00	0.06	0.000	0.000
Body	Average Parent Mass	0.08	0.09	1.17	0.003	0.011
Mass	Group size	-23.5	9.29	0.04	0.000	0.000
Transmission	Intercept	375.8	124.40	-0.07	0.000	0.000
Body Length	Average Parent Length	0.19	0.17	-0.71	-0.002	-0.007
Random Effects Standard Deviations and sensitivities						
Function	Social Group	Year Error	Residuals*	$\Delta\mu(N^{adult})$	$\Delta CV\left(N^{adult}\right)$	$\Delta CV\left(G^{adult}\right)$
Survival	0.43	0.45	-	-1.80	0.023	0.011
Fecundity	0.37	1.14	-	0.57	0.006	0.010
Movement	0.54	0.38	-	0.06	0.000	0.000
Development Mass	36.07	33.54	88.05	0.04	0.000	0.001
Development Length	10.75	5.77	27.79	0.06	0.000	0.000
Transmission Mass	28.30	17.42	60.27	0.02	0.000	0.001
Transmission Length	12.48	14.69	39.43	0.05	0.000	0.000
* Linear mixed effects models only						

Table 4.2: Parameter values and associated sensitivities of population size and the coefficient of variation of population and group size from the inter-intra-group regulation individual-based model.

Linear Functions

Mean population size, its coefficient of variation and the coefficient of variation in group size, averaged across groups, were all driven by coefficients influencing body condition. Increased development of weight for heavier individuals and increased birth weight for individuals from heavier parents, increased both population size ($\Delta\mu(N^{adult})$ = 6.55 and 1.17, respectively), its coefficient of variation ($\Delta CV(N^{adult})$ = 0.010 and 0.003) and the coefficient of variation averaged across groups ($\Delta CV(G^{adult})$ = 0.052 and 0.011). Parameter coefficients that decreased body condition acted inversely. Increased development of length for

longer individuals and increased birth length for individuals from longer parents, decreased both population size ($\Delta\mu(N^{adult}) = -5.95$ and -0.71, respectively), its coefficient of variation ($\Delta CV(N^{adult}) = -0.008$ and -0.002) and the coefficient of variation averaged across groups ($\Delta CV\left(G^{adult}\right) = -0.041$ and -0.007).

4.4 Discussion

The individual-based model investigated the extent to which socio-spatial structure influences population dynamics of badgers in Wytham Woods, Oxfordshire, UK. Group living in parts of their range, they are solitary foragers that experience few fitness benefits of sociality. Coefficients associated with socio-spatial structure were not the primary determinants of population size or fluctuations (Table 4.2). Population size was determined by individual body condition that in turn influences many demographic rates. Although sensitivities of trait based functions could not be directly compared with binomial process, these functions identified, adult survival followed by female fecundity, then cub survival and environmental stochasticity acting through survival, to be key determinants of population size and both population and group level fluctuations. The sensitivity analysis of group and population fluctuations identified intra-group regulation of both adult and cub survival to be an additional driver. Similarities in the drivers of fluctuations at the group and population level indicate that groups fluctuate with a level of synchrony. Sensitivities of the coefficient of variation in both adult group and adult population sizes were small, indicating the amplitude of fluctuations to increase directly proportionally with population size. A sensitivity of zero for the coefficient of variation does not represent no change in the size of fluctuations, only that the standard deviation changed to the same extent as population, or group size. In the following discussion changes in population size also represent changes in the amplitude of fluctuations except where the sensitivities of adult group or population sizes are non-zero.

4.4.1 Group Level Dynamics

Fluctuations at the group level were driven by changes in survival rates, with intra-group regulation acting through both adult and cub survival rates determining the coefficient of variation in group size. Intra-group regulation acting through both adult and cub survival increased fluctuations to a greater extent than their effect on population size. Environmental stochasticity, acting through survival also determined group level fluctuations, previously identified by Macdonald and Newman [2002], Macdonald et al. [2010], Nouvellet et al. [2013] .

4.4.2 Hierarchical structure and Movement

The concept of a fixed number of breeding positions is supported by the correlation between years in breeding individuals, with individuals breeding one year experiencing increased fecundity the following year

(Table 4.2) supporting previous work in Wytham Woods [Woodroffe et al., 1995, Annavi et al., 2014a]. If the same individuals reproduce each year, the social group can be viewed as reproducers and floaters, where the floaters are essentially queuing for breeding positions to become available [Woodroffe and Macdonald, 1995]. This first would imply that individuals move to groups with an available breeding position, ceasing to move when all positions are taken, queuing where resources permit. This is observed in the statistical models, with movement rates decreasing with the number of individuals outside of the focal group. This idea is in agreement with field observations post culling known as the perturbation effect, whereby movement increased after culling [Tuyttens et al., 2000a,b]. Individuals may also be queuing to obtain body condition high enough to successfully reproduce. The queuing for condition hypothesis is interpreted from the strong correlation between body condition and fecundity relative to survival and movement. Similarities can be drawn to dynamics observed in meerkat (*Surricata suricatta*) populations [Young and Clutton-Brock, 2006, O'Riain et al., 2000, Clutton-Brock et al., 2008, Hodge et al., 2008] where females intensely compete for breeding positions, with reproductive success upon obtaining dominance based on individual body weight. Meerkat cub survival is also influenced by group size, although inversely to that observed here, benefitting from conspecifics [Hodge et al., 2008]. In meerkats it was proposed that females should invest in increasing body weight over investment in cooperative activities. Given badgers exhibit few cooperative traits, queuing females should optimise increasing body condition and should spatially aggregate in areas of richest resources.

4.4.3 Regulatory Mechanisms

Macdonald and Newman [2002] found fecundity to decrease with group size but here the analysis found inter-group competition to be a better predictor. This reflects the number of breeding positions in a social group, and therefore the population, being limited. Increased group size decreases the probability of obtaining a breeding position within the group, but the number of individuals competing for the breeding positions outside of the group gives a better estimate of breeding success. There are more positions available outside the group than inside and high movement rates at low densities indicates that social group affiliation may not be limiting in obtaining an available breeding position in another social group. In retrospect the best predictor of female fecundity would most likely have been the number of adult females in the population relative to the total number of breeding positions.

A consequence of this is that the number of cubs born each year is relatively constant. If adult survival is high cub survival decreases stabilising group sizes in agreement with the findings of Fell et al. [2006] and similar to dynamics observed in the banded mongoose, *Mungos mungo* [Rood, 1975, Cant, 2000]. Weak adult regulation on survival (the primary driver of population growth [Macdonald and Newman, 2002]) and the small size of the habitat relative to other social carnivores result in adult populations fluctuating with environmental variables in relative unison [Macdonald and Newman, 2002, Macdonald et al., 2010, Nou-

vellet et al., 2013]. If adult population size is high recruitment will remain low until group sizes decrease to carrying capacity. This results in gradual declines that prevent population crashes. The variability in the environment is not large enough to produce spikes and crashes alone. These dynamics are similar to those exhibited by red deer (*Cervus elaphus*) [Albon et al., 2000, Benton et al., 1995] where environmental stochasticity on adult survival does not produce crashes in adult population size, in contrast to those seen in Soay sheep where crashes in adult survival due to environmental conditions can coincide with density regulation on calf survival, producing population crashes [Coulson et al., 2001]. Thus juvenile regulation in the presence of weak environmental stochasticity and weak adult survival regulation appears stabilising. An additional stabilising effect not modelled here is that all females mate but only a subset implant later in the year. This may mitigate against effects of breeder loss, as there is always an individual ready to implant in their place, further minimising the variance in cub production between years.

4.4.4 Implications for Restricted Population Growth

Multiple carnivore systems experience restricted population growth either during periods of improving ecological conditions [e.g. lions, *Panthera leo* Packer et al., 2005], during recolonisation of an environment from which they were previously extirpated [e.g. wolves, *Canis lupus* Hurford et al., 2006] or after disease outbreaks [e.g. ethiopian wolves, *Canis simensis*, and african wild dogs, *Lycaon pictus*, Marino et al., 2013, Courchamp and Macdonald, 2001]. These examples all exhibit cooperative behaviours and have strong evidence for potential Allee effects [Sillero-Zubiri et al., 1996, Creel and Creel, 1998, Courchamp et al., 2002, Hurford et al., 2006]. Badgers in the south-west of the United Kingdom experienced rapid increases in population size in the early nineties, before which populations did not increase with increasingly favourable conditions [Rogers et al., 1997, Macdonald and Newman, 2002]. The model here demonstrates how increasing adult survival would not increase population sizes due to decreases in cub survival and birth weight, feeding through and decreasing the other demographic rates, explaining decreased condition in larger groups observed by Macdonald and Newman [2002] but also why condition did decrease after the population increase. Formation of new groups alleviated intra-group regulation on cub birth weight.

As the number of breeding positions in the population is fixed and regulation on cub survival is strong, population growth can only occur if new groups form, if all groups have reached carrying capacity. New group formation opens new breeding positions, decreases crowding in the social group, increasing recruitment. As adult survival is weakly regulated by intra-group competition, population sizes will increase until the fecundity rates decrease to levels that stabilise population growth at unity. It is not the number of breeders that changes during the increase; it is the ratio of breeders to adult population size that decreases average fecundity in the population. Formation of new groups requires new territories to become available. This was observed during the rapid population increase in Wytham Woods where previous social groups contracted territory ranges as resource densities increased eventually permitting new social groups to form

when available space became available [Macdonald and Newman, 2002].

Chapter 5

Factors restricting new group formation in densely populated social systems

Abstract

Territoriality imposes spatial structure on social carnivore populations, with individuals occupying areas of higher real estate value experiencing fitness benefits. These benefits can be shared with related individuals that remain philopatric giving them an advantage over competitors. Investigated here is the extent to which fine scale habitat quality, and post-dispersal relationships, influence population dynamics in a lion (*Panthera leo*) population on the Serengeti plains of Tanzania. Social-spatial structure has been shown to produce step jumps in population densities in multiple carnivore populations, with the formation of new groups essential for population density increases, especially when groups experience strong intra-group regulatory mechanisms. Using an individual based model, parameterised to a 40 year intensive study, the model investigates the relative contributions of deterministic and stochastic processes in determining lion pride growth rates and extinction, the frequency of dispersing group production and the size of the dispersing group produced. Larger prides, and prides with a younger age structure, rear larger offspring cohorts, which due to reduced recruitment in larger groups are evicted from the pride. A key determinant of variance in pride size is fine scale habitat features that partition the ecosystem into a small set of optimal territories around bifurcations in river confluences, around which other prides congregate, essentially queuing for an optimal territory to become vacant. The optimal territories produce variance in pride sizes, but differences in pride sizes within the optimal territory residents is primarily driven by demographic stochasticity. The key determinants of dispersing group production, and pride extinction, are therefore stochastic effects, both environmental and demographic, that change the age structure and size of prides in a random manner. This has important implications for population growth as increases in density are limited to years of high recruitment across a number of prides. An interesting corollary from the analysis is that detection of non-linear effects of group size on individual fitness, found across many obligate cooperators, may be due to smaller groups occupying sub-optimal territories and not due to increased costs of cub-rearing, territory maintenance and reduced hunting efficiency in small groups.

Keywords: Lions, *Panthera leo*, group formation, restricted population growth, social species dynamics

5.1 Introduction

Sociality has been shown to inhibit population growth in many social carnivores, primarily acting through limitations on new group formation [African wild dogs, *Lycaon pictus* Courchamp et al., 2000a], [Eurasian badgers, *Meles meles* Macdonald and Newman, 2002] [lions, *Panthera leo* Packer et al., 2005]. In obligate cooperators these limitations can be fitness costs experienced by small groups known as Allee effects [Allee, 1931, Allee et al., 1949, Courchamp et al., 1999b], whereby hunting efficiency is reduced, individuals experience increased costs of pup rearing and territory maintenance while experiencing greater inter-group pressures, potentially driving them away from optimal territories [Packer et al., 1990, Rood, 1990, Stephens et al., 1999, Courchamp et al., 1999a, 2000a]. Many social carnivores have high reproductive skew and reproductive suppression of subordinates, such that forming new groups is the only process that increases the number of breeders in the population thus generating population growth [Clutton-Brock, 1998, Creel, 1998]. When new groups manage to form, increasing the number of breeders and effective population size, populations rapidly increase up to a new equilibrium, as seen in badgers [Macdonald and Newman, 2002] lions [Roelke-Parker et al., 1996, Packer et al., 2005] and Ethiopian wolves, *Canis simensis* [Marino et al., 2006, 2013]. Therefore understanding the demographic processes that limit new group formation is an integral part of understanding whether sociality increases extinction risk relative to their non-social counterparts [Rood, 1990, Stephens et al., 1999, Courchamp et al., 1999a, 2000a, Angulo et al., 2013]. Modelling a long-term study of lions (*Panthera leo*) on the Serengeti plains, Tanzania, the determinants of new pride formation and the characteristics of parental prides that enable them to produce dispersing groups that establish on the landscape are investigated.

Multiple mechanisms will interact to determine the success of a dispersing group establishing within an ecosystem. These will be both deterministic and stochastic, with small dispersing groups being susceptible to extinction through demographic stochasticity [Lande, 1993, Stephens et al., 1999]. In the absence of inter-group pressures, groups that disperse as juveniles may experience reduced individual fecundity and survival rates, increasing their extinction risk relative to groups with more prime-aged individuals. The dispersing group may experience increased inter-group pressures if dispersal group size is small relative to established prides and they may have to settle in sub-optimal territories. Their success may also be aided by environmental conditions during dispersal, with good years aiding in their establishment while they experience the costs outlined above. Modelling the demographic functions through which these processes act and how interactions between demographic rates amplifies each process, enables their contributions to observed patterns at the population level to be understood.

Many social species experience non-linear effects of group size on fitness, resulting in an optimal range

that maximises individual fitness [Caraco and Wolf, 1975, Koenig, 1981, Packer et al., 1990, Thurber and Peterson, 1993]. An optimal strategy in such species is to forcefully evict juveniles if recruiting them would drive the group above an upper threshold, keeping them in the group otherwise. In this scenario the structure of the dispersing group will correlate with the fitness of the parental pride. Groups with higher individual fitness will consistently rear larger cohorts without needing to keep them in the group to maintain adult group size. These may be driven by individual structure; age specific survival and fecundity, by territory quality, that may be group-specific or act over localised neighbourhoods, and by the competition between groups for access to the optimal territories. Therefore understanding the mechanisms that restrict formation of new groups requires consideration of not only the structure of the dispersing group, but also of the parental group the enables it to produce dispersing groups with this structure.

Post-dispersal, a group may be able to remain philopatric within the neighbourhood of its natal group, potentially receiving post-dispersal benefits from their natal pride but also guaranteeing a local competitor [VanderWaal et al., 2009]. Groups that disperse to new areas may find empty optimal patches which will not be available in their natal location [Clobert et al., 2009, VanderWaal et al., 2009] but may be dispersing to poor quality areas. This decision may be based on local densities, or available territories, but also the habitat quality of their natal area [Mosser and Packer, 2009]. New groups will have to compete with pre-existing groups for territories such that the level of inter-group competition will be an important factor in determining their chances of establishing.

These deterministic drivers will interact with stochastic processes. When group size is small the potential for demographic stochasticity to produce variance in the production of successful dispersing groups and the successful establishment of dispersing groups is high. When fecundity is low, stochasticity may be the largest driver of variance in cohort size and acting through juvenile survival, it may also produce variance in cohort size at maturity. Differences in dispersal group size within years may be driven by demographic stochasticity and between years this may also be influenced by environmental stochasticiy, producing years of many, large dispersing groups and other years with few dispersing groups.

The relative importance of each mechanism can be determined using mathematical models. Individual based modelling is a natural framework to incorporate socio-spatial structure, having been used to model a variety of social systems including bottlenose dolphins, *Tursiops*, [Hall et al., 2006], Eurasian badgers [Shirley et al., 2003], grey wolves, *Canis lupus* [Pitt et al., 2003], lions [Whitman et al., 2004], meerkats, *Suricata suricatta* [Bateman et al., 2013] and many more [See Grimm, 1999a, DeAngelis and Mooij, 2005, for multiple examples] . Here, an individual based model is used to map lion populations over an annual time step, tracking changes in pride size, dispersing group production and dispersing group size for each pride throughout the simulation.

Lions on the Serengeti plains were buffered against gradual population growth during increasing prey availability and vegetative cover that increased hunting efficiency, instead, experiencing step jumps between

equilibria [Packer et al., 2005]. A canine distemper outbreak in the 1990's caused populations to crash [Roelke-Parker et al., 1996], after which recovery was delayed, only recovering after a year of exceptionally high recruitment, suggesting environmental stochasticity and dispersal group size to be important factors [Roelke-Parker et al., 1996, Packer et al., 2005]. The optimal group size on the Serengeti plains is 3-6 adult females [VanderWaal et al., 2009] so population growth occurs primarily through new group formation. The model investigates the factors influencing the success of dispersing group establishment, the role of demographic and environmental stochasticity, the influence of habitat real estate value and the resolution over which it differs. Demographic rates; dispersal, fecundity and survival are parameterised to a long-term field study which are then used to simulate the population. From this simulation the deterministic drivers of pride extinction, the probability of producing a dispersing group and dispersing group size are analysed.

5.2 Methods

5.2.1 Data Collection

The study area covers 1700 km^2 of the open plains area in the Serengeti National Park, Tanzania, located at the centre of the Serengeti-Mara Ecosystem. A south-east to north-west gradient of rainfall and soil type partitions the park into two distinct ecosystems, the open grassland plains and the acacia woodland area. The model focuses on the plains lions that aggregate around sparsely distributed waterholes and rocky outcrops. Plains lions have been continuously studied since 1975 with population sizes ranging from 70 to 170 adult individuals [Mosser et al., 2009]. Observations recorded between 1975 and 1983 were opportunistic and since the beginning of 1984 each study pride has contained a minimum of one radio collared adult female. Monitoring since 1984 has relied on radio tracking and opportunistic observations that occur at a minimum of once per fortnight. Individual lions are identified by facial markings with demographic events (birth, death, immigration and emigration) determined by direct observation and reproductive behaviour/status. Fates of some individuals are unknown when they disperse outside of the study area. For this analysis these individuals are considered as mortalities as they no longer influence dynamics.

5.2.2 Study Species

Lions on the Serengeti plains experience strong non-linear effects of pride size on fitness, with the optimal pride size being between three and six adult (2+ years) females [Mosser and Packer, 2009, VanderWaal et al., 2009]. All males disperse as juveniles and females are either recruited to the adult pride or forcibly evicted by adult females if the pride size exceeds the optimal range [VanderWaal et al., 2009]. A secondary driver of dispersal is after successful male takeover events, where young cubs are killed and all other juveniles are forcibly evicted by the invading male coalition. Whitman et al. [2004] showed takeover events to be an important driver of dynamics and extinction risk.

Prides congregate around optimal hunting areas in fragments generated by river confluences [Mosser et al., 2009]. Dispersing prides that remain philopatric experiencing reduced inter-group competition for a limited time, continuing to use parts of their natal territory [Mosser et al., 2009]. The benefits of this depend on the location of its natal pride, with different fragments (or neighbourhoods) possessing different real estate values. Differences in habitat quality produce source-sink dynamics between different fragments [Mosser et al., 2009].

Over the course of the study it has become clear the certain prides experience long tenureships and produce multiple dispersing groups in comparison to others (Packer personal communication). The work of Packer et al. [2005], Mosser et al. [2009] and VanderWaal et al. [2009] is extended to identify the primary demographic variables behind; dispersal group production and size, of pride tenureship and the whether habitat features at a finer scale to that of the neighbourhood influence individual fitness.

5.2.3 Hypothesis

The Serengeti population is structured around a set of optimal hunting territories produced by river confluences fragmenting the habitat [Mosser et al., 2009]. Multiple prides inhabit each neighbourhood, but what has hitherto not been explored, is whether variation in habitat quality, at a finer resolution than the neighbourhood, produces fitness differences between prides, that is large enough to generate the observed variance in the production of dispersing groups or whether observed differences are driven by demographic stochasticity acting on a small optimal pride size. It is hypothesised that within each neighbourhood there exists an optimal territory around which all other prides queue, waiting for the optimal territory to become vacant. Adopted hereafter is the terminology of resident and floater-pride as used in ornithology to describe the occupants of optimal territories and those queuing.

It is known that each neighbourhood has its own real estate value and and is therefore hypothesised that the neighbourhood resident will experiences fitness benefits across an *A-Priori* unknown demographic rate(s), relative to the floaters queuing around it. These benefits will enable the residents to recruit larger juvenile cohorts and/or maintain adult pride size, and therefore pride tenureship, generating the observed variance in pride tenureship and dispersing group production.

Dispersing group size will be an important factor determining the success of the dispersing group in establishing by decreasing the likelihood of extinction due to demographic stochasticity. Post-dispersal relationships should aid groups that disperse from optimal neighbourhood territories and dispersers from neighbourhood residents are hypothesised to have an increased propensity to remain philopatric.

The relative effect of these mechanisms in comparison to individual level (age specific demography), pride level (intra-group regulation) and local and global competition factors can be understood using mathematical models. Definitions of optimal territory residency, post-dispersal relationships and how explanatory variables for the statistical analyses are constructed from these concepts are now introduced.

Definitions

Post-Dispersal Relationship

VanderWaal et al. [2009] demonstrated that the portion of shared territory with natal prides halved around 5 years post dispersal. Post-dispersal relationships are defined as a pride being within five years of dispersal and in the same neighbourhood as its natal pride (that is still alive). As prides share their natal territory it is assumed that they also experience reduced levels of inter-pride strife but also benefit from sharing a territory with a neighbourhood resident, more than with a floater pride. Therefore two binary factors are fitted separately, one indicating post-dispersal relationships with a neighbourhood resident, the other with a floater pride.

Neighbourhood Resident

To test whether prides experience additional territory specific benefits at finer spatial scales than neighbourhoods, prides that manage to produce a minimum of one dispersing group that successfully establishes are denoted as 'residents'. Successful establishment is defined as surviving for 5 years, the period that the pride experiences post-dispersal relationships. Spatial data at a finer scale to that of neighbourhood was not available so true locations of optimal territories could not be used. Therefore in the statistical analysis residency denotes being a member of a pride that produced a successful dispersing group whereas in the simulation it denotes occupying an optimal territory. This is explained further in the individual based model section below.

Local and Global Competition

Density dependence is fitted both at the neighbourhood (local competition) and habitat (global competition) level as the analysis focuses on how neighbourhood level processes affect population dynamics. Global competition is defined as the number of adult females in the population and local competition as the number of adult females within a neighbourhood.

5.2.4 Statistical Analyses

To identify the demographic rates through which the fitness benefits of optimal territory residency and post-dispersal relationships act, Generalised Linear Mixed Effects Models (GLMM) were fitted to the long-term data constrained to females only. Individual level dispersal, fecundity, defined as whether an individual reproduces or not, and survival were modelled using a binomial error structured GLMM. Litter sizes are randomly sampled from the observed sizes, with probabilities defined by their frequency in the data.

The statistical models tested for non-linear effects of group size, age dependencies, local and global competition and responses to takeover events. A takeover event is when a coalition of adult males invades an existing pride, killing all adult males, taking the breeding positions. Most cubs below six months of age are killed with other juveniles forced to disperse [Packer and Pusey, 1983]. A full list of explanatory variables are given in the Appendix Table C.1.1. Binary factors were also fitted to account for a canine distemper

outbreak in 1994 and for changes in the intercepts of demographic rates that occurred due to changes in ecological conditions [Roelke-Parker et al., 1996]. Year and neighbourhood were fitted as random effects to account for environmental variation and neighbourhood real estate value, respectively. Model selection was performed using Akaikes Information Criterion adjusted for small sample size (AIC_c) with the lowest value taken as the optimal model. AICc values are given in the Appendix Table C.1.2.

5.2.5 Model Structure

The optimal models from the statistical analyses are then used to predict individual demographic rates of a simulated population, an outline of which is given in Figure 5.1. The simulation initialises by sampling a population based on observed densities. These individuals are assigned prides and neighbourhoods. The number of neighbourhoods in the population is fixed at the number observed on the Serengeti Plains, with their associated real estate value for each demographic rate extracted from the neighbourhood random effect term in the GLMM. Therefore the real estate value of the neighbourhoods in the simulated population are representative of the Serengeti Plains. Each neighbourhood is assigned a single optimal territory that only one pride can occupy.

At the beginning of each iteration the model randomly samples wether a male takeover event occurs for each pride, based on the observed frequency of successful takeover events. Random samples are achieved by sampling a random number from a uniform distribution between 0 and 1, if the value exceeds the observed frequency of takeover events then no event occurs, if it is less than or equal to the observed frequency then a takeover event occurs. The same method is used to sample individual demographic processes. The expected value of the demographic rate is estimated based from the GLMM. A random number is then sampled from a uniform distribution between 0 and 1. If the number is greater than the expected value, the event does not occur, occurring otherwise.

This introduces demographic stochasticity into the model as individuals with the same expectation can experience different events. Environmental stochasticity is incorporated into the model by sampling a change in the intercept value of each demographic rate in the GLMM from the year random effect term. This number is randomly sampled from a normal distribution with mean zero and variance equal to the variance in the random effect. The same shift is used for every individual in the population, sampling a new shift each time step and a unique shift for each demographic rate.

After assigning takeover events to prides the model assigns dispersal events to individuals by randomly sampling from a binomial distribution, with expected values taken from the dispersal GLMM. After assigning dispersal events to every individual in the population, individuals dispersing from the same pride are pooled together to form new prides. The decision to disperse is modelled at the individual level but individuals disperse as a group from a pride.

The model then samples whether the dispersing group remains philopatric or disperses to a new neigh-

bourhood. This decision is conditional on the residency status of the parental pride. The decision to remain philopatric is sampled from a binomial distribution, with the expected value taken from the observed frequency in the data, constrained by parental residency status. i.e. if the parent is a resident, the probability of remaining philopatric is based on the frequency with which dispersing groups from resident prides remained philopatric in the data. If a pride does not remain philopatric, a neighbourhood is randomly sampled from the the non-natal neighbourhood set. Movement of prides between neighbourhoods is not modelled as a unique process, instead occurring when every individual in a pride is predicted to disperse through the dispersal function. This is not recorded as a dispersal event in the simulation but is used as a dispersal event in the statistical analysis of dispersal using GLMM's.

The model proceeds by randomly sampling whether each individual produces a litter with expectations predicted by the fecundity GLMM. If an individual produces a litter, the litter size is randomly sampled from the observed litter sizes, with probability of each litter size given by their observed frequencies. The offspring enter a pool of recruits that join the pride at the end of the iteration.

The final process to occur is survival, which is randomly sampled following the same procedure as dispersal and fecundity. Individuals that die are removed from the simulation with survivors continuing to the next iteration. Surviving individuals increase in age by a year and cubs that were born are now assigned to their natal pride.

If the neighbourhood resident goes extinct an individual from the neighbourhood population is randomly sampled with equal probability and their pride is assigned the residency. This results in the largest pride having the greatest probability of obtaining the optimal territory. If no prides occupy the neighbourhood the territory remains vacant until a dispersing pride enters the neighbourhood.

The simulation models the population after the increase in demographic rates due to ecological change and in the absence of canine distemper outbreaks. The canine distemper outbreak is fitted in the GLMM's to account for reduced demographic rates in that year but is not included in the simulation.

The model records:

- The date each pride was formed.
- The neighbourhood the pride settled in (whether it remained philopatric).
- The pride from which it dispersed.
- Pride size at each time step.
- The date the pride obtains an optimal territory (if at all).
- When the pride went extinct.
- Adult population and neighbourhood size through time.

- Whether a pride produced a dispersing group each time step.

This generates a simulated data set that can be used to understand population dynamics. The analytical methods used on the simulated data set are described below.

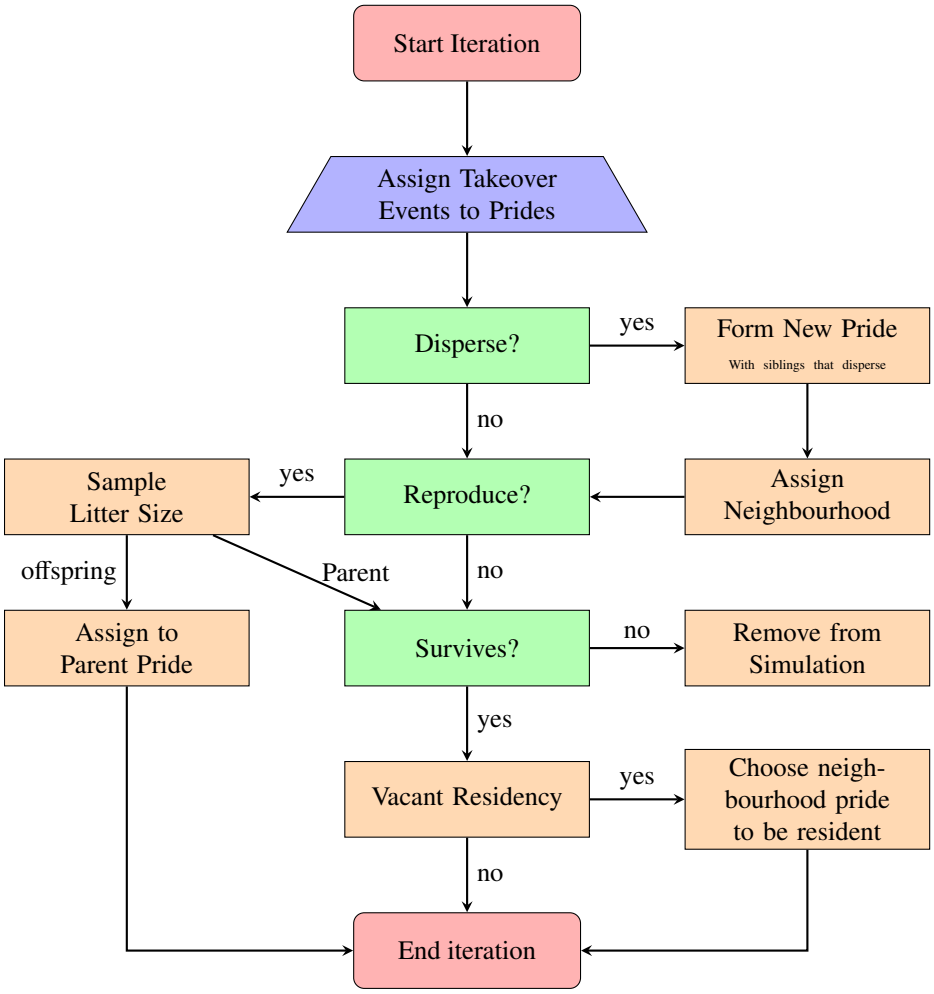


Figure 5.1: A flow-chart representation of the individual based model iterative cycle.

5.2.6 Identifying contributions of fine scale habitat quality and post-dispersal relationships on individual fitness.

Tracking each individual through the simulation permits analysis of age specific survivorship, fecundity and dispersal rates as well as life history metrics across the four pride types: optimal territory resident and floater and experiencing post-dispersal relationships with territory residents and floaters. These identify the fitness differences experienced due to territory heterogeneity and post-dispersal relationships. This identifies the potential drivers of variance in dispersing group production and tenureship but their relative contribution compared to other mechanisms are identified using regression analyses. The life history metrics calculated for prides experiencing post-dispersal relationships are estimated as though a pride can exist within this state indeterminately even though the maximum time a pride can experience these relationships is five years. They must therefore be interpreted as an index of fitness during the post-dispersal period.

5.2.7 Identifying determinants of pride extinction, dispersing group production and size.

At each time step a pride has the potential to go extinct and produce a dispersing group. Both of these are binomial processes that may be driven by intra-pride processes such as pride size, age structure and territory quality, competition between prides within a neighbourhood and population wide density regulation. A generalised linear model (GLM) with a binomial error structure is used to regress pride extinction (extinct/survived) and propagule production (produced/did not) as a function of intra-pride, local and global variables. Each explanatory variable is removed individually from the GLM and the percentage increase in deviance relative to the full model is taken to represent the relative explanatory power of each variable. Interactions between pride size and each explanatory variable are fitted in each GLM, with the interactions that explain 0.5% of the variance or greater reported. Fitting the environmental stochasticity intercepts as explanatory variables identifies the effect of environmental stochasticity (without time lags) and the remaining variance is attributed to demographic stochasticity. A second linear regression analysis (LM) investigates the determinants of dispersing group size and pride growth rates between years, regressing pride size at time t+1 against pride size at time t, that indicates the mechanisms that enable prides to self-maintain within the optimal region identified by VanderWaal et al. [2009].

5.2.8 Statistical Software

All data manipulation, statistical analyses and simulations were implemented in the statistical programme R [R Core Team, 2015] with GLMM's implemented using the package 'lme4' [Bates et al., 2013]. Models were run for $7.5e^5$ iterations.

5.3 Results

Function	Parameter	Est.	s.e
Cub	Intercept	0.47	0.54
Survival	Distemper	2.18	1.38
	Female Adult Group Size	-0.14	0.11
	Global Competition	-0.53	0.36
	Local Competition	-0.18	0.15
	Optimal Residency	0.47	0.20
Adult	Intercept	0.60	0.17
Survival	Distemper	-1.56	0.28
	Age	0.56	0.05
	Age^2	-0.04	$3e^{-3}$
	Post D-R with Resident	0.35	0.21
	Post D-R with Floater	-0.94	0.42
	Local Competition	-0.20	0.08
	Global Competition	-0.13	0.07
	Optimal Residency	0.36	0.13
	Takeover	-0.33	0.12
Fecundity	Intercept	-5.77	0.26
	Takeover	0.80	0.12
	Optimal Residency	0.35	0.12
	Age	1.08	0.06
	Age^2	-0.06	$4.e^{-3}$
	Post D-R with Floater	1.01	0.53
	Post D-R with Resident	0.35	0.18
Dispersal	Intercept	-4.93	0.41
	Age	0.36	0.11
	Age^2	-0.05	0.01
	Female Adult Group Size	0.78	0.10
Philopatry	Residents	0.92	-
Dispersers	Floaters	0.57	-
Takeover	Probability	0.35	-
Random	Cub Survival	0.75	-
Effect	Adult Survival	0.00	-
Standard	Fecundity	0.47	-
Deviation	Dispersal	1.51	-

Table 5.1: Parameter coefficients

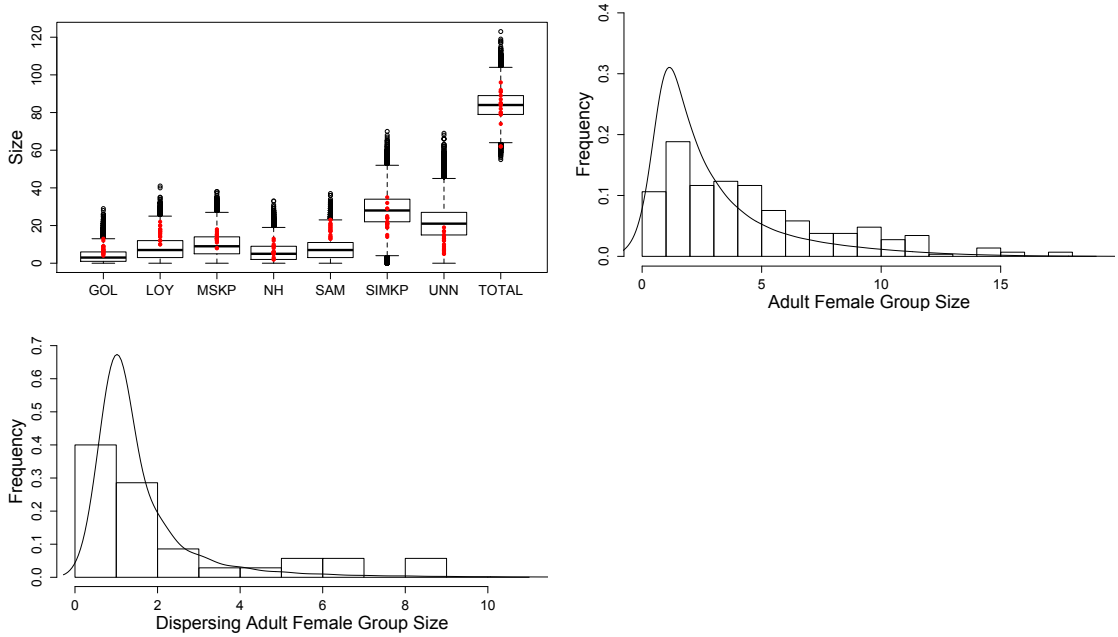


Figure 5.2: Observed neighbourhood densities (top left: red points), pride sizes (top right: solid bars) and dispersing group sizes (bottom left: solid bars) plotted against model predictions

Variable	Pride Extinction		Dispersing Group Production		Dispersing Group Size		Pride Size at t+1	
	GLM Coefficient	% Change in Deviance	GLM Coeff	% Change in Dev	GLM Coeff	% Change in Dev	GLM Coeff	% Change in Dev
Optimal Residency	-0.63	0.2	0.04	0.0	-0.14	0.2	0.52	2.4
Post-Dispersal Resident	0.08	0.0	-0.14	0.0	0.00	0.0	-0.04	0.0
Post-Dispersal Floater	0.15	0.0	-0.62	0.0	0.13	0.0	-0.08	0.0
Pride Size	-1.70	10.9	0.60	4.8	0.15	13.1	0.90	291.2
*Pride Size^2	-	-	-0.02	1.1	-	-	-	-
Mean Age	-0.32	1.2	0.07	0.0	-0.04	0.2	-0.08	3.2
*Mean Age^2	0.03	2.8	-0.02	0.1	-	-	-	-
Local Competition	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
Global Competition	0.02	0.4	0.00	0.0	0.00	0.0	-0.01	0.9
Neighbourhood (min:max values)	-0.3:0.1	0.1	-0.0:0.1	0.0	-0.1:0.0	0.0	0.0:0.3	0.3
**Dispersal Event Occurred	1.53	0.3	-	-	-	-	-1.11	4.6
Takeover Event Occurred	0.18	0.1	-0.04	0.0	-0.03	0.0	0.15	0.5
Explained Variance = $1 - \frac{\text{residual deviance}}{\text{null deviance}}$	23%		25%		19%		86%	

*only included where there is a non-linear relationship

**Not included on dispersal analyses as it is the response variable

Table 5.2: Likelihood ratio test tables for binomial GLM'S regressing pride extinction (event = extinction), dispersing group production (event=produced), dispersing group size and pride growth rates (size at t+1 against size at t) against intra-pride, local and global habitat variables (n prides = 68180).

5.3.1 Data Series

In total, 934 unique individuals were included in the study, covering 3886 unique events denoting whether an individual survived/reproduced/dispersed in a given year. The oldest individuals reached 19 years of age and female adult pride sizes varied from 1 to 18 individuals (mean 4.63, 95% CI 4.36, 4.90). Population sizes ranged from 56 to 155 individuals, averaging 97 individuals (87, 107) from 1975 to 2014 and 129 (121, 137) individuals between 1997 and 2014. Neighbourhood densities varied from 0 to 51 individuals averaging 13.9 (12.6, 15.2). The coefficient of variation within a neighbourhood, an index of fluctuation in size relative to average size ranged from 0.27 to 1.32 (mean 0.61) indicative of neighbourhood specific dynamics. There were 195 successful takeover events occurring at a rate of 0.35 per pride per year. Only 35 dispersal events were recorded, with dispersal group size averaging 3.2 individuals (3.1,3.3). Of these 92% (n=27) of dispersing groups coming from a pride satisfying the residency condition remained philopatric, in comparison to 57% (n=8) that dispersed from floater prides. This observed difference is in line with our hypothesis that dispersers have a higher propensity to remain philopatric when dispersing from an optimal territory. A single distemper outbreak was recorded during the study in 1994. There were 526 females born during the study with litter size varying between 1 and 5 females. A single female in the litter was the most common occurrence (n = 293) followed by 2 (n = 163), 3 (n = 60), 4 (n = 9) with a single recorded event of 5 females. Certain maternities were known but in cases were maternity could not be established, a mother was chosen randomly out of the adult females in a given pride. Litters that died before sexing were removed from the analysis such that litter size accounts for early natal mortality.

The AIC_c tables for the statistical analysis are given in the Appendix C.1.2 and the parameters estimates in Table 5.1. The model identified an increase in cub survival after 1997 due to ecological change and the model is simulated after this change.

The next section discusses the fit of the individual based model compared to the data series and is followed by a description of the key parameters coefficients (β) identified in the statistical analysis along with their standard errors (s.e) and how they influence the metrics of interest. The final section of the results discusses the relative contribution of un-modelled and stochastic processes in comparison to the deterministic drivers.

5.3.2 Individual Based Model Fit

The number of adult individuals predicted from the IBM in each neighbourhood and in total, are given in Figure 5.2. Population sizes captured observed densities (observed = 82.3, s.d = 9.22, n = 18; model = 84.2, sd = 7.64) although predicted neighbourhood densities were lower in the low density neighbourhoods than observed (Figure 5.2). The number of prides predicted by the model exceeded the observed frequency (observed μ = 16.2, σ = 1.63, n = 18; predicted μ = 29.4, σ = 4.5). This resulted in a smaller predicted mean pride size than observed (observed μ = 5.1 σ = 3.6, n= 292 ; predicted μ = 2.9 , σ = 2.7), although

the distribution of pride sizes was captured well (Figure 5.2). The frequency of dispersing group production predicted by the individual based model was lower than observed (observed μ=0.08, σ = 0.08, n = 18; predicted μ = 0.04, σ = 0.06). Mean dispersing group size was also smaller than observed (observed μ = 3.5, σ = 2.7; predicted μ = 1.6, σ = 1.4, Figure 5.2) indicating the dispersal function to over-estimate the number of individuals dispersing alone.

Mean pride size when dispersal events occurred was also slightly lower than observed (observed μ = 9.3, σ = 3.9, n = 23; Predicted μ = 7.7, σ = 4.2), with 63% (σ = 0.49) of prides producing a dispersing group in the simulation. This was higher than the observed value (0.34 estimated from the period 1975 to 2014) although not all prides had been tracked to extinction (study finished) so this is an under estimate.

	Resident	Floater	P-D-Relationship		All Individuals
			From Resident	Floater	
R_0	1.36	0.76	1.39	0.40	1.00
T_c	7.90	7.64	7.90	5.91	7.73
e_0	4.20	3.23	4.27	1.68	3.62

Table 5.3: Individual life history metrics; lifetime reproductive success (R_0), generation length (T_c) and life expectancy at birth (e_0) for the four different pride types and all pride types pooled predicted from the individual based model.

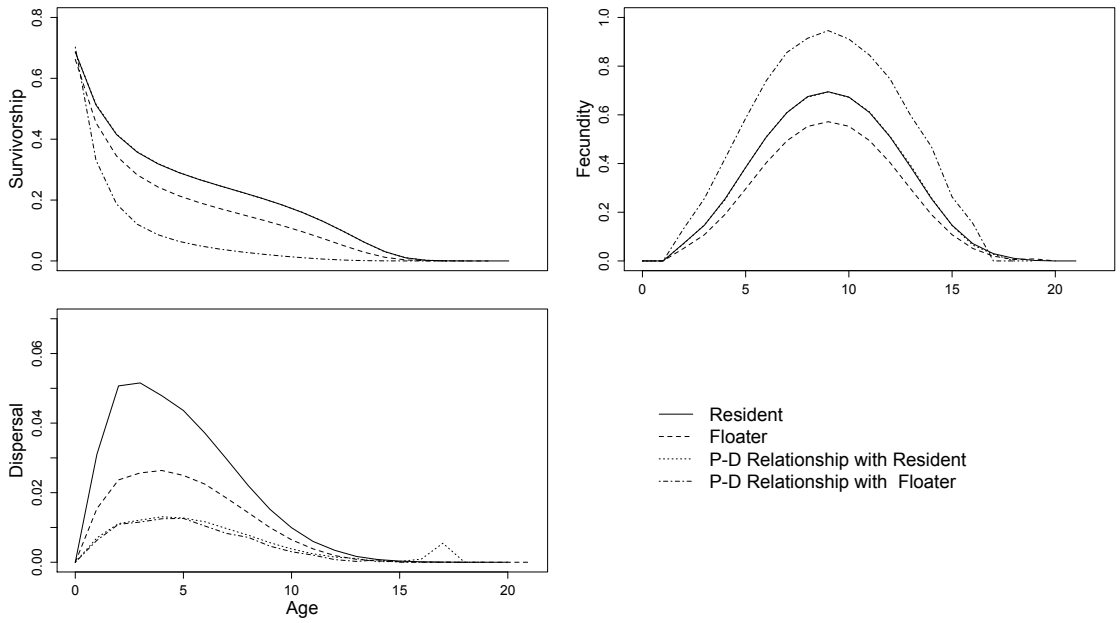


Figure 5.3: Survivorship, age specific fecundity and dispersal rates for the four pride definitions predicted from the IBM.

5.3.3 Deterministic Drivers

Generalised linear modelling of the deterministic drivers of dispersing group production, pride extinction and dispersing group size highlighted pride size as the primary determinant (Table 5.2). Larger prides are less susceptible to extinction through demographic stochasticity as average pride size is small (predicted = 2.9, σ = 2.7). Larger prides also produce more offspring, rearing larger cohorts that have a higher chance of surviving to adulthood, dampening the effects of demographic stochasticity. This enables the pride to maintain larger adult pride sizes, forcing individuals to disperse otherwise. This is observed in the mean pride size being almost three times as large when dispersal events occur than in prides where it does not (7.7 against 2.6). Therefore the key predictor of pride extinction, dispersal group production and dispersal group size, which in turn determines the success of the dispersing group, will be that which maintains pride size.

The GLM analysis of pride growth rates, analysed by regressing pride size at time t+1 against pride size at time t found a strong correlation in pride sizes between years (β = 0.90). Prides experiencing post-dispersal relationships decreased in size relative to prides of similar size although this explained little variance in the data and can therefore be viewed as having negligible effect. Prides occupying resident territories were larger and prides with an older age structure grew faster than younger prides (Table 5.2). Mean pride size for floater prides was 1.6 adult females (σ = 2.1), increasing to 1.7 in floater prides experiencing post dispersal relationships with either floaters (σ = 1.4) or residents (σ = 1.5). Prides occupying resident territories were significantly larger with an average of 5.7 (σ = 3.7) individuals. Therefore occupying an optimal territory enables the pride to maintain pride size better than floater prides due to increased individual fitness, demonstrated by the differences in lifetime reproductive success (Table 5.3) generating tenureship over five times longer for prides that obtain residency (residency obtained μ = 102, σ = 185; residency not obtained μ = 19, σ = 20). Floater prides experience low lifetime reproductive success (0.76) in comparison to optimal territory residents (1.36) indicating that floater prides will quickly tend to extinction unless they obtain an optimal territory within a neighbourhood. Prides experiencing post-dispersal relationships with optimal territory residents experience similar lifetime reproductive success (1.39), experiencing the same fecundity and adult survival benefits as residents (Table 5.1). This is most likely why groups dispersing from optimal territory residents have a higher propensity to remain philopatric than those dispersing from floater prides (0.92 in comparison to 0.57). The post-dispersal relationship enables them to increase pride size to within the optimal range identified by VanderWaal et al. [2009] while also increasing the age structure of the pride to ages that optimise fitness (Figure 5.3). This is contradicted, however, by the GLM analysis with post dispersal relationships explaining no variance in the data. The small size of prides experiencing post-dispersal relationships and lack of explanatory power indicates demographic stochasticity to be the primary mechanisms influencing changes in pride size of newly dispersed prides.

A second benefit from occupying an optimal territory, along with a larger pride size is a younger age

structure (residents μ = 4.5, σ =1.8; floaters μ = 5.1, σ = 2.8). Fecundity and survival are maximised around 9 years of age (Figure 5.3) but it is the younger individuals that have a higher propensity to disperse. Therefore, for a pride to produce dispersing groups it must be both large enough, and possess individuals of the dispersing age. This is seen in the statistical analysis of demographic rates with probability of dispersal increasing with group size (β = 0.78, s.e = 0.1) and the GLM analysis of pride extinction and dispersal group production, where an older age structure increases extinction and reduces dispersal. Occupying an optimal territory was not a significant predictor of dispersal, only of increased fitness on all other demographic functions, although the fitness benefits of occupying an optimal territory increases pride size, enabling them to produce more dispersing groups (0.12 per year in comparison to 0.02). The size of the dispersing groups did not differ between residents and floaters (μ = 1.6) indicating that floater prides produce dispersers when they are large enough and that the increased fitness experienced by optimal territory residents results in them reaching this size more frequently.

Fitting interactions between pride size and all other explanatory variables did not greatly improve the explanatory power of the GLM's. Only in the size of dispersing groups GLM did the explained variance increase by more than 1%, with all interactions fitted. The size of dispersing groups found an interaction between pride size and optimal territory residency and with neighbourhood density, that increased the explained variance from 0.19 to 0.21. The results reported in Table 5.2 do not contain these interactions as their explanatory power was small and is omitted for ease of comparison with the other GLM's. The interaction found that within prides occupying an optimal territory, large residents produced larger dispersing groups (β = 0.09, σ = 0.02), and that larger prides were affected to a lesser extent by local densities, with respect to dispersing group size (β = 0.002, σ = $4.8e^{-}5$).

5.3.4 Relative contributions of Stochastic Effects

Apart from pride growth rates, the deterministic drivers only explained a maximum of 25% of the variation indicating either a missing explanatory variable or strong stochastic effects. The GLM of growth of pride size between years explained 86%, with the majority explained by size the previous year. 14% was still unexplained and given the small number of individuals in each pride it is not surprising that demographic stochasticity drives changes between years. Fitting the environmental stochasticity shifts in intercept terms of each demographic function as an explanatory variable did not improve model fit except on dispersing group production where environmental stochasticity on dispersal explained 18% of the variance, although this still left 56% unexplained.

5.4 Discussion

An individual based model was used to investigate the relative contributions of deterministic and stochastic processes in determining the frequency that groups disperse from prides and the rate at which prides go extinct. The model tested whether the habitat was partitioned into a set of optimal hunting territories that invoke fitness benefits to their occupants, around which prides form in the suboptimal territories. Also tested was wether the sharing of territory with related prides that remained philopatric gave similar benefits during the initial period (5 years) post-dispersal. The statistical analysis of demographic rates found prides in optimal territories to experience fitness benefits across survival and fecundity that were also experienced with related prides that remained philopatric, except on cub survival (Table 5.1). Seeing that the benefits identified were almost identical for the parental and dispersed pride there is strong evidence for fine scale habitat quality influencing individual fitness, as previously identified by Mosser et al. [2009]. Using the parameterised demographic functions to simulate the population in an individual based modelling format, identified pride size to be the primary deterministic driver of pride extinction, dispersing group production and dispersing group size. Optimal territory occupancy resulted in larger prides, although this produces only variance between residents and floaters, the change in pride size between years was driven by demographic stochasticity within these two subsets.

Fine scale habitat heterogeneity results in the population consisting of two distinct pride types, those occupying optimal territories, that persist for long periods and produce many dispersing groups, and floaters queuing for an optimal territory that will go extinct, within three generations on average, if they do not obtain one (generation length = 7.6, tenureship μ = 19). The differences in habitat quality at the neighbourhood are offset by the differences in local densities. Neighbourhoods of higher real estate value experiencing higher densities that reduce fitness through inter-pride competition (Figure 5.2, Table 5.1). This is due to dispersing groups remaining philopatric, such that source areas quickly become densely populated, primarily through dispersal from optimal territory residents. The probability of a pride producing a dispersing group that disperses to another neighbourhood is equal for both floaters and residents, taken my multiplying the compliments of rates of philopatry with dispersal rates (Table 5.1). Therefore increasing the rate at which floater prides produce dispersing groups will influence source-sink dynamics to a greater extent than residents due to the population consisting primarily of floater prides.

Lifetime reproductive success of floater prides is less than one (Table 5.3). This means that the only self-sustaining prides are the optimal territory residents. In many other social carnivores the viability of the population is considered in terms of the number of breeding females. In meerkats (*Surricata suricatta*) they discuss breeding and floater individuals [O'Riain et al., 2000, Young and Clutton-Brock, 2006, Clutton-Brock et al., 2008, Hodge et al., 2008] with similar dynamics observed in badgers (*Meles meles*) [Dugdale et al., 2008]. In grey wolves (*Canis lupus*) where packs are family units only the alpha female reproduces, with other individuals dispersing long-distances to find mates [Brainerd et al., 2008]. All these

species exhibit reproductive suppression and the restricted number of breeding individuals is the proposed mechanism through which the populations may have increased susceptibility to extinction, and restricted population growth [Berec et al., 2007, Courchamp et al., 1999b,a, Macdonald and Newman, 2002, Vucetich et al., 1997]. In Lions all adult females attempt to rear cubs. In the Serengeti plains system occupying an optimal territory increases the probability of reproducing and cub survival (Table 5.1) resulting in increased lifetime reproductive success (Table 5.3). Given floater prides have lifetime reproductive success less than one, the population is effectvely being constantly colonised by the resident prides. The stability of the system should therefore be measured by the number of adult females occupying optimal territories. This may have important implications for sustainable harvest, as removal from floater prides may be more sustainable than from optimal territory residents, especially when harvest increases the rate of male takeover events, inhibiting recruitment and declining population growth rates [Whitman et al., 2004].

Environmental stochasticity on adult survival was effectively zero. Therefore for floater prides to be able to persist for long periods they must experience favourable demographic stochasticity on adult survival, and to produce dispersing groups this must be combined with a year of high reproductive success followed by high cub survival. This results in occasional dispersal events although they are rare (1% chance). This has important implications for limiting population growth. Each pride in an optimal territory can produce a maximum of one dispersing group per year. The model predicted a 12% chance of a resident pride producing a dispersing group, such that a new pride enters a neighbourhood approximately every nine years. It is therefore necessary for the floater prides to also produce dispersing groups if the population is to grow and for this, environments must be favourable. This is inline with the findings of Packer et al. [2005]. The analysis of demographic rates identifies cub survival to be the demographic rate that increased during the rapid increase in population size [Packer et al., 2005], increasing from 0.5 (s.e = 0.3) to 0.6 (s.e = 0.3). This will have had two consequences on population dynamics. Optimal territory residents would have produced larger cohorts and thus larger dispersing groups that will have been less susceptible to extinction through demographic stochasticity (Table 5.2) but also will have enabled floater prides to recruit more individuals such that during favourable environmental conditions, pride sizes reached levels that enabled dispersal events to occur. This is similar to the dynamics observed in badgers (*Meles meles*) where floater individuals queuing for breeding opportunities required favourable environmental conditions to achieve group sizes large enough, to carve out new territories within a saturated ecosystem. After favourable environmental conditions the population jumped to a new equilibrium [Macdonald and Newman, 2002]. Here it is not floaters within a social-group, but floater prides within a neighbourhood, that facilitated the jump in population size.

Interestingly the analysis of demographic rates did not identify the non-linear effects of group size on fitness identified by [VanderWaal et al., 2009]. The cost to larger prides was identified as acting through cub survival but no costs to small prides were observed. The differences in pride size between optimal territory

residents and floaters may explain this, with smaller prides (floaters) experiencing reduced fitness due to poor habitat. This may have important consequences for work on fitness costs to small groups identified in other species where costs to small groups may appear associated with group size when in fact they are due to small groups occupying the poorest habitats [Courchamp et al., 1999b], although removal of the neighbourhood random efect in the GLMM's here did not render the quadratic terms significant. This could have important consequences for extinction risk and management of low density endangered social carnivores.

Chapter 6

General Discussion

6.1 Overview

In this thesis, the demography and dynamics of three social carnivores, from three different families have been investigated. Each species shares similarities and differences in their demography with one another, that contribute to the observed similarities in population dynamics. Lions (*Panthera leo*) and grey wolves (*Canis lupus*) both invest in communal hunting, in the majority of their range, and rearing of offspring [Peterson, 1977, Harrington et al., 1983, Packer et al., 1990, Cooper, 1991]. Cooperators have been proposed to exhibit Allee effects at both the group and population level, due to small groups experiencing fitness costs [Courchamp et al., 1999a, Stephens et al., 1999]. Component Allee effects, a reduction in a component of fitness, have been demonstrated in African wild dogs (*Lycaon pictus*), meerkats (*Surricata suricatta*) and dwarf mongooses (*Helogale parvula*) [Rood, 1990, Creel and Creel, 1998, Courchamp and Macdonald, 2001, Courchamp et al., 2002, Clutton-Brock et al., 2001]. Each of these species experience a trade-off when group size is small. Adult group members may be required to both hunt and guard offspring from predators, resulting in reduced hunting efficiency or reduced offspring survival [Courchamp et al., 2000b]. More recently studies are beginning to question whether these component Allee effects reduce total fitness and result in reductions in group specific growth rates [Gusset and Macdonald, 2010, Woodroffe, 2011, Bateman et al., 2012]. Here, I, along with a range of collaborators in multiple countries, investigated the dynamics of three contrasting social carnivores, each of which are the top order predator such that predation, a component Allee effect identified in African wild dogs, meerkats and dwarf mongooses, is not present. Two experience reproductive suppression; badgers and wolves, two have exhibited step jumps in population size; lions and badgers, two are communal hunters with strong intra-group regulation; lions and wolves, with each species exhibiting contrasting litter sizes, the primary mechanism through which long lived species can increase population growth.

6.2 Presence of component and demographic Allee effects

The demographic model of wolves was the only model to detect a component Allee effect that was independent of density, although increasing per capita recruitment in smaller groups did not produce a threshold group size, below which groups tend to extinction. The larger component Allee effect detected in the Interior of Yellowstone National Park corresponded with increased litter size, that offset the reduced cub survival, such that recruitment was equal, at similar densities, to that observed in the resource dense interior of the park. Recruitment varied between 2 and 6 individuals at high and low densities, correlating closely with that observed in the Superior National Forest, Beltrami Island State Forest and Isle Royale populations [Harrington et al., 1983, Peterson et al., 1998]. High per capita recruitment in small packs resulted in no cost to total fitness associated with small group size, in the absence of global density regulation, such that demographic Allee effects were not identified.

No component Allee effects were found on lion demographic rates, although smaller prides experienced reduced cub and adult survival due to them occupying sub-optimal territories. At high densities small badger groups experienced reduced survival rates, though this was not present at low densities. It is this additional strength of inter-group competition that restricts population growth when carrying capacity increases, imposing a minimum group size that can successfully establish. I do not view this as an Allee effect as in the absence of inter-group competition small groups would not experience reduced fitness. Therefore predation and anthropogenic pressures appear the common mechanisms across social species that produce a minimum viable group size [see Gusset and Macdonald, 2010, Woodroffe, 2011, Bateman et al., 2012, for examples of no demographic Allee effect] and [Rood, 1990, Creel and Creel, 1998, Courchamp et al., 2002, Courchamp and Macdonald, 2001, Clutton-Brock et al., 2001, for demographic Allee effects].

6.3 Impacts of reproductive suppression

Reproductive suppression was present in the wolf and badger systems, with all adult females in the lion population attempting to breed. This has important consequences on population dynamics when populations are perturbed away from carrying capacity. In badgers it appears that 2-3 females reproduce in each social group, taken from the probability of reproducing relative to group size identified by Annavi et al. [2014a] and Woodroffe and Macdonald [1995]. In grey wolves it is predominantly the dominant male and female that reproduce, such that removal of non-reproducing individuals from each population will not influence the number of individuals born in the population each year. Evidence for multiple breeding individuals has been documented in wolves [Murie, 1944, Harrington et al., 1982, Mech, 2000], although work by Stahler et al. [2013] indicates that the number of pups recruited to one year of age is not affected as increased cub mortality offsets increased number born. Therefore multiple breeders appear to reduce survival of the dominant pairs pups, so removal of a secondary breeder will see an increase in recruitment of the dominant

pair.

In grey wolves and badgers, pack growth rates are maximised in smaller groups. Additional group members decrease cub survival in badgers and do not reproduce. In wolves, although additional conspecifics provide a small increase in cub survival through alloparental care, they reduce per capita recruitment by partitioning the litter among a larger pride. This enables rapid population growth when densities are reduced, as the number of offspring sired each year is unchanged, increasing per capita recruitment rates. Strong regulation through cub survival in both systems at high densities, produces stable dynamics, as years when adults do well see a decrease in per capita recruitment, stabilising growth rates. The banded mongoose, *Mungos mungo*, exhibits similar dynamics, with high juvenile mortality, driven by strong intra-group density dependence, generating stable groups through time [Rood, 1975, Cant, 2000]. The primary cause of population crashes in wolves is when there are canine distemper outbreaks that result in extremely low recruitment, similar to lions where adults experience increased mortality as well [Roelke-Parker et al., 1996, Almberg et al., 2010]. Therefore, in both systems, the only mechanism that will limit growth, is if the number of adult females decreases below the number of groups that the ecosystem can support, i.e. the number of denning sites that can successfully rear offspring. This is identical to the dynamics observed by Marino et al. [2006, 2013] in Ethiopian wolves (*Canis simensis*). Therefore species with high reproductive suppression should experience rapid population growth when populations are perturbed below carrying capacity, with the number of breeding positions, determined by the number of groups an ecosystem can support determining its return rate.

Lions do not exhibit reproductive suppression, such that declines in adult numbers do not see such large increases in per capita recruitment when population densities decline [Roelke-Parker et al., 1996, Packer et al., 2005]. This is why the Serengeti plains population was captured at an equilibrium density below carrying capacity after a canine distemper outbreak [see Roelke-Parker et al., 1996, for details]. Therefore reproductive suppression appears to produce dynamics more stable than in groups where all females reproduce. When all females reproduce the group may need to limit group size to restrict the number of individuals born as opposed to permitting additional non-reproducing members to join the group. This produces strong intra-group regulation such that new individuals cannot join pre-existing groups. If new groups need to form to generate growth this may be delayed until cohorts can be raised not only to the dispersing age, but then survive long enough to recruit themselves. In this time demographic stochasticity may result in group extinction.

6.4 Formation of new groups

Decreases in population size can occur through the extinction of groups, or through reductions in the mean group size in the population. Reductions in group size can decrease intra-group competition, increasing

individual fitness, resulting in population growth back to equilibrium. Extinction of groups can produce step jumps in population size, with populations fixed at densities below carrying capacity, until new groups can establish on the landscape. The latter is present in lions that experience strong intra-group competition, inhibiting new individuals from joining pre-existing groups. This is also present in grey wolves and yet they do not exhibit step jumps in population size. The primary difference between the two is litter size, with wolves in Yellowstone around 7 individuals and 4 in the Serengeti plains lions [Harrington et al., 1983, Packer and Pusey, 1995]. Large lion prides can produce large cohorts of offspring as all females reproduce, but small wolf packs can produce large cohorts, with additional pack members increasing cub survival but not litter size [Harrington et al., 1983, Stahler et al., 2013]. Therefore small wolf packs can grow quickly, but small lion prides will struggle to persist as dispersing group size is small, decreasing cohort size and increasing risk of extinction due to demographic stochasticity [Lande, 1993]. This does not, however, result in lions experiencing increased extinction risk in comparison to wolves and badgers when heterogeneity in territory quality is considered.

6.5 Effective population size

Heterogeneity in territory quality was fitted to all species, although the wolves were only partitioned across large spatial scales, far bigger than an individual territory. In badgers, areas of increased resource richness did not result in increased demographic rates due to increased number of subordinate individuals, increasing intra-group competition. Similarly, in lions, increased neighbourhood quality was offset by increased densities and inter-pride competition. The lion population did exhibit fitness differences between individuals occupying optimal territories within a neighbourhood. This generates two types of prides, those in optimal territories that have lifetime reproductive success greater than one, and those in sub-optimal territories with lifetime reproductive success less than one, tending to extinction. The effective population size is therefore the number of adult females occupying the optimal territories as these are the individuals driving population growth. In badgers, it is the number of females with breeding positions, equivalent to three times the number of social groups, and in wolves the number of packs. Therefore the majority of individuals in the population are not contributing to population growth. Even in wolves, were group members increase the number of individuals recruited, they decrease per capita recruitment rates. Therefore if non-breeding individuals are removed in badgers and wolves, and individuals from sub-optimal territories in lions, population viability would most likely be unaffected.

6.6 Implications for sustainable control

Culling of badgers results in increased immigration and disease transmission [Tuyttens et al., 2000a,b]. Nonselective removal may open breeding opportunities or change the relative size of queues for breeding

opportunities in each social group, incentivising individuals to change group affiliation, increasing movement and disease transmission. This process has been well documented and is known as the 'perturbation effect' [Tuyttens et al., 2000a,b]. One may be able to offset this effect by identifying the number of floater individuals within each social group and reducing each 'queue' proportionally. This would result in the relative size of each queue to the others in the population remaining constant. The benefits of changing social group would be zero.

In lions, population growth is produced by a subset of prides, such that changes to the structure of these prides may have profound influences on population size. Whitman et al. [2004] demonstrated increased takeover events, due to reductions in male pride size, decreased population viability. Extending this, hunting should be concentrated on floater prides in sub-optimal territories. These prides are smaller and thus more likely to experience takeover events, but also are more susceptible to extinction through demographic stochasticity [Lande, 1993] and experience decreased lifetime reproductive success. Removing individuals from these prides would reduce inter-group pressures on optimal territory residents, enabling them to rear larger cohorts that are forced to disperse, compensating for the anthropogenic pressure. In wolves reducing mean pack size and therefore territory size could enable more packs to exist within the ecosystem, increasing the number of breeding individuals and population growth. Promoting large packs, that experience reduced per capita recruitment but also inflict increased inter-pack pressures on small packs may reduce population growth, although I can never envisage this actually being implemented as management policy.

6.7 Stochasticity in socio-spatially structured populations

In spatially structured populations demographic stochasticity can manifest at the population level even at high densities [Lande et al., 1999]. In all three systems intra-group regulation acted predominantly through cub survival, except on the Northern Range of Yellowstone National Park. In badgers this mitigates against stochastic variation by reducing recruitment when adults do well and vice-versa, dampening group level fluctuations. This is achieved as group size never greatly exceeds carrying capacity, but also rarely crashes to levels where inter-group competition drives them to extinction. Badger group sizes, in the south west of the United Kingdom, are relatively large compared to lions and wolves [Kruuk and Parish, 1982, Harrington et al., 1983, Packer et al., 1990] so it is not surprising that stochastic effects are less prominent at the population level. In lions, stochasticity was the primary driver of population dynamics due to the small pride size that maximises fitness [VanderWaal et al., 2009]. This effect primarily increased extinction rates of floater prides, with optimal territory residents experiencing extremely long tenureship (100 years). As lifetime reproductive success of floater prides is less than one, tenureship of floater prides is primarily driven by demographic stochasticity, as adult individuals are rarely replaced by younger cohorts. Stochasticity was not incorporated into the wolf model but conclusions can be drawn from the model. Intra-group per

capita recruitment will fluctuate with changes in adult numbers, which will be influenced by demographic stochasticity as pack size is small.

A common theme here is that stochastic effects influence the individuals queuing for breeding rights or optimal territories, but if one were to focus on the number of breeding individuals, or individuals within the optimal territories, the dynamics would probably appear relatively constant in comparison. In lions, optimal territory residents regularly rear offspring cohorts that can be maintained in the pride if many adults die, dispersing otherwise, such that pride size of optimal territory residents remains constant. In wolves, if a pack goes extinct, then local dispersal most likely increases, forming a new pack and maintaining the number of breeding females, this was observed in Ethiopian wolves by Marino et al. [2006, 2013]. Therefore populations may fluctuate, but within each population there appears to exist a subpopulation, driving population growth, that remains relatively constant between years.

6.8 Importance of Results for General Social Species Dynamics

All of the results do not indicate additional Allee effects to be produced by social structure, although lack of evidence is not proof they do not exist [Liermann and Hilborn, 2001]. Thus, the results here do not lend support to the hypothesis that socially structured species exhibit increased extinction risk [Courchamp et al., 1999a]. The results also highlight the importance of considering individual demographic rates when testing for Allee effects to avoid arriving at erroneous conclusion such as Stahler et al. [2013], where reductions in recruitment at the group level, do not correlate with reductions in per capita rates.

This thesis has demonstrated how simple models can be used to understand the strength and direction of different regulatory mechanisms, but to accurately capture group dynamics requires extensive data and complex models, if one is to capture socio-spatial structure and demographic stochasticity.

To generalise the conclusions here to other social systems is difficult when similar models have not been fitted. Comparisons can only be drawn when the same model has been fitted to multiple systems, such as the two areas of Yellowstone National Park in Chapter 3. The decomposition of regulatory mechanisms derived in Chapter 3 provides the simplest method for testing different regulatory mechanisms across species and species ranges. The more complex models derived in Chapters 4 and 5, provide greater insights into the interactions between individual, group and habitat variables, but require very detailed and long time series, which are not always available. Both of these indicate local habitat features to greatly influence the distribution of group sizes within a system. When considering general social species dynamics it is important to account for habitat quality, as well as group size, to avoid attributing decreased demographic rates to group size, when they may be due to habitat, as demonstrated by the statistical analyses of lion demographic rates.

A limitation of all the models parameterised in this thesis have been their ability to accurately capture dispersal dynamics. In wolves dispersal is often long-range and may not be detected [Van Ballenberghe,

1983, Mech et al., 1995, Boyd and Pletscher, 1999]. In badgers, a species that spends the majority of its life underground, using a trapping record with three time series points a year, it is difficult to determine dispersal and movement from an individual trapped transitioning through territory. In lions capturing dispersal events that involve multiple individuals is difficult even with perfect knowledge of the system. An important future direction would be to document dispersal processes to a greater extent and to develop mathematical models that can accurately capture these events. This will require models that incorporate individual processes and correlations between individuals (group level decisions). Once these models have been derived, the dynamics of social species in general will be captured to a greater extent by models, providing greater insights for ecologists and enable more successful management plans to be constructued.

6.9 Future directions

This aim of this thesis was to identify whether general rules governing the dynamics of social species could be drawn. An application of the first study was to understand how populations respond to anthropogenic caused mortality. I begin by discussing the future directions for the Northern Rocky Mountain grey wolf system and associated wolf management, followed by directions for furthering understanding of social species dynamics.

If wildlife managers in the Northern Rocky Mountains wish to understand the demographic responses of wolves to harvest, they should adopt an individual based modelling approach, following the methods of Whitman et al. [2004]. This requires knowledge of how new packs form, such as fission fusion dynamics, how individuals and packs migrate to new areas, and how these processes are influenced by density. Currently few of these processes are known and the majority of collared individuals are the dominant individuals that rarely disperse. It would be interesting to set up experimental zones within the Northern Rocky Mountains, where densities and pack sizes are artificially manipulated under an experimental design. This would require more intensive tracking of packs within this area, but would uncover the demographic responses required to use complex population models. This would enable accurate predictions of population responses to harvest, while simultaneously creating a simulated environment, where a variety of different strategies could be simulated, permitting robust management strategies to be derived.

This thesis highlighted reproductive strategies as a key predictor of population dynamics, with reproductive suppression enabling rapid population growth, in comparison to species where multiple females reproduce. Currently the latter is only tested on lions and it would be interesting to see whether multiple social species where many females reproduce also exhibit strong intra-group regulation and step jumps in population size. Is reproductive suppression a more stable strategy than permitting multiple females in a group to reproduce? If this imposes a lower upper bound on group size through strong intra-group regulation, extinction risk may increase, especially given the lion population contained only a few prides which

drive population growth.

This thesis has identified a few patterns across species, but more modelling is required, across a greater variety of social structures, if we are to find general rules. Simple models can provide valuable insight into demography, but socio-spatially structured populations do require complex models to capture dynamics given the dependence of group size on demographic rates. Complex population models also permit the contribution of stochasticity to be analysed, an important process when mean group size is small. However, few models of social species dynamics exist, either due to fear of using complex models, or lack of data on key demographic processes. If general trends are to be uncovered, these factors need to be addressed.

Bibliography

S. D. Albon, T. Coulson, D. Brown, F. E. Guinness, J. M. Pemberton, and T. H. Clutton-Brock. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. *Journal of Animal Ecology*, 69(6):1099–1110, 2000.

W. C. Allee. Co-operation among animals. *American Journal of Sociology*, pages 386–398, 1931.

W. C. Allee, O. Park, A. E. Emerson, T. Park, and K. P. Schmidt. *Principles of animal ecology*. Saundere Co. Ltd., 1949.

E. S. Almberg, P. C. Cross, and D. W. Smith. Persistence of canine distemper virus in the greater yellowstone ecosystem's carnivore community. *Ecological Applications*, 20(7):2058–2074, 2010.

E. Angulo, G. S. A. Rasmussen, D. W. Macdonald, and F. Courchamp. Do social groups prevent allee effect related extinctions?: The case of wild dogs. *Frontiers in Zoology*, 10(1):11, 2013.

G. Annavi, C. Newman, C. D. Buesching, D. W. Macdonald, T. Burke, and H. L. Dugdale. Heterozygosity–fitness correlations in a wild mammal population: accounting for parental and environmental effects. *Ecology and Evolution*, 4(12):2594–2609, 2014a.

G. Annavi, C. Newman, H. L. Dugdale, C. D. Buesching, Y. W. Sin, T. Burke, and D. W. Macdonald. Neighbouring-group composition and within-group relatedness drive extra-group paternity rate in the european badger *Meles meles*. *Journal of Evolutionary Biology*, 27(10):2191–2203, 2014b.

A. W. Bateman, T. Coulson, and T. H. Clutton-Brock. What do simple models reveal about the population dynamics of a cooperatively breeding species? *Oikos*, 120(5):787–794, 2011.

A. W. Bateman, A. Ozgul, T. Coulson, and T. H. Clutton-Brock. Density dependence in group dynamics of a highly social mongoose, *Suricata suricatta*. *Journal of Animal Ecology*, 81(3):628–639, 2012.

A. W. Bateman, A. Ozgul, J. F. Nielsen, T. Coulson, and T. H. Clutton-Brock. Social structure mediates

environmental effects on group size in an obligate cooperative breeder, suricata suricatta. *Ecology*, 94 (3):587–597, 2013.

D. Bates, M. Maechler, B. Bolker, and S. Walker. lme4: Linear mixed-effects models using eigen and s4. *R package version*, 1(4), 2013.

T. G. Benton, A. Grant, and T. H. Clutton-Brock. Does environmental stochasticity matter? analysis of red deer life-histories on rum. *Evolutionary Ecology*, 9(6):559–574, 1995.

L. Berec, E. Angulo, and F. Courchamp. Multiple allee effects and population management. *Trends in Ecology & Evolution*, 22(4):185–191, 2007.

B. J. Bergstrom, S. Vignieri, S. R. Sheffield, W. Sechrest, and A. A. Carlson. The northern rocky mountain gray wolf is not yet recovered. *BioScience*, 59(11):991–999, 2009.

B. M. Bolker, M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H Stevens, and J. S. S. White. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3):127–135, 2009.

D. K. Boyd and D. H. Pletscher. Characteristics of dispersal in a colonizing wolf population in the central rocky mountains. *The Journal of Wildlife Management*, 63(4):1094–1108, 1999.

S. M. Brainerd, H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P Wabakken, and A. P. Wydeven. The effects of breeder loss on wolves. *The Journal of Wildlife Management*, 72(1):89–98, 2008.

C. Brown and K. N. Laland. Social learning in fishes: a review. *Fish and Fisheries*, 4(3):280–288, 2003.

K. P. Burham and D. R. Anderson. Tests of compensatory vs. additive hypotheses of mortality in mallards. *Ecology*, 65(1):105–112, 1984.

J. B. Calhoun. The social aspects of population dynamics. *Journal of Mammalogy*, 33(2):139–159, 1952.

M A. Cant. Social control of reproduction in banded mongooses. *Animal Behaviour*, 59(1):147–158, 2000.

T. Caraco and L. L. Wolf. Ecological determinants of group sizes of foraging lions. *American Naturalist*, 109(967):343–352, 1975.

K. A. Cassidy. Group composition effects on inter-pack aggressive interactions of gray wolves in yellowstone national park. *University Of Minnesota PhD Thesis*, 2013.

M. H. Cassini. Consequences of local allee effects in spatially structured populations. *Oecologia*, 165(3): 547–552, 2011.

H. Caswell. *Matrix population models*. John Wiley & Sons, Ltd, 2001.

E. A. Catchpole, B. J. T. Morgan, and T. Coulson. Conditional methodology for individual case history data. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, 53(1):123–131, 2004.

C. L. Cheeseman, J. W. Wilesmith, J. Ryan, and P. J. Mallinson. Badger population dynamics in a high-density area. In *Symposia of the Zoological Society of London*, volume 58, pages 279–294. Clarendon Press, 1987.

D. Z. Childs, M. Rees, K. E. Rose, P. J. Grubb, and S. P. Ellner. Evolution of complex flowering strategies: an age–and size–structured integral projection model. *Proceedings of the Royal Society of London B: Biological Sciences*, 270(1526):1829–1838, 2003.

D. Z. Childs, T. Coulson, J. M. Pemberton, T. H. Clutton-Brock, and M. Rees. Predicting trait values and measuring selection in complex life histories: reproductive allocation decisions in soay sheep. *Ecology letters*, 14(10):985–992, 2011.

R. Choquet, L. Rouan, and R. Pradel. Program e-surge: a software application for fitting multievent models. In *Modeling demographic processes in marked populations*, pages 845–865. Springer, 2009.

J. Clobert, J. M. Galliard, J. Cote, S. Meylan, and M. Massot. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology letters*, 12(3):197–209, 2009.

J. Clobert, M. Baguette, T. G. Benton, J. M. Bullock, and S. Ducatez. *Dispersal ecology and evolution*. Oxford University Press, 2012.

T. H. Clutton-Brock. Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution*, 13(7):288–292, 1998.

T. H. Clutton-Brock, D. Gaynor, G. M. McIlrath, A. D. C. Maccoll, R. Kansky, P. Chadwick, M. Manser, J. D. Skinner, and P. N. M. Brotherton. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology*, 68(4):672–683, 1999a.

T. H. Clutton-Brock, A. Maccoll, P. Chadwick, D. Gaynor, R. Kansky, and J. D. Skinner. Reproduction and survival of suricates *Suricata suricatta* in the southern kalahari. *African Journal of Ecology*, 37(1): 69–80, 1999b.

T. H. Clutton-Brock, A. F. Russell, L. L. Sharpe, P. N. M. Brotherton, G. M. McIlrath, S. White, and E. Z. Cameron. Effects of helpers on juvenile development and survival in meerkats. *Science*, 293(5539): 2446–2449, 2001.

T. H. Clutton-Brock, S. J. Hodge, and T. P. Flower. Group size and the suppression of subordinate reproduction in kalahari meerkats. *Animal Behaviour*, 76(3):689–700, 2008.

S. M. Cooper. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology*, 29(2):130–136, 1991.

T. Coulson, E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. Age, sex, density, winter weather, and population crashes in soay sheep. *Science*, 292(5521):1528–1531, 2001.

T. Coulson, S. Tuljapurkar, and D. Z. Childs. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *Journal of Animal Ecology*, 79(6):1226–1240, 2010.

T. Coulson, D. R. MacNulty, D. R. Stahler, B. vonHoldt, R. K. Wayne, and D. W. Smith. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science*, 334 (6060):1275–1278, 2011.

F. Courchamp and D. W. Macdonald. Crucial importance of pack size in the african wild dog *Lycaon pictus*. *Animal Conservation*, 4(2):169–174, 2001.

F. Courchamp, T. Clutton-Brock, and B. Grenfell. Inverse density dependence and the allee effect. *Trends in Ecology & Evolution*, 14(10):405–410, 1999a.

F. Courchamp, B. Grenfell, and T. H. Clutton-Brock. Population dynamics of obligate cooperators. *Proceedings of the Royal Society of London B: Biological Sciences*, 266(1419):557–563, 1999b.

F. Courchamp, T. H. Clutton-Brock, and B. Grenfell. Multipack dynamics and the allee effect in the african wild dog, *Lycaon pictus*. *Animal Conservation*, 3(4):277–285, 2000a.

F. Courchamp, B. T. Grenfell, and T. H. Clutton-Brock. Impact of natural enemies on obligately cooperative breeders. *Oikos*, 91(2):311–322, 2000b.

F. Courchamp, G. S. A. Rasmussen, and D. W. Macdonald. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology*, 13(1):20–27, 2002.

S. Creel. Social organization and effective population size in carnivores. *Behavioral Ecology and Conservation Biology*, 1(1):246–265, 1998.

S. Creel. Social dominance and stress hormones. *Trends in Ecology & Evolution*, 16(9):491–497, 2001.

S. Creel and N. M. Creel. Communal hunting and pack size in african wild dogs, *Lycaon pictus*. *Animal Behaviour*, 50(5):1325–1339, 1995.

S. Creel and N. M. Creel. Six ecological factors that may limit african wild dogs, *Lycaon pictus*. *Animal Conservation*, 1(01):1–9, 1998.

S. Creel and J. J. Rotella. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves *Canis lupus*. *PLoS One*, 5(9), 2010.

J. H. Crook. Social organization and the environment: aspects of contemporary social ethology. *Animal Behaviour*, 18:197–209, 1970.

S. Cubaynes, D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. Density-dependent intraspecific aggression regulates survival in northern yellowstone wolves *Canis lupus*. *Journal of Animal Ecology*, 83(6):1344–1356, 2014.

J. da Silva, D. W. Macdonald, and P. G. H. Evans. Net costs of group living in a solitary forager, the eurasian badger *Meles meles*. *Behavioral Ecology*, 5(2):151–158, 1994.

D. L. DeAngelis and W. M. Mooij. Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, 36:147–168, 2005.

C. A. Donnelly, R. Woodroffe, D. R. Cox, F. J. Bourne, C. L. Cheeseman, R. S. Clifton-Hadley, G. Wei, G. Gettinby, P. Gilks, and H Jenkins. Positive and negative effects of widespread badger culling on tuberculosis in cattle. *Nature*, 439(7078):843–846, 2006.

H. L. Dugdale, D. W. Macdonald, L. C. Pope, P. J. Johnson, and T. Burke. Reproductive skew and relatedness in social groups of european badgers, *Meles meles*. *Molecular Ecology*, 17(7):1815–1827, 2008.

H. L. Dugdale, S. A. Ellwood, and D. W. Macdonald. Alloparental behaviour and long-term costs of mothers tolerating other members of the group in a plurally breeding mammal. *Animal Behaviour*, 80 (4):721–735, 2010.

O. Duriez, S. A. Sæther, B. J. Ens, R. Choquet, R. Pradel, R. H. D. Lambeck, and M. Klaassen. Estimating survival and movements using both live and dead recoveries: a case study of oystercatchers confronted with habitat change. *Journal of Applied Ecology*, 46(1):144–153, 2009.

J. Eisenberg. *The social organisation of mammals*. Walter de Gruyter, 1983.

S. P. Ellner and M. Rees. Integral projection models for species with complex demography. *The American Naturalist*, 167(3):410–428, 2006.

S. T. Emlen and P. H. Wrege. Breeding biology of white-fronted bee-eaters at nakuru: the influence of helpers on breeder fitness. *The Journal of Animal Ecology*, 1(1):309–326, 1991.

S. Engen, Ø. Bakke, and A. Islam. Demographic and environmental stochasticity-concepts and definitions. *Biometrics*, 1:840–846, 1998.

R. J. Fell, C. D. Buesching, and D. W. Macdonald. The social integration of european badger *Meles meles* cubs into their natal group. *Behaviour*, 143(6):683–700, 2006.

R. D. Fernald and N. R. Hirata. The ontogeny of social behavior and body coloration in the african cichlid fish *Haplochromis burtoni*. *Zeitschrift fuer Tierpsychologie*, 50(2):180–187, 1979.

J. M. Fryxell, A. Mosser, A. R. E. Sinclair, and C. Packer. Group formation stabilizes predator–prey dynamics. *Nature*, 449(7165):1041–1043, 2007.

T. K. Fuller. Population dynamics of wolves in north-central minnesota. *Wildlife Monographs*, 1:3–41, 1989.

T. K. Fuller, L. D. Mech, and J. F. Cochrane. *Wolf population dynamics*. University of Chicago Press, 2003.

O. Gimenez, A. Viallefont, A. Charmantier, R. Pradel, E. Cam, C. R. Brown, M. D. Anderson, M. Bomberger Brown, R. Covas, and J. M. Gaillard. The risk of flawed inference in evolutionary studies when detectability is less than one. *The American Naturalist*, 172(3):441–448, 2008.

O. Gimenez, J. D. Lebreton, J. M. Gaillard, R. Choquet, and R. Pradel. Estimating demographic parameters using hidden process dynamic models. *Theoretical Population Biology*, 82(4):307–316, 2012.

V. Grimm. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling*, 115(2):129–148, 1999a.

V. Grimm. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling*, 115(2):129–148, 1999b.

J. A. Gude, M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D Mech, and R. R. Ream. Wolf population dynamics in the us northern rocky mountains are affected by recruitment and human-caused mortality. *The Journal of Wildlife Management*, 76(1):108–118, 2012.

M. Gusset and D. W. Macdonald. Group size effects in cooperatively breeding african wild dogs. *Animal Behaviour*, 79(2):425–428, 2010.

J. D. Hadfield. Package "masterbayes": Maximum likelihood and markov chain monte carlo methods for pedigree reconstruction, analysis and simulation. *Cran Project Viniette*, 2012.

A. J. Hall, B. J. McConnell, T. K. Rowles, A. Aguilar, A. Borrell, L. Schwacke, P. J. H. Reijnders, and R. S. Wells. Individual-based model framework to assess population consequences of polychlorinated biphenyl exposure in bottlenose dolphins. *Environmental Health Perspectives*, 114(1):60, 2006.

I. Hanski. Metapopulation dynamics. *Nature*, 396(6706):41–49, 1998.

I. Hanski. *Metapopulation ecology*. Oxford University Press, 1999.

F. H. Harrington, P. C. Paquet, J. Ryon, and J. C. Fentress. Monogamy in wolves: a review of the evidence. *Wolves of the world*, 1(1):209–222, 1982.

F. H. Harrington, L. D. Mech, and S. H. Fritts. Pack size and wolf pup survival: their relationship under varying ecological conditions. *Behavioral Ecology and Sociobiology*, 13(1):19–26, 1983.

R. Heinsohn and S. Legge. The cost of helping. *Trends in Ecology & Evolution*, 14(2):53 – 57, 1999.

S. J. Hodge, A. Manica, T. P. Flower, and T. H. Clutton-Brock. Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology*, 77(1):92–102, 2008.

A. Hurford, M. Hebblewhite, and M. A. Lewis. A spatially explicit model for an allee effect: why wolves recolonize so slowly in greater yellowstone. *Theoretical Population Biology*, 70(3):244–254, 2006.

M.D. Jimenez and S.A Becker. Northern rocky mountain wolf recovery program 2012 interagency annual report. Technical report, US Fish and Wildlife Services, 2012.

D. D. P. Johnson, W. Jetz, and D. W. Macdonald. Environmental correlates of badger social spacing across europe. *Journal of Biogeography*, 29(3):411–425, 2002.

O. R. Jones and J. Wang. Colony: a program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources*, 10(3):551–555, 2010.

Y. Kaneko, C. Newman, C. D. Buesching, and D. W. Macdonald. Variations in badger *Meles meles* sett microclimate: Differential cub survival between main and subsidiary setts, with implications for artificial sett construction. *International Journal of Ecology*, 2010, 2010.

K. Kilshaw, C. Newman, C. Buesching, J. Bunyan, and D. Macdonald. Coordinated latrine use by european badgers, *Meles meles*: potential consequences for territory defense. *Journal of Mammalogy*, 90(5):1188–1198, 2009.

J. A. King. The ecology of aggressive behavior. *Annual Review of Ecology and Systematics*, 1(1):117–138, 1973.

D. G. Kleiman and J. F. Eisenberg. Comparisons of canid and felid social systems from an evolutionary perspective. *Animal behaviour*, 21(4):637–659, 1973.

W. D. Koenig. Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *American Naturalist*, 1(1):421–443, 1981.

R. Kowalczyk, A. N. Bunevich, and B. Jędrzejewska. Badger density and distribution of setts in białowieża primeval forest (poland and belarus) compared to other eurasian populations. *Acta Theriologica*, 45(3): 395–408, 2000.

R. Kowalczyk, A. Zalewski, B. Jedrzejewska, and W. Jedrzejewski. Spatial organization and demography of badgers *Meles meles* in bialowieza primeval forest, poland, and the influence of earthworms on badger densities in europe. *Canadian Journal of Zoology*, 81(1):74–87, 2003.

C. J. Krebs. Demographic changes in fluctuating populations of microtus californicus. *Ecological Monographs*, 36(3):239–273, 1966.

H. Kruuk. Foraging and spatial organisation of the european badger, *Meles meles* l. *Behavioral Ecology and Sociobiology*, 4(1):75–89, 1978a.

H. Kruuk. Spatial organization and territorial behaviour of the european badger *Meles meles*. *Journal of Zoology*, 184(1):1–19, 1978b.

H. Kruuk. The social badger, ecology and behavior of a group-living carnivore *Meles meles*, 1989.

H. Kruuk and T. Parish. Factors affecting population density, group size and territory size of the european badger, *Meles meles*. *Journal of Zoology*, 196(1):31–39, 1982.

P. Kuss, M. Rees, H. H. Ægisdóttir, S. P. Ellner, and J. Stöcklin. Evolutionary demography of long-lived monocarpic perennials: a time-lagged integral projection model. *Journal of Ecology*, 96(4):821–832, 2008.

R. Lande. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, 1(1):911–927, 1993.

R. Lande, S. Engen, and B. E. Sæther. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *The American Naturalist*, 154(3):271–281, 1999.

J. D. Lebreton. Dynamical and statistical models for exploited populations. *Australian & New Zealand Journal of Statistics*, 47(1):49–63, 2005.

J. D. Lebreton and R. Pradel. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics*, 29(1-4):353–369, 2002.

J. D. Lebreton, K. P. Burnham, J. Clobert, and D. R. Anderson. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62(1): 67–118, 1992.

B. H. Letcher, J. A. Priddy, J. R. Walters, and L. B. Crowder. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. *Biological Conservation*, 86(1):1–14, 1998.

A. Leticia, P. Abbot, and A. D. Cutter. Population ecology, nonlinear dynamics, and social evolution. i. associations among non relatives. *The American Naturalist*, 159(2), 2002.

Martin Liermann and Ray Hilborn. Depensation: evidence, models and implications. *Fish and Fisheries*, 2 (1):33–58, 2001.

J. D. Ligon. Behavior and breeding biology of the red-cockaded woodpecker. *The Auk*, 1(1):255–278, 1970.

V. P. W. Lowe. Population dynamics of the red deer, *Cervus elaphus*, on rhum. *The Journal of Animal Ecology*, pages 425–457, 1969.

D. W. Macdonald. The ecology of carnivore social behaviour. *Nature*, 301(5899):379–384, 1983.

D. W. Macdonald and P. D. Moehlman. *Cooperation, altruism, and restraint in the reproduction of carnivores*. Springer, 1982.

D. W. Macdonald and C. Newman. Population dynamics of badgers *Meles meles* in oxfordshire, uk: numbers, density and cohort life histories, and a possible role of climate change in population growth. *Journal of Zoology*, 256(01):121–138, 2002.

D. W. Macdonald, C. Newman, J. Dean, C. D. Buesching, and P. J. Johnson. The distribution of eurasian badger, meles meles, setts in a high-density area: field observations contradict the sett dispersion hypothesis. *Oikos*, 106(2):295–307, 2004.

D. W. Macdonald, C. Newman, C. D. Buesching, and P. J. Johnson. Male-biased movement in a high-density population of the eurasian badger *Meles meles*. *Journal of Mammalogy*, 89(5):1077–1086, 2008.

D. W. Macdonald, C. Newman, P. Nouvellet, and C. D. Buesching. An analysis of eurasian badger *Meles meles* population dynamics: implications for regulatory mechanisms. *Journal of Mammalogy*, 90(6): 1392–1403, 2009.

D. W. Macdonald, C. Newman, C. D. Buesching, and P. Nouvellet. Are badgers 'under the weather'? direct and indirect impacts of climate variation on european badger *Meles meles* population dynamics. *Global Change Biology*, 16(11):2913–2922, 2010.

R. W. Mackereth and M. .. A/ Keenleyside. Breeding territoriality and pair formation in the convict cichlid. *Canadian Journal of Zoology*, 71(5):960–967, 1993.

D. R. MacNulty, D. W. Smith, L. D. Mech, J. A. Vucetich, and C. Packer. Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology*, 23(1):75–82, 2012.

M. H. MacRoberts and B. R. MacRoberts. Social organization and behavior of the acorn woodpecker in central coastal california. *Ornithological Monographs*, 1(21):iii–115, 1976.

J. R. Malcolm and K. Marten. Natural selection and the communal rearing of pups in african wild dogs *Lycaon pictus*. *Behavioral Ecology and Sociobiology*, 10(1):1–13, 1982.

J. Marino, C. Sillero-Zubiri, and D. W. Macdonald. Trends, dynamics and resilience of an ethiopian wolf population. *Animal Conservation*, 9(1):49–58, 2006.

J. Marino, C. Sillero-Zubiri, D. Gottelli, P. J. Johnson, and D. W. Macdonald. The fall and rise of ethiopian wolves: lessons for conservation of long-lived, social predators. *Animal Conservation*, 16(6):621–632, 2013.

G. W. McLaren, P. D. Thornton, C. Newman, C. D. Buesching, S. E. Baker, F. Mathews, and D. W. Macdonald. The use and assessment of ketamine–medetomidine–butorphanol combinations for field anaesthesia in wild european badgers *Meles meles*. *Veterinary Anaesthesia and Analgesia*, 32(6):367–372, 2005.

P. J. McLeod. Infanticide by female wolves. *Canadian journal of zoology*, 68(2):402–404, 1990.

L. D. Mech. *The wolf: Ecology and behaviour of an endangered species.* Doubleday. New York, 1970.

L. D. Mech. Buffer zones of territories of gray wolves as regions of intraspecific strife. *Journal of Mammalogy*, 75(1):199–202, 1994.

L. D. Mech. Leadership in wolf, *Canis lupus*, packs. *Canadian Field-Naturalist*, 114(2):259–263, 2000.

L. D. Mech and L. Boitani. *Wolves: behavior, ecology, and conservation*. University of Chicago Press Chicago, 2003.

L. D. Mech, S. H. Fritts, and D. Wagner. Minnesota wolf dispersal to wisconsin and michigan. *American Midland Naturalist*, 133:368–370, 1995.

m. C. Metz, D. W. Smith, J. A. Vucetich, D. R. Stahler, and R. O. Peterson. Seasonal patterns of predation for gray wolves in the multi-prey system of yellowstone national park. *Journal of Animal Ecology*, 81 (3):553–563, 2012.

M. D. Morecroft, M. E. Taylor, and H. R. Oliver. Air and soil microclimates of deciduous woodland compared to an open site. *Agricultural and Forest Meteorology*, 90(1):141–156, 1998.

A. Mosser and C. Packer. Group territoriality and the benefits of sociality in the african lion, *Panthera leo*. *Animal Behaviour*, 78(2):359–370, 2009.

A. Mosser, J. M. Fryxell, L. Eberly, and C. Packer. Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, 12(10):1050–1060, 2009.

R. L. Mumme. Do helpers increase reproductive success? *Behavioral Ecology and Sociobiology*, 31(5): 319–328, 1992.

A. Murie. *The wolves of Mount McKinley*, volume 5. US Government Printing Office, 1944.

D. L. Murray, D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyhan, and J. A. Valpha. Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biological Conservation*, 143(11):2514–2524, 2010.

C. Newman, Y. B. Zhou, C. D. Buesching, Y. Kaneko, and D. W. Macdonald. Contrasting sociality in two widespread, generalist, mustelid genera, *Meles* and *Martes*. *Mammal Study*, 36(4):169–188, 2011.

M. J. Noonan, A. Markham, C. Newman, N. Trigoni, C. D. Buesching, S. A. Ellwood, and D. W. Macdonald. Climate and the individual: inter-annual variation in the autumnal activity of the european badger *Meles meles*. *PLoS One*, 9(1), 2014.

P. Nouvellet, C. Newman, C. D. Buesching, and D. W. Macdonald. A multi-metric approach to investigate the effects of weather conditions on the demographic of a terrestrial mammal, the european badger *Meles meles*. *PLoS One*, 8(7), 2013.

T. D. Nudds. Convergence of group size strategies by mammalian social carnivores. *American Naturalist*, 112(987):957–960, 1978.

M. J. O'Riain, N. C. Bennett, P. N. M. Brotherton, G. McIlrath, and T. H. Clutton-Brock. Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats *Suricata suricatta*. *Behavioral Ecology and Sociobiology*, 48(6):471–477, 2000.

A. Ozgul, D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, 466(7305):482–485, 2010.

A. Ozgul, A. W. Bateman, S. English, T. Coulson, and T. H. Clutton-Brock. Linking body mass and group dynamics in an obligate cooperative breeder. *Journal of Animal Ecology*, 83(6):1357–1366, 2014.

C. Packer and A. E. Pusey. Male takeovers and female reproductive parameters: a simulation of oestrous synchrony in lions (panthera leo). *Animal Behaviour*, 31(2):334–340, 1983.

C. Packer and A. E. Pusey. The lack clutch in a communal breeder: lion litter size is a mixed evolutionarily stable strategy. *American Naturalist*, 145(5):833–841, 1995.

C. Packer, L. Herbst, A. E. Pusey, J. D. Bygott, J. P. Hanby, S. J. Cairns, and M. Borgerhoff Mulder. Reproductive success of lions. *Reproductive Success*, pages 363–383, 1988.

C. Packer, D. Scheel, and A. E. Pusey. Why lions form groups: food is not enough. *American Naturalist*, 136(1):1–19, 1990.

C. Packer, R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. E. Sinclair. Ecological change, group territoriality, and population dynamics in serengeti lions. *Science*, 307 (5708):390–393, 2005.

G. Péron. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *Journal of Animal Ecology*, 82(2):408–417, 2013.

R. Peterson. Wolf ecology and prey relationships on the isle royale. *US National Park Service Scientific Monographs*, 11:1–210, 1977.

R. O. Peterson, N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. Population limitation and the wolves of isle royale. *Journal of Mammalogy*, 79(3):828–841, 1998.

W. C. Pitt, P. W. Box, and F. F. Knowlton. An individual-based model of canid populations: modelling territoriality and social structure. *Ecological Modelling*, 166(1):109–121, 2003.

R. Pradel. Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics*, 61(2):442–447, 2005.

R. Pradel and A. Sanz-Aguilar. Modeling trap-awareness and related phenomena in capture-recapture studies. *PLoS One*, 7(3), 2012.

R. Pradel, O. Gimenez, and J. D. Lebreton. Principles and interest of gof tests for multistate capture-recapture models. *Animal Biodiversity and Conservation*, 28(2):189–204, 2005.

A. Purvis, J. L. Gittleman, G. Cowlishaw, and G. M. Mace. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B: Biological Sciences*, 267(1456):1947–1952, 2000.

R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2015.

E. Revilla and F. Palomares. Spatial organization, group living and ecological correlates in low-density populations of eurasian badgers, *Meles meles*. *Journal of Animal Ecology*, 71(3):497–512, 2002.

W. E. Ricker. Stock and recruitment. *Journal of the Fisheries Board of Canada*, 11(5):559–623, 1954.

M. L. Riedman. The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology*, 57(4):405–435, 1982.

W. J. Ripple and R. L. Beschta. Wolves, elk, willows, and trophic cascades in the upper gallatin range of southwestern montana, usa. *Forest Ecology and Management*, 200(1):161–181, 2004.

A. Rodríguez, R. Martín Franquelo, and M. Delibes. Space use and activity in a mediterranean population of badgers meles meles. *Acta Theriologica*, 41(1):59–72, 1996.

M. E. Roelke-Parker, L. Munson, C. Packer, R. Kock, S. Cleaveland, M. Carpenter, S. J. O'Brien, A. Pospischil, R. Hofmann-Lehmann, H. Lutz, G. L. M. Mwamengele, M. N. Mgasa, G. A. Machange, B. A. Summers, and M. J. G. Appe. A canine distemper virus epidemic in serengeti lions, *Panthera leo*. *Nature*, 379(6564):441–445, 1996.

L. M. Rogers, C. L. Cheeseman, P. J. Mallinson, and R. Clifton-Hadley. The demography of a high-density badger *Meles meles* population in the west of england. *Journal of Zoology*, 242(4):705–728, 1997.

J. P. Rood. Population dynamics and food habits of the banded mongoose. *African Journal of Ecology*, 13 (2):89–111, 1975.

J. P. Rood. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour*, 39(3):566–572, 1990.

B. E. Sæther. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution*, 12(4):143–149, 1997.

B. E. Sæther, S. Engen, and R. Lande. Density-dependence and optimal harvesting of fluctuating populations. *Oikos*, 76(1):40–46, 1996.

C. E. Sanderson, S. E. Jobbins, and K. A. Alexander. With allee effects, life for the social carnivore is complicated. *Population Ecology*, 56(2):417–425, 2014.

P. Savill, C. Perrins, K. Kirby, and N. Fisher. *Wytham Woods: Oxford's ecological laboratory*. Oxford University Press, 2010.

M. Schaub, J. D. Lebreton, et al. Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. *Animal Biodiversity and Conservation*, 27(1):73–85, 2004.

P. A. Schmidt and L. D. Mech. Wolf pack size and food acquisition. *The American Naturalist*, 150(4): 513–517, 1997.

M. D. F. Shirley, S. P. Rushton, G. C. Smith, A. B. South, and P. W. W. Lurz. Investigating the spatial dynamics of bovine tuberculosis in badger populations: evaluating an individual-based simulation model. *Ecological Modelling*, 167(1):139–157, 2003.

C. Sillero-Zubiri, A. A. King, and D. W. Macdonald. Rabies and mortality in ethiopian wolves (canis simensis). *Journal of Wildlife Diseases*, 32(1):80–86, 1996.

D. W. Smith, T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. Winter prey selection and estimation of wolf kill rates in yellowstone national park, 1995-2000. *Journal of Wildlife Management*, 68(1):153–166, 2004.

D. W. Smith, E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, and T. J. Meier. Survival of colonizing wolves in the northern rocky mountains of the united states, 1982–2004. *The Journal of Wildlife Management*, 74(4):620–634, 2010.

D. R. Stahler, D. R. MacNulty, R. K. Wayne, B. VonHoldt, and D. W. Smith. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. *Journal of Animal Ecology*, 82(1):222–234, 2013.

P. A. Stephens, W. J. Sutherland, and R. P. Freckleton. What is the allee effect? *Oikos*, pages 185–190, 1999.

P. D. Stewart and D. W. Macdonald. Badgers and badger fleas: Strategies and counter-strategies. *Ethology*, 109(9):751–764, 2003.

P. D. Stewart, L. Bonesi, and D. W. Macdonald. Individual differences in den maintenance effort in a communally dwelling mammal: the eurasian badger. *Animal Behaviour*, 57(1):153–161, 1999.

G. E. Svendsen. Behavioral and environmental factors in the spatial distribution and popualtion dynamics of a yellow-bellied marmot population. *Ecology*, 55(4):760–771, 1974.

M. Taborsky. Broodcare helpers in the cichlid fish lamprologus brichardi: their costs and benefits. *Animal Behaviour*, 32(4):1236–1252, 1984.

G. Tavecchia, J. Adrover, A. M. Navarro, and R. Pradel. Modelling mortality causes in longitudinal data in the presence of tag loss: application to raptor poisoning and electrocution. *Journal of Applied Ecology*, 49(1):297–305, 2012.

J. M. Thurber and R. O. Peterson. Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy*, 74(4):879–889, 1993.

N. Tinbergen. *The herring gull's world: a study of the social behaviour of birds.* Frederick A. Praeger, Inc., 1953.

L. W. Traill, S. Schindler, and T. Coulson. Demography, not inheritance, drives phenotypic change in hunted bighorn sheep. *Proceedings of the National Academy of Sciences*, 111(36):13223–13228, 2014.

S. Tuljapurkar, J. M. Gaillard, and T. Coulson. From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1523):1499–1509, 2009.

F. A. M. Tuyttens, R. J. Delahay, D. W. Macdonald, C. L. Cheeseman, B. Long, and C. A. Donnelly. Spatial perturbation caused by a badger *Meles meles* culling operation: implications for the function of territoriality and the control of bovine tuberculosis *Mycobacterium bovis*. *Journal of Animal Ecology*, 69 (5):815–828, 2000a.

F. A. M. Tuyttens, D. W. Macdonald, L. M. Rogers, C. L. Cheeseman, and A. W. Roddam. Comparative study on the consequences of culling badgers *Meles meles* on biometrics, population dynamics and movement. *Journal of Animal Ecology*, 69(4):567–580, 2000b.

U.S. Fish and Wildlife Service. Northern rocky mountain wolf recovery plan. Technical report, U.S. Fish and Wildlife Service, Denver, Colorado, 1987.

V. Van Ballenberghe. Extraterritorial movements and dispersal of wolves in southcentral alaska. *Journal of Mammalogy*, 64(1):168–171, 1983.

K. L. VanderWaal, A. Mosser, and C. Packer. Optimal group size, dispersal decisions and postdispersal relationships in female african lions. *Animal Behaviour*, 77(4):949–954, 2009.

B. M. Vonholdt, D. R. Stahler, E. E. Bangs, D. W. Smith, M. D. Jimenez, C. M. Mack, C. C. Niemeyer, J. P. Pollinger, and R. K. Wayne. A novel assessment of population structure and gene flow in grey wolf populations of the northern rocky mountains of the united states. *Molecular Ecology*, 19(20):4412–4427, 2010.

J. A. Vucetich, R. O. Peterson, and T. A. Waite. Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conservation Biology*, 11(4):957–965, 1997.

J. A. Vucetich, D. W. Smith, and D. R. Stahler. Influence of harvest, climate and wolf predation on yellowstone elk, 1961-2004. *Oikos*, 111(2):259–270, 2005.

J. R. Walters. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. *Annual Review of Ecology and Systematics*, 22:505–523, 1991.

J. R. Walters, P. D. Doerr, and J. H. Carter. The cooperative breeding system of the red-cockaded woodpecker. *Ethology*, 78(4):275–305, 1988.

S. K. Wasser and D. P. Barash. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Quarterly Review of Biology*, 58(4):513–538, 1983.

K. Whitman, A. M. Starfield, H. S. Quadling, and C. Packer. Sustainable trophy hunting of african lions. *Nature*, 428(6979):175–178, 2004.

B. D. Wisenden. Alloparental care in fishes. *Reviews in Fish Biology and Fisheries*, 9(1):45–70, 1999.

J. O. Wolff. Population regulation in mammals: An evolutionary perspective. *Journal of Animal Ecology*, 66(1):1–13, 1997.

R. Woodroffe. Demography of a recovering african wild dog *Lycaon pictus* population. *Journal of Mammalogy*, 92(2):305–315, 2011.

R. Woodroffe and D. W. Macdonald. Female/female competition in european badgers meles meles: effects on breeding success. *Journal of Animal Ecology*, 64(1):12–20, 1995.

R. Woodroffe, D. W. Macdonald, and J. Silva. Dispersal and philopatry in the european badger, meles meles. *Journal of Zoology*, 237(2):227–239, 1995.

A. J. Young and T. H. Clutton-Brock. Infanticide by subordinates influences reproductive sharing in co-operatively breeding meerkats. *Biology Letters*, 2(3):385–387, 2006.

E. Zimen. On the regulation of pack size in wolves. *Zeitschrift für Tierpsychologie*, 40(3):300–341, 1976.

Appendix A

Wolf Survival

A.1 Design matrices

$$Migration = \begin{array}{c} \\ Y \\ I \\ W \\ M \end{array} \begin{array}{c} \begin{array}{cccc} Y & I & W & M \end{array} \\ \begin{pmatrix} * & \phi^{Y,I} & \phi^{Y,W} & \phi^{Y,M} \\ \phi^{I,Y} & * & \phi^{I,W} & \phi^{I,M} \\ \phi^{Y,W} & \phi^{W,I} & * & \phi^{W,M} \\ \phi^{M,Y} & \phi^{M,I} & \phi^{M,W} & * \end{pmatrix} \end{array}$$

$$Survival = \begin{array}{c} \\ Y^{obs} \\ I^{obs} \\ W^{obs} \\ M^{obs} \\ I^{unobs} \\ M^{unobs} \end{array} \begin{array}{c} \begin{array}{cccccccccc} Y^{obs} & I^{obs} & W^{obs} & M^{obs} & I^{unobs} & M^{unobs} & \mu^Y & \mu^I & \mu^W & \mu^M \end{array} \\ \begin{pmatrix} \phi^Y & - & - & - & - & - & * & - & - & - \\ - & \phi^I & - & - & - & - & - & * & - & - \\ - & - & \phi^W & - & - & - & - & - & * & - \\ - & - & - & \phi^M & - & - & - & - & - & * \\ - & - & - & - & \phi^I & - & - & * & - & - \\ - & - & - & - & - & \phi^M & - & - & - & * \end{pmatrix} \end{array}$$

$$Mortality\ Source = \begin{array}{c} \\ \mu^Y \\ \mu^I \\ \mu^W \\ \mu^W \end{array} \begin{array}{c} \begin{array}{cccc} \mu_{gov} & \mu^Y & \mu^I & \mu^W & \mu^M \end{array} \\ \begin{pmatrix} * & \mu^Y & - & - & - \\ * & - & \mu^I & - & - \\ * & - & - & \mu^W & - \\ * & - & - & - & \mu^M \end{pmatrix} \end{array}$$

$$Recapture = \begin{array}{c} \\ Y \\ I^{obs} \\ W \\ M^{obs} \\ I^{unobs} \\ M^{unobs} \end{array} \begin{array}{c} \begin{array}{cccccc} Y & I^{obs} & W & M^{obs} & I^{unobs} & M^{unobs} \end{array} \\ \begin{pmatrix} 1 & - & - & - & - & - \\ - & P^I_{ons} & - & - & * & - \\ - & - & 1 & - & - & - \\ - & - & - & P^M_{ons} & - & * \\ - & P^I_{unobs} & - & - & * & - \\ - & - & - & P^M_{unobs} & - & * \end{pmatrix} \end{array}$$

$$Recovery\ /\ Recapture = \begin{array}{c} \\ Y \\ I^{obs} \\ W \\ M^{obs} \\ I^{unobs} \\ M^{unobs} \\ \mu^{control} \\ \mu^Y \\ \mu^I \\ \mu^W \\ \mu^W \end{array} \begin{array}{c} \begin{array}{ccccccccccc} NotSeen & Y & I^{obs} & W^{obs} & M & \mu^{control} & \mu^Y & \mu^I & \mu^W & \mu^M \end{array} \\ \begin{pmatrix} - & P^Y & - & - & - & - & - & - & - & - \\ - & - & 1 & - & - & - & - & - & - & - \\ - & - & - & P^W & - & - & - & - & - & - \\ - & - & - & - & 1 & - & - & - & - & - \\ 1 & - & - & - & - & - & - & - & - & - \\ 1 & - & - & - & - & - & - & - & - & - \\ - & - & - & - & - & 1 & - & - & - & - \\ * & - & - & - & - & - & \lambda^Y & - & - & - \\ * & - & - & - & - & - & - & \lambda^I & - & - \\ * & - & - & - & - & - & - & - & \lambda^W & - \\ * & - & - & - & - & - & - & - & - & \lambda^M \end{pmatrix} \end{array}$$

Variable	Symbol	Definition
Sex	S	[Male , Female]
Age	$A^{location}_{classes}$	Factor: Defined at 1st january. Age x years and 10 months
Capture Reason	C	[Representative , targeted] sample
Time intercept	I_t	Year [05, 06, 07, 08, 09], additive effect
Location	$L^{location}$	[Y, I, W, M], subscripted t if temporal variation
State	[O,U]	Observed and Unobserved at previous time step*
Migration	[F, T]	State of departure (from) and arrival state (to)

*Idaho and Montana only. Accounts for trap-dependence (See methods)

Table A1: Definition of variables and their associated code used in the AIC table.

Recapture			
	Est	LCI	UCI
Y	1.00	-	1.00
I^O	0.87	0.82	0.91
I^U	0.24	0.12	0.42
W	0.91	0.83	0.95
M^O	0.81	0.74	0.86
M^U	0.17	0.07	0.34
Recovery			
Y	0.65	0.54	0.74
I	0.64	0.52	0.74
W	0.46	0.34	0.58
M	0.61	0.46	0.74

Table A2: Recapture and Recovery rates in the 4 management areas.

Survival	Recapture	Recovery	Dev	AIC
$L_t^{Y,I,W,M}$+C+S+$A^W_{1,2,3^+}$	$L^{Y,I^O,I^U,W,M^O,M^U} + L_t^W$	$L^{Y,I,W,M} + I_t$	6027.2	6177.2
$L_t^{Y,I,W,M}$+C+S+$A^W_{1,2,3^+}$	L^{Y,I^O,I^U,W,M^O,M^U}	$L^{Y,I,W,M} + I_t$	6037.6	6179.6
$L_t^{Y,I,W,M}$+C+S+$A^W_{1,2,3^+}$	$L^{Y,I^O,I^U,W,M^O,M^U} + L_t^W$	$L^{Y,I,W,M} + L_t^Y$	6029.6	6179.6
$L_t^{Y,I,W,M}$+C+S+$A^W_{1,2,3^+}$	$L^{Y,I^O,I^U,W,M^O,M^U} + L_t^W$	$L^{Y,I,W,M}$	6034.0	6183.0
$L_t^{Y,I,W,M}$+C+S	L^{Y,I^O,I^U,W,M^O,M^U}	$L^{Y,I,W,M}$	6055.0	6187.0
$L_t^{Y,I,W,M}$+C	L^{Y,I^O,I^U,W,M^O,M^U}	$L^{Y,I,W,M}$	6060.5	6190.5
$L_t^{Y,I,W,M}$	L^{Y,I^O,I^U,W,M^O,M^U}	$L^{Y,I,W,M}$	6068.3	6196.3

Table A3: AIC table for the temporal variation in survival and cause specific mortality models, used to model correlations between survival rates and population growth.

Migration	Survival	Mortality Cause	Recapture	Recovery	ID Pars	QAIC (Δ QAIC) $\hat{c} = 1$	2
F:T	$L_t^{I+M,W} + L^Y + C + S + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	40	6157.0 (0)	3119.5 (0)
F:T	$L_t^{I,W} + L^{Y,M} + C + S + A^W_{1,2,3^+}$	$L^{Y,I,W,M}$	$L^Y + L_t^W + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M} + I_t$	50	6159.3 (2.3)	3130.6 (11.1)
F:T	$L_t^{I+M,W} + L^Y + C + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,I} + L^{[W,M]^{[O,U]}}$	$L^{Y,I,W,M}$	39	6159.7 (2.7)	3119.9 (0.4)
F:T	$L_t^{I,W} + L^{Y,M} + C + S + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	41	6160.6 (3.6)	3123.3(3.8)
F:T	$L_t^{I,W} + L^{Y,M} + C + S + A^W_{1,2,3^+}$	$L^{Y,I,W,M} + L_t^M$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	46	6160.7 (3.7)	3127.4 (7.9)
F:T	$L_t^{I,W} + L^{Y,M} + C + S + A^W_{1,2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}} + L_t^I$	$L^{W,I,Y,M}$	46	6160.8 (3.8)	3127.4 (8)
F:T	$L_t^{I,W} + L^{Y,M} + C + S + A^W_{1,2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M} + I_t$	46	6160.9 (3.9)	3127.5 (4)
F:T	$L_t^{I,W} + L^{Y,M} + C + S + A^W_{1,2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	42	6160.9 (3.9)	3123.5 (2)
F:T	$L_t^{I,W} + L^{Y,M} + C + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	40	6161.3 (4.3)	3121.7 (2.2)
F:T	$L_t^{I+M,W} + L^{Y,I,M} + C + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	40	6161.3 (4.3)	3121.7 (2.2)
F:T	$L_t^{I+M,W} + L^{Y,I,M} + C + S + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	42	6162.2 (5.2)	3125.1 (5.6)
F:T	$L_t^{I,W} + L^{Y,M} + C + A^W_{1,2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	41	6163.1 (6.1)	3123.5 (4)
F:T	$L_t^{I,W} + L^{Y,M} + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	39	6167.8 (10.8)	3121.8 (2.3)
F	$L_t^{I,W} + L^{Y,M}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	38	6173.2 (16.2)	3124.6 (5.1)
F:T	$L_t^{I,W} + L^{Y,M} + C + S + A^W_{1,2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	37	6178.6 (21.6)	3127.3 (7.8)
F:T	$L_t^{I+M,W} + L^Y + A^W_{1:2,3^+}$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	38	6166.2(9.2)	3122.1 (2.6)
F:T	$L_t^{I+M,W} + L^Y + C$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	38	6165.2 (8.2)	3120.6 (1.1)
F:T	$L_t^{I+M,W} + L^Y$	$L^{Y,I,W,M}$	$L^{Y,W} + L^{[I,M]^{[O,U]}}$	$L^{W,I,Y,M}$	37	6171.6 (14.6	3122.8 (3.3)

Table A4: AIC and associated AIC weights for a set of best fit models.

Appendix B

Badgers

B.1 Statistical Analysis

Social group and Year were fitted as random effects. Likelihood ratio tests were used to compare significance of variables using the 'drop1' function in R. The significance tables of the maximal and minimum adequate models, using a chi-squared test are given below.

B.2 Comparison with Mark-Recapture Results

Mark-recapture models were fit using the program E-Surge accounting for trap-awareness effects [Pradel and Sanz-Aguilar, 2012, Choquet et al., 2009]. Interactions between continuous variables cannot be fitted using E-Surge so the reported rates below are for a reduced version of the model reported in Table B.2.1. Model selection was performed on recapture rates but is not reported here. The mark-recapture analysis was restricted to individuals first caught as cubs as models including additional age classes were computationally very slow.

B.3 Parameter Values

Variable	ID	Details
Body Mass	M	Measured in grams
Body Length	L	Measured in centimetres
Body Condition	BC	Mass per unit Length measured in gcm^{-1}
Sex	S	Male / Female
Age Class	A	[0, 1-9, 10^{+}] measured in Years
Group Size	G	Number of individuals in the social group
Population Size	P	Number of individuals in the population
Inter-group competition	(P-G)	Number of individuals in other social groups
Recruited at t-1	R_{t-1}	Indicating an individual reproduced the previous year
Average Parental Mass	$\bar{M}^{Parental}$	Mean parental mass the year prior to birth
Average Parental Length	$\bar{L}^{Parental}$	Mean parental length the year prior to birth
Cub Sex	S_{cub}	Offspring sex used in inheritance analysis

Table B.1.1: Variables and their ID used in the AIC_c tables.

Function (Error Structure)	Variable	Degrees of Freedom	LRT	$P(> Chi)$
Development Weight (Gaussian)	SG	1	0.4	0.54
	SG^2	1	2.7	0.09
	M	1	266.3	$< 2e^{-}16$
	R_{t-1}	1	1.22	0.27
	S	1	164.5	$< 2e^{-16}$
	IC:A	2	16.0	$3.4e^{-4}$
	L	1	439.7	$< 2e^{-16}$
Development Length (Gaussian)	SG	1	3.5	0.06
	SG^2	1	5.2	0.02
	R_{t-1}	1	2.9	0.09
	S	1	183.3	$< 2e^{-16}$
	IC:A	2	10.3	0.01
	M^{parent}	1	0.6	0.06
Inheritance Weight (Gaussian)	SG	1	0.4	0.02
	SG^2	1	0.0	0.9
	IC	1	0.2	0.7
	S^{Cub}	1	1.2	0.3
	L^{parent}	1	0.7	0.4
Inheritance Length (Gaussian)	SG	1	0.0	1.0
	SG^2	1	0.3	0.6
	IC	1	0.1	0.8
	S^{Cub}	1	0.4	0.5
Movement (Binomial)	SG	1	3.3	0.1
	SG^2	1	3.0	0.1
	BC	1	1.1	0.3
	R_{t-1}	1	2.8	0.1
	S	1	1.0	0.3
	IC:A	2	1.5	0.5
Survival (Binomial)	BC	1	0.2	0.7
	R_{t-1}	1	1.9	0.2
	S	1	11.5	$6.9e^{-4}$
	SG:A	2	11.6	$3.0e^{-3}$
	SG^2:A	2	9.8	$7.2e^{-3}$
	IC:A	2	0.5	0.8
	IC:SG	2	14.5	$1.4e^{-4}$
Recruitment(Binomial)	SG	1	0.8	0.4
	SG^2	1	1.1	0.3
	BC	1	17.0	$3.7e^{-5}$
	R_{t-1}	1	23.6	$1.2e^{-6}$
	A	2	34.9	$2.6e^{-6}$
	IC	1	6.7	$9.5e^{-3}$

Table B.1.2: Likelihood ratio tests for the maximal models fitted for each demographic rate

Function (Error Structure)	Variable	Degrees of Freedom	LRT	$P(> Chi)$
Development Weight (Gaussian)	M	1	268.1	$< 2e^{-}16$
	S	1	165.1	$< 2e^{-}16$
	SG	1	11.5	$6.9e^{-4}$
	IC:A	2	15.6	$4.1e^{-4}$
Development Length (Gaussian)	L	1	448.0	$< 2e^{-16}$
	S	1	179.3	$< 2e^{-16}$
	IC:A	2	11.2	$3e^{-3}$
Inheritance Weight (Gaussian)	M^{parent}	1	0.3	0.6
	SG	1	6.8	$09.3e^{-3}$
Inheritance Weight (Gaussian)	L^{parent}	1	1.1	0.3
Movement (Binomial)	BC	1	0.5	0.5
	IC	1	4.3	$4.8e^{-3}$
	A	2	11.8	$2.8e^{-3}$
	BC	1	0.2	0.7
Survival (Binomial)	S	1	11.8	$5.9e^{-}4$
	SG:A	2	11.3	$3.0e^{-}3$
	SG^2:A	2	9.5	$8.5e^{-}3$
	IC:SG	1	14.6	$3.0e^{-}5$
	BC	1	17.4	$3.0e^{-}5$
	R_{t-1}	1	23.7	$1.1e^{-}6$
Recruitment(Binomial)	A	1	35.9	$1.6e^{-}8$
	IC	2	7.8	$5.2e^{-}3$

Table B.1.3: Likelihood ratio tests for the minimum adequate models fitted for each demographic rate

Parameter	MR Estimate	MR-Lower 95% CI	MR-Upper 95% CI	GLMM Estimate
Intercept	0.98	0.81	1.16	1.00 (Scaled up)
Body Condition	0.09	-0.00	0.18	0.01
Adult	0.69	0.47	0.89	0.41
Old Adult	-0.81	-1.15	-0.47	-1.02
Group Size	1.83	1.54	2.12	0.81
Group Size^2	-1.47	-1.77	-1.17	0.15
Inter-Group Competition	-0.12	-0.22	-0.02	-0.15
Male	-0.01	-0.20	0.20	-0.27

Table B.2.1: Comparisons of survival analysis estimates under a mark-recapture and GLMM framework

Function	Variable	Coefficient	Standard Error
	Intercept	0.67	0.19
	Body Condition	-0.003	0.04
	Male	-0.26	0.08
	Adult	0.42	0.09
	Old Adult	-1.03	0.20
	Intercept	-4.00	0.39
Survival	Body Condition	0.75	0.19
	Recruited t-1	1.42	0.29
Fecundity	Adult	1.52	0.30
	Old Adult	0.39	0.49
	Population Size	-0.59	0.22
	Intercept	-2.77	0.20
	Body Condition	0.07	0.11
Movement	Adult	0.60	0.18
	Old Adult	0.15	0.37
	Intercept	620.58	13.07
	Population Size	-24.64	7.63
Development	Adult	-56.34	7.70
Body	Old Adult	-120.43	13.95
Mass	Weight	0.28	0.02
	Male	54.78	4.25
	Population Size:Adult	25.83	5.82
	Population Size:Old Adult	11.08	19.55
	Intercept	513.1	7.78
	Length	0.29	0.01
Development	Population Size	-7.63	1.93
Body	Adult	-27.28	2.42
Length	Old Adult	-32.84	4.44
	Male	18.18	1.32
	Population Size:Adult	5.81	1.80
	Population Size:Old Adult	8.21	6.15
Inheritance	Intercept	201.5	73.9
Body Mass	Average Parent Mass	0.15	0.08
Inheritance	Intercept	375.8	134
Body Length	Average Parent Length	0.19	0.17
Random Effects Standard Deviations and Elasticities			
Function	Social Group	Year	Residuals (LMER only)
Survival	0.68	0.53	-
Fecundity	0.37	1.13	-
Inheritance Mass	25.10	18.32	62.56
Inheritance Length	12.48	14.69	39.43
Development Mass	37.38	31.80	88.19
Development Length	10.62	5.94	27.76
Movement	0.55	0.42	-

Table B.3.1: Parameters used in the population regulation individuals based model.

Appendix C

Lions

C.1 Statistical Analysis

Variable	ID	Definition
Age	A	Age in years fitted as a linear and quadratic term
Population Density	P	Number of Adult females in the habitat
Neighbourhood Density	N	Number of Adult females in the neighbourhood
Distemper	D	Binary variable indicating whether a distemper outbreak occurred
Group Size	G	Number of adult females in the pride
Residency	R	Binary variable indicating whether a pride has residency status
Post-Dispersal Relationship Status	$W_5^{res/non}$	Binary variable indicating whether a pride is in the same neighbourhood and within 5 years of dispersing from the resident or non-resident (floater) pride
Takeover	T	Binary Variable indicating whether a male takeover event occurred
Ecological Change	$Y_{(t_i:t_j)}$	A factor denoting a change in intercept in years i to j

Table C.1.1: Variables used in the statistical analysis and their identification code used in the AIC tables

Model	Function	Model	n_{fixed}	AIC_c	ΔAIC_c
Plains	Cub Survival	$Y_{97:14} + D + G + G^2 + P + N + R + T + W_5^{res} + W_5^{non}$	11	1115.4	6.28
		$Y_{97:14} + D + G + G^2 + P + N + R + T + W_5^{non}$	10	1113.4	4.27
		$Y_{97:14} + D + G + G^2 + P + N + R + T$	9	1112.1	2.93
		$Y_{97:14} + D + G + P + N + R + T$	8	1110.0	0.80
		$Y_{97:14} + D + G + P + N + R$	7	1109.4	0.27
	Adult Survival	$Y_{97:14} + D + G + G^2 + P + N + R + T + W_5^{res} + W_5^{non} + A + A^2$	13	2257.5	3.95
		$Y_{97:14} + D + G + P + N + R + T + W_5^{res} + W_5^{non} + A + A^2$	12	2255.5	1.97
		$D + G + P + N + R + T + W_5^{res} + W_5^{non} + A + A^2$	11	2254.0	0.44
		$D + P + N + R + T + W_5^{res} + W_5^{non} + A + A^2$	10	2253.5	0.00
		$D + N + R + T + W_5^{res} + W_5^{non} + A + A^2$	9	2254.8	1.27
	Recruitment	$Y_{97:14} + D + G + G^2 + P + N + R + T + W_5^{res} + W_5^{non} + A + A^2$	12	2378.8	7.37
		$Y_{97:14} + D + G + G^2 + R + T + W_5^{res} + W_5^{non} + A + A^2$	11	2376.9	5.43
		$Y_{97:14} + G + G^2 + R + T + W_5^{res} + W_5^{non} + A + A^2$	10	2375.8	4.42
		$Y_{97:14} + G + R + T + W_5^{res} + W_5^{non} + A + A^2$	9	2375.1	3.66
		$Y_{97:14} + R + T + W_5^{res} + W_5^{non} + A + A^2$	8	2373.1	1.68
		$R + T + W_5^{res} + W_5^{non} + A + A^2$	7	2372.3	0.84
	Dispersal	$Y_{97:14} + D + G + P + R + T + W_5^{res} + W_5^{non} + A + A^2$	11	851.4	9.67
		$Y_{97:14} + D + G + P + R + T + W_5^{res} + A + A^2$	10	849.8	8.07
		$Y_{97:14}G + P + R + T + W_5^{res} + A + A^2$	9	849.3	7.52
		$Y_{97:14}G + P + R + T + A + A^2$	8	847.5	5.80
		$Y_{97:14}G + P + T + A + A^2$	7	845.9	4.13
		$Y_{97:14}G + P + A + A^2$	6	844.3	2.61
		$Y_{97:14}G + A + A^2$	5	843.5	1.74
		$G + A + A^2$	4	841.7	0.00

Table C.1.2: AICc values for residency model.