Modelling sociality in carnivores

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Thesis submitted to the School of Natural and Environmental Sciences
in fulfilment for the requirements of the degree of Doctor of Philosophy
Newcastle University

July 2020

Abstract

Many theories have been put forward as potential explanations for social behaviour in carnivores, yet there is little consensus as to the factors that drive the formation of groups and social behaviours. Traditionally two selection pressures have been postulated to explain why animals are social; the exploitation of resources and avoidance of predation. Much of the work investigating sociality has focussed on single factors to explain group formation. However, many of these factors such as life history, diet, predation risk, and habitat use are confounded, operating at different temporal and spatial scales but interacting nonetheless. Thus it is important to investigate sociality in the context of multiple factors to understand how their complexity may influence social behaviours. This work investigates factors affecting sociality across narrowing scales to test hypotheses of the factors driving the formation of social groups and the resulting social behaviours. Topic modelling of descriptive data was used to understand behavioural similarities between species. Formalising the hypotheses of sociality as models and testing them with quantitative data demonstrated the relative importance of life history and environmental factors on the formation of social groups in different species. At a population level this interaction between the group and their environment is demonstrated to influence the demography of the group in a socially plastic species. Within populations individual based models show support for the hypothesis that the formation of social groupings is driven by energetic demands. Understanding the conditions that favour sociality within a species or population beyond predation and resource exploitation could prove useful for informing the management and conservation of carnivores, many of which are under threat. This thesis has evidenced, through multiple modelling approaches, the importance of integrating life history data and environmental information when considering the conditions under which social behaviours are exhibited.

Acknowledgements

First and foremost I would like to thank my supervisors, Steve, Aileen and Pete for all of their help and guidance throughout my time at Newcastle. Particular thanks to Aileen and Steve, without whom I wouldn't have even attempted postgraduate study, thank you for all of your support and encouragement, for always believing in me, and for all the cake. I feel very lucky to have had supervisors as kind and caring as you. Thanks to Pete for putting me in touch with the team at Woodchester and to Andy and Dez for allowing me access to the data that their team has collected and to observe the cuteness of the badger cubs and the hard work that goes into collecting such rich data.

Thanks to all of the MEPers for being such a lovely group of people to work with, thanks to Carys and Andy for the cups of tea and the twirls. Thanks to Louise for the topic modelling expertise, to Kirsty and to Zarah for all the corridor conversations, to my R ladies, Rike and Laura thank you for your friendship and for always being willing to get together eat pizza and say hello to every dog we encounter.

Thank you to Alanna and Sarah for being great friends, for the writing sessions, and for providing perspective when I needed it most. Thanks to my family for all of their support, to my mum who has more confidence in me than I ever will and whose constant support and encouragement has helped me to become the person that I am today. Last but by no means least to Stu, thank you for putting up with me and for all that you do to make life better. I am eternally grateful for your love and support and I'm already looking forward to our next great adventure.

Declaration

Data used in Chapter 4 were provided by Dr Andrew Robertson and Dr Richard Delahay, collected by the team involved in the Woodchester Park long term monitoring programme.

All other work was done by Jessica Kate Rowntree Ward.

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Chapter 1

Introduction

1.1 The order Carnivora

The order Carnivora is the fifth largest extant mammalian order, comprising thirteen terrestrial and three marine Families. Species in the order Carnivora (henceforth reffered to throughout this thesis as carnivores) are spread across every continent and members of the 245 species of terrestrial carnivores can be found in every major habitat on earth (Hunter & Barrett, 2018). Descended from the Miacids, a group of small civet-like mammals whose fossils date back to the Upper Eocene (approximately 50 million years ago), the divergence across the order has given rise to species with a wide variety of life histories. From the Least weasel (*Mustela nivalis*) weighing as little as $25g$, to the Polar bear (*Ursus maritimus*) weighing in excess of $650kg$. From the hypercarnivorus Caracal (*Caracal caracal*) to the completely herbivorous Giant panda (*Ailuropoda melanoluca*), the diversity of present-day species encompasses animals of greatly varying shapes and sizes all exhibiting a myriad of different behaviours.

The Miacids were thought to be mostly arboreal and present-day arboreal carnivores have retained the adaptations such as small body size and slim bones that favour their tree dwelling lifestyle (Eisenberg, 1989; Taylor, 1989). Only a few species, however, have retained this arboreal lifestyle. Many carnivores are cursorial species, such as the Cheetah (*Acionyx jubatus*) which have developed skeletal adaptations that maximize limb acceleration for high speed running (Taylor, 1989). Other carnivore species such as the Raccoon (*Procyon lotor*), have largely given up on predation and rarely use a gait faster than a walk (Thweatt & Hammond, 2010). Present-day carnivores can be separated into two major suborders (Caniforma and Feliforma) representing a divergence estimated around 45-50 million years ago (Fig.1.1). Whilst most feliform families originated in the Old World, and have primarily remained in the tropics, caniforms have spread further through the northern temperate regions and show a greater tendency towards omnivory than their feliform cousins (Pedersen et al., 2014).

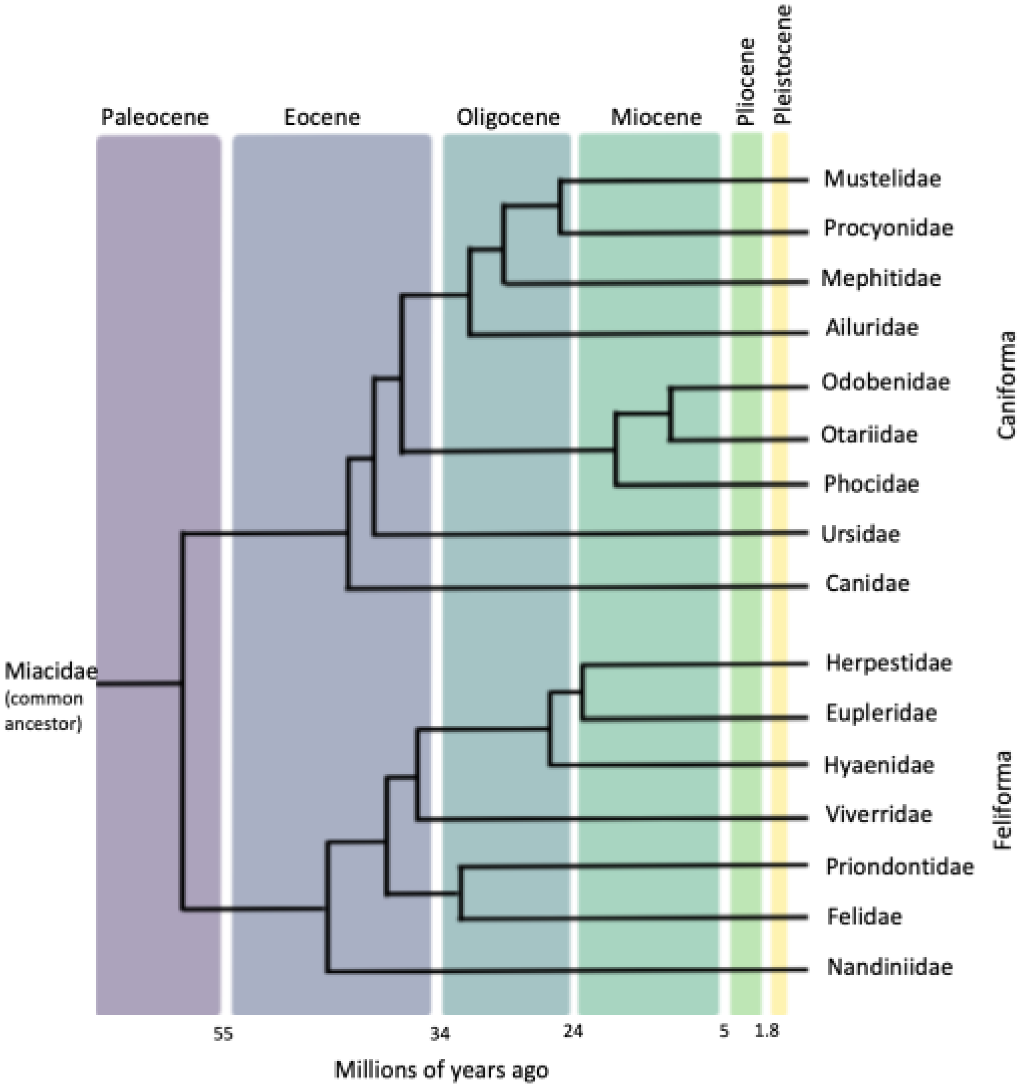

Figure 1.1: Phylogeny of Carnivora showing family level carnivores descended from Miacids. Reproduced from Hunter and Barrett (2018)

Despite these omnivorous adaptations, the characteristic condition of carnivores is the adaptation of the scissor like carnassials, giving rise to the name Carnivora which translates as "flesh eaters". Having evolved from premolars and mesial molars the purpose of the carnassials is to shear flesh. However, the high rates of evolution in teeth and the varied diets that species have developed has led to a great array of dental morphologies amongst present day carnivores (Fig. 1.2) (Brocklehurst & Benevento, 2020).

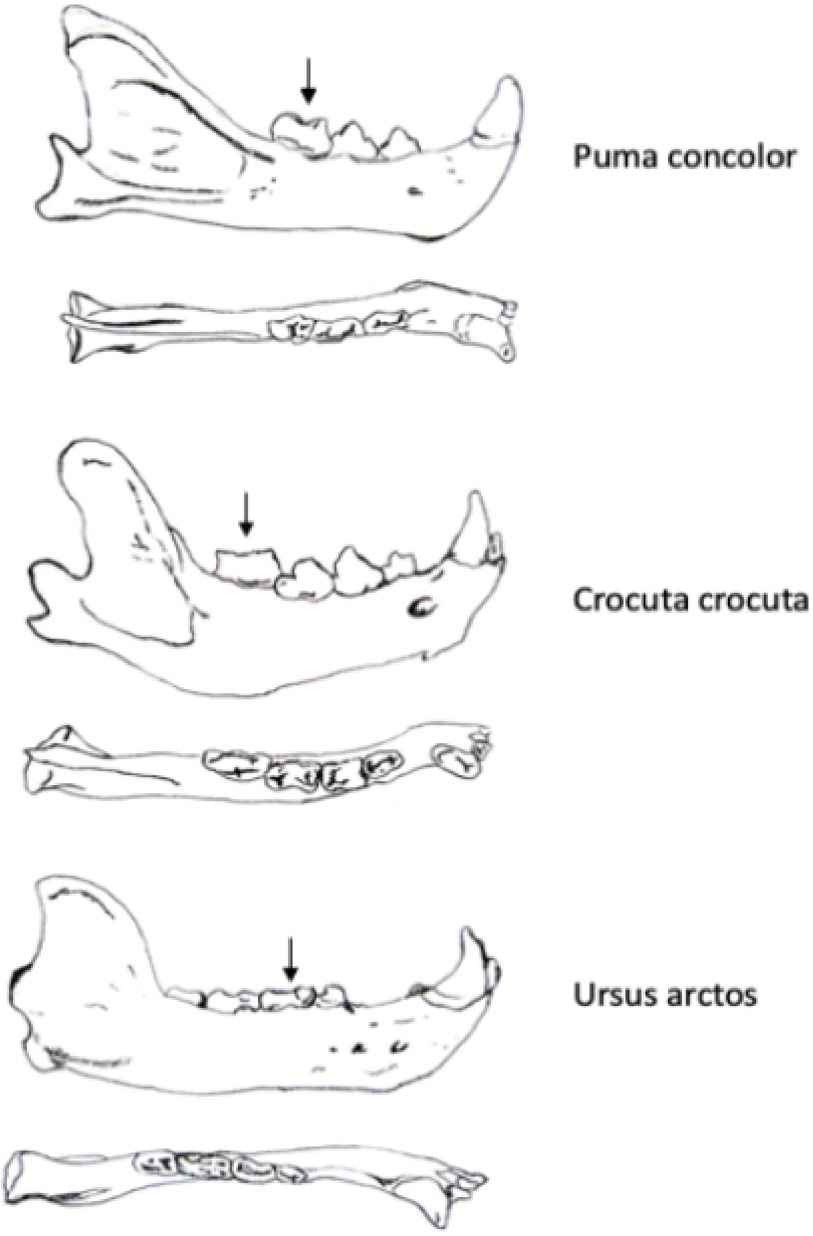

Figure 1.2: Dental diversity among carnivores. Right mandibles of a meat specialist (puma); a meat/bone eater (spotted hyaena) and an omnivore (brown bear) with carnassial teeth indicated by the arrows. All drawn to the same anterioposterior length, drawn from Van Valkenberg (1989).

The versatility in their dentition that led to the evolution of divergent dental patterns and diets, is thought to contribute to the present success of the group, with species adapting to exploit the environments in which they have found themselves (Asahara et al., 2016; Van

Valkenburgh, 1989). This ability to adapt, particularly to human modified environments may also contribute to the intense conflict and persecution that many species now face at the hands of humans (Boitani & Powell, 2012).

1.2 Carnivore status

Within mammalian research the order Carnivora dominates the literature whilst carnivores are among the most threatened group of mammalian species (Brooke et al., 2014; Treves & Karanth, 2003). Over a quarter of carnivore species populations are currently in decline with species thus being classified by the International Union for the Conservation of Nature (IUCN) as Vulnerable (43), Endangered (31), or Critically Endangered (4) (van de Kerk et al., 2013). The species that are at greatest risk are not confined to a single Family of similar individuals, but include the Malabar civet (*Viverra civettina*), Red wolf (*Canis rufus*), European mink (*Mustela lutreola*) and the Pygmy raccoon (*Procyon pygmaeus*), suggesting that species declines are not limited by life history or geography. The conservation of carnivores is crucial for the maintenance of biodiversity as carnivores play important roles in regulating ecosystems (Ripple & Beschta, 2004; Wolf & Ripple, 2016). Through intra-specific competition carnivores can regulate the density of other carnivore species (Linnell & Strand, 2000). Carnivores typically occupy the highest trophic niche in a habitat and thus the impacts they have through predation can cascade through ecosystems, making them pivotal to maintaining biodiversity (Karanth et al., 2017; Ripple et al., 2014; Treves & Karanth, 2003; van de Kerk et al., 2013).

Predators typically require more space than herbivores to maintain their populations (Terborgh, 2015). This is particularly true of large carnivore species, 60% of which have lost more than half of their historic range (Wolf & Ripple, 2018). Coupled with the increasing human population, species are increasingly having to share space with human populations (Pereira et al., 2012). Human encroachment often leads to habitat loss as landscapes are modified to suit human needs, and these modifications threaten biodiversity beyond the order Carnivora (Farris et al., 2015; Western, 2001). For carnivores, several life history characteristics can however exacerbate the difficulties of species having to coexist with humans. Many carnivores are hunters, eating meat to sustain themselves, a trait which is often exhibited by human populations as well. Where human habitation encroaches on the territory of a carnivore, the depletion of prey by humans can negatively impact the potential survival of carnivores through indirect competition (Henschel et al., 2011; Miller et al., 2014). Due to their nature as hunters, carnivores are prone to attacking livestock and people where they encounter them (Barlow et al., 2013; Boitani & Powell, 2012; van de Kerk et al., 2013). The response of humans to such attacks often ends in the killing of individual predators in retaliation which can have significant negative impacts for populations (Swanepoel et al., 2011; Woodroffe & Frank, 2005). Many carnivores exist at low population densities (Pedersen et al., 2017), with individuals often being slow to grow, where a population experiences declines resulting from direct or indirect conflicts their ability to recover can be severely limited (Jetz et al., 2004; Manlik, 2019).

Carnivores evolved as meat eaters, a lifestyle that necessitates the ability to catch and kill prey items. Such behaviours can become problematic for the coexistence of carnivores, not just with humans but with numerous other species. Coyotes (*Canis latrans*) for example are aggressive predators that are known to kill foxes and bobcats (*Felix rufus*), and their use of human modified landscapes has resulted in attacks on humans and contributed to the popular belief that they are a pest species across much of their range (Draheim et al., 2019; Fedriani et al., 2000). Where species such as this have evolved in order to be efficient hunters, interactions between any individuals have the potential to become antagonistic. For carnivores another animal is a potential prey item, potential competitor, or a potential mate. Carnivory may therefore appear antipathetic to sociality, yet amongst several species, including coyotes, social behaviours have been observed. Understanding why some species risk associating with other conspecifics could allow us to understand how better to protect carnivores and conserve populations of these highly threatened species.

1.3 Sociality

The word social is commonplace in our vernacular and yet its definition is often vague. Amongst the extensive entries under its definition by the OED there is variation in how the word pertains to the description of animal groups (Oxford English Dictionary, 2020). Sociality is often broadly defined as cooperative group living, comprising a set of organisms that remain together for a period of time (Mason & Shan, 2017; Rubenstein & Abbot, 2017). More specifically, it has been suggested that social interactions include cohesive behaviours (Armitage, 1981). At their most complex, social systems have been defined as those in which individuals frequently interact in different contexts, with different individuals, and often repeatedly interact with many of the same individuals in networks over time (Dröscher & Kappeler, 2013). The most advanced groups are thought to be those that include overlapping generations, cooperative care of young and reproductive division of labour (Rubenstein & Abbot, 2017).

From early work investigating animal societies Espinas (2015) explored the idea that societies were highly structured relationships among individuals of a species, the variation in which he interpreted as expressions of direct adaptation to ecology rather than phylogenetic descent (Standen & Foley, 1989). Sociality and the perceived advanced behaviours associated with it, has been suggested to increase cognitive demands on individuals and impart a selective pressure for increased encephalisation among social animals (Finarelli & Flynn, 2009). Built upon a principle of comparative neurology that behavioural specialisation corresponds to an increase in neural processing and a complimentary expansion of neural tissue devoted to that specialisation (Arsznov & Sakai, 2013). If sociality imposes cognitive demands it would be expected that changes in relative brain size with sociality would be coupled over evolutionary time (Pérez-Barbería et al., 2007). Amongst the order Carnivora, however, there seems to be limited evidence supporting this theory. Although an association between increased encephalisation and highly social behaviours has been found amongst canids it cannot be generalised across the whole order (Finarelli & Flynn, 2009), and such measurements do have constraints (Healy & Rowe, 2007).

Such a 'social brain' might not be necessary for species to act socially, but when group formation is favoured the size and structure of the group can have diverse effects on the morphology, behaviour and fitness consequences of individuals (Silk, 2007a; Wey et al., 2008). In primates, for example, the sex ratio within a social group can impact the extent of size related sexual dimorphism (Clutton-Brock et al., 1977). The structure of a group and the relationships that individuals form play an important role in the acquisition of dominance rank and associated behaviours (Johnson, 1987), and group size can impact breeding success, particularly in mammals whose young are reared by 'helpers' in the group (Clutton-Brock et al., 2001c). The behaviours resulting from such social associations are often studied in respect to the costs and benefits to individuals. Amongst carnivores where the costs of acting socially includes the potential that a conspecific could kill you there must be great benefit to adapting to such a lifestyle for it to have evolved in so many species.

1.4 Fitness

Fitness is an important evolutionary concept used as a mechanism to explain persistent behaviours. Individuals are thought to act in ways that enhance their fitness, with natural selection favouring the survival of the fittest. Fitter individuals are often defined as those individuals that not only maximise their offspring but those whose offspring themselves survive to become reproductive adults (Armitage, 1987). Sociality for example is only thought to persist where the benefits outweigh the costs and thus an individual's fitness is increased (Gittleman, 1989a). The individual fitness gain from acting socially is not always clear, particularly where social individuals within a group forfeit their chances of reproducing. The concept of inclusive fitness arose, describing the outcomes of an individual that detract from its own reproductive success while enhancing the reproductive success of others (Costa, 2013). The term inclusive fitness was first put forward by Hamilton (1964) who suggested that social behaviours will only be favoured by natural selection if

$$rb > c \tag{1.1}$$

where r denotes the coefficient of relatedness between the recipient (of a given behaviour) and the donor, b is the benefit conferred by the trait or behaviour and c is the cost to the individual exhibiting the trait (Hamilton, 1964). It is not always the case, however, that individuals within a social group are related. In such cases, where sociality persists it may reflect a trade-off between current fitness benefits, and costs that emerge from individual's decisions to join or leave groups (Ebensperger et al., 2012).

The costs and benefits to an individual's fitness are greatly impacted by the behaviours that individuals or groups exhibit. Fitness is the currency by which the outcomes of behaviours are assessed. When social behaviours are investigated the (fitness) costs and benefits are assessed as a means of understanding the persistence and evolution of that behaviour. Typically, where sociality is studied the fitness benefits that are thought to have contributed to the persistence of sociality include behaviours pertaining to the acquisition of food, defence against predation, the defence of resources and the rearing of young. Understanding the context in which these behaviours are impacted by social grouping can help in determining the conditions under which sociality occurs within the order Carnivora.

1.5 Social foraging and hunting

Behaviours relating to food acquisition are well documented and social foraging has been studied in many species from ants to humans (Bailey et al., 2013; Carbone et al., 2005; Clark & Mangel, 1986; Holekamp et al., 1997; Lamprecht, 1981; Lührs & Dammhahn, 2010; Sand et al., 2006; Stander, 1992; Wallace et al., 2002). Where food resources are clumped and animals forage in groups the food discoveries of a few can be of great benefit to the entire group (Giraldeau, 1984). As well as having the potential to increase feeding rates and survival probabilities, group foraging may be important in facilitating knowledge transfer between individuals, thus enhancing survival (Clark & Mangel, 1986; Giraldeau, 1984). There may however be costs to group foraging, where group mates make inefficient foraging decisions, individuals in a social group may have to sacrifice their own foraging efficiency to remain social (Valone, 1993). Such a sacrifice may be acceptable where the presence of group mates offers additional benefits such as protection against predators (Abrahams & Dill, 1989; Ramos-Fernández et al., 2006). Carnivores themselves are often predators and for many species foraging is characterised by hunting, with cooperative hunting often being cited as a key benefit of sociality (Bailey et al., 2013; Rasmussen et al., 2008; Stander, 1992).

Social hunting is thought to exist among 7% of carnivore species, it is well documented amongst numerous species in the Canidae, Felidae and Hyaenidae Families (Bailey et al., 2013; Macdonald, 1983). More recently cooperative hunting has been recorded in the otherwise solitary Malagasay fossa (*Cryptoprocta ferox*) (Lührs & Dammhahn, 2010). Although grey wolf (*Canis lupus*) pack hunting strategies have been demonstrated to emerge from simple rules (Muro et al., 2011), there have also been recordings of advanced behaviours including foresight, understanding and planning, suggesting higher order mental processing (Mech, 2007). In African wild dogs (*Lycaon pictus*), group hunting has been reported to include higher level cooperative strategies such as coordination and collaboration (Hubel et al., 2016a). Amongst lions (*Panthera leo*) differentiation in the roles executed by individuals during a hunt has been noted (Stander, 1992). Whether a group hunt involves complex collaboration and higher order processing capabilities or not, the benefits conferred by the behaviour remain the same. Cooperative hunting is thought to increase the average fitness benefits to individuals involved (Bailey et al., 2013) and cooperative hunters have been found to have increased reproductive outputs (Smith et al., 2012). Hunting as part of a group allows the potential for larger prey to be caught compared to animals of comparative size hunting alone, and the sharing of the workload may allow for more efficient hunting (Bailey et al., 2013; Clements et al., 2016; Palomares & Caro, 1999). Carnivores that are able to form groups can kill prey that weigh up to twelve times their mass, a feat which would be almost impossible if hunting alone (Palomares & Caro, 1999). Group hunting can reduce energetic expenditure of a hunt, particularly among cursorial hunters chasing prey over long distances (Rasmussen et al., 2008). It may be a means not only of increasing hunt success but of reducing the risk of accruing injuries during a hunt (Stander, 1992).

The potential to increase the range and frequency of prey that can be incorporated into the diet through group hunting does not however come without a cost. Hunting as part of a group inevitably means that individuals have to share their spoils with group mates. In several species this occurs through dominance rank with individuals having access to a carcass according to their status within the group (Chen, 2019; Holekamp et al., 1997). This can have implications for the energy that an individual gains from a hunt which is important, not only for individual survival but for enhancing one's fitness through reproduction. If the finite energy that is available from hunting is partitioned between maintenance and reproductive effort it may be that individuals whose energy intake is reduced have less energy to invest in reproduction (Rasmussen et al., 2008). As many carnivores are hunters their behaviours often have to account for more extreme temporal and spatial availability of prey resources than species such as social herbivores. Where food availability is a limiting resource, carnivorous individuals may be less likely to act socially and form groups unless other benefits that could arise from grouping outweigh the potential for reduced energy intake.

1.6 Social breeding

Social breeding, cooperative breeding and alloparental care are terms used to describe a reproductive system in which individuals invest in the evolutionary fitness of non-descendant young (Hatchwell & Komdeur, 2000; Montgomery et al., 2018; Rosenbaum & Gettler, 2018b). The behaviours encompassed in such care systems can include guarding, grooming, carrying, playing, teaching, feeding and even nursing of young and have been recorded amongst six of the terrestrial carnivore Families (Montgomery et al., 2018). For young, receiving such care can be important in shaping their development and life history trajectories, influencing their abilities to acquire physical resources as well as social rank (Montgomery et al., 2018; Rosenbaum & Gettler, 2018a). Reproduction is energetically expensive, as such the sharing of this cost between group members can be hugely beneficial to the successful rearing of young (Fryxell et al., 2007; Silk, 2007b; Smith et al., 2012). Helpers may provide food or even milk for young allowing an increased investment in their growth. The benefits of large size in juveniles are known to extend to the reproductive years and in several species positive relationships between pup size and survival have been documented (Sparkman et al., 2011). Helpers may also provision the reproductive female increasing her energy intake (Macdonald et al., 2004). Such behaviours can allow mothers to invest more in current reproduction, weaning offspring at later ages than mothers of non-cooperative species (Smith et al., 2012). Helpers may provide more indirect benefits, by acting as babysitters. Mothers able to leave their pups with babysitters, offering protection against predators, may be able to increase the amount of time spent away from the den gathering resources that can be channeled towards the development of a litter (Knight et al., 1992; Chen, 2019). The protection of babysitters may also reduce offspring losses due to infanticidal killings. Whilst there is some thought that social groups evolved to combat male infanticide (Opie et al., 2013; Shultz et al., 2011) most recent work supports the idea of male infanticide as a consequence rather than as a driver of sociality amongst mammals (Lukas & Huchard, 2014). Most records of helpers in cooperatively breeding species suggest that they are related and it has even been suggested that delayed dispersal of juveniles is a prerequisite to helping (Hatchwell & Komdeur, 2000). Helpers are thought to gain benefits through increases to their indirect fitness. It has been suggested that in some species acting as a helper may increase an individuals rank, or be a means of an individual getting experience and increasing their chances of successfully rearing young independently in the future (Emlen, 1982; Rosenbaum & Gettler, 2018a). For some species in which social breeding occurs, reproductive suppression has been recorded (Montgomery et al., 2018; Saltzman, 2010). Reproduction in non-breeding individuals can be suppressed either hormonally as seen in meerkats (*Suricata suricatta*) (Carlson et al., 2004) or behaviourally. Female wolves that have not had mating opportunities have been recorded to have the hormone profile of postpartum mothers suggesting a lack of hormonal reproductive suppression (Montgomery et al., 2018). These subordinate wolves have been observed to have been aggressively prevented from mating by dominant individuals with the suggestion that reproduction is suppressed through behaviours (Derix et al., 1993).

Where social reproduction is observed, the costs to an individual of not breeding, or helping are assumed to be outweighed by the benefits associated with group living being enough to increase their overall lifetime fitness. Social breeding is not a uniform phenomenon and thus may have multiple evolutionary origins and a myriad of consequences (Rosenbaum & Gettler, 2018b). It has been suggested that the costs and benefits associated with social breeding are impacted by resource availability (Ebensperger et al., 2012). In communally breeding red wolves helpers were shown to increase the survival of young in a population where density was low and food was abundant, but had negative effects in a population where density was high and food was scarce (Sparkman et al., 2011). In instances where an individual does not benefit from increased production of young or food intake as a result of being part of a social group, why then might they act socially? Perhaps simply surviving is enough to drive the evolution of sociality.

1.7 Social defence

Defence against predation is often cited as a driving force influencing the evolution of sociality (Beecham & Farnsworth, 1998; Gittleman, 1989a; Ramos-Fernández et al., 2006; Rands et al., 2004). Forming a group dilutes the risk to an individual of being predated (p) simply by spreading the risk across all members of the group (p/N). Further to the benefits from simple aggregation, many social species have developed behaviours that aid in defence against predators. Species that are subject to extreme predation pressure have developed the use of sentinel systems (Clutton-Brock et al., 1999; McBride et al., 2004). Taking turns to act as sentinels keeping watch and informing conspecifics of impending danger allows group mates to focus on foraging activities and reduce their individual vigilance behaviours (Clutton-Brock et al., 1999; Townsend et al., 2012a).

Predation may be age specific with several species that face little predation as adults having to group to defend young from infanticidal killings (Ebensperger et al., 2012;

Lukas Dieter & Huchard Elise, 2019; Robertson et al., 2015). Lions, for example, are known to benefit from sociality in the defence of cubs against infanticidal males (Fryxell et al., 2007). Further to the direct impact of defence on life and death, group defence can greatly impact the fitness of species through the abilities of a group to defend resources. Most African carnivores that group, successfully defend prey more often than solitary individuals (Palomares et al., 1999). Lions and wolves hunt in groups larger than is thought to be optimal in order to successfully defend kills from scavenging losses (Caraco & Wolf, 1975; Vucetich et al., 2004).

Not only can social grouping act as a means of defending prey once hunted it can also be used to monopolize the access to prey items for hunting in the first place. Defending a territory is a means by which animals can exclude competitors from an area and ensure access to the resources contained within that area, and has been cited as the primary benefit to group living (Verdolin, 2009). Defence of a territory by proxy can include defence of prey resources, mates and breeding sites (Baird & Dill, 1996). Most often territory defence involves the use of scent marks to indicate territory boundaries (Johnson, 1973). Larger territories are inherently more difficult to defend and the extent to which they are successfully marked and defended varies with territory boundary length (Jetz et al., 2004; Kruuk, 1972). The idea of defensible territoires providing resources has been suggested to be a driver of social group formation, formalized by the resource dispersion hypothesis (RDH) (Macdonald, 1983). The RDH suggests that groups may develop where resources are dispersed so that the smallest economically defensible territory for a pair can also support additional animals (Macdonald & Johnson, 2015). Explored in more detail in Chapter 4 the RDH, however, was developed to explain sociality in carnivore species that were not obviously explained by cooperation. Evidence of cooperation in territory defence suggests that sociality may impact the defence of territories and the resources that they encompass, thus potentially conferring fitness benefits to species exhibiting such behaviours (Robertson et al., 2015).

1.8 Thesis aims and outlines

The aims of this thesis are to assess the drivers of sociality across the Order Carnivora. These drivers operate across a range of different scales and thus require a vast amount of data in order to be thoroughly interrogated. As environmental systems are highly dimensional with many unmeasurable or unobservable processes, and with over 200 species in the Order inhabiting every continent of the globe, gathering sufficient data for investigations would require a gargantuan effort. To be able to effectively study complex systems such as the occurrence of social behaviours across a large Order in a controlled setting would be near impossible without the use of ecological models. Statistical models which test hypotheses about specific phenomena based on statistical distributions, and simulation models that evaluate the dynamics of a system though a mechanical representation of it, allow a focus on the features of interest within a system (Jørgensen & Bendoricchio, 2001). Where statistical analyses can reveal relationships between data, models can represent a synthesis of what we know about an ecosystem. They can be used to reveal system properties and to test hypotheses about ecosystem behaviour which would be almost impossible to carry out in the field. Throughout this thesis I aim to understand the factors driving sociality by using different modelling approaches to investigate the phenomenon of sociality through synthesis of extant data allowing novel insight from pre-existing information.

In **Chapter 2** I start by identifying two factors (diet and habitat) that are thought to influence sociality to try and understand how they might influence the patterns in social behaviour seen across species within the Order. I explore how the aforementioned factors can be investigated in a way that makes the most of existing data sources. Natural history has been an important factor in developing our understanding of the natural world. Much of this learning comes from observations and descriptions, by harnessing the computing power of modern linguistics methods we can now assess this information more formally. In an attempt to highlight the potential for use of textual data in analysis of behaviours such as sociality I used descriptive texts from the Handbook of The Mammals of the World (Wilson & Mittermeier, 2009) as a data source for a topic model. Using descriptive texts as a data source the model identifies similarities between species based on the language that is used to describe them, and demonstrates the importance of descriptive language in the analysis of behaviours.

Chapter 3 further investigates diet and habitat as variables that impact sociality and extends analyses to include life history traits including morphology, lifespan and reproduction as factors that may interact to influence sociality. The aim of this chapter is to understand patterns in sociality across different species, why some species act socially but others do not, and to understand the extent to which environmental and life history factors interact to influence social group formation. The variables of interest are thoroughly investigated using multivariate statistical models to identify patterns that occur across all terrestrial carnivore species for which data were available. Structural Equation Modelling (SEM) is then used to assess the relative contributions of the examined variables in driving animals to form social groups.

Where life history traits were demonstrated to be important in impacting sociality across different species, the interaction with environment was further investigated in an attempt to understand why some species show variability in their sociality in different environments. **Chapter 4** aims to quantify the drivers of sociality and the subsequent impacts on space use within a single species that exhibits plasticity in it's social behaviours. The European badger (*Meles meles*) is used as a model species due to the variation it exhibits in its sociality across different environments. The models developed in this chapter incorporate environmental and demographic variables identified in the previous chapter to investigate variation within a population. Using population demographic data and space use data from a long running monitoring project the impacts of exogeneous and endogenous variables including habitat, weather, group demography, territory size and population size are investigated.

Chapter 5 takes the factors identified in the previous two chapters, life history traits and their interaction with the surrounding environment and incorporates them into an Individual Based Model (IBM) to investigate the potential that energy is a driver of social behaviours. The IBM is built from energetic principles and is used to simulate the behaviours of groups of carnivores to understand the potential energy benefit to grouping. The model is parameterised for two social carnivore species the grey wolf and the meerkat, species that represent carnivores with extremely different life history strategies inhabiting wildly different environments.

Chapter 6 examines the range of different modelling approaches that have been used throughout the preceding chapters. The integration of the models to enhance the outputs from synthesising different data types is discussed in relation to the investigation of aspects of sociality that have not previously been explored. This critique highlights the rationale behind the investigations and evaluates the strengths and weaknesses of the approach. The findings from each chapter are then synthesised to demonstrate how this work has added to our knowledge and understanding of carnivore sociality and concludes by suggesting avenues for future work in this area.

Two

The order Carnivora is the fifth largest extant mammalian order, comprising thirteen terrestrial and three marine Families. Carnivores are spread across every continent and members of the 245 species of terrestrial carnivores can be found in every major habitat on earth [@hunter2018field]. Descended from the Miacids, a group of small civet-like mammals whose fossils date back to the Upper Eocene (approximately 50 million years ago), the divergence across the order has given rise to species with a wide variety of life histories. From the Least weasel (*Mustela nivalis*) weighing as little as 25g to the Polar bear (*Ursus maritimus*) weighing in excess of 650kg. From the hypercarnivorus Caracal (*Caracal caracal*) to the completely herbivorous Giant panda (*Ailuropoda melanoluca*) the diversity of present day species encompasses animals of greatly varying shapes and sizes all exhibiting a myriad of different behaviours.The miacids were thought to be mostly arboreal and present-day arboreal carnivores have retained the adaptations such as small body size and slim bones that favour their tree dwelling lifestyle [@eisenberg1989introduction; @taylor1989locomotor]. Only a few species, however, have retained this arboreal lifestyle. Many carnivores are cursorial species such as the Cheetah (*Acionyx jubatus*) which have developed skeletal adaptations that maximize limb acceleration for high speed running [@taylor1989locomotor]. Other carnivore species such as the Raccoon (*Procyon lotor*) have largely given up on predation and rarely use a gait faster than a walk [@thweatt2010hip]. Present day carnivores can be separated into two major suborders (Caniforma and Feliforma) representing a divergence estimated around 45-50 million years ago. Whilst most feliform families originated in the Old World and have primarily remained in the tropics, caniforms have spread further through the northern temperate regions and show a greater tendency towards omnivory than their feliform cousins [@pedersen2014macroecological]. Despite these omnivorous adaptations the characteristic condition of carnivores is the adaptation of the scissor like carnassials which gave rise to the name Carnivora which translates as "flesh eaters". Having evolved from premolars and mesial molars the purpose of the carnassials is to shear flesh. However, the high rates of evolution in teeth and the varied diets that species have developed has led to a great array of dental morphologies amongst present day carnivores [@[illegible]hurst dental[illegible]]. The versatility [illegible] dentition that led to the evolution of divergent dental patterns and diets, is thought to contribute to the present success of the group, with species adapting to exploit the environments in which they have found themselves [@asahara_unique_2016; @van1989carnivore]. This ability to adapt, particularly to human modified environments [illegible] contribute to the intense conflict and persecution that many species now face at the hands of humans [@boitani2012carnivore]. Within mammalian research the order Carnivora dominates the literature and carnivores are among the most threatened group of mammalian species [@brooke_correlates_2014; @treves_human-carnivore_2003].Over a quarter of carnivore species populations are currently in decline with species thus being classified by the International Union for the Conservation of Nature (IUCN) as Vulnerable (43), Endangered (31), or Critically Endangered (4) [@van_de_kerk_carnivora_2013]. The species that are at greatest risk are not confined to a single Family or similar individuals but include the Malabar civet (*Viverra civettina*), Red wolf (*Canis rufus*) European mink (*Mustela lutreola*) and the Pygmy raccoon (*Procyon pygmaeus*) suggesting that species declines are not limited by life history or geography. The conservation of carnivores is crucial for the maintenance of biodiversity as carnivores play important roles in regulating ecosystems [@ripple_wolves_2004]. Through intra-specific competition carnivores can regulate the density of other carnivore species [@linnell2000interference]. Carnivores typically occupy the highest trophic niche in a habitat and thus the impacts they have through predation can cascade through ecosystems making them pivotal to maintaining biodiversity [@karanth_k._ullas_spatio-temporal_2017; @ripple_status_2014; @treves_human-carnivore_2003; @van_de_kerk_carnivora_2013].Predators typically require more space than herbivores to maintain their populations [@terborgh_toward_2015]. This is particularly true of large carnivore species, 60% of which have lost more than half of their historic range [@wolf_rewilding_2018]. Coupled with the increasing human population, species are increasingly having to share space with human populations [@pereira2012global]. Human encroachment often leads to habitat loss as landscapes are modified to suit human needs and these modifications threaten biodiversity beyond the order Carnivora [@farris2015hunting; @weste[illegible]2001human]. For carnivores, several life history characteristics can, however, exacerbate the difficulties of species having to coexist with humans. Many carnivores are hunters, eating meat to sustain themselves, a trait which is often exhibited by human populations as well. Where human habitation encroaches on the territory of a carnivore, the depletion of prey by humans can negatively impact the potential survival of carnivores through indirect competition [@miller_amur_2014]. Due to their nature, [illegible] con[illegible]ans is more common among carnivores than other species, as hunters they are prone to attacking both livestock and people [@barlow2013profiling; @boitani2012carnivore; @van_de_kerk_carnivora_2013]. The response of humans to such attacks often ends in the killing of individual predators in retaliation which can have significant negative impacts for populations. Many carnivores exist at low population densities [@pedersen_shallow_2017] with individuals often being slow to grow, where a population experiences declines resulting from direct or indirect conflicts their ability to recover can be severely limited [@jetz_scaling_2004; @manlik_importance_2019]. Carnivores evolved as meat eaters, a lifestyle that necessitates a certain degree of aggression. Such aggressive behaviours, whilst essential to catch and kill prey items can become problematic f[illegible] carnivores not just with humans but with numerous other species. Coyotes (*Canis latrans*) for example are aggressive predators that are known to kill foxes and bobcats (*Felix rufus*), and their use of human modified landscapes has resulted in attacks on humans and contributed to the popular belief that they are a pest species across much of their range [@draheim[illegible]19pu[illegible]; @fedriani20[illegible]competition]. Where species such as this have evolved to be aggressive in order to be efficient hunters, interactions between any individuals have the potential to become antagonistic. For carnivores another animal is a potential prey item, potential competitor, or a potential mate. Carnivory may therefore appear antipathetic to sociality, yet amongst several species, including coyotes, social behaviours have been observed. Understanding why some species risk association with other potentially aggressive conspecifics could allow us to understand how better to protect carnivores and conserve populations of these highly threatened species. The word social is commonplace in our vernacular and yet it's definition is often vague. Amongst the extensive entries under it's definition in the OED there is variation in how the word pertains to the description of animal groups [@oxford_english_dictionary_social_nodate]. Sociality is often broadly defined as cooperative group living comprising a set of organisms that remain together for a period of time [@m[illegible]_valence-f[illegible]_2017; @rubenstein_evolution_2017]. More specifically it has been suggested that social interactions include cohesive behaviours [@[illegible]itage1981sociality]. At their most complex, social systems have been defined as those in which individuals frequently interact in different contexts with different individuals and often repeatedly interact with many of the same individuals in networks over time [@dros[illegible]_defining_2013]. The most advanced groups are thought to be those that include overlapping generations, cooperative care of young and reproductive division of labour [@rubenstein_evolution_2017]. From early work investigating animal societies Espinas [-@espinas2015societes] explored the idea that societies were highly structured relationships among individuals of a species, the variation in which he interpreted as expressions of direct adaptation to ecology rather than phylogenetic descent [@standen1989comparative]. Sociality and the perceived advanced behaviours associated with it has been suggested to increase cognitive demands on individuals and impart a selective pressure for increased encephelisation among social animals [@finarelli_brain-size_2009]. Built upon a principle of comparative neurology that behavioural specialisation corresponds to an increase in neural processing and a complimentary expansion of neural tissue devoted to that specialisation [@arsznov_procyonid_2013]. If sociality imposes cognitive demands it would be expected that changes in relative brain size with sociality would be coupled over evolutionary time [@perez-barberia_evidence_2007]. Amongst the order Carnivora, however, there seems to be limited evidence supporting this theory. Although an association between increased encephalisation and highly social behaviours has been found amongst canids it cannot be generalised across the whole order [@finarelli_brain-size_2009]. Such a 'social brain' might not be necessary for species to act socially, but when group formation is favoured the size and structure of the group can have diverse effects on the morphology, behaviour and fitness consequences of individuals [@silk_adaptive_2007-1; @wey_social_2008]. In primates, for example, the sex ratio within a social group can impact the extent of size related sexual dimorphism [@clutton1977sexual]. The structure of a group and the relationships that individuals form play an important role in the acquisition of dominance rank and associated behaviours [@johnson1987dominance], and group size can impact breeding success, particularly in mammals whose young are reared by 'helpers' in the group [@clutton2001effects]. The behaviours resulting from such social associations are often studied in respect to the costs and benefits to individuals. Amongst carnivores where the costs of acting socially includes the potential that a conspecific could kill you there must be great benefit to adapting to such a lifestyle for it have evolved in

Chapter 2

Data synthesis: Making the most of species data collections

2.1 Introduction

It has been hypothesised that sociality is driven by the potential to increase food acquisition, the potential to increase reproductive output, and the potential to decrease an individuals risk of predation (Fryxell et al., 2007; Gittleman, 1989a; MacNulty et al., 2012a). However much research has focussed on the role of each of these factors in determining sociality individually. The cooperative hunting of wolves, the anti-predator alarm calls of meerkats, or the cooperative breeding of lions are just a few examples (Chakrabarti & Jhala, 2019; MacNulty et al., 2012a; Townsend et al., 2012b). In reality sociality must be dependent on multiple processes and not the single behaviours alluded to above. Assessing the relative importance of each of these life history features in determining sociality is difficult as it is often reliant on data from studies where the interest has had a narrow process focus (eg. predator avoidance behaviour in meerkats) within a well defined social group in a small geographical area. The spatio-temporal domains of such studies are inevitably narrow because of the fine-scale nature of the process being considered. Despite being among some of the most well studied species, demographic data for all carnivores can be particularly hard to obtain due to the tendency of carnivores to be elusive, nocturnal, and often dangerous (Treves & Karanth, 2003; van de Kerk et al., 2013). Of the 245 terrestrial species within the order Carnivora most species are however well described, in part due to their charismatic nature and so even where individual carnivore species have been less frequently studied and demographic data may be missing there still exists a large amount of anecdotal information relating to their life histories and behaviours (Brooke et al., 2014). For species, particularly those lacking in published demographic data, museum collections are often cited as an important source of data. Yet the natural history reports that accompany museum specimens and detail observed behaviours are under-utilised as a source of data consistent across an entire Order (Gaubert et al., 2006; Lister, 2011). To what extent could this data be used to investigate social behaviours across the order Carnivora? The use of natural history data such as species descriptions could be used as a means of unifying information across species to investigate how their interactions with the environment might impact appearance of behaviours such as sociality.

Data tend to be thought of as facts and numbers that describe an object, idea, condition or situation (Borg et al., 2015). Scientific uses of data most often focus on quantitative analyses, thus museum collections are thought to house a wealth of data (e.g. morphological measurements and genetic material) that can be analysed numerically. Much of the early ecological research that accompanies such museum specimens consists of detailed accounts of observations of the interactions between species and their surroundings. Many of these early works such as that of Mech (1966) have been recognised for their important role in shaping our current knowledge of species behaviours. More recently however, such observational and descriptive information is often overlooked in favour of intensive field-based studies which measure behaviour over fine spatial and temporal scales under a highly localised set of environmental conditions. Highly detailed data, however, are often not generalisable to other populations of the same species. Descriptive texts are a key data source in domains such as digital humanities and social sciences (Gentzkow et al., 2019; Jänicke et al., 2017). The wealth of information that exists in books and collections of natural history observations could therefore, given appropriate analytical procedures, serve as a data source previously under-utilized in ecology. Further, such data are often collected over a wide range of environments and hence capture the breadth of responses that individual carnivore species may show to changing environmental conditions. Such untapped information could be vital in understanding how behaviours such as sociality have developed across species, knowledge that could aid efforts towards the conservation of many threatened carnivore species.

Bibliometric analyses have been gaining traction within ecology and conservation as a method by which a body of literature can be analysed, using linguistics methods such as topic modelling which attempts to deconstruct documents to find the structure within them (Brooke et al., 2014; Mair et al., 2018; Srivastava & Sahami, 2009). The topics addressed by a paper are one of the primary pieces of information that a reader tries to extract from a document (Griffiths & Steyvers, 2004). Techniques such as topic modelling can therefore assist quantitative research relating to text documents as a means of quantifying topics and relationships between documents (Chang et al., 2009; Nikolenko et al., 2017). Methods such as these can yield connections between documents that are not visible to the naked eye (Srivastava & Sahami, 2009). Coupled with techniques such as hierarchical clustering, the relationships between documents can be identified and quantified allowing a synthesis of different data types. Descriptive accounts, although not commonly used scientifically, have intrinsic value, and with the application of a topic modelling approach they can be analysed in the more quantitative manner typical of scientific studies. The application of such methods to bodies of text such as species accounts and descriptions, may be a valuable way to gain novel insight from existent but often neglected data, particularly with regards to behaviour. Behaviours are most commonly recorded as descriptions of what is seen, thus making the language that is used for that description a key piece of information that is most often ignored (Kamath & Wesner, 2020). By using techniques more commonly used in humanities research to extract and quantify textual information this data can be used to gain insights into the similarities or differences in behaviours between species beyond the patterns that are contained within numerical datasets. Texts such as The Handbook of Mammals of the World (Wilson & Mittermeier, 2009) contain information drawn from across the scientific literature and are well suited to analyses such as this. With information from over four thousand scientific publications and reports collated by a group of expert authors reference books such as this contain a vast amount of information, collated in a standardised format that can be used as part of an informed analysis. Here topic modelling is used to investigate whether descriptive data relating to habitat use and diet can be used to identify core habitat and diet features that might discriminate between social and non-social species.

Topic modelling

Topic modelling defines groupings (topics) from a collection of text (corpus) based on the co-occurrences of words (terms) and the frequency with which these co-occurrences arise.

Similar to clustering on numeric data it can be used to find natural groups of items that are defined by the data rather than the user. The model assumes that every document is a mixture of topics, each document is likely to contain words from several topics in differing proportions. It also assumes that every topic is a mixture of words and that words may be shared between topics. A matrix of document-word frequencies and the number of topics to be identified are used as inputs to the model which then provides frequency distributions for all words and all topics across all documents. The weight that each word contributes to a topic, i.e. the probability of a term occurring in a topic (β) can be used to infer the main ideas of each topic based on the words most strongly associated with the topic. The model also calculates the weight of each topic within each document (γ) which allows the documents most strongly associated with each topic to be identified.

The aim of this chapter is to analyse the extent to which descriptive texts, specifically those collated in the Handbook of Mammals of the World (Wilson & Mittermeier, 2009) can be used to investigate processes that determine behaviours such as sociality in carnivores. Topic modelling is used to analyse the descriptions of habitat and diet preferences in an attempt to determine the importance of language in understanding how these factors relate to behaviours such as sociality.

2.2 Methods

2.2.1 *Data*

The data comprised text accounts for species within the Canidae, Felidae and Herpestidae families extracted from Wilson and Mittermeier (2009) as detailed descriptions were available for all 106 species. The diet and habitat sections from each species account were read through Optical Character Recognition (OCR) using the *tesseract* package (Ooms, 2018) for the statistical software R (R Core Team, 2019) and then manually checked and corrected against the original text where necessary. Texts were transformed into a corpus and manipulated using the *tm* package (Feinerer et al., 2008). The pre-defined list of stop words defined in the *tm* package and all punctuation (including hyphens and slashes) were removed from the corpus. The suffixes of all words were removed to reduce words to their common root leaving a final corpus containing 4976 words with each 'document' representing one of the 106 individual species. Species within the dataset were classed as social or non-social through manual evaluation of records. Social animals were classed as those where associations of three or more individuals are recorded to exist outside of the breeding season. Where no such information exists within the text description species were classed as non-social.

2.2.2 *Models*

A Latent Dirichlet Allocation (LDA) topic model using Gibbs sampling was fitted to the corpus with an allocation of 10 topics using the *topicmodels* package (Hornik & Grün, 2011). The allocation of 10 topics was determined from the *a proiri* calculations resulting from block cross validation of the model data, in which the corpus was randomly divided into ten equal parts with each part in turn being witheld from the model fitting process. Perplexity was then used as a measure of model fit (Hornik & Grün, 2011) and was calculated over a range of values to determine the number of topics to be used as a model input. Results showed that perplexity plateaus at ~20 with a steep decline between 5 and 10 topics suggesting that a greater number of topics more accurately describes the corpus (Fig.A.1). The number of topics included in the model was set to 10 in order to balance the need to capture the complex nature of the corpus with the need to clearly interpret the results.

The topic model determines the weight of each words contribution to a topic (β) as well as the weights of each topic within each document (γ). The β values are used to determine the strength of the association between a word and a topic, similarly γ values can be used to determine the strength of the association of each document (species) with any of the identified topics. For each species account a dissimilarity matrix was calculated based on the distributions of γ values of each topic within the document. Hierarchical clustering was then carried out using a complete linkage method based on euclidean distances to investigate patterns derived from the textual descriptions of species.

All analyses were carried out in R 3.3.1. (R Core Team, 2016) using the following packages: dplyr (Wickham et al., 2020b), readr (Wickham et al., 2018), here (Müller, 2017), bibliometrix (Aria & Cuccurullo, 2020), tm (Feinerer & Hornik, 2019), slam (Hornik et al., 2019), lme4 (Bates et al., 2020), topicmodels (Grün & Hornik, 2020), tidyr (Wickham & Henry, 2020), conflicted (Wickham, 2019), ggplot2 (Wickham et al., 2020a), viridis (Garnier, 2018), phytools (Revell, 2020), recluster (Dapporto et al., 2020), treeman (Bennett, 2020), dendextend (Galili & Jefferis, 2020).

2.3 Results

The 20 highest weighted terms per topic were used to manually assess the nature of each topic and to assign each to a broad theme of habitat, diet or behaviour (Top 20 terms for each topic are detailed in Table.A.1). Two topics are strongly described by terms relating to habitat (eg.*woodland*, *forest*, *lowland*, *desert*) (Fig.2.1). Four topics are strongly described by terms relating to diet (eg. *rat*, *rodent*, *fruit*, *insect*, *bird*) and four topics were assigned to the theme of behaviour as the terms describing them are more varied, containing a mix of terms relating to diet and habitat and containing more descriptive terms that relate to behaviours of animals (eg. *hunt*, *avoid*, *use*, *consum*). The 'Habitat2' topic had the most skewed word association with a single word (*forest*) having a β value ($\beta = 0.08$) more than twice as high as the next strongest weighted word within the topic. The 'DietC' topic has the most even distribution of β values among the highest weighted words within the topic (range = 0.005).

Four of the topics were most strongly associated with species of a single family (Fig. 2.2). Topics 'BehaviourA' and 'HabitatB' were most strongly associated with members of the Felidae family, topic 'DietA' was strongly associated with species from the Canidae family and topic 'DietC' was strongly associated with herpestid species. The remaining six topics were most strongly associated with species from a mix of families with topic 'DietA' having strong associations with species from all three families. Of the topics that were strongly associated with species from multiple families two were classified as representing diet themes, one representing habitat themes and three representing the behaviour theme.

Topics 'DietA' and 'BehaviourB' shared strong affiliations with a single species, the Ethiopian wolf (*Canis simensis*) and the Canada lynx (*Lynx canadensis*), respectively (Fig. 2.2), yet much lower affiliations for the next strongest associated species. Around 60% (γ = 0.6) of the terms in the Canada lynx 'document' were generated by the 'BehaviourB' topic yet for the other species that were most strongly associated with the topic that value is reduced to around 20% (γ = ~0.2).

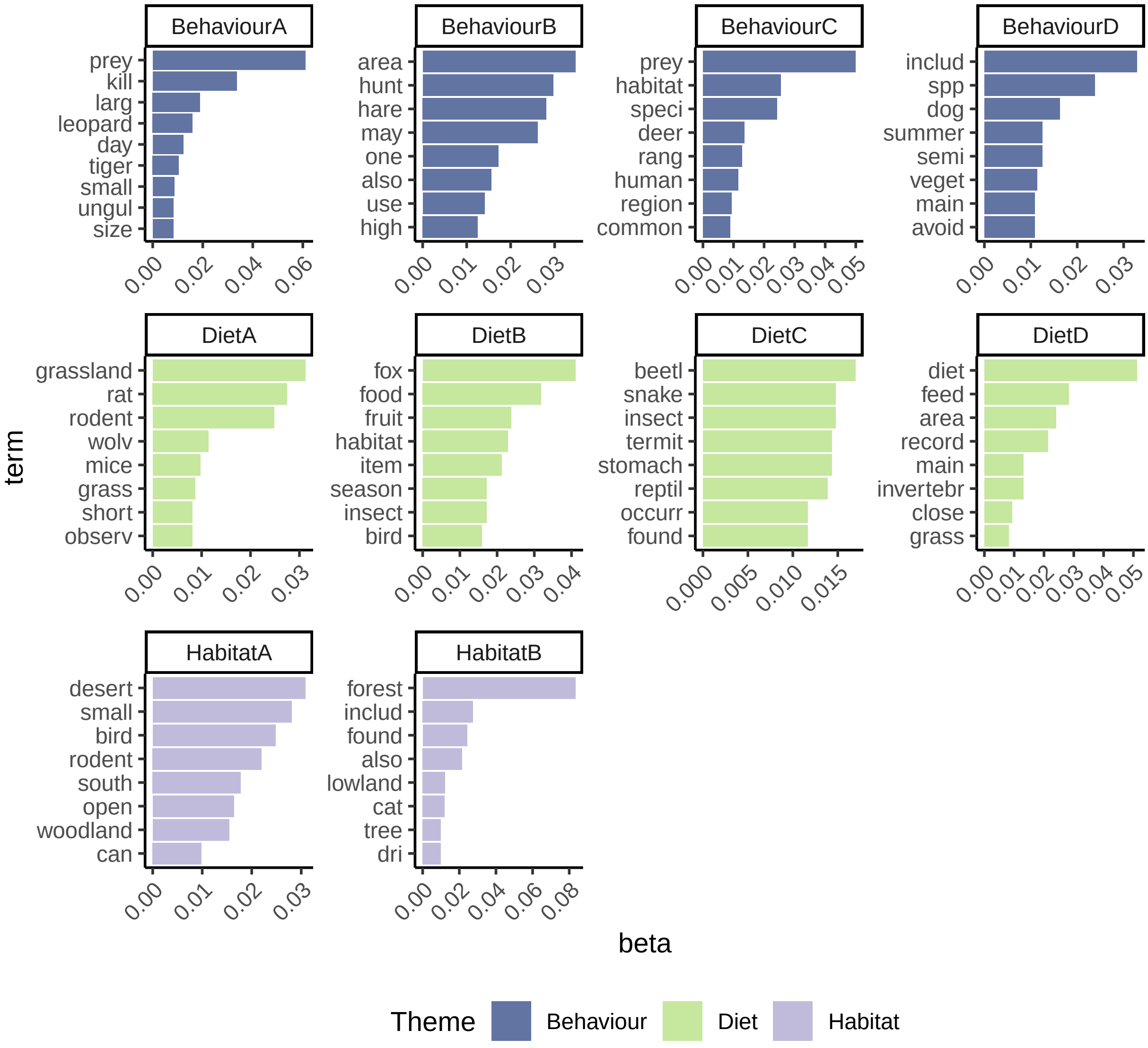

Figure 2.1: Top weighted words in the ten topics as determined by the topic model based on habitat and diet descriptors with the probability of each word being generated from its assigned topic (beta). Ranked in order of descending beta value for the top eight words in each topic, ‘BehaviourA’ displays nine words as ‘ungul’ and ‘size’ are equally weighted.

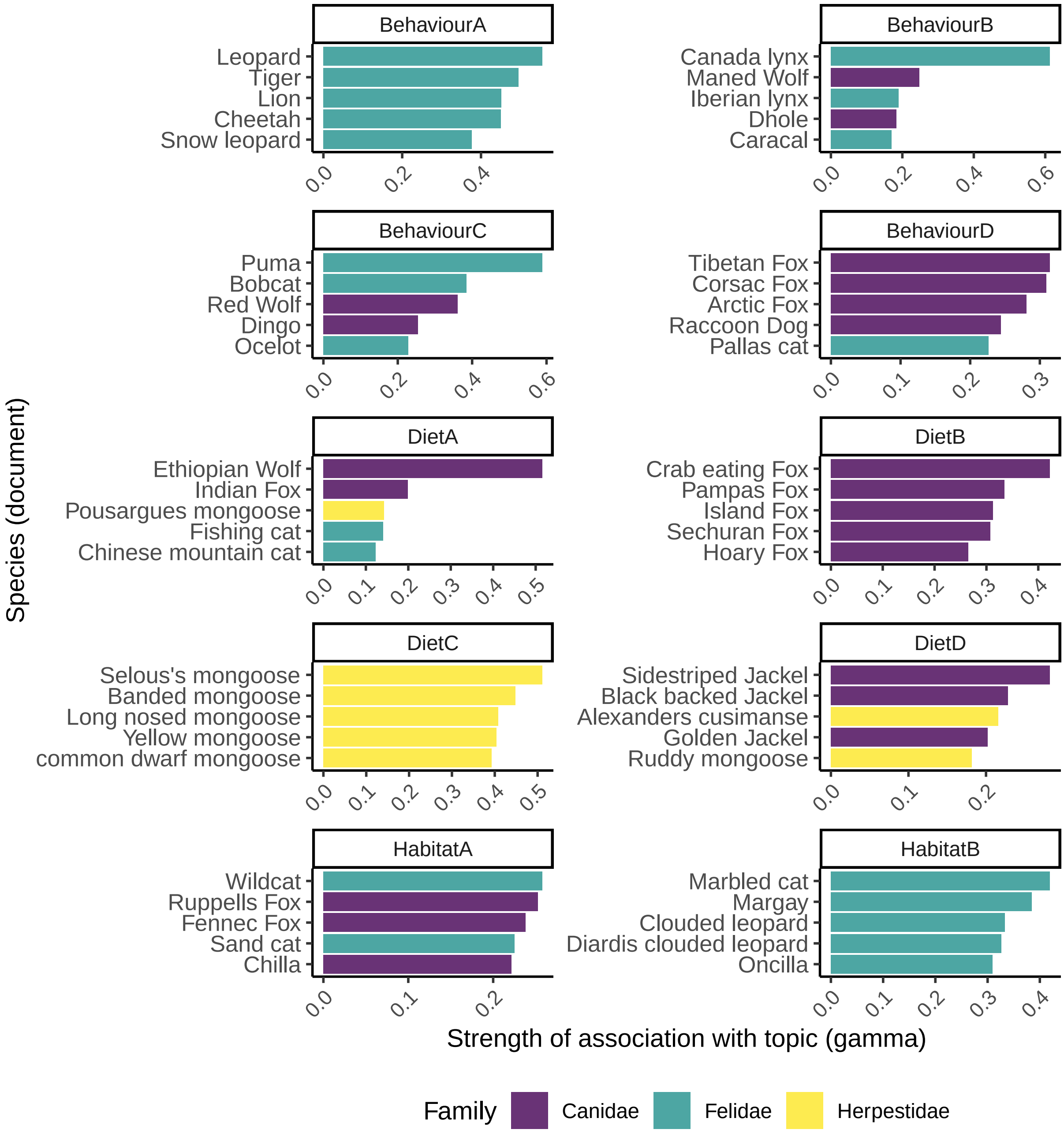

Figure 2.2: Top five species with strongest association (gamma) for each topic as determined by the LDA topic model

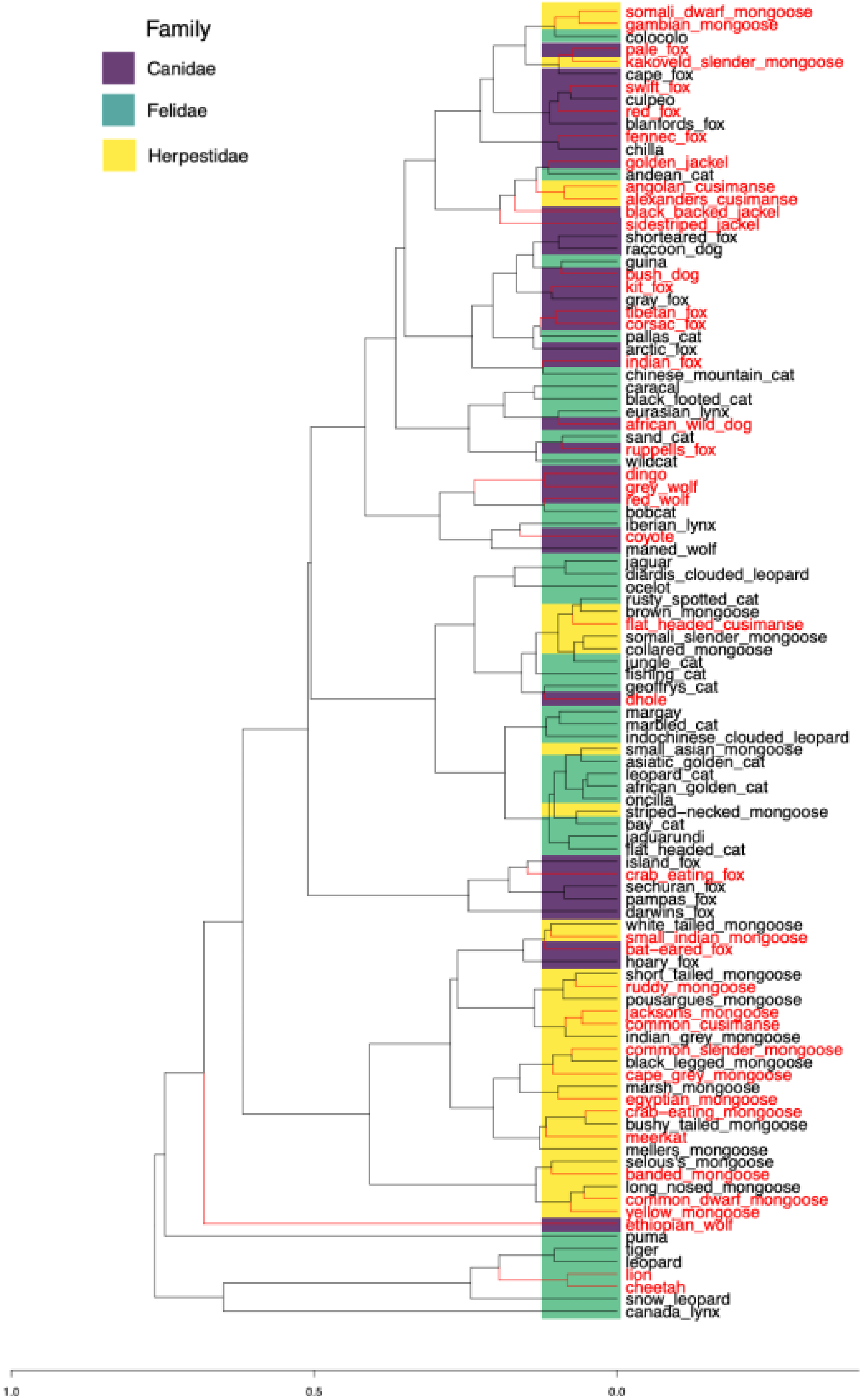

Figure 2.3: Heirarchical clustering of species (social = red, non-social = black) based on distributions and co-occurences of words derived from a topic model built on descriptive data of habitat and diet information.

Hierarchical clustering of the topic distributions across species failed to identify a simple discrimination between social and non-social species. Very few clusters contained more than two or three species that were solely composed of social (or non-social) species (Fig.2.3). The largest cluster containing only non-social species was comprised of ten felid species and two herpestid species.

Of the 33 herpestid species 22 were clustered together. Two canid species, the bat eared fox (*Otocyon megalotis*) and the Hoary fox (*Pseudalopex vetulus*) were more closely associated with the herpestids including the Small Indian mongoose (*Herpestes auropunctatus*) and the white-tailed mongoose (*Ichneumia albicauda*) than with the other phylogenetically similar canid species. The most distinct cluster was comprised of large bodied felids such as the Canada lynx, Leopard (*Panthera pardus*), Snow leopard (*Panthera unica*), Tiger (*Panther tigris*), Lion, and Cheetah. Within this cluster the topic model grouped the social lion and cheetah more closely than with the rest of the group.

2.4 Discussion

The topic model identified groups of species that are ecologically meaningul such as those with similar diets or habitat preferences based on the descriptive texts. The model also identified groupings of species based on words relating to the behaviours that they exhibit. Not only does this highlight the importance of descriptive data as a source that can be used to understand behaviours, but it also demonstrates the influence of the language that is used by humans in describing species, in identifying similarities between different species. Quantifying textual information in order to assess similarities between species highlighted patterns that may not have been obvious were a human attempting to infer relationships from numeric data alone. The clustering of species based on accounts of habitat and diet descriptions showed that there were similarities in the descriptions of behaviours that can be used to group species from phylogenetically distinct families. However there were no inherent differences in the way that descriptions of diet and habitat preferences in the literature could be used to identify whether carnivore species are social or not. Diet and habitat information alone were not sufficient in explaining sociality; some social species were seen to be similar based on this information however there was spread in social species across clusters. As diet and habitat are factors that have been hypothesised to influence sociality (Gittleman, 1989a) this analysis used the descriptions of these factors in an attempt to identify patterns among social (and non-social) species across three different families of carnivores. The model was used to demonstrate the similarity of behaviours of species with regards to the interactions between the species and their environment. As the model was built on the words used to describe species it may give an indication of species that behave in similar ways, with words such as *prey*, *kill* and *hunt* being important across topics, suggesting that the foraging behaviours and the manner in which we describe them can give information about similarities between species.

It is important to note that no one topic as identified by the model was described by terms such as *social*. It seems obvious that species that exhibit social behaviour are not explicitly described in a different manner to those that are not social. Sociality did not unduly skew the model, where clusters of social species are identified, although relatively small, it is because of the similarities in their habitat and diet descriptions not because they are described as being social. Such clusters of social species may therefore give clues as to the development of social behaviour among species that are in similar habitats or interacting with their environment in similar ways.

The clustering of the Lion and Cheetah, for example, is unsurprising as these species often co-occur, with overlapping ranges and the habitats that they occupy being similar. The use of sociality in hunting may contribute to the grouping according to the topic model with descriptions detailing the high success rates of groups and coalitions in bringing down large prey. In addition, the descriptors of the hunting methods employed by these species such as *rushing*, *charges* and *chases* suggests that similarities between the species may contribute to the grouping obtained from the model. In this instance the use of sociality to influence the hunting strategy of the species may be a driver of these species clustering more closely than with sympatric non-social species such as the leopard. The inclusion of descriptive language therefore demonstrates the importance of incorporating information pertaining to behaviours in analyses seeking to investigate the patterns of their appearance.

The majority of the mongoose species are clustered together with no clear groupings of social or non-social species within the cluster. Two fox species, the bat eared fox and the hoary fox are clustered more closely with mongooses such as the Small Indian mongoose and the white-tailed mongoose than they are with any other canid species. Similarities in the descriptions of habitats used by these species with *arid* habitats being *preferred* indicate the importance of language in our understanding of how a species interacts with its environment. Such information would be easily overlooked in traditional analyses that simply aggregate based on categorical data such as presence or absence as a measure of habitat use.

In addition, the species within this cluster are recorded as having similar diets, relying heavily on invertebrates. The inclusion of descriptors detailing how the species incorporate such prey in to their diet shows that the term *digging* may be an important descriptor used to group these species together. Whilst phylogenetically these species may be distantly related the similarities in their behaviours described in this data suggest similarities between the species that could be missed were the descriptive language not incorporated into analysis.

The Small Indian mongoose and the Bat eared fox may behave similarly in the open environments that they inhabit digging for invertebrate prey. Both species exhibit social behaviours yet the differences in these behaviours may be impacted by the life history traits of the species. For the mongoose, inhabiting open habitats that may be rich in invertebrate prey leaves them exposed to predators (Palomares et al., 1998). Sociality may therefore be an important mechanism of defence against predation with individuals being able to dig for prey whilst group mates keep watch and warn of the presence of predators (Kern & Radford, 2014). For the bat eared fox, that is larger in size than the mongoose predation may be less of a cause for concern. Defending enough territory to maintain a sufficient supply of invertebrate prey might however be more important (Emlen, 1982; Robertson et al., 2014). Territory defence however takes time, but if the task of defending an area is shared by a group an individual maybe able to devote more time foraging for prey. Whilst the diets and habitat preferences may be similar in these species the motivations for acting socially may differ.

Sociality is known to have the potential to impact the diet of a species and can alter their foraging behaviours (Metz et al., 2011; Périquet et al., 2015). As highlighted by the model the way in which a species forages, through hunting or scavenging is an important consideration when assessing similarities between species. Foraging behaviours are often heavily impacted by the habitat in which an animal lives (Gittleman, 1989b; Hubel et al., 2016a; Smith et al., 2012). From this model however it is obvious that whilst these factors can go some way to explaining groupings of social species additional factors such as life history traits and population demographies need to be considered in order to truly understand the drivers of sociality.

The inclusion of life history traits is particularly important in order to understand the extent to which this model may be biased according to the data source. Wilson and Mittermeir (2009) was used as a source as it is one of the most extensive collections of standardised descriptions for species within the Order. The texts themselves were contributed by experts and as such there is a small potential for bias in the descriptions due to differences in author styles between authors contributing information to different families. As the model used examined the language used, similarities in the style of descriptions could impact the outputs, thus the incorporation of additional data regarding life history characteristics of species could further our understanding of the difference that are seen between different Family groups.

The use of this technique demonstrates the effectiveness of utlilising existing data for synthesis of novel information, a theme that is carried through the analyses in the following chapters of this thesis. With the advances in open science and data sharing practices the potential for advancing knowledge through novel analysis of extant data can only increase. By re-examining extant data we can make great use of the wealth of information that exists without having to invest large amounts of time and money that would be required to achieve studies of this nature encompassing an entire Order of species.

Three

Chapter 3

Comparative trends of sociality among terrestrial carnivores: a multivariate analysis

3.1 Introduction

Across the order Carinvora species exhibit great differences in their social behaviours, from the obligate social breeding meerkats (Ozgul et al., 2014) to the solitary brown bear (*Ursus arctos*) (Lamb et al., 2017). Grey wolves frequently interact with conspecifics forming multi-male multi-female groups (Cassidy et al., 2015), yet maned wolves (*Chrysocyon brachyurus*) barely even associate with their chosen mate (Dietz, 1984). Only 10-15% of carnivores live in social groups (Gittleman, 1989a) and among those that do there is great variation in the extent to which social behaviours are exhibited. Why then do some species form social groups and exhibit social behaviours when others do not?

In seeking to answer such questions the benefits that arise from social grouping have often been considered (Gittleman, 1989b). Wolves may group in order to hunt together with a pack being able to take down prey much larger than can be taken by an individual (Muro et al., 2011). Groups may form where they offer a competitive benefit to the individuals within the group, for example, where a group of hyaenas may be able to defend a carcass against lions an individual may have been displaced (Pangle & Holekamp, 2010). Increased protection against predation is one of the fundamental benefits that sociality is thought to confer (Gittleman, 1989b). The sentinel system of meerkats is a well-documented example by which the presence of groupmates allows individuals to forage whilst being warned of the presence of predators (Clutton-Brock et al., 2002; Santema & Clutton-Brock, 2013; Townsend et al., 2011). Understanding why not all carnivores are social requires an appreciation of the fact that the benefits of sociality are not the same amongst different species and are impacted by both the life history traits of an individual as well as the environment it inhabits. Grouping to reduce predation pressure has little benefit for large bodied species such as the lion but for smaller bodied species such as the meerkat the benefits can be great (Terborgh, 2015). Additionally meerkats, living in open savannah habitats may obtain a greater benefit from group predator defence than mongooses living in densely vegetated habitats where their risk from aerial predators is greatly reduced (Gilchrist et al., 2009). To understand what factors drive species to form social groups therefore requires an understanding of how the benefits differ according to the characteristics of the species and the environment in which it lives.

Geographical patterns in the level of sociality show variation in a number of lineages, including social insects (Kaspari & Weiser, 2012; Kocher et al., 2014), spiders (Majer et al., 2015), birds (Jetz & Rubenstein, 2011) and mammals (Faulkes et al., 1997). Such studies demonstrate the impacts of environment on group size, nest size, or other social traits and suggest a strong influence of ecology and the environment on the evolution and complexity of cooperation (Majer et al., 2015). Latitudinal gradients in primary productivity and vegetation diversity can determine the habitats and communities that develop (Hawkins et al., 2003). Such gradients can impact carnivores, and the way in which they need to interact with their environment in numerous ways that are not independent of each other. While diverse habitats may be more productive, providing greater resources for individuals to exploit (Cusens et al., 2012), those resources may also support a higher density of predators and competitors of a species (Carbone & Gittleman, 2002; Creel, 2001). The extent to which a species is impacted by predation and competition not only varies with habitat but is largely impacted by body size (Terborgh, 2015); a factor that is itself impacted by geographic variation (Ferguson & Larivière, 2002)). The interlinked nature of all these factors needs to be accounted for when seeking to explain why some species form groups and others do not.

Many studies have investigated the relationship between individual variables such as latitude and body size or home range and body size however the impacts of multiple factors, their interlinked nature and any indirect effects on species may not appear obvious. The influence of habitat on the diet of a species may be well studied (Ferretti et al., 2020; Li et al., 2013; McGregor et al., 2015) but how this relationship relates to confounding factors such as predation risk, body size and survival likely impacts the relationship that we see. Examining the relationship between body size and diet in relation to behaviours such as sociality will only provide part of the picture because the impacts of diet are confounded by the interaction with habitat which in turn is impacted by the latitude at which a species is found, which itself impacts body size. In such systems with large numbers of predictors and responses with complex causal connections Structural Equation Modelling (SEM) offers a framework for interpretation. SEM is well suited for studying hypotheses about multiple processes operating in systems (Grace et al., 2010). In order to assess the relative contributions of individual factors a SEM framework is used in which hypothesised paths between variables, that are based on the literature supporting the relationship are tested (Grace et al., 2010). The nature of SEM allows separation of concept from measurement and through the inclusion of direct and latent variables in SEM it is made explicit how observation is being related to theory (Grace, 2006).

This chapter sets out to study multiple factors that might influence sociality simultaneously. SEM is used to study the relationships between factors involved in sociality (bionomics, demography, habitat and diet) across all terrestrial carnivore species. Linear regression and ordination approaches are first used to identify major trends and to develop a conceptual model of the drivers of sociality. The derived habitat, diet and demographic data are then used as covariates describing each species as test data with which to challenge the conceptual model of carnivore sociality with SEM, with each species effectively being a replicate sample in the analysis.

3.2 Methods

3.2.1 *Data*

In order to achieve a global data synthesis data for all terrestrial carnivores were collated from the Handbook of the Mammals of the World, Carnivores (Wilson & Mittermeier, 2009) and A field Guide to the Carnivores of the World (Hunter & Barrett, 2018). The data within these texts are comprised of information from over 4000 published studies and offer a comprehensive overview of global populations of terrestrial carnivores. The

PanTHERIA database (Jones et al., 2009) was used as a supplementary data source to fill in gaps where possible giving a dataset detailing 235 species.

Data were recorded for each species where available for the following variables: Head-Body length, Tail length, Shoulder height, Weight, Skull length, Footprint length, Home range, Density, Gestation period, Litter size, Juvenile mortality, Adult mortality, Lifespan (wild and captive), Red list status, Social (Y/N), Territorial (Y/N), Predated (Y/N), Group size (Table B.1). Data relating to competition were not available from the text. Guild overlap was calculated as a proxy variable representing potential competition and was calculated for each species as the number of carnivore species of greater body size with overlapping geographic distribution.

Linear regressions were used to investigate correlations between variables contained within the data to gain a thorough understanding of each variable being used in subsequent modelling analyses. Multivariate analysis methods were used to investigate patterns in different sets of variables simultaneously, and allow a comparison of patterns among social and non-social species. Principal Component Analysis (PCA) was conducted using the *factoExtra* (Kassambara & Mundt, 2020) and *PerformanceAnalytics* (Peterson & Carl, 2020) R packages in order to assess the variation among the demographic variables.

3.2.2 *Diet*

As grouping facilitates the capture of large prey items the size of prey items included in the diet of each species was investigated. The size range of each species diets were calculated based on the items detailed in the texts describing species' diets. Diet data were frequently recorded in the text as common names and these were matched to binomials using the names listed by the IUCN database. Body weights for diet items were recorded where possible, where diet items were detailed as a specific species the weight for that species was extracted from the PanTHERIA database (Jones et al., 2009), from Lislevand et al. (2007), or from the AnAge database (De Magalhaes & Costa, 2009). Where recorded items were vague in detail the most appropriate estimate of weight was deduced using the mean weight from the genus or family. Where diet items were recorded as young or juvenile of a species the birth weight of that species was recorded as the weight of the diet item. From the weights of recorded diet items the prey size range (excluding plant materials) was calculated for each species. Where the recorded maximum or minimum prey items did not contain sufficient detail (e.g. mammals) the item was excluded and the next largest/smallest prey item was used to provide the range limits. To give an indication of the prey size range relative to the size of the predator proportional prey weight was calculated as, prey weight/predator weight, for each diet item. Texts detailed diet items but did not contain explicit detail regarding the frequency of each prey item within a species diet. To give a indication of the spread in prey sizes kurtosis was calculated as a measure of the distribution of prey size in the diets of each species using the *moments* (Komsta & Novomestky, 2015) R package. Bite force data estimated by Christiansen and Wroe (2007) were included for 151 species. Hierarchical clustering of species based on the presence or absence of recorded diet items was used to investigate potential groupings of species based purely on dietary information using the *phytools* (Revell, 2020), *reculster* (Dapporto et al., 2020) and *treeman* (Bennett, 2020)R packages.

3.2.3 *Habitat*

Habitats used by a species according to the text were recorded as presence/absence data and classified using 40 habitat types noted by the IUCN habitat classification scheme (Version 3.1). These data were ordinated using Principle Component Analysis (PCA) to assess the variation amongst the habitats used by the species. Simpsons Alpha diversity of habitat variation was calculated based on habitats that each carnivore species was recorded as using. Hierarchical clusters of species were determined using an average linkage method based on the habitats that species are recorded as inhabiting.

Leaf Area Index (LAI) was used as a proxy for the openness of habitats. Annual median LAI values were extracted (pixel resolution of 500m^2) from the MODIS 4 day product (Myneni et al., 2015) using the google earth engine and the mean value across a 5000m^2 area was computed for each sample point. LAI values attributed for each species were calculated as the mean value derived from points randomly sampled accross a species geographic range (IUCN, 2019) at a density of one point per 500km^2 of global range area. For each species the LAI value was used as a proxy for primary productivity and habitat structure in subsequent models with higher LAI scores denoting areas with greater leaf cover and therefore more densely vegetated.

3.2.4 *Interaction models*

Hypothesised pathways of interaction amongst demographic and environmental variables supported by evidence from the published literature were defined (Table 3.1) and conceptual models were developed to describe these interlinkages (Fig.3.1). Structural Equation Models (SEM) were used to test the conceptual models with the collated data and assess the relative contributions of each variable in relation to social group size using the *piecewiseSEM* package (Lefcheck et al., 2019). The conceptual model was used as a framework for the development of the structural equation models with all parameters included in the framework bing incorporated into the SEM. The model was optimized by assesment of model AIC and the significance of covairates with non significant parameers being removed. The results of the most parsimonious model are presented with estimated values for direct effects reproted for all pathways.

To incorporate sociality as a categorical variable (with social species being defined as those which associate in groups of three or more at any point outside of the breeding season) and to investigate the relationships between variables not explicitly defined in the SEM Bayesian network models were developed (Marcot et al., 2006) using the *bnlearn* (Scutari & Ness, 2019) R package. A Bayesian network model with and 'expert elicited' structure was derived from the conceptual model (Fig.3.1) challenged with SEM but with the group size variable replaced with sociality as a binary variable. An additional relationship between body size and extinction risk, as denoted by IUCN Red list category was included in the expert elicited model structure. The model was compared to two additional candidate models with structures derived from machine learning algorithms (Silander-Myllymaki (SM) and Min-Max Hill Climbing (MMHC)) to investigate the relative strengths of pathways between variables and to determine if any pathways not identified in the conceptual model were important. All three candidate models were constructed using a subset of the data (70%) and subsequently tested using the remaining (30%) data.

Table 3.1: Structural Equation Model (SEM) pathways and the rationale for their inclusion in the model

Path description	Rationale	References
Latitude impacts body size, habitat, guild overlap and home range size	At higher latitudes populations exist at lower densities and as a result resources such as food and mates can be scarce. In addition the impacts of seasonality and snow cover are amplified at greater latitudes and general species diversity decreases reducing the potential for overlap between carnivore species. With lower diversity the variation in habitats available for exploitation by carnivores is decreased despite the increased home range sizes that compensate for the reduced resource availability. It is hypothesised that at greater latitudes body size will be larger which may facilitate the increased movement required to cover the larger home ranges required to cope with lower food availability.	(Ferguson & Lariviere, 2008; Hillebrand & Azovsky, 2001; Meiri, Yom-Tov, & Geffen, 2007; Stevens, 1989)
Bite force impacts diet	Bite force limitations are thought to have influenced the evolution of mechanisms by which predators subdue their prey after a successful hunt. Bite force thus may be important in determining prey range and prey capture.	(Christiansen & Wroe, 2007)

Habitat impacts home range size, body size, guild overlap and diet	Habitats that are densely vegetated may favour small bodied species for which rapid movements amongst dense vegetation may be easier and which offer more protection from predation. The primary productivity of more densely vegetated habitats is greater than for open habitats. More productive habitats are thought to support a greater diversity of species and thus can indicate the resource availability, in terms of food contained within it and potential for overlap with other carnivore species. At higher resource densities individuals may be able to reduce the area over which they need to range in order to meet their energetic requirements.	(Ferguson & Lariviere, 2008; Gittleman, 1985; Janis, Damuth, & Theodor, 2000; Reed, Finley, Romme, & Turner, 1999)
Lifespan impacts reproduction	Reproductive measures such as interbirth interval, birth weight and gestation length are positively correlated with longevity, with larger longer lived individuals having longer gestation lengths and producing larger young in their litters.	(Gittleman, 1986)

Body size impacts home range size, lifespan, reproduction, social group size, guild overlap and diet	Home range size is strongly dependent on organism size, scaling with metabolic requirements which are themselves known to scale with body size. Lifespan also scales positively with body size, thought to be regulated by metabolism this relationship is unsurprising. The impacts are, however, far reaching particularly when considering the reproductive strategy of an individual and its relationship with body size. There is a negative relationship between body weight and litter size with larger species generally having fewer young. Body size has a strong influence over the diet, with metabolic thresholds needing to be met the size of an individual is important in determining the amount of energy that it needs to consume and thus the type of prey that it targets. The size of an individual may limit the prey that it is physically able to successfully capture and consume. The size of an individual can be an important determinant of predation pressure and the degree to which it must compete with other species in the guild, with smaller species being at higher risk of being predated by organisms larger than themselves and this may impact extent to which sociality is seen amongst species.	(Carbone, Teacher, & Rowcliffe, 2007; Haskell, Ritchie, & Olff, 2002; Lindstedt, Miller, & Buskirk, 1986; Owen-Smith & Mills, 2008; Speakman, 2005; Tuomi, 1980)

Social group size impacts home range size, diet and reproduction	Larger groups require more energy to sustain the larger number of individuals and thus may need to range over a larger area in order to encompass the required resources. Groups having potential for a greater prey range may increase their energetic intake but may need to range over larger areas to catch larger prey. Social group size can increase the energy available for reproduction and impact investment in and success of rearing young.	(Christiansen & Wroe, 2007; Creel & Creel, 1991; Montgomery et al., 2018; Muro et al., 2011; Owen-Smith & Mills, 2008)
Home range impacts diet and guild overlap	The diet of a species is likely limited by the prey that it encounters in its home range. Larger home ranges may encapsulate more variable prey items and may contain more large prey items. The presence or absence of larger carnivores may impact the dietary choices of a species.	(Gittleman & Harvey, 1982)

Guild overlap impacts diet, reproduction and social group size.	Where there is a greater number of carnivore species within a guild, spatially and/or temporally overlapping in their ranges interspecific competition may restrict the size of prey that individuals can succesfully defend against competitors and competition may impact the amount of energy available to individuals for reproduction. Where interspecific competition is greater individuals likely gain greater benefits from grouping and thus larger groups may form among species that have to compete with other large carnivores.	(Bekoff et al., 1984; Ebensperger et al., 2012; Karanth K. Ullas et al., 2017; Ramos-FernÃndez et al., 2006)

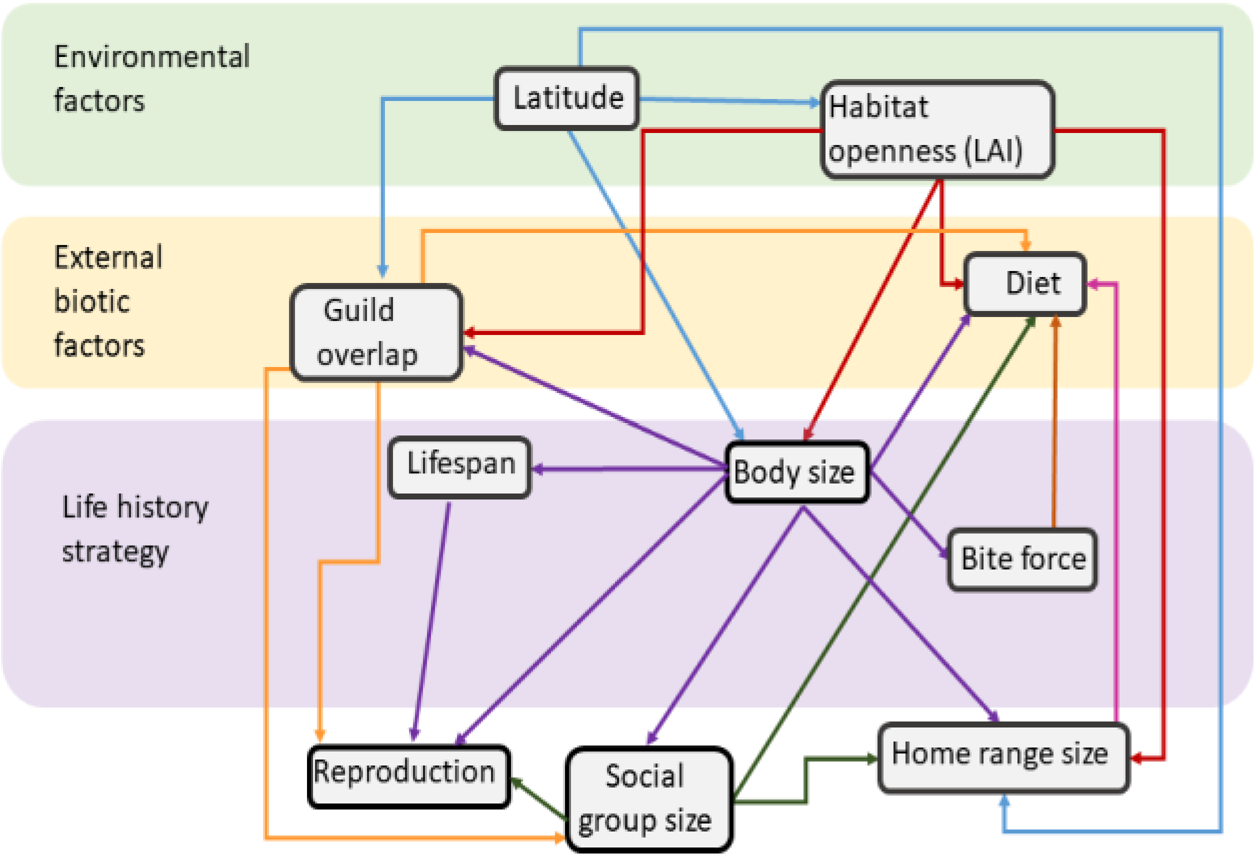

Figure 3.1: Conceptual model of hypothesised variable relationships which informed the structure of the SEM and the Expert elicited Bayesian network (which included the additional variable of extinction threat relating to body size)

3.3 Results

3.3.1 *Life history*

Data regarding body size (Head-body length) were the most complete being available for all species (n = 235), weight data were available for all but one recorded species (*Lyncodon patagonicus*) and skull sizes were available for all but 12 species (*Herpestes fuscus*, *Herpestes ochraceus*, *Herpestes flavescens*, *Genetta cristata*, *Poiana leightoni*, *Pseudalopex fulvipes*, *Procyon pygmaeous*, *Bassaricyon medius*, *Bassaricyon calleni*, *Spilogale angustifrons*, *Melogale everetti*, *Martes gwatkinsii*). Strong positive correlations existed between morphometric traits (Weight, Body length, Footprint length, Skull length) across all species. Population density correlated negatively with body size and this effect was stronger amongst social species (Fig. 3.2.). Litter size was negatively correlated with morphometric traits with larger animals having smaller litters. The length of gestation was positively correlated with morphology and the effects were stronger amongst social animals. Morphometric variables (Skull size, body size, footprint size, body weight) are all positively associated with the first principal component of the model which explains 49.8% of the variance in the data (Fig. 3.3.). Breeding investment, as a function of body mass is negatively related to axis one suggesting that breed investment is higher in smaller animals. Axis two explains a smaller proportion of the variation but is strongly influenced by maximum home range size and negatively impacted by gestation length suggesting that animals with smaller home ranges may also have longer gestation lengths.

3.3.2 *Diet*

Diet ranges calculated from the available lists of prey items are variable between species. Amongst the canids social species generally have a larger upper size limit to prey with the Culepo (*Pseudalopex culapeus*) and the Arctic fox (*Alopex lagopus*) being the only solitary canids eating prey larger than themselves (Fig. 3.4.). In some instances however the quality of the diet data may have skewed the analyses. The largest diet item recorded for the arctic fox was the reindeer (*Rangifer tarandus*) however as the diet data were comprised of records of occurrence of diet items it is unlikely that arctic fox can predate upon reindeer rather than merely scavenge at carcasses. Amongst felids many species were recorded to eat prey larger than themselves and only large bodied species were recorded as social (Fig. 3.5.). Social lions, whilst smaller in size than Tigers had a larger upper size limit to their prey relative to their body weight. Amongst the felids there was a general trend of prey size decreasing as body size decreased. Amongst viverrids, herpestids and procyonids diets were more variable. Of the 16 species that ate items larger or the same size as themselves ten are social however an equal number of social species were recorded with a diet consisting only of smaller items (Fig. 3.6.).

Analysing diet data using hierarchical clustering based on the presence or absence of prey items in their diet showed no clear patterns or obvious clusters based on hunting or foraging strategies of species. As the data contained only records of items in a diet much of the associated information from the text regarding how the item was incorporated into

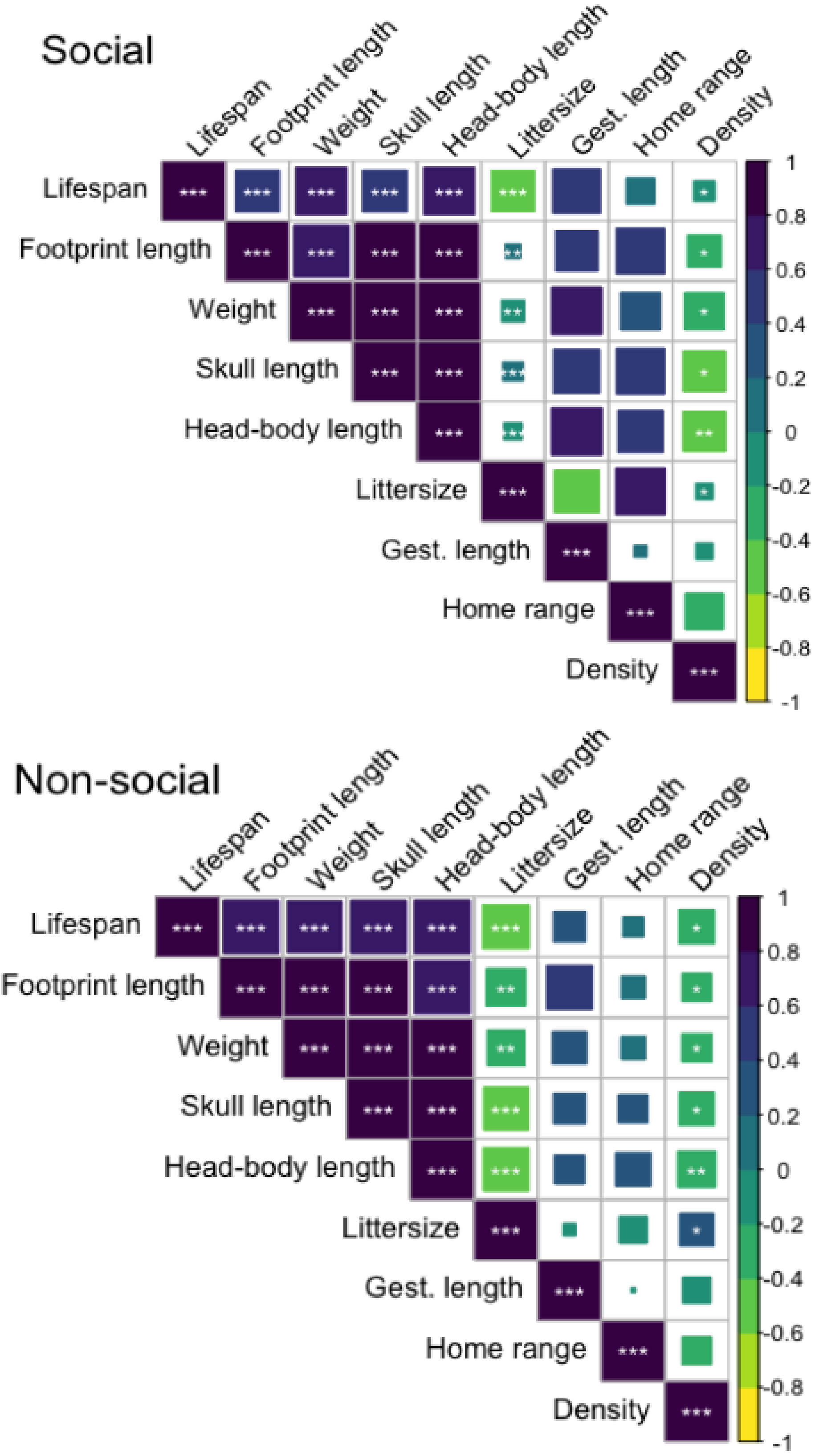

Figure 3.2: Pairs plot dispalying data from correlation matrix of species for which data were available for all ten variables examined in social (top) and non-social (bottom) carnivore species. Correlation strength is denoted by the size of the tile. Colours represent the correlation coefficient. Significance of correlations are denoted by asterisks where *** (0.001), **(0.01), *(0.05).

the diet was lost. Information regarding the acquisition of recorded diet items, hunted or scavenged, actively sought or opportunistically taken, is likely important in trying to understand patterns relating to group formation and the potential benefits gained in relation to energy acquisition. For several species detailed diet studies do exist but for many of the species, particularly small elusive species detailed information is lacking.

The distribution of the size of diet items was quantified using kurtosis as a measure of the spread of variation with high kurtosis scores denoting platykurtic distributions and low kurtosis scores denoting leptokurtic distributions. Kurtosis was slightly higher amongst non social than social species (Fig. 3.7.) suggesting that the prey size for social species is more narrowly distributed that that of non social species. Kurtosis of diet distribution is higher in social than non social herpestids, suggesting social herpestids generally have

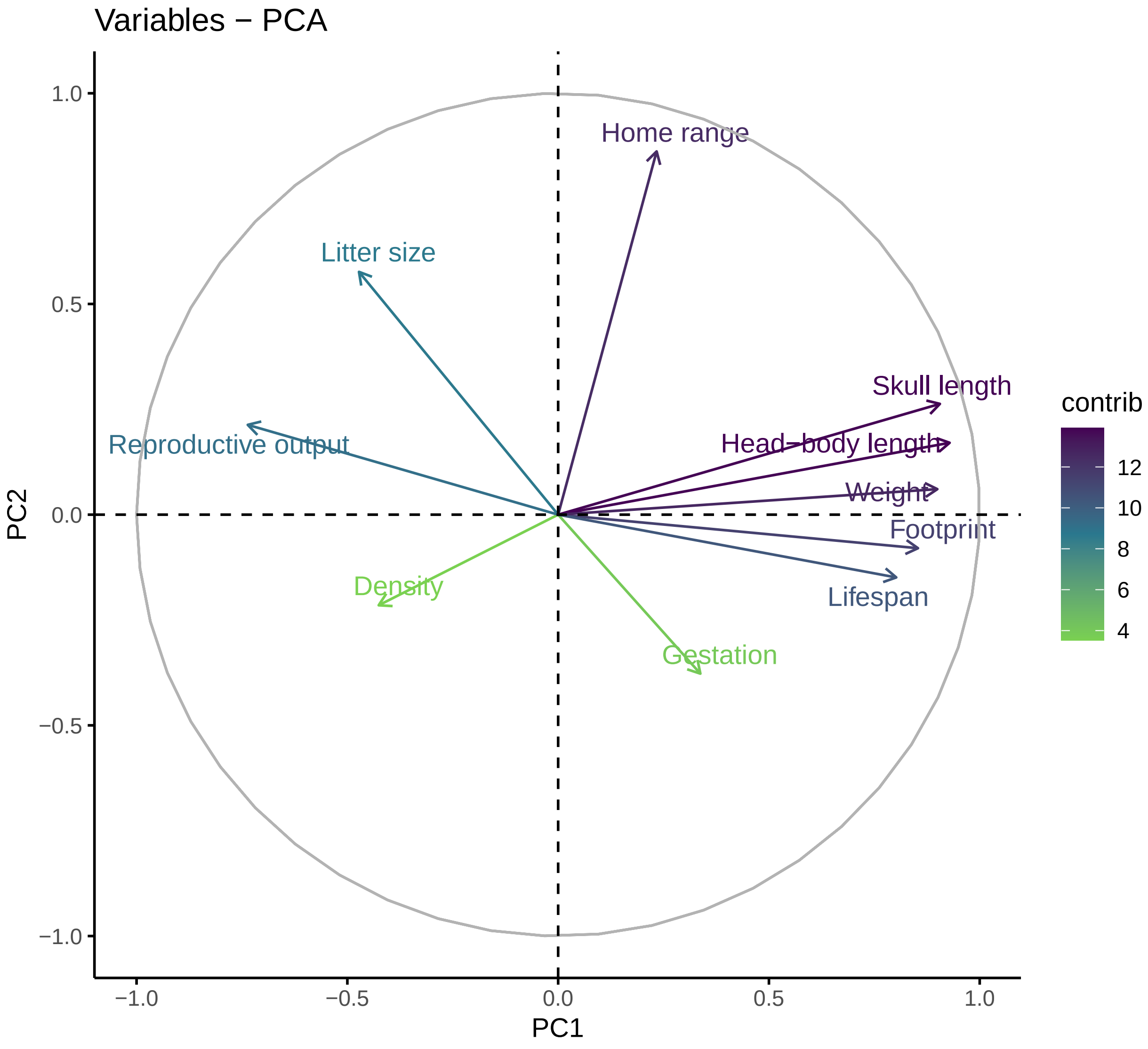

Figure 3.3: Biplot displaying the association of modelled variables with the first and second principal components coloured according to the strength of their contributions.

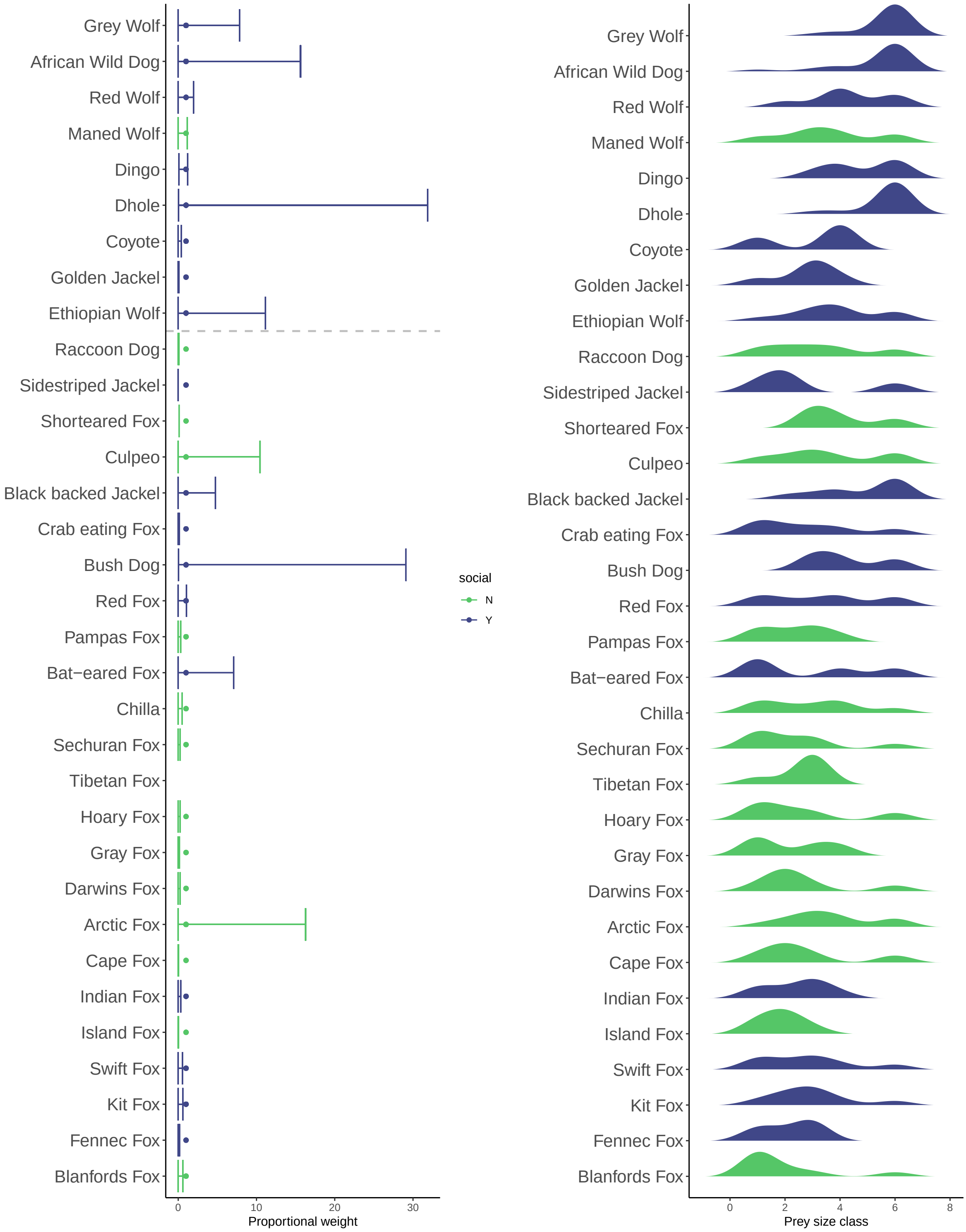

Figure 3.4: Diet range for Canidae showing (left) minimum and maximum size of recorded prey standardised by the weight of the predator with points representing predators (predator weight relative to it's individual weight = 1) and distributions (right) of recorded prey items according to their size (<10g, 10-100g, 100g-1kg, 1-10kg, >10kg). Species along the Y axis are listed in descending body size (based on weight). Grey dashed line indicates 20kg threshold above which species are predicted to feed on large prey (Carbone et al., 1999). Green indicates non-social and blue indicates social species.

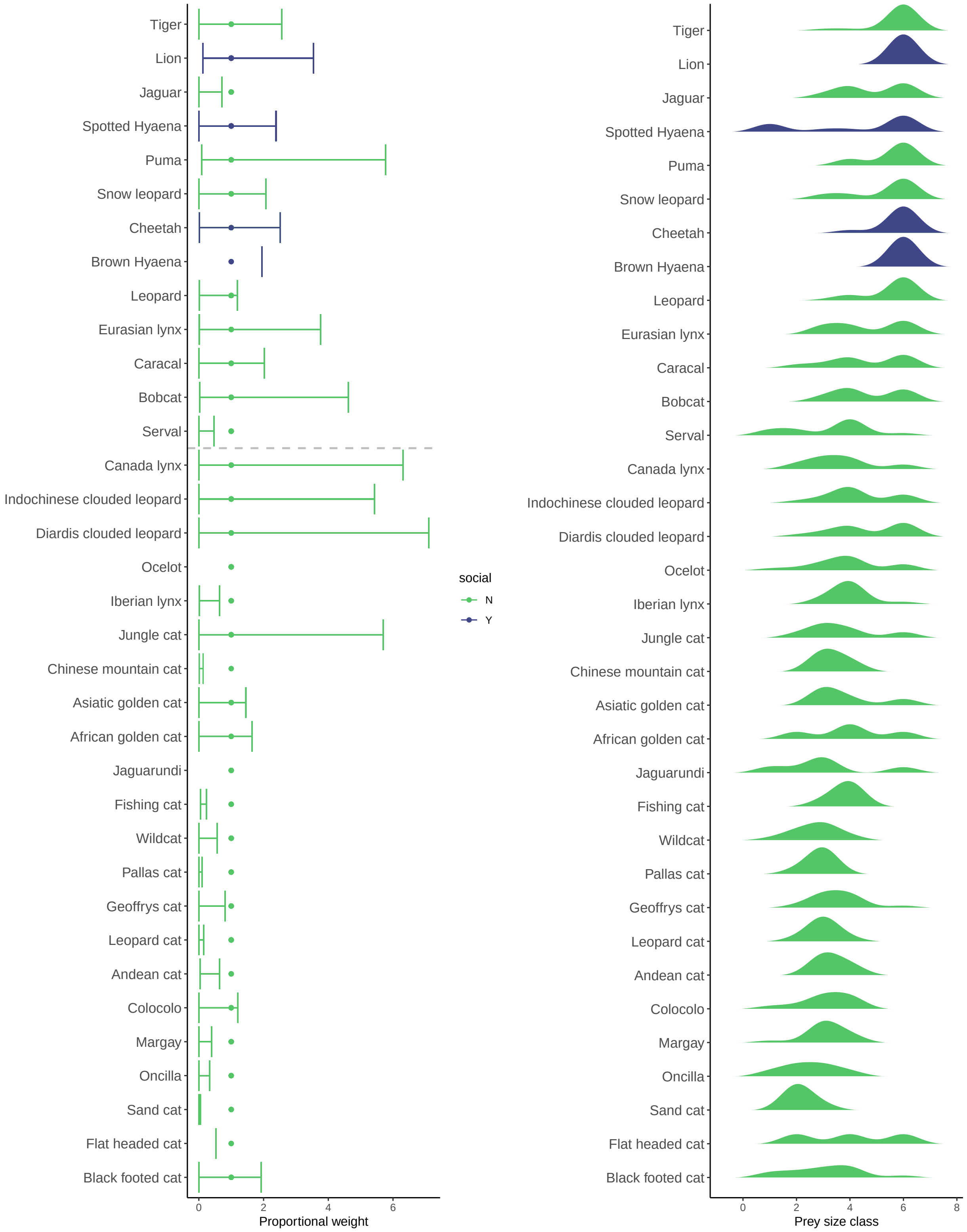

Figure 3.5: Diet range for Felidae and Hyaenidae showing (left) minimum and maximum size of recorded prey standardised by the weight of the predator with points representing predators (predator weight relative to it's individual weight = 1) and distributions (right) of recorded prey items according to their size (<10g, 10-100g, 100g-1kg, 1-10kg, >10kg). Species along the Y axis are listed in descending body size (based on weight). Grey dashed line indicates 20kg threshold above which species are predicted to feed on large prey (Carbone et al., 1999). Green indicates non-social and blue indicates social species.

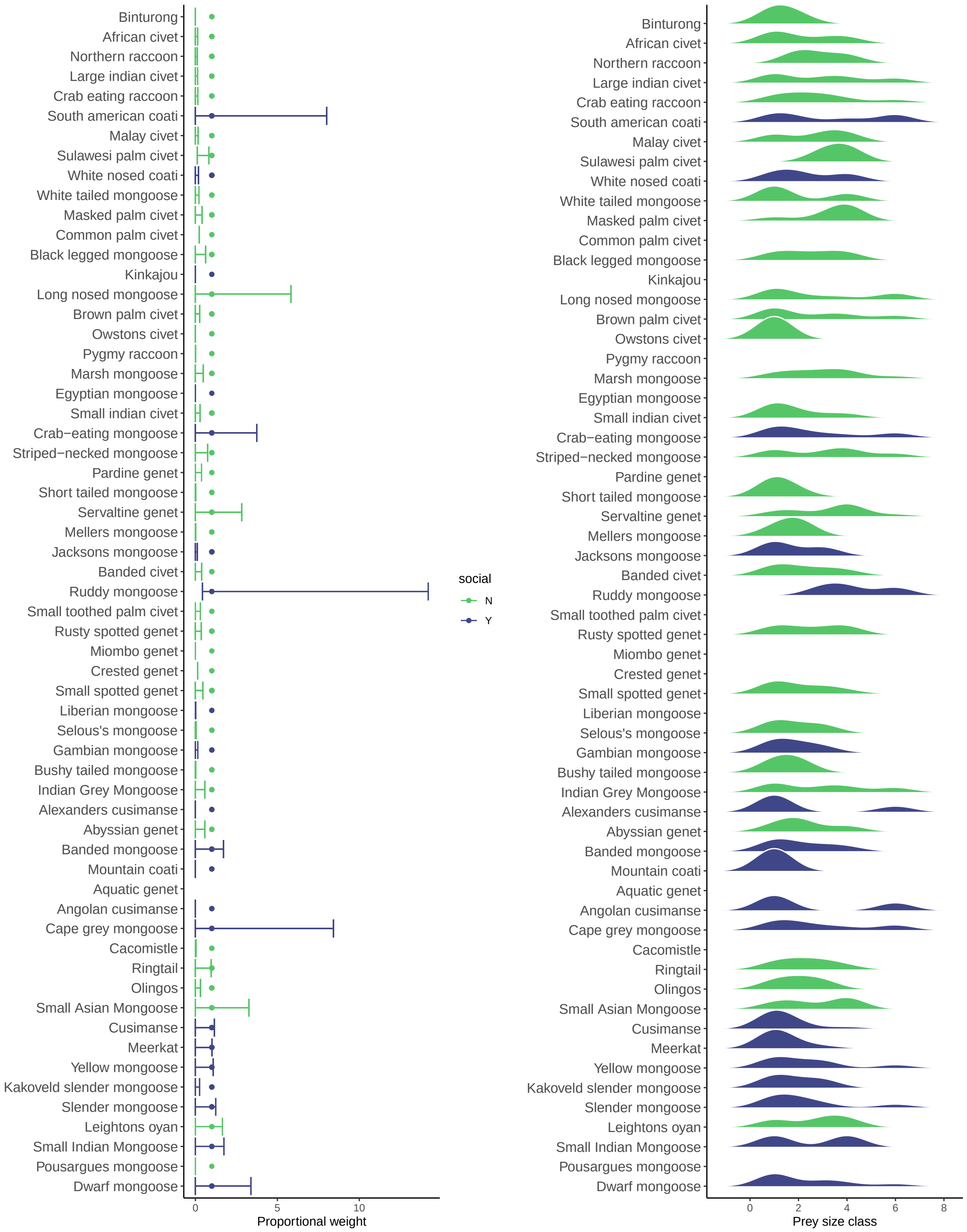

Figure 3.6: Diet range for Viverridae, Herpestidae and Procyonidae showing (left) minimum and maximum size of recorded prey standardised by the weight of the predator with points representing predators (predator weight relative to it's individual weight = 1) and distributions (right) of recorded prey items according to their size (<10g, 10-100g, 100g-1kg, 1-10kg, >10kg). Species along the Y axis are listed in descending body size (based on weight). Green indicates non-social and blue indicates social species.

a wider diet range than non social species within the family. Amongst the felids lions are the only social species and the distribution of their diet has a very high kurtosis suggesting that they also have a wide prey range.

Prey size range may be limited by the physical capabilities of a predator in chewing flesh or bone. Prey range and predator size were both significant predictors of bite forces quantified from Christiansen and Wroe (2007). Predictions from a linear model with body weight, family, mean prey size and prey size range as predictors highlighted hyaenidae (β = 459.377, SE = 55.617, P <0.001) and ursidae (β = 433.173, SE = 116.382, P <0.001) as having significantly higher bite forces than predicted based on their size and diet.

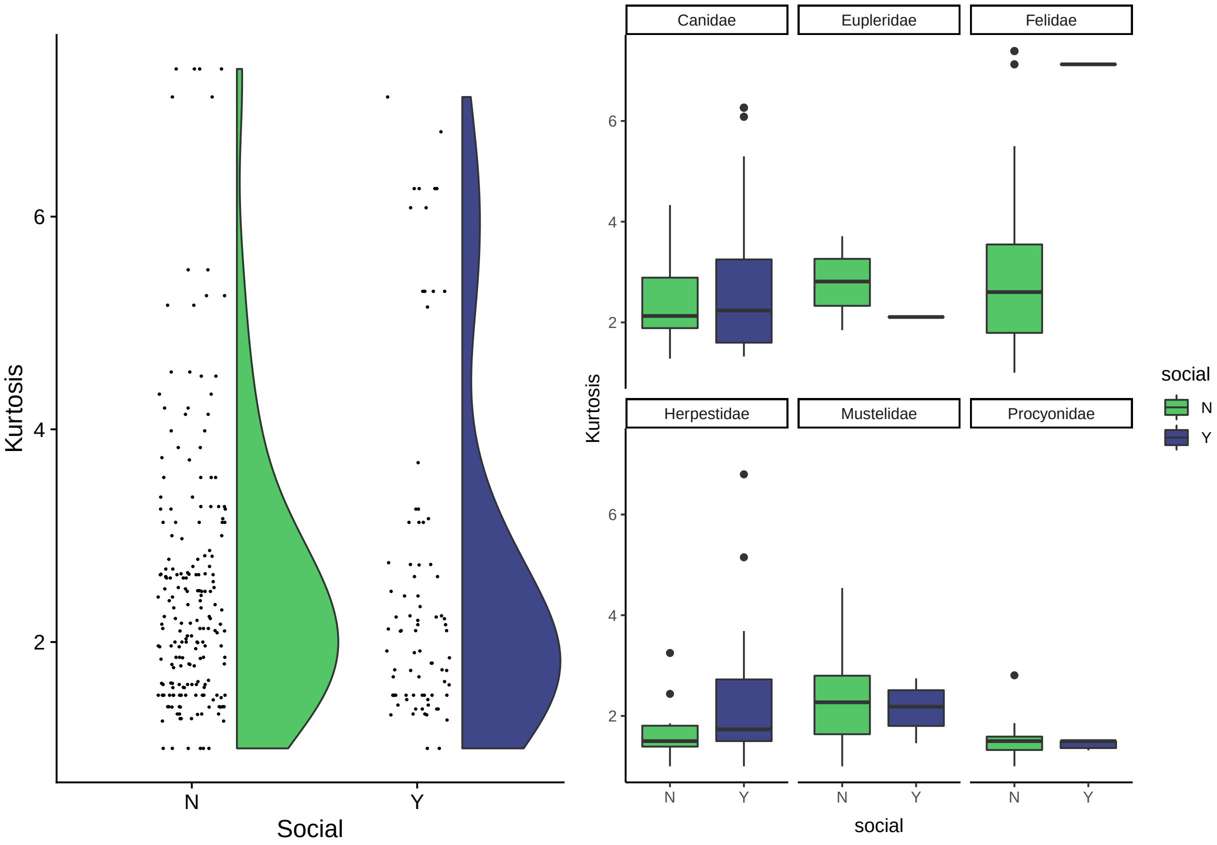

Figure 3.7: Kurtosis scores for diet distributions shown for all species and split by family for those with available data in both the social and non social classes. High kurtosis values represent a wide ranging diet distribution (in terms of size of items incorporated in the diet), low values denote a narrow distribution.

3.3.3 *Habitat*

Habitat data were ordinated using PCA to constrain the variation seen across species (Fig. 3.8.). Axis one relates to the variation in moisture within habitats with generally dry habitats (dry_forest, dry_shrub, artificial pastures) having high axis one scores and

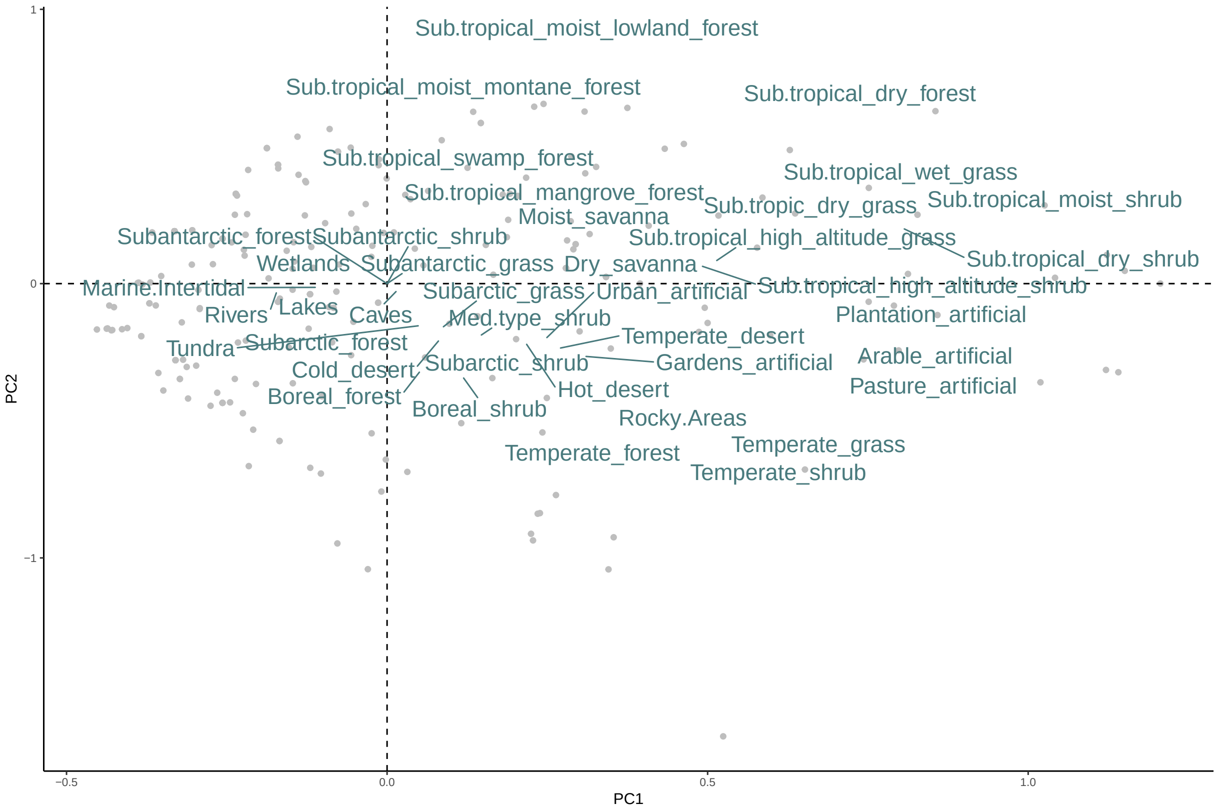

Figure 3.8: Principle Component Analysis of habitat types used by carnivore species

wetter habitats having lower axis 1 scores (marine inter-tidal, rivers, lakes, swamp forest boreal forest subarctic forest) however explains only 22.3% of the variation in habitats used. Axis 2 relates to latitudinal gradient with lower scores denoting more northern habitats (temperate habitats, boreal habitats) and higher scores for more tropical habitats (sub tropical forests, swamps etc.) however it only explains 14.3% of the variation in habitats used. Across all carnivore species the distribution of average LAI was lower in social species than in non social species (Fig. 3.9.). Whilst members of the Hyaenidae and Ursidae are all found in habitats with low LAI measures large variation was seen between species in other families.

Hierarchical clustering of species based on habitat types used by each species showed some clear groups with otters, and mink in a distinct group separate from all other species (Fig. 3.10.). Amongst this cluster all social species (with the exception of the Smooth Coated otter (*Lutrogale perspicillata*)) were closely grouped. In General social species were seen across the dendrogram suggesting no strong clustering of social species based on their habitat preferences. Some small social clusters were seen such as the grouping of Lions , Cheetahs and the Spotted hyaena (*Crocuta crocuta*). Branching at about 0.25

this group represents species that spatially overlap in their ranges and occupy similar habitats. Despite the close phylogenetic relationship between members of the Hyaenidae family the Brown hyaena (*Parahyaena brunnea*) and the Striped hyaena (*Hyaena hyaena*) were not closely grouped with the Spotted hyaena or the Ardwolf (*Proteles cristata*) but were instead contained in a small social cluster with the Gambian mongoose (*Mungos gambianus*). Whilst such groupings may hint at similarities in habitat use by social species the dendrogram shows that there was much variation in habitats used by social species across families. Habitat alone was not sufficient in driving social behaviours to develop amongst species.

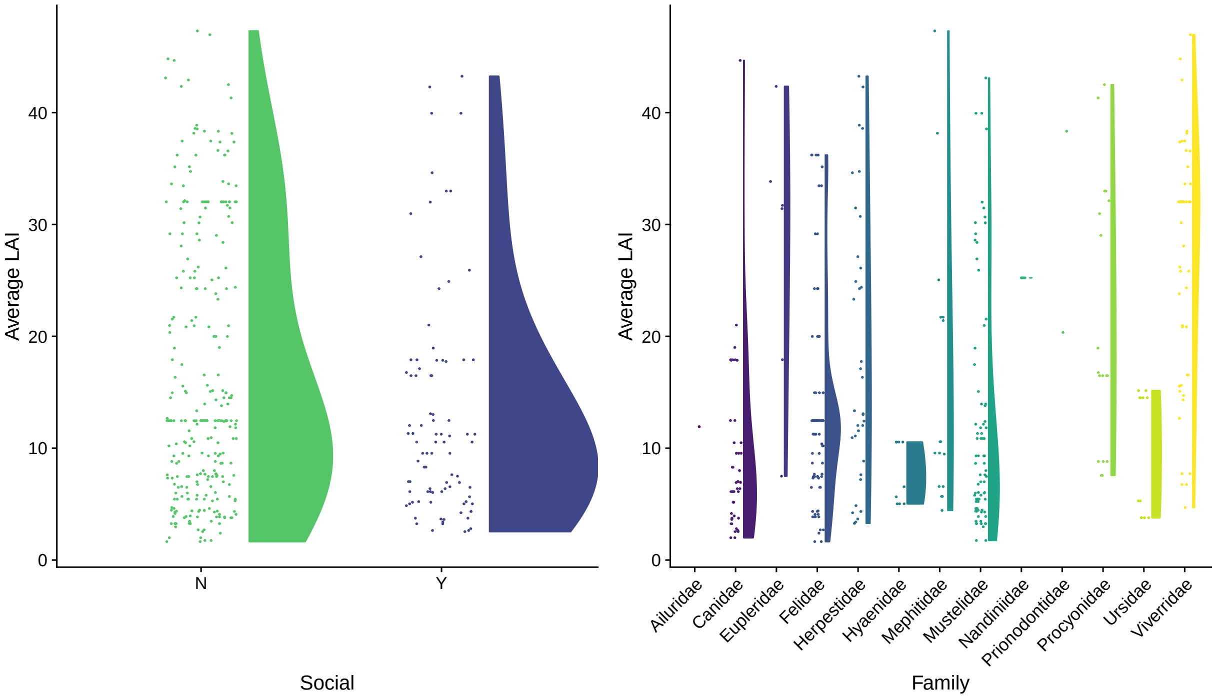

Figure 3.9: Variation in Leaf Area Index (LAI) of habitats within the geographic range of social and non social species and for species in each family

3.3.4 *Interaction Models*

The conceptual model included two variables under diet, maximum prey size and mean prey size as calculated from the available data. The hypothesised relationships were the same for both diet variables and in all cases mean prey size was non significant and therefore removed from the model for clarity. Standardised (Fig. 3.11) and unstandardised (Tab. 3.2) were calculated for all model pathways.

The strongest relationship as identified by the SEM was that of Carnassial bite force on the maximum size of diet items (Std. Est. = 1.061, P <0.001) suggesting that species

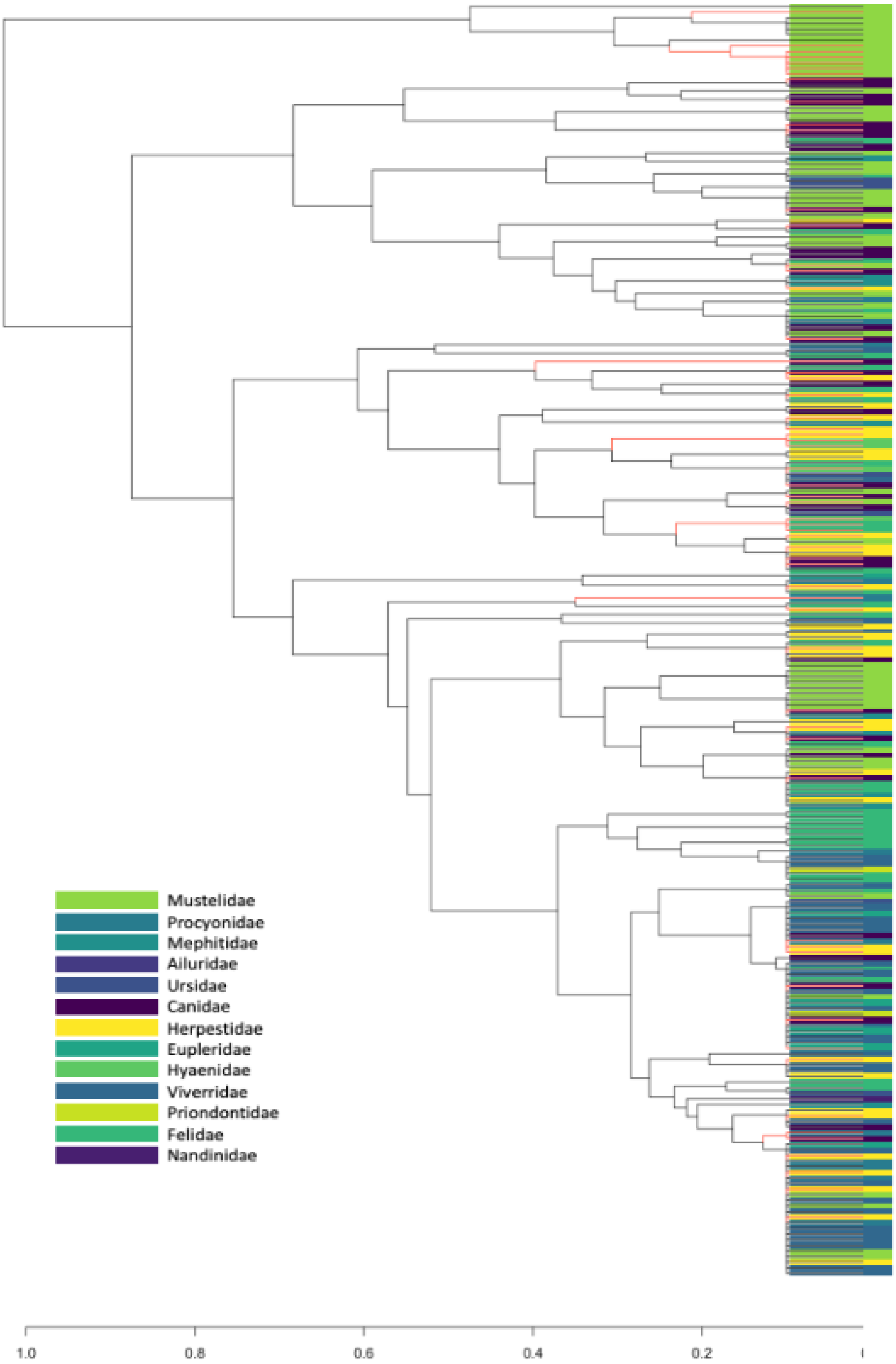

Figure 3.10: Heirarchical clustering of species relationships based on habitat types used by each species coloured according to the family of the species. Red branches denote social species, black branches denote non-social species.

with stronger bite forces had a larger maximum prey size. Maximum prey size was also positively impacted by home range size (Std. Est. = 0.458, P <0.001) and negatively impacted by habitat productivity with max prey size being smaller in more productive, densely vegetated habitats (Std. Est. = -0.157, P = 0.0322). In addition a negative relationship between habitat and home range size was predicted (Std. Est. = -0.196, P = 0.036). Whilst this indirectly links habitat to diet the direct impacts are much greater. The model predicted a latitudinal gradient of habitat productivity which was predicted to increase with increasing distance from the equator (Std. Est. = -0.58, P <0.001). The impact of latitude on body size, although non significant supports the idea that body size increases with increasing distance from the equator. Body size was a significant predictor of home range size (Std. Est. = 0.21, P <0.001), lifespan (Std. Est. = 0.428, P <0.001) and carnassial bite force (Std. Est. = 0.628, P <0.001) suggesting that larger animals have larger home ranges, live longer and have stronger bite forces. The model showed body size to significantly positively impact maximum social group size (Std. Est. = 0.115, P = 0.0189) and negatively impact maximum prey size (Std. Est. = -0.361, P <0.001). However when the indirect effects of body size on maximum prey size (mediated through home range size and through bite force) are considered the overall impact was positive (Std. Est. = 0.411), suggesting that a greater body size increases the upper limit of prey size that can be obtained.

The model predicted maximum social group size to positively impact reproductive output suggesting that larger social groups can produce larger or heavier litters (Std. Est. = 0.213, SE = 3.182, P <0.001). Body size impacted reproduction, which here was a measure of the litter weight relative to body size. The direct interaction suggests that larger individuals have relatively smaller litters (Std. Est. = -0.426, P <0.001). The overall contribution of body size to reproduction when including the indirect effects was negative but the magnitude of the effect is smaller (Std. Est = -0.184).

Group size also positively impacted home range size suggesting that larger groups inhabit larger ranges (Std. Est. = 0.326, P <0.001). The impact of group size on maximum prey size although insignificant was predicted to be negative by the model. The direct impact was negative (although non significant) however when the indirect impact (mediated through home range size) is considered the overall influence of Social group size on diet was positive (Std. Est. = 0.136).

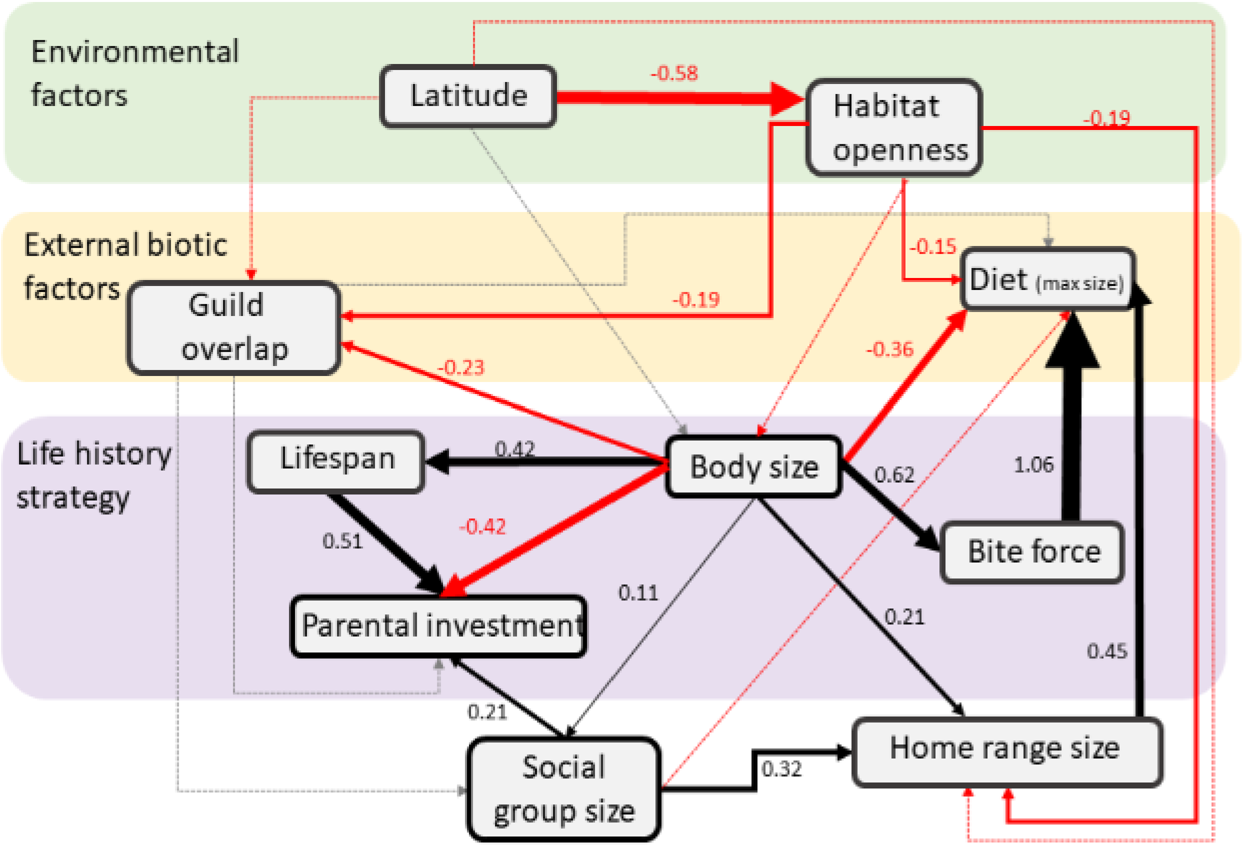

Figure 3.11: Structural Equation Model (SEM) output for all species with standardised coefficients, non significant relationships are denoted by dashed lines, positive relationships (black) and negative relationships (red) are shown with the relative strength of the relationships indicated by the thickness of the path.

Table 3.2: Structural Equation Model (SEM) coefficients resulting from the testing of the conceptual model against species data.

Response	Predictor	Estimate	Std.Error	DF	P.Value	Std. Est.
Size	Latitude	0.1019	0.0888	348	0.252	0.0819
Size	LAI	-0.0902	0.1357	348	0.5067	-0.0475
LAI	Latitude	-0.3800	0.0285	349	<0.001	-0.5797
Prey size	LAI	-2087.3802	966.9022	184	0.0322	-0.1567
Prey size	Size	-2534.8866	462.2117	184	<0.001	-0.3611
Prey size	Biteforce	349.6499	32.1565	184	<0.001	1.0613
Prey size	Group size	-168.0717	581.4638	184	0.7729	-0.0134
Prey size	Home range	103.9495	11.6757	184	<0.001	0.4584
Prey size	Competition	185.8351	794.1919	184	0.8153	0.0138
Home Range	LAI	-11.5223	5.4666	252	0.036	-0.1962
Home Range	Latitude	-0.5952	2.6734	252	0.824	-0.0155
Home Range	Size	6.5124	1.5074	252	<0.001	0.2104
Home Range	Group size	18.0791	2.8968	252	<0.001	0.3257
Reprod. Inv.	Size	-14.3566	1.9303	139	<0.001	-0.4258
Reprod. Inv.	Lifespan	70.7516	14.0649	139	<0.001	0.5078
Reprod. Inv.	Group size	12.8601	3.1822	139	<0.001	0.2126
Reprod. Inv.	Competition	6.3557	5.8265	139	0.2772	0.0980
Group size	Size	0.0640	0.0272	435	0.0189	0.1147
Group size	Competition	0.0672	0.0524	435	0.2006	0.0626
Lifespan	Size	0.1037	0.0098	172	<0.001	0.4284
Biteforce	Size	13.3763	0.6393	239	<0.001	0.6278
Competition	Size	-0.1213	0.0250	347	<0.001	-0.2333
Competition	LAI	-0.1885	0.0634	347	0.0032	-0.1911
Competition	Latitude	-0.0581	0.0415	347	0.1632	-0.0898

Body size had a negative impact on reproduction suggesting that relative to their size larger individuals had smaller litters (Std. Est. = 0.21, P <0.001). The indirect impacts of body size however predict a positive relationship with reproduction. Through the positive impact of body size on lifespan (Std. Est. = 0.428, P <0.001) which in turn positively impacts reproduction (Std. Est. = 0.508, P <0.001) and through the positive impact of body size on group size and maximum group size positively impacting reproduction (P <0.001) there is positive indirect effect of body size on reproduction although this does not outweigh the direct negative impact.

The use of Bayesian networks did not highlight any relationships that were not already included in the SEM. The expert learned structure was the best Bayesian network model (area under ROC: 0.936). The model derived from the Min-Max Hill-Climb algorithm was the next best candidate model (area under ROC: 0.701) (Table. 3.3.). The structure

Table 3.3: Results of Bayesian networks built using three different structures used to test the social node with data.

Model structure	Error rate %	Log loss	Quadratic loss	Spherical payoff	Gini coefficient	Area under ROC
Expert learned	13.95	0.637	0.1744	0.904	0.873	0.936
MMHC	22.48	0.973	0.376	0.8	0.401	0.701
SM	34.88	1.78	0.559	0.705	0.366	0.683

of the expert learned network was similar in structure to the SEM suggesting that the structure as determined by hypothesised relationships, based on biological knowledge performs better than machine learned structures for this data.

3.4 Discussion

Life history traits strongly interact with environmental factors in influencing social group size, this analysis has shown that rather than investigating isolated relationships the system should be viewed holistically in order to fully understand how these interactions impact sociality among carnivores. Understanding what drives sociality requires an appreciation of how factors such as reproductive output and diet breadth, which may increase amongst social animals, interact with environmental factors and impact other behaviours such as ranging. Because sociality can impact a species in numerous ways a broad approach to its study is required in order to fully understand what drives it in different species and populations.

Environmental gradients in primary productivity impact the diets of carnivores, through determining the extent of heterotrophic production which in turn impacts herbivore productivity and ultimately determines the prey base and the energy available to consumers such as carnivores (Creel et al., 2018; Cusens et al., 2012; Ferguson & Lariviere, 2008). Individual carnivores are then constrained in their choice of prey not only by what they encounter but by only being able to consume prey that are of a size they can physically capture (Christiansen & Wroe, 2007; Gittleman, 1985; MacNulty et al., 2009). Therefore the diet of a species is impacted by both the environment and life history traits, with larger carnivores ranging over larger areas and being able to tackle larger prey. The impacts of social grouping in relation to the diet are often considered through the potential for a group to cooperate during hunting to capture large prey (Bailey et al., 2013; Creel, 1997) or to increase the success of hunts (Carbone et al., 2005; MacNulty et al., 2012a). The model demonstrates, however that sociality can indirectly impact the diet of a species and this should be considered when investigating resource acquisition as a potential driver of social group formation. Social group size was seen to impact home range size, with larger groups inhabiting larger areas. A group having a larger territory than an individual may therefore inhabit an area that encompasses more prey, or larger prey, with the increased range having the potential to overlap the large ranges of big prey species. Altering behaviours such as social grouping and ranging may then provide opportunities for individuals to attempt to maximize their fitness in the face of both the physical and environmental conditions with which they are challenged.

With the diet determining an individuals energetic intake the factors that influence diet choices can greatly impact the reproductive capabilities, and thus fitness of an individual. Reproduction is impacted by environmental constraints with mothers needing to gain sufficient energy from their diet to fulfill their own requirements and to support the development of a litter (Angerbjörn et al., 1991; Creel & Creel, 1991; Woodroffe, 1995). In addition to the impact of the environment, individual traits such as size and lifespan can impact the reproductive strategies that have evolved for different species (Borg et al., 2015; Manlik, 2019). Reproduction is a behaviour that is mediated by sociality,the model here showed that larger groups have the potential for higher reproductive outputs.

Reproduction is energetically costly, particularly for mothers who must first support the growth and development of a foetus, birth, and then support a growing offspring. Where an individual is reproducing or supporting young it must invest a significant amount of time and energy into supporting its offspring thus the benefit of being able to share the load of this work would greatly reduce their individual energy burden. Where a reproducing individual is part of a group they may have the ability to extend foraging bouts by benefiting from group members babysitting or group members may provision young (Chen, 2019; Knight et al., 1992). These behaviours can lead to increased energy intake for young which may result in higher survival from faster growth rates. The birthweight of young will be limited by the size of the species, as larger young with higher growth rates have been demonstrated to have increased fitness (Sparkman et al., 2011) the potential for social behaviours to increase the energy available to young therefore may offer a means by which individuals can increase their fitness despite the evolutionary constraints of traits such as size. The data suggests that social species had longer gestational periods relative to their body size with sociality potentially increasing the production of more precocial young. Although the longer gestation period comes at a greater cost to the reproducing mother the costs may be absorbed by groupmates through mechanisms such as groupmates provisioning mothers due to the potential future benefits to the group from larger or more numerous young (Macdonald et al., 2004; Smith et al., 2012). If group members can compensate for the reduced capabilities of a reproducing mother enough to allow her to produce more or larger young it may have future benefits to the group. A greater number of young may bolster group numbers allowing them to expand their territory or increase their hunting success. Yet a litter of larger young may develop more rapidly and sooner be able to contribute to the group and help to defend a groups territory or increase their foraging success or strengthen the groups ability to drive away predators or competitors.

In addition to the variation in reproductive strategy that can be impacted by sociality there exists variation in the structure of social groups that can impact reproduction. Several social species restrict the number of individuals that can be reproductively active within the group at any one time (Carlson et al., 2004; Derix et al., 1993; Montgomery et al., 2018). Data detailing the complexities of different social breeding behaviours including group structure and tradeoffs between size of young and litter size were too sparse for inclusion in this model. Inclusion of such information along with detailed information regarding predation risk among different species could be an interesting area for future investigation using this approach. It is worth noting that the modelling undertaken here comprises information smmarised over large geographic ranges thus indicating the average representation of widely distributed species. The nature of comparing species across an entire Order requires data that it is of a more general resolution, investigations of finer scale variation in the behaviour of a species would be beneficial but was beyond the scope of this study.

Here factors relating to life history strategy have been shown to have the largest contribution to behaviours including sociality, space use and reproduction. Whilst external and environmental factors are still important in the context of sociality their influence is not as great as the life history factors. It is argued that sociality, space use, and reproduction are plastic behavioural traits that are driven by energetic processes and are used as a means of maximizing fitness in the face of rigid factors that are altered on an evolutionary timescale rather than in response to environmental changes. In order to truly understand what drives behaviour a holistic approach accounting for the interdependencies of various important factors is required. Through examining the processes occurring across different scales we can begin to understand the relative importance of different contributing actors. Only then can a deep understanding be gained that can be used to inform the conservation and management of threatened species. By studying only parts of a system, diet, habitat use, reproduction we can only hope to gain an understanding of individual processes. In order to truly understand systems such as sociality and not just understand responses we need to use methods such as these to investigate the interactions between processes that drive the system both directly and indirectly.

Four

Chapter 4

Factors affecting territory size and group composition in a social carnivore

4.1 Introduction

Sociality amongst animals is thought to have evolved as a result of the functional benefits it confers, generally persisting only when the benefits of social behaviour outweigh the potential costs (Krause & Ruxton, 2002). Amongst carnivores only a small proportion (10-15%) of species live in social groups often deriving different functional benefits from doing so (Gittleman, 1989a). Meerkats use social grouping as a mechanism for minimizing predation risk through enhanced vigilance offered by group membership (Clutton-Brock et al., 2001a). Through social hunting African wild dogs are able to take down and feed on large equids, and spotted hyaenas in groups are able to displace lions from a carcass (Kruuk, 1972).

In addition to inter-specific differences of carnivore social behaviour, intra-specific variation also occurs, such as the difference in female lions associating with males in African prides (Schaller, 2009) but not in Asiatic prides (Chakrabarti & Jhala, 2019). Perhaps the most socially plastic carnivore is the European badger whose social groups vary across their geographic range, from large groups (up to 33) in the UK to small groups, pairs or even solitary animals in Europe (Rogers et al., 1997; Delahay et al., 2000;

Revilla et al., 2001; Johnson et al., 2002; Revilla & Palomares, 2002; Molina-Vacas et al., 2009). Badgers have few predators so they do not benefit from social predator defence in the same way as meerkats. The diet of the badger largely consists of small prey so there is no benefit to them from the potential for groups to co-operate and hunt large prey as African wild dogs do. Group living has the potential, however, to increase disease risk through close proximity to other individuals and can reduce resource availability through increased intra-specific competition (Lindenfors et al., 2007). There are clearly costs to sociality in badgers and any benefits are not obvious, yet they must exist in order for sociality to persist.

Several hypotheses have been postulated trying to explain group living in badgers (Table. 4.1). Many of these hypotheses focus on the interaction between groups and the territory which they inhabit. Badgers hold territories which must contain the resources required for individuals and groups to persist; a sett (underground burrow system), areas in which to forage and access to mates for reproduction.

Setts represent considerable resources, requiring specific soil composition to support the network of tunnels and chambers that can be used by numerous individuals comprising a social group (Balestrieri et al., 2006; Kruuk, 1978a). Once established they may constrain the ability of badgers to disperse to new areas (da Silva et al., 1993). Where individuals share a territory they forage individually relying on a diet largely comprised of earthworms (*Lumbricus sp.*) requiring energy equivalent to an estimated 169 earthworms per day (Kruuk, 1978a). Badger populations are generally stable in the UK with low dispersal rates and stable territory boundaries (da Silva et al., 1993; Dugdale et al., 2007; Pope et al., 2006; Rogers et al., 1997; Roper et al., 1986). Variation exists between social groups in their use of space and it is this variation that has been a crucial component of the development of the Resource Dispersion Hypothesis (RDH) (Carr & Macdonald, 1986).

The RDH has been progressively synthesised into a hypothetical model that proposes a mechanism by which sociality in carnivores may have developed (Macdonald, 1983). Crucial to the RDH is the idea of heterogeneity in the environment (Macdonald & Johnson, 2015). The hypothesis generates three predictions for carnivore populations. 1: that territory size is determined by the dispersion of resources. 2: that social group size is determined by resource richness. 3: that group size and territory size are independent of each other (Johnson et al., 2001a). Since it was first proposed there have been several

Table 4.1: Hypotheses put forward to explain group living in Badgers.

Hypothesis Poroponents	Mechanism	Predictions and Interpretations
Resource Dispersion Hypothesis (RDH). Kruuk (1978)	Resource availability varies with space and time and animals will hold territories that account for this variability by sometimes defending extra resources.	Territory size is determined by dispersion of resource patches. Larger territories will be seen where the distances between resource patches are greater. Group size is determined by the heterogeneity of resources and the richness of resources. Larger groups willl persist where resource patches are richer. Territory size and group size are unrelated.
Constant Territoriy Size Hypothesis (CTSH). Lindstrom (1980)	Good years give excess resources. Larger group sizes can exist in better years. The group should be reduced to its primary members at least once every lifetime with group size limited by emigration of subordinate animals under poor conditions.	Territory size is constant despite interannual variation in food supply. Group size is dependent on resources. Long term studies have rarely seen the reductions predicted and when food availability is low breeding females and their cubs rather than subadults are more likely to suffer mortality (Woodroffe and Macdonald, 1993). Regarded as a temporal extreme of RDH.
Prey Renewal Hypothesis (PRH). Waser (1981)	Prey renewal rate determines territoriality.	Low rates of prey renewal favour territoriality. Rapid rates of prey renewal would increase the number of conspecifics that could be tolerated on the territory.

Territroy Inheritance Hypothesis (TIH). Lindstrom (1986)	Secondary animals reach reproductive status by inheriting natal territory. Group formation depends exclusively on food abundance.	Groups only form in small territories. Maximum group size is 4-5 adults. Assumes no cost to an adult maintaining a territory that is sustaing a group even before it has assembled a group - the model is concerned with the maintenance rather thant the origin of group living (Woodroffe and Macdonald, 1993). Thought to require RDH as an underlying driver.
Antikleptogamy Hypothesis (AKH). Roper et al. (1986)	Territories are maintained by males and act to prevent access to females.	Predicts seasonal changes in territory defence and latrines on borders between groups. Older females have been found to spend more time visiting latrines than males. Both males and females are found living in exclusive territories defended against both sexes (Latour, 1990; Pigozzi, 1987). Gives no explanation of the lack of correlation between group size and territoriy size.
Cub Defence Hypothesis (CDH). Wolff (1993)	Territoriality in females has evolved to reduce infanticide and is independent of the distribution and abundance of food. Predicts a seasonal pattern of defence and aggression.	A territory is defended to keep intruders as far as economically possible from the nest site. Assumes that the spacing of females is dependent on resources and that the spacing of males is dependent on the spacing of females. No explanation of male groupings that are seen in badgers.
Den Site Hypothesis (DSH). Doncaster and Woodroffe (1993)	Location and size of the den determine the asymmetrical configuration of territory borders and thus determine territory size and shape.	The resource quantity and quality contained within a territory is dependent on the location of the main sett.

Passive Range Exclusion Hypothesis (PREH). Stewart et al. (1997)	Central foraging place creates a gradient in resource availability which maintains territory size and shape which in turn regulates group size.	Predicts that once a resource gradient is establisehd, a strategy of preferential feeding optimizes food intake. Theory predicts that the presence of a territory owner signals unprofitable foraging which increases avoidance by intruders. Range exclusion theory is expected to break down at low food patch densities (regardles of patch richness). Range Exclusion shoud be strong in non-kin groups living in restricted locations (e.g. limited resting sites), where food is not highly mobile relative to the predator, where individauls forage solitairliy or in subgroups and where food has a homogeneous or multi patch distribution.
Integrative Hypothesis (IH). Revilla and Palomares (2002)	Ecological constraints determined by the availability of key resources shapes the degree of competition between individuals. Demographic constraints are defined by mortality rates of dominant individuals and of animals during dispersal. Behaviour is constrained by the same conditions that favour philopatry over dispersal.	Assumes the basic social unit of a pair with high competition during periods of food stress encouraging young animals dispersing from their natal territory. Predicts philopatry to be adopted where competition for food is low.

variations on the RDH in addition to alternative hypotheses. Proponents of the RDH however maintain that most of the variations rely on the RDH as an underlying mechanism (Macdonald & Johnson, 2015).

Badgers are territorial, defending areas containing resources through scent marking and defecating at territory boundaries (Roper et al., 1986, 1993; Tinnesand et al., 2015). For badgers a trade off therefore must exist between the need for territories that are large enough to encompass sufficient resources for all, but that are simultaneously economically and energetically defensible. Badgers have been considered to be contractionists, defending the smallest territory possible (Kruuk & Parish, 1985). A group of badgers will require more energy than an individual and thus more resources are required to sustain the per capita energy intakes (Johnson et al., 2001b). According to the RDH social groups are only able to exist provided that all individuals can satisfy their resource needs without imposing unsustainable costs on each other (Macdonald & Johnson, 2015).

Challenging the RDH and understanding the drivers of sociality in badgers has always been limited by difficulties in measuring the resources they use, both their availability and dispersion (Johnson et al., 2001a, 2001b). Food has been the resource of primary focus, (Macdonald, 1983; Kruuk & Parish, 1985; da Silva et al., 1993) whilst the distribution of setts has been postulated to influence territory size and shape (Doncaster & Woodroffe, 1993) the availability of females (Roper et al., 1993) has also been investigated as the potential resource determining space use. Individual habitat features have also been identified as being important in determining badger demography (da Silva et al., 1993; Delahay et al., 2006; Johnson et al., 2001a). Few studies, however, have recognized the fact that many of the habitat components of relevance to badgers, food availability, habitat type, and climate are not independent of each other and may interact. A natural consequence of this is that attempts to explain badger social structure and space use may have missed or mis-identified key ecological processes determining the observed space use characteristics and ultimately the potential drivers of sociality. Because many of the processes are interdependent it is impossible to assess their relative contribution to badger demography unless their joint contribution and interdependence is analysed together with the badger demographic response. This can be achieved using Structural Equation Modelling (SEM) which provides a robust framework for studying hypotheses about multiple processes operating in a system (Palomares et al., 1998; Grace et al., 2010) and has been successfully used in ecological research to demonstrate interconnected factors regulating populations (Elmhagen et al., 2010; Elmhagen & Rushton, 2007; Eisenhauer et al., 2015). Understanding the relative contributions of different factors may help in understanding their impact on the social grouping of badgers which in turn would give clues as to the plasticity of social behaviours seen among different populations of the species. Incorporating both direct and indirect drivers that can influence the environment in which a badger inhabits could give insight as to how such factors directly and indirectly impact the social organisation of these animals.

4.2 Methods

4.2.1 *Conceptual model*

A conceptual model of space use was developed based on resource acquisition and territory defense (Fig.4.1). The pathways that comprise the conceptual model are detailed fully in (Table.4.2). The model relates to space use in the context of fixed spatial resources and temporally varying phenomena such as weather which impact on resource acquisition. Badgers occupy territories which provide them with a sett and space in which they can forage for food resources, predominately invertebrates. Competition for space with other social groups leads to defence behaviour at territory boundaries. Here it is hypothesised that the density of animals in territories is a function of numerous interacting exogenous variables with varying temporal and spatial domains that cannot be influenced by the badger, and endogenous biological phenomena, such as reproduction, that can be. A badger has no control over the landscape composition, this is a fixed spatial domain and for the most part has a long temporal dimension, ultimately individuals only occupy landscapes that are suitable. Overlying the landscape is the more temporally varying exogenous driver of weather, which includes rainfall and temperature. These two variables are key drivers of the population processes that lead to food generation such as earthworm reproduction (Edwards & Bohlen, 1996) as well as influencing the behaviours that cause the invertebrates to be active and therefore available to badgers. Food availability thus varies through both time and space. Whilst variation in weather conditions may be predictable at a seasonal scale, short term variations in weeks and months may not be. Badgers therefore face issues in ensuring their sustained presence in the face of short-term unpredictable food resources and thus must vary their demography and behaviour, and maximize fitness as a response.

Table 4.2: Hypothesised pathways of relationship incorporated in Structural Equation Model

SEM Pathway and description	Rationale	References
1. Cub production and territory defence are influenced by adults in the group	The number of adults belonging to a social group will impact the amount of territory that can be defended, for a territory area to be defended the individuals in the group have to be able to produce enough scent marks and faeces to mark boundary latrines with adult males making the greatest contribution. The number of adults in a social group can also impact on the production of cubs, with per individual productivity decreasing with group size increases and groups with non breeding female helpers having been shown to have smaller litters.	(Brown, Cheeseman, & Harris, 1992; Dugdale et al., 2007; Kilshaw, Newman, Buesching, Bunyan, & Macdonald, 2009; Mallinson, Cresswell, Harris, & Cheeseman, 1992; Woodroffe & MacDonald, 1995; Woodroffe & Macdonald, 2000)

2. Larger territories have more resources	Larger territories likely contain more resources and must be more heterogeneous than smaller territories. Female reproductive success is related to body condition and the size of home range territory that females use. Resource availability is correlated with bodyweight of both adults and cubs and may therefore impact on the survival of cubs to emergence from the den. In addition larger territories are more likely to have resources such as annexe setts which are important in the successful rearing of cubs where multiple females are breeding in any one year. With a greater amount of resources available to a group more cubs can be supported by that group.	(Carpenter et al., 2005; da Silva et al., 1993; Delahay et al., 2006; Rogers et al., 1997; Woodroffe & MacDonald, 1995)
3. Possession is 9/10ths of the law	Setts represent a considerable resource and once established may constrain the ability of badgers to disperse to new areas. The stability of territory borders through time has been well documented, with little change in territories between years the resources that were held in the previous year will likely impact what is held by any group in a given year. Low dispersal rates of badgers suggest that variation in group size and demography between years is strongly influenced by the group size in the previous year. Thus it is hypothesised that the number of individuals (adults and cubs) within a group and within a neighbouring group will be hghly dependent on the size of that group in the previous year.	(da Silva et al., 1993, 1993; Dugdale et al., 2007; Kamath and Wesner, 2020; Pope et al., 2006 ; Rogers et al., 1997; Roper et al., 1986)

4. Neighbours create conflict and competition	A greater number of neighbouring territories will impact on a groups territory by reducing opportunities for territory expansion. Although known neighbours may decrease between group aggression their presence will restrict the available space for territory expansion.	(Palphramand & White, 2007; Tinnesand et al., 2015)
5. Land aspect influences the quality of habitat area	At a larger-scale land aspect influences the environment through its impact on local scale ambient temperatures and water movements which can affect vegetation and subsequent habitat quality. In addition to the land aspect, habitat type will also impact food availability, topographical and vegetation differences interact and can influence the micro climatic or soil characteristics that relate to the biomass and emergence behaviour of worms, the primary prey item for badgers.	(Curry, 2004; Delahay et al., 2006; Holland & Steyn, 1975)
6. Winter weather impacts reproduction and survival	Winter weather will impact food availability which can in turn affect breeding and population survival. Thus winter weather may impact the number of neighbouring individuals that a badger is subjected to and the numbers of young that can be supported.	(Macdonald, Newman, Buesching, & Nouvellet, 2010; Woodroffe, 1995)
7. Habitat type impacts territory size	Habitat type impacts the availability of resources with different habitats provisioning different resources (food, setts etc.).	(Feore and Montgommery, 1999)

Territory defense in badgers, involves repeated marking at boundaries by several individuals. This also serves to communicate the magnitude of space use across adjacent boundaries and possibly also the population densities present (Palphramand & White, 2007). Having to defend a territory and also forage within it to feed creates an optimization problem for badgers. The larger the territory, the more food is likely to be available as habitat and landscape diversity will likely increase, but the more energetically costly it becomes to defend the boundary of that territory. The greater the number of defenders the easier a territory becomes to defend, however, constraints on food availability are imposed, as the larger the group size the smaller the per capita availability of food resources in the territory.

Taken together it is hypothesised that it is this interaction between exogenous and endogenous drivers that determines group size and territory size in badgers. Having identified the exogenous drivers of habitat and climate and endogenous drivers of reproduction and behaviour the relationships that arise from this conceptual model can be challenged using demographic data in an attempt to partition the relationships among potential driving processes and their effects on badger space use and sociality.

4.2.2 *Data*

Data comprised records of social group demography and records of sett size and location for 25 badger social groups from 1982-2010. Data were collected four times per year as part of routine capture-mark-recapture and bait-marking studies undertaken at the Woodchester Park Study site in Gloucestershire. Study site and data collection methods are detailed in full by Robertson et al.(2015).

Demographic data including group size and composition (number of males, number of females, number of adults, number of cubs, number of neighbours) for each social group, were coupled with spatial information (habitat cover, slope aspect cover) from the 2015 Landcover map (Rowland et al., 2015) for each territory area for each year. Eight different habitat types were found in the study area (broad-leaf woodland, coniferous woodland, arable and horticultural land, improved grassland, calcareous grassland, freshwater, salt-marsh and urban habitat types) and covered all eight aspect classifications (N, NE, E, SE, S, SW, W, NW). Habitat and land aspect composition were ordinated using Principal Component analysis (PCA). PCA ordinations were used

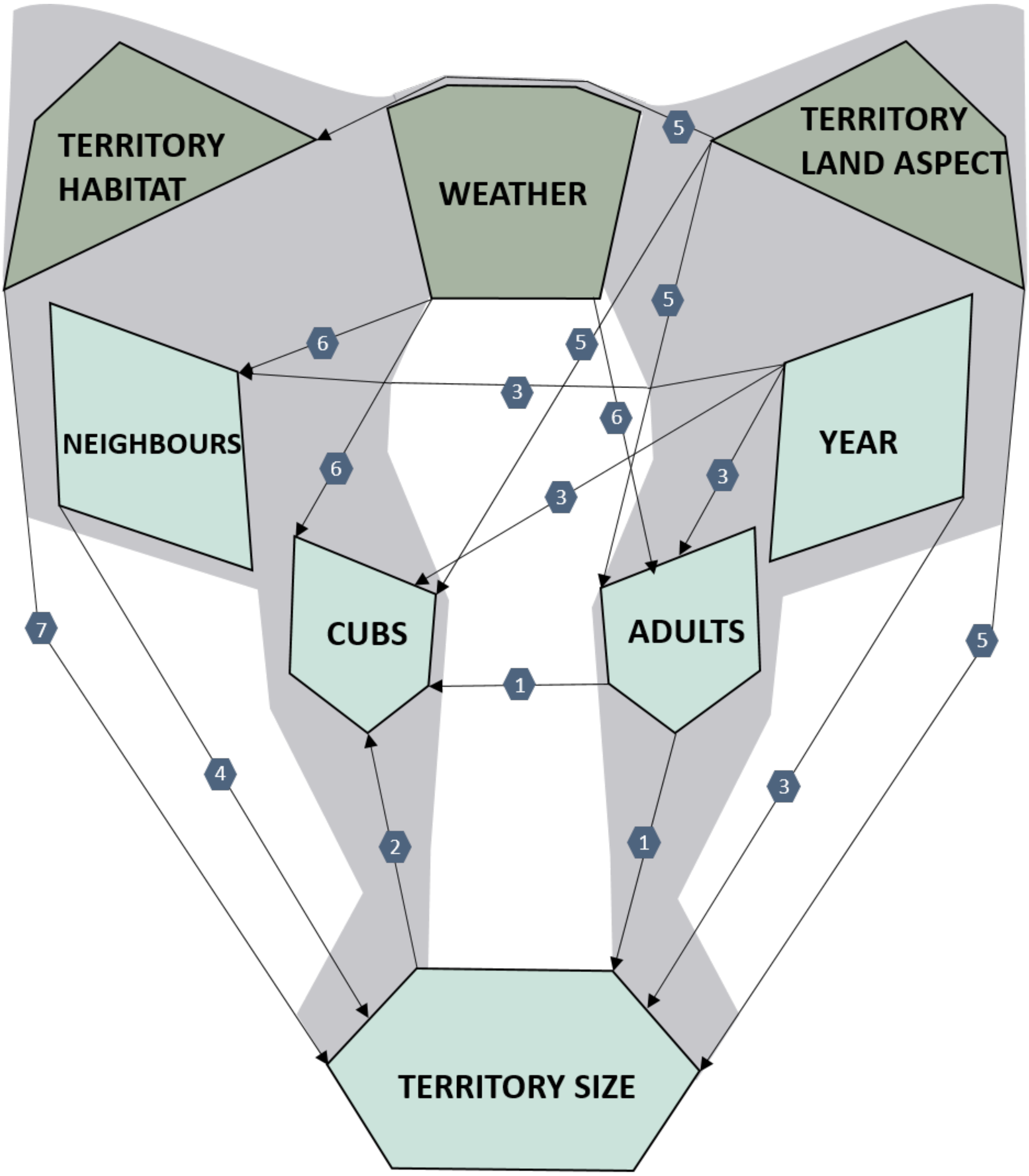

Figure 4.1: Conceptual model detailing hypothesised pathways of interaction influencing badger space use and demography. Pathways between exogeneous (Dark green) and endogeneous (Light green) variables are detailed according to their number in Table 4.2

to reduce the dimensionality of the data in order to identify major trends in the variation in habitat and land aspect composition (respectively) across territories. The principal component loadings derived from these analyses were used in subsequent modelling analyses. Shannon's Alpha diversity of habitat and land aspect were calculated for each group's territory in each year to give an indication of resource variation within territories. Weather data was incorporated as the North Atlantic Oscillation (NAO) scores from January of each year giving an indication of large scale climate variation and thus a proxy for earthworm populations as food availability.

4.2.3 *Models*

To investigate the potential impacts of social group demographics and environmental factors on territory size a series of linear models using generalized least squares (adjusting for temporal correlation with an off diagonal correlation structure (Pinheiro & Bates, 2000)) were used. The models include territory size as a response with predictor variables all modeled at the level of the social group. Predictors were: territory size in the previous year, number of cubs in the group, the number of adults that were in the group, habitat composition and aspect. The indirect and direct effects of drivers on the temporal and spatial pattern of home range sizes were then quantified using Piecewise Structural Equation Modelling (SEM).

Since the data on individual territories were not independent of each other in either time or space, parameters estimated from a Structural Equation Model that assumes independence are likely to be biased. This would lead to an overestimation of significance in putative relationships between variables. Piecewise SEM uses a mixed effect model formulation where it is possible to adjust for the effects of serial dependence in the data through the inclusion of an off-diagonal covariance matrix in the estimation of the standard errors associated with the parameter estimates. This effectively adjusts for the variation associated with repeated measures through time.

However it was hypothesised that individual territories were spatially dependent in that territories were adjacent to each other. Parameter estimates from a piecewise SEM are therefore also likely to be biased from this source of non-independence in the data. This was addressed by simulation with 1000 runs with different permutations. The observed parameter values for the SEM paths were then compared with the sample distributions from the permutation runs. If the model parameters for the observed data differed, were greater or smaller than 95% of the estimates from the 1000 repeat runs it was assumed that the estimate was not likely to have arisen by chance following Manley (2006).

All analyses were carried out in R 3.3.1. (R Core Team, 2016) using the following packages: lattice (Sarkar, 2008), mapview (Appelhans et al., 2017), nlme (Pinheiro et al., 2016), piecewiseSEM (Lefcheck, 2016), raster (Hijmans, 2016), rgdal (Bivand et al., 2017), rgeos (Bivand & Rundel, 2017), semPlot (Epskamp & Stuber, 2017), tidyverse (Wickham, 2017) and vegan (Oksanen et al., 2017).

4.3 Results

4.3.1 *Creating habitat and aspect summary variables*

The first two axes of the Principle Component Analysis of land aspect explained 87.5% of the total variation across territories with axis one component loadings relating to a North-South plane (Fig. 4.2). In the habitat ordination the first two axes of the ordination explained 92.1% of the total variation in the territory location data. Woodland habitat areas had high axis one scores and grassland areas, particularly improved grassland areas had low axis one scores (Fig. 4.2). Axis one scores from each ordination were then used as surrogate simplified variables for aspect and habitat in the subsequent modelling. High aspect values therefore represented territories with more Northern facing land and low aspect values represented territories with more Southern facing land. High habitat values corresponded to territories that contained more woodland habitat and low habitat scores indicate territories with more grassland areas.

4.3.2 *The dynamics of territory size*

Territories in the study area remained relatively stable through time. There were no recorded major changes in land use within the Woodchester park study area through the 28 year study period suggesting that habitats remained stable. Territory size was highly dependent on the size of the territory in the previous year ($\beta = 35.310$. P <0.001). There was a significant relationship between territory size in a given year and the number of cubs born in it ($\beta = 2.844$, P = 0.004), the number of adults it supported ($\beta = -1.5$, P = 0.131) and the weather in that year ($\beta = 1.972$, P = 0.049). This indicates that after

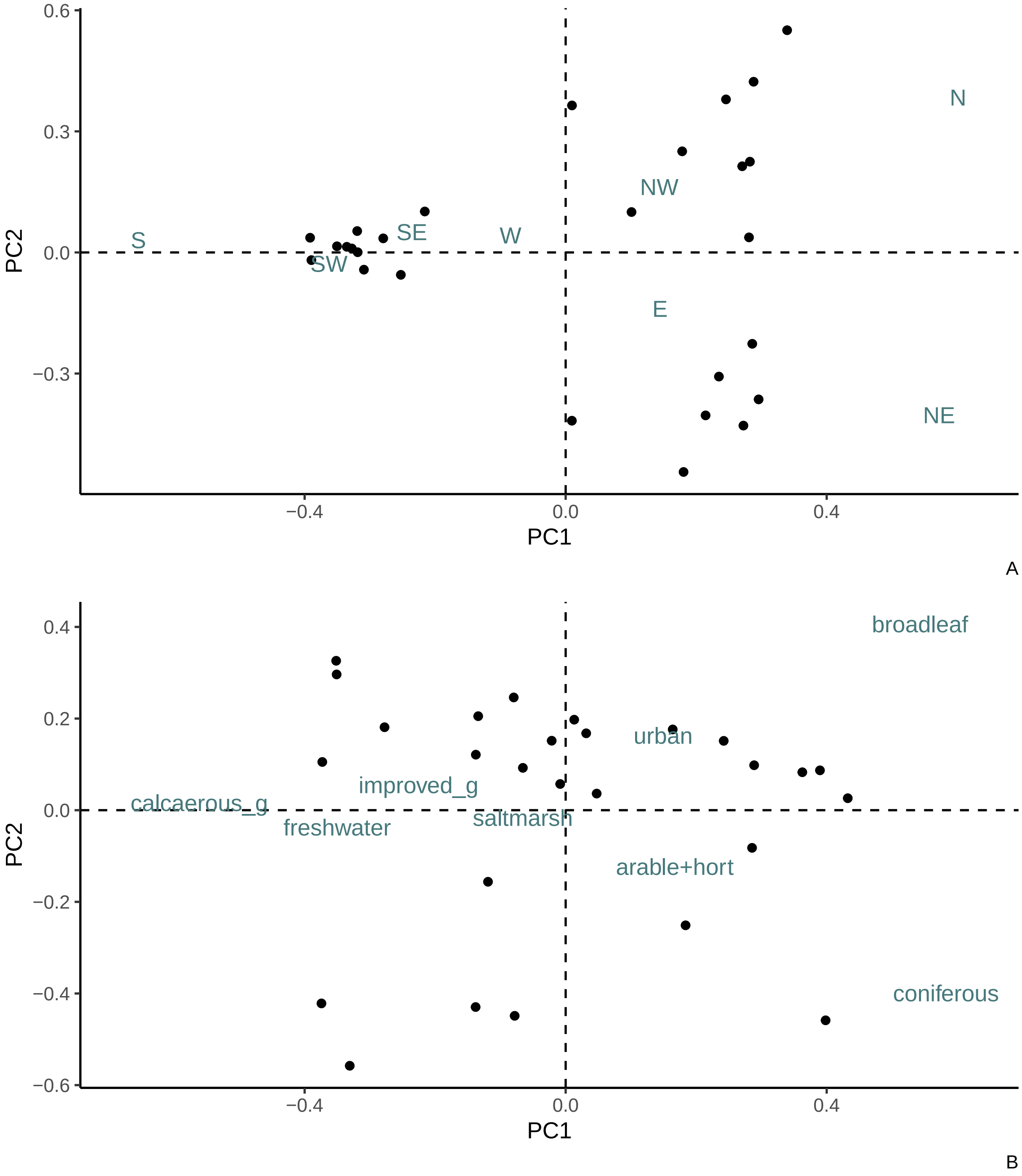

Figure 4.2: PCA ordination of mean proportions of land aspect (A) and habitat cover (B) for all territories through time. Axis one used as habitat variable in subsequent modelling detailing high habitat scores to be territories containing higher proportions of woodland and low habitat scores detailing territories containing more grassland. Abbreviations in the plot represent the component loadings for each of the cardinal points.

adjusting for the previous years territory size, the number of animals present (both cubs and adults) was related to territory size (Fig. 4.3).

The significant relationship between territory size and NAO (β = 1.97, P = 0.049) for the winter suggests that territory size was also linked to weather in the preceding winter. Territory size was highly dependent on the diversity of habitat (β = 3.33, P <0.001) and land aspect (β = 13.38, P <0.001) with larger territories being more diverse than smaller territories. Overall territory size was found to decrease throughout the 28 year study period (1982 mean TSA: 0.286km2, SD = 0.146, 2010 mean TSA: 0.246km2, SD = 0.101). The decrease in territory size is contrasted with an increase in mean group size through time (1982 mean group size: 5.923, SD = 2.326, 2010 mean group size: 8.071, SD = 3.54. The increase in group size coupled with the decrease in territory size led to a decrease in the area per badger contained within each territory.

4.3.3 *Analysing the direct and indirect drivers of space use with SEM*

The full SEM was developed based on the conceptual model (Fig. 4.1) with the addition of an assumed covariance between Neighbours (defined as the total number of adults in all territories that are directly adjacent to a group) and Adults. The full SEM was compared to an alternate with a uni-directional relationship between Neighbours and adults, upon comparison of model AIC the model without the assumed covariance between the two variables was shown to be the better fit and was used as the final model. The final model (Fig. 4.4) had non significant pathways removed for clarity, as their removal had little impact on the modeled estimates. All parameter estimates were either larger or smaller than 95% of the estimates derived from the 1000 permutation model runs. That is they were at extreme values of the permutation coefficient distribution. This suggests that the relationships observed between territory area and the modeled variables assumed determine it did not arise by chance.

Territory size was shown to be strongly negatively influenced directly by habitat (Observed coefficient = -0.337, position in permutation distribution = 995, P = 0.005) with territories containing more woodland being smaller than those containing high proportions of grassland. Territory size was strongly negatively influenced by land aspect both directly (Observed coefficient = -0.28, position in permutation distribution

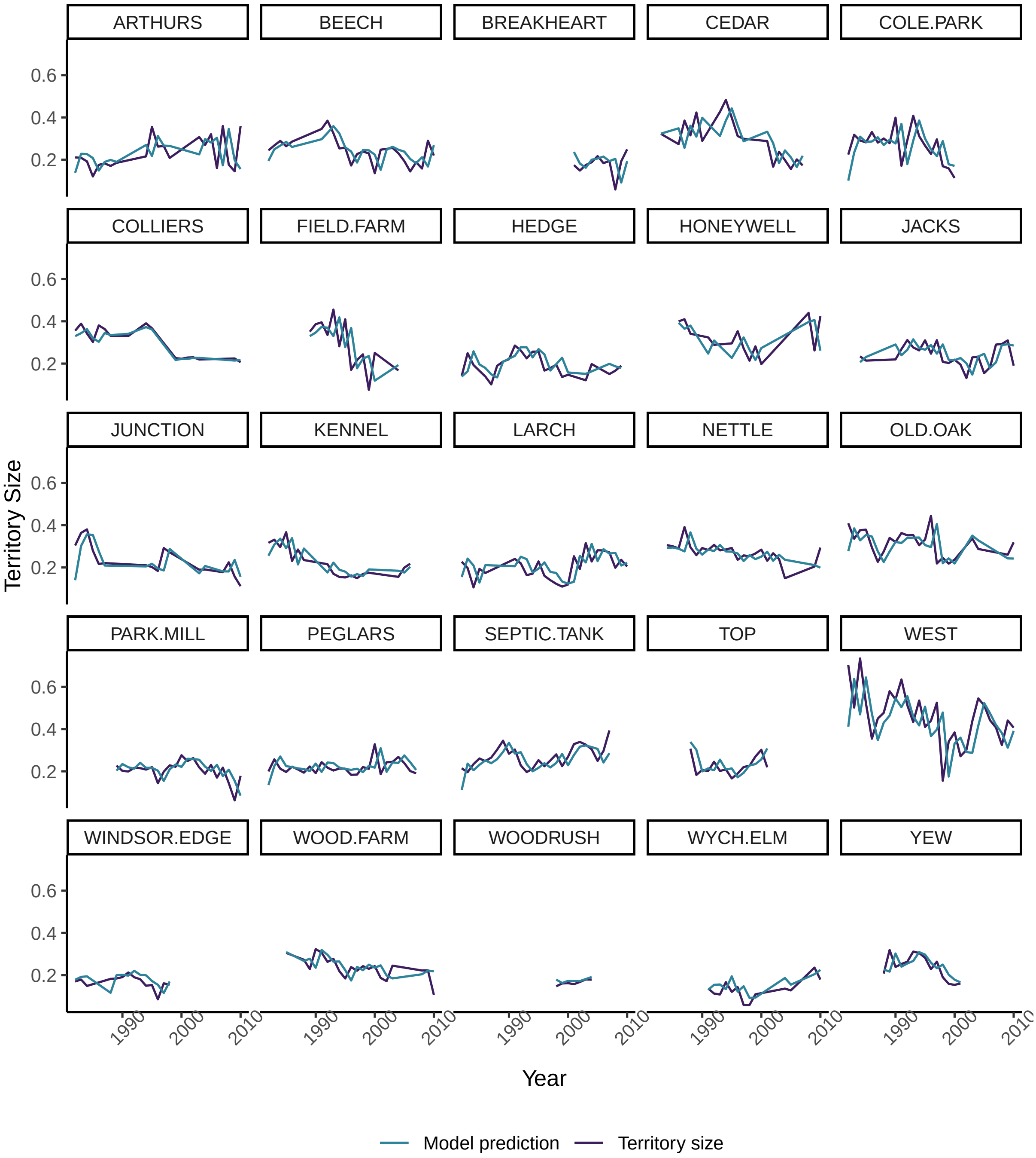

Figure 4.3: Predictions of a Linear model compared to actual territory size for social groups through the study period from years 1982:2010. Linear model relates territory size (TSA) to sett demographics (number of cubs, number of adults and territory size in the previous year) and NAO score.

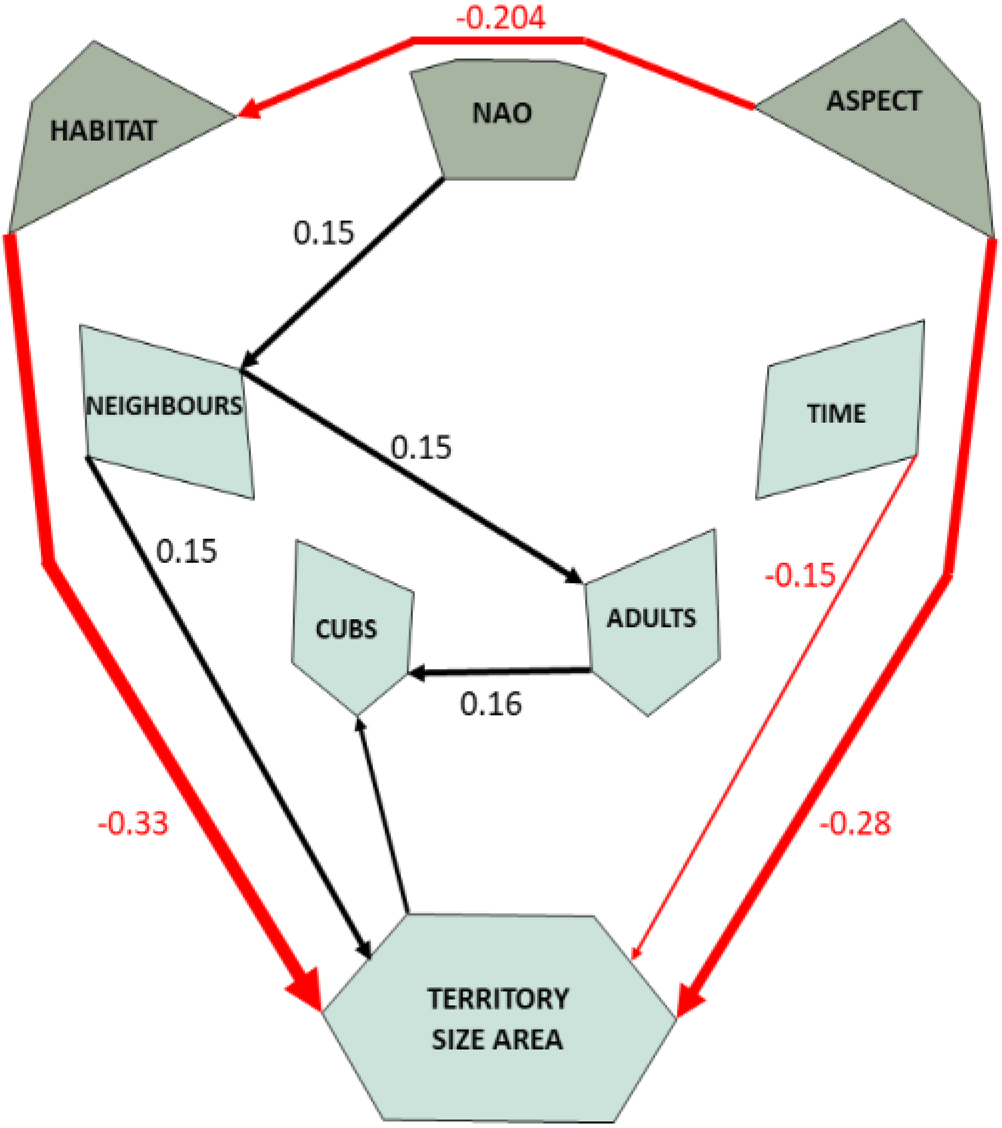

Figure 4.4: Parsimonious refined SEM including standardised coefficients of direct and indirect drivers of territory size in badger social groups at Woodchester park. Arrows indicate the directionality of the relationship. Red arrows indicate significant negative relationships and black arrows indicate significant positive relationships.

= 1000, P <0.001) and indirectly through the negative impact of aspect on habitat type (Observed coefficient = -0.2, position in permutation distribution = 1000, P <0.001). There was a direct negative impact of time on territory size (Observed coefficient = -0.15, position in permutation distribution = 998, P = 0.002) with territories decreasing in size throughout the study period. NAO positively impacted numbers of neighbours (Observed coefficient = 0.15, position in permutation distribution = 995, P = 0.005) which in turn had a positive impact on territory size (Observed coefficient = 0.15, position in permutation distribution = 995, P = 0.005). Neighbours also had a positive impact on adult numbers (Observed coefficient = 0.15, position in permutation distribution = 996, P = 0.04). Cub numbers were impacted directly by both Territory size (Observed coefficient = 0.11, position in permutation distribution = 971, P = 0.029) and by the number of adults (Observed coefficient = 0.16, position in permutation distribution = 998, P = 0.002) with larger territories supporting more cubs, and groups with more adults producing more cubs. NAO did not have any significant direct impacts on Cub or adult numbers however it did exert an indirect influence through its impact on neighbours.

4.4 Discussion

Despite the relative stability in the social groupings of badgers at Woodchester Park variation in the territory size of a social group still exists between groups in a given year, and within groups between different years. There exists a relationship between group size and territory size but the relationship is complex and is impacted by many interacting factors. The variation in climate and habitat strongly impact factors regulating resources that are available to badgers. In response to this variation badgers need to regulate several biological processes such as their utilization of space and their production of young. By using a Structural Equation Model identification of the interlinked factors that impact this relationship has been possible.

Much previous research on territoriality and social behaviour in carnivores has centered on identifying individual factors impacting on single metrics such as territory size. Territories are by definition spatially defined, animals pre-empt space from which they obtain necessary resources. However few if any studies have recognized that many of the factors that may influence territory formation and defence are non-independent and many may interact or have indirect effects on the outcome. Here the close interdependence of features that may impact on territory formation have been identified and their relative significance quantified in relation to their direct and indirect effects.

The model showed that social group, habitat type, land aspect, diversity of land and climatic variation all impact territory size. These factors influence space use through both direct and indirect effects with the badger territorial space use system consisting of a network of relationships that together impact the observed territory size. The model showed a direct impact of weather (NAO) on neighbour numbers (the total number of individuals in all territories neighbouring a given group). Earthworms are the primary prey item for badgers in the UK (Kruuk, 1978a) and their distribution and abundance are strongly impacted by climatic conditions (Edwards & Bohlen, 1996; Rutgers et al., 2016). NAO represents a large scale climatic index with high values denoting European climates experiencing mild wet weather (Stenseth et al., 2003), conditions favourable for earthworm emergence (Gerard, 1967; Johnston et al., 2014; Nuutinen et al., 2014). The model therefore uses NAO as a surrogate for food availability and in weather suited to worm emergence numbers of neighbouring individuals are increased. The increase in numbers of neighbouring individuals that is driven by the mild wet winter may reflect increased survival at a population level, the result of greater food availability. Where food resources are abundant individuals may be able to increase their energy stores and therefore increase survival as well as reproductive effort (da Silva et al., 1993). Whilst there was no direct impact of weather on adult numbers the indirect effect (through impacting neighbours which in turn impact adult numbers) acts to increase group sizes in years of favourable earthworm conditions.

Habitat and land aspect both influence territory size directly and indirectly. At a fine scale land aspect impacts primary productivity (Holland & Steyn, 1975). In turn the effects on the habitat scale up through the community composition influencing the landscape and therefore resources such as food and sett sites that are available to badgers within their territories. Setts require specific habitat and soil properties and have previously been considered in the context of the RDH (Doncaster & Woodroffe, 1993; Molina-Vacas et al., 2009). The focus of studies on setts as a single resource to explain sociality and space use, however, may have ignored the interaction with habitat as a driving factor. Earthworm populations vary with land use and habitat and are particularly prevalent in grassland areas (Kruuk et al., 1979; da Silva et al., 1993), which have been previously identified to be important to badgers (Palphramand et al., 2007). Such grassland areas however are not suitable sett locations with covered areas such as woodlands being preferred (Byrne et al., 2012; Huck et al., 2008). Territories are required for the provision of multiple resources each with different requirements. With multiple resources being impacted by the landscape composition of the area the interlinked nature of resource provision and space use becomes evident.

The model tested the hypothesis that larger territories would have more resources to support cubs being born and there was a direct impact of territory size on cub numbers. Larger territories were able to support greater numbers of cubs and likely provide more resources such as additional setts in which cubs produced from extra pair matings can be reared (Rogers et al., 2003). As the territories within the Woodchester park study area mostly contained fewer than five distinct habitat patches Shannons Index of alpha diversity of both land aspect and habitat was used as a measure of resource variation within each territory. If territory size were determined by resource dispersion smaller territories would contain the same resources and thus be equally as diverse as larger territories with the difference due to the dispersion of resources. Territory size, however, was strongly related to the diversity of land contained within that territory. Larger territories were more heterogeneous with greater diversity of both land aspect and habitat than smaller territories. In a highly heterogeneous territory the number of areas that are suitable at any one time for worm emergence are likely to be greater than for a more homogeneous environment. In contrast, a more homogeneous territory may have larger areas of suitable worm habitat but there will be larger areas suffering the same conditions at any one time. Therefore under changing conditions the worm emergence may be more coherent over larger areas in a homogeneous territory but the number of areas that are potentially capable of being continuously suitable will be reduced. Whilst the annual fluctuations in climate that regulate earthworm populations are relatively predictable (Shukla & Kinter III, 2006) small scale variation is much more difficult to predict but likely has a large impact on the availability of worms as food for badgers. Maintaining a larger territory may therefore buffer against the uncertainty surrounding local scale availability of earthworms as a food resource on a daily basis.

At Woodchester larger more diverse territories were those that contained more grassland habitat and these territories were more changeable through time. Woodlands buffer temperature variation more than open habitats such as grasslands (Suggitt et al.,

2011) and therefore may offer greater predictability in the availability of surface dwelling earthworms allowing badgers to maintain smaller territories whilst ensuring their resource needs are met.

According to the RDH such ‘patchiness’ of resource availability both spatially and temporally is important in determining the space used by a social group. Previously attempts to assess patchiness, particularly with regards to resource dispersion, have investigated the number of distinct habitat ‘patches’ within a territory (Johnson et al., 2001a). With the scales at which ecosystems are observed being critical in shaping our understanding of their structure and function (Estes et al., 2018) assessing variation at an appropriate scale is key. Earthworms operate at a small spatial scale with clusters occurring in areas $< 10m^2$ (Rossi, 2003) and population dispersal peaking at $10m$ per year (Stein et al., 1992). Although habitat composition of a territory is undoubtedly important (Palphramand et al., 2007) the use of habitat ‘patches’ as a measure of resource dispersion may be too coarse to capture the variation in earthworm availability at a scale that impacts badgers.

The model showed that cub numbers are strongly directly influenced by two factors, adult numbers within the group and the size of the group’s territory. Although declines in productivity per adult have been recorded with increasing group size (Dugdale et al., 2007) reproductive suppression may be a mechanism for adjusting group size in response to the local availability of resources (Woodroffe, 1995). Groups with greater cub numbers had larger territories in any given year with the potential to provide more resources thus allowing increased reproductive successes (Mallinson et al., 1992; Woodroffe & Macdonald, 2000; Rogers et al., 2003). The strong link between territory size and cub numbers suggests that reproduction is impacted by the amount of territory space and thus the diversity of that space that is available to individuals. With a greater amount of resources available to a group, annexe setts for rearing young in groups with multiple breeding females (Rogers et al., 1997) and feeding areas more cubs can be supported by that group (da Silva et al., 1993; Delahay et al., 2006). With a strong link between resources and reproduction, larger territories providing more resources and producing more cubs increases social group size. With cubs driving their integration into the group (Fell et al., 2006) such a link between cub numbers and territory size provides evidence of the indirect nature of the link between social group size and territory size.

Throughout the study period the badger population increased, a trend also seen across the UK (Johnson et al., 2001b; Macdonald & Newman, 2002). Despite the increase in badger numbers the amount of space used decreased through time effectively leading to a reduced area per individual badger within a territory. There is no evidence of any significant increases in resources through time (Johnson et al., 2001a; Macdonald et al., 2010) suggesting that badgers may have been inhabiting territories larger than the absolute minimum contradicting the thinking that badgers are contractionists (Kruuk & Parish, 1985). As such it may not simply be the dispersion of resources that drives the variation in the territory size of a social group.

Coordinating the timing of behaviours such as breeding and space use with knowledge of resource availability ensures that groups will have sufficient resources within their territories to ensure their survival. In areas such as the UK where climatic conditions support greater numbers of earthworms it may be the case that badgers can share territories with large numbers of conspecifics at little or no detriment to themselves. In areas across Europe where climatic conditions are less favourable for earthworms, the increased variation in resource availability may lead to alternate food sources including fruits (Balestrieri et al., 2009; Pigozzi, 1988), cereals (Madsen et al., 2002), amphibians (Goszczynski et al., 2000) and mammals (Fischer et al., 2005; Martin et al., 1995) being more important. The variation in diet as a response to different landscape conditions (Requena-Mullor et al., 2016) will impact the space used by an individual or group and may impact the tendency to act socially and form groups that defend territories. The results point to the need to consider the spatial dynamics of territory maintenance. What is needed now is more precise knowledge of the spatio-temporal dynamics of food availability as mediated by weather. This may go some way to explain the observed variation in space use in the badger and could lead to a better understanding of the factors impacting the conditions under which social group living is exhibited.

Five

Chapter 5

Individual based model of carnivore energetics

5.1 Introduction

Energy, often termed ‘the currency of life’, is the driver of all processes on earth (Gallagher et al., 2017; Pace, 2001). Constraining the richness of an ecosystem via trophic cascades, energy generation, use and cycling can limit the number of individuals able to coexist in an environment (Gillman et al., 2015; Hawkins et al., 2003). Within an ecosystem variation results from the aggregation of individual environment interactions into large scale energy fluxes (Desforges et al., 2019; Grimm et al., 2016). Energy can therefore be considered a critical driver of fitness, with individual energy fluxes being dependent on the life history traits, and metabolic characteristics of individuals (Abrahams & Dill, 1989; Brown et al., 2004; Desforges et al., 2019).

In order to survive individuals must gain sufficient energy to thermoregulate and maintain metabolic processes. Metabolic rate is a commonly used measure of the energetic expenditure for a resting animal in it’s thermoneutral zone (Aldama et al., 1991). As the rate of metabolic processes are fundamentally governed by biochemical reactions the metabolic rate of an individual is heavily impacted by temperature and is known to scale with body size (Brown et al., 2004; Gillooly et al., 2001). Large or cold organisms retain more resources in their bodies by fluxing them through metabolic pathways at a slower rate (Brown et al., 2004). Whole organism metabolic rate is limited by the rates of resource uptake across surfaces and by the distribution rates of materials through fractally branching networks of blood vessels in the body which causes a 1/4 power scaling with body mass (West et al., 1999). The rate at which an individual processes energy, and the amount of energy required to maintain cellular functions each day therefore varies according to the body size of that individual. The energy demands that are imposed on an individual due to it's body size can greatly impact how they behave and interact with their environment (Rasmussen et al., 2008). Not only do individuals need energy for cellular metabolism they also need energy in order to deal with daily processes such as foraging and predator avoidance (Brown et al., 2004). Whilst climate (Clarke et al., 2010), diet quality (Bozinovic et al., 2007), and predation threat (Abrahams & Dill, 1989; Ward et al., 2000) are all factors that might influence an individual's metabolism it is the potential to link metabolic traits with behaviours that may be important when considering energy as a driver of behaviours such as sociality (Killen et al., 2016).

The purpose of any activity can ultimately be linked to fitness but all activities are driven by energy. Fitness enhancing behaviours may therefore be viewed in terms of energy as those which maximize energy intake relative to expenditure and where there is a relationship between energy and fitness animals are expected to behave so as to maximize their energy intake (Abrahams & Dill, 1989). The dynamic energy budget (DEB) theory suggests that a fixed fraction of energy gains go towards the maintenance of metabolic processes with the surplus being available for maturity and reproduction (Kooijman et al., 2008). Processes that directly contribute to fitness, such as gestation and lactation can only be afforded if the energetic demands of a mothers metabolism have been met (Jackson et al., 2014; Nisbet et al., 2000). Such metabolic constraints may have important impact on the behaviours that an individual exhibits.

More often than not it is behaviours that are investigated in relation to the optimization of fitness yet on a day to day basis these behaviours are driven by energy availability. Behaviours that maximize fitness should be those that minimize energy expenditure or maximize energetic intake. Some behaviours such as foraging and predator avoidance are, however, energetically costly (Brown et al., 2004). Foraging decisions are thought to be driven by natural selection to optimize nutrient intake at the minimum energy expenditure and the least risk to the forager (Balme et al., 2007). Decisions regarding social behaviours may therefore be expected to be similar. If acting socially decreases the energy expenditure of an individual through reduced predation stress, reduced energetic expenditure associated with reproduction or increased energetic intake then the drivers of social behaviours may be explained in terms of energy. The model developed here explores the role of energy in relation to group size, with sociality hypothesised to be a mechanism by which individual energy gain relative to expenditure can be increased.

Energy is a useful and popular concept for comparative purposes (Kooijman et al., 2008). Mass and energy balances can be calculated for individuals and integrated into Individual Based Models (IBM's) allowing a link between individual and population processes (Martin et al., 2012; van der Vaart et al., 2016). Using energy budgets that are derived from first principles has the potential to make IBM's more coherent (Grimm et al., 2016). Energy budgets have been incorporated into IBMs for various species ranging from daphnia to elephants (Boult et al., 2018; Martin et al., 2013; Sibly et al., 2013). IBMs incorporating energetic components have been used largely for studies focused on animal movement (Hooten et al., 2019; Latombe et al., 2014; Zhang et al., 2017), individual growth (Desforges et al., 2019; English et al., 2012; MacNulty et al., 2009; Speakman, 2005) and population dynamics (Cuddington & Yodzis, 2000; McCauley et al., 1993).

Here an IBM built on metabolic scaling rules is used to explicitly model energy gain and expenditure in carnivores to investigate the energetic consequences of sociality. The model is generalised in the sense that it simulates hunting behaviour, energy gain and population demographics for any species in idealised landscapes. The model is used to investigate the energetic benefits of sociality at the level of the individual for large hunters and invertebrate feeders to assess the differences brought about from feeding on such different sized prey resources.

Wolves and meerkats are social species representing almost opposite ends of the spectrum of diversity contained within the Order Carnivora. Wolves are large bodied, hunt in groups to capture prey that can be up to 10 times their own weight (Chapter 3), as such, hunting can be both dangerous and energetically expensive for a wolf (Vucetich et al., 2004). Meerkats however are small in size and rarely eat anything larger than themselves, with diets largely consisting of invertebrate prey (Doolan & MacDonald, 1996). Given that invertebrate prey is several orders of magnitude smaller than the meerkat they have to consume a large number of prey items in order to meet their energetic requirements.

The large relative size of it's prey may be enough for a single hunt to satisfy a wolf for several days, however, a meerkat must operate a more consistent grazing approach in order to gain enough energy from their small prey to see them through a single day. The energetic costs relative to expenditure of these different behavioural strategies may be mediated through the use of social grouping and the associated behaviours as a means of maximising individual fitness.

5.2 Methods

The purpose of the model is to find the energetic cost or benefit associated with living as part of a social group and assess the impact of any costs or benefits in relation to individual fitness through reproduction. Through simulating foraging behaviour and interactions with neighbouring groups the energy expenditure of daily activities is balanced with the energy intake from foraging gains. Energy gains are allocated to survival, growth or reproduction to allow an assessment of the impacts of group living to predators. The model is generic, built on metabolic scaling rules that are determined by the body size of the predator being investigated and is parameterised here for grey wolves in a high and low food density environment and for meerkats.

5.2.1 *State variables and scale*

The model simulates activities at the level of the group calculating the energy balance at each ten-minute time-step throughout a single breeding period in which predators restrict their movements to maintain the use of a den site whilst reproducing and supporting young. Predators are characterised by the state variables: Body size, energy reserves, litter size, and group size. Parameters specific to the predator species being modelled include activity pattern, movement speed, gestation length, birth-weight, critical size, and daily movement distance. Parameter values are detailed in Table 5.1.

Model Environment

Den sites were randomly distributed across the model landscape and were used as centroids from which territory boundaries were created as Thiessen polygons filling the model landscape.

Table 5.1: Table detailing parameters for the modelled species

Parameter	Wolf	Meerkat
Activity pattern	Diurnal	Diurnal
Maximum daily movement distance (km)	13.38 estimated from Kusak et al. (2005)	1.81 estimated from Gall et al. (2017)
Movement speed (kmph)	3.78 estimated from Musiani et al. (1988)	5.95 estimated from Bosquet et al. (2011)
Individual weight (kg)	Initial value sampled from a triangular distribution with maximum of 55kg and minimum of 19kg as recorded by Wilson and Mittermeier (2009)	Initial value sampled from a triangular distribution with maximum of 0.97kg and minimum of 0.62kg as recorded by Wilson and Mittermeier (2009)
Critical size (kg) below which predator cannot survive	19kg minimum weight recorded by Wilson and Mittermeier (2009)	0.62kg minimum weight recorded by Wilson and Mittermeier (2009)
Breeding threshold weight (kg) below which predator must priorities growth over reproduction	30kg estimated on the assumption that individuals in the lower quartile (assuming a triangular distribution centered around the median of 37kg) would be unable to breed.	0.75kg estimated on the assumption that individuals in the lower quartile (assuming a triangular distribution centered around the median of 0.795kg) would be unable to breed.
Gestation length (days)	62 minimum length recorded by Wilson and Mittermeier (2009)	70 minimum length recorded by Wilson and Mittermeier (2009)
Birthweight of young (kg)	0.41kg as denoted by De Magalhaes et al. (2009)	0.0386kg as denoted by De Magalhaes et al. (2009)

Litter size (individuals)	Sampled from a triangular distribution assuming a maximum of 13 as denoted by Wilson and Mittermeier (2009)	Sampled from a triangular distribution assuming a maximum of 7 as denoted by Wilson and Mittermeier (2009)
Age (years) at atart of model run	2	2
Group size	Modelled as a discrete entity between 1-29	Modelled as a discrete entity between 1-29

Predator movement was constrained to the model environment assuming that individuals are unable to disperse to new territories or environments for the duration of the model run. The density of animals simulated is altered to ensure that the mean home range size is representative of data recorded for the predator species. Predator movement is constrained to the model area thus assuming that individuals do not disperse to new territories or environments for the duration of the model run.

Food

Food was placed in to the model environment at densities that reflect recorded prey availablities for the species being modeled. Full details of the prey items incorporated in to the model environment and the densities at which they were available are detailed in Table. 5.2. Prey densities remained constant throughout the model runs with prey items that were successfully hunted and consumed being subsequently replenished and randomly positioned in the model environment.

Table 5.2: Table detailing modelled prey items and the densities at which they are incorporated into the individual based foraging model

PREY	SIZE (KG)	DENSITY (N/KM2)	REFERENCE
Caribou	109	0.50	Dale et al. 1994
Bison	624	2.81	Becker et al. 2008

Elk	146	1.35	Becker et al. 2008
Invertebrates	0.003-0.3	116979.00	Davis et al. 2010

Daylight hours

Annual variation in daylight was incorporated to allow for seasonal variations in activity periods to be simulated as part of the model with each environment representing the mid range latitude for the predator species or a latitude for which specific data were available. Day length was simulated according to the latitude at which the model landscape was located and the day of the year (1-365) to account for the variation in sunlight hours experienced and its potential impact on activity and behaviour (Fig. C.1). The activity pattern of the predator determines the time-steps in which it has the potential to be active. Where the latitude and day of the year were such that true darkness was not achieved and twilight lasted for the entire night time period predators with a crepuscular activity pattern were effectively modelled as being nocturnal and had the potential to be active throughout the night.

Survival

Where energetic intake was not sufficient for the payment of metabolic costs, energy from the metabolization of body tissue was used to pay metabolic costs and the body size of individuals were reduced accordingly. At the end of each day where the mean individual body size was lower than the smallest recorded adult body size (critical size parameter) for the species one individual from the group was removed in order to ensure the survival of the rest of the group. Where the model was parameterised for meerkats daily predation risk scaled with group size was calculated from Golabek et al.(2008) and applied at the end of each day. Where predation was successful an individual was removed from the group.

5.2.2 *Process overview and scheduling*

Simulations of the individual based model were run for a minimum time period of 100 days and iterated through each day in time-steps of ten minutes. Animal activity was determined for each time-step according to their behaviour pattern (nocturnal, diurnal or crepuscular) and the decisions detailed in Fig.5.1. At each time-step each predator is simulated in a random order, where a predator is not already carrying out an activity (e.g. travelling towards an identified prey item) they are able to carry out an activity only when they have enough time to travel home before the end of their activity period and if they have not already exceeded the daily maximum movement distance. Where predators are able they forage, travelling towards the target prey item before capturing/handling the item and storing any energy gained. Decisions are made according to a hierarchy that can be seen in Fig.5.1. Where a predator has intruders in their home territory they will only confront the intruder if they are closer to the intruder than they are to a prey item. In confrontations between intruders and territory owners the predator with the largest body size wins out and the smaller individual or group retreats to a random point within its home territory. In this way intruders are able to act as kleptoparasites stealing kills from neighbours if they are larger than them.

Foraging

Where the predator was in it's activity period it was able to forage to gain the energy required for metabolic processes, growth and reproduction. Predators moved about the landscape in order to consume prey items that were available to them. Foraging was not restricted to being within the predators home territory however where the target prey item was not in a predators home territory that prey was only be pursued if the predator was closer to the prey than it was to any other (non group) predators, and the predator was closer to that prey item than they were to any other predators (e.g. the owner of the territory in which the prey item was situated).

On pursuit of a prey item the hunt success rate was determined as the rate predicted from a linear model (based on data from (Bothma et al., 1997; Fanshawe & Fitzgibbon, 1993; Jędrzejewski et al., 1992; MacNulty et al., 2014, 2012b; McGregor et al., 2015; Stander, 1992)) in which predator mass and prey size were significant predictors of hunt success (Fig. C.2). Where a hunt was successful the predator was able to feed on the prey item. When hunts were deemed unsuccessful the prey item was removed from the landscape and a new prey item of the same size was generated elsewhere in the model environment in its place.

Upon successful capture of a prey item prey processing followed immediately after. Prey processing encompassed the time required to capture, subdue, kill and eat a prey item. Values of prey processing time in the model were predicted from a generalised linear model

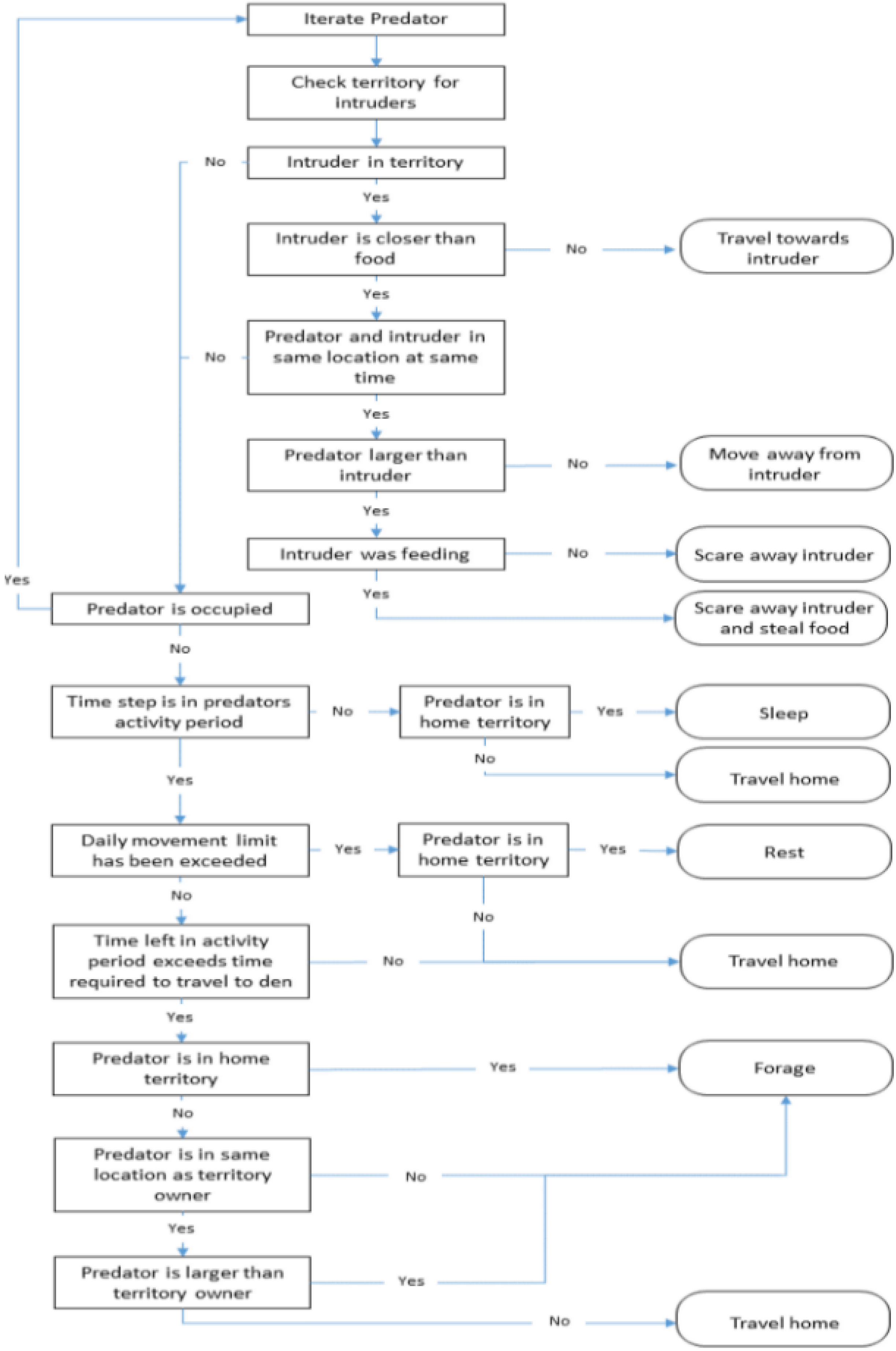

Figure 5.1: Flow diagram detailing model run order within each timsetep

based on data from (DeLong & Vasseur, 2012) which showed proportional prey weight to be a significant predictor of handling time (Fig. C.3).

Conflict competition

Where a predator strayed outside of its home territory or was faced with an intruder entering its home territory there was potential for conflict to occur. Where two predators spatially and temporally overlapped the larger bodied predator won the competition and the smaller bodied predator was forced to retreat. Where the retreating predator was within its home range they moved towards their den location for a single time-step. In the case that the intruding predator was defeated they returned to a random point within their home territory before being able to occupy themselves with another action. Where the defeated predator was processing prey the victorious predator was able to act as a kleptoparasite and consume any remaining prey.

Reproduction and growth

Reproduction and growth occurred based on energetic thresholds and was incorporated into the model at the end of each day. Female animals had the potential to breed only if their body size was above a certain threshold weight. For reproducing individuals once their metabolic costs had been paid, excess energy that could be put towards growth was used to develop foetuses for the duration of the animals gestation period. At any point during gestation if the mothers body weight dropped below the critical size excess energy was diverted and growth was prioritised over the growth of the foetus until the mothers body weight exceeded the breeding threshold once again. After the birth of a litter the group was responsible for provisioning food to the young to ensure that they could meet metabolic demands and grow where possible. After birth, once the metabolic costs of all adults had been paid the metabolic costs of young were paid. Where excess energy was available if a predator’s body weight had dropped below the breeding threshold the growth of that predator was prioritised over the growth of young in that day. Where a predators body weight was not below the breeding threshold the excess energy gained was used for the growth of young (Fig. 5.2).

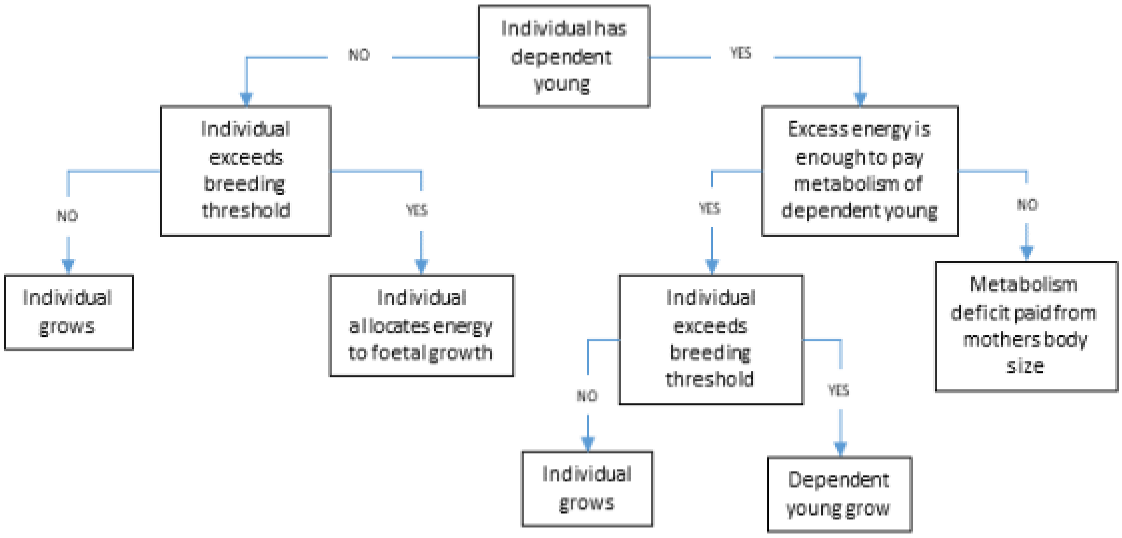

Figure 5.2: Flow diagram detailing prioritisation of excess energy (energy accrued after having accounted for individuals metabolic needs) towards growth and reproduction at the end of each modelled day

Energy

Energy gains and losses were recorded at each model time-step. Predators gained energy through the successful capture and consumption of prey items from the environment. The energy gained from prey items was recorded in Kcal assuming that 80% of the prey item is consumed (Brzeziński & Marzec, 2003) with an energetic value of 5.59Kcal per kg of flesh (Waterlow, 1981) and 5325Kcal per kg of invertebrate matter (Kouřimská & Adámková, 2016).

Energetic costs were determined according to the activity which the individual was undertaking.

$$BMR = 67.61 * M^{0.75} \tag{5.1}$$

Basal metabolic rate (BMR) (Kcal/day^{-1}) was calculated from (Lavigne, 1982) Eqn. (5.1) where M refers to body mass (kg). BMR per time-step was used for sleeping and resting activities. For traveling activities (including foraging and retreating from competitors) metabolic expenditure per time-step was calculated according to Eqn. (5.2) as predicted by Taylor et al. (1970) where V represents the velocity of movement.

$$MR = \frac{1.7 * BMR}{V} \tag{5.2}$$

At each time-step energy intake was balanced against energetic cost according to the activity that was being carried out in that time-step. At the end of each day surplus energy was diverted towards either growth or reproduction (depending on reproductive threshold having been met). Growth was calculated as the conversion of energy to flesh tissue with a conversion factor of 4.9Kcal per g of tissue synthesized (Waterlow, 1981). Where individuals were reproductively active and supporting the growth of a litter all metabolic calculations included the weight of the litter as part of the mothers size during the gestation period. Foetal growth occurred only after maternal energetic costs had been paid. Post-partum neonate growth was dependent on the mother where the model simulated solitary animals. Where the model simulated social animals all adults within the group were able to share the cost of feeding young.

5.2.3 *Design concepts*

The model was designed to be generic with the potential to be parameterised for a broad range of species. Two components differ between the model as parameterised for wolves and for meerkats, prey detection and social foraging.

Prey detection: wolves

The detectability of each prey item was calculated according to the size of the prey item and its distance from the predators location. Detectability for each prey item within the predators maximum daily movement distance was determined and the target prey item was selected as that which maximized the ratio between prey item size and distance required for the predator to travel to the prey item.

Prey detection: meerkats

Where the model represented predators that forage for invertebrates it was assumed that the most detectable prey would be that which was closest to the predator regardless of size.

Social foraging: wolves

All individualswithin a group were modeled as contributing equally to the hunting and processing of prey with successful hunts being shared equally among the group (wolves). Group mass (individual mass * group size) was used a predictor of hunt success and processing time in the model in the same way that individual mass was used for solitary species. The potential benefits of social grouping were incorporated into the model as the increased hunt success and processing rate.

Social foraging: meerkats

All individuals in a group foraged simultaneously occupying an area with individuals feeding individually (i.e. caught prey was not shared among the group). Group mass (individual mass * group size) was used a predictor of hunt success and processing time in the model in the same way that individual mass was used for solitary species. The potential benefits of social grouping were incorporated into the model as the increased hunt success and processing rate, reflecting increased foraging efficiency.

Fitness

Predators are not explicitly modelled to behave in a manner that maximises fitness. Fitness consequences are included in the model as the product of reproductive effort, governed by the empirical rules relating to energy gain.

Interaction

Predators interact with neighbours when spatiotemporal overlap occurs. Within group interactions between individuals are not included in this model.

Stochasticity

Stochastic processes within the model include the distribution of den sites and resulting territories, distribution of food items, and the determination of initial body size, and litter size parameters.

Collectives

The model simulated social groups to act as the modelled agent. In any given time period the group carried out a single activity. Energetic calculations were balanced at the level of the individual (within the group) and then adjusted according to the size of the group. The model assumes that all individuals within a group grow equally, the critical mass (weight below which individuals die) for the group is therefore determined as the critical mass for an individual multiplied by the number of individuals within the group. It was assumed that a single individual within the group has the capability to reproduce in a given year and that all individuals within the group share the costs of developing and raising young. The maximum litter size for a group is determined as the maximum recorded litter size for the species (the same as for a group size of 1) and litter weight is used as a measure of reproductive success.

Metabolic costs were calculated at the individual level, assuming that all individuals within the group have the same body mass (group mass/ group size). Although only a single individual within the group has the capability to breed in a given year, all group members were able to contribute to the growth and maintenance of a litter of young. Where the environment did not provide enough resources to sustain a group and support the growth of young, the maintenance of adults within the group was prioritised over reproduction.

Observations

The model was parameterised for the grey wolf in a low density prey environment (Alaska, Caribou prey only (Dale et al., 1994)) and high density prey environment (Yellowstone, Bison and Elk prey (Becker et al., 2008)). Groups up to the maximum recorded group size for the species as recorded by Wilson and Mittermeier (2009) were modeled at a fixed density within each model environment. Fifteen model runs of 100 days in length each simulating 15 group sizes (1-29) were used to generate model outputs for analyses. The model was subsequently prameterised for meerkats to give an indication of the impacts among a small bodied predator. The meerkat model simulated 15 group sizes (1-29) over 100 days for fifteen simulation runs.

Data generated by the models that were used for analysis included annual survival, annual reproductive output and daily energy intake/expenditure. Generalised Linear models were used to assess the impacts of group size on survival, reproduction and energy intake/expenditure in each model environment. Linear mixed effects models fit by restricted maximum likelihood were used to assess the significance of group size on reproduction and energy intake/expenditure. For mixed models the model environment was included as a random effect in all instances. The extent to which group size led to a unimodal response in any of the outcomes was investigated by the inclusion of a quadratic term for the independent variable in the linear model. Where unimodal models were significant, the group size that led to the maximum response was identified through analysis of solving for the independent variable when the gradient from the first derivative of the regression equation was zero.

5.3 Results

5.3.1 *Survival*

The number of groups in which there was no mortality (where survival is highest) varied across model runs (Fig. 5.3). The size of a group had a small negative effect on the chances of all individuals within the group being able to survive (β = -0.007, SE = 0.001, P <0.001) for wolves and had a small positive but non significant effect for meerkats (β = 0.001, SE = 0.002, P = 0.639). Amongst the wolf models individual survival was significantly lower in the high food density environment than the low food density environment (β = 0.093, SE = 0.023, P <0.001).

5.3.2 *Reproduction*

For wolves group size had a significant positive impact on the group level reproductive output in high food density (β = 1.474, SE = 0.058, P<0.001) and low food density (β = 1.4, SE = 0.043, P <0.001) environments (Fig. 5.4). The impact of group size on reproductive output in the meerkat model was small but significant and suggested an increase in reproductive output with increased group size (β = 0.005, SE = 2×10^{-4}, P = <0.001). Across all models accounting for model environment (wolf high food density, wolf low food density, meerkat) as a random effect, individual body size had a small positive impact on reproductive output (β = 0.004, SE <0.001, P <0.001).

The response of reproductive output was unimodal in both the high food density (β = -0.431, SE = 0.015, P <0.001) and low food density (β = -0.186, SE = 0.011, P <0.001) environment for wolf models as well as for the meerkat model (β = -0.002, SE = 5×10^{-4}, P <0.001). Where reproductive output showed a unimodal response, the optimum group size

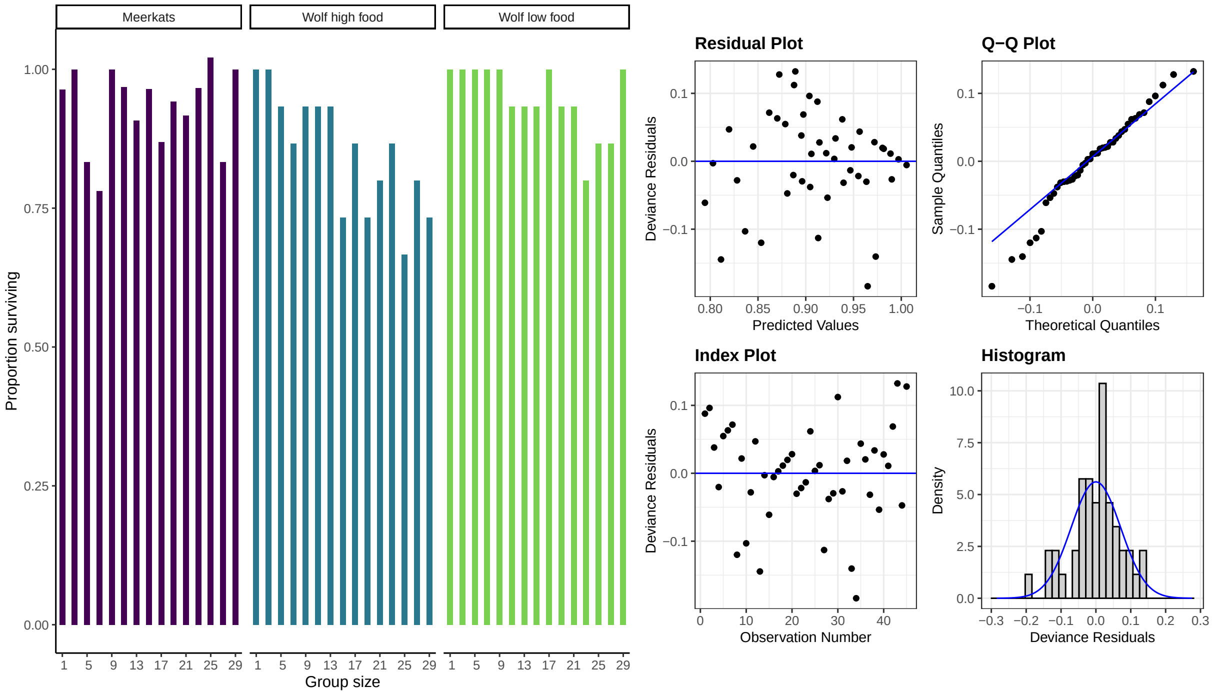

Figure 5.3: Survival (left) across group sizes in modelled meerkat groups, and grey wolf groups in high density (Elk and Bison prey) and low density (Caribou prey) prey environments. Residuals (right) from a Generalised Linear Model (GLM) in which group size and prey environment are significant predictors of survival.

was found by differentiating the regression equation ((C.1)) relating output to group size and evaluating the value of group size where the gradient of the derivative was zero. This gave estimates of optimal group sizes for maximisation of reproductive output for wolves in a high density food environment of 29, for wolves in a low density food environment of 36, and of 4 for meerkats.

5.3.3 *Energy Expenditure*

The median individual daily energy expenditure for wolves was 963 Kcal and was 42 Kcal for meerkats, across both species the values obtained are similar to previous estimates (Scantlebury et al., 2002; Vucetich et al., 2004). Group size was a significant predictor of daily energy expenditure with energy expenditure decreasing as group size increased for wolves in high ($\beta = -3 \times 10^{-5}$, SE $= 2 \times 10^{-6}$ P <0.001) and low ($\beta = -2 \times 10^{-6}$, SE $= 4 \times 10^{-7}$ P <0.001) food density environments. For meerkats group size had a small significant positive impact on energy expenditure ($\beta = 8 \times 10^{-6}$, SE $= 3 \times 10^{-8}$ P <0.001).

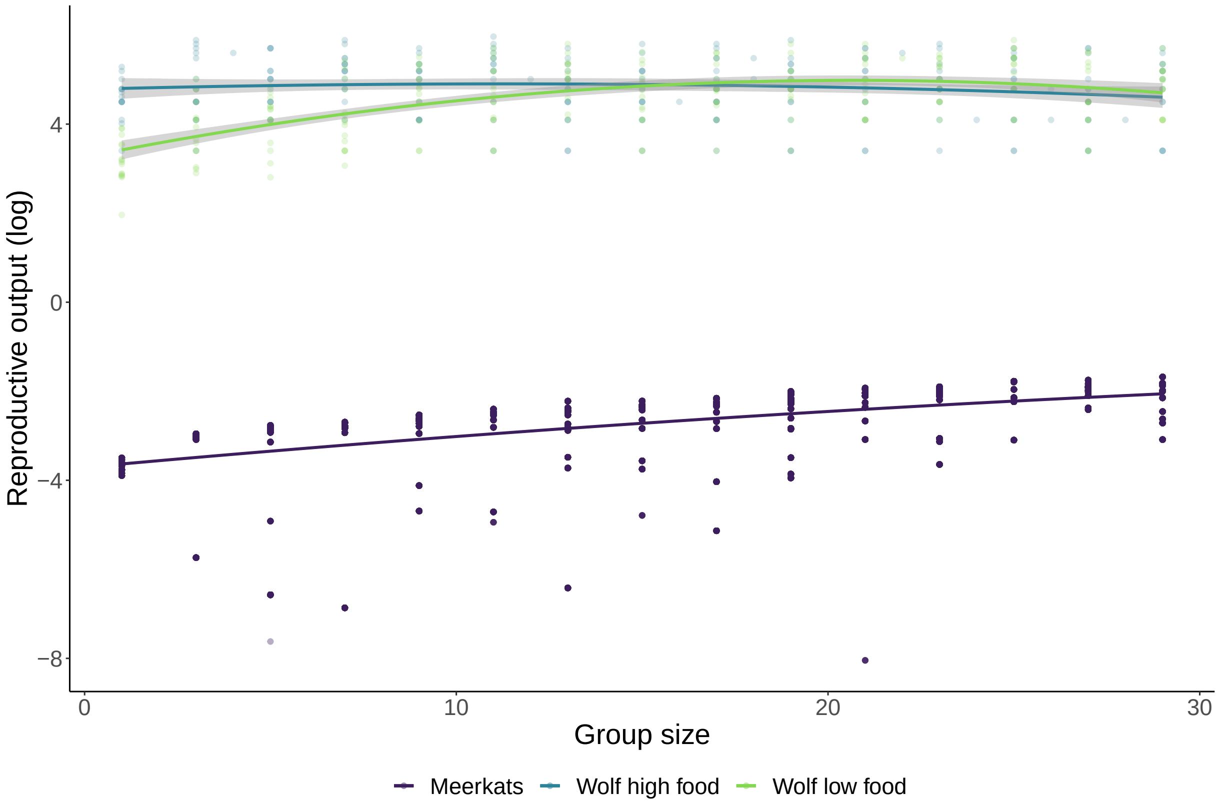

Figure 5.4: Reproductive output (log) measured as total litter weight scaled by group mass for groups containing between 1-29 individuals under different model scenarios

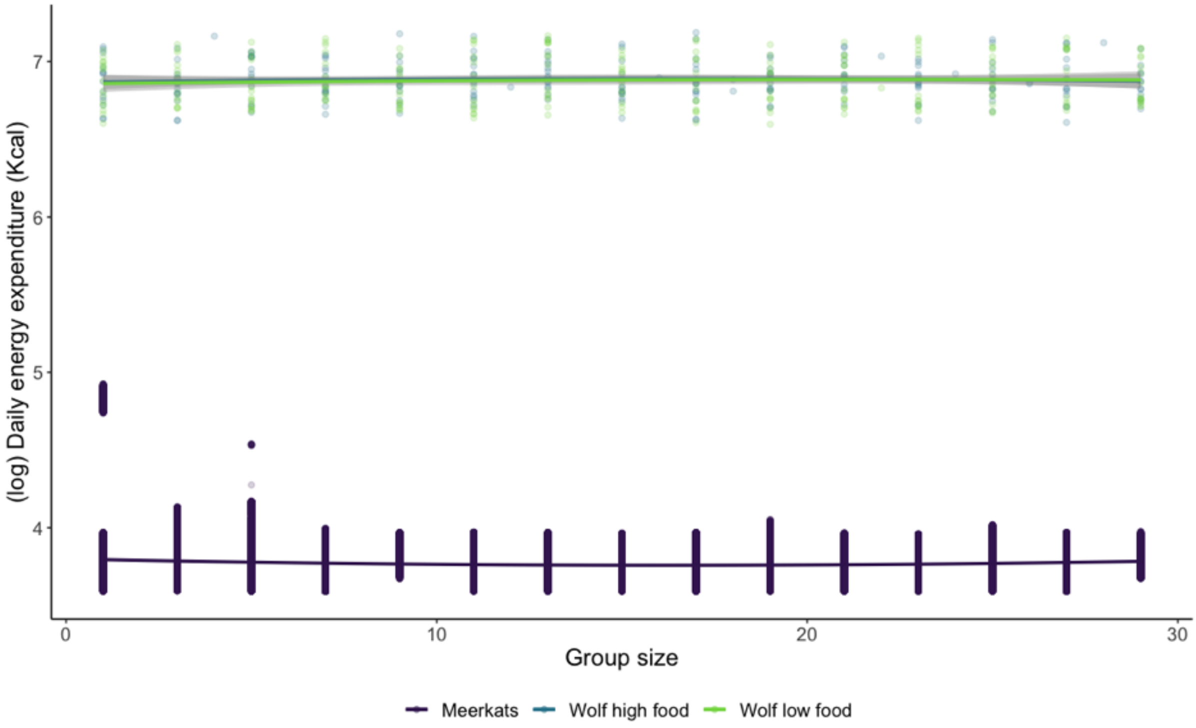

Figure 5.5: Daily energy expenditure (Kcal) of individuals in groups of varying size as determined from simulation model outputs

5.3.4 *Energy intake*

Energy intake was investigated independently for each model run to assess the relative impact of the prey environment in each case. Energy intake was generally stable across groups of differing sizes (Fig. 5.6).

In the meerkat model group size had a small significant positive impact on daily energy intake (β = 0.0016, SE =2×10^{-5}, P <0.001) with larger groups having higher energy intakes. For wolves group size had a positive impact on daily energy intake. The effect was large in the high density food environment (β = 3.3913026×10^{4}, SE =356.328, P <0.001) and small in the low density food environment (β = 0.095, SE =3×10^{-4}, P <0.001).

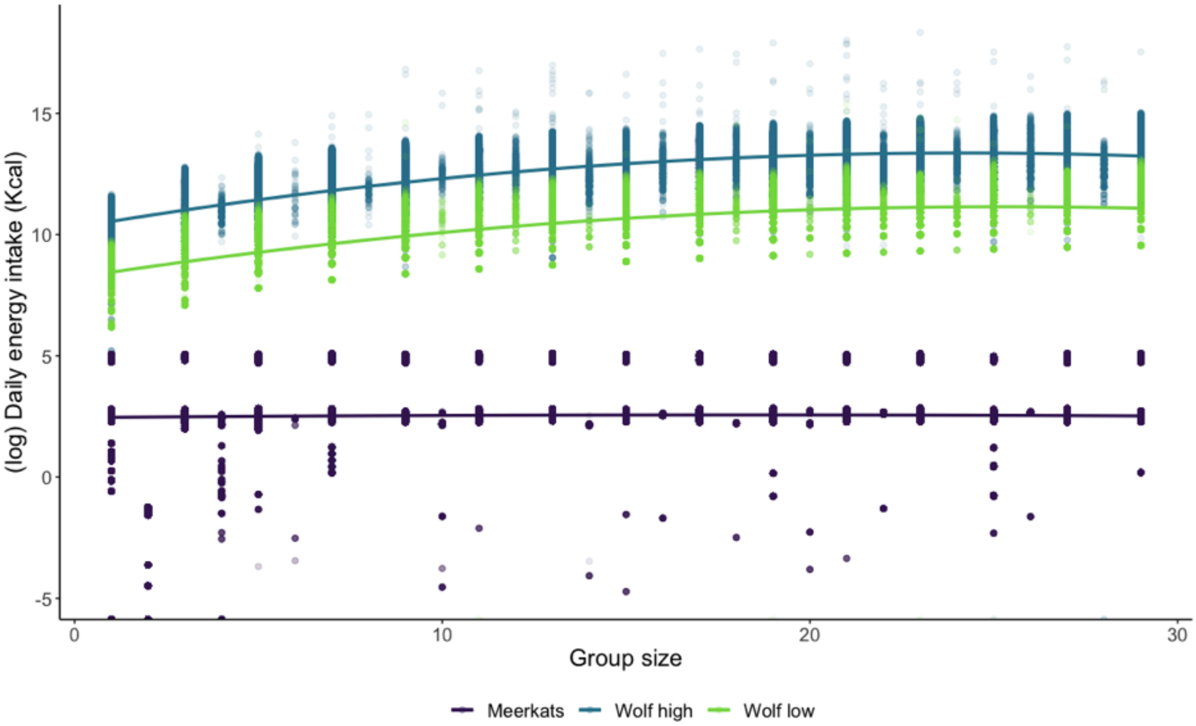

Figure 5.6: Logged daily energy intake (Kcal) of individuals in groups of varying size as determined from simulation model outputs

5.4 Discussion

For both the meerkat and the wolf, the model predicted an increase in energy intake with group size, suggesting that individuals in larger groups have the potential to be energetically better off than solitary animals or those in small groups. Despite the difference in the bioenergetics of the two species the model suggested that there may be energetically determined optimum group sizes for populations of both species. The predicted optima for wolves was higher than previous estimates of optimum group sizes (Hayes et al., 2000; MacNulty et al., 2012a). Group sizes have often been recorded to be higher than predictions which tend to be based on hunting and ignore confounding benefits of sociality (Baird & Dill, 1996) that have been accounted for by this model. The predicted optimum group sizes for wolves, whilst variable according to the modelled environment were close to the upper end of recorded pack sizes such as Yellowstone's druid pack that was recorded to reach 37 individuals in 2001 (Smith et al., 2005). Among small bodied mammals, predicting group sizes has been noted to be difficult (Waser, 1981) and here the predicted group size from the model was smaller than the majority of groups seen in the wild (Drewe et al., 2009). The outputs from the model and the deviations from what we see in reality can be explained by the behavioural differences between the two species coupled with the simplifications of those behaviours used in generating the model.

Energetic models have predicted that large carnivores have to eat large prey in order to sustain themselves (Carbone et al., 1999). Although a preference for large prey is surely influenced by the energetics constraints of large size there is some evidence to suggest that large species such as lions for example, are poor hunters of small prey (MacNulty et al., 2009). Hunt success may therefore be a driver of prey choice in large bodied species due to protracted hunting locomotion having high energetic costs (Hubel et al., 2016b). Many large carnivores have diets that encompass wide ranges of prey sizes (Chapter 3) however much of the smaller prey may be scavenged or opportunistically caught with hunting likely focused on larger prey items. If the pursuit of a prey item is unsuccessful it will result in a large waste of energy for an individual pursuing a hunt. Maximizing hunt success is therefore an attractive way of ensuring the maximisation of energy intake relative to expenditure and this factor likely extends to grouping. For large species such as wolves, not only is hunt success thought to increase to a certain degree with group size (MacNulty et al., 2014, 2012a) but the excessive energetic cost of chasing prey may give rise to tangible energetic benefits for individuals hunting as part of a group (Rasmussen et al., 2008). The benefits do not increase linearly with group size, as the prediction of an optimum group suggests, as a group gets bigger there will be more room for individuals to 'free-ride' rather than to co-operate and the extent to which individuals benefit from the grouping is diminished (MacNulty et al., 2012a). In addition as the size of the group increases internal group threats increase and competition reduces food intake per individual thereby potentially imposing an upper limit to the size of a group (Bekoff et al., 1984; Pangle & Holekamp, 2010). Additional behavioural regulation including overt aggression at kills has been seen to fragment groups onto smaller more energy efficient units, particularly where the quality of prey is variable (Nudds, 1978; MacNulty et al., 2012a). Such behaviours suggest an energy driven regulation of grouping behaviours in wolves.

The same however cannot be said for meerkats, although they forage in the presence of group mates, the lack of cooperative hunting eliminates the possibility of group size impacting hunt success. Their propensity to act as grazers limits the potential need to share prey with groupmates. Their need to successfully forage for a large number of small prey items may however lead to time acting as a limiting factor to the rate at which energy can be gained. Foraging for food is a mechanism required for energy intake but it must be balanced with other activities that take place on a daily basis to ensure survival such as predator avoidance. Meerkats are small bodied carnivores, a factor that makes them vulnerable to predators (Townsend et al., 2012a). In order to reduce the risk of being predated upon individuals have to devote time to vigilance behaviours and this is particularly important in the context of foraging. A foraging meerkat has it's head down digging for invertebrates (Doolan & MacDonald, 1996), as meerkats are commonly predated upon by aerial predators (Manser, 2001) individuals with their head to the ground digging for prey are unable to be looking up for predators at the same time. As a result individuals must partition their time between the two behaviours in order to maximize the time that can be devoted to foraging whilst remaining vigilant for predators. If the time available for foraging is a limiting factor because it has to be balanced with vigilance behaviours, mechanisms that can increase time available for foraging would have the potential to increase energy intake. Sociality may be that mechanism for meerkats, where the presence of group mates can allow individuals to increase the amount of time that they are able to forage through the sharing of vigilance behaviours (Santema & Clutton-Brock, 2013). If increases in group size reduce vigilance time then individuals can forage more efficiently which translates to fitness gains (Silk, 2007b).

Whilst the partitioning of time between foraging and vigilance might offer a behavioural explanation of the energetic benefit of grouping it was not explicitly included in the model. Predation risk in the model was implemented daily with the relative risk to an individual decreasing as the size of the social group to which it belongs increased. Such an application of predation risk allows this important factor to be incorporated into the model however for a more thorough understanding of the impact the functional response of predators should be investigated as a future priority. The results of the model suggested that there was an increase in energy intake with group size but it was not clear what process caused this emergent behaviour. It is possibly linked to reduced per capita inter-group vigilance in that time spent defending a territory (in this case by chasing off non-group members from food sites within the home range) could be reduced as group size increases, a factor that warrants further investigation in future.

The energy, and therefore resource requirements of a group will be greater than that of an individual, as groups get bigger they will need to consume more resources in order for all individuals to satisfy their energy requirements. Groups may therefore deplete the resources in a given area at a faster rate than individuals. The consequences of this could lead to individuals in larger groups having to travel over greater distances when foraging to ensure that they can obtain enough food. For meerkats foraging in unknown areas can reduce success (Kranstauber et al., 2020) and so larger groups may have to increase the size of their range to ensure that they have enough known areas to forage in effectively. As territorial animals meerkats defend territories through the use of scent marks at latrines (Jordan et al., 2007), for groups defending larger territories the cost of travelling to the latrines to replenish scent marks will be higher and could increase the energetic burden on individuals. However there is the potential for this cost to be shared across individuals within the group (Robertson et al., 2015) which may offer an additional energetic benefit to grouping that outweighs the increase in energy expenditure that is seen.

European badgers, which are midway between wolves and meerkats in terms of body size may act socially to gain a similar benefit in the UK where they are seen to live in large groups. Like meerkats they eat prey that is relatively small and thus could be considered grazers where they live socially; they may benefit from the shared defence of territory areas through scent marking at latrine sites (Kilshaw et al., 2009). However in parts of Europe where badgers live alone a difference in their diet and foraging strategy is seen, with individuals eating larger prey that requires them to hunt rather than graze (Martin et al., 1995). This switch from grazing to hunting may be important in determining the tendency to act socially. Where a species can graze on small prey there may be little cost to sharing a territory, particularly if sharing can act to reduce the energetic cost of territory defence. However, where individuals have to hunt for larger prey the potential to save energy by sharing territory defence may be outweighed by the cost of having to share prey or to share the territory area where that larger prey may be sparse and unpredictable in its distribution.

The primary factors determining home range size in carnivores are thought to be the dispersion of available prey, and the energetic needs of individuals as determined by their body size (Newsome et al., 2013). For wolves, whose large ungulate prey are themselves prone to ranging over large distances (Ofstad et al., 2016), their ranges are large enough that active defence such as is seen in meerkats and badgers would likely be impossible to maintain, even if the effort was shared among group mates. Group defence may however manifest differently in the species, defence of captured prey may be more important than defence of a territory area. Larger groups are better able to defend kills from competitors which may be more efficient than defending the space in which prey could be found and killed (Atwood & Gese, 2008; Vucetich et al., 2004; Wallach et al., 2015). For hunters such as wolves in which the energetic cost of a hunt is high the loss of that kill to competitors has a large impact (Hubel et al., 2016b). Energetic benefits associated with group size therefore likely extend beyond hunt success. Not only do their prey range over large distances but being larger bodied they are slower to reproduce and grow, thus if a wolf pack were to restrict their movement to an energetically defensible area they may risk not encountering enough prey to sustain them which could have important implications for reproduction.

In models of both species the reproductive output of a group was predicted to increase with group size. Carnivorous species have been thought to have shorter gestation periods, giving birth to lighter young as a way of reducing the maternal energetic burden, particularly in the face of fluctuating prey (Bekoff et al., 1984). As gestation and lactation must be constrained by the metabolic rate of a mother (Jackson et al., 2014) the help of group mates in supporting a reproducing individual may be a means of increasing reproductive output. The help of group mates in supporting reproduction could result in faster growth and better energetic status of young which in theory leads to earlier age at first reproduction and would have the potential to increase lifetime reproductive output of offspring (Rosenbaum & Gettler, 2018b). In both Meerkats and wolves reproduction is most usually limited to the a single dominant individual or pair (Borg et al., 2015; Clutton-Brock et al., 2001b; Doolan & Macdonald, 1999). The high ranking reproductively active individuals within the group are able to benefit from the help of group mates in order to increase the size or growth rate of young. The extent to which this is seen however is likely to vary with environment, with group mates prioritizing their own energetic needs over the help of young where populations have been recorded at carrying capacity for the environment (Sparkman et al., 2011).

Individual based models allow a simulation of processes at a very fine scale and they are optimal when focused at a scale below the output of interest, with individuals being the key unit of interest for understanding dynamic systems at higher levels of organisation (Martin et al., 2012). By modelling at a bioenergetic scale the emergent behaviours that impact populations can be assessed in relation to those which have been observed and recorded in the field. For wolves and meerkats group size has been correlated with reproductive output (Clutton-Brock et al., 2001b; Sparkman et al., 2011). Where the energy balance favours grouping sociality can evolve, restricted , however, by the environment in which the predator exists. To further improve the outputs from this model factors such as the spatial and temporal variability of prey should be incorporated. In addition strengthening the implementation of predation in the model to include a functional response of predators would greatly enhance the predictions made by the model. Where the data allows the model has the potential to be adapted and parameterised for a suite of carnivore species which could strengthen the evidence for energy as the driving factor influencing social behaviours among different species in different environments. Parameterised for different species of carnivore the model could be used to investigate differences in the energetic benefits from sociality across different clades.

The model developed here has greatly simplified the processes that are associated with sociality. Perhaps the most important of these is the representation of behaviour. It is perhaps ironic that it is the behaviour associated with sociality in carnivores that has attracted a large amount of research interest yet it is also the most severe criticism aimed at the use of Individual Based models (Rushton et al., 1997). Nonetheless, the IB model developed here shines a light on the relative importance of considering bioenergetics as a driver of behaviour. On this basis IB models of the kind developed here can act as a bridge between descriptive behaviour and populations dynamics.

Chapter 6

Discussion

The numerous factors that impact the extent to which sociality is exhibited are inextricably interlinked and as such must be investigated in a manner that accounts for this. Here I have shown that social grouping can be energetically efficient, but to understand the energy saving mechanism requires an understanding of the interactions between individuals and their environments. The use of ecological models as tools to examine the complexities of the development of carnivore social groups has allowed a deeper understanding of the contributing factors that can act as a foundation which future studies can build upon. If energetic principles, coupled with a knowledge of a species environment can be used to predict the extent to which individuals in a given population might exhibit social behaviours this could be a vital conservation tool.

6.1 The modelling approach

Models as formal expressions of the essential elements of a problem are most often initially represented verbally, before being translated into conceptual diagrams and formally challenged with data. Here I have extended this initial verbal representation to explore the potential for word models, and analysis of language to be used to complement numerical analyses. When investigating a behaviour such as sociality it is important to consider how that behaviour is recorded. Whilst many ecological processes can be measured and interrogated numerically, behaviours are described before they are analysed. These descriptions and the language that is used is extremely important and could provide information that can be quantified.

Language is an abstraction, used to describe observations or phenomena, although we may not be conscious of it the structure of the language that we use, the words that we choose, contain a great amount of detail about the subject of our description (Erk, 2012). Where two behaviours are perceived to be similar perhaps the language used to describe them is similar. Such a similarity may be obvious when comparing a small number of texts but for comparisons across large numbers of texts such similarities may not be visible to the naked eye (Chang et al., 2009). Topic modelling allows a deconstruction of texts identifying structures and topics that are hidden in the composition of language (Blei, 2012).

Using a topic modelling approach has the potential to harness information from existing data, bodies of text, that have not been commonly used in ecological analyses. Here it was used to demonstrate that the textual descriptions of a species' habitat use and diet preferences could be used to demonstrate similarities between species in different families that coupled with additional information could be useful in understanding the emergence of social behaviours in carnivore species.

Analysis of text in this manner relies on the assumption that words have meaning and that those meanings depend on the context in which they appear, the objects and subjects of sentences and the words surrounding them (Srivastava & Sahami, 2009). The word chase, for example, could be preceded by words such as short or long, the choice of that word drastically alters our perception of the behaviour being described. As a method topic modelling can be limited by the length of texts (Blei, 2012), whilst many carnivore species are well described there are some species for which we have relatively little information and this limited the analysis with only three families of terrestrial carnivores having texts for all species that were long enough to be used for the model.

Sociality is a complex behaviour and is unable to be explained by the language used to describe habitat and diet preferences alone. Some similarities were seen in the descriptions of social species based on their habitat and diet descriptions but these factors are just components of a larger system. Additional interlinked factors such as life history traits are important in impacting behaviour and thus analyses need to be extended to incorporate these variables. The incorporation of such information requires the synthesis of different data types and the use of more complex distribution models.

Multivariate models seek to find common trends or groupings in complex data where there are many variables measured on multiple individuals. Through the use of information about the relationships between variables, these techniques can be used to identify the structure underlying a dataset with multiple correlated variables (Everitt & Hothorn, 2011; Rencher, 2005). Such statistical models can be used to reduce the dimensionality of data, where multiple correlated variables such as life history variables are of interest to identify patterns. These models tend to focus on static patterns rather than the dynamic processes that produce them (Bolker, 2008) thus offering a jumping off point for more dynamic investigations.

Multivariate analyses are however limited in their assumption that all variables are equal when this in fact is not the case in most systems. Structural Equation Modelling (SEM) does not make the same assumption and can be used to investigate the relative contributions of the different variables being investigated. The emphasis of SEM is on the study of simultaneous influences not to isolate causes which makes it appropriate for use in complex systems such as ecosystems (Shipley, 2016). As scientists we are too often taught that conclusions can only be deemed acceptable if based on accepted statistical conventions. We develop a null hypothesis and only reject that where our analyses produce test results that fit with our selected cut-off criteria. SEM's offer an alternative; they are built on the complete available body of knowledge and models are only rejected if the observed data do not match the expectations derived from the model (Grace, 2006).

Using a SEM approach allows an interrogation of the interactions between variables that influence the behaviour of interest. Models built *a priori* incorporating all existing knowledge are used as vehicles for testing ideas where the intention is to understand a response variable in the context of the system in which it exists (Kline, 2015). To do this requires us to approach the problem with a system perspective, it would be meaningless to isolate a single relationship and examine it carefully aiming to reveal its details because the relationship may be different when it works in nature with interactions from many other processes. SEM also allows comparisons across variables that are measured at different scales through the use of standardised coefficients. Being based on covariance rather than correlation standardised and unstandardized results can be calculated. This is particularly important for analyses such as these where the factors of interest vary from being at the scale of an individual's home range to being at a latitudinal scale (Grace, 2006).

There are however limitations to SEM particularly when using standardised coefficients for comparison. The sample sizes used in these analyses are likely large enough to estimate a consistent sample variance however a potential limitation of the method is the assumption within SEM of multivariate normal distribution (Finney & DiStefano, 2006). When looking at sociality, the numbers of individuals of adults or cubs within a group we are dealing with individuals and thus in reality are limited to whole numbers. SEM is limited in its capacity to model categorical variables, therefore sociality can not be included as a binary variable (animals being classed as social or non-social) which has led to the use of group size as a proxy for sociality. Given the plasticity of social behaviours the classification of sociality as binary would likely be inaccurate, particularly given that a suite of social behaviours exist and individuals within a population can vary in the extent of social behaviours that they exhibit. Proponents of SEM have stressed the idea that statistics should be used only to aid in interpretation rather than as a set of rigid protocols for establishing facts with model evaluation needing to be theoretically plausible rather than simply the result of statistical criteria (Grace, 2006; Kline, 2015). Through the use of SEM, I have shown that although life history variables may have the biggest influence on sociality the interaction with external biotic factors and the environment are important in influencing sociality across different species. This allowed the important environmental variables to be included in models investigating variation within a species which again demonstrated the impact of the environment in shaping the social groups seen within a population.

For processes that may be driven by more than one mechanism, as SEM suggests is the case for sociality it is important to ensure that the underlying mechanism is captured. Energy potentially represents that mechanism and energetic principles can be scaled up from a cellular to an individual level in order to simulate it's impact on individuals (Martin et al., 2012). Population level properties such as sociality emerge from the interactions of individuals with each other and their environment with an individual's adaptive behaviour giving rise to emergent properties (DeAngelis & Mooij, 2005). Individuals are the building blocks of ecosystems; the properties and behaviours of individuals are what determines the properties of the systems they compose. Individual based models (IBMs) link all of the separate levels in the ecological hierarchy, the responses of individuals to their local environment are based on physiological and behavioural responses (van der Vaart et al., 2016). The aggregation of all individuals of many species interacting with each other and with their environment produces community dynamics. Ecosystem dynamics result from the aggregation of individual environment interactions into large scale material and energy fluxes and this can be captured by the use of IBMs (Grimm et al., 2016).

The continued behavioural adaptation that results from process based rules that allow individuals to respond flexibly not only allow for more detail to be captured by the model but allow more flexibility for individual action than compartmental modelling approaches which operate at the population scale (Jørgensen & Bendoricchio, 2001).
IBMs are often developed for very specific research questions which can create problems for researchers meaning that they often have to develop models from scratch for the particular scenario that they wish to model (Martin et al., 2012). The development of a specific model however does ensure that the property of interest is modelled at an appropriate scale. The development of a specific model requires a large amount of pre-existing knowledge of the system in order to effectively parameterise a model and this can be a limiting factor for species for which relatively little data exists. The species modelled here, the grey wolf and the meerkat are well studied and provide an opportunity to thoroughly investigate the energetic impacts of sociality which could be further explored for other well described species.

Ecological models represent a simplified picture of reality that can be used as a tool to investigate a problem (Jørgensen & Bendoricchio, 2001). They represent a synthesis of what we know about a system that extends beyond simple relationships between data. When trying to understand a concept such as sociality, a behaviour that is not only exhibited in different species across the order Carnivora but is also seen to vary within species, it would be impossible to survey the many components of an ecosystem and their reactions in each instance of social behaviour in order to try and understand it. With the use of models as a holistic tool the different conditions under which social behaviours are seen have been examined allowing some insight into the driving factors influencing social behaviours.

When evaluating the outputs of such models the scale at which they focus is an important consideration. Here models investigated both broad scale global variations, as well as finer scale single species systems. The different scales at which these models are focussed appears to show environmental variables to be more important in local, single species models than global cross species comparisons. For the badger models the availability of fine scale longitudinal data allowed a detailed investigation of a population that was able to account for the environmental heterogeneity of the habitat area over an extended time period. The nature of this data, combined with the fact that badgers are a species that largely live and therefore feed in temperate climates where food availability is driven by the environment, allows for the detailed analysis of the fine scale environmental variables that are influential to their sociality. Where investigations are focused at a broader scale, investigating the impacts of different species across their global ranges, the models suggested environmental variables to have an impact but to a lesser extent. The data available for these models include a more generalised representation of the environments in which species are found. In contrast to the longitudinal data that is available for badgers the global models do not account for fine sale environmental heterogeneity and as such the model outputs emphasise more broadly on the life history factors that impact social behaviour. No single model can hope to capture the complexity of a real world behavioural situation (Clark et al., 2000). Ecological modelling is not a one size fits all approach to understanding behaviour; different techniques can be used for different purposes, and multiple approaches may be required to gain a thorough understanding of a system. Ecological models are tools, much like geographic maps, they are representations of reality. The map (or model) that will be of most use in a given situation will differ depending on the scale at which it is focussed. Using different modelling approaches to examine sociality at different scales I have demonstrated the importance of environmental interactions with individuals in shaping the social behaviours that they exhibit.

6.2 Understanding sociality

So why be social, to increase food intake to increase reproductive output or to decrease predation risk? All of these benefits ultimately boil down to energy. The pressures of each will differ depending on the individual, (how big it is, what it eats, the environments that it lives in etc.) but ultimately the behaviours that are exhibited are shaped by a balance of numerous factors. Individuals have to maximise energy intake relative to expenditure in order to maximise the amount of excess energy that can be devoted to reproduction and ultimately enhance their fitness. This fitness is what drives the evolution of behaviours that are impacted by multiple drivers, life history traits, environment and the interaction between the two.

If it is energetically beneficial to be social, whether it means that an individual gets more energy from eating bigger things or spending less energy by sharing costs such as territory defence then it will surely be in an individual's best interests to act socially. Most previous research has focused on the perceived costs and benefits of sociality but as I have demonstrated these factors are not independent and must be investigated as part of a bigger system. Sociality is a complex system so breaking it down to then build it back up is a solid approach to its investigation as it leads not only to an understanding of the component parts but also how they interact. Thoroughly investigating each component before attempting to understand how it relates to other components within the system has given a structure to the modelling approach that has allowed an investigation of interacting processes that are occurring at different scales to impact social behaviours.

The results of Chapter 2 showed that language could be used in analyses aiming to understand behaviours, demonstrating the importance of natural history data in modern analyses. The results highlighted some similarities in the way that similar foraging behaviours are described that can be used to start to understand the context in which social behaviours might arise. The results also highlighted the differences between different Families of carnivores which suggested that life history characteristics might strengthen our understanding of the patterns in sociality seen across different species. Sociality is known to have evolved multiple times across numerous phylogenetic groups (Smith et al., 2012), investigating life history traits (which tend to be similar across closely related groups) without accounting for the interaction between a species and its environment would not yield a full picture of the conditions under which sociality occurs. Further investigating this Chapter 3 demonstrated that numerous factors that influence sociality are interlinked and as such need to be examined in a manner that accounts for this. When considering differences between species life history traits were shown to be more important than the environment, these traits have evolved at a slower pace than the pace at which environmental changes take place and so are shaped by the interactions between an individual and its environment. Behaviours are a result of life history and environmental interactions. Evidenced by the bush dog (*Spethos venaticus*) for example, which has developed as one of the smallest canid species, it's relatively small size allows efficient navigation of the densely vegetated forests of south america that they inhabit. This small size allows them to use burrows as a means of predator avoidance but also means that they can enter burrows of other species to take advantage of them as prey.

Their tendency to live in social groups has also allowed them to develop group hunting strategies that can be used to take down large prey allowing the species to have a wide prey range but still be small enough in size to effectively manoeuvre in the environment that they find themselves in. Even though the model suggests that life history traits are relatively more important in impacting sociality it is evident that the environmental interaction necessitates an ecosystems approach in which environment is also considered. This interaction with the environment is important when considering variation within a species.

Chapter 4 demonstrated the interaction between environmental conditions and territory size of a group which impacts the demography of the group itself, particularly how many cubs can be supported. If these factors are important in driving the size of social groups this could be important factor in understanding the variation in social groups and the conditions under which sociality arises. Focusing on the European badger, a species that has long been identified as a social anomaly, living in groups, pairs or individually and not exhibiting social behaviours such as cooperative breeding, predator defence, or hunting (Balestrieri et al., 2011). UK populations have been extensively studied, lots of detail is known about their behaviours (Buesching & Macdonald, 2001; Carpenter et al., 2005; Cresswell & Harris, 1988; da Silva et al., 1993; Doncaster & Woodroffe, 1993; Dugdale et al., 2007; Fell et al., 2006; Kruuk & Dekock, 1981; Kruuk, 1978b; Mallinson et al., 1992; McClune et al., 2015; Palphramand & White, 2007; Roper et al., 1993; Woodroffe & MacDonald, 1993; Woodroffe, 1995; Woodroffe & Macdonald, 2000). European populations however have not been studied to the same extent. Most studies of European populations have focused on the diet (Asprea & Marinis, 2005; Barea-Azcón et al., 2010; Fischer et al., 2005; Goszczynski et al., 2000; Henry, 1984) which in turn impacts the not only the size of territories that they occupy but the extent to which they occupy themselves with territory defence (Balestrieri et al., 2006, 2011). Where the unpredictability of food resources leads to larger ranges that are not systematically defended to the same extent as in UK populations the energetic benefit of forming a social group may be reduced. The energetic optimum group size under such conditions is likely lower.

The idea of energy as a driver of group formation was explored further in Chapter 5 and demonstrated that energy driven optimum groups sizes can be predicted and that the optima varies between species and environments. Understanding that energy likely drives social grouping through the development of the Individual Based Model based on energetics allowed an investigation of which aspects of an individuals resources are optimised when individuals group. Testing the method with two species that are different in their life histories and behaviours but that both benefit from social grouping allowed a demonstration of the energetic benefit brought about through social behaviours. If energy regulates behaviours the formation of a social group will result when grouping can bring about behaviours that will maximize the energetic intake of an individual relative to expenditure. The environment and characteristics of the individual will determine the social behaviours that the individual benefits from in order to bring about this energy maximization. Grouping might reduce individual energy expenditure during hunting, reproduction or defence or it might increase energy intake and survival. Further investigations incorporating intra-group interactions would provide a deeper understanding of the differences between theoretical optima and the real world observations that are recorded, an understanding which could be a vital conservation tool.

6.3 Recommendations for future work

In order to understand what conditions favour the formation of social groups several aspects of how an individual interacts with it’s environment need to be investigated. As a synthesis aiming to understand sociality in numerous species this work was limited by the availability of appropriate data, particularly with regards to predation. Information regarding the predation threats to each carnivore species were not well documented within the data sources used for these analyses (Hunter & Barrett, 2018; Jones et al., 2009; Wilson & Mittermeier, 2009). Collation of information on the predators threatening each carnivore species was difficult to extract due to many carnivores themselves being predators, thus where literature was searched using the terms ‘species name’ and ‘predator’ manual interrogation of each study was required to determine whether the study detailed the predators of a carnivore or described that carnivore as a predator. As predation threat is impacted by factors such as body size and habitat, demonstrated as factors that are important in influencing sociality (Chapter 3) the collation of such information could be used to further understand the relative contribution of predation pressure as a driver of social behaviours. In addition to a better understanding of the impacts of predation across species a more detailed incorporation of the functional response of predators, such as those that predate on meerkats would be an interesting point of further development for individual based models such as that used in Chapter 5.

European badgers remain puzzling in their sociality, whilst there is a plethora of information relating to populations in the UK (largely due to their implications in the transmission of bovine tuberculosis (Brown et al., 1992; Delahay et al., 2000; Garnett et al., 2005; Mullen et al., 2013; Rogers et al., 2003; M. Tuyttens et al., 2000; Weber et al., 2013)) their behaviours are less well studied on the continent. Studies that do exist largely center on diet (Asprea & Marinis, 2005; Balestrieri et al., 2009; Myslajek et al., 2013; Rosalino et al., 2005) or home range size (Molina-Vacas et al., 2009; Revilla & Palomares, 2002; Rosalino et al., 2004; Zabala et al., 2002) but less is known about the extent to which their behaviours differ from what is known of UK populations. Such information would provide invaluable knowledge of behavioural plasticity with relation to sociality and could feed in to models such as that developed here (Chapter 5).

A particularly interesting area of further research would be the incorporation of intra group relationships and behaviours which may impact the group sizes that exist in the wild. Recent work has suggested group composition and the resulting behaviours to be equally as important as group size in determining the outcomes of inter group interactions for species such as wolves (Schell, 2020). Incorporation of information on lesser known social dynamics within a group (Bauduin et al., 2020) into an energetic based model could be an interesting avenue for the development of the work detailed here in order to give further clues as to the drivers of social groups.

6.4 Conclusion

To have the best chance at successfully conserving carnivores it is crucial to have a good understanding of their behaviours and how these interact with their environment. The more that we know the more informed our conservation efforts can become. The global biodiversity crisis is well acknowledged, protecting carnivores we protect the ecosystems in which they are found, they act as an umbrella species and their success can increase the success of numerous other species. We have limited resources to devote to conservation, well informed investments therefore offer a greater promise. Understanding what drives sociality, between and within species must include an understanding of the interaction between a species and its environment. With energy potentially driving the extent of social grouping, varying between species and environments we have to account for its impact on social behaviours. Ecological models not only offer a mechanism by which we can deconstruct ecosystems in order to understand them but have the potential to be used as tools for conservation, predicting the outcomes of different scenarios. By harnessing the power of ecological models to better understand and predict species responses we may have a chance to reduce biodiversity loss.

Appendix A

Chapter 2 appendix

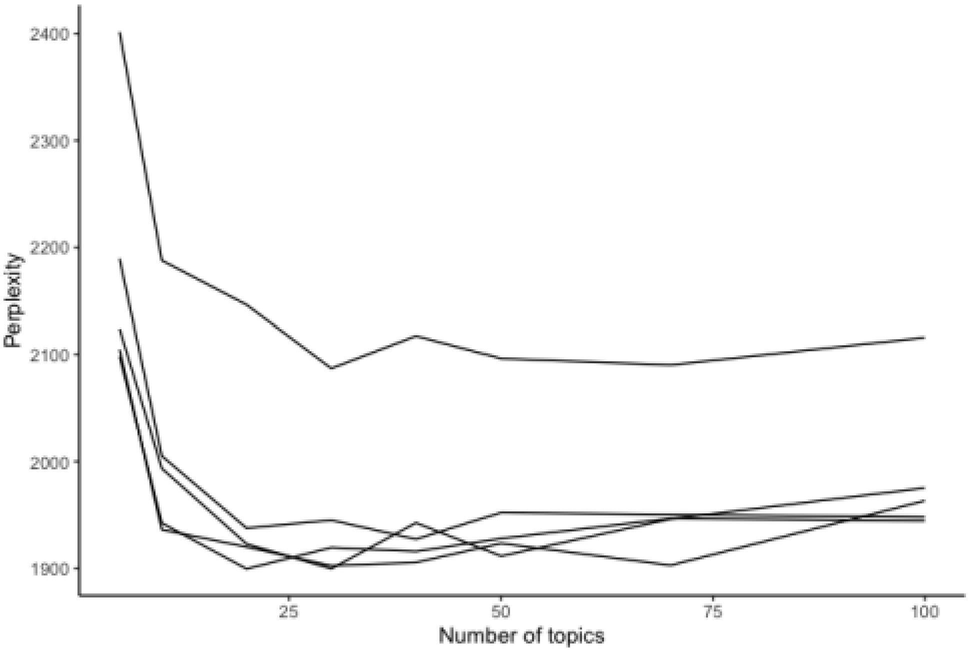

Figure A.1: Perplexity scores of different topic numbers as determined by block cross fold validation

Table A.1: Top 20 weighted words assigned to topics in LDA model

BehavA	DietA	DietB	HabitatA	BehavB	BehavC	HabitatB	DietC	DietD	BehavD
prey	grassland	fox	desert	area	prey	forest	beetl	diet	includ
kill	rat	food	small	hunt	habitat	includ	snake	feed	spp
larg	rodent	fruit	bird	hare	speci	found	insect	area	dog
leopard	wolv	habitat	rodent	may	deer	also	stomach	record	summer
day	mice	item	south	one	rang	lowland	termit	invertebr	semi
tiger	grass	season	open	also	human	cat	reptil	main	veget
small	observ	insect	woodland	use	region	dri	found	close	avoid
size	short	bird	can	high	common	tree	occurr	grass	main
ungul	burrow	vertebr	also	mountain	rabbit	decidu	africa	most	stepp
anim	occasion	forag	prefer	studi	occur	water	egg	jackal	bird
will	seen	mammal	appear	consum	red	river	mongoos	varieti	arid
scat	hole	rang	inhabit	success	occupi	along	food	montan	bush
young	found	avail	rainfal	snowsho	use	ground	african	frequent	elev
cover	carcass	plant	water	site	although	habitat	mammal	rocki	near
taken	marsh	collect	opportunist	like	import	tropic	seat	habitat	report
larger	east	seed	speci	relat	wild	dens	frequenc	dens	eat
africa	indian	carrion	primarili	cover	can	open	dri	dig	lizard
park	black	coastal	wildcat	per	puma	evergreen	open	accord	general
cat	mole	island	import	year	occasion	known	coleoptera	level	northern
less	ethiopian	southern	central	occur	terrain	associ	percentag	specimen	environ

Appendix B

Chapter 3 appendix

Table B.1: Table detailing modelled data extracted from Wilson and Mittermeier

Variable	Detail (units)
Head-Body length	Max. recorded (cm)
Tail length	Max. recorded (cm)
Shoulder height	Max. recorded (cm)
Weight	Max recorded (kg)
Skull length	Max. recorded (cm)
Footprint length	Max. recorded (cm)
Home Range	Max. recorded (km2)
Density	Max recorded (individuals per km2)
Gestation period	Max recorded (days)
Litter size	Max recorded (n)
Juvenile mortality	Proportion
Adult mortality	Proportion
Lifespan	Max recorded (years)
Red List status	one of: Data deficent, Least concern, Near threatened, Vulnerable, Endangered, Critically endangered, Extinct in the wild, Extinct
Social	Binary (yes/no) determined from text descriptions
Territoral	Binary (yes/no) determined from text descriptions

Predated	Binary (yes/no) determined from text descriptions
Group size	Max recorded (n)
Guild overlap	Number of species of greater body size with overlapping geographic distribution

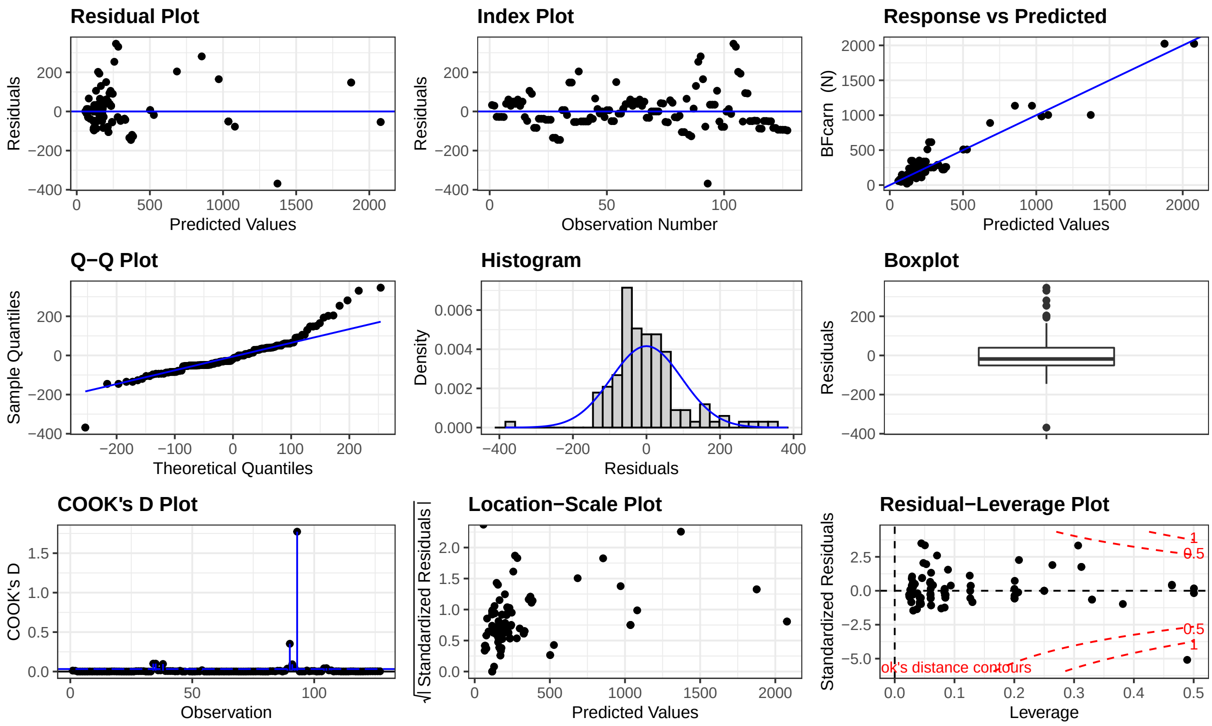

Figure B.1: Residual outputs from model predicting bite force as a function of predator weight, prey range, mean prey size and family

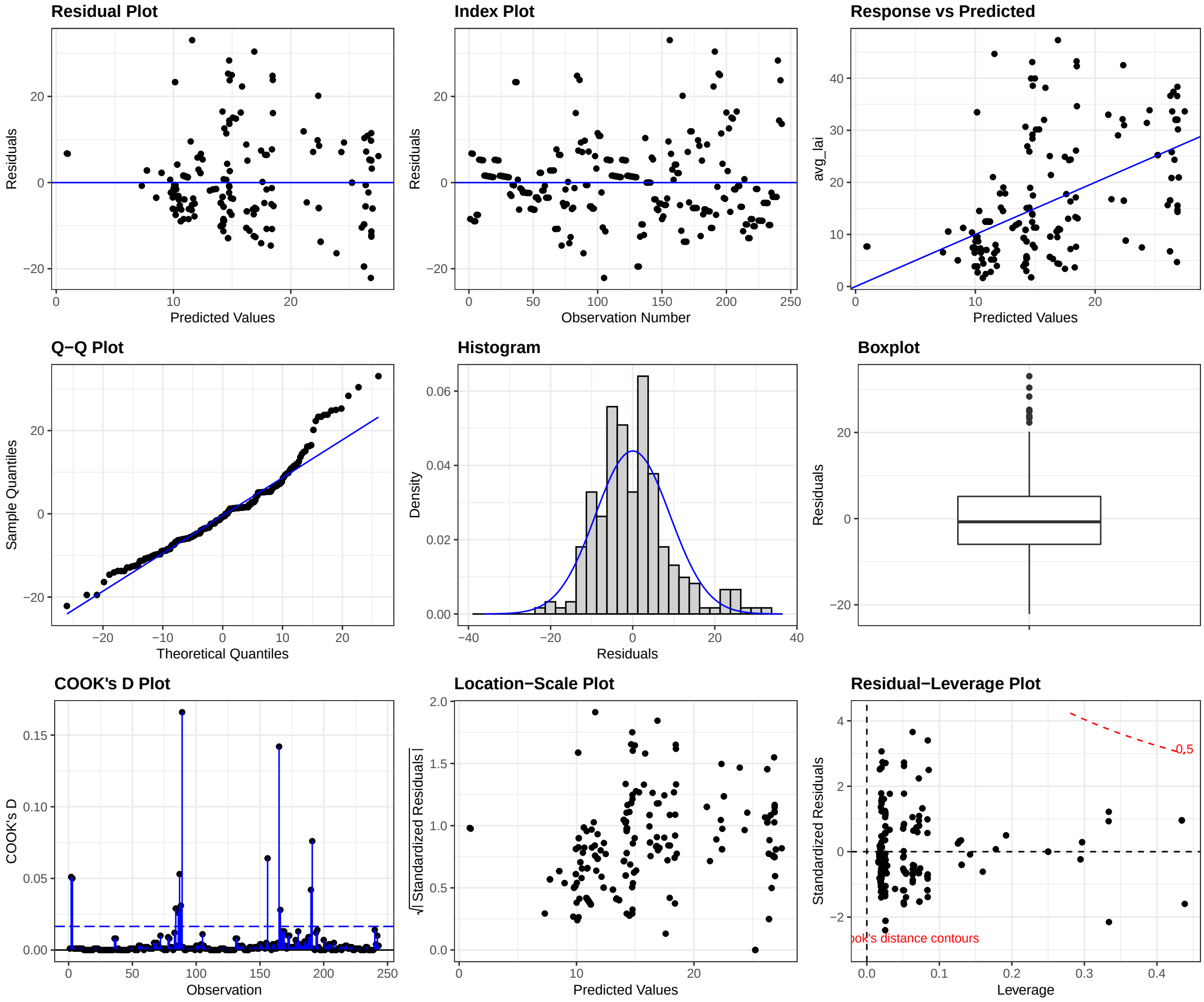

Figure B.2: Residual model outputs using weight, prey mean weight, prey size range and family as predictors of LAI

Figure B.3: Reference image used as a reminder of the difference between platykurtic and leptokurtic distributions for using kurtosis as a measure of the shape of a distribution.

Appendix C

Chapter 5 appendix

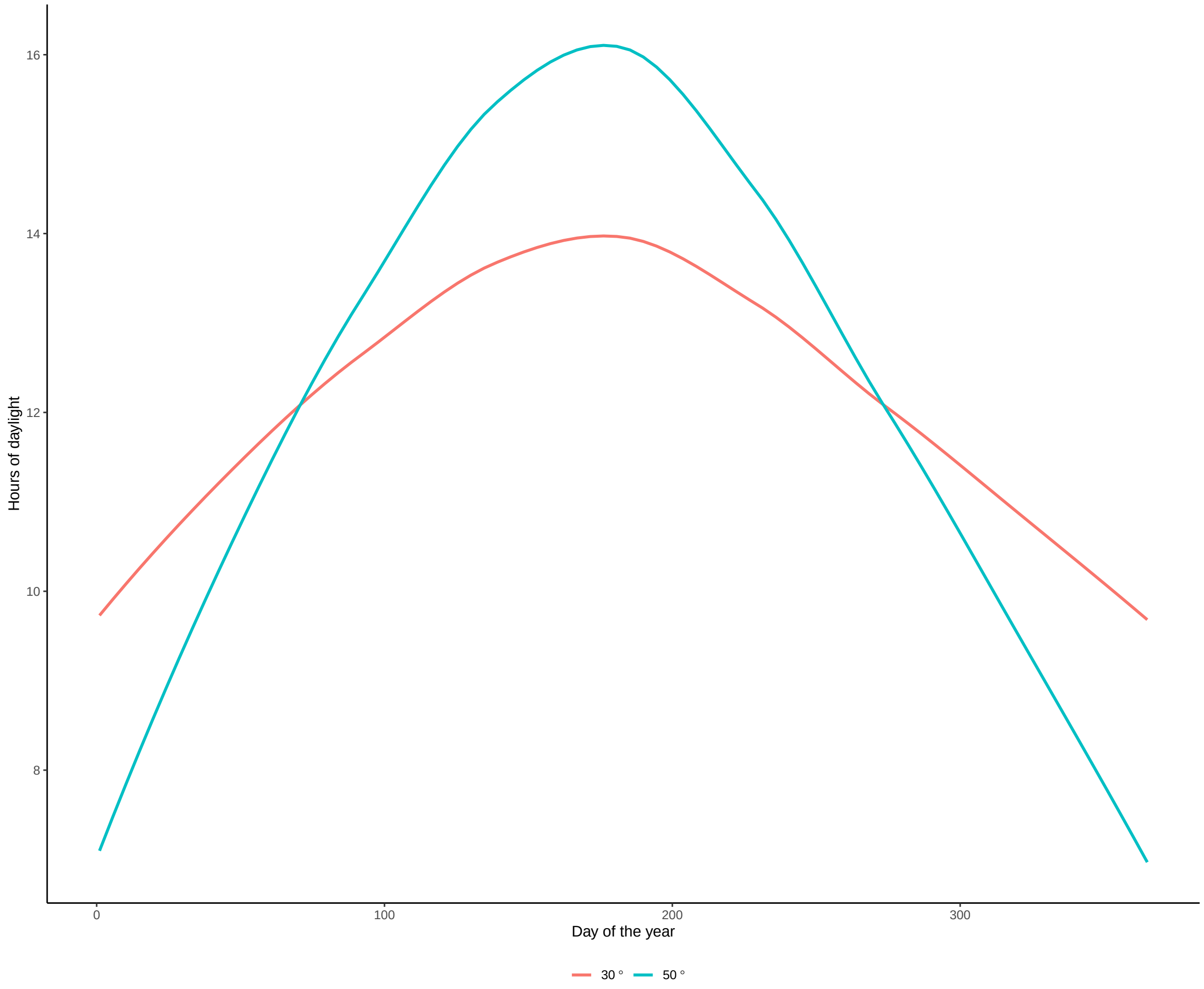

Figure C.1: Day length (hours) as predicted by the model for latitudes of 30° (red) and 50°(blue) demonstrating diferences that can occur between ranges at different latitudes.

Hunt success

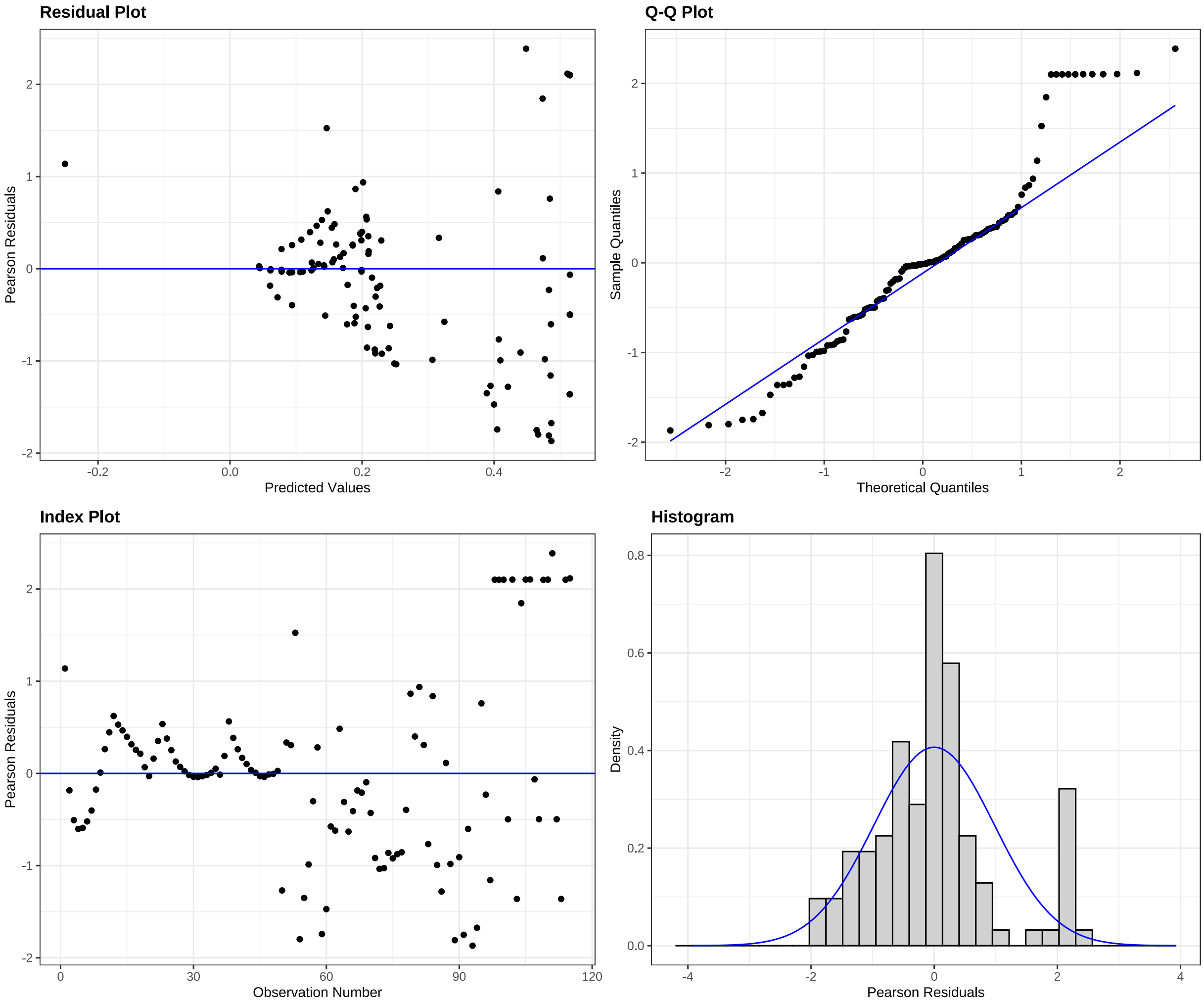

Figure C.2: Residual plots from hunt success model with hunt success rate as a function of group mass with Family as a random effect

Processing time

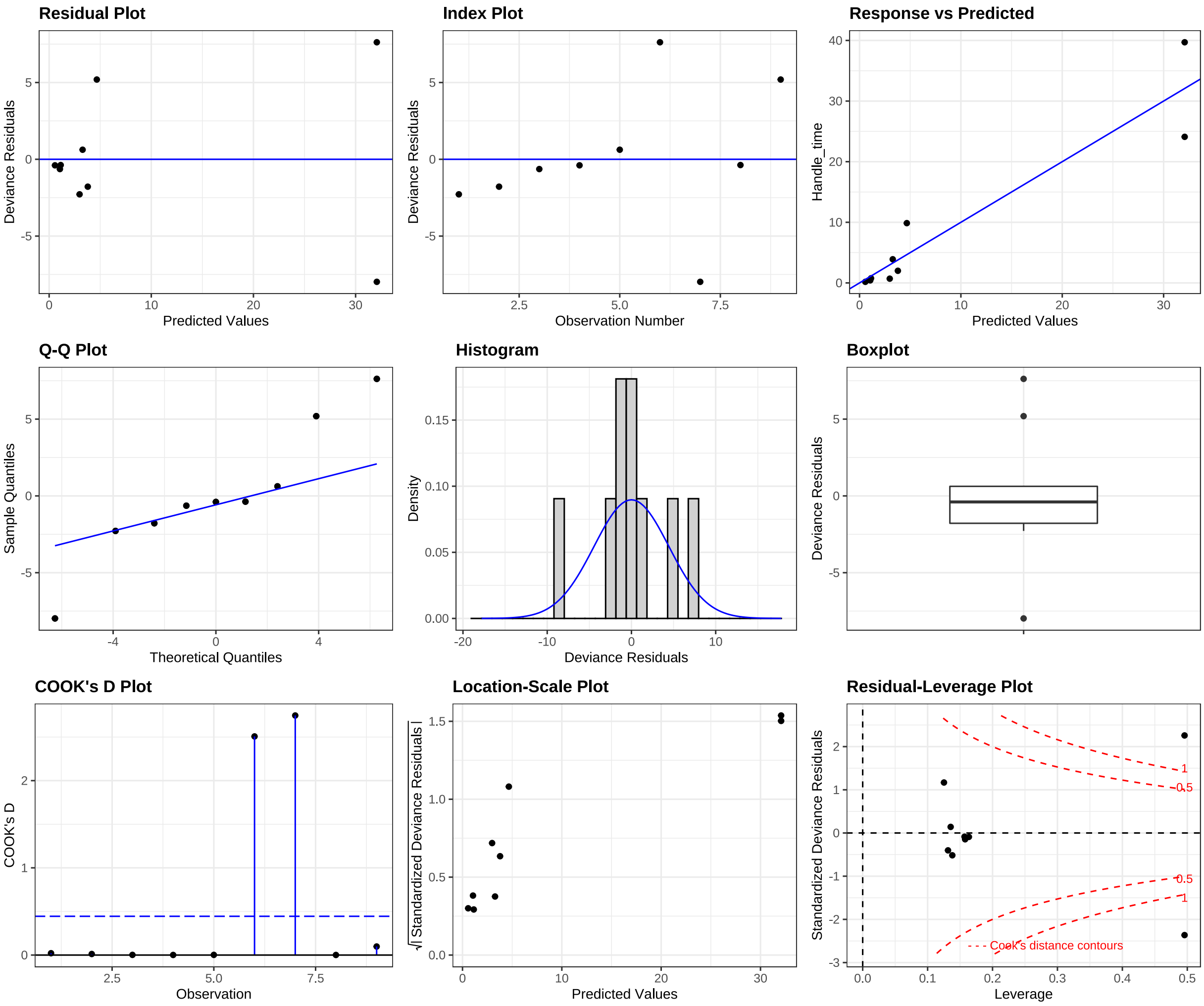

Figure C.3: Residual plots from prey processing time model with (log) mean prey size as a function of predator size and group size with Family as a random effect

Prey processing time was significantly predicted by the proportional weight of a prey item as compared to the predators weight(β= 4.015, p = <0.05). Predictions from this linear model were used to inform the processing time parameter of the Individual Based Model

Regression equation

Differentiated to predict optimum group size

$$Reproductiveoutput\ Groupsize + Groupsize^2 \tag{C.1}$$

Body size

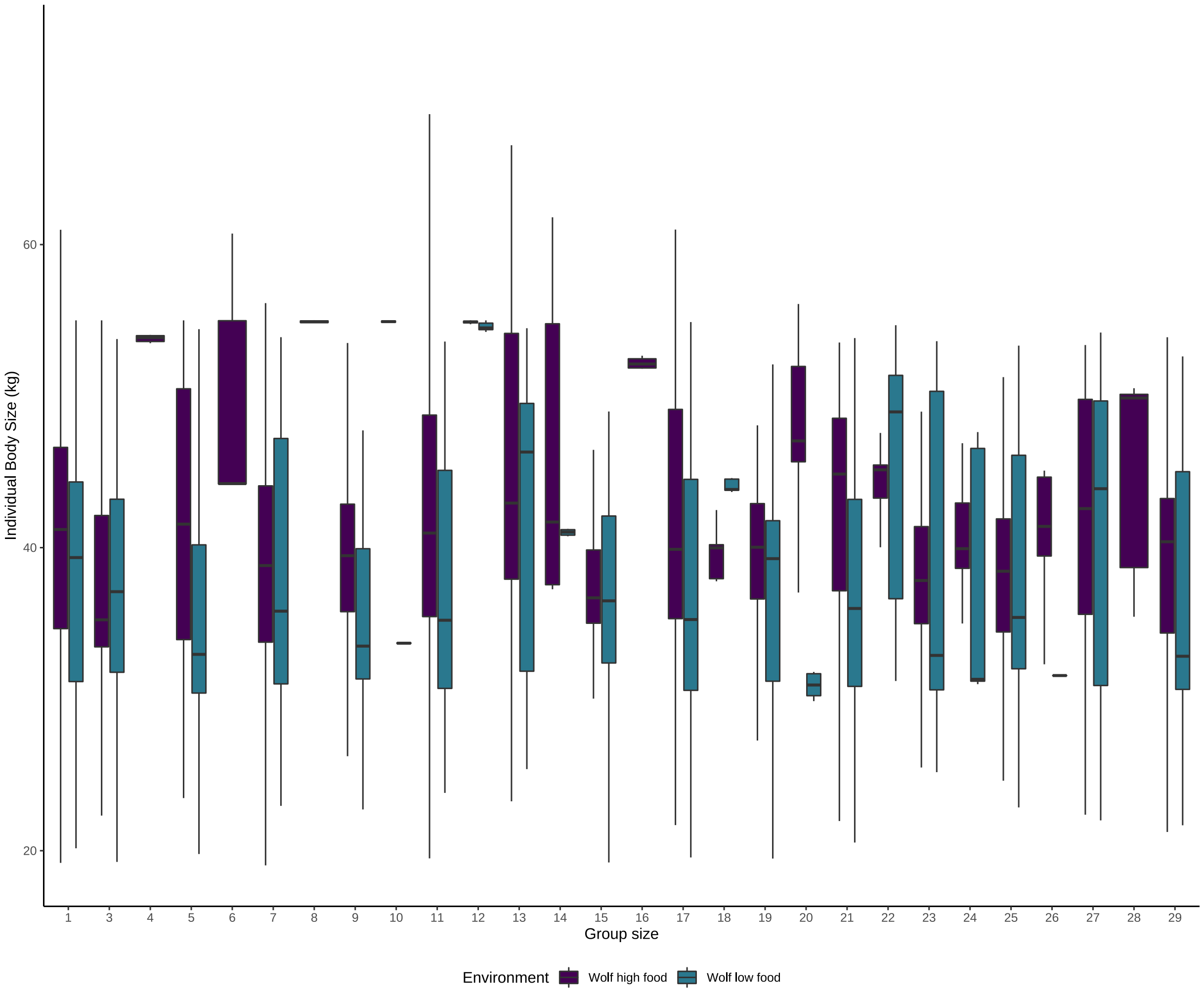

Figure C.4: Variation in mean individual body size with group size at the end of simulated model runs. For wolves a very small positive influence of group size on body size was seen (beta = <0.001, P = <0.001)

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