

The evolution of individual foraging specialisation in a group-living mammal



Submitted by

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Thesis summary

Individual foraging specialisation has received much attention in the past few decades, however the causes and consequences of such specialisation in group-living and cooperative species remain poorly understood. These species merit special consideration as many of the key drivers associated with individual foraging specialisation, such as intrapopulation competition and social learning, are likely to be influenced by the intensified local social environment. In this thesis, I aim to investigate such social influences on individual foraging niche. I first explore current theory behind individual foraging specialisation and apply this to the social group in order to predict how living in groups may impact the development of such specialisation (Chapter 1). I also discuss the consequences of between-individual variation in foraging niche and consider how the development of this may feedback on the social environment of group-living species (Chapter 1).

Following my review of current theoretical and empirical work in Chapter 1, I investigate the causes of individual foraging specialisation in a population of wild banded mongooses, *Mungos mungo*. I begin by outlining the general methods used in this thesis, detailing the study species, study site, data collection and sample preparation and processing (Chapter 2). Presenting my findings, I first show that increasing group size results in smaller individual foraging niche, suggesting that intragroup competition drives individual foraging specialisation (Chapter 3). Second, I present evidence for the non-genetic social inheritance of foraging niche and explore the influence of role models on the transmission of behavioural traditions (Chapter 4). This work highlights that the social group environment, in particular increased local competition and

opportunity for social learning, has a substantial effect on individual foraging niche in banded mongooses. I hypothesise that the ability to specialise may reduce intragroup competition, promoting group stability and propose further work to explore how living in groups influences both the causes and consequences of individual foraging specialisation.

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Author's declaration

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Definitions and abbreviations

Behavioural tradition: persistent behavioural traits shared by several members of a species and transmitted through social learning (Fragaszy & Perry 2003)

Concerted (many-to-one) transmission: acquisition of behaviours from multiple role models acting in concert; often exhibited by older group members transmitting behaviours to younger individuals

Ecological release: an increased wealth of underutilised resources, often as a result of reduced interpopulation competition, but also environmental factors such as patch size, microhabitat diversity, resource diversity and environmental stability

Eusocial: species of the highest level of sociality, which feature high relatedness, cooperative brood care and a pronounced division of labour

Haplodiploid: species in which males develop from unfertilized eggs and are haploid (possessing a single set of chromosomes), and females develop from fertilized eggs and are diploid (possessing two sets of chromosomes)

Increased degree: individuals with wider foraging niches interact with more species, resulting in a greater number of network connections (Bolnick et al. 2011)

Individual specialisation: when individual niche is substantially lower than that of its population for reasons not attributed to age, sex or morphology (Bolnick et al. 2003)

Isodistance: the distance in isotopic niche space between two individuals

Isotopic niche: an area (in δ space) with axes defined by isotopic values (δ values, Newsome et al. 2007)

Local competition: competition within a social group for shared resources

Oblique transmission: transmission of behaviours between generations irrespective of relatedness (Cavalli-Sforza & Feldman 1981)

RINI: Relative Individual Niche Index

SEA: Standard Ellipse Area; represents the area of isotopic niche space occupied by an individual or social group (Jackson et al. 2011)

Type A generalism: expansion of population niche through increased within-individual variation, resulting in a population of generalists (Van Valen 1965)

Type B generalism: expansion of population niche through increased between-individual variation, resulting in a population of specialists (Van Valen 1965)

Vertical transmission: transmission of behaviours between mother and offspring (Cavalli-Sforza & Feldman 1981)

Chapter 1: General introduction

Abstract

Recent research has demonstrated the widespread occurrence of individual foraging specialisation and the numerous causes and consequences associated with it. However, one key area that has received relatively little attention, is the presence of such specialisation in group-living species. This warrants special consideration as the social group environment often has a greater impact on the individual than the total population and mechanisms driving specialisation may differ. This article summarises current theories regarding individual specialisation and applies these to group-living species, discussing how the causes and consequences may differ to those in non-social species. Both intra- and interpopulation competition are thought to be key drivers in the development of foraging specialisation. We might expect similar effects in group-living species, but driven by competition within and between social groups, rather than whole populations. Living in groups also presents greater opportunity for social learning; a widely recognised mechanism through which foraging niche can be acquired. Our review suggests that living in groups may profoundly alter the mechanisms behind and the consequences of, individual foraging specialisation, highlighting the importance of further study within this area.

Introduction

The observation that individuals of the same species exhibit much phenotypic variation provided the basis for Darwin's theory of evolution by natural selection (Darwin 1859), and continues to intrigue ecologists and evolutionary biologists. Such phenotypic variation can lead to differences in individual niche use, due to intrapopulation variation in traits such as age (Engen & Stenseth 1989; Newland et al. 2009), sex (Bearhop et al. 2006; Stauss et al. 2012; Camphuysen et al. 2015; Burke et al. 2015) or morphology (Galicia et al. 2015; Hopwood et al. 2015; Pegg et al. 2015; Chavarie et al. 2016). However, when individual niche is substantially lower than that of its population for reasons not attributed to these three variables, it is termed individual specialisation (Bolnick et al. 2003). An upsurge in research into individual specialisation over the past two decades (Fig. 1) has revealed that it is widespread, affecting many ecological factors and evolutionary outcomes (Araújo et al. 2009; English et al. 2010; Newsome et al. 2009, 2015; Robertson et al. 2014, 2015; Rossman et al. 2015). However, one key area has received little attention: the causes and consequences of individual specialisation in group-living species.

The occurrence of individual specialisation in group-living species merits special consideration, as the environment created by a social group should have a greater impact on individuals than the environment created by the whole population. Therefore, we might expect mechanisms behind individual specialisation, and the implications of this specialisation, to be different in group-living species. For example, a significant consequence of group-living is an increase in competition between conspecifics (Krause & Ruxton 2002); competition being widely considered a key driver in the development of individual specialisation (Tinker et al. 2008; Svanbäck & Persson 2009; Bolnick

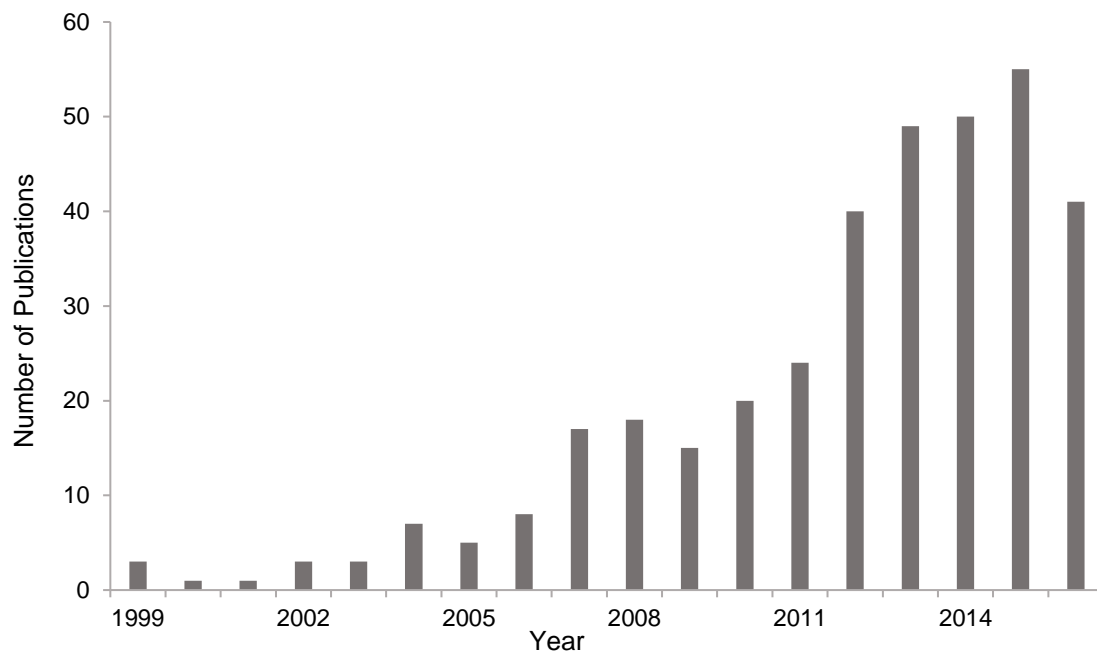


Figure 1: Number of scholarly publications on individual specialisation published per year since 1989 (Papers identified using Web of Knowledge™ search terms ‘Individual specialisation/specialization’). Between 1978 and 1998, 16 articles were published (<1 per year). Bar at 2016 represents publications up to 12/12/2016

et al. 2010; Newsome et al. 2015). In group-living species, group size can be considered the effective population size influencing ecological and evolutionary processes (Chepko-Sade & Halpin 1987). Thus we might expect group-living species to exhibit a higher degree of individual specialisation when intragroup competition increases. Individual specialisation can also affect reproductive success in non-social species, both positively (Patrick & Weimerskirch 2014; Otterbeck et al. 2015; Pagani-Núñez et al. 2015) and negatively (Navarro-López et al. 2014). Although the effects of reproductive success are unlikely to differ in group-living species at the individual level, individual specialisation may have important implications for reproductive success at the group-level. Group-living species, particularly cooperative species, often rely on the help of other group members to raise their young (Packer et al. 1990; Hodge 2005; Doerr & Doerr 2007; Cameron et al. 2009; Klauke et al. 2013). Helpers are often energetically limited in the amount of care they can provide (Gaynor et al. 1998; van de

Crommenacker et al. 2011; Nichols et al. 2012; Cant et al. 2013). Therefore, any benefits of individual specialisation that increase energy resources, such as increased body condition or foraging efficiency, may promote helping behaviour. This in turn could increase the reproductive success of the group.

One way in which individuals from the same population exhibit specialisation is in their foraging niche, with intrapopulation variation in foraging niche documented across a variety of different taxa (birds: Harris et al. 2014; Potier et al. 2015; mammals: Newsome et al. 2009, 2015; Robertson et al. 2014, 2015; Rossman et al. 2015; sharks: Matich et al. 2011; amphibians: Araújo et al. 2009). Studies of European badgers, *Meles meles*, found substantial variation in diet between individuals of the same social group, independently of age or sex, suggesting individual foraging preferences (Robertson et al. 2014, 2015). These differences were consistent over time, indicating long-term foraging specialisation (Robertson et al. 2014).

The purpose of this review is to summarise current theories underlying individual foraging specialisation and how these apply to group-living species. We focus on variation in foraging niche, however the concepts and arguments proposed may be applied to other forms of individual specialisation. We discuss how the mechanisms and consequences of individual foraging specialisation may differ in group-living species, compared to non-social species. We then propose future work to address the gaps in our knowledge regarding individual specialisation in group-living species (Table 1).

Table 1: Future research areas and predictions based on current theory

	Future work	Prediction
Causes		
<i>Intragroup competition</i>	Examine indices of individual foraging behaviour against proxies of increased intragroup competition such as declines in resource abundance or group size	Increased intragroup competition drives increased individual foraging specialisation
<i>High relatedness</i>	Investigate the impact of increased intragroup competition on individual foraging specialisation as a function of within-group relatedness	High within-group relatedness drives generalist foraging behaviour under increased intragroup competition
<i>Intergroup competition</i>	Long-term monitoring of populations, measuring individual foraging specialisation within social groups before and after the removal of neighbouring groups	Ecological release from intergroup competition leads to increased individual specialisation within groups
Consequences		
<i>Group stability</i>	Long-term monitoring of social groups, measuring individual specialisation and within-group variation. Comparing indices between stable groups and those that experienced collapse	Groups displaying greater individual specialisation exhibit long-term stability and reduction in risk of collapse
<i>Social network</i>	Studies combining indices of individual specialisation and social network analysis of competitive interactions, investigating degrees of connectivity and central nodes	Generalist individuals appear as central nodes, whilst specialist individuals exhibit lower degrees of connectivity and are positioned on the periphery
<i>Sub-group communities</i>	Identifying individual specialist behaviours and preferentially associations within social groups	Social groups divided into smaller sub-group communities displaying different specialist behaviours
<i>Group reproductive success</i>	Measure helping effort against individual speciation indices. Quantify individual specialisation across group and examine group level reproductive success	Specialist individuals display greater helping effort. Social groups comprised of individual specialists show increased reproductive success

What is individual specialisation?

Bolnick et al (2003) describes an “individual specialist” as an individual whose niche is substantially narrower than that of its population, for reasons not attributable to its sex, age or discrete morphological group. Total population niche width can be separated into two components; between-individual and within-individual variation (Roughgarden 1972). Populations comprised of generalist foragers have greater within-individual variation in niche, as each individual utilises a wide range of resources relative to total population niche width. In contrast, between-individual niche differences make up the majority of the variation in total niche in populations of individual specialists, as each individual uses a small proportion of the resources available to them.

Causes of individual specialisation

Although many studies have identified individual specialisation in foraging behaviour (Tinker et al. 2008; Araújo et al. 2009; Harris et al. 2014; Robertson et al. 2014, 2015; Rossman et al. 2015; Sanz-Aguilar et al. 2015), the ecological causes underlying this intrapopulation variation remain debated. Proposed mechanisms behind individual foraging specialisation in non-social species vary widely, including intra- and interpopulation competition (Svanbäck & Bolnick 2005; Svanbäck & Persson 2009; Bolnick et al. 2010), ecological opportunity (the wealth of underutilised resources as a result of decreased interspecific competition or environmental/habitat changes; Schluter 2000; Darimont et al. 2009) and predation (Darimont et al. 2007). Empirical evidence for these mechanisms is well reviewed by Araújo et al. (2011). The effects of ecological opportunity and predation are unlikely to differ between non-social and group-

living species, however the effects of competition are likely to differ. In addition, there is a far greater opportunity for social learning in social groups; also likely to play a role in the development of individual foraging specialisation. Here, we discuss these two mechanisms – competition and social learning – in the development of individual foraging specialisation in group-living species.

Intrapopulation competition

In group-living species, it is likely that individuals are more greatly impacted by the characteristics of their social group rather than those of the whole population. In particular, local competition is likely to be a major influence on the development of specialisation in group-living species. Both theoretical and empirical studies in mainly non-social species have demonstrated the contradictory outcomes of competition on individual foraging specialisation (Table 2). Classic foraging theory predicts that under increased competition, individuals should add new prey items to their diet, widening individual niche and driving generalist foraging strategies (Type A generalism; Van Valen 1965; Stephens & Krebs 1986; Fig. 2a). However, classic competition theory (such as niche partitioning; Schoener 1974; Pianka 1976) predicts that as competition between species increases, stable coexistence is achieved through niche differentiation, reducing dietary overlap between competitors (Type B generalism; Van Valen 1965; Fig. 2b).

These contrasting models can be applied to group-living species to form two opposing hypotheses, regarding the consequences of intragroup competition on individual foraging specialisation: (1) as competition increases, all individuals in the group add new items to their diet, widening individual niche and promoting

Table 2: Examples of the effects of intrapopulation competition on the degree of individual foraging specialisation

Study species	Effect	Summary	Method	Reference
Non-social species				
<i>Anaxyrus americanus</i> , <i>A. fowleri</i> , <i>Lithobates catesbeianus</i> , <i>L. clamitans</i> , <i>L. sphenoccephalus</i> (American toad, Fowler's toad, American bullfrog, Northern green frog, Southern leopard frog)	No effect	Variation in individual specialisation indices was not explained by conspecific density	SCA/ SIA	Cloyed & Eason 2016
<i>Enhydra lutris nereis</i> (Sea otter)	Increase	Higher total population dietary diversity under decreased prey abundance driven by greater variation between individuals	DO	Tinker et al. 2008
	Dependent upon environment	Populations in rocky habitats exhibited increasing individual foraging specialisation with intraspecific competition, whereas in a mixed substrate habitat specialisation declined	DO/ SIA	Newsome et al. 2015
<i>Gasterosteus aculeatus</i> (Three-spine stickleback)	Increase	Increased population density led to increased foraging niche variation between individuals	SCA	Svanbäck et al. 2007
	Increase	Total population niche expanded with increased density. Some individuals switched exclusively to new prey items, altering foraging niche position but not niche size	SCA	Araújo et al. 2008
<i>Tribolium castaneum</i> (Red flour beetle)	Dependent upon environment	Increased density drove greater use of novel food source when food sources mixed. When able to choose (food sources not mixed), increased density reduced use of novel food source	SIA	Parent et al. 2014
Group-living species				
<i>Arctocephalus gazelle</i> , <i>A. tropicalis</i> (Antarctic fur seal, Sub-Antarctic fur seal)	Decrease	Larger individual isotopic niches observed in higher intraspecific competition environments	SIA	Kernaléguen et al. 2015
<i>Bombus terrestris</i> (Bumblebee)	Decrease	Individual bees visited more plant species at increased forager density promoting generalist behaviours	BO	Fontaine et al. 2008
<i>Meles meles</i> (European badger)	No effect	Group size had no significant effect on individual specialisation	FS/ SIA	Robertson et al. 2015

Note: Method: SCA, stomach content analysis; SIA, stable isotope analysis; DO, dietary observation; BO, behavioural observation; FS, faecal sampling

type A generalism across the social group (foraging theory; Stephens & Krebs 1986; Fig. 2a); (2) competition leads to niche partitioning within the group, increasing foraging specialisation and minimising dietary overlap between conspecifics through type B generalism (niche partitioning; Schoener 1974; Pianka 1976; Fig. 2b).

A significant cost of living in groups is a high level of local competition for resources between group members (Krause & Ruxton 2002). Applying predictions made under competition theory to the social group (Schoener 1974; Pianka 1976), high levels of local competition experienced by group-living species will drive dietary diversification between conspecifics (Table 1), facilitating their stable coexistence. Conflict within social groups has significant consequences, including eviction and infanticide (Stephens et al. 2005; Cant et al. 2010; Thompson et al. 2016). This suggests that any mechanism which reduces intragroup conflict, such as increased individual foraging specialisation under type B generalism, is more likely to be selected for in group-living species.

It is important, however, to consider species' characteristics and the environmental conditions experienced by individuals, when investigating the effect of competition on foraging specialisation in group-living species.

Populations of southern sea otters, *Enhydra lutris*, demonstrated a greater degree of individual foraging specialisation under increased competition, resulting from food limitation (Tinker et al. 2008). However, subsequent studies found that this was context dependent (Newsome et al. 2015). Sea otters inhabiting rocky habitats exhibited an increase in foraging specialisation under increased competition, whereas populations living in habitats with a mixed

substrate (rocky and soft-sediment) displayed lower individual specialisation (Newsome et al. 2015). Upon examination, it appeared that sea otters living in mixed-substrate habitats had narrower total population niches, suggesting specialisation at the population rather than individual level. This study highlights the importance of considering the local environment rather than that of the whole population. In group-living species, this is particularly important as social groups are often highly territorial (Kruuk 1978; Lazaro-perea 2001; Cooney 2002; Schradin 2004; Cant et al. 2013, 2016) suggesting that increased intragroup competition may only promote individual specialism (type B generalism) where a group's territory contains a diverse enough range of resources.

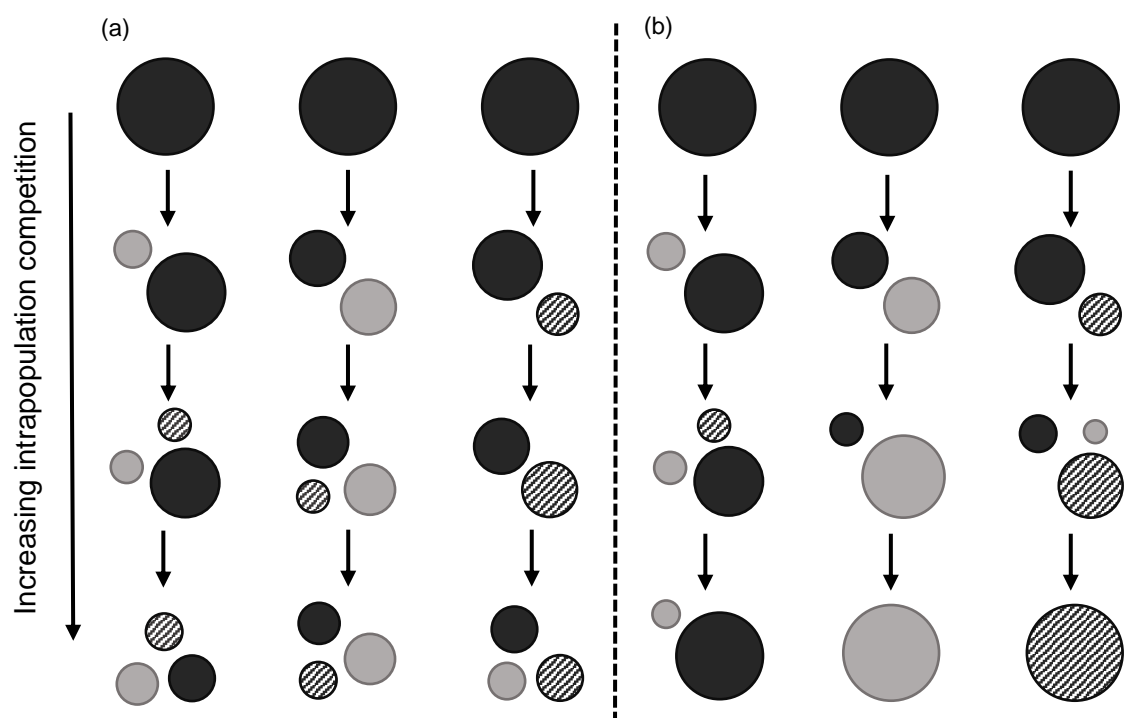


Figure 2: Competition driven type A and type B generalism. Schematic diagram depicting how increasing competition can result in a) type A generalism (all individuals utilise all prey available) and b) type B generalism (individuals utilise different prey items). Each column represents the diet of one individual at increasing levels of intrapopulation competition. Different colours and circle areas represent different prey items and proportion of diet respectively

A further aspect of the local environment that is likely to play an important role in the development of individual foraging specialisation in social groups is the social environment. For example, the degree of relatedness within social groups may affect how competition influences individual foraging specialisation. As individual specialisation can be seen as a mechanism to improve individual foraging efficiency (Tinker et al. 2008; Potier et al. 2015; Rossman et al. 2015), it is reasonable to assume that it generates a cost to conspecifics. Individuals specialising on top-ranked prey items become more efficient at foraging this particularly resource and better able to compete with conspecifics.

Subsequently, individuals less able to compete for top-ranked food items are forced to forage on those of poorer quality. Therefore, where intragroup relatedness is high, although individuals specialising on top-ranked prey items will benefit from greater access to the best food resource, they may also incur inclusive fitness costs by forcing close relatives to forage on less-preferred resources. An example of this can be seen in bumblebees, *Bombus terrestris*, where a study found that intrapopulation competition resulted in an expansion of niche width at both the individual and colony level (Fontaine et al. 2008).

Bumblebees are a haplodiploid, eusocial species, which feature high relatedness, cooperative brood care and a pronounced division of labour.

Competing with conspecifics to increase individual gain at a cost to other group members will be detrimental to the whole colony, increasing subsequent individual costs. Therefore, in groups with low levels of relatedness, selection to avoid intragroup conflict is likely to lead to type B generalism and an increase in individual foraging specialisation, as long as the range of resources available is diverse enough. However, in groups with high levels of relatedness the inclusive fitness costs of increased individual specialisation may select against increased

specialisation, making type A generalism and greater levels of individual generalism more likely (Table 1).

Interpopulation competition

Population niche width represents a balance between the expansive forces of intrapopulation variation and constraining forces of interpopulation competition (Roughgarden 1972). It is widely held that total population niche width expands as a result of fewer interspecific competitors (Van Valen 1965; Taper & Case 1985), termed 'ecological release'. Ecological release suggests that in a community of multiple species occupying distinct niches, removal of one or more species promotes the expansion of total niche width in the remaining species (Roughgarden 1972). There are, however, contrasting theories as to how reduced interpopulation competition affects individual niche width: (1) the niche variation hypothesis predicts that individual foraging specialisation will increase in environments with lower interspecific competition, as expansion of total niche width occurs through increasing between-individual variation (Van Valen 1965; Bolnick et al. 2003). This would lead to type B generalism (Van Valen 1965); (2) alternatively, quantitative genetic models predict that, if niche expansion does not incur costs to the individual, total population niche expansion will occur through increases to within-individual variation, promoting type A generalism (Taper & Case 1985; Ackermann & Doebeli 2004). This suggests that whether release from interspecific competition increases (e.g. Bolnick et al. 2010; Kernaléguen et al. 2015) or decreases individual specialisation (as proposed by Ackermann & Doebeli 2004) within a population depends on the overall payoff associated with individual niche expansion.

In studies of group-living species, the analogous effect is intergroup competition, with the removal of a neighbouring group leaving a vacant niche that other groups can expand into. Therefore, we can test these differing predictions regarding the effect of interpopulation competition by investigating the effects of intergroup competition on individual foraging specialisation. Intergroup conflict is common in group-living species, which are often highly territorial and compete for access to resources (Kruuk 1978; Lazaro-perea 2001; Cooney 2002; Schradin 2004; Cant et al. 2013, 2016). Similarly to non-social species, ecological release from intergroup competition would be expected to allow total group niche expansion, either through increasing individual niche (type A generalism) or between-individual variation in foraging niche (type B generalism). Which of these outcomes occur depends on the overall payoff of individual niche expansion. This payoff is likely to be determined by the presence of functional trade-offs which constrain individual niche, preventing the development of generalist strategies (Taper & Case 1985; Svanbäck & Bolnick 2005). For example, the morphology of Eurasian perch has been found to affect the efficiency of foraging in different habitats. More stream-lined individuals exhibited higher efficiency than deeper-bodied individuals when foraging in open water, whereas the opposite is true near shorelines, indicating a trade-off between foraging on littoral and pelagic prey items (Svanbäck & Eklöv 2004). As such, if stream-lined individuals were removed from the population, leaving a vacant niche in open water, we would not expect deeper-bodied individuals to expand their niche to include both open and shoreline habitats at a cost to their foraging efficiency. Instead, we would predict that some individuals move completely into the vacant open water niche, developing a more stream-lined morphology and maintaining foraging specialisation.

Many functional trade-offs associated with foraging specialisation, such as morphology and physiology (Afik & Karasov 1995; Svanbäck & Eklöv 2004), are likely to be similar in group-living species as in non-social species. However, increased opportunity for social learning in group-living species may affect individual foraging specialisation through learning trade-offs (Tinker et al. 2009). Theoretical studies have suggested that individuals have a limited ability to retain multiple foraging techniques, when complex learned skills are required to exploit dietary resources, constraining individual niche (Tinker et al. 2009). Therefore, individuals face trade-offs between learning to efficiently forage a certain food item (specialism) and maintaining the ability to forage alternative resources (generalism). Many studies demonstrate the importance of learned foraging behaviour in group-living species (Sherwin et al. 2002; Galef & Laland 2005; Whiten et al. 2007; Thornton & Malapert 2009; Hopper et al. 2011). Thus, where foraging behaviours are socially transmitted, we would expect greater opportunity for social learning through group-living to generate greater learning trade-offs. This predicts that, individual foraging specialisation in social groups is more likely to increase with reduced intergroup competition, in accordance with the niche variation hypothesis, leading to type B generalism (Van Valen 1965; Table 1).

Social learning

In addition to its role in how intergroup competition affects individual specialisation (above), social learning is likely to have its own independent effects on the development of specialisation in group-living species.

Social learning has been suggested as a likely mechanism behind the acquisition of foraging behaviour in both group-living and non-social species (Galef & Laland 2005; Kenward et al. 2006; Thornton & Malapert 2009; Hopper et al. 2011; Webster & Laland 2015). However, solitary and group-living animals differ in their opportunity for social learning in the number and type (e.g. mother or older sibling) of demonstrators from whom they can learn. Non-social species rely predominantly on their mothers to facilitate learning of foraging behaviours (Rymer et al. 2008), whereas individuals living in groups may have the opportunity to learn from other adults (Visalberghi & Addessi 2001; Nicol 2006; Rymer et al. 2008; Thornton & Malapert 2009; Müller & Cant 2010). Increased opportunity for social learning may enhance the development of individual foraging specialisation in group-living species by providing alternative routes through which to acquire foraging skills.

Different types of group-living species, however, likely vary in their degree of social learning and who they acquire skills from (e.g. Nicol 2006; Rymer et al. 2008; Müller & Cant 2010; Kendal et al. 2015). Therefore, in this instance, it may be beneficial to assess the effects of different social systems on specialisation separately, particularly the difference between non-cooperative and cooperative breeders. Bottlenose dolphins, a communal breeding species where females travel together but care for their own offspring, display social inheritance of foraging behaviour (Rossman et al. 2015). Individuals were found to continue using their natal foraging habitat after independence from their mother, indicating that foraging strategy is transferred through matrilineal lineages (Rossman et al. 2015), as in non-social species (Rymer et al. 2008). However, in cooperative breeding species, offspring have a greater potential to learn from other group members, as they are cared for by other 'helper' group

members (Komdeur 1994; Hodge 2005; Russell et al. 2010; Cant et al. 2013; Thompson et al. 2016). This provides alternative avenues for social transmission of foraging techniques. For example, a study investigating the social acquisition of foraging strategies in banded mongooses, *Mungos mungo*, found that juveniles exhibited the same foraging technique of a prized dietary item as their primary care-giver, known as escorts (Müller et al 2010). Mongoose escorts are most often non-breeding members of the group (Cant et al. 2013; 2016), demonstrating that foraging strategies can be learned from non-parental adults in a cooperative breeding group (See also Thornton & Malapert 2009). As social learning provides a likely mechanism in the development of foraging specialisation (Tinker et al. 2009; Robertson et al. 2014), increased opportunity for social learning in cooperative animals may increase the degree of individual foraging specialisation at an early age in these species.

Unlike solitary species who leave their parents and siblings upon independence, social learning in group-living species can continue throughout an individual's life (Rymer et al. 2008). Examples of this can be seen in the cultural inheritance of tool-use by adult group members in chimpanzees, *Pan troglodytes* (Tonooka 1997; Biro et al. 2003), and Goffin cockatoos, *Cacatua goffini* (Auersperg et al. 2014). Models by Tinker et al. (2009) predict that the opportunity to learn and improve foraging efficiency over time can lead to an increase in specialisation. This suggests that, although individual specialisation is defined as between-individual variation not attributable to age (Bolnick et al. 2003), experience gained whilst ageing can increase the degree of foraging specialisation displayed by an individual (Tinker et al. 2009). That is, age correlates with size of individual foraging niche, rather than position in niche space. Where prey-

specific foraging strategies can be learned or improved through practice, greater access to conspecifics may allow for continued development of individual niche in group-living animals. This continued availability of others to learn from throughout life may, therefore, increase the degree of individual specialisation in group-living species compared to non-social species. This effect, however, may be dampened by an individual's ability and/or willingness to learn from others decreasing with age, despite the opportunity still existing (Nicol 2004; Thornton & Malapert 2009; Carter et al. 2014). For example, a study of chacma baboons, *Papio ursinus*, found that older individuals demonstrated reduced propensity in learning to exploit novel food items (Carter et al. 2014).

The increased opportunity for social learning in group-living species is likely to have particular effects on the development of individual specialisation. The greater availability of individuals for offspring to learn from, particularly in cooperative breeding groups, is likely to increase levels of specialisation during development. The continued presence of other group members throughout an individual's life will further increase the opportunity for social learning, in cooperative and non-cooperative species, potentially leading to increased levels of specialisation with age. However, as individuals learning propensity often decreases with age, this age effect is likely to tail off and reach a maximum level of specialisation past a certain age.

Ecological importance of individual specialisation

Many of the consequences of individual specialisation exhibited by non-social species will be reflected in group-living species (e.g. increased predation:

Darimont et al. 2007; improved body condition: Robertson et al. 2015; improved reproductive success: Otterbeck et al. 2015; Pagani-Núñez et al. 2015).

However, certain characteristics of living in groups may cause specialisation to affect group-living species differently. Firstly, social groups can be looked upon as small, organised populations. Just as specialisation can affect population dynamics (Van Valen 1965; Łomnicki & Ombach 1984; Bolnick et al. 2003), it can be expected to influence group dynamics in a similar, but potentially stronger, manner. Secondly, the effects of individual foraging specialisation on reproductive success may be seen at the group-level, with important implications for cooperatively breeding species in particular.

Social dynamics

Group stability

Within-group variation in behavioural traits can have important ecological implications. Both theoretical and empirical research suggests that behavioural homogeneity increases the risk of population collapse (Whitehead & Richerson 2009). For example, killer whales, *Orcinus orca*, have high levels of mortality within groups in which all individuals feed primarily on Chinook salmon, *Oncorhynchus tshawytscha*, when salmon populations decline (Ford et al. 2010), demonstrating that group-level specialisation can increase the risk of group collapse when resources fluctuate. Phenotypic diversity is important as it can promote population resilience in changing environments (Whitehead 2010). However, in populations dependent on social learning of behaviour, behavioural diversity is also important in promoting population resilience (Whitehead et al. 2004). Therefore, social groups exhibiting high degrees of individual-level

specialisation will likely demonstrate greater resilience to environmental change, reducing the risk of group collapse (Table 1).

The relationship between individual specialisation and groups' resilience to environmental change has important implications for our understanding of the evolution of specialisation in social groups. It also has important implications for the conservation and population management of threatened species (Bolnick et al. 2003), many of which live in social groups (e.g. African wild dog, *Lycaon pictus*, African elephant, *Loxodonta Africana*, and Barbary macaque, *Macaca Sylvanus*; IUCN 2015). Incorporating an understanding of how individual specialisation affects resilience to environmental change will allow population management strategies to better identify at-risk social groups or populations of group-living species.

Social interactions

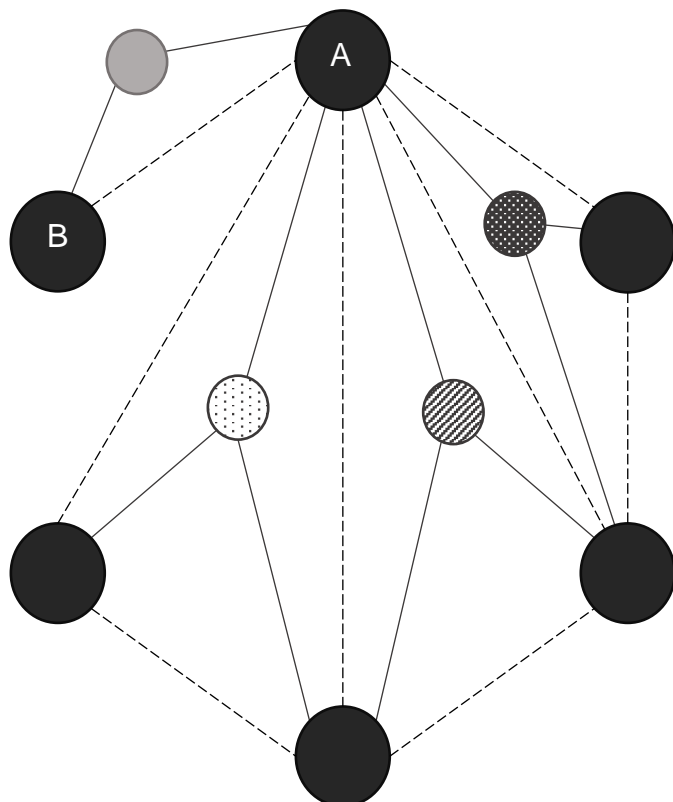
It is intuitive that individuals with wider foraging niches interact with more species, known as 'increased degree' in network theory (Bolnick et al. 2011). Using the same reasoning, a wider individual niche may also increase the degree of connectivity between individuals of the same species. Members of social groups often forage in close proximity to each other (De Luca & Ginsberg 2001; Radford & Ridley 2008; Hirsch 2011), increasing the frequency of competitive interactions between conspecifics. Generalist foragers in group-living species may, therefore, experience an increase in their degree of connectivity as they compete with a greater number of group members for a wider range of prey items (Table 1). For example, a highly generalised individual foraging on all prey items will compete with all group members,

exhibiting a greater degree of connectivity within their social group (individual A in Fig. 3). In contrast, a specialised individual foraging exclusively on a single prey item will only compete with other individuals foraging on the same food item (individual B in Fig. 3). This suggests that, in addition to reducing intragroup competition (see ‘Intrapopulation competition’ section above), an additional consequence of individual specialisation may be effects on the social networks of group-living species. In particular, generalists are expected to be more central and have a greater number of social connections than specialists (Table 1; Fig. 3).

Individual specialisation may also affect social network sub-groupings through behavioural matching. This is where animals with similar socially-determined behaviours preferentially associate (Cantor & Whitehead 2013). Examples of this have been documented in societies of bottlenose dolphins (Ansmann et al. 2012; Mann et al. 2012). One of the most well-known foraging specialisations in

Figure 3: Social network implications of generalist/specialist foraging on degree of connectivity within social groups.

Large black circles depict different group members and different patterned smaller circles represent different prey items. Solid lines illustrate food web and dashed lines denote social interaction network, representing competition for food resources. Individual A exhibits generalist foraging strategies and has a degree of five, competing with five other group members. Individual B is a specialist forager and has a degree of one, only competing with individual A for food resources



dolphins is sponging; a behaviour where individuals place a sponge on their nose to aid foraging in rocky substrates (Krützen et al. 2005; Bacher et al. 2010). Social network analysis revealed that spongers preferentially associate with other spongers, driving social network structure through behavioural matching (Mann et al. 2012). Similarly, dolphin populations in Moreton Bay, Australia, formed two distinct communities based on their foraging behaviour during periods of prawn trawling; those who followed trawlers, feeding on discards, and those who did not (Chilvers & Corkeron 2001; Ansmann et al. 2012). Subsequent analysis of social structure revealed that, upon cessation of prawn trawling, trawler and non-trawler dolphins were integrated into one social network (Ansmann et al. 2012). By influencing preferential association, individual foraging specialisation alters social networks and can drive the development of distinct communities based around different specialities within social groups (Table 1).

Reproductive success

It is widely recognised that foraging specialisation can improve individual reproductive success and fitness (Votier et al. 2004; Patrick & Weimerskirch 2014; Otterbeck et al. 2015; Pagani-Núñez et al. 2015). Although this influence is likely to be similar in group-living and non-social species at the individual level, cooperative breeding species may exhibit further reproductive consequences at the group level. In these species, care provided by non-breeding helpers can increase the reproductive success of breeders (Hodge 2005; Doerr & Doerr 2007; Russell et al. 2007; Klauke et al. 2013). However, helpers are energetically limited in the amount of care they can provide (Gaynor

et al. 1998; van de Crommenacker et al. 2011; Nichols et al. 2012; Cant et al. 2013). Individual foraging specialisation is thought to increase foraging efficiency (Strickler 1979; Tinker et al. 2008; Potier et al. 2015) and so may be particularly favoured in cooperatively breeding species, as it will promote helping behaviour by easing energy constraints. Subsequent increased levels of care may therefore improve overall group reproductive success (Table 1), having significant implications in terms of increased territory defence (Mosser & Packer 2009) and prey capture (Gusset & Macdonald 2010) through expansion of social group size.

Conclusion

Living in groups can alter both the causes and consequences of individual foraging specialisation (Table 1). Increased local competition for resources between group members and opportunity for social learning is likely to result in greater levels of individual specialisation. However, these effects may be moderated by the levels of relatedness within the group and whether the group exhibits cooperative care. Increased levels of specialisation may make social groups more resilient to environmental changes and lead to greater levels of sub-grouping in the group's social network structure. It may also promote greater levels of helping in cooperative breeding species. These effects are likely to have important implications for our understanding of individual foraging specialisation and the functioning of social groups, yet are largely unexplored.

Chapter 2: General methods and thesis aims

Study species

In this thesis, I investigate individual foraging niche in group-living species in cooperatively breeding wild banded mongooses, *Mungos mungo*. Banded mongooses are small social mammals (<2kg) that typically live in groups of 10 to 30 individuals (Cant 2000; Cant et al. 2013, 2016). Groups forage in close proximity to each other (typically within 10-20m; Fig. 4), however foraging is carried out individually and group members aggressively defend prey items from each other (De Luca & Ginsberg 2001). Banded mongooses display a wide dietary niche, with prey items varying widely to include insects, small vertebrates, eggs and fruit (Rood 1975; Gilchrist 2004). Banded mongoose social groups contain 1-8 breeding females, who give birth synchronously to large litters of up to 23 pups (Cant et al. 2010, 2013, 2016; Hodge et al. 2011).



Figure 4: Banded mongooses foraging in a group

Both parents and nonbreeding members of the group help to raise these communal litters, through babysitting and escorting (Gilchrist & Russell 2007). Babysitting commences after birth where new born pups are guarded each day by usually one to two adult 'babysitters', who remain at the den while the rest of the group leaves to forage. Escorting behaviour begins when pups emerge from the den to accompany the group at around 3-4 weeks old. During this time, some pups may form one-on-one relationships with an adult helper who feeds, grooms and protects the pup until maturation (Gilchrist 2004; Bell 2007). Termed 'escorts', these individuals are often not the biological parent of the pup and are no more related to the pup than the average group member (Cant et al. 2013, 2016). Although escorting relationships are initiated by pups, who aggressively defend their escorts from littermates (Gilchrist 2008), escorts actively maintain relationships later on in the provision period, responding to the call of 'their' pup (Gilchrist et al. 2008).

Past study has demonstrated the importance of these escorting relationships in learning foraging techniques. After observing their escorts behaviour during dependence, pups displayed the same preference for foraging technique as their escort in later life, suggesting that foraging preferences are socially transmitted (Müller & Cant 2010).

Study site and data collection

Research for this thesis was conducted on a population of habituated wild banded mongooses that reside on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E). Here, a long-term research project was established in 1995 by Mike Cant and Tim Clutton-Brock.



Figure 5: Mongoose territory on the edge on Lake Edward

Mweya Peninsula is a 5km² promontory connected to the mainland by a narrow isthmus, extending into Lake Edward on the border of Uganda and the Democratic Republic of Congo. The habitat mostly consists of medium-height grassland with dispersed *Euphorbia candelabra* trees, *Euphorbia candelabrum*, and thickets of woolly caper bush, *Capparis tormentosa*, and needle bush, *Azima tetraacantha* (Cant 2000; Cant et al. 2016; Fig. 5). The peninsula is divided by a 40m high slope, creating upper and lower halves. The banded mongoose population share the peninsula with large herbivores including African elephant, *Loxodonta Africana*, Cape buffalo, *Syncerus caffer*, and warthog, *Phacochoerus africanus*. Large predators such as leopard, *Panthera pardus*, and African lion, *Panthera leo*, are also seen regularly. The climate is equatorial with little fluctuation in temperature (Marshall et al. 2016). There is, however, seasonal variation in rainfall, with two dry periods spanning January-February and June-July (Cant et al. 2016; Marshall et al. 2016).

My study involved 115 individual banded mongooses, living in nine social groups. All individuals in the population are identifiable using unique shave patterns and pit tags (TAG-P-122IJ, Wyre Micro Design Ltd., UK) and are habituated to the presence of an observer within 5m. Individuals are captured every 3 to 6 months to maintain shave patterns and collect tissue and blood samples for physiological analysis. Vibrissae samples were collected between September 2013 and October 2015 for stable isotope analysis. Pups are first captured at approximately 3 weeks old upon emergence from the den, and a tail tip tissue sample is taken for genetic analysis (Nichols et al. 2010). Using the DNA extracted from these tissue samples, a pedigree has been constructed and parentage assigned (for further details, see Sanderson et al. 2015). Individuals are captured using box traps (67 x 23 x 23 cm; Tomahawk Live Trap Co., Tomahawk, WI, USA) and anaesthetised using isoflurane (for further details of the trapping procedure, see Jordan et al. 2010). One or two individuals within each group are fitted with a VHF radio collar (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., UK) that allows groups to be located. To record life history and behavioural data, groups are visited at least every 3 days. When groups contain heavily pregnant females or there are dependent pups, groups are visited daily to establish accurate birth dates and collect babysitting and escorting behavioural data.

Sample preparation and stable isotope analysis

I used stable isotope analysis to investigate individual foraging niche within and between banded mongoose groups (Bearhop et al. 2003, 2004; Araújo et al. 2007; Newsome et al. 2007). Within the past decade, stable isotope analysis

has risen in popularity for investigating individual foraging niche variation (Bearhop et al. 2004; Newsome et al. 2007), providing an efficient method for measuring individual- and population-level dietary niche (Newsome et al. 2009, 2015; Robertson et al. 2014). It relies on the premise that the isotopic ratio of consumer tissue reflects that of their prey items over which the tissue was synthesised (Hobson & Clark 1992; Bearhop et al. 2004). Metabolically inert tissues such as vibrissae, preserve stable isotope ratios, recording diet over a discrete period (Hobson & Clark 1992; Bearhop et al. 2003). Repeated measurements of the isotopic composition of an individual's tissues offers an indication of the degree of individual foraging specialisation, allowing for the temporal variation of niche width to be investigated (Bearhop et al. 2004).

To quantify individual banded mongoose foraging niche, I analysed stable isotopes of carbon and nitrogen ($^{13}\text{C}/^{15}\text{N}$) in vibrissae, which vary with habitat and trophic level respectively (Crawford et al. 2008). Vibrissae from individual mongooses were repeatedly sampled during each live trapping, by plucking under general anaesthetic. Vibrissae grow fully between each 3-monthly trapping, therefore each sample represented the diet of the individual over the preceding 3 months. Vibrissae samples from individual banded mongooses (4-5 vibrissae per sample) were scraped to remove debris and cut into small fragments using scalpel and forceps. This produced a total sample size of 786 vibrissae samples from 117 individuals (samples per individual: mean \pm sd = 2.31 ± 1.53). Each sample was weighed to around 0.7mg (mean \pm sd: $0.78\text{mg} \pm 0.34$; $n = 786$) and sealed in small tin capsules (Elemental Microanalysis) in preparation for stable isotope analysis. Carbon and nitrogen isotope ratios ($\delta^{13}\text{C}/\delta^{15}\text{N}$) were determined using continuous flow isotope ratio mass spectrometry (CF-IRMS), using a Sercon Integra integrated elemental analysis

and mass spectrometer (Cheshire, UK). Expressed as δ values, isotope ratios are reported in parts per mil/thousand (‰), according to the equation

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where X represents ^{13}C or ^{15}N , and R represents the ratio of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). International standards of V-PDB (Vienna Pee Dee Belemnite) and air were used for calibrating $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively.

Thesis aims

Although foraging specialisation has been widely noted across a variety of taxa, the causes of individual foraging specialisation in group-living species remain largely undiscussed. This area of study merits special consideration as some of the proposed drivers of foraging specialisation, in particular competition (Tinker et al. 2008; Svanbäck & Persson 2009; Bolnick et al. 2010; Newsome et al. 2015) and social learning (Tinker et al. 2009), are amplified by group-living (Krause & Ruxton 2002). In this thesis, I aim to investigate the causes of individual foraging specialisation in group-living species by examining individual foraging niche in a population of banded mongooses, both within and between social groups.

In Chapter 3, I explore the effects of intragroup competition on individual foraging niche size. Two confounding theories exist regarding how individual foraging specialisation is driven by intrapopulation competition. Classic optimal foraging theory suggests that as competition increases, individuals should add new prey items to their diet, increasing their foraging niche and reducing individual foraging specialisation (Stephens & Krebs 1986). On the other hand,

classic competition theory (such as niche partitioning; Schoener 1974; Pianka 1976) predicts that as competition between species increases, stable coexistence is achieved through niche differentiation, reducing dietary overlap between competitors and increasing foraging specialisation. Niche partitioning can also be driven by competition at the intraspecific level, observed in pike, *Esox Lucius* (Kobler et al. 2009), three-spine sticklebacks, *Gasterosteus aculeatus* (Svanbäck & Bolnick 2007), and sea otter, *Enhydra lutris nereis* (Tinker et al. 2008). Applying these opposing theories to social groups, I form two predictions of the effects of intragroup competition on individual foraging niche size in group-living species: (1) Increased intragroup competition leads to greater individual foraging niche size and a reduction of individual foraging specialisation (optimal foraging theory; Stephens & Krebs 1986); and (2) Intragroup competition drives niche partitioning between members of the same social group, increasing the degree of individual foraging specialisation (competition theory; Schoener 1974; Pianka 1976). Using group size as a proxy for intragroup competition, I test these hypotheses by investigating the effects of group size on relative individual isotopic niche size; an indicator of foraging niche size (Bearhop et al. 2004).

In Chapter 4, I explore the non-genetic social inheritance of individual foraging niche. Social learning is widely noted as a mechanism through which foraging behaviours can be acquired (Rymer et al. 2008; Tinker et al. 2009; Thornton & Malapert 2009; Müller & Cant 2010; Hopper et al. 2011). Social transmission of behavioural traditions, defined as persistent behavioural traits shared by several members of a species and transmitted through social learning (Fragaszy & Perry 2003), is suggested to promote behavioural uniformity (Whitehead & Richerson 2009). However, where foraging behaviours are learned from several

different individual role models, social transmission may promote behavioural heterogeneity within social groups (Cavalli-Sforza & Feldman 1981; Müller & Cant 2010). I test these predictions by comparing pair-wise distances in isotopic niche space, investigating (1) whether individuals inherit their foraging niche from their escorts or their parents; (2) whether individual foraging niche persists into adulthood; and (3) how association strength between pups and escorts affects the social transmission of foraging niche.

Chapter 3: Intragroup competition predicts individual foraging specialisation in a group-living mammal

Abstract

There has been much research investigating individual foraging specialisation, but little discussion about its causes in group-living species. Foraging theory predicts that with increased competition, individuals should add new prey items to their diet, widening their foraging niche. However, classic competition theory suggests that competition leads to niche partitioning, increasing individual foraging specialisation. Applying these two theories, I formed two opposing hypotheses of the effects of intragroup competition on individual foraging specialisation in group-living species: (1) increased competition erodes individual foraging specialisation (foraging theory hypothesis); and (2) increased competition drives niche partitioning, resulting in increased specialisation (competition theory hypothesis). I tested these two hypotheses by analysing the stable isotope values of banded mongoose, *Mungos mungo*, whiskers to quantify individual niche size as a function of social group size. Individual isotopic niche size declined with increasing group size, despite larger groups occupying larger niches. My findings suggest that individuals utilise a smaller proportion of the resources available to them when intragroup competition increases, supporting my prediction that local competition can promote niche partitioning within social groups.

Introduction

Within animal populations there is often remarkable heterogeneity in foraging behaviour (birds: Harris et al. 2014; sharks: Matich et al. 2011; mammals: Newsome et al. 2009; Robertson et al. 2014, 2015). This intraspecific variation in foraging niche can often be attributed to differences in sex (Bearhop et al. 2006; Stauss et al. 2012), age (Newland et al. 2009) or morphology (Pegg et al. 2015). However, where individual niche is substantially narrower lower than that of its population for reasons not attributed to these three variables, it is termed individual specialisation (Bolnick et al. 2003).

Individual specialisation in foraging niche has important implications for ecology and evolution. Increased foraging specialisation is associated with both positive and negative effects, with empirical evidence of improved reproductive success (Otterbeck et al. 2015; Pagani-Núñez et al. 2015), increased overall body condition (Robertson et al. 2015) and higher predation risk (Darimont et al. 2007). Individual foraging specialisation in European badgers, *Meles meles*, has been found to improve body condition when competition is more intense (Robertson et al. 2015), demonstrating how foraging specialisation can be beneficial and that between-individual variation in foraging behaviour can have important individual-level effects.

Variation in individual foraging behaviour can have particularly important implications in species that live in stable social groups, because individuals are likely to be influenced by the local social environment more than the characteristics of the broader population. Particularly where dispersal is limited, the social group can be considered the effective population when considering the adaptive value of different behavioural and life history strategies (Chepko-

Sade and Halpin 1987). Yet, the implications of individual foraging specialisation in group-living species remain poorly understood. It has been suggested that individual variation may play an important role in the evolution of cooperation (Barta 2016), however this lacks empirical support.

Classic foraging theory predicts that in the face of increased competition, individuals should add new prey items to their diet, widening their trophic niche and forming a population of generalist foragers (Stephens and Krebs 1986). However, classic competition theory (e.g. niche partitioning: Schoener 1974; Pianka 1976) predicts that as competition between species increases, stable coexistence is achieved through niche differentiation, reducing dietary overlap between competitors. Niche partitioning can also be driven by competition at the intraspecific level (Svanbäck & Bolnick 2007; Tinker et al. 2008; Kobler et al. 2009)(Tinker et al. 2008). I apply these theories to form two opposing hypotheses of the effect of local competition (competition within a group for shared resources) on individual foraging specialisation in group-living species: (1) intragroup competition promotes generalist foraging behaviours and a reduction of individual foraging specialisation (foraging theory hypothesis); and 2) intragroup competition leads to niche differentiation between conspecifics, increasing individual foraging specialisation (competition theory hypothesis).

I test these hypotheses in a population of wild banded mongooses, *Mungos mungo*, by exploring the effects of group size, a proxy of intragroup competition, on individual isotopic niche size; an indicator of foraging niche size (Bearhop et al. 2004). Banded mongooses present a good model species for testing how intragroup competition influences the development of individual specialisation in a group-living species. They live in mixed-sex groups of typically 10-30 individual members occupying distinct territories (Cant et al. 2013, 2016).

Although they forage in close proximity to one another (10-20m), banded mongooses aggressively defend prey items from other group members, fiercely competing for dietary resources (De Luca and Ginsberg 2001). Their diet is broad and they feed on a variety of invertebrates such as millipedes, ants and beetles, and occasionally vertebrates including frogs and reptiles (Rood 1975). Previous studies on the system have also demonstrated the co-existence of multiple foraging strategies within banded mongoose groups (Müller and Cant 2010), suggestive of between-individual variation in foraging niche. I measured individual and total group isotopic niches by repeatedly sampling the isotope values of individuals' vibrissae over a 2 year period, using group size as a measure of intragroup competition to explore our two opposing hypotheses.

Materials and methods

Study system and sample collection

My study was carried out on a population of wild banded mongooses on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E). As part of a long-term research project, life history data has been collected on this population since 1995. Below, I provide details specific to my study; for further information about banded mongoose biology and the study site see Cant et al. (2013, 2016).

Between September 2013 and October 2015, vibrissae were collected under light anaesthetic (isoflurane) from individual banded mongooses as part of routine trapping undertaken every 3 months (see Jordan et al. 2010 for details of trapping procedure). All mongooses are individually identified using unique hair-shave patterns on their back and pit tags (TAG-P-122IJ, Wyre Micro

Design Ltd., UK) inserted under the skin in the scruff of the neck. Each social group is visited at least every three days to collect basic life history data and groups containing heavily pregnant females are visited daily to record accurate birth dates.

Sample preparation and stable isotope analysis

I used stable isotope analysis to investigate patterns of individual isotopic niche within and between mongoose groups (Bearhop et al. 2003; Bearhop et al. 2004; Araújo et al. 2007; Newsome et al. 2007). Previous studies demonstrate that analysis of ^{13}C and ^{15}N stable isotopes provides an efficient method for measuring individual- and population-level dietary niche (Newsome et al. 2009, 2015; Robertson et al. 2014). Isotopes of ^{13}C and ^{15}N vary with habitat and trophic level respectively, representing foraging location and trophic position (Crawford et al. 2008). Repeated measurements of individual isotope values over time provide an indication of the degree of individual foraging specialisation (Bearhop et al. 2004). I repeatedly sampled banded mongoose vibrissae at each live trapping, with vibrissae growing back fully between each 3-monthly trapping session. Vibrissae from individual banded mongooses (4-5 vibrissae per sample) were scraped to remove debris and cut into small fragments using a scalpel and forceps. Each sample was weighed to around 0.7mg (mean \pm sd: $0.78\text{mg} \pm 0.34$; $n = 786$) and sealed in small tin capsules (Elemental Microanalysis) for stable isotope analysis. Carbon and nitrogen isotope ratios ($\delta^{13}\text{C}/\delta^{15}\text{N}$) were determined using continuous flow isotope ratio monitoring mass spectrometry (CF-IRMS), using a Sercon Integra integrated

elemental analyser and mass spectrometer (Cheshire, UK). Isotope ratios are expressed as δ values, reporting parts per mil (‰), according to the equation

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where X represents ^{13}C or ^{15}N , and R represents the ratio of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). International reference materials (IAEA, Vienna) were analysed within each run for calibrating $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ sample values scaled to V-PDB and air respectively.

Statistical analysis

I quantified dietary variability of individual mongooses using the standard ellipse area (SEA), representing the area of isotopic niche space occupied by the individual (Jackson et al. 2011). After a small sample size correction, SEAs have been shown to be insensitive to sample size (Jackson et al. 2011). I calculated SEAs for all individual banded mongooses with three or more isotope samples ($n = 115$) and applied a sample size correction to give SEAc, following the methods outlined by Jackson et al. (2011). The number of samples per individual varied from three to seven (mean \pm sd = 4.02 ± 1.21).

When investigating between-individual variation in foraging niche size, is it important to consider the size of the total population niche and the proportion of this total niche the individual occupies (Roughgarden 1972). In group-living species, particularly species such as banded mongooses that forage as a group, individual niche is likely more influenced by social group niche than the broader population niche. I therefore calculated a relative individual niche index (RINI) using group niche sizes as the baseline, which were quantified using

standard ellipse areas, applying a sample size (SEAc) (Jackson et al. 2011). To match individual niche and group niche temporally, I calculated group SEAc for each individual separately, using all samples taken from the group between the dates over which the focal individual was sampled. I then calculated a RINI for each individual by dividing individual niche size by their social group niche size. Standard ellipses are comparable to standard deviations in univariate analysis and are therefore, sensitive to small sample size. The number of samples used to calculate group niche was larger than that used to calculate individual niche, ranging from 10 to 136 (mean \pm sd = 68.80 \pm 33.79). Applying a sample size correction to small sample sizes leads to larger SEA, therefore as a consequence, individual SEAc is often larger than group SEAc, resulting in a RINI above one. This index does not have the property that individual values necessarily must be less than one. Nevertheless it is a valid non-dimensional measure to compare between individuals and groups.

To investigate the effects of increased intragroup competition on individual isotopic niche size, I square-root transformed RINI to meet assumptions of normality and fitted the index against group size in a linear mixed-effects model (LMM). To calculate group size, I first calculated the mean number of individuals within the social group on each day that each vibrissae sample was synthesised (estimated growth time from trapping observations = 90 days). I then calculated the mean group size value across each individuals' vibrissae samples. Age (in years) and sex were also included as explanatory variables in the model to confirm that the variation in isotopic niche between individual mongooses was not age or sex specific, and therefore due to individual specialisation. To investigate the effect of competition on diet at the group level, I also fitted an LMM modelling group niche (SEAc) against group size using the baseline group

niches that were calculated for each individual. In both models, I included social group as a random effect to control for repeated measures from each group. Time (years) was included as a fixed effect to control for any temporal effects on niche size. As individual SEAc's covered time periods encompassing a range of seasons (mean = 365.5 days, range = 270 – 630 days; Marshall et al. 2016), seasonality was not included in linear models. My dataset consisted of 115 individuals from nine social groups.

All analyses were undertaken in R version 3.2.5 (R Core Team 2016) using the lme4 package version 1.1-12 to fit LMMs (Bates et al. 2015) and the SIBER package version 2.0.2 to fit bivariate ellipses and calculate SEAc (Jackson et al. 2011).

Results

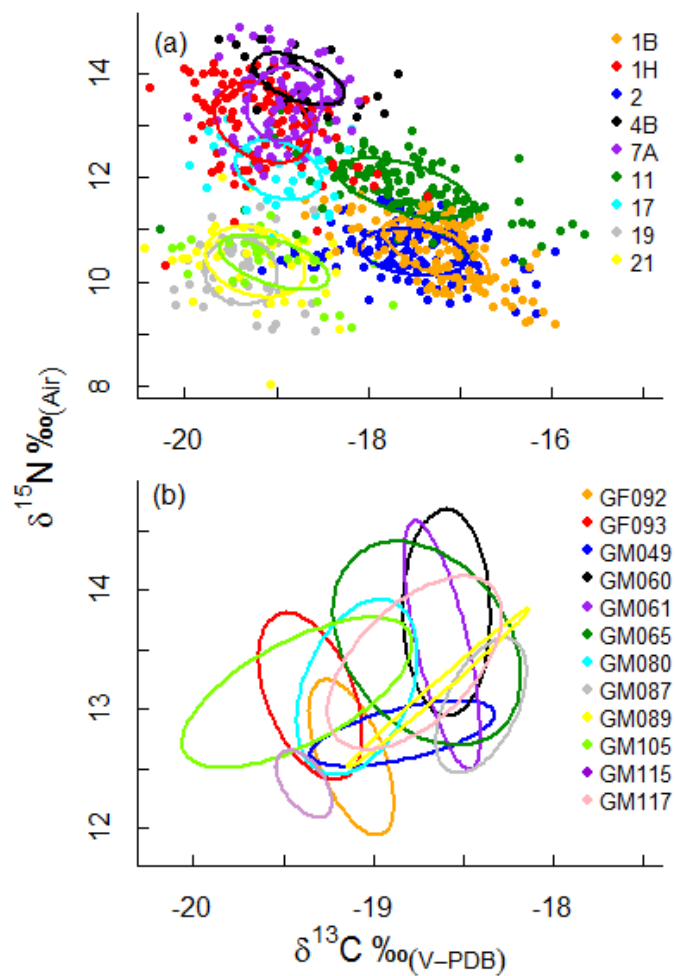
Banded mongooses varied greatly in the isotopic composition of their tissues, both for $\delta^{13}\text{C}$ (range -20.45‰ to -15.63‰) and $\delta^{15}\text{N}$ (range 8.05‰ to 14.89‰; Fig. 6). I observed marked variation in isotope values both between social groups (Fig. 6a) and between individuals within social groups (Fig. 6b).

Individuals in larger social groups displayed smaller isotopic niches relative to group isotopic niche (as measured by my relative individual niche index, RINI; LMM: $\beta \pm \text{se} = -0.01 \pm 0.01$, $t_1 = -2.20$, $p = 0.03$; Table 3; Fig. 7a). Individuals' relative niche did not vary with age (LMM: $t_1 = 0.81$, $p = 0.41$) or sex (LMM: $t_1 = -0.70$, $p = 0.52$). Observation time had no effect on individual niche size (LMM: $t_1 = -0.08$, $p = 0.85$). Group isotopic niche size varied between groups (Table 4) and increased with increasing group size (LMM: $\beta \pm \text{se} = 0.01 \pm 0.004$, $t_1 =$

Figure 6: Isotopic niche variation

between and within mongoose groups

groups. Variation in isotopic niche of vibrissae $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope values in banded mongooses, represented as standard ellipse areas (SEA), between a) social groups and b) individuals within a single social group. Individuals from Group 7A are shown here as an example. Different groups/individuals are represented by different colours. The centre of the standard ellipse is defined by the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each individual/group, and a covariance matrix determines the shape and size (Jackson et al. 2011)



2.09, $p = 0.03$; Table 3 & 4; Fig. 7b). Observation time increased the size of group niche (LMM: $\beta \pm \text{se} = 0.09 \pm 0.02$, $t = 3.92$, $p < 0.001$).

Discussion

I found that individual banded mongooses in larger groups had smaller relative isotopic niches (RINIs; Fig. 7a), despite larger groups occupying larger niches (Fig. 7b). This result supports my prediction made under classic competition theory; that greater intragroup competition drives between-individual variation in niche. In many group-living species, individuals frequently forage in close proximity to one another, resulting in high levels of local competition for resources (De Luca and Ginsberg 2001; Jolles et al. 2013; Burke et al. 2015; Eshchar et al. 2016). Therefore, sociality may play an important role in the

development of individual foraging specialisation, as this increase in local competition promotes foraging niche partitioning between group members.

My results may also suggest that the ability to specialise is a prerequisite for group-living. Partitioning of resources through individual specialisation is widely recognised as a mechanism through which to decrease competition (Schoener 1974; Pianka 1974, 1976; Correa and Winemiller 2014). A significant cost of living in groups is a high level in local competition between individuals (Krause and Ruxton 2002), therefore niche partitioning of foraging resources may serve

Table 3: Model results of the analysis of intragroup competition. Linear mixed model of relative individual niche index (RINI; square-root transformed) and total group isotopic niche size (SEAc) in banded mongooses. Individual RINI calculated as individual niche size (SEAc)/ group niche size (SEAc) over the time the individual was sampled. Significant effects shown in bold

Response	Effect	Estimate	SE	<i>t</i>	<i>p</i>
RINI (sqrt)	Intercept	1.28	0.19	6.77	
	Age	0.01	0.02	0.81	0.41
	Sex (male)	-0.05	0.07	-0.70	0.52
	Group size	-0.01	0.01	-2.20	0.03
	Time	-0.01	0.08	-0.08	0.85
Group SEAc	Intercept	0.58	0.11	5.11	
	Group size	0.01	0.004	2.09	0.03
	Time	0.09	0.02	3.92	0.0001

Table 4: Individual and group niche size. Mean and standard deviation of groups' size, relative individual niche index (RINI) and total group niche size (SEAc). Relative individual niche index (RINI) calculated as individual niche size (SEAc) / group niche size (SEAc) over the time the individual was sampled

Group ID	Group size (mean ± sd)	Individual RINI (mean ± sd)	Total group niche SEAc (mean ± sd)
4B	7.59 ± 0.18	1.14 ± 0.47	0.74 ± 0.06
21	10.88 ± 1.10	0.62 ± 0.31	1.06 ± 0.18
17	12.87 ± 0.61	1.98 ± 1.28	0.80 ± 0.06
19	20.33 ± 1.81	1.40 ± 0.81	0.65 ± 0.11
7A	25.54 ± 1.28	1.41 ± 0.79	0.78 ± 0.19
11	25.92 ± 1.40	0.70 ± 0.46	1.12 ± 0.06
1H	25.60 ± 1.19	0.85 ± 0.55	1.15 ± 0.13
2	30.91 ± 2.10	0.92 ± 0.88	0.78 ± 0.07
1B	32.32 ± 3.68	0.77 ± 0.66	0.77 ± 0.11

to reduce conflict between group members, allowing for their stable coexistence. Without the ability to specialise and reduce niche overlap, the costs of competition associated with group-living may be too high, which may explain why we observe foraging specialisation in group-living species such as banded mongooses.

My results contrast with the predictions of classic optimal foraging theory, which predicts that with increased competition, individuals should add new prey items to their diet, increasing their individual niche (Stephens and Krebs 1986). What might explain the reversal of this pattern in banded mongooses?

Between-individual variation in foraging niche as a result of increased competition can be driven by differences in individual rank-preference of prey. Optimal diet models predict that populations of individuals with the same top-ranked prey items but different lower-ranked items, known as 'competitive refuge', will display the highest levels of foraging specialisation when competition increases (Svanbäck and Bolnick 2005). In such a system, all individuals will forage a shared, most valuable prey item when competition is low, resulting in narrow population and individual niches. However, if individuals differ in their second and/or third choice prey, increased competition can lead to diversification in foraging niche, as individuals add different prey items to their diet. Under high competition, some individuals may not be able to compete for the most-prized items, switching completely to an alternative food source and forming a population of individual specialists. In a study where high competition was associated with increased foraging specialisation, some sea otter individuals were observed to eat proportionally more lower ranked prey items (indicated by a lower prevalence in total population diet) than the most popular prey item (Tinker et al. 2008). This may suggest that, under competitive

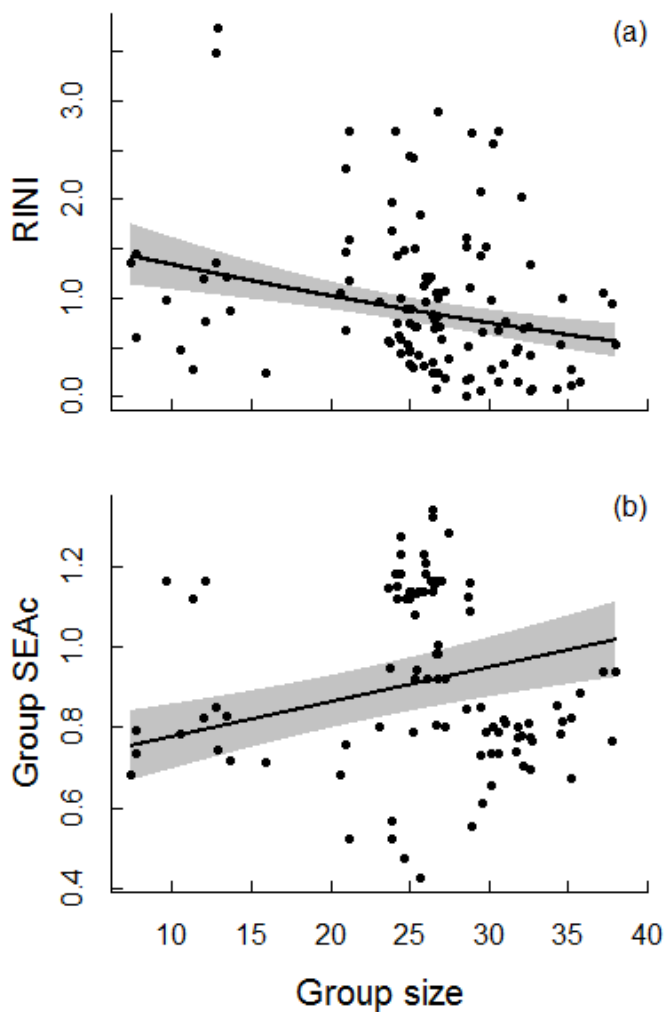


Figure 7: Effect of group size on individual and group isotopic niche size. Represented as a) individual niche size relative to total group niche (referred to as relative individual niche index (RINI) and calculated as individual standard ellipse area (SEAc)/ group SEAc over the time the individual was sampled (LMM; $n=115$, $P=0.03$), and b) total group isotopic niche (SEAc) (LMM; $n=115$, $P=0.03$). Figure represents 115 individuals from 9 different social groups. Group size was calculated as the mean group size over the time period sampled. Lines represent predictions from linear mixed models with standard error polygons

conditions, some individuals are unable to compete for top-ranked prey items and seek alternative food sources. Similarly, as the diet of banded mongooses is highly varied (Rood 1975), I suggest that conspecifics differ in their rank-preference of prey items. I propose that individual banded mongooses share the same top-ranked items but differ in their subsequent preferences, adding different prey items to their diet when competition increases, driving greater between-individual variation. This could be tested using a ‘cafeteria’ experiment, giving individuals simultaneous choice over various items to determine preference.

Although my study suggests that intragroup competition is a driving force in the development of individual specialisation in banded mongooses, the mechanism behind what determines an individual’s position in niche space is unclear. Social

learning is a widely proposed mechanism behind the development of individual foraging niche (Tinker et al. 2009; Thornton and Malapert 2009; Slagsvold and Wiebe 2011; Rossman et al. 2015). In both group-living and non-social species, individuals learn foraging technique from their parents (Slagsvold and Wiebe 2011; Rossman et al. 2015), however living in groups provides further opportunity to learn from other group member (Krause and Ruxton 2002; Müller and Cant 2010; Farine et al. 2015). In banded mongooses, pups form close relationships with adult group members known as escorts, most often not their parents, who care for and feed them until independence (Cant et al. 2013, 2016). Past studies have demonstrated the social transfer of foraging technique preferences between mongoose pups and their care-givers; preferences that remained even after independence (Müller and Cant 2010). This suggests that social learning during development may contribute to individual differences in the foraging niche of the banded mongoose. Increased opportunity for social learning from other group members may, therefore, increase development of individual foraging specialisation in group-living species.

Differences in individual niche size were not attributable to age or sex of the individual, suggesting that banded mongooses display true individual foraging specialisation within social groups (Bolnick et al. 2003). Isotope values of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ also varied between social groups. Past studies have found that the composition of an individual's habitat affects their isotope values (Robertson et al. 2014; Rossman et al. 2015), therefore the variation in isotope values between social groups is likely the result of habitat differences between group territories.

It is worth noting that individuals can differ in their isotope values due to variation in physiological stress. However, the variation between individuals

observed in this study (up to $\Delta 6.61\text{‰}$ for $\delta^{15}\text{N}$) is much larger than what would be expected from differences in stress-levels alone ($\sim\Delta 0.5 - 2.0\text{‰}$, Hobson et al. 1993; $\Delta 1.68\text{‰}$, Cherel et al. 2005).

Understanding how the social environment impacts specialisation has important ecological implications. For example, if group-living species benefit from intragroup variation in order to reduce conflict between members and maintain stable societies, then individual specialisation may play an important role in the evolution of social systems (see Barta 2016). Individual specialisation in group-living species is also an important consideration for conservation and population management, as many threatened species live in social groups (e.g. African wild dog, *Lycaon pictus*; African elephant, *Loxodonta africana*; Barbary macaque, *Macaca sylvanus*; IUCN 2016). Conservation programs must be aware of the importance of maintaining intragroup variation and its consequences to group-living animals if stable populations are to be maintained.

In conclusion, my study provides evidence that intragroup competition can lead to greater between-individual variation in group-living species; a pattern consistent with competition theory. Although larger groups occupied larger niches, individual isotopic niche size decreased with increased intragroup competition, suggesting that group-living species reduce conflict between group members through niche partitioning. These results suggest that the social group environment can impact the level of specialisation exhibited by individuals, highlighting the importance of addressing this gap in our knowledge.

Chapter 4: Non-genetic inheritance of lifelong foraging niche in a cooperative mammal

Abstract

Social transmission is a major mechanism for the non-genetic inheritance of behavioural traditions and is thought to promote behavioural uniformity within social groups. However, the presence of role models may influence the acquisition of foraging traditions. Using a unique system which exhibits both one-to-one and many-to-one caring, I tested theoretical predictions regarding the influence of role models on the transmission of distinct foraging traditions. Quantifying individual diet in a population of wild banded mongooses, *Mungos mungo*, I demonstrate that individual mongooses acquire lifelong foraging niches through non-genetic social inheritance, displaying behavioural traditions within social groups. My findings provide empirical evidence that one-to-one caring can promote the inheritance of distinct behavioural traditions, allowing for the coexistence of multiple traditions within social groups.

Introduction

Social transmission of behavioural traditions, defined as persistent behavioural traits shared by several members of a species and transmitted through social learning (Fragaszy & Perry 2003), is thought to erode behavioural variation within social groups and promote uniformity (Laland & Janik 2006; Kendal et al. 2009; Whitehead & Richerson 2009). However, the social inheritance of foraging behaviours can be affected by the presence of role models. Learning behaviours from multiple role models, known as many-to-one or “concerted” transmission, assumes that individuals are influenced by many role models acting in concert and is often exhibited by older group members transmitting behaviours to younger individuals (Cavalli-Sforza & Feldman 1981; Hewlett & Cavalli-Sforza 1986). Studies have demonstrated many-to-one transmission in groups of chimpanzees, *Pan troglodytes*, where younger lower-ranked individuals exhibit a ‘copying dominants’ bias in acquiring foraging behaviours (Hopper et al. 2011; Kendal et al. 2015). Individuals are seen to preferentially adopt the behaviour of the majority, also known as conformist transmission, which restricts the accumulation of multiple traditions within groups (Henrich & Boyd 1998; Haun & Rekers 2012; Luncz et al. 2012). These transmission patterns lead to behavioural uniformity within groups and high between-group variation (Cavalli-Sforza & Feldman 1981; Hewlett & Cavalli-Sforza 1986), of the kind reported for chimpanzee tool use (Tonooka 1997; Biro et al. 2003) and cetacean dialect (Weilgart & Whitehead 1997; Rendell & Whitehead 2005; Burtenshaw & Whitehead 2012).

By contrast, learning foraging behaviours from single role models may allow the coexistence of multiple behavioural traditions within social groups (Cavalli-

Sforza & Feldman 1981). Most commonly, examples demonstrate the inheritance of behaviour from parent-to-offspring, known as vertical transmission. Previously observed in populations of bottlenose dolphins, *Tursiops truncatus*, individuals demonstrated inheritance of foraging habits from mother to calf, displaying behavioural variation within social groups (Rossman et al. 2015). An alternative pattern of one-to-one learning is oblique transmission, where behaviours are passed between generations irrespective of relatedness (Cavalli-Sforza & Feldman 1981). Populations of banded mongooses, *Mungos mungo*, have been shown to exhibit oblique transmission of foraging behaviours, as individuals were found to display the same preference for foraging technique as their carer from when they were pups (Müller & Cant 2010). However, it is unknown whether this social inheritance outweighs genetic inheritance, or whether the influences are long-lasting.

While the social transmission of foraging behaviour is widely documented (Nicol 2006; Thornton & Malapert 2009; Müller & Cant 2010; Kendal et al. 2015; Rossman et al. 2015), there is a lack of empirical research concerning how the mechanism of transmission influences the acquisition of foraging behaviour. My study aims to address this gap by investigating how the number and type of role model affects the social transmission of diet in a population of wild banded mongooses; a species which exhibits both one-to-one and many-to-one caring. Specifically, I address three main questions: 1) Do pups inherit their foraging niche from their caregivers or parents (oblique or vertical transmission)? 2) Do inherited differences in foraging niche persist into adulthood? 3) Does the number of role models alter the extent to which foraging niche is acquired? By investigating alternative transmission mechanisms side-by-side, I aim to test the theoretical prediction that learning from single role models can allow the

coexistence of multiple foraging behaviours within social groups (Cavalli-Sforza & Feldman 1981).

Methods

Study system

Banded mongooses present a valuable model for investigating the social transmission of foraging niche, as individuals form close associations with adult group members in early life (Cant et al. 2013, 2016). They live in social groups of between 10 and 30 individuals in which reproduction is highly synchronised (Hodge et al. 2011). Females give birth in an underground den, usually on the same night, to a communal litter which adult group members help to raise. Upon leaving the den at around 30 days old, banded mongoose pups form close relationships with adult group members known as escorts, who look after and feed the pup until the age of around 3 months (Gilchrist & Russell 2007; Cant et al. 2013, 2016). Previous experimental work on this species demonstrated social inheritance of foraging behaviour from escorts (Müller & Cant 2010), however whether the number of escorts affects this social transmission remains unknown. Escorts are most often non-breeders (Cant et al. 2016), allowing us to distinguish between social and genetic influences on foraging niche. Escort-pup pairings are actively maintained by mongoose pups who aggressively defend access to their escort (Gilchrist 2008). The duration and strength of these pairings can vary, with some pups having the same escort throughout the dependent period, whilst others may have many. Further details of the study species and study site can be found in Cant et al. (2013, 2016).

Sample collection

Vibrissae were collected from individual banded mongooses under general anaesthetic every three months, between October 2013 and September 2015, as part of routine trapping. Individuals were captured using box traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) and anaesthetised using isoflurane (see Jordan et al. 2010 for further details of trapping procedure). All individuals in the population are identifiable through use of unique shave patterns on their backs and pit tags (TAG-P-122IJ, Wyre Micro Design Ltd., UK) inserted under the skin of their nape. Social groups containing pregnant females and/or dependent pups are visited for at least 20 minutes every day.

As part of the long-term banded mongoose research project, escorting behaviour is observed in communal litters each day after emergence through to nutritional independence. Escorting behaviour is conspicuous and adult individuals are recorded as an escort in a particular group visit if they associated closely with a focal pup (observed within 0.5m of the focal pup for over half of the 20-minute observation session). My study utilises escorting behavioural data from 23 communal litters. I calculated escorting relationship strength index as the proportion of group visits during the escorting period that a particular adult was recorded as a pup's escort.

Pup parentage was assigned from a pedigree built using genetic data from small 2-mm skin samples taken at first capture. For further details on sampling procedure and genetic analysis, please see Sanderson et al. (2015).

Sample preparation

I used stable isotope analysis to measure individual foraging niches of banded mongooses. This method is based on the premise that the stable isotope ratios of a consumer's tissue reflect those of its dietary sources over which the tissue was synthesised (Hobson & Clark 1992; Hobson 1999). I analysed the stable isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which vary with habitat and trophic level respectively, representing foraging location and trophic position (Crawford et al. 2008).

Vibrissae samples from individual banded mongooses (4-5 per sample) were scraped to remove debris and cut into smaller fragments using a scalpel and forceps. Samples were then weighed to around 0.7mg (mean \pm sd: 0.78mg \pm 0.34; n = 786) and sealed in small tin capsules in preparation for stable isotope analysis. Analyses of carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$ / $\delta^{15}\text{N}$) were carried out using a Sercon Integra integrated elemental analyser and mass spectrometer (CF-IRMS; Cheshire, UK). Expressed as δ values, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios are reported in parts per mil (‰), with reference to international standards (IAEA, Vienna) V-PDB and air respectively.

Statistical analysis

1) Do pups inherit their foraging niche from their caregivers or parents?

I collected 107 isotope measures from individual banded mongooses, across ages from 29 days to over five years old, for which I had a corresponding measure from the individual's escort when they were a pup (49 individuals from 6 social groups). Corresponding measures were collected within one month of

the focal sample. To test whether there was non-parental social transmission of foraging niche between escorts and pups, I compared individuals' distances in isotopic niche (hereafter referred to as 'isodistance') from their escort with the isodistance from a random group member. Random group members were chosen from individuals who met the following criteria: i) a vibrissae sample was available from them within one month of the focal individual's sample; ii) they were not the escort, mother or father of the focal individual; and iii) they were an adult group member (>1 year old) on the day the focal individual was sampled. Random group members were assigned for each of the 107 individual-escort pairs 10,000 times and the mean individual-random group member isodistance from each permutation used to create a null isodistance distribution. I then compared mean observed individual-escort isodistances to this null distribution and calculated a one-tailed *P*-value testing my *a priori* prediction that individual-escort isodistances would be smaller than individual-random group member distances. To assess whether any effect on isodistances I found was driven by either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, I repeated this process comparing individual-escort and individual-random group member differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ separately.

To test whether there was parental transmission of foraging niche, I compared individual-father and individual-mother dyad isodistances with individual-random group member isodistances. In order to maximise sample sizes, analyses were undertaken separately for pup-father and pup-mother dyads. As social group has a strong effect on individual isotope signature, individuals whose father was part of a different social group at the time of sampling were excluded. All mothers in the sample were in the same social group as their offspring at the time of sampling. The resultant datasets were comprised of 17 (eight individuals from four social groups) and 27 (17 individuals from four social groups)

individual isotope samples with corresponding father and mother samples, respectively. I used the same random sampling procedure as above and calculated a one-tailed *P*-value. This tested my *a priori* prediction that individual-father/mother isodistances would be smaller than individual-random group member distances, if foraging behaviour was transmitted from parent to offspring.

2) *Do inherited differences in foraging niche persist into adulthood?*

In order to investigate the development of foraging niche, I repeated the above analysis for samples taken from pups (< 90 days; n=11), subadults (≥ 90 days to a year; n=32) and adult (≥ 1 year; n=64) individuals separately. This allowed me to investigate the ontogeny of foraging niche and whether individuals continue to use similar niches to their escort after independence.

3) *Does the number of role models alter the extent to which foraging niche is acquired?*

I used my randomisation procedure to explore the effect of escort relationship strength on the social transmission of foraging niche. I divided the data into six categories based on the characteristics of all the escorting relationships an individual formed as a pup: 1) strong one-on-one association, 2) weak one-on-one association, 3) strong association with one escort as well as associations with other escorts (strongest relationship only), 4) multiple weak associations (strongest relationship only), 5) strong association with one escort as well as associations with other escorts (all relationships), 6) multiple weak associations (all relationships). Associations were classified as strong if they spent over half of their provisioning period (e.g. association index above 0.5) with that particular

escort. I conducted permutations of pair randomisations for these six categories separately, comparing observed values with the null distribution.

Results

In terms of isotopic distance, individuals were closer to the individual that escorted them as a pup than to random group members (Fig. 8; mean observed value = 0.67, null distribution mean = 0.77, $p = 0.002$). Individuals were closer to their escort than a random group member in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values when examined separately (Fig. 8b and 8c; $\delta^{13}\text{C}$: observed value = 0.48, null distribution mean = 0.54, $p = 0.03$; $\delta^{15}\text{N}$: observed value = 0.40, null distribution mean = 0.46, $p = 0.02$). Individuals were not closer to either parent compared with a random group member (Fig. 9a and 9b; father: $p = 0.91$, $n = 17$; mother: $p = 0.85$, $n = 27$).

Exploring the ontogeny of foraging niche formation, isotopic niches of pups (<3 months) were not closer to those of their escorts than a random group member (Fig. 10a; $p = 0.78$). However, subadult individuals (3-12 months) and adult individuals (1 year+) were closer in isotopic niche to their escort than a random group member (Fig. 10b and 10c; subadult: mean observed value = 0.94, null distribution mean = 1.13, $p = 0.002$; adult: mean observed value = 0.53, null distribution mean = 0.62, $p = 0.03$).

Individuals who had a strong relationship with a single escort were closer in isotopic niche to their escort than to random group members (Fig. 11a; mean observed value = 0.63, null distribution mean = 0.76, $p = 0.03$, $n = 35$).

Individuals who had a strong association with one escort along with other

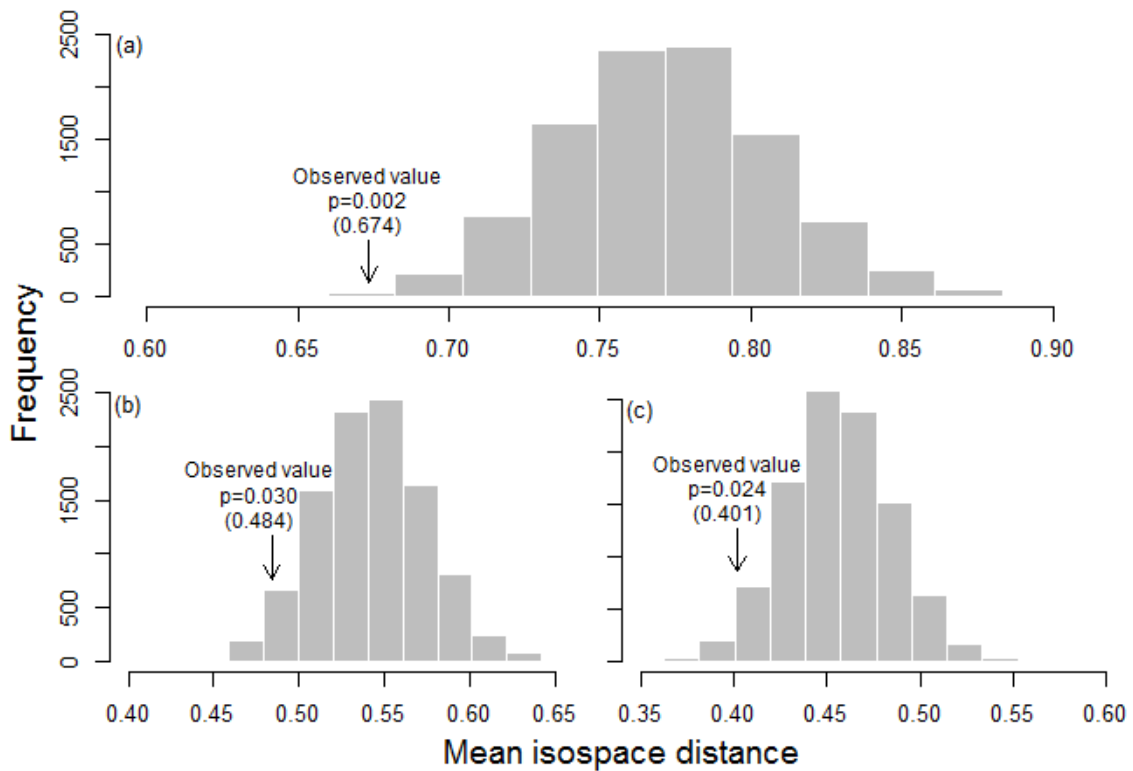


Figure 8: Social transmission of foraging niche. Randomisation histograms depicting a) the null distribution mean isodistances between individuals and a random group member compared to the observed mean isodistance between individuals and their escort as a pup; b) distance between individuals in $\delta^{13}\text{C}$ isotope values; and c) distance between individuals in $\delta^{15}\text{N}$ isotope values (arrows represent p-values from one-tailed tests)

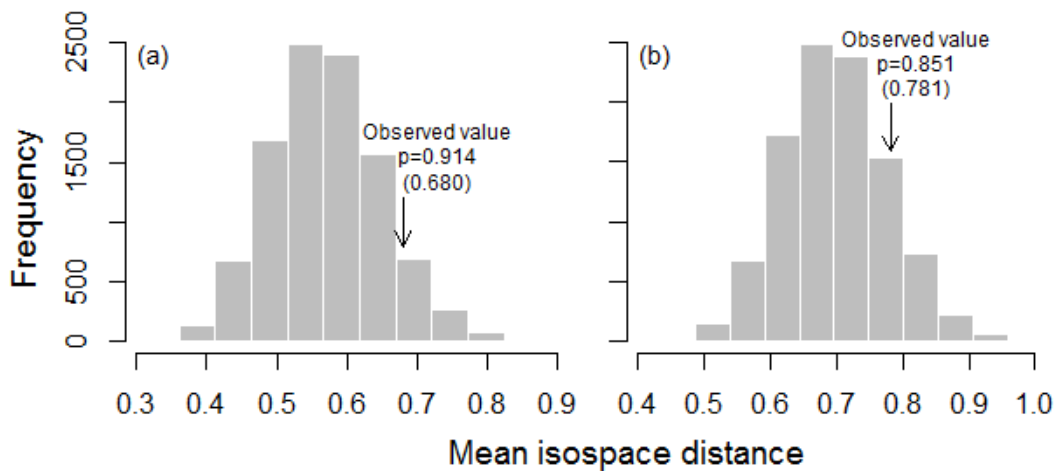


Figure 9: Parental inheritance of foraging niche. Randomisation histograms of the null distribution of mean isospace distance between the isotope signature of focal pups and a random group member for a) individuals with corresponding sample from father; and b) individuals with corresponding sample from mother. Corresponding samples of mothers and fathers were classified as being taken within one month of the focal sample (arrows represent p-values from one-tailed tests)

associations were not significantly closer to their escort. This lack of effect was apparent when analysing all relationships (Fig. 11e; $p = 0.19$, $n = 22$) and when examining only the strongest relationships separately (Fig. 11c; $p = 0.22$, $n = 12$). Escort pairings with weak associations were not significantly closer in isotopic niche than what would be expected under random pairing, whether associations were one-on-one (Fig. 11b; $p = 0.07$, $n = 19$) or multiple (Fig. 11d and 11f; strongest relationship only: $p = 0.06$, $n = 22$; all relationships: $p = 0.08$, $n = 31$).

Discussion

My results demonstrated that the isotopic niche of individual banded mongooses were closer to that of their escorts (Fig. 8), but not their parents (Fig. 9), presenting evidence for non-genetic transmission of foraging niche. The social influence of escorts on the foraging niche of their pups took time to manifest: only individuals over three months were closer in isotopic niche to their escort compared with other group members (Fig. 10). This shift in diet indicates the social inheritance of foraging niche, a key component in defining a behavioural tradition (Fragaszy & Perry 2003). Here I demonstrated that individual adult mongooses (1-5 years old) shared similar diets to their escorts from infancy, suggesting that an individual's socially learned foraging niche is conserved. Therefore, I conclude that individual foraging niche in banded mongooses is both socially acquired and persists into later life and can be considered a behavioural tradition (as defined by Fragaszy & Perry 2003).

Social transmission of behavioural traditions is thought to promote uniformity of behaviour within social groups (Whitehead & Richerson 2009). However, my

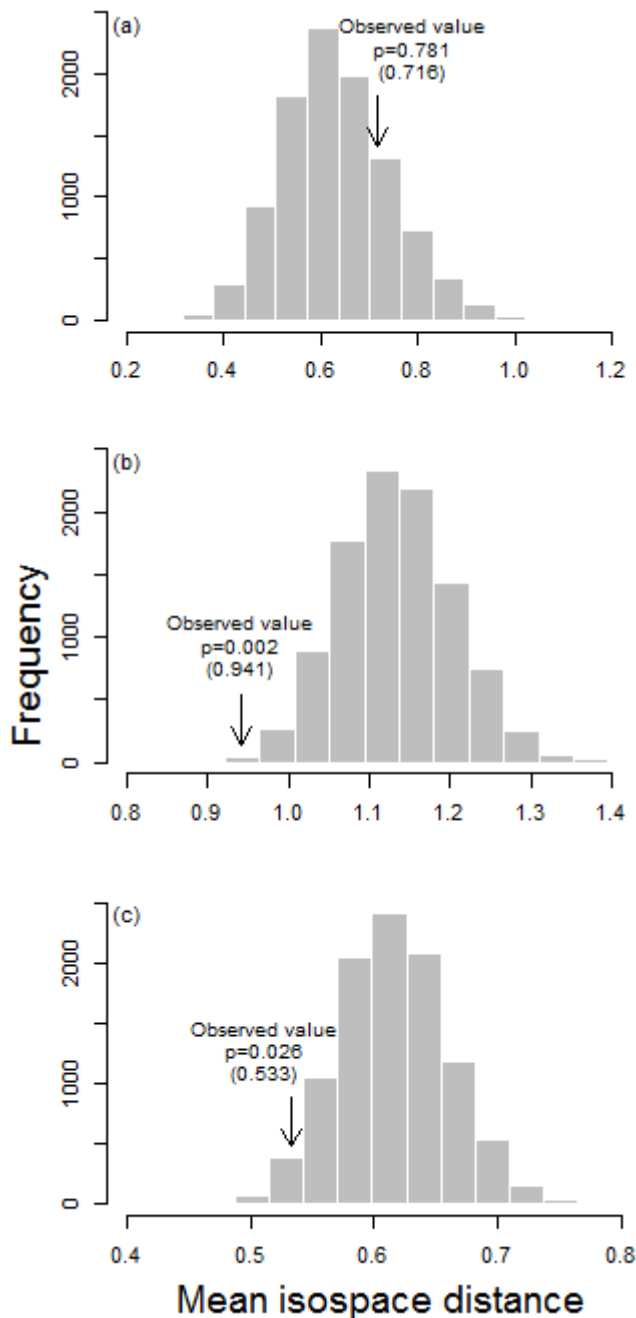


Figure 10: Ontogeny of foraging niche. Randomisation histograms of the null distribution of mean isodistance between individual-random pairings, compared with individual-escort isodistance for individuals aged a) <math>< 3</math> months; b) 3-12 months; and c) 1 year + (arrows represent p-values from one-tailed tests)

Together, these results provide support for the theoretical prediction that oblique transmission (i.e. one-to-one social inheritance irrespective of relatedness) allows multiple traditions to coexistence in a single social group

work supports theoretical arguments which suggest that this can be influenced by the presence of role models. Individuals who associated with multiple escorts did not share a similar diet to their escort (Fig. 11b, 11d and 11f), suggesting that distinct foraging behaviours are less likely to be inherited when social transmission is many-to-one. This finding supports the prediction that social learning erodes behavioural heterogeneity when multiple role models are present (Cavalli-Sforza & Feldman 1981). By contrast, individuals that exhibited strong associations with a single escort were significantly closer in diet (Fig. 11a), inheriting distinct behavioural traditions.

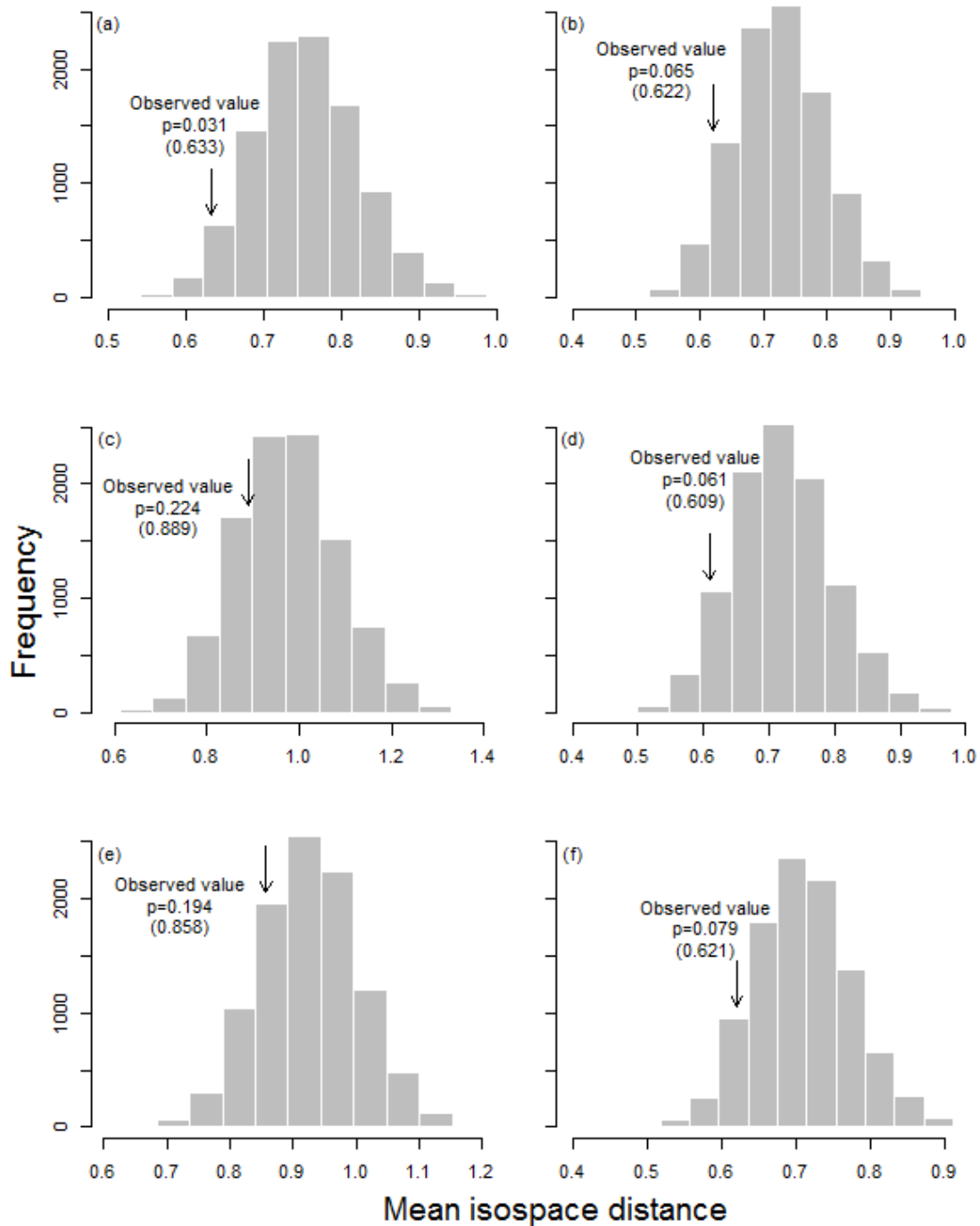


Figure 11: Influence of role models on foraging niche. Randomisation histograms of the null distribution of the mean isodistance between individual-random pairings, compared with individual-escort isodistances of different relationship strengths, showing a) strong one-on-one relationships; b) weak one-on-one relationships; c) pups who had a strong relationship with one escort but also spent time with other escorts (strongest relationship only); d) weak relationships with multiple escorts (strongest relationship only); e) pups who had a strong relationship with one escort but also spent time with other escorts (all relationships); and f) weak relationships with multiple escorts (all relationships) (arrows represent p-values from one-tailed tests)

(Cavalli-Sforza & Feldman 1981). Behavioural heterogeneity within social groups can have important ecological implications. Both theoretical and empirical studies suggest that behavioural homogeneity increases the risk of population collapse (Whitehead & Richerson 2009). For example, studies have documented high levels of mortality in groups of killer whales in which all individuals feed primarily on Chinook salmon when salmon populations declined (Ford et al. 2010), demonstrating that group-level specialisation can increase the risk of population collapse when resources fluctuate. Phenotypic diversity is generally thought to promote population resilience as environments change, therefore genetic diversity is valued (Whitehead 2010). However, in populations dependent on social learning of behaviour, cultural diversity within populations is also important (Whitehead et al. 2004). Many cooperatively breeding animals live in relatively closed (or 'viscous') groups which can be viewed as miniature populations embedded in a larger metapopulation (Thompson et al. 2016). In this study, I provide evidence for the social inheritance of foraging behaviour and demonstrate that role models can alter the transmission of such foraging traditions. By influencing how behavioural traditions are transmitted, the presence of role models may affect behavioural variation within social groups and subsequent group stability. In accordance to previous theoretical models (Cavalli-Sforza & Feldman 1981), it can be predicted that one-to-one transmission of behavioural traditions will promote behavioural heterogeneity within social groups and reduce the risk of group collapse.

Social transmission of behavioural traditions is also likely to be affected by the strength of association between individuals. It can be predicted that the more frequent the interaction between student and role model, the more likely they are to acquire more specific information (Coussi-korbel & Fragaszyt 1995). My

findings support this prediction, as only those individuals who exhibited strong one-on-one associations shared a similar diet to their escort (Fig. 11a).

Individuals who spent less than half of their time with a single escort did not exhibit the same foraging behaviours (Fig. 11b). I suggest that these individuals acquire their foraging niche through individual learning. Individual learning has costs including energy, time and predation (Boyd & Richerson 1988; Whitehead & Richerson 2009). However, it can reduce the risk of population collapse by promoting innovation and the development of new foraging behaviours (Whitehead & Richerson 2009). I hypothesise that through individual learning, banded mongooses maintain the ability to innovate and adapt to changing environments. This hypothesis could be tested in my system by exploring intraspecific variation in the distribution of transmission types. I predict that groups in which one-to-one escorting relationships are frequent and strong will be more robust (in terms of group numbers) to fluctuations in resource availability and the ecological environment.

Exploring the ontogeny of foraging niche, pups were not closer to their escort in diet during their first three months (Fig. 10a). Although, as the isotope values of a tissue reflect the time period over which the tissue was synthesised (Hobson & Clark 1992; Bearhop et al. 2004), isotope values taken from young pups will likely have derived from their mothers whilst in-utero or from suckling.

Therefore, I predict that isotopic niches of pups (<3 months) will be closer to that of their mothers, however due to small sample size I was unable to test this prediction.

In conclusion, I demonstrate that individual banded mongooses acquire lifelong foraging niches through non-genetic social inheritance, displaying behavioural traditions within social groups (defined by Fragaszy & Perry 2003). Using a

unique system which exhibits both one-to-one and many-to-one caring, I was able to test predictions that the number of role models can affect the transmission of distinct foraging traditions. My findings provide empirical evidence that one-to-one caring can promote the inheritance of distinct behavioural traditions, allowing for the coexistence of multiple traditions within social groups.

Chapter 4: General discussion

Individual foraging specialisation has been documented across a wide range of taxa, including both non-social (Araujo et al. 2009; Newsome et al. 2009, 2015; Matich et al. 2011) and group-living species (Robertson et al. 2014, 2015; Rossman et al. 2015). Many causes have been proposed to account for the development of such specialisation (Araújo et al. 2008, 2011; Tinker et al. 2009; Bolnick et al. 2010; Newsome et al. 2015). However, the prevalence of individual foraging specialisation and the causes behind such between-individual variation in group-living species, are currently poorly understood. In this thesis, I argued that some causes of individual specialisation, such as competition and social learning, are likely to have a greater impact on group-living species compared to less social species (Chapter 1). I then investigated the causes behind individual foraging specialisation in a group-living mammal, the banded mongoose, *Mungos mungo*. I examined how intragroup competition affects the size of individual and group foraging niches (Chapter 3). I also explored the transmission mechanisms driving differences in individual foraging niches and how they may affect behavioural traditions within social groups (Chapter 4). Below, I discuss the key findings of this thesis and the implications for our understanding of individual foraging specialisation in group-living species, highlighting potential areas for future research.

Intragroup competition and foraging specialisation

Intrapopulation competition is widely considered to be a main driver of individual foraging specialisation (Svanbäck & Bolnick 2005; Tinker et al. 2008; Araújo et al. 2011; Parent et al. 2014; Newsome et al. 2015). However, there are

contrasting theories predicting how competition affects individual niche size. Classic optimal foraging theory predicts that individuals should add new prey items to their diet under increased competition, expanding individual niche and promoting generalist foraging behaviours (Stephens & Krebs 1986). Alternatively, classic competition theory, such as niche partitioning, suggests that resource diversification allows for the stable coexistence of populations, promoting specialisation at the species level (Schoener 1974; Pianka 1976). These predictions can be applied to social groups to predict how intragroup competition may affect individual foraging specialisation.

In Chapter 3, I tested the two opposing hypotheses of these contrasting theories: (1) intragroup competition leads to larger individual niche and generalist foraging strategies (optimal foraging theory); (2) intragroup competition promotes individual foraging specialisation through niche partitioning (competition theory). I show that individual banded mongooses in larger social groups displayed smaller relative niches, despite larger groups having larger niches. These results demonstrate that larger group size, a proxy for intragroup competition, promotes individual foraging specialisation, supporting the prediction about the effect of intragroup competition on individual specialisation I generated from niche partitioning theory.

One important cost of living in groups is the increased level of local competition (Krause & Ruxton 2002), therefore any mechanism that reduces conflict between conspecifics and reduces these costs should be favoured. Niche partitioning theory predicts that individual specialisation reduces conflict between populations, allowing for their stable coexistence (Schoener 1974; Pianka 1976). Similarly, partitioning resources within social groups through individual foraging specialisation may reduce conflict between group members,

lessening some of the costs of group-living and promoting stable societies.

Thus, greater local competition may mean that individual foraging specialisation is more prevalent in group-living than non-social species.

In order to test my finding that intragroup drives individual foraging specialisation, I propose further study using naturally occurring group fluctuations during eviction events, demonstrated by many group-living species including banded mongooses (Thompson et al. 2016), meerkats (Stephens et al. 2005) and cichlids (Dey et al. 2015). Evictions in banded mongooses are common and conspicuous, driving groups of females, and occasionally males, away from the group (Thompson et al. 2016). I predict that individual foraging specialisation will decrease after such eviction events, as competition between the remaining group members relaxes.

Social learning and foraging niche

Social learning is widely recognised as a mechanism through which foraging behaviours are acquired (Thornton & Malapert 2009; Tinker et al. 2009; Müller & Cant 2010; Hopper et al. 2011; Auersperg et al. 2014; Rossman et al. 2015). It is suggested that the social transmission of foraging traditions reduces within-group variation in foraging behaviour and promotes behavioural uniformity (Henrich & Boyd 1998; Whitehead & Richerson 2009; Hopper et al. 2011; Luncz et al. 2012; Kendal et al. 2015). However, both theoretical and empirical studies demonstrate that the presence of role models may affect how foraging behaviours are transmitted (Cavalli-Sforza & Feldman 1981; Thornton & Malapert 2009; Müller & Cant 2010; Kendal et al. 2015). Learning from a single role model promotes the transmission of distinct foraging behaviours, whereas

learning from multiple role models can have a 'concerted' or 'averaging' effect, acquiring behaviours from all role models (Cavalli-Sforza & Feldman 1981).

In Chapter 4, I investigated transmission pathways of socially inherited foraging niche in banded mongooses, examining from whom individuals acquire foraging behaviours and whether the number of role models affects the extent to which individuals inherit traditions. Previous studies have shown that foraging behaviours are socially acquired in banded mongooses (Müller & Cant 2010), however it is unclear whether individuals learn from their parents or caregivers, or if the acquired behaviours persisted throughout adulthood (>1 year). My findings build upon this research, demonstrating that foraging behaviours are transmitted through non-genetic inheritance and persist into later life, suggesting that banded mongooses exhibit foraging traditions (as defined by Fragaszy & Perry 2003). However, testing both one-to-one (oblique) and many-to-one transmission, I found this social inheritance of foraging niche was influenced by the number of role models an individual associated with.

Individual banded mongooses who displayed a strong association with a single escort had a similar diet to this escort, suggesting that the presence of a single role model promotes the transmission of distinct foraging traditions. By contrast, mongooses who engaged in multiple associations did not inherit the same foraging behaviours as their escort, corresponding with the theoretical argument that many-to-one transmission erodes behavioural heterogeneity (Cavalli-Sforza & Feldman 1981). However, further inspection of social networks combined with more detailed information of foraging niche may shed light on how the foraging niches of these individuals are shaped. For example, individuals who learn from multiple role models may display all foraging behaviours exhibited by all role models. In this instance, individuals who engage in multiple learning

associations may demonstrate generalist foraging strategies. On the other hand, individuals may adopt an average of their role models niches, acquiring the most common foraging behaviours; a tactic shown to promote behavioural uniformity within social groups (e.g. Chimpanzees; Kendal et al. 2015).

Both theoretical and empirical studies suggest that greater within-group variation in behavioural traditions can reduce the risk of population collapse (Whitehead & Richerson 2009; Ford et al. 2010). Our findings demonstrate that learning from distinctly different role models promotes between-individual variation in foraging niche. Learning from single role models may, therefore, reduce the risk of group collapse by maintaining behavioural diversity.

Identifying the mechanism of transmission behind foraging traditions may prove crucial in predicting within-group variation in behavioural traditions and the subsequent risk of group collapse (Cavalli-Sforza & Feldman 1981).

Demonstrating the social inheritance of distinct foraging traits, I provide evidence that social networks influence behavioural traditions. However, it is also thought that behavioural traditions can shape social networks (Cantor & Whitehead 2013). By exploiting a wider range of resources, individuals who exhibit generalist foraging strategies are likely to compete with more conspecifics and so increase their number of social connections (known as increased degree: Bolnick et al. 2011), placing them in central network positions. To investigate this prediction, competition interaction networks can be built by quantifying individual foraging specialisation and identifying the components of individuals' diets. This information can be used to predict which individuals compete with one another for dietary resources, constructing a social interaction network based on resource competition (as shown in Fig. 3). Overlaying these competition networks with others depicting different social

interactions, such as grooming or aggression, will allow us to examine any similar trends in association.

By influencing individuals preferred associations, behavioural matching can shape social networks by forming sub-group communities (Krützen et al. 2005; Ansmann et al. 2012; Mann et al. 2012). Network based diffusion analysis can be used to investigate whether patterns of socially transmitted behaviours correspond with patterns in the relevant social network (Franz & Nunn 2009; Hoppitt & Laland 2011; Aplin et al. 2012). Empirical evidence comparing social networks with and without a particular foraging behaviour has been presented in populations of bottlenose dolphins (Ansmann et al. 2012). In order to experimentally test for behavioural matching, similar models could be established in species that demonstrate the ability to learn foraging behaviours from human role models, such as New Caledonian crows, *Corvus moneduloides* (Kenward et al. 2006). Alternative methods of foraging a specific food item could be taught to individuals and social networks analysed in the presence such dietary item. The social networks generated could then be compared to those exhibited upon removal of the food item. This would allow the comparison of social networks in the presence and absence of different behavioural traditions, testing the occurrence of behavioural matching.

Synthesis

In this thesis, I show that individual foraging niche in banded mongooses is affected by both intragroup competition and social learning from role models. However, one question that remains is whether social group size influences the number of role models an individual associates with. It is intuitive that larger

groups contain more available role models, therefore we may anticipate that individuals in larger groups learn from multiple role models. As demonstrated in Chapter 4, learning from distinctly different role models promotes between-individual variation in foraging niche. Consequently, we would expect increasing group size to lead to reduced individual foraging specialisation; the opposite of what was observed in Chapter 3. Larger groups are, however, likely to produce more offspring, which may counterbalance the greater number of role models resulting in little effect of group size on the number of role models an individual associates with. Alternatively, individuals in larger groups may preferentially associate with single role models, acquiring a distinct niche and reducing the level of competition they experience. Niche partitioning reduces conflict between conspecifics for limited resources (Schoener 1974; Pianka 1976). Therefore, increasing group size may promote one-to-one transmission of foraging traditions, maintaining behavioural diversity within social groups. Studies investigating how increasing group size alters the number of learning associations may shed light on how these two drivers of individual foraging specialisation work together to shape an individual's foraging niche.

My finding that intragroup competition drives individual foraging specialisation relies on the assumption that resources are limited and that individuals are competing with other group members for dietary items. However, where resources are abundant, intragroup competition may not strongly influence individual foraging specialisation. Theory predicts that low levels of intragroup competition allow all individuals to forage on prey items of the best quality (Svanbäck & Bolnick 2005). Where individuals have the same top-ranked prey item, reduced competition leads to group-level foraging specialisation and low between-individual variation in foraging niche, as all individuals forage the same

preferred item (Svanbäck & Bolnick 2005). In such systems, how might individual foraging specialisation develop? As demonstrated in Chapter 4, social transmission of foraging behaviours can promote behavioural heterogeneity within social groups in the presence of role models (as theorised by Cavalli-Sforza & Feldman 1981). Learning from a single role model leads to the inheritance of distinct foraging niches, promoting between-individual variation in foraging niche. Therefore, where foraging behaviours are learned from single role models, social transmission of foraging niche may drive between-individual variation in foraging niche in systems where resources are abundant and competition is low.

Studies documenting individual foraging specialisation are numerous (Svanbäck & Bolnick 2007; Tinker et al. 2008; Araujo et al. 2009; Matich et al. 2011; Robertson et al. 2014; Robertson et al. 2015; Newsome et al. 2015; Rossman et al. 2015), however research concerning such between-individual variation in group-living species is scarce. I demonstrate that these species merit special consideration as the findings included in this thesis (Chapters 3 and 4) reveal that the social group environment can significantly influence the development of individual foraging specialisation. By partitioning resources, individual foraging specialisation presents a mechanism to reduce conflict between group members, supporting their stable coexistence. Continuing to explore the causes and consequences of individual specialisation in group-living species will expand our knowledge of between-individual variation and potentially further our understanding of the evolution of living in groups.

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