

**SCROUNGING HERBIVORES USE BOTH PATCH QUALITY AND
DOMINANCE STATUS OF PATCH HOLDERS WHEN DECIDING WHICH
PATCH TO JOIN**

By

KEENAN STEARS

Submitted in fulfilment of the
requirements for the degree of Master of Science,
University of KwaZulu-Natal.

2011

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for a Master of Science Degree at the University of KwaZulu-Natal. It has not been submitted before for any degree or examination in any other University.

Supervisor:

Dr Adrian M. Shrader

University of KwaZulu-Natal, Pietermaritzburg, South Africa.

December 2011

ABSTRACT

One of the major costs of group living is increased competition due to social information. Social information allows foragers to gain information about the location and the quality of food patches from observing other group members. Ultimately, this allows social foragers to use resources more efficiently. However, the distribution and quality of food varies both spatially and temporally and social information may result in aggregations of foragers around favourable food patches when they are available. This results in individuals of various dominance ranks aggregating around food resources and competing for food. In order to understand how dominance and patch quality interact to determine foraging behaviour, various foraging models have been created. In particular, producer-scrounger social foraging models are used to understand foraging behaviour and patch choice under competitive conditions.

In producer scrounger games, individuals can either find their own food patches (produce) or join other individuals at food patches (scrounge). This study focused on how the combination of patch holder dominance status and patch quality interacts to influence patch joining decisions by scroungers. According to producer-scrounger models scroungers only join patches held by subordinate individuals. However, I found that a scrounger will join any patch as long as the patch holder is not within the top five most ranked individuals in the herd. However, as patch quality increased, fewer of the top ranked patch holders were avoided at each patch quality. This suggests that foraging is a trade-off between the costs of an aggressive interaction and the benefits gained from each patch. Behavioural titrations found that the initial density of food at a patch needs to be 2.3 times greater for a scrounger to feed from the next dominant patch holder. At high patch qualities there was a threshold point where patch quality became the driving force behind patch joining decisions and no patch holders were avoided, no matter their dominance status. Scroungers that fed from the top ranked patch holders had the same intake rate when compared with feeding with subordinate patch holders. This could be due to an increased level of vigilance by the scrounger in order to avoid an aggressive interaction with the dominant patch holder. However, scrounger's intake rate increased when they fed from dominant patch holders that were not the top ranked herd members.

This suggests that only the top ranked herd members are aggressive enough to prevent scrounging attempts.

A novel discovery of this study was that although the goats formed a linear dominance hierarchy, they did not forage in accordance with it, with lower ranking individuals avoiding dominant patch holders. This suggest that in social herbivores dominance hierarchies are not maintained to determine who has priority access to food. This study shows that even large differences in dominance are not sufficient enough to prevent scrounging decisions and only the top ranked patch holders have the ability to prevent joining attempts.

ACKNOWLEDGEMENTS

Firstly I would like to thank my supervisor Dr Adrian M. Shrader for supervising me as well as this project. Without his continued advice and support throughout, this study would not have been possible.

Professor Graham I.H. Kerley, my co-supervisor, for his assistance and constructive criticisms.

Professor David Ward, for his help with the statistical analysis of my results.

I would also like to thank the staff at Ukulinga Research Farm. Special thanks to Sam Khumalo, who lent me his herd of goats, and the workers on the farm who helped with the daily herding of the goats. Thanks to the farm manager, Mangesh Deepap, for allowing me to conduct this project using the farm facilities and animals.

Thank you also to my assistant, Melissa H. Schmitt, for her hard work and help with data collection.

Lastly, I would like to thank my parents who have supported me throughout the last two years.

TABLE OF CONTENTS

DECLARATION	i
ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
LIST OF FIGURES	vii
LIST OF TABLES	viii

Chapter 1

Introduction.....	1
1.1. Broad aim	1
1.2. Group living	1
1.3. Optimal foraging theory and producer-scrounger games.....	3
1.4. Dominance in producer-scrounger games.....	5
1.5. Dominance hierarchies.....	6
1.6. Patch quality in producer-scrounger games	9
1.7. Scrounger joining decisions	11
1.8. Layout.....	12
References.....	13

Chapter 2

2.1. Introduction.....	20
2.2. Methods.....	22
2.2.1. Dominance relationships	24
2.2.2. Patch choice between different quality patches	26
2.2.3. Patch quality and dominance status of patch holder	27
2.2.4. Patch quality and dominance status of the top five ranked patch holders.....	27
2.2.5. Data Analysis	28
2.3. Results.....	29
2.3.1. Patch quality	30
2.3.2. Linear hierarchy	30

2.3.3. Scrounger’s intake rate against close, intermediate and far dominance category patch holders	30
2.3.4. Scrounger’s patch choice against close, intermediate and far dominance category patch holders	31
2.3.5. Scrounger’s patch choice against the top ranked patch holders.....	31
2.3.6. Scrounger’s intake rate against the top ranked patch holders	31
2.4. Discussion	32
2.4.1. Scrounger’s intake rate against close, intermediate and far dominance categories	33
2.4.2. Scrounger’s patch choice for close, intermediate and far dominance categories	34
2.4.3. Scrounger’s patch choice against the top five ranked patch holders.....	36
2.4.4. Scrounger’s intake rate against the top five ranked patch holders	40
References.....	43

Chapter 3

Conclusions and implications for producer-scrounging models and foraging behaviour	59
References.....	65

LIST OF FIGURES

Figure 1: Testing arena used in the experiment. Thick lines denote non-transparent fences. Goats were held in the holding area and were transferred to the testing arena when needed for testing. Feeding patches (indicated by square) were placed on each side of the non-transparent divider 50

Figure 2: Type two functional response curve of scroungers' intake rate when they fed from patch holders from the close, intermediate and far dominance categories. 51

Figure 3: The lowest ranked goat that was avoided by scroungers at each patch quality. Ranking is set so that rank one is the most dominant individual, rank two is the second most dominant, etc. 52

LIST OF TABLES

Table 1: Chi-square results confirming that the herd of 45 goats could identify the patch quality from visual cues.....	53
Table 2: Linear dominance hierarchy for the goat herd with the total number of wins and losses and non-interacting pairs calculated from the win-loss matrix. Clutton-Brock Index (CBI) value was calculated using the formula: $CBI = (B+b+1)/(L+l+1)$, Where B = the number of individuals whom the subject dominates, b = the number of individuals whom those dominated by the subject in turn dominate, L = the number of individuals who dominate the subject, and l = the number of individuals who dominate those dominating the subject (Clutton-Brock et al., 1979).....	54
Table 3: Significant and non-significant effects of patch quality, distance (close, intermediate, far), status (dominant, subordinate) and their inter interactions on the intake rate of scroungers from an ANOVA analysis. The influence of patch quality, status and their interaction on scrounger's intake rate when feeding from the top five ranked patch holders in the herd is also shown.	56
Table 4: Chi-square results from the saturated log linear model showing the main effects and two way interaction of the variables patch quality (40 g, 100 g, 200 g, 400 g, 1000 g), distance (close, intermediate, far) and status (dominant, subordinate) had no influence on the number of scroungers that fed from a dominant or subordinate patch holder.	57
Table 5: Chi-square test results showing the difference in the number of scroungers that fed from a dominant or subordinate patch holder. Significant p values indicate that scroungers avoided the dominant rank and fed more from subordinate patch holders. Non-significant p values indicate that scroungers fed equally from patches held by the top individuals and subordinates.....	58

CHAPTER 1

Introduction

One of the main costs of group living is competition. Herbivores that forage in groups continuously interact with group members of different dominant ranks as well as forage in patches of different quality. The role of dominance and patch quality on foraging behaviour has been well documented. However, the interaction of these factors on scrounging behaviour has not been explored.

1.1. Broad aim:

To determine how the combination of patch holder dominance status and patch quality interact to influence scrounging behaviour of group-living goats.

Objectives:

1. Determine the dominance hierarchy of a herd of goats.
2. Determine whether individuals within this herd can determine patch quality via visual cues.
3. Determine whether patch quality or dominance status of patch holders has a greater influence on the patch-joining decisions of scroungers.
4. Determine how the interaction of dominance and patch quality influences patch-joining decisions of scroungers across patches of different quality.
5. Determine whether scroungers adjust their intake rate in response to the patch holder's dominance rank.

1.2. Group living

Many animal species live in groups (Krause and Ruxton, 2002). However, for individuals living in groups there are costs and benefits. One of the greatest benefits of group living is decreased predation risk. This can be the result of increased group vigilance (Pulliam, 1973) and anti-predatory benefits (Ranta et al., 1996). Vigilance can be costly to an individual as it decreases the available time spent foraging (Smith and Cain, 2008). In

order to minimise the amount of time spent being vigilant, individuals congregate in groups. As group size increases individual vigilance decreases (Roberts, 1996). This decrease in individual vigilance, while still getting the same level of protection (i.e. many eyes hypothesis, (Lima, 1990)) allows individuals to spend more time foraging. Grouping also allows individuals to avoid predators through the dilution effect where a predator may only prey upon one individual in the group (Mooring and Hart, 1992). Group defence also decreases predation risk as individuals band together to deter predators (Robinson, 1985). Hence, the risk of being a victim of predation is a function of group size. Another means of avoiding predation is through the selfish herd effect where individuals reduce the probability of predation by moving close to other herd members or to the centre of the herd (Hamilton, 1971). This grouping together to form large group sizes can also lead to a confusion effect, where predators are confused by the movement and shifting of the feeding group (Landeau and Terborgh, 1986).

Group-living animals have another advantage: that of having access to social information (Shrader et al., 2007; King et al., 2009). As the distribution of good quality food varies both spatially and temporally within an environment, herbivores are faced with the challenge of estimating the quality of food patches (Valone and Templeton, 2002) as well as to locate high quality food (Shrader et al., 2007). A lot of focus has been put on how foragers obtain this information and how they use it to determine foraging decisions. Solitary as well as social animals can obtain information about patch quality through personal sample information while searching and exploiting patches (Valone, 1991). However, social foragers have access to another source of information which is not available to solitary foragers, known as social information (Valone, 1989). Social information is obtained when foragers observe the foraging behaviour of other herd members (Giraldeau et al., 2002). Social foragers can combine both personal and social information to estimate patch quality faster and more accurately (Valone and Templeton, 2002). This allows for a more efficient use of resources as foragers are able to find and assess the quality of food patches (Vickery et al., 1991; Ranta et al., 1996; Beauchamp et al., 1997; Shrader et al., 2007), far easier than if they were foraging on their own. For example, Smith et al. (2001) found that foraging blackbirds, *Turdus merula*, dominant individuals had an increase in foraging success after displacing a subordinate individual.

This suggests that these individuals use social information to locate and obtain high quality food patches. By using information gained from others, foragers may experience an increase in average feeding rate and a reduction in its variance (Pulliam and Millikan, 1982).

There are however, costs involved with social living. These include the increased probability of disease and parasite transmission (Hart and Hart, 1992; Arnold and Lichtenstein, 1993) and competition for food (Smith et al., 2001). This competition may be intense as a result of social information (Barnard, 1984). For example, Smith and Cain (2008) found that impala, *Aepyceros melampus*, changed their foraging behaviour due to a change in resources due to intraspecific competition. As individuals fed in close proximity to each other the abundance of food decreased. To compensate, individuals increased the number of steps they took per minute in order to eat the best forage before neighbouring herd members (Smith and Cain, 2008). Smith et al. (2001) found that in blackbirds, *Turdus merula*, top-ranked birds experienced greater foraging success compared to bottom-ranked birds when feeding in small groups. This increased foraging success was due to the dominant birds being able to out-compete subordinate birds while experiencing little interference competition themselves. The foraging efforts (i.e. number of feeding movements per unit time) of subordinates were found to be lower than that of dominants even if no interference competition occurred. This was likely due to the subordinates spending time monitoring the aggressive behaviour of dominant individuals rather than feeding (see Cresswell, 1997). This ensures that subordinates are able to avoid costly aggressive interactions with dominant birds.

For herbivores the distribution and quality of food varies both spatially and temporally across the environment. As a result, individuals may aggregate around favourable food patches when and where they are available (Giraldeau and Dubois, 2008). With this increase in competition around patches how do individuals, both dominant and subordinate, determine where to feed and how does their foraging tactic influence their intake? To answer this, social foraging models are used to determine how the behaviour of an individual influences the decisions and payoffs of others (Giraldeau and Dubois, 2008).

1.3. Optimal foraging theory and producer-scrounger games

For any animal, foraging decisions are based on many factors such as the quality and quantity of food and the current energetic requirements of the forager (Lendvai et al., 2006). These decisions are complicated further for animals that live and feed in groups (Giraldeau and Caraco, 2000). In order to understand the choices that individuals face while foraging, various foraging theories have been developed. The optimal foraging theory (Charnov, 1976) has been relied on as a means to formalise foraging problems (Owen-Smith and Novellie, 1982). Optimal foraging theory relies on simple optimality in order to understand foraging problems. This approach does not deal effectively when animals interact and affect each other's payoffs. For example, when determining the optimal diet for a single forager the payoffs of including and not including certain prey types are calculated and it is predicted that the forager will choose the diet which maximises its payoff. However, many species congregate in herds and compete with each other for resources, the payoff gained from choosing a diet is determined by the frequency with which other herd members also choose that diet. As a result, this results in payoffs that are frequency-dependant and thus simple optimality models cannot be used to predict the best diet choice (Giraldeau and Dubois, 2008).

What is needed is an evolutionary game-theoretical approach which expects tactic choice to converge on an evolutionary stable strategy (ESS) (Giraldeau and Dubois, 2008). Social foraging theory addresses frequency-dependant payoffs and provides a method to understand food exploitation and patch selection under competitive conditions (Giraldeau and Dubois, 2008). Social foraging theory is divided into four categories: group membership, decisions within patches, descriptive models of phenotypic diversity and producer-scrounger games. In this thesis, I will only be focusing on producer-scrounger games.

The models used in producer-scrounger games focus on the stable frequencies of alternative foraging strategies, the payoffs of each strategy and the optimal tactic choice (Liker and Barta, 2002). In group living animals, some members of the group exploit the finding efforts of other herd members (Liker and Barta, 2002). This results in some individuals searching for food patches (producers), while others (scroungers) watch other individuals find a food patch and then join them at the patch or displace them (Barnard

and Sibley, 1981; Giraldeau and Caraco, 2000; Valone and Templeton, 2002; King et al., 2009). Recent literature suggests that producer-scrounger models can successfully predict foraging tactic use (Giraldeau and Caraco, 2000; Coolen et al., 2001).

Before producer-scrounger models can be applied to group foraging situations, two assumptions need to be met (Ohtsuka and Toquenaga, 2009). First, the choice to be a producer or a scrounger is mutually exclusive, a forager can choose either to be a producer or a scrounger, but cannot simultaneously play both (Coolen et al., 2007; Ohtsuka and Toquenaga, 2009). The second assumption is that the scrounger's payoffs are negatively frequency-dependent on their frequency within the group so that they do very well when rare but very poor when common (Barnard and Sibley, 1981; Vickery et al., 1991; Beauchamp and Giraldeau, 1996). Under these conditions, it is assumed that scroungers do better than producers when scroungers are rare in the group, because there are many exploitable food patches made available by the producers. However, when scroungers are common the scrounger option does worse due to the decrease in available patches as a result of fewer producers locating food patches. This also leads to increased competition at already located food patches (Barnard and Sibley, 1981). This strong negative frequency dependence leads to a mixed evolutionarily stable strategy (ESS) where both foraging choices coexist and obtain the same pay-offs (Maynard Smith, 1982; Vickery et al., 1991). Therefore foragers can either be pure producers or pure scroungers or will alternate between tactic choice at the evolutionary stable strategy frequency (Vickery et al., 1991).

1.4. Dominance in producer-scrounger games

The dominance rank of a forager can influence its ability to compete for food. If dominance influences competition then dominance relationships between foragers are expected to influence social foraging tactic use (Giraldeau and Beauchamp, 1999). Barta and Giraldeau (1998) developed a phenotype limited producer-scrounger model in which they assumed competitive abilities differed among individuals. They found that the difference in competitive ability between individuals determines their use of the producer or scrounger tactic.

When competitive differences between foragers are high, foragers are predicted to specialise exclusively on one tactic. Specifically, dominant individuals should scrounge whereas subordinate individuals should produce. Liker and Barta (2002) found that in house sparrows there was a strong association between dominance and foraging method. They found that dominant individuals obtained food by joining other individuals at patches more often than subordinates. However, when differences in competitive abilities are narrow, all foragers can use both tactics. In an experiment with Mexican jays, *Aphelocoma ultramarine*, it was found that the foraging choice of birds varied continuously (McCormack et al., 2007), and that producer-scrounger tactic choice was not related to dominance *per se* as in Liker and Barta (2002). The greater the difference in dominance rank between two birds, the more likely it was that a joining event would occur, with the dominant bird joining the subordinate (McCormack et al., 2007). Prior to joining a patch a bird takes the dominance rank of the producer into account and generally, individuals prefer to join patches held by lower-ranked individuals (McCormack et al., 2007). This is important in understanding the role of dominance in producer-scrounger games, as joiner preference has not been included in theoretical models or interpretations of results (McCormack et al., 2007).

1.5. Dominance hierarchies

One of the major costs of group living is competition. Dominance plays a large role in this with dominant individuals out-competing subordinates through aggressive interactions (contest competition) or through the removal of a limited resource from an area before others are able to feed (scramble competition) (Vogel, 2005). The role of dominance has also been seen in producer-scrounger games. Social dominance has been introduced as a means of understanding social organization (Hind, 1974; Côté, 2000). Dominance can be defined as repeated, agonistic interactions between two individuals. Furthermore, it is characterized by a consistent outcome in favour of the same individual and an avoiding response of its opponent rather than escalation (Drews, 1993). The status of the winner of the interactions is the dominant and the loser the subordinate.

There are two major benefits of social dominance. First, dominant individuals may be allowed access and exclusivity to limited resources. For example, dominant red

deer stags, *Cervus elaphus* (Appleby, 1980), and woodland caribou, *Rangifer tarandus caribou* (Barrette and Vandal, 1986), had priority access to food resources over subordinate individuals. Secondly, dominance may reduce aggression between individuals within a herd, as individuals would avoid costly interactions. This benefits both dominant and subordinate individuals. Dominant individuals benefit by not having to re-establish dominance at every new contact, which saves energetic costs as well as costs of injury (Fournier and Festa-Bianchet, 1995). Subordinates would benefit by not interacting with a dominant individual over a resource as it would most probably not obtain the resource and also risk injury in an agonistic interaction. Maynard-Smith and Price (1973) showed that animals appear to use individual characteristics that are related to an individual's dominance rank to determine whether to initiate or escalate an agonistic encounter. These include: body mass, body size, or weapons such as horns (Côté, 2000).

Various methods of constructing dominance hierarchies have been proposed. Bang et al. (2010) compared three different indices to construct dominance hierarchies, viz Clutton-Brock et al. (1979) index (CBI), David's score (DS) and frequency-based index of dominance (FDI). CBI considers for each individual, both direct and indirect wins and losses (Clutton-Brock et al., 1979). Direct wins are given by the number of individuals against whom the focal animal wins and indirect wins are given by the total number of individuals against whom each individual that the focal animal wins against in turn wins. CBI has been widely used for vertebrate species (Watts, 1994; Mateos and Carranza, 1997). However, there is a problem with CBI as it doesn't take into account the total number of wins and losses, but rather measures wins as a binary decision between pairs of individuals (Bang et al., 2010). DS accounts for this problem by considering the proportion of the interactions that result in wins and losses (David, 1987). Bang et al. (2010) modified CBI to take into account the frequency of direct and indirect wins and losses creating what they call the frequency-based dominance index (FDI).

Bang et al. (2010) tested these three indices against natural and artificially generated data sets of the eusocial wasps, *Ropalidia marginata* and *R. cyathiformis*. They found that the dominance ranks obtained by the three indices were positively and significantly correlated with each other. However, the three indices differed in their

ability to create unique ranks due to non-interacting pairs and reversals in the direction of dominance. The question then is which index do you use to construct a dominance hierarchy? The answer lies in the number of unique ranks that each index gives with the given data. The index that gives the largest number of unique ranks is therefore preferable to one that gives many tied ranks (Bang et al., 2010). The reason is, if each individual has a unique rank it is easier to arrange individuals into a linear hierarchy. This approach assumes that dominance is transitive (Jameson et al., 1999). For example, for every three individuals A, B and C, if A dominates B and B dominates C, then it is probable that A dominates C (Appleby, 1983; de Vries, 1995). If individuals have tied ranks then the assumption of transitivity is not met and the hierarchy will not be linear. Bang et al. (2010) found that there is not one universal dominance index but rather each index is suitable to different species as the number of non-interacting pairs and reversals may vary between species. DS is useful for species where there is high percentage of reversals. FDI is useful in species where there are many non-interacting pairs and CBI is useful in species where information on rates of interactions is absent.

Once the dominance relationship between individuals has been determined, the next question is, can these relationships be ordered into a linear hierarchy? Individuals form a linear hierarchy if for every dyad A and B in the group, A dominates B, or vice versa and if every triad is transitive (Jameson et al., 1999). The common method of dealing with dominance relationships is to organise group members in rank order, so that individuals do not dominate those higher in rank. However, this may increase the overall impression of linearity and it may produce hierarchies from groups that actually have no structure (Beilharz and Mylrea, 1963). Dominance is assumed to be transitive when individuals are ranked into a linear hierarchy. Therefore, a statistical test (adapted from Kendall, 1962) can be used to test whether dominance in a group is transitive (see Appleby, 1983). This method can be used on groups where some dyads did not interact, although this will bias the test and decreases the probability of dominance transitivity being significant (Appleby, 1983). The linearity of a hierarchy is denoted by Kendall's coefficient K. K can have values ranging from 0, indicating absence of linearity, to 1, indicating complete linearity (Appleby, 1983).

Although the majority of hierarchies of interest are linear, there are however different types of hierarchies (de Vries, 1995). In wolf packs, *Canis lupus*, dominance is held in check by an alpha pair, the alpha male and female (Mech, 1970; Peterson, 1977). All members, including the alpha female, are subordinate to the alpha male (Schenkel, 1967) and the alpha female is dominant over all other individuals except the alpha male (Clark, 1971; Mech, 1999). Even among yearlings and two year olds there were very few rank displays (Mech, 1999). The same behaviour in dominance can be seen in the African hunting dog, *Lycaon pictus*, which is ecologically very similar to the wolf (Mech, 1975). This suggests that although there is a dominance hierarchy only the top ranked individuals are important and there is no difference in rank between the rest of the individuals in the pack. This was also found in captive bonobos, *Pan paniscus*, where linear rank order among males were rigid among high-ranking males but less clear among middle- to low-ranking males (Furuichi, 1992; Furuichi and Ihobe, 1994). In chimpanzees, *Pan troglodytes*, males rank either in linear hierarchies (Boesch and Boesch-Achermann, 2000) or at least in narrow rank categories (Goodall, 1986; Newton-Fisher, 2002). For female chimpanzees, dominance relationships were ordered in broad rank categories (Pusey et al., 1997) and linear hierarchies have never been detected.

1.6. Patch quality in producer-scrounger games

Patch quality and diet selection are important factors in understanding the mechanisms that determine foraging decisions (Illius et al., 1999). Illius et al. (1999) found that goats selectively grazed on vegetation that gave the highest intake rate and the density of the above ground biomass of the vegetation influenced the goat's intake rate. Wilmshurst et al. (1995) also found that the density of a resource influenced foraging. For example, wapiti, *Cervus elaphus*, preferred to forage from patches of intermediate biomass. In general, grazing ruminants should prefer, short, intermediate biomass grass swards over tall, high biomass swards (Wilmshurst et al., 2000). If animals are selecting patches of intermediate biomass in order to maximise their foraging efforts, this could lead to an aggregation of foragers within these patches (Wilmshurst et al., 1995). Aggregation around a resource can lead to increased competition and increased aggression to obtain the whole resource (Giraldeau and Dubois, 2008). Producers should aggressively defend

food patches, whereas only a fraction of scroungers should aggressively attempt to appropriate a producer from its patch (Dubois and Giraldeau, 2005). This is because the producer obtains the finder's share and thus should be more willing to pay for defence compared to the scroungers' willingness to pay for appropriation (Dubois and Giraldeau, 2005). The finder's share is the proportion of food that is available to the producer before a scrounger joins the patch, and it is inversely proportional to patch quality (Giraldeau and Dubois, 2008).

Vickery et al. (1991) was the first to present the rate maximizing model. The model predicts that the frequency of the scrounger tactic within a group depends on the finder's share as well as group size. The larger the finder's share, the lower the equilibrium proportion of scroungers (Giraldeau and Dubois, 2008). The finder's share is a vital component of the rate maximising model so it is important to determine whether it exists within foraging situations. Experiments on nutmeg mannikins, *Lonchura punctulata*, and zebra finches, *Taeniopygia guttata*, strongly suggested the existence of a finder's share when foraging in clumps of different quality, as producers were able to capitalise on the first two or three seeds in a patch before they were joined by scroungers (Giraldeau et al., 1990; Coolen et al., 2001). The finder's share has also been found in capuchin monkeys, *Cebus paella* (Di Bitetti and Janson, 2001). Food provisions were placed on platforms and the process of platform discovery was noted. The platform's finder enjoyed the finder's share of fruit. The size of the finder's share was determined by the dominance of the discoverer, the amount of food on the platform, the distance between individuals and the extent to which the food discovery was broadcast to the rest of the group (Di Bitetti and Janson, 2001). Coolen et al. (2001) found that nutmeg mannikins allocated more time to the scrounging tactic as food clumps became more clumped, this is because the producer can only monopolise a small proportion of the available food before the scrounger arrives (Beauchamp, 2008). A scrounger can only benefit from its tactic choice if there is a large proportion of food available in the patch when the scrounger arrives (Giraldeau and Livoreil, 1998). Another factor that influences the finder's share is how easily a patch can be defended. The more clumped a resource is, the easier it is to defend. Aggressive producers can delay the arrival of scroungers by aggressively defending a patch, thereby reducing the share that is available

to the scrounger (Vickery et al., 1991). The effects of patch quality on producer-scrounger tactic choice have been well documented. However, one factor that has not been explored is what role does patch quality play in determining where scroungers feed?

1.7. Scrounger joining decisions

Dominance and patch quality have been shown to influence producer-scrounger tactic choice (Vickery et al., 1991; Barta and Giraldeau, 1998; Liker and Barta, 2002). Dominant individuals tend to scrounge, whereas subordinate individuals normally produce. At present, producer-scrounger games only focus on how foragers choose between the producer and scrounger tactic and how dominance influences their payoff. One aspect of producer-scrounger games that has not been explored is how do scroungers use the combination of dominance and patch quality to determine what patches they join? The influence of dominance on scrounger foraging decisions has been looked at, for example, scroungers tend to scrounge mainly from subordinate individuals (McCormack et al., 2007). However, the influence of patch quality on scrounger decisions is lacking. For example, individuals likely forage in a way that maximises their intake of resources. How does the dominant status of a patch-holder influence that intake rate? Will scroungers always avoid feeding from dominant individuals even when food quality and payoffs are extremely high, or will dominant patch-holders only be avoided at low patch quality? These are important questions that at present are not included in producer-scrounger games and their understanding will greatly increase our knowledge of scrounger foraging behaviour.

With the adaptive plasticity of foraging choices, any individual, no matter its dominance rank, can use the scrounger tactic. In this study, a scrounger needs to assess its own dominance rank, the dominance rank of others surrounding it as well as patch quality before joining a patch. So how does a scrounger use these different factors to determine which individual to scrounge from and how does its choice influence its payoff?

1.8. Layout

The following thesis consists of three chapters. The first chapter is a broad introduction which provides information on the topics that are being investigated. The second chapter follows the format of a scientific paper and deals with the experiment of how the combination of patch holder dominance status and patch quality drives the patch joining of scroungers. The third chapter then ties in the findings of this experiment to generate a broad conclusion which links to the literature. Each chapter is independent and has its own references. As a result, there may be slight overlap in information between chapters.

References

- Appleby, M.C. 1980. Social rank and food access in red deer stags. *Behaviour* 74, 227-265.
- Appleby, M.C. 1983. The probability of linearity in hierarchies. *Animal Behaviour* 31, 600-608.
- Arnold, W., Lichtenstein, A.V. 1993. Ectoparasite loads decrease the fitness of alpine marmots (*Marmota marmota*) but are not a cost of sociality. *Behavioral Ecology* 97, 36-39.
- Bang, A., Deshpande, S., Sumana, A., Gadagkar, R. 2010. Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices. *Animal Behaviour* 79, 631-636.
- Barnard, C.J. 1984. The evolution of food-scrounging strategies within and between species. In: Barnard, C.J. (Ed.), *Producers and scroungers: Strategies of exploitation and parasitism*. Chapman and Hall, New York, pp. 95-126.
- Barnard, C.J., Sibley, R.M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29, 543-550.
- Barrette, C., Vandal, D. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* 97, 118-146.
- Barta, Z., Giraldeau, L.-A. 1998. The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioural Ecology and Sociobiology* 42, 217-223.
- Beauchamp, G. 2008. A spatial model for producing and scrounging. *Animal Behaviour* 76, 1935-1942.
- Beauchamp, G., Belisk, M., Giraldeau, L.-A. 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *Journal of Animal Ecology* 66, 671-682.
- Beauchamp, G., Giraldeau, L.-A. 1996. Group foraging revisited: information sharing or producer-scrounger game? *American Naturalist* 148, 738-743.
- Beilharz, R.G., Mylrea, P.J. 1963. Social position and behaviour of dairy heifers in yards. *Animal Behaviour* 11, 522-528.

- Boesch, C., Boesch-Achermann, H. 2000. The chimpanzees of the Tai Forest. Oxford University Press, Oxford, UK.
- Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9, 129-136.
- Clark, K.R.F. 1971. Food habits and behavior of the tundra wolf on central Baffin island. Ph.D. thesis. University of Toronto, Toronto.
- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M., Guinness, F.E. 1979. The logical stag: adaptive aspects of fighting in red deer. *Animal Behaviour* 27, 211-225.
- Coolen, I., Giraldeau, L.-A., Lavoie, M. 2001. Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour* 61, 895-903.
- Coolen, I., Giraldeau, L.A., Vickery, W. 2007. Scrounging behaviour regulates population dynamics. *Oikos* 116, 533-539.
- Côté, S.D. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137, 1541-1566.
- Cresswell, W. 1997. Interference competition at low competitor densities in blackbirds (*Turdus merula*). *Journal of Animal Ecology* 66, 461-471.
- David, H.A. 1987. Ranking from unbalanced paired-comparison data. *Biometrika* 74, 432-436.
- de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour* 50, 1375-1389.
- Di Bitetti, M.S., Janson, C.H. 2001. Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour* 62, 47-56.
- Drews, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour* 125, 283-311.
- Dubois, F., Giraldeau, L.-A. 2005. Fighting for resources: the economics of defense and appropriation. *Ecology* 86, 3-11.
- Fournier, F., Festa-Bianchet, M. 1995. Social dominance in adult female mountain goats. *Animal Behaviour* 49, 1449-1459.
- Furuichi, T. 1992. Dominance relations among wild bonobos (*Pan paniscus*) at Wamba, Zaire. *In* Abstracts of the XIVth Congress of the International Primatological Society, Strassbourg, France.

- Furuichi, T., Ihobe, H. 1994. Variation in male relationships in bonobos and chimpanzees. *Behaviour* 130, 211-228.
- Giraldeau, L.-A., Beauchamp, G. 1999. Food exploitation: searching for the optimal joining policy. *Trends in Ecology and Evolution* 14, 102-106.
- Giraldeau, L.-A., Caraco, T. 2000. *Social Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Giraldeau, L.-A., Dubois, F. 2008. Social foraging and the study of exploitative behavior. *Advances in the Study of Behavior* 38, 59-104.
- Giraldeau, L.-A., Hogan, J.A., Clinchy, M.J. 1990. The payoff to producing and scrounging: what happens when patches are divisible? *Ethology* 85, 132-246.
- Giraldeau, L.-A., Livoreil, B. 1998. Game theory and social foraging. In: Dugatkin, L.A., Reeve, H.K. (Eds.), *Game Theory and Animal Behavior*. Oxford University Press, New York, pp. 16-37.
- Giraldeau, L.-A., Valone, T.J., Templeton, J.J. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 357, 1559-1566.
- Goodall, J. 1986. *The chimpanzees of Gombe - Patterns of behavior*. The Belknap Press of Harvard University Press, Cambridge, MA.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31, 295-311.
- Hart, B.L., Hart, L.A. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour* 44, 1073-1083.
- Hind, R.A. 1974. *Biological bases of human social behaviour*. McGraw-Hill, New York.
- Illius, A.W., Gordon, I.J., Elston, D.A., Milne, J.D. 1999. Diet selection in goats: a test of intake-rate maximisation. *Ecology* 80, 1008-1018.
- Jameson, K.A., Appelby, M.C., Freeman, L.C. 1999. Finding an appropriate order of hierarchy based on probabilistic dominance. *Animal Behaviour* 57, 991-998.
- Kendall, M.G. 1962. *Rank correlation methods*, 3rd edn. Charles Griffin, London.
- King, A.J., Isaac, N.J.B., Cowlshaw, G. 2009. Ecological, social, and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology*, 1039-1049.

- Krause, J., Ruxton, G.D. 2002. Living in groups. Oxford University Press Inc., New York.
- Landeau, L., Terborgh, J. 1986. Oddity and the 'confusion effect' in predation. *Animal Behaviour* 34, 1372-1380.
- Lendvai, A.Z., Liker, A., Barta, Z. 2006. The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. *Animal Behaviour* 72, 747-752.
- Liker, A., Barta, Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* 139, 1061-1076.
- Lima, S.L. 1990. The influence of models on the interpretation of vigilance. In: Bekoff, M., Jamieson, D. (Eds.), *Interpretation and explanation in the study of animal behaviour: Explanation, evolution and adaptation*. Westview Press, California, pp. 246-267.
- Mateos, C., Carranza, J. 1997. The role of bright plumage in male-male interactions in the ring-necked pheasant. *Animal Behaviour* 54, 1205-1214.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Maynard Smith, J., Price, G.R. 1973. The logic of animal conflict. *Nature* 246, 15-18.
- McCormack, J.E., Jablonski, P.G., Brown, J.L. 2007. Producer-scrounger roles and joining based on dominance in a free-living group of Mexican jays (*Aphelocoma ultramarina*). *Behaviour* 144, 967-982.
- Mech, L.D. 1970. *The wolf: the ecology and behavior of an endangered species*. Doubleday Publishing Co., New York.
- Mech, L.D. 1975. Hunting behavior in two similar species of social canids. In: Fox, M.W. (Ed.), *The wild canids*. Van Nostrand Reinhold Co., New York, pp. 363-368.
- Mech, L.D. 1999. Alpha status, dominance, and division of labor in wolf packs. *Canadian Journal of Zoology* 77, 1196-1203.
- Mooring, M.S., Hart, B.L. 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123, 173-193.

- Newton-Fisher, N.E. 2002. Relationships of male chimpanzees in the Budongo Forest, Uganda. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioral diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, UK, pp. 124-137.
- Ohtsuka, Y., Toquenaga, Y. 2009. The patch distributed producer-scrouter game. *Journal of Theoretical Biology* 260, 261-266.
- Owen-Smith, N., Novellie, P. 1982. What should a clever ungulate eat? *American Naturalist* 119, 151-178.
- Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service Science Monographs Series 11, Washington, D.C.
- Pulliam, H.R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38, 419-422.
- Pulliam, H.R., Millikan, G.C. 1982. Social organisation in the nonreproductive season. In: Framer, D.S., King, J.R., Parkes, K.C. (Eds.), *Avian Biology*, Vol. 6. New York Academic Press
- Pusey, A., Williams, J., Goodall, J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277, 828-831.
- Ranta, E., Peuhkuri, N., Laurila, A., Rita, H., Metcalfe, N. 1996. Producers, scroungers and foraging group structure. *Animal Behaviour* 51, 171-175.
- Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* 51, 1077-1086.
- Robinson, S.K. 1985. Coloniality in the yellow-rumped cacique as a defense against nest predators. *The Auk* 102, 506-519.
- Schenkel, R. 1967. Submission: its features and function of the wolf and dog. *American Zoologist*. 7, 319-329.
- Shrader, A.M., Kerley, G.I.H., Kotler, B.P., Brown, J.S. 2007. Social information, social feeding, and competition in group-living goats (*Capra hircus*). *Behavioral Ecology* 18, 103-107.
- Smith, R.D., Ruxton, G.D., Cresswell, W. 2001. Dominance and feeding interference in small groups of blackbirds. *Behavioral Ecology* 12, 475-481.

- Smith, S.M., Cain, J.W. 2008. Foraging efficiency and vigilance behaviour of impala: the influence of density and neighbour density. *African Journal of Ecology* 47, 109-118.
- Valone, T.J. 1989. Group foraging, public information, and patch estimation. *Oikos* 56, 357-363.
- Valone, T.J. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. *Animal Behaviour* 41, 569-577.
- Valone, T.J., Templeton, J.J. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society of London: Biological Sciences* 357, 1549-1557.
- Vickery, W., Giraldeau, L.-A., Templeton, J.J., Kramer, D.L., Chapman, C.A. 1991. Producers, scroungers, and group foraging. *The American Naturalist* 137, 847-863.
- Vogel, E.R. 2005. Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. *Behavioral Ecology and Sociobiology* 58, 333-344.
- Watts, D.P. 1994. Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). *Behavioral Ecology and Sociobiology*. 34, 347-358.
- Wilmshurst, J.F., Fryxell, J.M., Bergman, C.M. 2000. The allometry of patch selection in ruminants. *Proceedings of the Royal Society of London: Biological Sciences* 265, 345-349.
- Wilmshurst, J.F., Fryxell, J.M., Hudson, R.J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* 6, 209-217.

CHAPTER 2

Scrounging herbivores use both patch quality and dominance status of patch holders when deciding which patch to join.

Abstract

Two key factors that influence foraging behaviour of group living herbivores are dominance and patch quality. As a result, group living herbivores need to gauge the dominance status of a patch holder as well as patch quality before joining a patch to feed. However, in producer-scrounger games the role of dominance and patch quality on scrounger joining decisions has not been explored. By using artificial feeding patches I was able to test the influence of dominance status and patch quality on scrounger's patch choice as well as intake rate. In the first experiment where the dominance status of patch holders was split into close, intermediate and far categories, dominance played no role in determining which patch scroungers decided to join. Scroungers joined patches held by subordinate and dominant patch holders across all the dominance categories. However, scroungers that fed from dominant patch holders had a higher intake rate when compared to scroungers that fed from subordinate patch holders. The highest intake rate was observed when scroungers fed from patch holders from the close dominance category, followed by the far category and lastly the intermediate dominance category. This suggests, that scroungers perceived these patch holders as competitors and increased their intake rate to account for it, rather than as dominant individuals and avoid them. To determine whether dominance played any role, scroungers were tested against the top five ranked patch-holders. Against the top ranked individuals, dominance did play a role in patch choice and scroungers avoided the top ranked individuals and only joined subordinate patch holders across all patch qualities. However, as patch quality increased the number of top ranked goats that were avoided declined. Behavioural titrations found that the initial density of food at a patch needs to be 2.3 times greater for a scrounger to feed from the next dominant patch holder. However, there was no difference in intake rate between whether scroungers fed from subordinate or dominant patch holders across all patch qualities. This suggests that only the top ranked individuals being aggressive

enough to prevent patch joining. Although there was a decline in the number of top ranked patch-holders that were avoided, patch quality never broke down the dominance hierarchy, except when patch quality was extremely high and unrealistic.

Key words: scrounger, group living, intake rate, patch choice.

2.1. Introduction

Living in groups has two major benefits, safety from predators and increased foraging efficiency (Clark and Mangel, 1986; Elgar, 1989). Reduction in predation risk comes from increased group vigilance levels (Pulliam, 1973), dilution effect (Mooring and Hart, 1992) and reduced domains of danger (i.e. Selfish herd: (Hamilton, 1971)). Increased foraging efficiency can be obtained through social information (Valone, 1993; Giraldeau and Caraco, 2000). Social information is where through watching other group members individuals are able to obtain broader information about the environment (Danchin et al., 2004; Dall et al., 2005). Individuals use this information to increase their ability to find and assess the quality of food (Valone and Templeton, 2002; Shrader et al., 2007). Individuals can locate food patches (i.e. local enhancement), join patches found by others, and kleptoparasitize patch holders (Barnard, 1984; Vickery et al., 1991; McCormack et al., 2007; Shrader et al., 2007). This leads to increased interactions and competition between foragers at feeding sites.

In order to predict the effect of group living on feeding behaviour it is important to determine when such exploitative relationships occur and the subsequent effect on individual's foraging rates (Vickery et al., 1991). As individuals congregate and compete with each other for resources, the payoffs obtained can be explained using game theory in the form of producer-scrounger games (Barnard and Sibley, 1981; Giraldeau and Beauchamp, 1999).

In producer-scrounger games an individual can either search for food patches themselves (produce) or join other individuals at their patches (scrounge) (Beauchamp, 2008; Ohtsuka and Toquenaga, 2009; Kurvers et al., 2010). Although producer-scrounger models assume that an individual is unable to produce and scrounge simultaneously (Coolen et al., 2007), it does not mean that an individual can only be a producer or a

scrounger. Foragers can switch between foraging tactics at any given time, depending on circumstances (King et al., 2009; Ohtsuka and Toquenaga, 2009), the environment and the behaviour of others (Katsnelson et al., 2008). Therefore any individual within a herd has the ability to be a producer as well as a scrounger.

The position of an individual within a dominance hierarchy has a large effect on its foraging behaviour as well as its intake rate (Rands et al., 2006). Reduced intake rates by subordinates, while in the presence of dominants have been recorded in wood pigeons, *Columba palumbus* (Murton et al., 1971), oystercatchers, *Haematopus ostralegus* (Ens and Goss-Custard, 1984), and barnacle geese, *Branta leucopsis* (Black et al., 1992). Barta and Giraldeau's (1998) phenotype-limited producing-scrounging model found that dominant individuals tend to scrounge whereas subordinates generally produce. An experiment with Harris' sparrows, *Zonotrichia querula*, showed that dominant birds displaced subordinate birds from patches that they had found (Rohwer and Ewald, 1981). This was also found in chacma baboons, *Papio ursinus* (King et al., 2009), house sparrows, *Passer domesticus* (Liker and Barta, 2002; Lendvai et al., 2006), and Mexican jays, *Aphelocoma ultramarina* (McCormack et al., 2007).

When it comes to patch joining decisions in producer-scrounger games various studies have shown that scroungers only join patches held by subordinate individuals (Liker and Barta, 2002; McCormack et al., 2007). However, some studies have indicated that dominance can have little effect on tactic use, even when individuals formed dominance hierarchies and competed for food (Giraldeau et al., 1990; Beauchamp, 2006). This suggests that the role of dominance in determining foraging decisions may be influenced by external factors. In producer-scrounger games the role of dominance has not been studied in terms of how it influences a scrounger's foraging decision. When an individual has chosen the scrounging tactic, how does it use dominance to determine where to feed and how does its choice influence its payoff? For example, does a scrounger feed from a dominant or a subordinate individual's patch and how does its choice influence its intake rate?

Another important factor that influences foraging choice is patch quality. Individuals forage in a way that maximises their intake rate (Wilmshurst et al., 1995; Illius et al., 1999) and if availability of food is high, foragers should prefer to feed from

high quality patches rather than low quality patches (Distel et al., 1995). Surprisingly, despite the important role of patch quality, the effect of patch quality has not been explored with regard to scrounger patch-joining decisions.

When individuals make patch-joining decisions, it is likely that they are faced with different combinations of patch quality as well as dominance status of patch holders. For example, when individuals feed on highly aggregated and rich food patches, it is expected that dominance will play a large role in determining foraging decisions (Barta and Giraldeau, 1998). However, the degree to which patch quality and dominance level of a patch holder interact to govern the joining preference of scroungers has not been explored (McCormack et al., 2007). As a result, I have focused this study on how dominance and patch quality interact to determine the joining preference of scroungers. If dominance is the driving force, I expect scroungers to prefer to join subordinate patch holders, irrespective of patch quality. However, in contrast, if patch quality is the main factor, scroungers should feed from any patch, irrespective of the dominant status of the patch holder.

2.2. Methods:

Experiments ran from April 2010 to May 2011 at the Ukulinga Research Farm of the University of KwaZulu-Natal in Pietermaritzburg, South Africa. The University of KwaZulu-Natal's Animal Ethics Committee cleared all animal husbandry and experimental procedures (permit number 068/10/Animal).

I used 22 goats, *Capra hircus*, (7♂; 15♀) in the experiments from an initial herd of 45 goats. Only one male was not castrated and all female goats were reproductively active during some or all of the experiments. Goats ranged from ten months to three years of age. Goats provided a good species with which to test my predictions as they have a clear dominance structure (Barroso et al., 2000; Côté, 2000). Furthermore, they have been shown to use social information (Shrader et al., 2007) and dominant goats scrounge from lower ranking individuals by displacing them from food patches (Barroso et al., 2000; Van et al., 2007).

For eight months prior to the experiments the goats were habituated to the testing arena and the artificial feeding patches. In the mornings, before the experiments began, the goats were released into paddocks to feed for an hour. This provided the goats with food to ensure that they were not starved during the experiments, which could alter their foraging behaviour. The goats were not provided with food during the night but had *ad libitum* access to water; this mimics common husbandry practices (Shrader et al., 2008). When the experiments were completed, the goats were released into natural pastures to graze. In the afternoons (~15h00), the goats were returned to the experimental arena and allowed to feed from the artificial feeding patches. This ongoing exposure to the patches ensured that the goats were accustomed to feeding from them. I used commercial sheep pellets (Complete sheep finisher, Meadow Feeds, South Africa) for all the experiments.

I used two types of artificial patches in the different experiments. The first type was similar to the ones used by Shrader et al. (2008). They were rectangular with the dimensions of 570 x 365 x 230 mm. The second was a 67 mm diameter round shallow bucket. All feeding trays had a 3 x 3 grid of 2 mm wire on top. In addition, the square patches and the smaller round patches contained five litres and two and a half litres respectively of an inedible medium of a combination of equal amounts of dried corncobs and 20 cm length plastic tubing. This provided diminishing returns in these patches and prevented all the food from being consumed. For my experiments, I used four different patches: black and white square patches, and black and white round patches. The black square patch represented the second highest quality patch (400 g of food), followed by the white square patch (200 g of food), and then the black round patch (100 g of food) and finally the white round patch (40 g of food). The highest quality patch (1000 g of food), was used to see what the effects would be when the goats are presented with a patch of extremely high quality. I did not use an artificial patch for this, but rather poured the food into a pile on a large sheet of plastic with no inedible medium.

Experiments were conducted in a 7 x 4.5 m pen that had the outer walls covered with black plastic (Figure 1). I did this to ensure that the goats focused their attention on the feeding trays and patch holders. The end of the pen was divided in half by a non-transparent fence (3 x 2 m) that ran from the back wall (de Nood, 2007). I placed one feeding tray and a goat acting as the patch holder on either side of the divider (de Nood,

2007). The feeding trays were placed 0.3 m inside each half, which ensured that the test goat had to choose between the sides, and enter one side of the pen in order to feed. Before each goat was released to join a patch, it was able to see both feeding trays as well as the associated patch-holder and was therefore able to decide which patch to join before it was released. Patch choice was recorded as the first side entered by the test goat. Patch holders were tethered to the back of the pen with rope attached to a dog collar around the neck. The combination of patch quality and the patch holder's dominance status varied according to each experiment (see below). Experiments ran from 7 to 11 am everyday (April 2010 – May 2011) and each goat was only tested once a day. Each goat, however, was tested in every experiment (N=22 goats).

2.2.1. Dominance relationships

In order to determine the dominance hierarchy of the herd, I tested the interactions of two goats at a time. For each of the dyads, I provided a single feeding tray with 200 g of food poured into the corner. The goats were allowed to feed from the tray and dominance was determined by visual cues (Barroso et al., 2000; Côté, 2000). Aggressive behaviour included horn threats (head butting or other use of the horns) and rush threats (sudden charge at an antagonist). Submissive behaviour included avoiding the dominant individual after an interaction or complete avoidance with no feeding. For each dyad, the dominant individual as well as the subordinate was identified and a win-loss matrix was constructed to determine dominance (Fournier and Festa-Bianchet, 1995). All individuals in the herd were tested against each other. The factors that determine dominance (i.e. age and size) were not considered, only the dominance rank of individuals was important and where they fell in the dominance hierarchy of the herd.

A concern with using win-loss matrices is that they can result in several inconsistencies when calculating dominance rank (Côté, 2000). Ranks that are calculated using win-loss matrices are likely to be biased as goats interact more often with other goats of a similar rank. This may result in an increased chance of defeat when compared to random interactions. Fournier and Festa-Bianchet (1995) found that low-ranking individuals avoided interactions with higher ranked individuals. If certain goats interact more often than other goats, this could lead to biased or inaccurate results which would

affect the dominance hierarchy. However, for my experiment I ensured that every individual was tested against every other individual. Therefore, it is unlikely that the inconsistencies of the win-loss matrix, referred to by Côté, play a role.

Dominance was calculated for each individual, using the Clutton-Brock et al. (1979) index (CBI). CBI was chosen as the dominance index for my data as data was qualitative and was recorded in a win-loss matrix and no information regarding the rate of interaction was obtained (Bang et al., 2010). Bang et al. (2010) suggest that dominance should be calculated with an index that gives the highest number of unique ranks. I compared the number of unique ranks that each index tested in Bang et al. (2010) achieved and found CBI to yield the highest number of unique ranks. CBI for each member of the herd was calculated using the formula:

$$CBI = (B+b+1)/(L+l+1)$$

Where B = the number of individuals whom the subject dominates, b = the number of individuals whom those dominated by the subject in turn dominate, L = the number of individuals who dominate the subject, and l = the number of individuals who dominate those dominating the subject (Clutton-Brock et al., 1979).

Individuals were ranked according to their CBI values, a high CBI value indicating a superior rank. This then gave an estimate of an individual's overall dominance and position within the herd. These results were then compared to a method used by Fournier and Festa-Bianchet (1995) to test the reliability of my rank calculations. They ranked individuals according to the following ratio of wins versus losses: Rank = wins +1/losses +1, where the highest ratio indicated a higher rank. The dominance ranking using the Fournier and Festa-Bianchet (1995) equations yielded very similar results. As a result, I decided to use the CBI measure of dominance as it gave fewer tied ranks between dyads and it is also a more complex index that takes into account the success of opponents.

Although all the goats had unique ranks within the herd, Barroso et. al. (2000) found that in stable hierarchies there was a possibility of slight changes of positions within the herd for individuals that had a similar dominance ranking. For example,

continuous interaction between two consecutively ranked individuals (e.g. rank 6 and 7) could yield results where the sixth ranked goat would dominate and other times the seventh ranked goat could dominate. This was supported by Reinhardt and Flood (1983) who found that in bison, *Bison bison*, dominance-subordinate relationships showed infrequent reversals. In order to account for this, goats with successive dominance ranks were never tested against each other in the patch joining experiments.

In order to determine the influence of dominance on patch joining by scrounging herbivores, different dominance classes were created (i.e. close, intermediate and far). This allowed me to determine whether a scrounger's patch choice would be different if a patch holder was close or far in rank. For example you would expect individuals to avoid more dominant individuals as the dominance gap between individuals increased. However, similarly ranked individuals interact frequently (Fournier and Festa-Bianchet, 1995) therefore more aggression could be shown between individuals from the close dominance category. A goat was considered close in dominance rank if it was between 3-5 goats in rank above the scrounger, intermediate 6-8 and far 9-12 goats above in rank. The size of these dominance classes was determined by the sample size of goats and will likely vary with smaller or larger herd sizes. These dominance classes were determined in relation to the dominance rank for each scrounger (N=22) that was used.

2.2.2. Patch choice between different quality patches

Prior to experimentation, I had to ensure that all the goats were able to differentiate between the artificial food patches based on visual assessment of patch quality. To test for this, I offered the goats a choice between a good food patch (black square) and a poor quality patch (white square). As I had four different patch qualities the different combination of patch qualities were tested against each other (Table 1). The combinations of the quality of the patches were altered so that every individual was subjected to every food patch combination (e.g. black square vs. white square, white square vs. black circle, etc.). The two patches were put either side of the divider at the end of the testing pen (Figure 1). The test goat was released from the front of the pen, from where it could see both patches. This allowed the goats to see the amount of food that was in each patch before joining. Once released, I recorded the patch that the goat

went to and fed from. In each situation, the goat went straight to a patch and started feeding. Goats were not tested against the 1000 g food patch, as I felt they would easily be able to see the large pile of food on the flat piece of plastic. In order to account for an area effect, I rotated the positions of the different patches between successive trials. For example, if the black square was on the right hand side of the pen it would then be moved to the left hand side for the next test. All goats within the initial herd (N=45) were tested twice at each combination of patches. Only goats that successfully identified the differences in all of the trials with the different patch qualities were used as scrounging individuals (N=22).

2.2.3. Patch quality and dominance status of patch holder

In order to understand the influence of patch quality and dominance status of a patch holder, I tethered a dominant and a subordinate goat behind separate artificial food patches which were separated by the pen divider (Figure 1). Dominant individuals were selected from the three dominance categories, which were calculated using the scrounger's rank. For the subordinate goat, I used any individual that had a lower rank than the scrounger. Patch holders were not able to feed from the patch. This followed the same experimental design as the patch choice experiment, but the two patches were of the same quality. As with the previous experiments, the test goat (i.e. scrounger) was released from the end of the pen and the patch quality and the dominance status of the patch holder it chose to feed from was recorded. Scroungers were allowed to feed for two minutes, which allowed their intake rates (g/min) to be determined. The patch holders were replaced for each scrounger. To ensure scroungers did not prefer to feed from a specific side of the pen (area effect), the position of the dominant and subordinate goats were switched between successive trials. This was repeated for each combination of the three dominance classes and different patch qualities.

2.2.4. Patch quality and dominance status of the top five ranked patch holders

As a large number of the individuals did not join patches based on the dominance hierarchy as expected, I tested to see if individuals high up in the hierarchy had a greater impact with regard to patch joining decisions of scroungers. To do this, I focused on only

the top five dominant goats. I followed the same experimental design as the previous experiment. However, instead of separating the dominance hierarchy into close, intermediate and far, all scroungers were tested against the top five goats of the dominance hierarchy. For example, the dominant patch holder fell within the top five ranked goats and the subordinate patch holder was, once again, any goat that had a lower rank than the scrounger. As with the previous experiment, a scrounger was released from the end of the pen and the patch quality and the dominance status of the patch holder it fed from was recorded. As with the other experiments scroungers were allowed to feed for two minutes in order to determine their intake rate. Each goat was tested against the top five goats individually across all five patch qualities. To avoid an area effect, the positions of the dominant and subordinate goats were alternated between successive trials.

2.2.5. Data Analysis

Linearity of the dominance hierarchy was tested using Kendall's coefficient, K (Kendall, 1962), which calculates the number of circular triads within a herd. This method was designed to take into account unknown relationships where individuals in a dyad did not interact. In the win-loss matrix dominant individuals in a dyad were assigned a value of 1 and subordinate individuals a zero. Where individuals in a dyad did not interact, a value of $\frac{1}{2}$ was given to each individual. Kendall's coefficient values range from 1, complete linearity, to 0, absence of linearity (Appleby, 1983). A dominance hierarchy is considered linear with a K value of greater or equal to 0.9 (de Vries, 1995; Fournier and Festa-Bianchet, 1995). When using win-loss matrices, the rearranging of individuals into a specific order may create a linear hierarchy, when in fact no linear relationship exists. To account for this a Chi-squared test, as described in Appelby (1983), was done to determine whether the constructed hierarchy occurred by chance.

To determine whether the goats could tell the difference between the patch qualities based on visual recognition, I ran a Chi-square test. A separate test was run for each combination of patch qualities. For example a Chi-square test was run for black square vs. white square and another for white square vs. black circle until all combinations were tested.

I used log linear analysis to determine whether scrounger's patch joining decisions varied across (i) patch quality (40 g, 100 g, 200 g, 400 g, 1000 g), (ii) dominance categories (close, intermediate and far), and (iii) dominance status of the patch holder (dominant or subordinate). The fully saturated model best fit of the data. This model takes into account all the variables being analysed and all possible interactions between the variables. The fully saturated model was compared against reduced models using the likelihood ratio tests. The statistics presented show the reduction in goodness of fit following the removal of certain variables from the model, based on chi-squared statistics and significance levels.

I also ran Chi-squared tests to determine whether there was a significant difference between the number of scroungers that fed from a dominant or subordinate individual. For example, a Chi-square test was run for each of the top five goats for each patch quality. This determined whether the scrounger's patch choice was random, or whether they cued off dominance. Furthermore, I ran an ANOVA to determine whether the reproductive status (pregnant versus not pregnant) influenced the intake rate of females.

To determine whether intake rates of the scroungers varied across the different patch qualities (40, 100, 200, 400 and 1000 g), dominance gap (close, intermediate and far), and rank (dominant or subordinate), I used a three-way ANOVA. This was repeated for the data from the second experiment using the top five ranked goats. In the ANOVA I used the goats' individual id as a blocking variable. I did this as it was important to account for the variability of the same goat across different treatments. All statistical tests were run with PASW Statistic 18 (SPSS) and all results are considered significant at $p = 0.05$. Prior to analysis, I log transformed the intake rate data to meet the assumption of normality.

2.3. Results

There was no significant difference ($F_{1,398} = 0.45$, $p = 0.833$) between the intake rates of females that were reproductively active compared to non-reproductively active females. This allowed for female intake rate data to be grouped for analysis.

2.3.1. Patch quality

From the total herd, a subset of the goats (N=22) were chosen which could successfully identify the difference in patch quality across all patch combinations from the initial herd (Table 1). A scrounger was considered to make successful choices if it repeatedly joined the better quality patch

2.3.2. Linear hierarchy

The interactions from the win-losses matrix confirmed the existence of a linear dominance hierarchy that was not created by chance ($K = 0.96$, $\chi^2 = 712.5$, $df = 50$, $P = 0.05$) (Table 2). The high value of K , when compared to other studies of Fournier & Festa-Bianchet (1995) and Barroso et al. (2000) is due to there being very few non-interacting dyads when compared to the size of the herd. The transitivity of dominance is one directional, so that a lower ranking individual never dominates a higher ranking individual. This shows that each individual is aware of its position as well as the position of others within the hierarchy. Individuals within the herd have been interacting repeatedly for thirteen months, which has allowed them plenty of opportunities to assess the dominance characteristics of other group members.

2.3.3. Scrounger's intake rate against close, intermediate and far dominance category patch holders

There was a significant increase in the intake rate of all goats as patch quality increased (Table 3). The dominance rank of the patch holders also had a significant effect on scrounger's intake rate (Table 3). However, counter to predictions, intake rate did not increase as dominance rank increased. Surprisingly, a Tukey post hoc test showed that the mean intake rates across the different patch qualities showed that scroungers had higher intake rates when they fed from patch holders that were close in rank (1.25 ± 0.53 g/min) and those far away (1.24 ± 0.54 g/min), compared to those at an intermediate distance (1.21 ± 0.58 g/min). There was no significant difference in intake rates between the close and far categories ($p = 0.916$), however there was a difference in intake rates between the close ($p = 0.010$) and far ($p = 0.029$) categories when compared to the intermediate dominance category. Scroungers' intake rates differed (Table 3) between

whether they fed from a patch holder that was close, intermediate or far in dominance rank at each patch quality (Figure 2). Not surprisingly, the intake rate pattern followed that of a type two functional response (Figure 2). There was a steep increase in intake rate at low patch qualities (i.e. food availability), which reached an asymptote as patch quality (i.e. food availability) increased.

The intake rates of scroungers feeding from a dominant patch holder (1.34 ± 0.62 g/min) were significantly greater than those from a subordinate (1.19 ± 0.56 g/min) (Table 3). However, the interaction of the three variables: patch quality, status (whether the scrounger fed from a subordinate or dominant) as well as distance (close, intermediate or far) did not influence intake rate (Table 3).

2.3.4. Scrounger's patch choice against close, intermediate and far dominance category patch holders

Contrary to expectation, I found that across all the different patch qualities, goats chose to feed equally between patches held by dominant and subordinate patch holders, irrespective of the dominance gap (Table 4). This was surprising as the goats had a well established linear hierarchy and thus were expected to avoid dominant patch holders.

2.3.5. Scrounger's patch choice against the top ranked patch holders

For the test of scroungers against the top five dominant individuals in the herd, results indicate that scroungers tend to only avoid the top four ranked patch holders. However, the number of top-ranked individuals that were avoided was determined by patch quality (Table 3). At the lowest patch quality, the top four individuals in the hierarchy were avoided (Figure 3). As patch quality increased, the number of top individuals that were avoided by scroungers decreased. At the highest patch quality (i.e. 1000 g), scroungers did not pay attention to dominance rank, but rather joined patches held by the top individuals in the hierarchy and subordinates equally (Figure 3).

2.3.6. Scrounger's intake rate against the top ranked patch holders

There was a significant effect of patch quality (i.e. food availability) on intake rate (Table 3) with intake rate increasing with an increase in patch quality, following a type two

functional response curve. However, there was no difference in intake rate if a scrounger fed from a dominant (top ranked patch holder) or subordinate patch holder, across all patch qualities (Table 3).

I compared the intake rates of when scroungers fed from patch holders from the far dominance category (from experiment one) and when feeding with the top ranked patch holders (from experiment two). Scroungers intake rate when feeding with patch holders from the far dominance category had a higher intake rate (1.24 ± 0.54 g/min) when compared to scroungers that fed from the five most dominant patch holders (0.82 ± 0.22 g/min).

2.4. Discussion

When herbivores scrounge both patch quality as well as the dominance status of patch holders determine patch joining decisions (McCormack et al., 2007). However, until now, the combined effect of these two factors on patch joining decisions has not been explored. Previous experiments on the influence of dominance on patch choice found that scroungers preferred to join subordinate individuals (Liker and Barta, 2002; Lendvai et al., 2006; King et al., 2009). My results contradict this, as scroungers joined both subordinate and dominant patch holders. This suggests that dominance may not be the most important factor driving joining decisions. However, these tests did not include the top ranked individuals. I expanded on these experiments to show that only the top ranked individuals in a hierarchy are able to influence scroungers patch choice. Only when scroungers faced the top ranked individuals, did they prefer to join subordinate patch holders. However, patch quality is also important in patch choice, as the number of top ranked goats that were avoided varied according to patch quality. I found that as patch quality increased, fewer dominant patch holders were avoided. This suggests that despite the risk of aggressive interactions, as patch quality increases, the benefits outweigh the costs and individuals scrounge from dominant patch holders. Ultimately, as patch quality increases it becomes more important than dominance with regard to determining scrounger patch joining decisions.

2.4.1. Scrounger's intake rate against close, intermediate and far dominance categories

In socially foraging herbivores, it is generally accepted that the position of an individual within a dominance hierarchy has a large influence on its foraging behaviour as well as its intake rate (Rands et al., 2006). In my experiment, the scrounger's intake rate was influenced by the difference in dominance rank between the patch holder and the scrounging individual. Scroungers had the highest intake rates when feeding from individuals close in rank, followed by those that were far in rank, and had the lowest when feeding from patch holders an intermediate number of ranks away. A likely reason for the intake rate being highest when a scrounger fed from a close ranking patch holder is because individuals tend to interact more often with individuals similar in rank (Clutton-Brock et al., 1979; Clutton-Brock et al., 1982). The increased interactions could be a means to try and out-compete the closely ranked individual and move up the dominance hierarchy. This increased level of interaction leads to an increased intake rate as the scrounger will try and maximise its payoff before an interaction occurs. In contrast, a forager will try and avoid interacting with a high ranking individual as they are unlikely to defeat it, as dominant individuals are usually larger and aggressively defend resources (Thouless and Guinness, 1986).

So then why did scroungers that fed from the far dominance category have the second highest intake rate? It has been shown that subordinate foragers tend not to interact with a highly ranked individual, as dominant individuals generally push subordinates off food patches (Smith et al., 2001; Liker and Barta, 2002; McCormack et al., 2007). So when a scrounger joins a dominant patch holder it will likely increase its intake rate to obtain as much food as possible before the possibility of it being excluded from the patch. Shrader et al. (2007) found that in free-living goats, individuals increased their intake rate in the presence of competitors.

Another possible explanation for an increased intake rate when feeding from a dominant patch holder is that the dominant goat may not have been alert when the scrounger was released. Therefore, the scrounger may have capitalised on this and fed from the patch as fast as possible before it was excluded. However, scroungers were only released into the pen when both patch holders were alert and standing behind their patches. As a result, this is unlikely to have played a role.

There are, however, a number of studies that have shown that the intake rate of subordinate individuals decrease in the presence of a dominant individual (Ens and Goss-Custard, 1984; Saito, 1996; Rands et al., 2006). A potential reason for these contrasting results is that the absolute differences in rank between dominant and subordinate individuals may have varied between the experiments thereby influencing the role of dominance (Stillman et al., 1997; Barta and Giraldeau, 1998). My results support this. For example, the intake rate of scroungers was higher when they fed from dominant patch holders from the far dominance category when compared to the top five ranked goats in the hierarchy. This shows that the difference in rank between dominant patch holders and subordinate scroungers determines the influence of dominance on intake rate and that only the top ranked patch holders can cause a reduction in intake rate. This is likely due to the subordinate being vigilant towards the dominant individual.

The scroungers that fed from dominant patch holders were making a trade-off between risking the costs of an agonistic interaction with a dominant patch holder and increasing their intake rate. Scroungers that fed from subordinate patch holders experienced lower intake rates as they were unlikely to be excluded by the subordinate patch holder. Furthermore, their lower intake rate could also have been from spending time excluding the subordinate from the patch and ensuring it didn't return to feed.

The intake rates of scroungers were relatively low across all patch qualities. Factors that influence intake rate are search and handling time (Spalinger and Hobbs, 1992). For my experiments, search time was zero as the food was presented to the goats in trays. In contrast, the handling time of the food pellets was likely high, because the concentrated pellets possible require time to chew and swallow compared to grass. Another explanation could be that although the goats did not show concern about joining a dominant patch holder, they still could have remained vigilant against possible aggressive interactions from the dominant patch holder.

2.4.2. Scrounger's patch choice for close, intermediate and far dominance categories

Although dominance influences the intake rate of scroungers, it did not seem to influence patch selection. In the initial tests, where the dominance hierarchy was separated into close, intermediate and far dominance categories, scroungers did not show any preference

in feeding from a dominant or subordinate patch holder. This was unexpected as an individual, when presented with equal patch qualities, should tend to avoid feeding from a dominant individual's patch. This would then reduce the possibility of costly confrontations (Stillman et al., 1997; Côté, 2000). Stillman et al. (1997) developed an individual-based model that predicts the level of interference between individuals based on their behaviour. The model predicted that all dominant individuals would dominate all subordinate individuals regardless of the difference in rank. This was supported by a field based study on oystercatchers (Goss-Custard et al., 1995). However, in other species it is the absolute difference in dominance between two individuals that is important (Stillman et al., 1997; Barta and Giraldeau, 1998). For example in white-faced capuchin monkeys, *Cebus capucinus*, top ranked monkeys benefited from significantly higher energy intake rates than medium and low ranking monkeys (Vogel, 2005). However, there was no difference in energy intake rate between medium and low ranking individuals. In Mexican jays, *Aphelocoma ultramarine*, there is a significant correlation between the difference in dominance rank between two birds and patch-joining attempts in the same dyad (McCormack et al., 2007). The greater the difference in rank, the higher the frequency of joining by the dominant bird. This could explain why the scroungers in my study did not choose a patch according to the dominance status of the patch holder at each patch quality. The absolute difference in dominance rank between the scrounger, and patch holders from even the far dominance category, may not have been large enough for the scrounger to deem them too dominant to join. Although there was a dominance gap of 9-12 goats this may not have been large enough to create a large competitive difference between scroungers and patch holders. A key factor with regard to my experiment is that goats in the far dominance category did not necessarily include the top ranked goats in the herd. As a result, there is a threshold response to patch joining and a scrounger may only avoid a patch if the patch holder's dominance is above a certain rank or if the patch holder is a top ranked individual in the herd.

It was also expected that patch quality would influence whether a scrounger fed from a dominant- or subordinate-held patch. Ultimately, there is likely a threshold where patch quality overrides dominance. The resource defence theory states that the aggressiveness with which a patch is defended should decrease with an increase in patch

quality (Dubois and Giraldeau, 2005). This is because when patch quality is high there is enough food for more than one individual to feed without their being a reduction in the amount of food available to each individual. Thus, at high patch qualities the payoffs would be high enough for a scrounger to risk feeding from a dominant patch holder. As a result, as patch quality increases more individuals should shift and feed from patches held by dominant individuals. In contrast, at low patch qualities, patches are defended aggressively (Vickery et al., 1991). Thus, in this situation, the costs of feeding with a dominant individual would outweigh the benefits. In turn, scroungers should select patches held by subordinates. However, the results of my study show that scroungers did not pay attention to the dominant status of patch holders regardless of patch quality. There was no significant difference in patch selection across all the patch qualities and across all the dominance categories (Table 2). Scroungers joined dominant individuals from both the close and far dominance categories which suggest that these dominant individuals do not present enough of a threat to prevent subordinates joining. This lack of aggression can explain why patch selection did not change with changing patch quality. At all patch qualities, the benefits outweighed the costs of an interaction, which allowed scroungers to join patches held by subordinate as well as dominant patch holders.

2.4.3. Scrounger's patch choice against the top five ranked patch holders

When scroungers were tested against the top five dominant goats they chose which patch to join according to the dominant status of the patch holder. As predicted in producer-scrounger models (Liker and Barta, 2002; Lendvai et al., 2006), scroungers preferred to join patches held by subordinate individuals. This is what I expected and suggests that dominance is important in determining patch choice when faced with the top ranked individuals. Thus, it seems in my study that only the top ranked individuals are dominant enough to prevent scroungers from joining their patches.

However, the number of dominant patch holders avoided varied with patch quality (Figure 3). At the lowest patch quality (40 g), only the top four dominant goats were considered too dominant to join at a patch. However, as patch quality increased fewer of these most dominant goats were avoided. At low food availability, the relative proportion of food available solely to the patch finder (i.e. finder's share) is high

(Giraldeau and Dubois, 2008). This leaves a small proportion of the available food left for the scrounger when it joins a patch. In addition, according to the resource defence theory, high levels of aggression are expected at low patch quality (Dubois and Giraldeau, 2005). This suggests that with only a small proportion of the food being available to the scrounger and high levels of aggression being shown, the costs of joining a dominant patch holder greatly outweigh the potential benefits of joining (Vickery et al., 1991).

Aggression shown by patch holders is related to their dominance rank, with normally the biggest, strongest individuals aggressively defending patches (Barta and Giraldeau, 1998). My results suggest that only the top four goats were dominant and aggressive enough to prevent scroungers from joining them. However, the number of dominant individuals that are avoided at each patch quality will vary according to herd size as well as the aggressiveness of individuals within the herd.

As patch quality increased, the relative finder's share as well as the level of competition likely decreased. As a result, the number of top ranked goats that were avoided decreased. At the highest patch quality (1000 g), scroungers key off only patch quality and joined all patch holders, irrespective of dominance rank at a patch. At such a high patch quality the relative finder's share is likely small and the amount of food available to a scrounger far outweighs any cost of feeding with a dominant patch holder.

From my results (Figure 3), I can make a prediction when patch quality becomes more important than dominance. Although there is a gap in patch quality between 400 g and 1000 g, I can use the logarithmic trendline to predict when patch quality becomes more important than dominance. Once put through my data, the equation for the trendline is:

$$y = -1.1611\ln(x) + 8.3519 \quad (\text{Equation 1})$$

Where y is the lowest ranked goat that is avoided and x is patch quality. If y is substituted with 1 and the equation is solved for x , the value obtained will be the patch quality where patch quality becomes more important than dominance (i.e. where no individuals are avoided by scroungers). This gives a patch quality of 563 g, therefore this represents the threshold where patch quality becomes the driving point behind patch joining decisions.

Although 563 g is the amount of food at which patch quality overrides dominance, it is a measure of how rich that patch needs to be so that the harvest rate obtained at that patch is equal to the harvest rate of a patch held by a less dominant patch holder.

Behavioural titrations provide an opportunity to quantify what goes into dominance and how it influences patch use behaviour (Kotler and Blaustein, 1995). An experiment on two gerbil species, *Gerbillus allenbyi* and *G. pyramidum*, used behavioural titrations to ask the question, ‘How much richer does a patch in the open (risky) have to be compared to a patch in a bush (safe) for animals to harvest equal amounts of seeds from the two microhabitats?’ (Kotler and Blaustein, 1995). The results show the open patch had to have an initial seed density of between 4 to 8 times greater (depending on the gerbil species) than the bush patch for the two patches to be of equal value. The differences in seed density between the two microhabitats reflect the differences in foraging costs due to predatory risk from owls (Kotler et al., 1991). In general, foragers will join a patch when the marginal benefits exceed the costs. Therefore, as the costs of predation increases between the bush and open microhabitats, the benefit (seed density) also needs to increase.

Similarly, in my experiment, the same question can be asked but instead of measuring the costs of predation you can get an understanding of the cost of an interaction with a top ranked patch holder. In order to determine how much richer a patch needs to be for a scrounger to join the next ranked individual one can use equation 1. If you substitute y with the dominance ranking of the top ranked goats (i.e. 1 – 5) you can determine the respective patch qualities at which scroungers will then join the next ranked patch holder. For example, a patch quality of 563 g is needed for scroungers to feed from the top ranked patch holder, 237 g to feed from the second highest ranked patch holder and 100 g to feed from the third highest ranked goat and so on. From this I can determine that a patch needs to be 2.3 times richer for the benefits to outweigh the costs of a scrounger joining the next highest ranked patch holder. The difference in quality between the two patches is a measure of the costs of an aggressive interaction with a dominant individual.

This pattern of patch selection suggests that scroungers weigh up the costs of feeding with a dominant patch holder and the benefits (amount of food) gained at each

patch quality (Rands et al., 2006). At low patch quality, the costs of feeding from a top ranked individual are too high and thus these patch-holders are avoided. As a result, at low patch quality dominance outweighs patch quality in driving joining decisions. However, as patch quality increased the benefits (amount of food gained) from each patch start to outweigh the costs of aggressive interactions. Therefore, when scroungers make patch-joining decisions they weigh up the amount of food they can gain against the cost of aggressive interactions due to dominance. For example, an experiment on Japanese macaques, *Macaca fuscata fuscata*, showed that when food was abundant, patch choice by a subordinate individual was unaffected by whether or not a dominant patch holder was present (Ihobe, 1989). In contrast, when food was limited, subordinates altered their perception of patches and avoided dominant patch holders. My results support this and suggest that there is a transition point, (i.e. 563 g of food per patch), where patch quality overrides dominance as the main factor that determines where scroungers feed.

This pattern of how patch quality determines the importance of the dominance hierarchy was also found in female chimpanzees, *Pan troglodytes*, in the Tai National Park, Côte d'Ivoire (Wittig and Boesch, 2003). Female chimpanzees had high levels of contest competition and formed clear dominance hierarchies as an adaptation to deal with the high levels of competition (Wittig and Boesch, 2003). By forming a hierarchy individuals avoided having to re-establish dominance at every new contact (Fournier and Festa-Bianchet, 1995), and allowed dominant females access to monopolizable food resources (Boesch and Boesch-Achermann, 2000). Foragers that are subjected to high levels of competition have despotic dominance relationships and usually form linear dominance hierarchies (Wittig and Boesch, 2003). In my experiment, at low patch quality, competition was likely high, so scroungers joined patches according to the dominance hierarchy, although it was only applicable to the top ranked goats in the herd. On the contrary, when foragers experience no competition, the hierarchy will not be as important in determining patch choice (Wittig and Boesch, 2003). As patch quality increased in my experiment, competition became less, which led to a decrease in the importance of dominance in determining patch choice and scroungers joined a patch regardless of the dominance status of the patch holder.

Another factor that influences foraging behaviour is the state (i.e. hunger) of the forager (Caraco et al., 1980; Godin and Crossman, 1994). The state of the scrounger could determine the number of dominant goats that are avoided at each patch quality. For example, the hungrier a scrounger is the greater the risks it would be willing to take as it balances the risk of starvation against the risk of predation (Sweitzer, 1996), or in the case of my experiment, the cost of an interaction with a dominant individual. My results show that at ~560 g the dominance hierarchy breaks down and all dominant goats are avoided. If, however, the scrounger is in a poor state the shifting point (patch quality) at which the dominance hierarchy breaks down would be less as the scrounger is taking more risks to meet its energetic demands. Ultimately, this means that the number of dominant goats that are avoided at each patch quality will be different when compared to scroungers that are in a good state versus a poor state. Altering the state of an individual also determines the amount of aggression that an individual shows when defending its patch (Janson and Vogel, 2006). As aggressive interactions are both costly in time and energy, the costs of joining patches outweigh the benefits and few scroungers would join dominant individuals at each patch quality. Once again you would get a shift in the patch quality where the dominance hierarchy breaks down, this time it would be greater than ~ 560 g. Unfortunately, testing these predictions was beyond the scope of the study. However, it does open up possibilities for future studies.

2.4.4. Scrounger's intake rate against the top five ranked patch holders

One of the main impacts of dominance in foraging is a reduced intake rate by subordinates (Barta and Giraldeau, 1998; Vogel, 2005; Rands et al., 2006). When scroungers were tested against only the top five most dominant goats in the herd, their intake rate was lower when compared to the close, intermediate and far dominance categories. This suggests that only the top five most dominant goats are viewed as dominant as they were able to cause a reduction in scroungers' intake rate. However, the scroungers' intake rate when they fed from a dominant (top five) did not differ to when they fed from a subordinate patch holder. However, the intake rate was higher when scroungers fed from dominant (close, intermediate and far) patch holders as scroungers increased their intake rate likely to account for competition. An explanation for the

decreased intake rate, when feeding from the top five most dominant patch holders, is that scroungers decreased their intake rate as they increased their vigilance against possible attack by dominants (Smith et al., 2001). An experiment on tufted titmice, *Pardus bicolour*, showed that subordinate intake rates decreased when in the presence of dominants (Waite, 1987). This was because individual's scanning, which would normally be associated with anti-predatory behaviour, was greatly increased in the presence of dominants. This increase in vigilance was likely to avoid aggressive interactions with the dominant patch holder.

One of the key assumptions of producer-scrounger models that include dominance is that dominant individuals will only scrounge from subordinate producers (Liker and Barta, 2002; McCormack et al., 2007). Ultimately, this limits the number of potential scrounging opportunities, especially if the scrounger has a low rank within the herd. For example if a scrounger has a dominance rank of 11 in the herd of 22 goats, according to producer-scrounger games, it would only scrounge from 11 goats, 50 % of the herd. The results from this study, however, indicate that scroungers no matter their rank can scrounge from both subordinate and dominant patch holders, as long as the patch holders are not the top ranked goats in the herd. So within the same herd, the scrounger with a rank of 11 will now be able to scrounge from 16 goats, 72% of the herd. This greatly increases the number of patch holders that scroungers can join, thereby increasing the opportunities for individuals to scrounge. As a result, it may affect the proportion of individuals within the herd acting as scroungers and producers (i.e. frequency dependence).

Dominance is a key factor in determining patch selection by scrounging herbivores and a good predictor of the outcome of competitive interactions. However, Wittig and Boesch (2003) found that chimpanzee social structure was more complicated and flexible than previously thought. The major determinant that influenced social structure was competition. This holds true for the goats in this experiment. As changes in the ecological conditions (i.e. patch quality) likely created more or less competition and as a result the relative importance of the dominance hierarchy changed. For example, producer-scrounger models predict that scroungers will not join dominant individuals. However, my results show that subordinates do in fact join dominant patch holders, as

long as the dominant individuals are not the top ranked individuals. Scroungers are making a trade-off between increasing their intake rate and risking feeding from a dominant patch holder. Scroungers joined patch holders from the close, intermediate and far dominance categories because they were able to achieve a higher intake rate when compared to feeding with a subordinate. This benefit outweighs the costs of an interaction due to these individuals not being aggressive enough to prevent joining attempts. However, scroungers did not feed from the top ranked patch holders because the costs of an interaction from these aggressive individuals was high and scroungers achieved the same intake rate whether they fed from a dominant- or subordinate-held patch. Although scroungers avoided the top ranked patch holders there was a threshold (i.e. 563 g of food per feeding station) where patch quality became the driving factor behind patch joining decisions and scroungers joined patches regardless of the rank of the patch holder.

However, 563 g of food at each feeding station (i.e. the area in which an animal can feed without taking a step (Ruyle and Dwyer, 1985)) under natural conditions is unrealistic. In order to achieve high biomass within the feeding station, the grass needs to be tall, but as grass matures and increases in height its nutritional quality as well as its digestibility decreases (Van Soest, 1994). The forage maturation hypothesis (McNaughton, 1984; Fryxell, 1991) suggests that ruminants should forage on swards of intermediate height and maturation stage rather than on taller more mature swards, in order to maximise dry matter intake and energy digestibility. An experiment on wapiti, *Cervus elaphus* (Wilmshurst et al., 1995), and red deer, *Cervus elaphus* (Langvatn and Hanley, 1993), showed that these herbivores selected swards of intermediate height and biomass, even when tall swards of high biomass were available. Wilmshurst et al. (1995) found that wapiti selected patches with a biomass of 1200 kg/ha (120 g/m²) when offered a mosaic of patches ranging from 800–2900 kg/ha (80-290 g/m²). An experiment with cattle showed that they selected for patches of short grass with a mean biomass of 379 g/m² and rejected tall patches that had a mean biomass of 738 g/m² (WallisDeVries et al., 1998). If you consider the feeding station of a goat to be 0.5 m² and use the above results then under natural conditions goats would select for patches that contained 30-95 g of grass per feeding station and would avoid patches that had 185 g of grass. In order to

achieve 185 g of grass per 0.5m² the biomass would be extremely high and of poor nutritional quality. This shows how unrealistic 563 g of food per feeding station that is required for the dominance hierarchy to break down. By using the equation from Figure 2 and 95 g as the maximum amount of food per feeding station that goats will select for, only the top three goats in the herd would be avoided under natural conditions.

This greatly increases scrounging opportunities and suggests that scroungers use both patch quality as well as the aggressiveness of each patch holder to make patch joining decisions to weigh up the costs and benefits of joining each patch. By doing this, scroungers forage in a way that maximises their payoffs and possibly minimizes the costs of social foraging.

References

- Appleby, M.C. 1983. The probability of linearity in hierarchies. *Animal Behaviour* 31, 600-608.
- Bang, A., Deshpande, S., Sumana, A., Gadagkar, R. 2010. Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices. *Animal Behaviour* 79, 631-636.
- Barnard, C.J. 1984. The evolution of food-scrounging strategies within and between species. In: Barnard, C.J. (Ed.), *Producers and scroungers: Strategies of exploitation and parasitism*. Chapman and Hall, New York, pp. 95-126.
- Barnard, C.J., Sibley, R.M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29, 543-550.
- Barroso, F.G., Alados, C.L., Boza, J. 2000. Social hierarchy in the domestic goat: effect on food habits and production. *Applied Animal Behaviour Science* 69, 35-53.
- Barta, Z., Giraldeau, L.-A. 1998. The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioural Ecology and Sociobiology* 42, 217-223.
- Beauchamp, G. 2006. Phenotypic correlates of scrounging behavior in zebra finches: role of foraging efficiency and dominance. *Ethology* 112, 873-878.

- Beauchamp, G. 2008. A spatial model for producing and scrounging. *Animal Behaviour* 76, 1935-1942.
- Black, J.M., Carbone, C., Wells, R.L., Owen, M. 1992. Foraging dynamics in goose flocks - the cost of living on the edge. *Animal Behaviour* 44, 41-50.
- Boesch, C., Boesch-Achermann, H. 2000. *The chimpanzees of the Tai Forest*. Oxford University Press, Oxford, UK.
- Caraco, T., Martindale, T.S., Whitman, T.S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* 28, 820-830.
- Clark, C.W., Mangel, M. 1986. The evolutionary advantages of group foraging. *Theoretical Population Biology* 3, 45-75.
- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M., Guinness, F.E. 1979. The logical stag: adaptive aspects of fighting in red deer. *Animal Behaviour* 27, 211-225.
- Clutton-Brock, T.H., Guinness, F.E., Albon, S.D. 1982. *Red deer: behavior and ecology of two sexes*. University of Chicago Press, Chicago.
- Coolen, I., Giraldeau, L.A., Vickery, W. 2007. Scrounging behaviour regulates population dynamics. *Oikos* 116, 533-539.
- Côté, S.D. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137, 1541-1566.
- Dall, S.R.X., Giraldeau, L.-A., Olsson, O., McNamara, J.M., Stephens, D.W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* 20, 187-193.
- Danchin, E., Giraldeau, L.-A., Valone, T.J., Wagner, R.H. 2004. Public information: from noisy neighbors to cultural evolution. *Science* 305, 487-491.
- de Nood, G.J. 2007. Patch quality and dominance status of producers affects the patch choice of scrounging herbivores. Honours thesis.
- de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour* 50, 1375-1389.
- Distel, R.A., Laca, E.A., Griggs, T.C., Demment, M.W. 1995. Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. *Applied Animal Behaviour Science* 45, 11-21.

- Dubois, F., Giraldeau, L.-A. 2005. Fighting for resources: the economics of defense and appropriation. *Ecology* 86, 3-11.
- Elgar, M.A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Review* 64, 13-33.
- Ens, B.J., Goss-Custard, J.D. 1984. Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe Estuary. *Journal of Animal Ecology* 53, 217-231.
- Fournier, F., Festa-Bianchet, M. 1995. Social dominance in adult female mountain goats. *Animal Behaviour* 49, 1449-1459.
- Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138, 478-498.
- Giraldeau, L.-A., Beauchamp, G. 1999. Food exploitation: searching for the optimal joining policy. *Trends in Ecology and Evolution* 14, 102-106.
- Giraldeau, L.-A., Caraco, T. 2000. *Social foraging theory*. Princeton University Press, Princeton, New Jersey.
- Giraldeau, L.-A., Dubois, F. 2008. Social foraging and the study of exploitative behavior. *Advances in the Study of Behavior* 38, 59-104.
- Giraldeau, L.-A., Hogan, J.A., Clinchy, M.J. 1990. The payoff to producing and scrounging: what happens when patches are divisible? *Ethology* 85, 132-246.
- Godin, J.-G.J., Crossman, S.L. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. *Behavioural Ecology and Sociobiology* 34, 359-366.
- Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., West, A.D. 1995. Deriving population parameters from individual variations in foraging behaviour. II. Model tests and population parameters. *Journal of Animal Ecology* 64, 277-289.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31, 295-311.
- Ihobe, H. 1989. How social relationships influence a monkey's choice of feeding sites in the troop of Japanese macaques (*Macaca fuscata fuscata*). *Primates* 30, 17-25.
- Illius, A.W., Gordon, I.J., Elston, D.A., Milne, J.D. 1999. Diet selection in goats: a test of intake-rate maximisation. *Ecology* 80, 1008-1018.

- Janson, C., Vogel, E. 2006. Hunger and aggression in capuchin monkeys. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), *Feeding ecology in apes and other primates: ecological, physical, and behavioural aspects*. Cambridge University Press, Cambridge.
- Katsnelson, E., Motro, U., Feldman, M.W., Lotem, A. 2008. Early experience affects producer-scrounger foraging tendencies in the house sparrow. *Animal Behaviour* 75, 1465-1472.
- Kendall, M.G. 1962. *Rank correlation methods*, 3rd edn. Charles Griffin, London.
- King, A.J., Isaac, N.J.B., Cowlshaw, G. 2009. Ecological, social, and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology*, 1039-1049.
- Kotler, B.P., Blaustein, L. 1995. Titrating food and safety in a heterogeneous environment: when are the risky and safe patches of equal value? *Oikos* 74, 251-258.
- Kotler, B.P., Brown, J.S., Hasson, O. 1991. Factors affecting gerbil foraging behaviour and rates of owl predation. *Ecology* 72, 2249-2260.
- Kurvers, R.H.J.M., Prins, H.H.T., van Wieren, S.E., van Oers, K., Nolet, B.A., Ydenberg, R.C. 2010. The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society of London: Biological Sciences* 277, 601-608.
- Langvatn, R., Hanley, T.A. 1993. Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia* 95, 164-170.
- Lendvai, A.Z., Liker, A., Barta, Z. 2006. The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. *Animal Behaviour* 72, 747-752.
- Liker, A., Barta, Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* 139, 1061-1076.
- McCormack, J.E., Jablonski, P.G., Brown, J.L. 2007. Producer-scrounger roles and joining based on dominance in a free-living group of Mexican jays (*Aphelocoma ultramarina*). *Behaviour* 144, 967-982.

- McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist* 124, 863-886.
- Mooring, M.S., Hart, B.L. 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123, 173-193.
- Murton, R.K., Isaacson, A.J., Westwood, N.J. 1971. The significance of gregarious feeding behaviour and adrenal stress in a population of wood pigeons *Columba palumbus*. *Journal of Zoology (London)* 165, 53-84.
- Ohtsuka, Y., Toquenaga, Y. 2009. The patch distributed producer-scrounger game. *Journal of Theoretical Biology* 260, 261-266.
- Pulliam, H.R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38, 419-422.
- Rands, S.A., Pettifor, R.A., Rowcliffe, J.M., Cowlishaw, G. 2006. Social foraging and dominance relationships: the effects of socially mediated interference. *Behavioral Ecology and Sociobiology* 60, 572-581.
- Reinhardt, V., Flood, P.F. 1983. Behavioural assessment of muskox calves. *Behaviour* 87, 1-21.
- Rohwer, S., Ewald, P.W. 1981. The cost of dominance and advantage of subordination in a badge signalling system. *Evolution* 35, 441-454.
- Ruyle, G.B., Dwyer, D.D. 1985. Feeding stations of sheep as an indicator of diminished forage supply. *Journal of Animal Science* 61, 349-353.
- Saito, C. 1996. Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and interpatch distance. *Animal Behaviour* 51, 967-980.
- Shrader, A.M., Brown, J.S., Kerley, G.I.H., Kotler, B.P. 2008. Do free-ranging domestic goats show 'landscape of fear'? Patch use in response to habitat features and predator cues. *Journal of Arid Environments* 72, 1811-1819.
- Shrader, A.M., Kerley, G.I.H., Kotler, B.P., Brown, J.S. 2007. Social information, social feeding, and competition in group-living goats (*Capra hircus*). *Behavioral Ecology* 18, 103-107.
- Smith, R.D., Ruxton, G.D., Cresswell, W. 2001. Dominance and feeding interference in small groups of blackbirds. *Behavioral Ecology* 12, 475-481.

- Spalinger, D.E., Hobbs, N.T. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *The American Naturalist* 140, 325-348.
- Stillman, R.A., Goss-Custard, J.D., Caldow, R.W.G. 1997. Modelling interference from basic foraging behaviour. *Journal of Animal Ecology* 66, 692-703.
- Sweitzer, R.A. 1996. Predation or starvation: Consequences of foraging decisions by porcupines (*Erethizon dorsatum*). *Journal of Mammalogy* 77, 1068-1077.
- Thouless, C.R., Guinness, F.E. 1986. Conflict between red deer hinds: the winner always wins. *Animal Behaviour* 34, 1166-1171.
- Valone, T.J. 1993. Patch information and estimation: a cost of group foraging. *Oikos* 68, 258-266.
- Valone, T.J., Templeton, J.J. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society of London: Biological Sciences* 357, 1549-1557.
- Van, D.T.T., Mui, N.T., Ledin, I. 2007. Effect of group size on feed intake, aggressive behaviour and growth rate in goat kids and lambs. *Small Ruminant Research* 72, 187-196.
- Van Soest, P.J. 1994. *Nutritional ecology of the ruminant*, Second edn. Cornell University Press, New York.
- Vickery, W., Giraldeau, L.-A., Templeton, J.J., Kramer, D.L., Chapman, C.A. 1991. Producers, scroungers, and group foraging. *The American Naturalist* 137, 847-863.
- Vogel, E.R. 2005. Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. *Behavioral Ecology and Sociobiology* 58, 333-344.
- Waite, T.A. 1987. Dominance-specific vigilance in the tufted titmouse: effects on social context. *Condor* 89, 932-935.
- WallisDeVries, M.F., Laca, E.A., Demment, M.W. 1998. From feeding station to patch: scaling up food intake measurements in grazing cattle. *Applied Animal Behaviour Science* 60, 301-315.
- Wilmshurst, J.F., Fryxell, J.M., Hudson, R.J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* 6, 209-217.

Wittig, R.M., Boesch, C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology* 24, 847-867.

Figures and tables

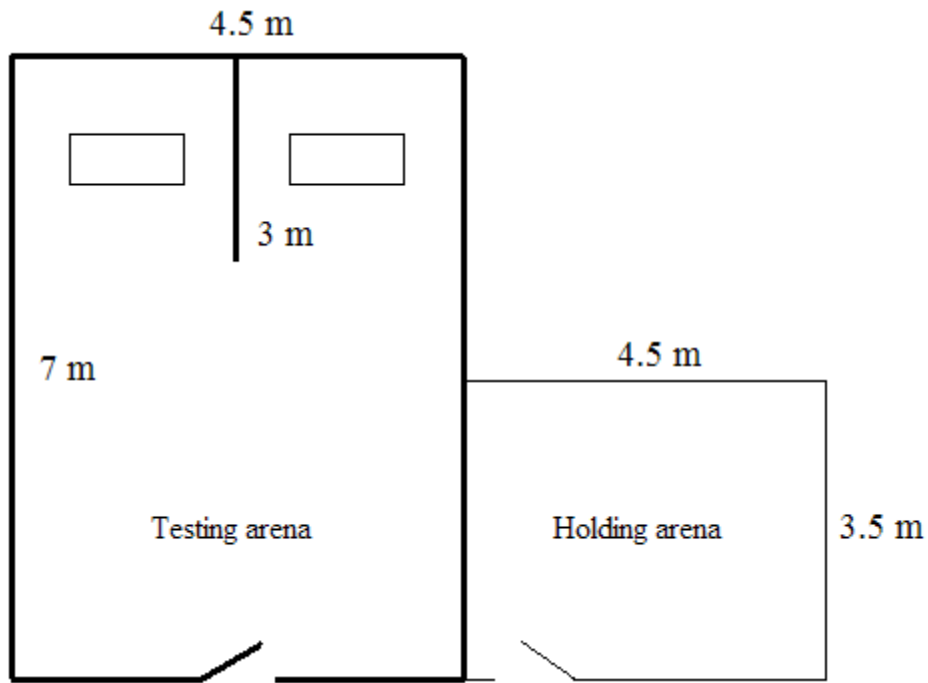


Figure 1: Testing arena used in the experiment. Thick lines denote non-transparent fences. Goats were held in the holding area and were transferred to the testing arena when needed for testing. Feeding patches (indicated by square) were placed on each side of the non-transparent divider

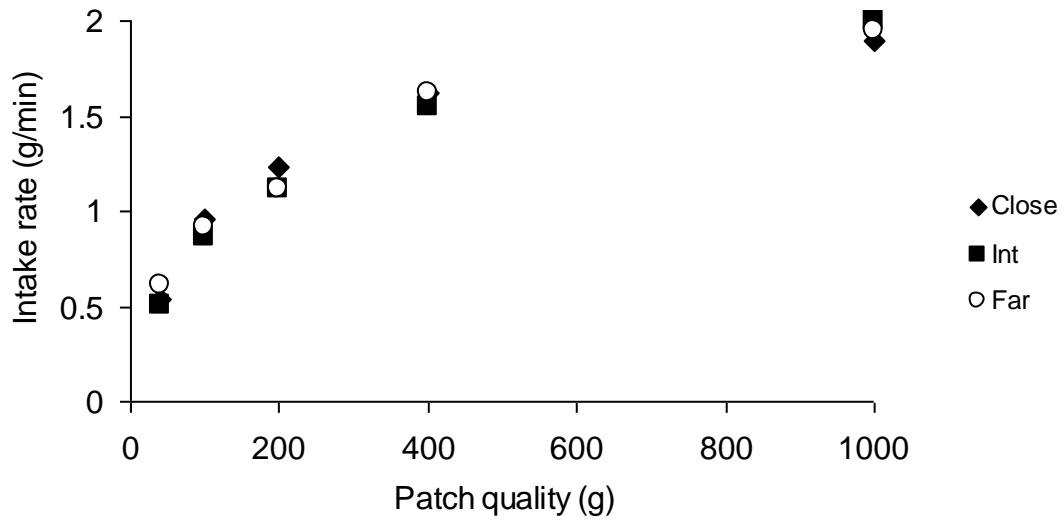


Figure 2: Type two functional response curve of scroungers' intake rate when they fed from patch holders from the close, intermediate and far dominance categories.

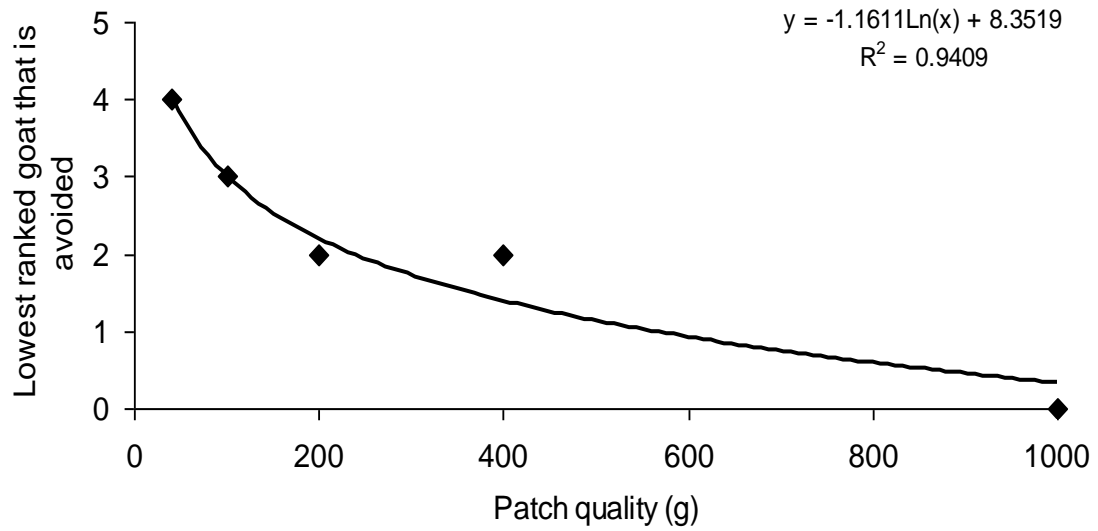


Figure 3: The lowest ranked goat that was avoided by scroungers at each patch quality. Ranking is set so that rank one is the most dominant individual, rank two is the second most dominant, etc.

Table 1: Chi-square results confirming that the herd of 45 goats could identify the patch quality from visual cues.

Patch quality (g)	Number of goats that fed from good quality patch	Number of goats that fed from poor quality patch	Chi-square value	p
400 vs. 200	33	12	5.18	0.023
400 vs. 100	34	11	6.29	0.012
400 vs. 40	39	6	13.98	<0.001
200 vs. 40	37	8	10.43	0.001
200 vs. 100	33	12	5.18	0.023
100 vs. 40	34	11	6.29	0.012

Table 2: Linear dominance hierarchy for the goat herd with the total number of wins and losses and non-interacting pairs calculated from the win-loss matrix. Clutton-Brock Index (CBI) value was calculated using the formula: $CBI = (B+b+1)/(L+l+1)$, Where B = the number of individuals whom the subject dominates, b = the number of individuals whom those dominated by the subject in turn dominate, L = the number of individuals who dominate the subject, and l = the number of individuals who dominate those dominating the subject (Clutton-Brock et al., 1979).

Goat Number	Number of wins	Numbers of losses	Non-interacting pairs	CBI value
Blue 05	44	0	0	978
IG 35	43	1	0	467
Blue 06	42	2	0	222.750
IG 41	41	3	0	121.286
Big beige	40	4	0	73.455
Blue 04	38	5	1	46
Tank	38	6	0	33.182
Matey	36	8	0	17.263
Mottled	36	8	0	16.073
IG 32	33	11	0	7.368
IG 36	33	11	0	6.902
Madash	32	12	0	6.212
Blue 03	32	11	1	5.577
IG 42	26	13	5	3.949
IG 46	30	14	0	3.545
Blue 01	29	15	0	3.414
IG 51	28	16	0	2.722
Blue 08	27	16	1	2.513
IG 57	27	17	0	2.384
S6K	28	18	0	1.916
S3K	25	19	0	1.718
Blue 02	22	22	0	0.981
S2K	22	22	0	0.980
S7K	21	23	0	0.820
Tiger	20	24	0	0.732
TK2	19	25	0	0.608
Blue 07	18	26	0	0.503
IG 55	18	26	0	0.476
S13K	15	29	0	0.281
Old brown beard	14	30	0	0.270
IG 44	15	29	0	0.269

Table 2 continued

Goat Number	Number of wins	Numbers of losses	Non-interacting pairs	CBI value
S9K	12	31	1	0.168
S12K	11	32	1	0.135
Curly brown	11	33	0	0.126
S10K	10	33	1	0.109
TK8	8	31	5	0.094
S8K	7	35	2	0.082
TK5	7	36	1	0.049
S14K	6	37	1	0.032
TK3	6	38	0	0.030
TK6	3	39	2	0.010
Blue 11	3	41	0	0.008
TK4	2	41	1	0.005
S15K	1	41	2	0.002
S16K	0	43	1	0.001

Table 3: Significant and non-significant effects of patch quality, distance (close, intermediate, far), status (dominant, subordinate) and their inter interactions on the intake rate of scroungers from an ANOVA analysis. The influence of patch quality, status and their interaction on scrounger's intake rate when feeding from the top five ranked patch holders in the herd is also shown.

	Type II Sum of Squares	df	Mean Square	F	Sig.
Patch quality	10.683	4	2.671	423.744	<0.001
Status (Dominant/subordinate)	0.025	1	0.025	3.989	0.047
Distance (Close/intermediate/far)	0.046	2	0.023	3.668	0.027
Status * Patch quality	0.027	4	0.007	1.088	0.363
Distance * Patch quality	0.102	8	0.013	2.024	0.044
Distance * Status	0.017	2	0.009	1.383	0.253
Distance * Status * Patch quality	0.022	8	0.003	0.446	0.893
Error	1.664	264	0.006		
Top five ranked goats					
Status (Dominant/subordinate)	0.006	1	0.006	0.212	0.646
Patch quality	78.275	4	19.569	684.663	<0.001
Status * Patch quality	0.042	4	0.01	0.367	0.832
Error	16.606	581	0.029		

Table 4: Chi-square results from the saturated log linear model showing the main effects and two way interaction of the variables patch quality (40 g, 100 g, 200 g, 400 g, 1000 g), distance (close, intermediate, far) and status (dominant, subordinate) had no influence on the number of scroungers that fed from a dominant or subordinate patch holder.

Effect	df	Chi-Square	Sig.
Patch quality*distance (Close/intermediate/far)	8	0.031	1.000
Patch quality*status (Dominant/subordinate)	4	5.508	0.239
Distance*Status	2	1.879	0.391
Patch quality	4	0	1.000
Distance	2	0	1.000
Status	1	0.303	0.582

Table 5: Chi-square test results showing the difference in the number of scroungers that fed from a dominant or subordinate patch holder. Significant p values indicate that scroungers avoided the dominant rank and fed more from subordinate patch holders. Non-significant p values indicate that scroungers fed equally from patches held by the top individuals and subordinates.

		Patch Quality (g)				
Goat						
rank	40	100	200	400	1000	
1	0.01*	0.03*	0.01*	0.03*	0.48	
2	0.00*	0.01*	0.03*	0.03*	0.48	
3	0.00*	0.03*	0.32	0.48	0.67	
4	0.01*	1.00	0.77	1.00	0.56	
5	0.29	0.77	1.00	0.77	0.24	

Note: *denotes $p < 0.05$.

CHAPTER 3

Conclusions and implications for producer-scrounging models and foraging behaviour

The purpose of this study was to explore how exploitative relationships in group living herbivores influence foraging decisions and its influence on individual's foraging rates. When making patch joining decisions, it is likely that individuals are faced with different combinations of patch quality as well as dominance status of patch holders. Therefore, the idea was that if dominance is the driving force behind patch choice, I expected scroungers to prefer to join subordinate patch holders, irrespective of patch quality. However, in contrast, if patch quality is the main factor, scroungers should feed from any patch, irrespective of the dominant status of the patch holder. Therefore, the broad aim of the study was to determine how the combination of patch holder dominance status and patch quality interacts to influence scrounging behaviour of group-living goats.

In order to determine the influence of dominance on patch joining decisions, I created three dominance categories; close, intermediate and far. This then allowed me to understand the influence of dominance on patch joining decisions as there are contrasting results on the role of dominance in foraging. For example, the phenotype-limited producing-scrounging game of Barta and Giraldeau (1998), predicts that dominance only plays a role when there are large differences in competitive ability between individuals. However, Stillman et al. (1997) developed an individual-based model that predicts the level of interference between individuals based on their behaviour. Their model predicts that a dominant individual will dominate any subordinate individual, regardless of the difference in rank (Stillman et al., 1997). Surprisingly, in this study dominance seemed to play no role in determining the patch joining decisions of scroungers as they joined patches irrespective of the dominance rank of the patch holder. This suggests that patch quality may be more important than dominance in determining patch joining decisions.

However, these results are unexpected as the goats formed a clear linear hierarchy. A key factor that determines the dominance rank of an individual is aggression (Liker and Barta, 2001), as it is normally the bigger, more aggressive individuals that out-

compete the smaller, less aggressive individuals (Barroso et al., 2000; Côté, 2000). So, if aggression plays a large role in dominance then these dominant individuals need to be able to aggressively defend their food patches in order to assert their dominance. It is clear that even patch holders from the far dominance category are not aggressive enough to prevent scrounger joining. As scroungers did not cue off dominance, the results seem to follow the predictions of Barta and Giraldeau's (1998) phenotype-limited producing-scrounging model and that the dominance gap between scroungers and patch holders may not have been large enough.

To explore this possibility, I then further increased the difference in dominance rank and only tested scroungers against the top five ranked (i.e. most dominant) individuals in the herd. Only when scroungers were tested against these five individuals in the herd did they avoid the dominant patch holders. This confirms that only the top ranked individuals are aggressive enough to prevent joining as perceived benefits are lower than the perceived costs. Although Barta and Giraldeau's (1998) phenotype-limited producing-scrounging model predicted that large differences in dominance rank would influence tactic choice, my results show that even large differences in gaps are not sufficient and that dominance only influences patch joining if scroungers are faced with the top ranked herd members. As a result, my results provide a unique set of data with which to determine if the model is robust enough to handle variations from the initial assumptions. These results may also help explain the contradicting influence of dominance on foraging behaviour.

A number of studies found that dominance had no influence on foraging behaviour (Giraldeau and Lefebvre, 1986; Giraldeau et al., 1990). For example, Robinette Ha and Ha (2003) conducted an experiment on how dominance influences the probability of individuals successfully retaining their prey or stealing from others. They found dominance to play no role. They calculated dominance so that male crows, *Corvus caurinus*, dominated females and adults dominated subordinates (Richner, 1989). However, this may be too simplistic, as there is no indication where these individuals would sit in a dominance hierarchy. There is no way of determining the difference in dominance rank between males and females as well as adults and juveniles from the information given in the paper. It is possible that two crows, one being dominant and the

other subordinate, were similarly ranked in the hierarchy and the difference in their competitive abilities may not have been large enough for dominance to influence foraging decisions. Barta and Giraldeau's (1998) model predicted that these contradictions may be the result of the difference in competitive ability between individuals not being large enough. However, they suggest that further studies should address this prediction (Barta and Giraldeau, 1998). My results showed that even large differences are not sufficient to prevent joining and that dominance only influences patch joining decisions if scroungers are faced with patches held by the top ranked individuals in the herd.

These findings can generate some important changes in producer-scrounger models as well as our understanding of foraging behaviour. One of the major assumptions of producer-scroungers models is that individuals avoid scrounging from dominant patch holders (Lendvai et al., 2006; King et al., 2009). In this study, this was not the case as scroungers only avoided the top ranked patch holders. This allows scroungers to greatly increase the number of individuals from which they can scrounge from. This benefits especially the low-ranking scroungers and may be a possible way in which these individuals are able to minimise the costs of competition associated with group living. Barta and Giraldeau's (1998) model predicted that when competitive differences are high, foragers should specialise exclusively on one tactic. For example, dominant individuals should scrounge whereas subordinates should produce. However, my results show that even large competitive differences are not enough and foragers will only specialise on one tactic when facing the most dominant (i.e. top ranked) individuals. For example, subordinates scrounged from dominant patch holders from the close, intermediate and far dominance categories but could also produce if necessary. This suggests that the competitive difference between the subordinates and the dominance categories are not that different. However, when faced against the top ranked individuals, subordinates would never scrounge and therefore specialise on one tactic, producing.

It is clear that both dominance and patch quality determine foraging decisions, so I then explored this further to determine how they interact to determine joining decisions across a range of different patch qualities. The results show that scroungers are making a trade-off between dominance and patch quality. As patch quality increases dominance

plays less of a role and fewer top-ranked patch holders are avoided. The shifting point where patch quality becomes more important than dominance suggests the importance of patch quality in producer-scrounger games. However, in producer-scrounger models there is a lack of information concerning the influence of patch quality on foraging behaviour. This study suggests the importance of further research on the influence of patch quality and although it was beyond the scope of this thesis, the influence of the finder's share on patch choice and foraging behaviour. The finder's share is important as it determines how much aggression a patch holder should show to defend a patch and how much aggression a scrounger should show in attempting to appropriate a patch holder. This aggression which is ultimately determined by patch quality could influence patch joining decisions of scroungers.

Although the patch holders were prevented from feeding from the patches, by being tethered to the pen, the tethers were long enough to allow interaction with the scroungers. The artificial patches were placed just out of reach from the patch holders but as the scroungers joined the patch and fed, the length of the tethers allowed the patch holders and scrounger to stand side by side. The dominant patch holders were still able to attempt to exclude the scroungers by horning them. The subordinate patch holders continuously tried to join the feeding scroungers which resulted in the scroungers interacting and aggressively trying to push the patch holders away. This simulated natural conditions and still allowed me to collect intake rate data. Although it was beyond the scope of this study, it would be interesting to determine if the scrounger's behaviour would change if the patch holders were allowed to feed from the patches as well.

Individuals try to and forage in a way that maximises their energetic gains (Wilmshurst et al., 1995). However, dominance may limit their ability to do this (Vogel, 2005; Rands et al., 2006). A reduced intake rate by subordinates is one way how dominance affects subordinates. However, in this study, scroungers had a higher intake when feeding from dominant individuals from the close, intermediate and far dominance categories. Scroungers only experienced reduced intake rates when feeding from the top ranked patch holders. This shows that only the top ranked herd members are able to influence patch choice as well as intake rates of scroungers. This clearly shows that although there is a clear linear hierarchy, the herd is split into two groups: the dominant

top ranked individuals and then the rest of the herd. This can generate some important changes in the way dominance hierarchies are viewed and their influence on foraging behaviour. Future research that deals with dominance, the top ranked individuals should be considered dominant and separating dominance into categories may not be sufficient enough for dominance to influence foraging decisions.

With only the top ranked individuals being able to influence foraging behaviour, what is the value of being dominant? Being able to defend a food patch influences the dominance hierarchy (Barta and Giraldeau, 1998). My results suggest that for group living herbivores dominance is not the driving factor that determines foraging decisions as only the top four ranked individuals influenced scrounger's foraging decisions. This also suggests that dominance hierarchies in herbivores are not maintained to determine who has priority access to food because when it comes to grazing under natural conditions, food patches are not always easily defensible (Fournier and Festa-Bianchet, 1995). When dominant individuals are not able to defend food patches, they are not able to prevent scroungers from joining them at their patch. For example, an experiment on dark-eyed juncos, *Junco hyemalis*, showed that dominant birds consumed significantly more seeds than subordinates when resources were clumped (Theimer, 1987). However, there was no difference in the amount of seeds consumed when food was dispersed and less defensible.

However, there are circumstances when dominance and dominance hierarchies are important. For example, when resources are defensible, such as oestrous females (Fournier and Festa-Bianchet, 1995) dominance is important as dominant individuals have priority to females (Emlen and Oring, 1977). Dominance is also correlated with age (Clutton-Brock et al., 1984; Rutberg, 1986; Barroso et al., 2000). As individuals age they will increase their rank in the hierarchy which will allow them access to females as well as reach the top ranked individuals in the herd and have increased foraging success by prevent joining behaviour by scroungers. Dominant individuals may use their social status to force subordinate individuals to the periphery of the herd where they are more exposed to predators, thereby forcing them to increase their vigilance (e.g. Schneider, 1984). By doing so, dominant individuals are able to take advantage of the selfish herd effect by reducing the probability of predation by moving to the centre of the herd

(Hamilton, 1971).

Overall, this study has contributed to our understanding of scrounging behaviour in group-living herbivores. It has shown how scroungers assess their own dominance rank, the dominance rank of patch holders as well as patch quality to determine patch joining decisions. It has challenged some of the major assumptions of producer-scrounger models as well as those of general foraging behaviour. It shows that scroungers forage in a manner that maximises their energetic gains by weighing up the costs and benefits of joining each patch. Although dominance is important in foraging behaviour, this thesis shows that when patch quality is high, patch quality is the driving factor behind scrounger's patch joining decisions.

References

- Barroso, F.G., Alados, C.L., Boza, J. 2000. Social hierarchy in the domestic goat: effect on food habits and production. *Applied Animal Behaviour Science* 69, 35-53.
- Barta, Z., Giraldeau, L.-A. 1998. The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioural Ecology and Sociobiology* 42, 217-223.
- Clutton-Brock, T.H., Guinness, F.E., Albon, S.D. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308, 358-360.
- Côté, S.D. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137, 1541-1566.
- Emlen, S.T., Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215-223.
- Fournier, F., Festa-Bianchet, M. 1995. Social dominance in adult female mountain goats. *Animal Behaviour* 49, 1449-1459.
- Giraldeau, L.-A., Hogan, J.A., Clinchy, M.J. 1990. The payoff to producing and scrounging: what happens when patches are divisible? *Ethology* 85, 132-246.
- Giraldeau, L.-A., Lefebvre, L. 1986. Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Animal Behaviour* 35, 797-803.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31, 295-311.
- King, A.J., Isaac, N.J.B., Cowlshaw, L. 2009. Ecological, social, and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology* 20, 1039-1049.
- Lendvai, A.Z., Liker, A., Barta, Z. 2006. The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. *Animal behaviour* 72, 747-752.
- Liker, A., Barta, Z. 2001. Male badge size predicts dominance against females in house sparrows. *Condor* 103, 151-157.

- Rands, S.A., Pettifor, R.A., Rowcliffe, J.M., Cowlshaw, G. 2006. Social foraging and dominance relationships: the effects of socially mediated interference. *Behavioral Ecology and Sociobiology* 60, 572-581.
- Richner, H. 1989. Phenotypic correlates of dominance in carrion crows and their effects on access to food. *Animal Behaviour* 38, 606-612.
- Robinette Ha, R., Ha, J.C. 2003. Effects of ecology and prey characteristics on the use of alternative social foraging tactics in crows, *Corvus caurinus*. *Animal Behaviour* 66, 309-316.
- Rutberg, A.T. 1986. Dominance and its fitness consequences in American bison cows. *Behaviour* 96, 62-91
- Schneider, K.J. 1984. Dominance, predation, and the optimal foraging in white-throated sparrow flocks. *Ecology* 65, 1820-1827.
- Stillman, R.A., Goss-Custard, J.D., Caldow, R.W.G. 1997. Modelling interference from basic foraging behaviour. *Journal of Animal Ecology* 66, 692-703.
- Theimer, T.C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate dark eyed juncos: *Junco hyemalis*. *Animal Behaviour* 35, 1883-1890.
- Vogel, E.R. 2005. Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. *Behavioral Ecology and Sociobiology* 58, 333-344.
- Wilmshurst, J.F., Fryxell, J.M., Hudson, R.J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* 6, 209-217.