

THE FORAGING BEHAVIOUR OF SHEEP IN
RESPONSE TO ENVIRONMENTAL
UNCERTAINTY

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DECLARATION

I hereby declare that I composed this thesis myself and it has not been accepted in any previous application for a degree. Unless otherwise stated, the work contained herein is my own. All quotations have been distinguished by quotation marks and sources of information acknowledged

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<i>Table of Contents</i>	<i>i</i>
<i>Acknowledgements</i>	<i>vii</i>
<i>List of Figures and Tables</i>	<i>viii</i>
<i>List of Abbreviations</i>	<i>xi</i>
<i>List of Appendices</i>	<i>xiii</i>
<i>List of Plates</i>	<i>xiii</i>
<i>Abstract</i>	<i>xiv</i>

Chapter 1: General Introduction	1
References	3

Chapter 2: Literature Review	4
Introduction	4
Structure of the review	4
The importance of scale	5
Spatial scale	5
Temporal scale	7
Foraging Theory	7
Optimality models	7
Foraging in a patchy environment	8
Rules of Thumb	9
Satisficing	11
Information primacy	12
Sampling	14
Sampling in Herbivores	16
The value of information over time	17
The use of information under social conditions	19
Methods of determining dominance relationships	23
Individual differences and the propensity to take risky decisions	26
Risk sensitive foraging – foraging with information	27
Reliable information in predictable environments: The use of spatial memory	30
Conclusions	31
References	32

<i>Chapter 3: Preference of Scottish Blackface ewes for commonly encountered foodstuffs: good quality grass hay and green keil pellets</i>	41
Introduction	41
Materials and Methods	41
Animals and Housing	41
Experimental set-up	42
Experimental Design	42
Measurements	42
Food rewards	42
Statistical Analysis	43
Results	44
Discussion	46
Summary	48
References	48

<i>Chapter 4: Foraging sheep adapt their patch leaving decisions in response to environmental quality and uncertainty</i>	51
Introduction	51
Materials and Methods	52
Animals and housing	52
Food rewards	53
Initial training	53
Experimental set-up	54
Data recording	54
Arena set-up	54
Experimental design	57
Treatments	57
Time periods	58
Buffer Days	58
Test Days	58
Treatment period	58
Trials	59
Measurements	59
Statistical analysis	59
Patch leaving decisions	59
Predicted behaviour	60
Learning about the environment	61
Walking speeds	61
Individual differences	62
Results	62
Patch leaving decisions	62
Expectation	64
How did the results of the test compare to those predicted?	65
How did sheep respond to change in patch quality?	65
Walking speed	66

Individual differences	69
Discussion	70
How did observed and predicted results compare?	72
Walking Speed	73
How did the sheep learn as the patch quality changed during the buffer period?	73
General discussion	74
Summary	75
References	76

Chapter 5: Does the behaviour of sheep in boldness tests reflect risk taking tendencies while foraging? 79

Introduction	79
Materials and Methods	80
Animals and Housing	80
Behavioural tests	81
Measurements	81
Leaving the pen.	81
Scores	81
Transit.	81
Scores	81
Novel Object.	82
Scores	82
Surprise Effect.	82
Results	83
Discussion	84
Summary	85
References	86

Chapter 6: The effect of conspecifics on foraging behaviour and the use of information 87

Introduction	87
Establishment of the dominance hierarchy	89
Materials and Methods	89
Animals and Housing	89
Data Collection	90
Training	90
Food competition trials	91
Measurements	92
Analysis	93
Results	93

The effect of social foraging on information and behaviour	96
Materials and Methods	96
Animals and Housing	96
Food Rewards	96
Initial training	96
Experimental Set-up	97
Experimental Design	97
Training Period	97
Training and Tests – 4 Periods.	98
Test Period	99
Analysis	100
Training period	100
Test Period	101
Results	103
Training	103
Test Period	104
The first sheep to move during a trial	104
Effect of run number	106
Following behaviour	108
Effect of run number	109
Discussion	111
Summary of results	111
First to move	111
Following behaviour	112
Producer-scrounger roles	113
Difference in rank	114
Sociability	115
Comparing natural with restricted foraging	115
Modifications to the experimental set-up	116
Summary	117
References	118

Chapter 7: The effect of a time delay on the choice between a stable and variable patch **120**

Introduction	120
Materials and Methods	122
Animals, Housing and Care	122
Experimental Set-up	124
Habituation to the procedure	125
Assignment to the treatments and initial training	125
Experimental design	126
Testing procedure	127
Measurements	128
Analysis	128
Learning the patch conditions	128
Patch choice in free choice trials	129

Results	130
Learning the patch conditions: The behaviour of the sheep during the training period	130
Patch choice in the free trials	132
Consideration of group size effect.	134
Discussion	135
Limitations of the experimental design	139
Summary	140
References	142

Chapter 8: The effect of spatial and temporal variation in patch quality on the foraging behaviour of sheep. **144**

Introduction	144
Materials and Methods	147
Animals and the pasture	147
Creation of resource sites	147
Treatments	148
Definitions	150
Stable (Figure 8.2a)	150
Intermediate (Figure 8.2b (I)-(V))	150
Variable (Figure 8.2c)	151
High (Figure 8.2d (I)-(V))	151
Formation of groups	164
Timing	164
Training	164
Testing Procedure	164
Measurements	165
Analysis	165
Training	165
Use of data	166
Efficiency	166
Sampling behaviour	167
Path similarity	167
Results	168
Training	168
Test	169
Truncation of the data	169
Group efficiency	171
Sampling behaviour	173
Search Paths.	176
Discussion	178
Training	178
Efficiency	178
Sampling	179
Sampling within sites	179
Sampling between sites	180
Search Path	181
Social influence on foraging efficiency	183

Summary	184
References	185
Chapter 9: General Discussion	188
Introduction	188
Summary of results	188
Implications for foraging in an uncertain environment	189
Win-stay vs. win-shift strategies for foraging	190
The cost of information	191
Cost of information in the indoor experiments	191
Costs of information in the pasture experiment	193
Spatial memory at the feeding station scale	194
Social complexity and information	195
Dominance and information	197
Social effects at pasture	200
Effect of dominance status on performance	201
Sociability	202
Summary	203
Future direction	204
Concluding remarks	205
References	205

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LIST OF FIGURES AND TABLES

Table 3.1	Results of the three preference methods
Table 3.2	Analysis of variance table
Table 3.3	Chemical composition of feeds
Figure 3.1	Individual differences in preference
Table 4.1	Chemical composition of feeds
Figure 4.1	The experimental arena
Figure 4.2	The amount of hay eaten across sheep and periods for different probability treatments
Figure 4.3	Prediction of hay eaten across the probability treatments based on the results of the hay eaten for the predictable treatments 0 & 1
Table 4.2	Prediction of hay eaten from the regression equation
Figure 4.4	Comparison of observed and predicted results
Figure 4.5	Change in treatment from low to high
Figure 4.6	Change in treatment from high to low
Figure 4.7	Travel time differed between the low treatments (0, 0.25) and the high treatments (0.5,0.75,1)
Figure 4.8	Individual differences between sheep in hay eaten at probability treatment 1
Figure 5.1	Correlation between the rank of hay eaten and the behaviour scores
Table 5.1	Results of the hay eaten and the behaviour scores
Table 6.1	The order and position of dyads in one day
Table 6.2	The win-loss matrix
Table 6.3	The win-loss matrix arranged by rank
Table 6.4	The division of the group into dominants and subordinates
Figure 6.1	The experimental arena
Table 6.5	The experimental design
Table 6.6	Definition of terms in the fixed model
Figure 6.2	Mean leaving time (s)
Figure 6.3	The likelihood of a dominant or subordinate being first to move,

	according to their previous treatment in the training environment
Table 6.7	Results of Generalised Linear Model for the analysis of first to move
Figure 6.4	The likelihood of being first to move during the first 4 runs of the test
Figure 6.5	The likelihood of being first to move during the last 4 runs of the test
Figure 6.6	Following behaviour during the first 4 runs of the pair trial
Figure 6.7	Following behaviour during the last 4 runs of the pair trial
Figure 7.1	Plan of the foraging arena
Table 7.1	“time to bin” for sheep after 5 high runs, 5 stable or 5 low runs
Figure 7.2	The change in walking behaviour for the two slow environment groups
Table 7.2	Results of the patch choice test after varying delays
Table 7.3	Power analyses over a range of different effects and group sizes
Figure 8.1	Plan of pasture showing the position of the 7 sites
Table 8.1	Structure of the treatments
Figures 8.2 a-d	Plan of pellet distribution across treatments
Figure 8.3	Increase in sites visited over the 6-day training period
Figure 8.4	Increase in the volume of pellets consumed over the 6-day training period
Figure 8.5	Variation in group efficiency across treatments
Figure 8.6	Variation in focal animal efficiency across treatments
Figure 8.7	Variation in the total volume of pellets consumed by the focal animal within the truncated period
Table 8.2	REML results for the comparison of efficiency measures across treatments
Figure 8.8	Sheep on treatments where within site variability was held constant made fewer site visits over the 20 minute trial period
Figure 8.9	Variation in the time until first grazing across treatments
Figure 8.10	Variation in the number of bowls checked before leaving the site
Table 8.3	Summary of means for efficiency measures across treatments
Figure 8.11	Path similarity across all treatments between days 4 and 5
Figure 8.12	There was no significant difference between treatment groups in

search path similarity

Figure 9.1

Comparison of leaving times across experiments in Chapter 4 and Chapter 6

LIST OF ABBREVIATIONS

ADF	Acid detergent fibre
cm	Centimetre
cPV	Crude preference value
df	Degrees of freedom
DM	Dry matter
dom	Dominant
g	Gram
h	Hour
kg	Kilogram
LW	Live weight
MAFF	Ministry of Agriculture, Fisheries and Food
ME	Metabolisable energy
min	Minute
MJ	Megajoule
mm	Millimetre
ms	Mean squares
MVT	Marginal Value Theorem
N	Elemental nitrogen
NS	Not significant
NDF	Neutral detergent fibre
OM	Organic matter
OMD	Organic matter digestibility
s	Seconds
SD	Standard deviation
SE	Standard error
SED	Standard error of difference
SEM	Standard error of mean

SET Scalar expectancy theory
sub subordinate

LIST OF APPENDICES

Appendix I: Order of pellet presentation for probability treatments

LIST OF PLATES

Plate 4.1 The experimental arena (used in Chapters 4 and 6)

Plate 4.2 The video set-up showing the four camera views displayed on the monitor

Plate 8.1 Close up of a bowl within the sward

Plate 8.2 View of a resource site

ABSTRACT

In a natural environment, foraging herbivores are faced with uncertainty as a result of heterogeneity in resource distribution over space and time. By gathering and using information about resources foragers can decrease uncertainty about the environment and hence increase foraging success. Determining the capacity of foragers to adapt their behaviour in response to variable resources will help the understanding of herbivore decision making in a complex environment. The behavioural response of sheep was studied under experimental variation in spatial and temporal distribution of resources and in social foraging conditions.

When foraging alone in an indoor arena, sheep adjusted their patch leaving behaviour according to their expectation of patch quality. This was achieved by combining information about the average probability of reward within a patch with recent patch experience. In a supplementary experiment no significant relationship could be found between the patch leaving behaviour of the sheep in this experiment and measures of personality traits for the individual animals. Under the same conditions, but paired with another sheep of known dominance status a second experiment investigated the effect of increased social complexity on patch leaving behaviour. The behaviour of individuals became less efficient as sheep of different social status diverged in behaviour. Dominant animals followed and challenged subordinate animals for patch access. Subordinate animals relinquished patch information to avoid conflict with dominants. When given a choice between predictable and variable patches offering the same mean reward in the third experiment, sheep selected the predictable patch

regardless of recent patch experiences. As the time between successive patch visits increased, sheep reverted to a random choice, except where recent experience on the variable patch had been negative. This highlighted the persistence in memory of sheep for negative over positive or neutral experience and provided evidence for a win-stay strategy of foraging. In a final pasture experiment combining spatial, temporal and social factors, sheep foraged more efficiently when resource distribution was stable and predictable. Sheep used spatial memory to return to feeding stations within a site as a strategy to avoid competition from other flock members.

This study found evidence that sheep behave flexibly and rapidly to changes in their foraging environment. Social constraints and the costs of obtaining and retaining information in a variable environment influenced efficiency in foraging behaviour.

CHAPTER 1

GENERAL INTRODUCTION

For a foraging animal in a natural, heterogeneous environment, uncertainty over resource distribution is inevitable. Defined by the Chambers English dictionary as “*a state of doubt, such as cannot be definitely forecast*” (Macdonald, 1967) uncertainty can be overcome by using information obtained through a range of experience to help make decisions. The ability of the forager to achieve this can determine their lifetime success (Green, 1984). This study is concerned with the way in which information is gathered and used by foraging herbivores under conditions of resource variability to reduce uncertainty, and focuses on spatial and temporal variability in resource distribution and the effect of conspecific competitors on the behavioural response of individuals. This research area has undergone extensive theoretical development (for review see Stephens & Krebs 1986) however, there is little understanding of the level of information used by foraging herbivores under variable environmental conditions.

This study aims to examine the use of information by foraging herbivores in overcoming uncertainty in a variable environment. The objectives are to examine the effects of

- 1) probability of reward in an alternative patch on patch leaving behaviour
- 2) a delay in time between successive patch visits
- 3) social constraints on information use
- 4) increased complexity in social systems and spatial and temporal variation in the resources

Sheep (*Ovis aries*) were chosen as a model with which to explore this problem as herbivores represent a special case of forager (Stephens & Krebs 1986). Herbivores are seldom food-limited, due to the low quality and abundant nature of their food supply. In order to forage efficiently however, herbivores may attempt to maximise energy gain over time (Belovsky 1978), select required nutrients (Belovsky 1978), maximise digestion rate (Westoby 1974) or avoid plant secondary compounds (Pfister et al. 1996). In consequence, herbivores forage in a complex environment requiring the ability to learn about resources and use that information to acquire food (Belovsky et al. 1999). This study will consider the ability of sheep to respond to changes in predictability and variability in food resources and the information used to do so.

As two of the four main experiments considered the choice for the forager between two feed resources, hay and pellets, it was necessary to establish that one food source was strongly preferred over the other. It was on this preference that the later experiments were based. This will therefore be discussed in Chapter 3. Predictability in reward and the response of individual sheep was examined in Chapter 4. An auxiliary experiment (Chapter 5) was then carried out in response to the results of Chapter 4 to test for a correlation between aspects of behaviour exhibited in that experiment and individual variation in personality characteristics of individuals. In an attempt to approach more naturalistic conditions, social foraging in a variable environment was examined (Chapter 6). The effect of the passage of time on a choice between patches varying in predictability was considered in Chapter 7. This was considered important as all experiments were concerned with behaviour over time periods of several weeks. Finally Chapter 8 describes an experiment designed to

incorporate these aspects of foraging to examine the response of foraging sheep to spatial and temporal variation in resource distribution.

The experiments described in Chapters 3 to 7 were carried out under highly controlled conditions. Artificial foraging environments were created within buildings of the research station, where sheep were familiar with housing and husbandry procedures. This set-up minimised stress on the animals and allowed experimental conditions, such as access to food, to be strictly controlled. The final experiment (Chapter 8) took place in a pasture in an attempt to approximate more natural grazing conditions, however resources were also manipulated using concentrate feeds.

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CHAPTER 2

LITERATURE REVIEW

INTRODUCTION

With limited time and knowledge in a heterogeneous environment how does an animal maximise foraging efficiency? This review examines the evidence describing how foragers gather information about the environment and use that information to increase their foraging efficiency. By increasing foraging efficiency animals can increase their net rate of energy gain, thereby increasing their fitness by passing on their genes to the next generation (Stephens & Krebs 1986; Brown et al. 1993).

The experiments presented in this thesis are concerned with the behaviour of foraging herbivores. Large herbivores represent a special case in foraging behaviour because, unlike the typical predators in traditional foraging models their food does not occur in discrete “packages” but as a relatively continuous resource of nutrients (Laca & Demment 1996). As such, many of the discussion points referring to the foraging models will consider herbivores independently.

Structure of the review

The relevance of different scales of study for foraging herbivores will firstly be discussed. Optimal foraging as a model with the effects of inherent constraints and assumptions will be considered. The review will also consider alternative models proposed to account for the observed behaviour of foragers. Aspects of foraging in predictable environments, the degradation of information over time in response to extrinsic and intrinsic factors, and the influence of conspecifics on the use of information by individuals are also discussed.

Natural selection drives efficiency. Those foragers not maximising their efficiency will lose out in the next generation to competitors that have done so.

THE IMPORTANCE OF SCALE

Landscape systems are characterised by heterogeneity (Freidel 1994), defined as “*the variety of qualities found in an environment*” (Levins 1968). Some changes in the spatial and temporal distribution of resources are predictable such as day length and tidal cycles; and some are less so, for example population cycling of prey and predators, food resources, and the weather. Under grazing conditions, differential exploitation of plants by herbivores leads to vegetation communities differing in species composition, structure, phenological stage and quality (Marriott & Carrère 1998). Consequently, grazed habitats become heterogeneous, and herbivores respond to this by altering their grazing distribution across these spatial and temporal scales (Bailey et al. 1996). For large herbivores, forage resources can be considered at the level of bites, feeding stations, plant communities, landscapes or regional systems (Senft et al. 1987) and foragers exhibit particular behaviour patterns associated with these hierarchical levels (Kotliar & Wiens 1990; Bailey et al. 1996).

Spatial scale

The lowest spatial level considered for a foraging herbivore is the single bite; ranging up through feeding station (the area within reach while the front feet are stationary), patch (a group of feeding stations), feeding site (where a feeding bout takes place) and camp (an area where animals drink and rest between feeding bouts) (Bailey et al. 1996). A resource patch can also be described as a cluster of preferred bites (Bailey et al. 1996) but ideally should be defined in response to the behaviour of the forager

rather than limits defined by the observer. The largest scale to be encountered by the herbivore is their home range (Senft et al. 1987).

In heterogeneous environments intake rate for herbivores is not constrained by selection at the scale of a single bite. It has been reported that cattle (*Bos taurus*) consume between 14,000 and 33,000 bites per day (Scarnecchia et al. 1985) and thus the significance of individual choices at the bite scale may be obscured (Illius & Gordon 1990). Instead it has been proposed that intake rate in herbivores is constrained by the efficient exploitation of resource patches (Roguet et al. 1998). The foraging environment of a herbivore is often composed of preferred vegetation distributed within a lower quality continuous background (Illius & Gordon 1990). Arditi & Dacorogna (1988) developed a model accounting for arbitrary distribution of resources in the environment such as a grazed ecosystem. It described the speed at which an animal should move through a continuous environment and found that animals should identify a threshold of quality below which resources should be rejected. Where resources are above this quality threshold the animal should slow down to feed there, but continue to walk through areas falling below this threshold. In essence, “*where patches do not exist...animals should invent them*”(Kacelnik & Bernstein 1988). Given the results of this model, and the evidence for the exploitation of patchy environments by herbivores, it appears justified to consider herbivore foraging at the patch level.

The mechanisms governing the movement of foragers in a heterogeneous environment have been extensively studied at the patch level (Stephens & Krebs 1986), but care must be taken to ensure that scaling up across larger spatial scales is representative of foraging behaviour (Laca & Ortega 1995; WallisDeVries et al.

1999). Beyond the bite scale, constraints unrelated to foraging come into play, such as avoidance of predation and requirements for water and shelter (Senft et al. 1987). Consideration of foraging decisions at multiple spatial scales (Jiang & Hudson 1993; Ward & Saltz 1994; Ginnett & Demment 1997) are only appropriate where the relationship between the scales can be justified and are relevant for the subject species (Wiens 1989).

Temporal scale

On a temporal scale, the frequency of decision-making also varies between the hierarchical levels. For example, at the bite scale, the question “which plant to consume next” occurs more often than “where to begin the next foraging bout” (Senft et al. 1987; Freidel 1994). Higher level decisions have the greatest impact on foraging success of a herbivore as these events occur more rarely, and the cost of a mistake in selecting a feeding site will be higher than, for example, the cost of a misplaced bite (Bailey et al. 1996). Despite this, there is evidence that foraging herbivores forgo long-term rate of intake maximisation for intake in the short-term (Fortin et al. 2002).

FORAGING THEORY

Optimality models

As a result of natural selection it is assumed that the fitness of an animal, or its genetic contribution to the next generation, is related to its behaviour while foraging (Pyke 1984). An optimal animal “*maximises or minimises behaviour subject to constraints*” (Krebs & McCleery 1984) and those animals operating optimally are most likely to survive, reproduce and contribute to the next generation (Pyke 1984).

Foraging has been a favoured ground for testing optimality theory for a number of reasons; foraging is assumed to be a series of discrete decisions made by the forager: where to search, for how long to search, which prey items to take, how to move through the environment. All these decisions represent trade-offs. For example, by choosing to stop and catch a particular prey item the forager misses the opportunity to search for further prey. The basic assumption in optimal foraging theory is that the behaviour that provides the maximum fitness benefit to the individual is that which maximises rate of energy gain.

Foraging in a patchy environment

Where food resources are distributed heterogeneously in the environment, how should a forager decide where and for how long to feed? The Marginal Value Theorem (MVT) developed by Charnov (1976) attempts to predict the optimal behaviour of an animal in such an environment. The time spent in every patch is dependent on the average profitability of the environment. The primary assumptions of the marginal value model are that (a) fitness increases linearly with the rate of energy intake and (b) the forager has complete knowledge of the environment. On the basis of these assumptions, the MVT predicts that an animal should leave one patch and move to the next when its instantaneous rate of energy intake from the current patch falls to a value equal to the average net rate of energy intake for the habitat. Patches where the instantaneous rate of intake is less than the average environmental rate should be ignored. According to the model, foraging takes place in cycles of patch visits and travelling. The foraging time allocated to patches of higher quality should be longer than the time spent in poorer quality patches. Although many tests of the model have shown good qualitative fit (Cowie 1977;

Krebs et al. 1978; Laca et al. 1993; Distel et al. 1995), in most cases there is discrepancy between the predictions of the model and the observed behaviour (Devenport & Devenport 1993; Kotler et al. 1994; Shipley & Spalinger 1995; WallisDeVries et al. 1999). Several theories have been proposed to explain these discrepancies including the desire for a nutritionally mixed diet (Belovsky 1978; Parsons et al. 1994), the maintenance of favourable rumen conditions (Cooper et al. 1994) and limits in the cognitive capacity of the animal (Illius & Gordon 1990). Animals stay longer than predicted in patches (Bazely 1990) when patches are not easily recognisable. This suggests that animals are gathering information while they forage and using this information to make patch leaving decisions. Rewards gathered at the start of the foraging bout can be used to estimate patch quality. By staying in the patch longer than predicted by the MVT, animals are continually updating their estimate of patch quality (Krebs & McCleery 1984), however they are also incurring a cost of lost opportunity to forage elsewhere. The inability to accurately assess patch quality according to the complete knowledge assumption of the MVT (Pyke 1984) is a problem of information. However, within every foraging bout there must be a point at which the search for information stops and the decision is made to leave the current patch and search for food elsewhere in the environment.

Rules of Thumb

The MVT does not specify a mechanism for identifying the time at which the intake rate falls to that achievable in the surrounding environment. It is widely believed that foraging animals use “rules of thumb” to solve the optimisation problems of foraging without complete knowledge. Green (1984) tested several rules that might be used to make these decisions, based only on information that the forager could gain in a

patch. The rules considered were (1) a fixed time rule where the forager should leave after a fixed time, regardless of success (2) a giving up time rule where the forager should leave after a fixed time without any successful captures and (3) an assessment rule where the forager should leave after its rate of capture drops to an unacceptable threshold. Overall, the assessment rule performed best across a range of environmental conditions, and could be considered analogue of the marginal value theorem where the unacceptable threshold is an estimate of the environmental average. This was shown in the study of a parasitoid wasp (*Nemeritis canescens*) in the search for unparasitised hosts. The wasp left the patch after a threshold encounter rate had been reached (Waage 1979). A study of patch departure rules for a large grazing herbivore, the wapiti (*Cervus elaphus canadensis*) was carried out by Jiang & Hudson (1993) at two hierarchical levels of resource heterogeneity, the feeding station and the patch. Patch was defined in this study as “*a cluster of feeding stations separated from others by a break in the foraging sequence when the animal reorients to a new location*”. There was no evidence that wapiti used foraging time as a patch departure rule. Instead it was concluded that they left patches when the intake rate at a feeding station fell to a rate that was below the seasonal expected intake rate, attributed to the large seasonal variation in patch quality. After a winter period, the grassland was considerably more heterogeneous and wapiti were disinclined to leave a patch. However, this study did not consider the effect of travel time between patches or the effect of patch depression during foraging.

Rules of thumb are highly species specific, and are only expected to work well in the natural foraging environment of the animal under study (Krebs & McCleery 1984).

Rules of thumb do not attempt to claim the observed behaviour is the best that an

animal can do, as does the MVT, however they do illustrate how simple behavioural rules can approximate optimal behaviour without the constraints of complete knowledge (Janetos & Cole 1981).

SATISFICING

An alternative hypothesis to optimal foraging when considering foraging behaviour in a variable environment is *satisficing* (Ward 1992). Satisficing, a Scottish word meaning “to satisfy”, is the process defined by setting desired levels, searching within those choices for an alternative that meets that minimum requirement and selecting that option (Simon, 1956). This appears to be a useful strategy when the forager does not know what is ahead. One of the major assumptions of optimal foraging theory is the monotonic increase in fitness with increasing foraging efficiency (Stephens & Krebs 1986). If in fact, the relationship between fitness and foraging was a step-wise function, then satisficing would be selected (Ward, 1992). This was shown in a study of the foraging trade-off between predation risk and food quality in ants (*Lasius pallitarsis*), where no significant difference in fitness was identified between ant colonies consuming optimal diets and those consuming diets only half as energetically valuable (Nonacs & Dill 1990).

Like a rule of thumb, by taking the satisficing shortcut, the forager solves the problem of optimal behaviour (Gigerenzer & Todd 1999). Although an animal that is foraging to satisfaction may not be using rules that optimise, an animal using the type of rules of thumb described above, are not always satisficers (Krebs & McCleery 1984). For example, foraging using rules of thumb may be a method of optimising under constraints (Goodie et al. 1999). In a stochastic environment, setting a

stringent level of attainment as done by satisficers has a high risk of failure. Krebs and McCleery (1984) illustrate this with the example of a blowfly, with the nerves between the brain and the gut severed. Such an animal with the highly simplistic foraging rules of a satisficer would only be able to survive in any environment if food was encountered at the exact rate allowing the fly to survive, but not to overfill its gut. In an unpredictable environment therefore, satisficing is a risky strategy. Another argument against satisfication is natural selection. Passing on genes to the next generation requires not just the minimum efficiency provided by satisficing that the animal can “get away with”, but the maximum efficiency to give offspring the best competitive advantage, i.e. following an optimisation strategy.

INFORMATION PRIMACY

The requirement for information about the environment may be more than just an aid to increasing efficiency but a motivational need in itself. The drive to reduce uncertainty and create a reliable cognitive model on which to base foraging decisions at the expense of maximising foraging efficiency is based on the “information primacy” theory (Inglis 1983). Suboptimal behaviour in the short-term is predicted to lead to optimal behaviour in the long-term as animals minimise uncertainty through gathering information. As animals increase in hunger, the motivation to gather information is reduced in favour of increasing feeding efficiency. This theory has been proposed to explain the observation that many animals will prefer to work for food rather than exploiting freely available food, a phenomenon known as contra-freeloading or learned industriousness (Inglis & Shepherd 1994). Wild rats (*Rattus norvegicus*) were presented with two patches accessed by lever pressing. Initially

both patches contained feed pellets; however, one patch was later switched to contain rodenticide pellets. Rats quickly learned to shift feeding preferences towards the safe patch, however, were also observed to sample the rodenticide patch though without consuming the pellets (Inglis & Shepherd 1994). This behaviour was attributed to information gathering on a previously rewarded patch. Another prediction of the information primacy hypothesis is, where all patches are equally predictable, i.e. there is no uncertainty associated with the environment, that animals should always exploit the most profitable patch, as there is no further information from feeding in the other patch. This was supported in a study by Forkman (1996) where Mongolian gerbils (*Meriones unguiculatus*) were observed to feed from an unprofitable food source when the food was hidden or camouflaged, resulting in suboptimal behaviour. However, when food was visible or easily accessible the profitable food source was almost always preferred. A major assumption of the information primacy hypothesis is that the continual gathering of information increases the long-term fitness of the animal at the expense of efficient behaviour in the short-term. However, these experiments cannot explicitly show that animals are forfeiting foraging behaviour in order to overcome an information deficit and predicts information gathering to occur without reference to the value of the information. The behaviour of the animals in these experiments could be attributed to a tendency to perform natural species-specific foraging techniques (Kacelnik 1987). However, one of the main criticisms of the Marginal Value Theorem is the assumption of complete information about the environment and despite concerns about the exact nature of the information being gathered (Kacelnik 1987), the information primacy hypothesis can explain the occurrence of partial preferences and sampling behaviour.

SAMPLING

Investing time in exploring patches to determine their quality may reduce the cost of feeding on a low quality patch in a variable environment. Sampling behaviour helps the forager overcome the problem of “incomplete information” (Stephens & Krebs 1986) by tracking environmental fluctuations and thereby increasing foraging efficiency. Sampling can be considered exploratory behaviour, where animals are observed to visit unprofitable parts of the environment (Shettleworth et al. 1988), and may explain “partial preferences” where seemingly non-preferred food items are consumed by the forager (Illius et al. 1992; Illius & Gordon 1993). In both cases information about the environment is gathered and can be applied in future foraging bouts.

A number of approaches have been taken towards the study of this problem (Dow & Lea 1987; Tamm 1987; Shettleworth et al. 1988; Krebs & Inman 1992; Devenport et al. 1997). Krebs et al (1978) argued that the most effective approach to foraging in a two patch environment, with one stable patch and the other variable in output, is to sample both patches for an optimal time and then focus on the most profitable. This strategy is termed optimal sampling. The time at which the forager should switch from sampling to exploiting the most profitable patch is dependent on the rate of change of a variable patch and the length of time that the patch is available. The longer the patch is available, the more can be gained from increased time spent sampling (Dow & Lea 1987). Stephens and Krebs (1986) and Stephens (1987) also examined sampling theoretically, asking the question how often should an animal sample to maximise intake? Sampling is most valuable at intermediate rates of change of the variable patch. Where the environment is near stable, a forager

sampling the unknown variable patch incurs a cost of lost opportunity to forage in the stable patch. Equally, when the environment is highly variable, information on patch quality gained through sampling is of little value because conditions are likely to change between runs and thus the forager incurs costs associated with sampling that include movement between patches and exposure to predation. As a result, a trade-off exists in less predictable environments between staying in one patch (the cost of missed opportunity to feed in a higher quality patch) and moving to exploit “pastures new” (the cost of walking and search time between patches). There has been limited success in testing the specific predictions of these models with either laboratory or field observations. Tamm (1987) examined sampling behaviour in hummingbirds (*Selasphorus rufus*), finding some support for qualitative but little for quantitative predictions. The discrepancy was attributed to inappropriate currencies and artificiality in the experimental set-up.

However, sampling is generally considered a low cost activity (Stephens & Krebs 1986; Kacelnik & Bernstein 1988; Illius & Gordon 1990) and has been shown to improve foraging efficiency. Under natural conditions, foraging eastern chipmunks (*Tamias striatus*) increased the time devoted to exploration when the quality of their current patch fell (Kramer & Weary 1991). This qualitatively supports the hypothesis that sampling is of greater value when foraging in a low quality patch because the quality of alternative patches is likely to offer a higher rate of gain. Further, in a study of great tits (*Parus major*) and blue tits (*Parus caeruleus*) with nestlings, the birds devoted more than one and a half times the search time predicted by exclusive use of the most profitable patch. However, by doing so, they increased their foraging efficiency by 30% over equal use of all trees (Naef-Daenzer 2000). In an extension

of the sampling theory, Dall et al (1999) produced a model accounting for the probability of interruption on sampling behaviour of a forager. The efficiency of a forager is not just constrained by the ability to maximise intake, but often by factors out-with its control, such as bad weather, interference from competitors, or vigilance behaviour. The probability of interruption, or the expected time that the forager has to sample, will affect the investment the forager makes in learning about the environment. Again, the forager was presented with a two patch environment. One patch offered a constant but stable reward; the second was stochastic with variable payoff. Animals had to sample to identify the most profitable patch. When there was a small probability of interruption a lot of time was invested in sampling the unknown patch. However, when the probability of interruption increased, and hence the expected time horizon for foraging decreased, the model forager switched to foraging from only the stable and known option. Therefore, the time that the forager expects to have available for sampling affects the value of information from the unknown patch.

Sampling in Herbivores

The food source of foraging herbivores does not occur in the discrete patches considered by traditional foraging theory (Stephens & Krebs 1986). Instead, vegetation is only partially consumed and nutrients are widely distributed and generally low in quality (Illius & Gordon 1993). Although it has been shown that foraging sheep can use environmental cues to assess patch quality (Edwards et al. 1996; Edwards et al. 1997), for example, brightness is significantly correlated with protein content in perennial ryegrass (Bazely & Ensor 1989), such informative cues are rarely as clear cut as in the studies mentioned above, and as such discrimination

problems are likely to arise. To assess patch quality it is may therefore be necessary for herbivores to invest time in sampling vegetation in unpredictable environments.

THE VALUE OF INFORMATION OVER TIME

Tracking patch quality by sampling allows an animal to integrate information from recent foraging bouts with information from the past to build up an assessment of average patch quality (Tamm 1987). When tracking patch conditions, the most recent information the forager has about patch quality is the most valuable, because the accuracy of information will decrease over time (Devenport & Devenport 1993) as a result of competition, avoidance of predation, adverse weather conditions or other demands on the animals time budget. The rate at which this information about the patch loses value will depend on the rate of change of the environment. Where the environment is stable, information is valuable to the forager for longer. In response to this the forager should discard outdated information according to current environmental conditions (Hirvonen et al. 1999). How is this achieved? Cowie (1977) proposed the notion of the memory window while investigating the Marginal Value Theorem (Charnov 1976). The memory window represents a time period over which information is remembered. Long memory windows are resilient to short term changes in the environment, but limit the ability of the forager to react quickly to long term environmental shifts. Conversely, short memory windows favour a quick response to short term change (Shettleworth 1998). This concept was later developed into the Exponentially Weighted Moving Average model (EWMA) (Killeen, 1981; McNamara & Houston 1987; Dow & Lea 1987). The EWMA is based on a parameter that adjusts the length of the memory window according to an average of

past experiences and the influence of the last patch experience on that average (summarised by Devenport and Devenport, 1994). This strategy allows the forager to track and respond to environmental change with optimal memory load (Hirvonen et al. 1999). The model was further developed in simulations that exponentially devalued weights for past events to investigate an individual forager's memory in response to environmental variability (Hirvonen et al. 1999). The weighting of experiences was altered according to a predefined devaluation rate. Where the devaluation rate was high weighting strongly favoured recent events and where devaluation rates were low past events still provided valuable information. These simulations found that in a stable environment foraging efficiency was improved by using a low memory devaluation rate. Conversely, where the environment was highly variable a high memory devaluation rate, i.e., information was quickly forgotten, was more efficient. This allowed foragers to overcome local fluctuations that did not affect the overall resource distribution.

For foraging herbivores changes in resource stability occur across temporal scales. Patch consumption by an individual or its conspecifics result in short-term depletion of resources. Animals can return to these patches within days to find the resource regenerated. However, large scale events such as vegetation transitions in rangeland systems, perhaps as a result of drought (Illius & Hodgson, 1996) require animals to adopt a flexible behavioural strategy in response to changes at any scale. Dumont and Hill (2001) successfully used a low memory devaluation rate in a stable environment to calibrate a model of sheep searching behaviour. By altering devaluation rate in response to variable patch conditions foragers could efficiently

track environmental change and incorporate the decreasing reliability of information over time (Beauchamp et al. 1997).

However, EWMA models have been criticised for producing scenarios of limited environmental realism (Kacelnik et al. 1987; Devenport & Devenport 1994). Devenport & Devenport (1993; 1994) developed a dynamic temporal weighting rule, avoiding the use of a floating parameter, as in the EWMA models and instead weighting patch experiences according to the rate of change of the environment. In an experiment with chipmunks (*Tamias minimus*) and ground squirrels (*Spermophilus lateralis*) Devenport and Devenport (1994) found that as the time since the last patch experience grew, animals relied less on their most recent patch experiences and foraged according to patch averages. This experiment also showed that the rate of change of the environment influenced patch choice. In environments where conditions changed only slowly i.e. a relatively stable environment, patch information was retained for longer. The simulation work by Hirvonen et al (1999) supported these findings. Devaluation of information should therefore be dependent on the rate of change of the environment.

THE USE OF INFORMATION UNDER SOCIAL CONDITIONS

Information loses value over time because the risk that the patch will have changed state increases with the time since the last visit. What causes patches to change? One explanation is the use of the same patch by competitors. For a social species such as the sheep, living in a group can offer many advantages. Principally, group living provides protection from predation through an increase in level of vigilance, and through dilution, the more animals in the group the less likely that an individual will

be captured (Krebs & Davies 1981; Olupot & Waser 2001). Group living can also influence foraging behaviour. There is increased opportunity for social learning (Nicol 1995) based not only on successful foraging but also where the conspecifics are unsuccessful (Templeton 1998).

Learning from others enables foraging animals to gain important information, aid decision making processes and track environmental change with increased efficiency, whilst minimising the risks of searching the environment and the consequent exposure to predation (Laland & Williams 1998). The study of social learning in sheep has been based around the acquisition of feeding preferences from kin and conspecifics in a group (Provenza & Balph 1987). During the early weeks of life the mother is the primary influence on the behaviour of an individual, for example, lambs exposed to wheat for one hour per day for 5 days in the presence of their mother consumed more wheat than lambs exposed without their mother and ingested 10 times more wheat after a period of three years with no intermittent exposure (Lynch et al. 1983). As the animal matures the influence of the mother diminishes and the presence of young conspecifics becomes increasingly important. At 7 weeks old, lambs are capable of learning from any adult conspecific (Lynch et al. 1992).

Foragers can therefore learn diet preferences from others - but how does the presence of conspecifics influence searching behaviour and patch choice in a heterogeneous environment? For an individual animal, knowledge about patch conditions may become less reliable with the introduction of competitors, adding an additional source of uncertainty. Conversely, learning about the existence of patches from conspecifics can increase the mean and reduce the variance in foraging success for

the group (Giraldeau & Beauchamp 1999; Stahl et al. 2001), hence increasing the available information and reducing environmental uncertainty. The information-sharing model of group foraging proposes that patch information is distributed evenly throughout the group and that the value of information increases as environmental patchiness increases (Clark & Mangel 1984). Whilst foraging, individuals remain alert to finds that other foragers are making, and move to join them. The best known example of this is Ward & Zahavi's information centre hypothesis (1973) explaining communal roosting in birds. Unsuccessful birds follow successful roost mates to rich but ephemeral food patches (Sonerud et al. 2001). In this model it is assumed that all animals are equally likely to find food and equally likely to join others. However, there is a high possibility that cheaters, animals that exploit the finds of others, will arise under these conditions. This alternative theory of group foraging is described as the producer-scrounger model, first proposed by Barnard & Sibly (1981). In this model, individuals use one of two tactics, producer - individuals that discover the food, or scrounger - individuals that do not search for food themselves but instead look for opportunities to exploit the finds of the producers, without incurring the risks of searching themselves. The payoffs for each tactic are strongly frequency dependent. Scroungers do better than producers when scroungers are rare in the group, but worse when scroungers are common (Mottley & Giraldeau 2000). In a study of foraging barnacle geese (*Branta leucopsis*) subordinate animals occupied leading positions in the group and therefore were first to encounter rich food sources, giving them a "finders" advantage. However, dominant geese quickly displaced the subordinates to monopolise the site (Stahl et al. 2001). In general dominant animals play the scrounger role and subordinate animals

the producer role (Barta & Giraldeau 1998) however, roles do not appear to be exclusive, an assumption of the producer-scrounger model. Individuals may shift opportunistically between producing and scrounging according to environmental conditions (Giraldeau & Lefebvre 1986).

Dominant animals are afforded the protection of a central position in the group (Hall & Fedigan 1997) while taking advantage of the information about patch resources from the subordinate producers. This was examined under controlled conditions with pairs of pigs (*Sus scrofa*) where the subordinate animal in a pair was given privileged knowledge about the patch positions and the dominant animal was uninformed. Subordinate animals were permitted to explore an arena where food was hidden in several bins. The dominant pig, with no previous experience of the arena was then introduced with the informed subordinate animal. It was found that uninformed pigs followed their informed companions and displaced them as the subordinates discovered food. As a result dominants consumed food more rapidly than predicted from a random search or from foraging alone (Held et al. 2000). It appears therefore that the use of public information in addition to personal information gained through sampling behaviour and previous experience can greatly enhance foraging efficiency (Templeton & Giraldeau 1996; Ksiksi & Laca 2000). However, as shown in the examples above, the benefits are highly dependent on the status of the individual within the group. Caraco et al (1989) carried out a study investigating the effect of co-foragers on intake rate in dark-eyed juncos (*Junco hyemalis*). In this experiment birds were given the opportunity to choose between social and solitary foraging. Subordinate birds had higher intake rates when foraging alone, and broke away from bouts of social foraging more often than dominant birds. In response dominant birds

tended to follow subordinates, initiating more than half the incidences of social foraging even when subordinates were feeding from poor patches. Group foraging is therefore more costly for subordinates than for dominants with subordinate animals experiencing lower foraging success (Smith et al. 2001) and lower bite rates (Thouless & Guinness 1986), possibly as a result of increased vigilance against attack. For subordinates to remain in a social group the benefits, for example, the potential to become dominant in the future, the increased protection from predation and the reduced variance in finding food must outweigh the costs of exploitation.

Methods of determining dominance relationships

How are dominant and subordinate individuals within the group identified? A proposed function of dominance hierarchies is to minimise aggression and the risk of injury in competitive interactions (Lynch et al. 1992). This was shown in examples above where subordinate animals relinquish their finds to dominants. Based on work by Schjelderup-Ebbe (1922, in Drews, 1993), Drews (1993) defines dominance as:

“...an attribute of the pattern of repeated agonistic interactions between two individuals characterised by a consistent outcome in favour of... ..a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and the loser subordinate”

The identification of dominance hierarchies under natural conditions is problematic, particularly given that a principle function of the hierarchy itself is to reduce escalated aggression. Where animals have been observed in the wild, assessment may centre on time budgets of animals, focusing on vigilance and foraging behaviour (Fournier & Festa-Bianchet 1995). A study of dominance in female red deer (*Cervus elaphus*) noted that subordinate deer feeding next to dominants had reduced feeding rates (Thouless & Guinness 1986). Festa-Bianchet (1991) found evidence for a relationship between dominance rank and age in bighorn sheep (*Ovis canadensis*),

but where age was controlled for in the analysis dominance was not correlated with reproductive success. Alternatively, wild animal studies follow direct agonistic interactions between focal group members (Eccles & Shackleton 1986; Festa-Bianchet 1991). Observing behaviour in the wild has the advantage of recording natural interactions. However, where resources are not restricted agonistic interactions may only occur infrequently.

Testing under controlled conditions has been extensively carried out on domestic species e.g. cattle (Arnold & Maller 1983); pigs (Lawrence et al. 1991; Brouns & Edwards 1994) and sheep (Erhard et al. 1998). These tests are frequently based on pair-wise competitive interactions for access to a limited food resource. Despite criticism for lacking realism (Craig 1986) pair-wise interactions for a limited food resource can provide useful information on the structure of paired relationships. Using the information obtained from observation of pair-wise competitive interactions, where all members of the group are in competition against each other, a dominance hierarchy can be formed from a win-loss matrix. The individual who is never supplanted in a pair-wise interaction is found at the top of the matrix and the individual always supplanted, at the bottom. Scores for the matrix may be calculated for number of wins, number of successful supplants within an interaction, or net number of aggressive acts directed towards the opponent. For example, for a group of three animals A, B and C, a matrix could be:

	A	B	C
A	-	1	1
B	0	-	1
C	0	0	-

where 1 indicates a successful supplant of another individual, and 0 indicates where an individual has been supplanted by another

This matrix is typical of a linear hierarchy exhibiting transitivity, where A supplants B and C, B supplants C, and C is subordinate to both A and B. Under most wild, and even controlled experimental conditions, perfectly linear transitive relationships are rare (Appleby 1983; Martin & Bateson 1993). Landau's index of linearity (h) can describe the extent to which a dominance hierarchy is linear, using the following equation

$$h = (12/n^3 - n) \cdot \sum (v_a - \frac{1}{2}(n-1))^2$$

where n is the number of individuals in the group, v_a is the number of individuals supplanted by individual a . A value of 1.0 represents perfect linearity.

However, Appleby (1983) has shown that the possibility of obtaining a linear hierarchy where none exists is greater than expected, i.e. that the dominance relationships between the individuals in the group have been observed by chance. In fact, due to the lack of degrees of freedom, a group of five or less individuals cannot be arranged in linearity at a significance of $P < 0.05$. A test of significance, adapted from Kendall (1962, *in* Appleby, 1983) is presented by Appleby (1983) to examine for the probability of a linear hierarchy occurring by chance and was developed by Devries (1995) to include ties or unknown rankings.

In foraging herbivores, food resources are generally not defendable and as such there is little evidence for dominance behaviour in domesticated sheep, particularly since groups of sheep tend to be of similar age and weight (Lynch et al. 1992). The high costs relative to the benefits of improving position in the rank for herbivores may prevent subordinate animals from challenging the established order. Thouless & Guinness (1986) note that

“the stability of dominance hierarchies is a result of weak and low ranking individuals accepting their position in preference to fighting for access to resources and losing”.

INDIVIDUAL DIFFERENCES AND THE PROPENSITY TO TAKE RISKY DECISIONS

Individual differences are not limited to the effects of dominance hierarchies on behaviour. The importance of individual differences has now been recognised in areas such as sexual behaviour (Zenchak & Anderson, 1980), sociability (Mills & Faure, 1990; Capitanio 1999), maternal behaviour (Dwyer & Lawrence, 1999) and aggression (Hessing, 1993). An important category of behaviour involves the propensity of individuals to make risky decisions, known as the shy-bold continuum. This behaviour was first recognised in humans (Kagan et al. 1988) and has been extensively studied. It was suggested that the high levels of arousal associated with risky behaviour interfere with decision-making processes (Addison & Schmidt 1999). However, under certain environmental conditions risk taking may be adaptive if the perceived benefits are strong enough. Studies on boldness have extended to other species: bighorn sheep (Reale et al. 2000), fish (Huntingford, 1976), cats (Feaver et al. 1986) and primates (Stevenson-Hinde et al. 1980) however examination of the shy-bold continuum has been carried out most extensively in the Pumpkinseed fish (*Lepomis gibbosus*) (Wilson et al. 1993; Coleman & Wilson 1998). In a laboratory experiment by Wilson et al (1993) individuals from a wild-caught population of pumpkinseed fish (*Lipomus gibbosus*) were grouped as shy or bold depending on their response towards a novel object placed in a familiar environment. This test is commonly used to assess boldness in children (Kagan et al 1988). The novel objects in this experiment were unbaited fish traps. Fish that entered the traps were described as bold and those that did not as shy. It was

predicted that those fish identified as being bold would be more likely to take risky decisions while foraging. It appeared that this prediction was upheld. After being marked and re-released into the original pond habitat it was found that bold pumpkinseed fish foraged at a greater rate and in a more risk prone manner than shy fish. In addition, when re-trapped and taken into the laboratory this pattern was again observed. However, once acclimatised to the laboratory no differences could be identified between the shy and bold groups (Wilson et al. 1993).

Wilson et al (1994) proposed that individual differences might be generated and maintained by variability in the natural environment, but that variation is lost when conditions become constant or predictable, such as those experienced in the laboratory. With this flexibility in behaviour, the fish are able to adjust their level of response to according to the frequency and density characteristics of the population. If an individual is feeding on a rich but ephemeral patch it will pay to be more risk prone to take advantage of that food source. In contrast, predictable environments, when the presence of food can be anticipated, favour shy-type behaviour to prevent the forager risking exposure to predation.

RISK SENSITIVE FORAGING – FORAGING WITH INFORMATION

Environmental stochasticity presents not only a problem of information for the forager, but also a problem of risk (Stephens & Charnov 1982; Caraco & Lima 1985). Even when a forager is fully informed about the values of different reward patches or the probabilities at which rewards might be offered, there still remains the problem of which foraging strategy to adopt to best exploit this knowledge. The fitness of the forager has been shown to depend on its response not only to the mean

long term intake rate offered by a patch but also to the variance of intake rate, a behaviour known as risk sensitivity (Caraco et al. 1980; Stephens & Charnov 1982). In an experiment with a small granivorous bird, the yellow-eyed junco (*Junco phaeontus*) Caraco et al (1980) showed that this species exhibited risk sensitive strategies dependent on the internal state of the animal. Two patches were offered to the birds within the aviary; one patch offered a constant reward, the other a variable reward, but with the same mean. If animals were maximising energy gains as predicted by optimal foraging theory, they should choose equally between patches. However, it was found after one hour of starvation, birds preferred the stable patch - risk averse behaviour, but after a longer period of starvation birds became risk prone - preferring the variable patch. This was explained by assuming that the birds were maximising their daily survival probability. Where the birds were at no risk of starvation, the best policy was to be risk averse. However, where there was a risk of starvation within that day, it was necessary for birds to choose the variable patch, as the mean reward offered by the stable patch was not sufficient to meet the birds' requirements. This is known as the "expected energy budget rule", and states that the forager should "*be risk averse if expected energy budget positive, be risk prone if energy budget negative*" (Stephens 1981).

However, there are a number of criticisms associated with this argument (Krebs & Kacelnik 1991; Bateson & Kacelnik 1998). For example, when starlings (*Sturnus vulgaris*) were presented with patches varying in food amount they were risk averse but with a delay to reward were risk prone, suggesting that the energy budgets of starlings could not solely account for the observed behaviour (Reboreda & Kacelnik 1991).

An alternative, mechanistic approach (as opposed to the functional energy budget rule) to account for risk sensitive behaviour is the Scalar Expectancy Theory (SET) (Gibbon 1977; Bateson & Kacelnik 1998). This model is based on the information processing abilities of the forager and centres on the scalar property of Weber's Law, which states that the standard deviation of a forager's estimate (of either amount of reward or time to reward) is proportional to the value of the parameter being estimated. The forager stores a distribution of, for example, the time intervals before reward in its memory. A normally distributed memory representation is stored for a fixed stimulus such as the stable patch but for a variable stimulus the median distribution is skewed to the left of the arithmetic mean (Bateson & Kacelnik 1995). With this information the forager chooses a patch by drawing a random sample from the memory distributions associated with both the constant and variable patch types. As a result of the probability distributions, higher values are normally associated with the constant patch and lower values with the variable patch. Therefore, when selecting for a patch offering the greatest reward the forager will prefer the patch offering the highest value, the constant patch. In contrast, when selecting for a time delay the forager will prefer the lowest option, the shortest time and hence the variable patch.

SET cannot, however, account for all observed behaviour, in particular the effect of energy budget on risk sensitive behaviour (Reboreda & Kacelnik 1991). To address the problem of conflicting predictions based on evolutionary or cognitive explanations of behaviour, Bateson & Kacelnik (1998) call for the incorporation of both mechanistic and functional aspects in future models of risk sensitivity.

RELIABLE INFORMATION IN PREDICTABLE ENVIRONMENTS: THE USE OF SPATIAL MEMORY

Where food resources occur in a highly stable temporal and spatial distribution, memory can be used to guide future foraging decisions. The ability to recall events and use memory is the basis for learning (Shettleworth 1998). A familiar example of memory at work is the caching behaviour of corvids and parids. Clark's nutcracker (*Nucifraga columbiana*) is a member of the Corvidae family of birds from the montane habitat of North America. Like other corvids, the nutcracker buries thousands of seeds over late summer, returning to the caching sites in winter and spring to retrieve the seeds. The caching sites are underground, protected from the elements and competing foragers. The over-winter survival and reproductive success of the Clark's nutcracker is dependent on the ability to relocate the sites several months later often retrieving up to 70% of the previous years store (Vander Wall & Balda 1981; Kamil & Roitblat 1985). The foraging environment for these birds represents a highly stable and predictable environment over both spatial and temporal scales. However, for all foragers in spatially heterogeneous environments, the ability to remember the location of high quality patches can improve foraging efficiency (Bailey et al. 1996). Memory in foraging herbivores can be considered at two levels. "Working memory" refers to short-term memory for sites of high quality within the foraging environment. An experiment carried out with steers (*Bos taurus*) found they were capable of associating sites within a maze with food sources and remembering these locations for up to 8 hours (Bailey et al. 1989a). Working memory allows foragers to avoid recently visited sites and, therefore, exploit the environment more efficiently. "Reference memory" is the long-term memory that foragers have of their

environment and is used to relocate patches after a break from foraging. Laca (1995) showed that reference memory can persist for up to 20 days in foraging steers presented with a relocation task. Evidence of spatial memory has been found in other herbivorous species. Black-tailed deer (*Odocoileus hemionus columbianus*) repeated previously successful search paths to relocate food items in an enclosure, resulting in foraging efficiency greater than expected by chance (Gillingham & Bunnell 1989). Cattle were capable of relocating food patches in radial and parallel arm mazes and of ordering their choices from large to small rewards (Bailey et al. 1989a; Bailey et al. 1989b). Sheep consistently returned to food patches over a six day period, were flexible in relearning locations when food distribution changes and could use cues to help make foraging decisions (Edwards et al. 1996). Approaching a more natural system, Dumont & Petit (1998) created high quality resource sites using concentrated feed within a natural pasture. The study found that sheep visited more sites and consumed more concentrate with increased experience of the feed distribution. In addition the sheep repeated a previously successful search path and showed area concentrated searching behaviour. Dense sites were exploited more efficiently than sparse sites. The studies of spatial memory in herbivores show, where food is distributed in a stable and predictable manner, animals are capable of learning this distribution and exploiting pasture heterogeneity.

CONCLUSIONS

The field of foraging behaviour has been extensively examined for a range of species and within a range of models. However, for foraging herbivores there is little verification of information gathering strategies used in complex and heterogeneous

environments. Complexity arises from variation in the availability, predictability and quality of resources, of the social environment and of degradation of resources with time. Successful foraging requires that animals can overcome this resource uncertainty to efficiently exploit their environment.

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CHAPTER 3

PREFERENCE OF SCOTTISH BLACKFACE EWES FOR COMMONLY ENCOUNTERED FOODSTUFFS: GOOD QUALITY GRASS HAY AND GREEN KEIL PELLETS

INTRODUCTION

The aim of this trial was to establish if sheep exhibit a preference between good quality hay and a concentrated pelleted sheep feed. Pelleted rations are appropriate to use under experimental conditions as they allow greater control over the presentation of feed and accuracy in recording results (Edwards et al. 1994). As a result of this convenience pellets have been used in a range of experiments examining motivational behaviour in foraging animals (e.g. sheep-Edwards et al. 1994; Edwards et al. 1996; Dumont & Petit 1998; cattle-Laca 1998). In the experiments reported below (Chapters 4-7) a strong preference for pelleted food rations over hay was necessary to provide a sufficiently powerful motivational force to direct foraging decisions in sheep in an experimental environment.

MATERIALS AND METHODS

Animals and Housing

Five 2 year old Scottish Blackface sheep were tested for feed preference in this experiment (mean live weight \pm SD=53 \pm 2.25kg). This group had previously been kept at pasture but all animals were familiar with both the pelleted concentrate and chopped hay used in this experiment. During the experiment the sheep were kept on maintenance rations, with the feed ration calculated according to the equation $0.435\text{MJ/kgLW}^{0.73}$ (MAFF 1984). Sheep were housed and tested in individual home

pens within visual contact of other animals. They were familiar with individual housing and consuming hay and pellets from feed bins similar to those presented in the test. The sheep had continuous access to drinking water in the home pens.

Experimental set-up

Tests were conducted twice per day, at 10:00h and 15:00h in the home pens of the sheep. Two feed bins were simultaneously placed in the pen. One bin contained 700g concentrate pellets (12.5MJ/kj/DM: Green Keil, NorthEastern Farmers, Rosehall, Turriff, Scotland) and the other, 200g good quality chopped hay. These values were based on pilot tests and allowed maintenance of intake rate without significant depletion of either feed type over the trial period. Bins were consistently used for one feed type only. All food was removed from the animals one hour before the five-minute preference test. After this time the bins were removed and re-weighed to the nearest gram.

Experimental Design

The sheep were tested in a balanced design accounting for position of the bins and time of day effects. The five sheep were tested twice per day over a four-day period resulting in a total of 40 trials.

Measurements

Food rewards

Samples of hay and pellets were oven-dried, and weighed. Samples were milled to 1mm and analysed for neutral detergent fibre (NDF) (Goering & Van Soest, 1970), organic matter digestibilities (OMD), metabolisable energy (ME) concentration

(Gallenkamp, FIS, Crawley, UK) as described by Blaxter (1962) and elemental nitrogen (N) (Pella & Colombo 1973) (Table 3.3).

Intake of each food type was based on the difference between pre and post-test feed weights measured to the nearest gram. Preference for food type was determined by proportion of the weight of food consumed over the five-minute period.

Statistical Analysis

Where animals fed from only one bin (this only happened during one trial, where no hay was consumed) a value of half the minimum previous hay consumption (5g) was assigned to the hay patch (2.5g), and removed from the pellet patch, so the total consumed remained the same. This enabled the use of log ratio analysis by preventing zero values of preference arising. Firstly, a preference value for each food type was calculated and expressed as a proportion of the total feed consumed and therefore varied between 0.0 and 1.0. Cases of non-discrimination resulted in a value of 0.5 (Bell 1959). To test the hypothesis that preference for pellets was significantly different to preference for hay, a paired t-test was carried out.

With proportional analysis, as described above, preference over a range of food types must sum to 1. This is known as the unit-sum constraint. As a result, preference for one feed is always linked to the other. For example, as preference for one feed increases, preference for the alternative consequently decreases (Aebischer et al. 1993). Log ratio analysis overcomes this by transforming the observed preference values onto an unconstrained scale and also accounts for lateral preferences of individuals. Non-discrimination in this case would result in a value of zero.

Preference values were converted to log-ratios according to the equation:

$$\log \text{ ratio} = \log (p_A/p_B)$$

where p_A = proportion of total feed consumed as pellets and p_B = proportion of total feed consumed as hay (Elston 1998; Illius et al. 1999). Variation in preference was determined by fitting a linear regression model in Genstat (Genstat 5 Committee 1998) containing the terms: individual sheep, effect of day, position of feed bin containing pellets, run number and the interaction of sheep and position. Log-ratios were back transformed to compare individual differences between the sheep using the standard error value.

RESULTS

The animals exhibited strong preference for pelleted food (mean preference value for pellets=0.930, SE=0.006) (Table 3.1). The preference for pellets was significantly greater than the preference for hay ($t_4 = 32.27$, $P<0.001$).

Table 3.1: Results of the three preference methods

Sheep	p_A	Log ratio	Back-transformed preference value
1	0.913 (\pm 0.006)	1.03 (\pm 0.033)	0.737 (\pm 0.006)
2	0.915 (\pm 0.007)	1.042 (\pm 0.038)	0.739 (\pm 0.007)
3	0.906 (\pm 0.006)	0.989 (\pm 0.03)	0.729 (\pm 0.006)
4	0.98 (\pm 0.006)	1.79 (\pm 0.105)	0.853 (\pm 0.014)
5	0.936 (\pm 0.01)	1.214 (\pm 0.092)	0.768 (\pm 0.015)
Mean (\pm SE)	0.930 (\pm 0.006)	1.213 (\pm 0.072)	0.765 (\pm 0.011)

Log ratio analysis gave a mean value of 1.213, and correspondingly -1.213 for hay. The regression analysis of the log ratios found individual sheep to be the only factor significantly accounting for a difference in preference ($F_{4,35} = 28.69$, $P<0.001$). There was no evidence that day or time of day effects (run) explained any of the variation observed. Neither position of the pellet bin nor any interaction between position and

individual sheep had an effect. This indicated that the sheep showed insignificant levels of lateral preference (Table 3.2).

Table 3.2: Analysis of variance table formed by adding terms in the order shown to a regression model for the log ratio preference data

Change	df	ms	Variance ratio	F-prob.
+ sheep	4	0.89	28.69	<0.001
+ day	3	0.08	2.71	0.069
+ run	4	0.04	1.31	0.295
+ pellet side	1	0.06	2.01	0.169
+ sheep.pellet side	4	0.02	0.69	0.609
Residual	23	0.03		
Total	39	0.12		

Differences between individual sheep were calculated from back-transformed log ratio preference values using the standard error value.

Sheep 4 showed significantly higher preference values than all other sheep. Sheep 1, 2 and 3 showed the same level of preference. Sheep 5 showed a higher level of preference but not significantly different from sheep 3.

In summary all animals showed a highly significant preference for pellets but this varied between individuals.

Chemical analyses of the feeds are shown below (Table 3.3).

Table 3.3: Chemical composition of feeds (g kg⁻¹ OM)

Feed type		OMD	NDF	N	ME
Hay	(mean)	57.54	71.09	1.26	17.95
	SD	2.99	3.11	0.01	1.21
Pellets	(mean)	75.81	31.84	3.04	18.67
	SD	4.01	1.47	0.02	0.89

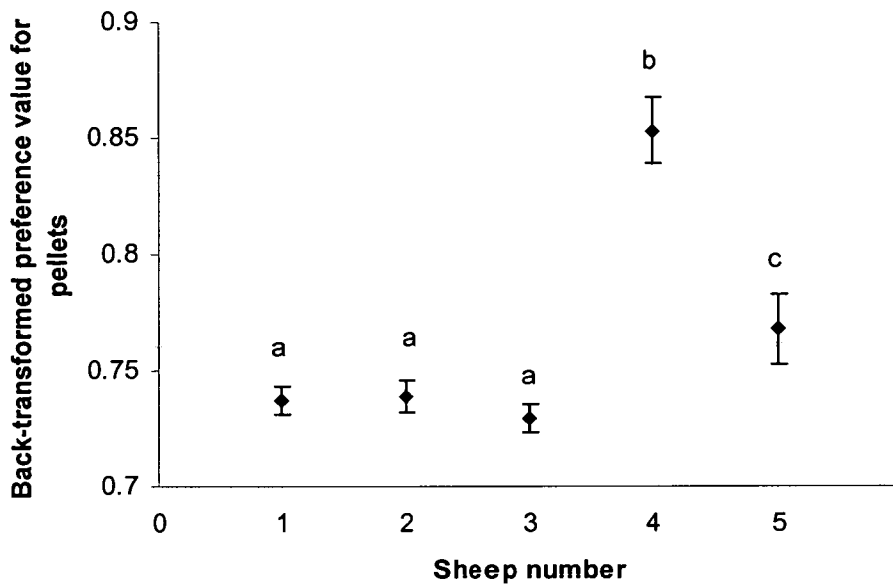


Figure 3.1: Graph showing individual differences in preference between sheep (Means \pm SE).

DISCUSSION

It is likely that pellets are preferred over hay by the sheep due to their high digestibility (Belovsky, 1978), higher protein content and lower fibre (Table 3.3). In addition, although energetic values of the two feeds are similar, the pellets are denser and more easily manipulated by the feeding sheep. Crude preference values were calculated following the procedure used by Bell (Bell 1959). Goatcher & Church (1970) classed values of 0.8 or above as 'strong preference', between 0.8 and 0.7 as 'moderate preference' and between 0.7 and 0.6 as a 'weak preference'. With the mean crude preference value here of 0.903, this suggests the sheep had a strong preference for the pellets. This supports other studies that use pellets as a preferred food source in manipulation experiments.

The log-transformed value obtained in the pellet and hay choice trial can be also compared with previous results on diet preference in grass species, by Illius et al (1999). Here, preference of goats (*Capra hircus*) for *Anthoxanthum*, *Agrostis*, *Deschampsia*, *Festuca* and *Holcus* species was examined. It was found that *Festuca* and *Deschampsia* were the most highly preferred, and *Holcus* and *Agrostis* were strongly avoided. For example, the choice between *Deschampsia* and *Holcus* gave a log-ratio value of 3.34 for *Deschampsia* and hence -3.34 for *Holcus*. This back-transforms to a preference value (where the proportion of a species consumed when paired with itself is 0.5) of 0.97 for *Deschampsia* over *Holcus*. Illius et al (1999) attributes the variation in preference for grass species largely to dry matter intake rate. When compared with the values found in the current experiment with hay and pellets, at a log ratio value of 1.78 (pellets) and back transformed value of 0.717, the relationship between hay and pellets is strongly favoured towards pellets.

Although all sheep showed a strong preference for pellets in this test, there was a difference in the strength of the preference across the group. Where one sheep favoured the pellets more strongly this could affect decision making in the main choice experiment, with sheep more willing to take a risk to obtain pellets. As such, individual differences in the main choice experiments may be attributed to differences in level of preference for the pellets.

For the purposes of the following experiments, it was important to strike a balance between the preference for pellets over hay. Pellets had to provide a highly motivating force for the sheep in an uncertain foraging situation. However, it was also important that the hay provided an acceptable alternative to pellets where sheep,

in response to the experimental treatment, were unwilling to take a risk. A transformed preference value of 0.717 suggests a good balance.

SUMMARY

For the purposes of experiments presented in Chapters 4 and 6 it was necessary to ensure that sheep selected one feed type preferentially over another. A feeding test was carried out on a group of sheep to determine the level of preference for green keil concentrated feed pellets over good quality hay. Sheep showed a strong tendency to select pellets over hay ($P < 0.001$), however, preference varied between individuals. Overall, the strong but not absolute preference for pellets over hay ensured that sheep were motivated to feed on pellets, but that hay provided an acceptable alternative.

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CHAPTER 4

FORAGING SHEEP ADAPT THEIR PATCH LEAVING DECISIONS IN RESPONSE TO ENVIRONMENTAL QUALITY AND UNCERTAINTY

INTRODUCTION

Natural environments are characterised by heterogeneity: between plant communities, animal populations and the resources available for exploitation (Freidel 1994). Large herbivores face an environment in which nutrients are widely distributed at low density (Senft et al. 1987) and disrupted by indigestible and toxic plant materials (Illius & Gordon 1990). Within this heterogeneous environment, there is evidence that grazing animals select diets based on the nutritional quality and quantity of the forage (Gordon & Illius 1992). Maximisation of intake rate depends on the ability of the forager to exploit these factors under conditions of environmental variability (Pyke 1984; Gordon & Lascano 1993).

A cluster of preferred bites could be considered a resource patch (Bailey et al. 1996) and it is the efficient exploitation of resource patches that influences foraging behaviour (Roguet et al. 1998). A forager capable of maximising the trade-off between the costs of leaving a depleting patch as against the benefits of finding an under-exploited patch will be at an advantage. So how is this achieved?

Optimal foraging models assume that animals have a complete knowledge of the environment (Pyke 1984). However, limitations in the sensory and information processing capabilities of the forager, and the stochastic nature of the environment result in a problem of uncertainty (Stephens & Krebs 1986; Nishimura 1992). How does a foraging animal overcome this problem? Fixed decision rules, such as “stay in



a patch for a set time” may work well where the environment is stable or predictable. Alternatively using information gained from previous foraging experiences i.e. learning, is a means of overcoming the uncertainty associated with variability in the environment (McNamara & Houston 1985). If learning about the environment improves foraging efficiency, information acquisition becomes an important activity (Ljungberg & Enquist 1986).

The present study focuses on this problem of information acquisition for foraging herbivores in an uncertain environment. The study animal was the Scottish Blackface sheep. The following objectives were based on the ability of the sheep to adjust their patch-leaving behaviour when patch conditions were more or less predictable and varied in potential reward. The objectives of the experiment were (1) to determine if sheep could assess the relative quality of an alternative patch when conditions were more or less predictable and (2) to determine the information used by the sheep to achieve this. During the experiment the quality of the alternative patch changed at regular intervals, allowing the investigation of learning behaviour as the sheep accumulated new information. The third question then was (3) when environmental quality changed, how did the sheep respond?

MATERIALS AND METHODS

Animals and housing

This experiment took place at Glensaugh Research Farm, Scotland (56°N 2°W) between October and December 1999. The subjects were the five yearling Scottish Blackface ewes (mean live weight at the start of the study \pm SD=55.6 \pm 3.4kg) that received the preference test described in Chapter three. The sheep were housed in

individual pens within visual contact of non-experimental conspecifics. During the experiment the animals were fed to maintenance via a morning feed and any food eaten during the training and experimental period, with the remainder fed in the evening. The feed ration was calculated according to the equation $0.435\text{MJ/kgLW}^{0.73}$ (MAFF 1984). The sheep were familiar with feeding from the bins used in the test. It was not necessary to restrict the diets of the sheep, as they were motivated to perform the task. In addition, there is evidence that fasted animals may select a less preferred diet to overcome a short-term hunger, which may confound the results of a patch choice experiment (Edwards et al. 1994; Dumont & Petit 1995). However, to ensure that all animals were equally motivated to perform the feeding task, any excess food was removed from the feed bins 60 minutes prior to the first test. The sheep had continuous access to drinking water in the home pens.

Food rewards

The food rewards used in this experiment were good quality chopped hay, a food reward of intermediate preference and a pelleted food ration (Green Keil, NorthEastern Farmers, Rosehall, Turriff, Scotland), a highly preferred reward. Sheep were familiar with these foods. The preference of the sheep for pellets over hay was established in a preference test (Chapter 3).

Initial training

Over a five-day period, animals were released into the experimental arena (Figure 4.1) to gain familiarity with the human handler, the test environment, feeding regime and to foraging individually. Individual runs in the arena initially lasted one minute but as the sheep became accustomed to the procedure this was increased to five minutes. For the first four days two feed bins were available and both contained hay.

Four trials per day took place. On the final day of initial training the variable bin was provisioned with pellets on two of the four runs. The pattern of provisioning was the same for all sheep. The dividing gate between the arena sections was closed as the sheep moved round. This training period allowed the sheep to learn the presence of two food patches and the behavioural consequence of the “no return” gate.

Experimental set-up

The foraging environment was simulated in an enclosed arena within a farm building (Figure 4.1, Plate 4.1).

Data recording

To minimise disturbance to the animals during the trial all runs were recorded on four video cameras. The cameras were connected to a quad, which allowed all images to be displayed on a monitor at the same time (Plate 4.2). The arrows shown on Plate 4.1 indicate the direction of the camera image.

All further experiments described in this thesis were video recorded in the same way.

Arena set-up

The arena measured 11m by 6m and was divided down the centre by a partition 9.5m in length. On entering the arena an individual sheep was faced with the stable patch, a large bin containing 500g of high quality chopped hay. Moving around the partition the sheep found the variable patch that may or may not have contained 50g of food pellets. Once the animal had made the decision to move from the stable to the variable patch, a gate at the top of the arena closed to prevent return to the stable patch. This was to ensure that taking the decision to move from the stable patch to the variable patch entailed some form of risk for the forager, namely that of missed opportunity to feed on the hay if the variable patch was empty. To eliminate the risk

of the animal identifying the presence of food through smell, pellets were placed outside the arena, near to the variable patch. The animal was unable to see into the variable patch from the stable patch.

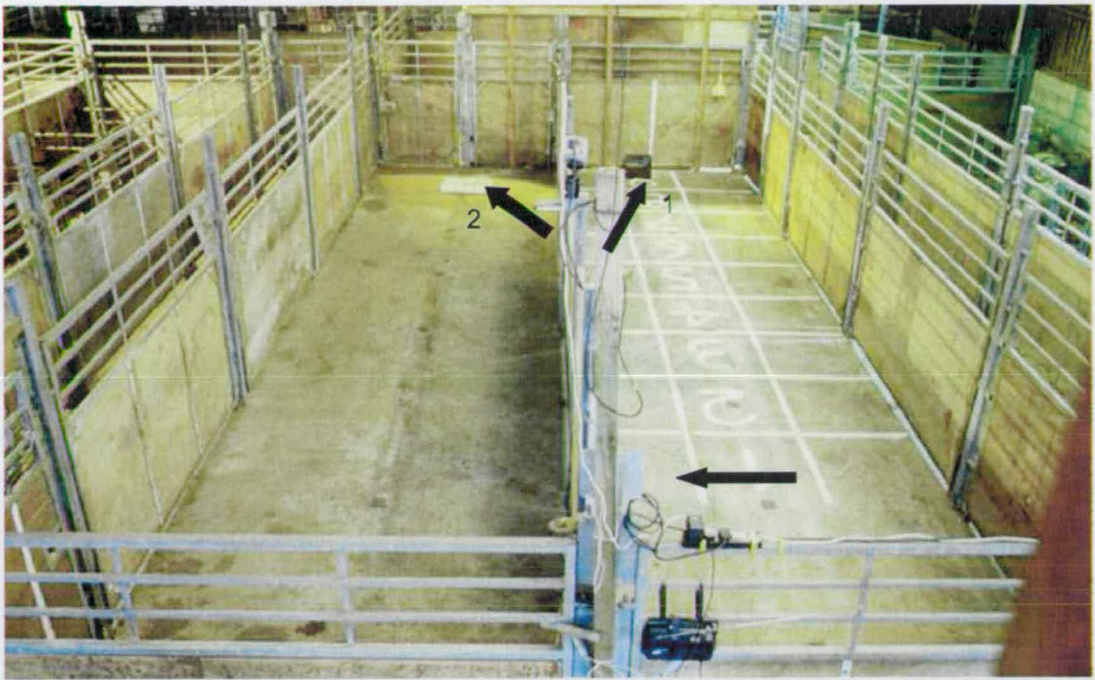


Plate 4.1: The experimental arena

← Arrows represent the camera view. This can be compared with the monitor view. The 4th camera was located above the arena. Plate 4.1 shows the image from this camera.

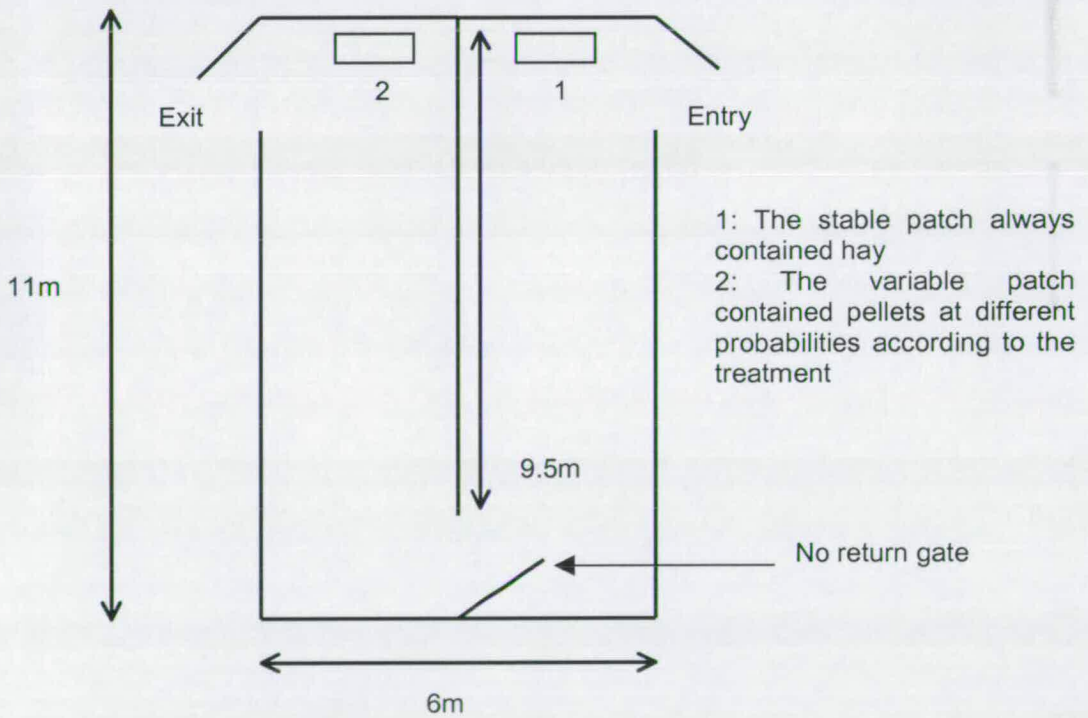


Figure 4.1: The experimental arena



Plate 4.2: The video set-up showing the 4 camera views displayed on the monitor

Experimental design

To simulate an environment, in which reward varied in predictability, five probability treatments were imposed upon the sheep. These probabilities were presented by varying the reward from the variable patch between '1' (50g feed pellets) and '0' (empty) according to the particular probability treatment, described below:

Treatments

These treatments were 0, 0.25, 0.50, 0.75 and 1 probabilities of the patch being encountered with pellets. For each treatment, four patterns of presentation were

established and rotated in a balanced order for each day of the treatment. Each sheep had four runs in the arena per day, experiencing one pattern per day according to their probability treatment. For example, a sheep on treatment 0.25 would have four runs in a day, with a possible presentation in the variable patch of 0, 0, 1, 0 (See Appendix D).

Time periods

Each sheep experienced a different probability during each of five experimental periods, with all sheep experiencing all probabilities in a Latin square design.

Buffer Days

A period consisted firstly of three training days of four runs per day, during which the animal was permitted to explore the arena and which operated as a buffer period to mitigate the effect of the previous treatment. During the buffer period, the variable patch was provisioned with pellets according to the treatment in that period (Appendix 1). However, in the buffer period, if the sheep did not move to the variable patch within the allotted time period, she was pushed round by the human observer.

Test Days

The second part of the period was five days of experimental runs, with four runs per day. In this section the observer did not interfere with the behaviour of the sheep for the five minutes of the test.

Treatment period

Each treatment period was therefore eight days long, a total of 32 runs per sheep per period. The presentation order of probability treatment and pattern for individual sheep was structured to minimise confounding effects.

Trials

A run began with the introduction of the sheep into the arena, and terminated when the sheep exhibited any of the following behaviours:

1. Fed only on the stable patch until the maximum time limit of five minutes was reached. A limit was placed to reduce the effects of satiation.
2. Moved around to the variable patch, and hence made the decision to leave the stable patch in favour of the variable. If the sheep had made the decision to move and the variable patch was full, the sheep was permitted to feed until the patch was depleted before being returned to the pen.
3. Appeared to have finished feeding, and was exhibiting other non-feeding behaviours

Measurements

Feeding behaviour was recorded by eye and by video. Details of sheep number, trial number, treatment tested, date and time of observation were recorded. During the trial, time spent feeding on the stable patch and variable patch, time of arrival and leaving each patch, times spent walking and idle (or other activities, such as abandonment of feeding), were recorded. Food weights before and after each trial were recorded to the nearest gram for both the stable and the variable patch.

Statistical analysis

Patch leaving decisions

This analysis was carried out to assess the effect of probability treatment on the patch-leaving behaviour of foraging sheep. The dependent variable used to measure the response of the sheep was the quantity of hay in grams consumed (“hay eaten”) before leaving the stable patch. The data used in this part of the analysis was taken

from the last five experimental days of the eight-day period. The first three days of each period were considered a buffer period and were analysed separately. Analysis was made using REML (REsidual Maximum Likelihood) in Genstat (1998). This technique was used because the carryover effects from one period to the next were not fully balanced. REML estimates the components of variance corresponding to all strata in the analysis and then assigns appropriate weights to comparisons. In this way information on treatment effects is combined across strata. Significance levels were determined using the Wald statistic (Elston 1998). The Wald statistic has an asymptotic chi-squared distribution with degrees of freedom equal to those of the fixed model term. The statistic determines the change in fit of the model when a new term is added to the current model containing all the previous terms.

“Hay eaten” was the response variate in the model. Predicted effects (described below), treatment, the state of the alternative patch on the previous run and run number were considered in the fixed model and individual sheep, period and their interaction in the random model. To satisfy the REML assumption of equal variances across treatments, a square root transformation was carried out. To investigate the fixed factors in more detail, the effect of run number within treatments was examined. REML analyses were carried out for each treatment with a fixed model of run number, and previous state, and the random model of sheep. Period was not included in this analysis because it was aliased with sheep. Again the variate tested was “hay eaten”, the quantity of hay consumed before leaving the stable patch.

Predicted behaviour

A model was developed to predict the behaviour of the sheep assuming no individual differences in behaviour and absolute preference for pellets. The results of hay eaten

for all sheep within the five-day experimental runs for treatments 0 and 1 were combined to produce a regression plot assuming that sheep were responding to their most recent experience in the variable patch. “Hay eaten” for the intermediate probabilities was extrapolated from this plot on the assumption that sheep responded to an average of their most recent experience. These predicted results were included in the Wald analysis as a continuous fixed effect and compared with those observed during the experiment.

Learning about the environment

This analysis was carried out to assess the capacity of sheep to respond to changing patch state and investigate if response varied with the direction of change of patch quality. The probability treatments were divided into groups “high” and “low”, where high was groups 0.5, 0.75 and 1.0 treatment probabilities and low was 0 and 0.25. This division was made on the basis of the analysis above. The average quantity of hay eaten for each run from the last 12 runs of the previous experimental period through the first 12 runs of the following period, or the buffer period, was taken for all sheep. This data was plotted as hay eaten over time and a regression equation calculated for each of the buffer periods; low to high and high to low. The slopes of the regression were compared with Students t-test.

Walking speeds

This analysis was carried out to examine the walking speed of the sheep under different probability treatments. Analysis of variance (ANOVA) was used. The time to walk between two points in the arena of a known distance apart was measured as the variate. The blocking factor was period plus individual animal nested within

period. Significant differences between levels of the treatment were identified using least significant differences (LSD) at the 5% level (Snedecor & Cochran 1980).

Individual differences

A one-way ANOVA was carried out to determine if individual sheep differed in their response to the test environment. The response variate was “hay eaten” when the probability treatment was 1. Only this probability treatment was used as it most closely represented the direct preference test, where both feeds were available and predictable. Significant differences between individual animals were identified using least significant differences (LSD) at the 5% level (Snedecor & Cochran 1980).

RESULTS

Patch leaving decisions

Sheep were seen to consume more hay when the probability of the variable patch containing pellets was low, and less hay when the probability of pellets was high. Thus, exploitation of the stable patch, in terms of the amount of hay consumed before leaving was strongly influenced by the probability of pellets being present in the variable patch ($W_4=13.825$, $P<0.001$; Figure 4.2). This difference lay between the 0 and 0.25 treatments and the other higher treatments (0.5, 0.75, 1), determined through analysis of least significant differences between the means of hay eaten across treatments (SED=9.924, df = 4)

Exploitation of the stable patch was also influenced by the state of the variable patch on the last visit. More hay was consumed at the stable patch when the variable patch was found to be empty on the last visit ($W_1=9.8$, $P=0.001$). However the second

($P=0.370$) and third ($P=0.681$) most recent patch experiences did not have a significant effect on the stable patch exploitation.

Over the five-day period, there was a change in stable patch exploitation, with the amount of hay consumed before leaving changing with run number, suggesting a learning effect over time ($W_{19}=1.789$, $P=0.02$). To test the hypothesis that learning about the environment occurred more quickly in more predictable patch treatments the effect of run number on hay eaten was examined within treatments. The only treatment where run number significantly affected the level of patch exploitation was 0.5 ($W_{19}=1.76$, $P=0.021$).

Previous treatment, the probability treatment before the current treatment did not have a significant effect on the amount of hay consumed before leaving the stable patch

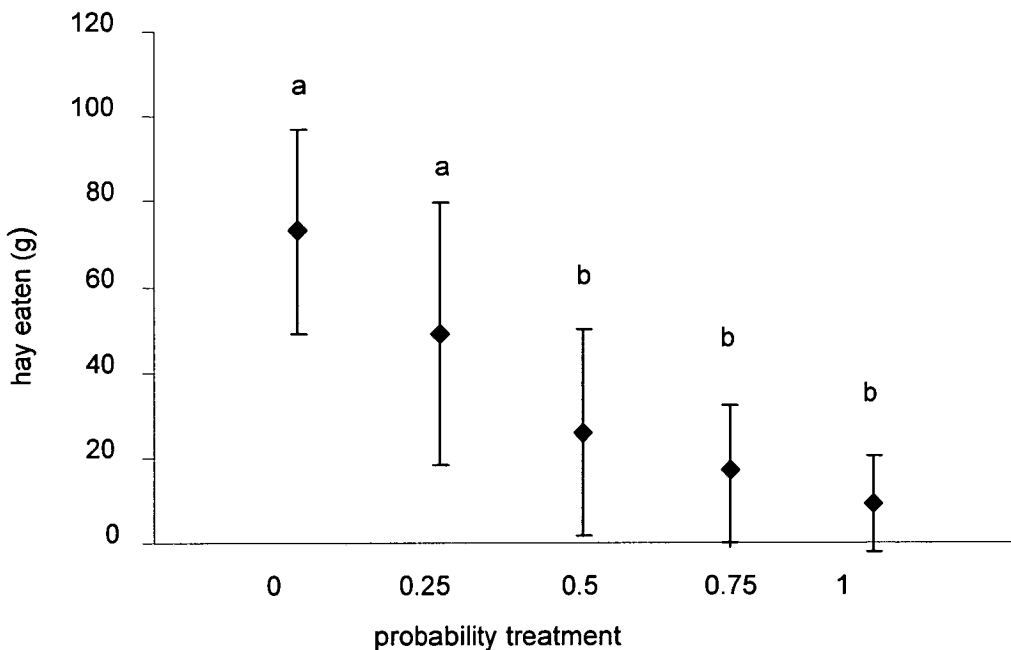


Figure 4.2. The amount of hay eaten across sheep and periods for different probability treatments. Means are shown with standard error bars. Means with different superscripts vary ($P < 0.05$)

Expectation

Figure 4.3 shows a plot of predicted behaviour based on the response variate “hay eaten”. The plot was based on the results of the trials for all animals at the probability treatments 0 and 1, as these probabilities represented a predictable environment.

On the basis of the regression equation for Figure 4.3, predicted values for the intermediate probability treatments were calculated (Table 4.2).

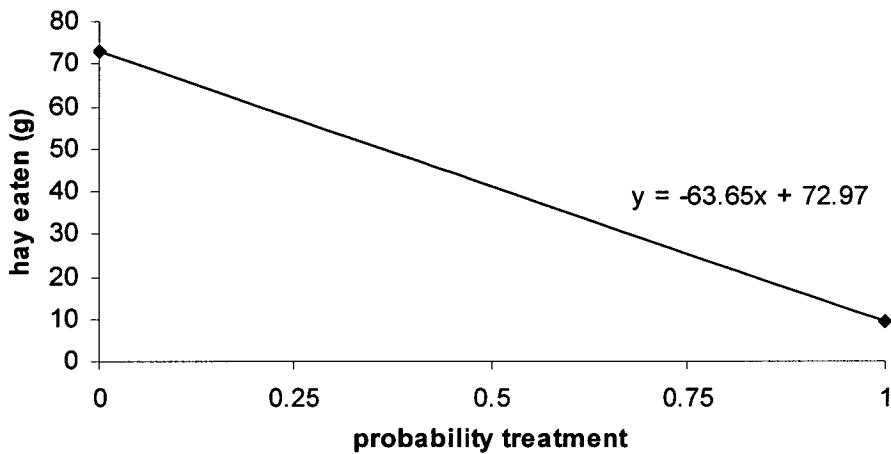


Figure 4.3: Prediction of hay eaten across the probability treatments based on the results of hay eaten for the predictable treatments 0 and 1.

Table 4.2: Predictions for “hay eaten” from regression equation

Probability treatment	Predicted “hay eaten”(g)
0	72.97
0.25	57.05
0.5	41.14
0.75	25.23
1	9.32

How did the results of the test compare to those predicted?

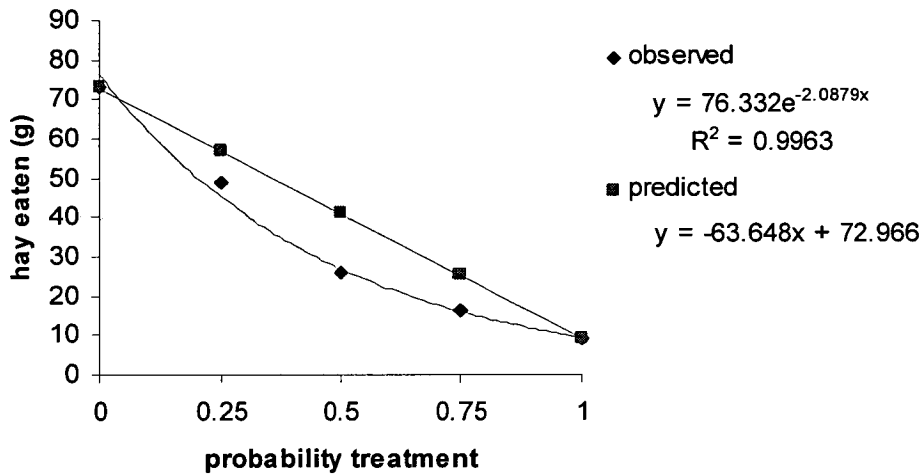


Figure 4.4: Comparison of observed and predicted results

Although all the observed “hay eaten” values for intermediate treatment probabilities fell below those predicted given complete knowledge of the environment, this difference was not significant ($P=0.170$).

How did sheep respond to change in patch quality?

To investigate the learning behaviour over time in more detail, the behaviour of the sheep during the three day (12 run) “buffer” period was examined. On the basis that there was no significant difference in the response variate between 0 and 0.25, and 0.5, 0.75 and 1 probability treatments, the data for the treatments were divided into low (0, 0.25) and high (0.5, 0.75, 1). Graphs 4.5 and 4.6 show the change in average “hay eaten” during the final 12 runs of the previous treatment, followed by the first 12 runs of the new treatment, the buffer period. The transition in response to the variable patch as conditions change is clear, however there is a significant difference between the gradients of the slopes (Students t-test: $t_{0.05(2),20}=3.85$, $P<0.01$). This

shows that the sheep are responding more strongly when the change in treatment was from high to low (Figure 4.5), compared to a change from low to high (Figure 4.6).

Walking speed

Sheep walked at different speeds to the variable patch according to their expectation of patch quality ($F_{4,12}=11.39$; $P<0.001$; Figure 4.7), with sheep walking more slowly to the variable patch when they expected a low probability of pellets. Analysis of least significant differences found that sheep on treatments 0 and 0.25 walked significantly slower than sheep on treatments 0.5, 0.75 and 1.

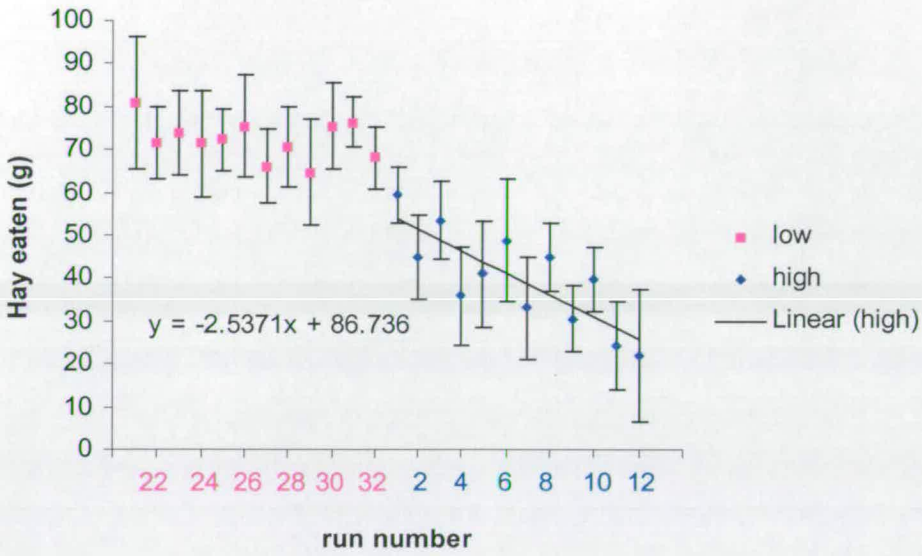


Figure 4.5 Change in treatment from low to high. 21- 32 represent the final runs of the last period, 1 – 12 represent the 12 runs of the buffer treatment (Means of hay eaten \pm SE).

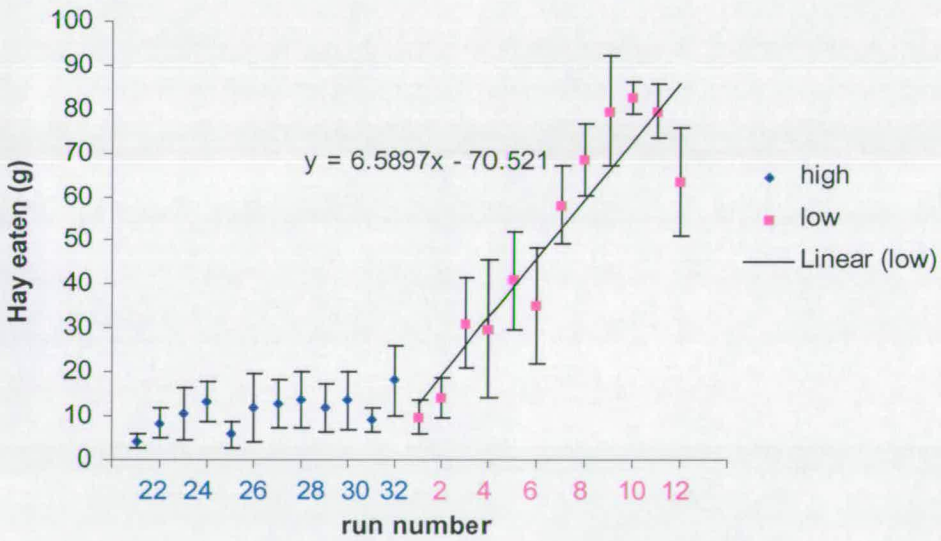


Figure 4.6 Change in treatment from high to low (Means of hay eaten \pm SE).

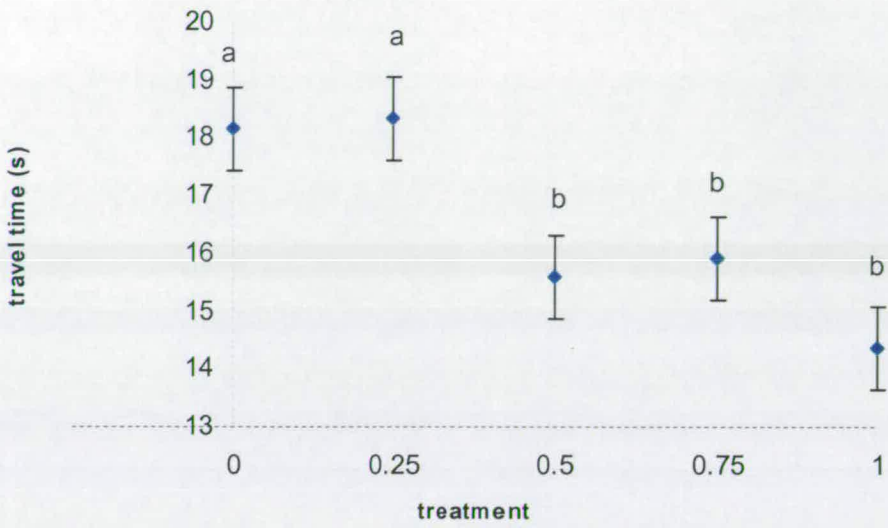


Figure 4.7: Travel time differed between the low treatments (0 and 0.25) and high treatments (0.5, 0.75, 1). Means with different superscripts vary ($P < 0.05$)

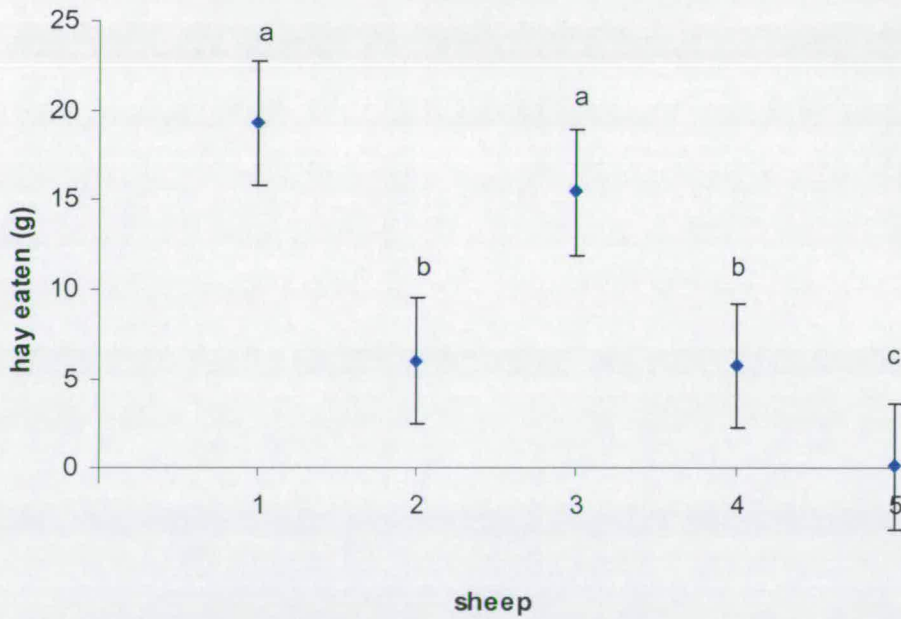


Figure 4.8: Individual differences between sheep in the “hay eaten” at probability treatment 1. Means with different superscripts vary ($P < 0.05$)

Individual differences

Individual sheep differed in their response to the test environment ($F_{4,95}=15.44$, $P<0.001$; Figure 4.8) when controlling for treatment. Sheep 1 and 3 tended to remain at the stable patch for longer, consuming more hay than the other sheep before moving to the variable patch. Sheep 5 moved to the variable patch the quickest, only stopping to sample the hay on two of 20 runs.

Analysis of individual differences in this chapter did not reflect the measures of preference observed during the preference trial in Chapter 3.

DISCUSSION

Despite the unpredictable nature of the variable patch in some treatments, sheep were capable of adjusting their behaviour according to their perceived average of environmental quality. The results of this trial suggest that foraging sheep use more than one rule to calculate this average.

The probability of reward (probability treatment) had the strongest influence on the amount of hay eaten before leaving for the variable patch. At the predictable probability of 0, where pellets were never present, the sheep generally stayed in the stable patch, feeding on the hay for the duration of the trial. At the probability of 1, sheep generally ignored the certain patch and went straight to the pellets. At intermediate probabilities conditions were relatively less predictable and this was reflected in the amount of hay consumed before moving. At low probabilities more hay was consumed than at high probabilities. However, sheep could not or did not distinguish between the individual probability treatments. Instead, sheep grouped the 0 and 0.25, treatments, as “low” and 0.5, 0.75 and 1 as “high”. This most likely occurred as a result of discrimination error, inability to calculate probability and unidentified interference with memory. It is possible that the decrease in probability led to a decrease in leaving behaviour as a result of aversion to unrewarded walking. For bumblebees (*Bombus pennsylvanicus*) foraging in a variable environment it was considered that where flowers had a reward variance that could extend down to zero there might have been an aversion to unrewarded flowers (Real 1991). Foraging cattle in a Y-maze set-up showed a tendency to switch patches after an unrewarded foraging bout, though there appeared to be no innate tendency for switching after a

successful foraging bout (Hosoi et al. 1995a). This win-stay, lose-shift tendency might explain the behaviour of the sheep in the current experiment. After experiencing empty runs in the variable patch the forager, possibly to minimise the risk of lost opportunity to feed at the hay patch, switched to remain at the hay patch for the following trial. Conversely, success at the variable patch encouraged the forager to return there on the following run.

In addition to a leaving rule based on the overall intake from the patch, the most recent experience in the variable patch affected the hay eaten on the stable patch. More hay was consumed when the last variable patch experience was negative, supporting the ideas presented above. The most recent information that a forager has about a patch is likely to be the most reliable (Devenport & Devenport 1994). Cuthill et al (1990) found that starlings (*Sturnus vulgaris*) used a similar rule, basing their patch leaving decisions on the time taken to travel between the last patch and the current patch i.e. relying on their most recent experience to gain information about the quality of the environment. In the current experiment, as for the starlings, it was found that the use of short-term information did not extend beyond the most recent patch visit.

Only at the two most extreme probability treatments was the information from the last patch visit completely reliable. Although the forager could learn the probability of reward, the precise state of the variable patch on a single run at intermediate treatments was not predictable. The tendency of sheep on the higher probability treatments to return to the variable patch suggests that they were willing to invest time in sampling the patch to assess its quality. Sampling to gather information about the environment is a low cost behaviour of value in a fluctuating environment where

memory of patch conditions is of “low informative value” (Stephens & Krebs 1986; Illius & Gordon 1993). Run number, as an indicator of the experience within a patch was found to have a significant influence on patch leaving decisions of sheep but only at treatment 0.5. This implies that the sheep had learnt the probability treatment before the start of the experimental runs for the other treatments and their patch leaving behaviour had reached an asymptote. McNamara & Houston (1985) simulated foraging in changing and unchanging environments and found that, although simple rules could be used to approximate optimal behaviour, it was more difficult to learn when the environment was highly variable. As a consequence of the variability at treatment 0.5 it is possible that the sheep found it more difficult to track change and consequently devoted more time to sampling the patch.

As previous treatment, the probability treatment before the current treatment, did not influence the “hay eaten” on the current treatment, it could be considered that the buffer period of 12 runs was sufficient to eliminate the carryover effect from the previous treatment. This time period supports the results of previous studies. For example, in operant conditioning in pigs, carryover effect was removed with a 48 hour buffer period (Lawrence & Illius 1989). In a similar arena set-up to the current experiment Dumont & Petit (1995) found that three daily tests were sufficient to teach animals a new reward level.

How did observed and predicted results compare?

As no difference was found between the predicted and observed results, the conclusion can be drawn that sheep were behaving as if they were fully informed about the state of the patch at intermediate probabilities. This emphasises the ability of sheep to collate information from previous foraging bouts to make patch leaving

decisions. However, as the predicted results were obtained from data already collected in this experiment a favourable comparison with the observed data was likely and, therefore, these results should be accepted with caution. All of the observed values for the intermediate treatments were lower than predicted so sheep were tending to leave the patch earlier after consuming less hay. This trend could be a result of the grouping of treatments by the sheep, where no difference in behaviour was found between 1, 0.75 and 0.5, and 0, 0.25.

Walking Speed

Expectation of reward was not only measured in the amount of hay consumed before leaving the variable patch, but also in the walking behaviour of the sheep. Sheep moved faster to the variable patch when their expectation of reward was higher. Previous studies have reported a relationship between incentive and behavioural response. Primates performed an operant response with shorter reaction times when the expected reward was highly preferred compared to non-preferred (Watanabe et al. 2001). In rats, reaction times were faster (Crespi 1942; Brown & Bowman 1995) and response effort was greater (Kirshenbaum et al. 2000) as the value of the expected reward increased. In the current experiment, the increased probability of reward was a greater incentive for the sheep to move and again reflects the high preference for the pelleted food.

How did the sheep learn as the patch quality changed during the buffer period?

Analysis of the change in behaviour over the buffer period revealed a significantly steeper learning curve as patch quality changed from high to low compared with a change from low to high. This suggests a stronger drive to learn when the environment decreases in quality. Hosoi et al (1995a) and Hosoi et al (1995b) have

shown that in cattle and goats losing experiences are more important in determining behaviour than winning experiences. Hosoi et al (1995a, b) attribute this to the nature of large herbivore foraging. Grazing environments, while containing patches of preferred food, usually offer a continuous food source and, therefore, winning experiences are more likely to occur than losing experiences. That a large grazing herbivore is more sensitive to losing experiences is thus unsurprising. The behaviour of the sheep in the current experiment appears to support this argument.

It is likely that within this experiment individual variation in foraging decisions between sheep obscured differences between treatments. It was predicted that individual variation in patch leaving behaviour reflected a difference in preference for pellets, e.g. an individual with a stronger preference for pellets would leave earlier than an individual with a weaker preference. However, the differences observed in patch leaving behaviour in the current Chapter could not be explained by the differing preferences for pellets observed in Chapter 3.

General discussion

This trial has shown that sheep are capable of assessing patch quality under unpredictable conditions. The probability of the variable patch containing pellets was assessed on the basis of average patch quality and recent patch experience. The cost of making the wrong decision, that of missed opportunity to feed at the variable patch, was minimised by the sheep by feeding in the stable patch for an amount of hay that corresponded to their perceived average of the environment.

In the current experiment the sheep could not predict the exact state of the patch on a single run. Patch leaving decisions were based on an estimate of the next patch quality derived from previously gathered information biased towards their most

recent experience in that patch. However, this experiment found that individual variation in behaviour played an important role in predicting patch-leaving behaviour. This is explored further in Chapter 5 where there is an attempt to make a link between individual variation and patch-leaving behaviour exhibited in this experiment.

The uncertainty arising from an information deficit is likely to occur in many natural foraging systems. This experiment showed that learning takes longer where environments are unpredictable. Using the set-up presented here, Chapter 6 will consider the effect of introducing another animal into the environment on the foraging behaviour of an individual. Chapter 7 will follow up on this by considering how time between experiences in a variable environment influences behaviour.

SUMMARY

In a natural heterogeneous environment a forager will inevitably experience variability and consequently uncertainty in resource distribution. To test the response of a forager to variability and uncertainty in the quality of food patches sheep were introduced into a two-patch environment. The first patch offered a stable reward of intermediate preference. The second patch offered a highly preferred reward with a predefined probability. The decision to leave the first patch was based on the perceived average quality of the environment. As the quality of the environment decreased sheep spent longer on the first patch ($P < 0.001$). However, decisions were also governed by recent patch experience ($P = 0.001$). Time within a period only had an effect in the most unpredictable treatment, indicating that the sheep learning about the environment. When environmental conditions changed from

high quality to low i.e. a negative change, a strong shift in behaviour was observed. This effect was weaker when the change was from low quality to high, suggesting that foraging behaviour in herbivores is more strongly influenced by losing experiences than by winning experiences.

Sheep apparently overcome environmental uncertainty by averaging information gained through patch experience. Learning about patch conditions takes longer when the environment is unpredictable.

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CHAPTER 5

DOES THE BEHAVIOUR OF SHEEP IN BOLDNESS TESTS REFLECT RISK TAKING TENDENCIES WHILE FORAGING?

INTRODUCTION

This test of individual characteristics within a group of sheep was carried out in response to the experiment presented in Chapter 4. The aim of that experiment was to examine the effects of uncertainty in the environment on the foraging decisions made by sheep. It is possible that particular behavioural characteristics, over and above the treatments imposed by the experiment, may have influenced their foraging decisions. In the experiment described in Chapter 4 five sheep were faced with foraging decisions that were more or less predictable in their outcome. A level of individual variation between the sheep in their response to the foraging scenario was observed, however, this could not be attributed to differences in the level of preference for pellets over hay, as established in Chapter 3. An alternative hypothesis to account for the differences observed in patch leaving behaviour refers to individual personality characteristics of the animal. Within a population animals can be identified as shy or bold, depending on their response to a novel or risky situation (Kagan et al. 1988; Wilson et al. 1994; Reale et al. 2000). Previous studies have found that shy individuals tend to shown avoidance behaviour and bold individuals, approach behaviour, commonly identified by observing behaviour of individuals towards a novel object (Wilson et al. 1994). Given the results of the experiment presented in Chapter 4, it was hypothesised that individual personality characteristics, in this case, boldness in a risky situation might explain the occurrence of individual differences in

patch-leaving behaviour. In this experiment, animals were identified as relatively shy or bold, dependent on their behaviour in a battery of tests, and these results were compared against their patch-leaving behaviour observed in Chapter 4.

To test the level of boldness in a fear-inducing situation four tests were designed. These consisted of pen leaving, transit, novel object and surprise effect, defined below. There is evidence that the propensity of an individual to elicit fear-related behaviour in one test is correlated with its response in further tests (Lyons et al. 1988; Lawrence et al. 1991; Boissy & Bouissou 1995). In addition the novel object test has been used to measure levels of fearfulness and curiosity that are related to boldness and exploratory motivation in response to novelty (Hemsworth et al. 1996; Wemelsfelder et al. 2000). In the current experiment I tested the hypothesis that levels of boldness in a fear-eliciting situation can predict the behaviour of sheep in a risky foraging test (Chapter 4).

MATERIALS AND METHODS

Animals and Housing

The behaviour trials were carried out at the Macaulay Institute's Glensaugh research facility (56°N, 2°W), Scotland, in March 2000. Five Scottish Blackface ewes, the same animals as had been used in the main experiment (Chapter 4) were the subjects (mean live weight \pm SD=53kg \pm 5.1). The sheep were housed in familiar individual pens indoors and within visual contact of non-experimental companion animals. The housing pens and experimental arena were naturally lit. Animals were fed to maintenance on good quality hay, calculated according to the equation $0.435\text{MJ/kg LW}^{0.73}$ (MAFF 1984) and had free access to water at all times in the home pen.

Behavioural tests

A series of four tests were presented to individual animals, typically reported to elicit fearful response and allow identification of individual characteristics. These tests were (1) handling in pen, (2) transit, (3) novel object test and (4) surprise test. The four tests were successively conducted in the same environment, which consisted of the home pen, a transit run along a corridor, a holding pen and an arena measuring 10m*10m. All tests took place on one day.

Measurements

The tests are described below. Behavioural scores are also shown.

Leaving the pen.

The handler opens the door of the pen to allow the sheep to escape

Scores

1. Leaves pen voluntarily without the interference of the observer
2. Observer enters the pen, the sheep leaves calmly and quietly
3. Observer enters the pen. The sheep is driven round the pen several times before running out
4. Observer enters pen. The sheep shows panic or distress by running round the pen, attempting to jump out, falling, or a combination of these behaviours.

Transit.

The sheep is moved down a corridor followed by an observer

Scores

1. Walking or running voluntarily down the corridor
2. Hesitating, but moving forward without observer interference
3. Reluctant, but moving forward on approach of observer

4. Resistant, running back past observer towards the home pen and companion sheep, once or repeatedly

Novel Object.

The sheep was introduced into a familiar arena in social isolation. A novel object, motorbike tyres piled 1m high with a base ~1m*1m was already present in the arena.

Scores

Instantaneous sampling of behaviour in arena

- a. Instantaneous sampling took place every 10s over a 5-minute period.

Behaviours recorded were:

- i. Running*
- ii. Walking
- iii. Immobility*
- iv. Vocalisation*
- v. Urination/Defecation*
- vi. Head through bars*
- vii. Attention to novel object
- viii. Other behaviours

Those behaviours marked with an asterisk represent fear-related behaviours (Boissy & Bouissou 1995). The number of scans where fear-related behaviours were shown over the five minute period was summed to give an overall measure of fearfulness within novel object arena.

Surprise Effect.

On return to the holding pen the sheep were subjected to a sudden fright stimulus simulated by opening an automatic umbrella in front of the animal.

Scores

1. No response
2. Flinching response
3. Retreat from umbrella with a start
4. Panic, attempt to escape

All trials were recorded on video and measurements taken from the recording. Behaviour was scored subjectively according to the response of the animals to the test by an unbiased observer. Scores were totalled across the 4 tests to give an overall score of fear-related behaviours over the tests. This was ranked and compared to the rank of hay eaten from Chapter 4 using Spearman rank correlation coefficient.

RESULTS

As levels of fearfulness increased within temperament trials, ranking of hay eaten by sheep also increased ($(r_s)_5=0.675$, $P<0.25$, Figure 5.1) indicating less risk prone-ness in more fearful animals. With only 5 animals in the sample the power of this test is very weak at 0.512. Even by doubling the number of animals at $r = 0.675$ would only increase the power of the test to 0.56. Increasing the sample size to 20 animals would increase the power of the test at this strength of association to 0.93.

Table 5.1: Results of the hay eaten and the behaviour scores.

Sheep	Mean hay eaten (g)	SE	Rank of hay eaten	Test 1	Test 2	Test 3	Test 4	Total Score	Rank of scores
1	51.06	2.26	5	2	1	4	1	8	3.5
2	29.78	2.59	3	2	4	3	2	11	5
3	43.14	2.80	4	2	2	2	2	8	3.5
4	25.39	2.16	1	1	3	1	1	6	1
5	28.19	2.34	2	2	4	2	2	10	2

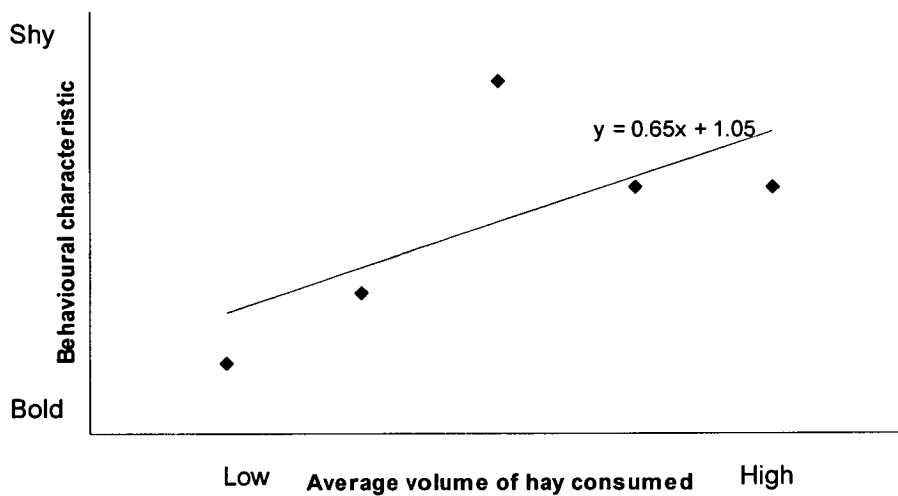


Figure 5.1: Correlation between the rank of hay eaten and behaviour scores

DISCUSSION

In the experiment described in Chapter 4 one patch in a two patch environment offered a reward that varied in the predictability of occurrence. The decision to move to the variable patch entailed a level of risk. If the variable patch was empty on an individual run, the sheep could not move back to the first patch to continue feeding and, therefore, incurred a cost of lost opportunity (Stephens & Krebs 1986). The sheep compensated for this risk by consuming more hay from the first patch before moving to the variable patch as the likelihood of receiving a reward from the variable patch decreased.

There was a high level of individual variation in the total volume of hay consumed across all treatments and it was hypothesised that those sheep consuming most hay were exhibiting risk-averse behaviour. It has been shown that behaviour in fear-eliciting situations can reflect levels of boldness, which in turn may reflect a

tendency to show risky behaviour. In the current experiment I attempted to relate the tendency to show fearful behaviour to the propensity of sheep to take risky foraging decisions in Chapter 4. This correlation, although not statistically significant, may reflect a relationship between these factors. The number of sheep used in the Chapter 4 imposed a statistical constraint upon the correlation analysis and as a result, significance was not achieved. The experiment described in Chapter 4 could not be carried out with more animals due to experimental design and time considerations. The temperament trials were carried out several months after completion of “rewards” and although the trials took place in a familiar environment, it would have been preferable to run the temperament trials alongside the foraging trials. Coleman & Wilson (1998) emphasise that individual differences in boldness are context specific. The behaviour of pumpkinseed fish towards a novel object was not correlated with their response to a threatening stimulus. While the quantity of hay consumed in the foraging trial may have been a reflection of risk taking tendency, the relationship between risk and fear behaviour was not sufficiently supported in this experiment.

For future consideration, a larger number of animals would be subjected to foraging trials, with character scoring in conjunction with the original experiment where individual differences were of specific interest.

SUMMARY

Evidence of bold behaviour in character tests may reflect the tendency to take risks in different environmental contexts. In the experiment presented here no significant correlation was found between fear scores and the tendency to leave the patch early

in the experiment presented in Chapter 4, however a trend was evident. Development of this theory in relation to patch leaving behaviour presents an interesting question for future work.

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CHAPTER 6

THE EFFECT OF CONSPECIFICS ON FORAGING BEHAVIOUR AND THE USE OF INFORMATION

INTRODUCTION

Living in a group can confer many advantages. The avoidance of predators is enhanced through increased vigilance and dilution within the group reduces the probability of capture by predators (Olupot & Waser 2001). A further function of group living may be to increase the mean intake rate or reduce the variability associated with finding food, particularly in patchy environments (Giraldeau & Beauchamp 1999; Stahl et al. 2001). Individuals can learn about ephemeral patches by following conspecifics (Sonerud et al. 2001) or through social facilitation. Theories of group foraging emphasise the importance of shared information in a socially foraging species (Giraldeau & Beauchamp 1999). However, there are potential disadvantages of living in a group when considering foraging behaviour, principally competition from other group members. A possible means of controlling aggression and intra-specific competition is through the formation of a dominance hierarchy (Gauthreaux 1978; Stahl et al, 2001). Dominant animals in the group can achieve improved fitness through increased opportunity to mate (Van Noordwijk & Van Schaik 2001) and access to food resources by following and displacing subordinates as they find food (the “producer-scrounger” model (Barnard & Sibly 1981).

Examination of foraging behaviour can determine the costs and benefits of sociality for individuals in the group that differ in rank. In a study of blackbirds (*Turdus*

merula) dominant birds showed increased foraging success and reduced effort after displacing or foraging with a subordinate. Subordinate birds, however, experienced a lower success rate when foraging with higher ranking individuals (Smith et al. 2001). Despite these disadvantages subordinate animals remain in a social group because the benefits of group living outweigh the costs. The experiment presented here examines the use of information in a variable environment. It builds on the results of Chapter 4 by introducing another animal, and hence another source of information into the environment. However, associated with additional information is an additional source of uncertainty. Even when fully informed about the probability of reward there is uncertainty over the probability of achieving that reward under competitive conditions.

This experiment considered the patch leaving response of an individual in the presence of another animal of known dominance status. The patches were adjusted to permit both animals to feed from a stable and predictable patch but only one animal could feed from an alternative variable patch. Foragers were individually trained to have an expectation of variable patch quality that varied between high and low. The interest in the current experiment is the use of information when foraging with conspecifics. The following hypotheses tested were (1) how is historical information about patch quality used and can new information be obtained? (2) Which of the animals, dominant or subordinate is most likely to take the initiative in moving between patches, and on what information is this behaviour based? (3) Do some animals follow other animals when moving between resource patches and if so, under what conditions?

It was predicted that animals would use information based on previous experience (training) to determine the quality of the alternative resource and adjust their patch leaving behaviour accordingly, as in the results of Chapter 4. In addition it was expected that the behaviour of an individual would be influenced by the information held by the other animal. If sheep were responding according to the producer-scrounger theory, dominant animals would be expected to exploit the information about the patch held by the subordinate. Conversely, subordinates were not expected to follow or challenge dominant animals for the resource, possibly relinquishing information about patch quality to achieve this.

Before this experiment could be carried out it was first necessary to establish the dominance hierarchy of the group. The methods and results for this part of the experiment will be presented before methods and results of the main experiment. The discussion section will refer to results concerning both experiments.

ESTABLISHMENT OF THE DOMINANCE HIERARCHY

MATERIALS AND METHODS

Animals and Housing

This experiment was carried out at the research facility Glensaugh farm, Scotland (56°N 2°W) in December 2000. The subjects in this experiment were eight 2-year-old non-pregnant, non-lactating Scottish Blackface ewes (mean live weight at the

start of the study \pm SD=66.6 \pm 3.65kg). Throughout the study the animals were housed in individual strawed pens, under natural light and ventilation. During the experiment the animals were fed to maintenance on good quality hay. The feed ration was calculated according to the equation $0.435\text{MJ/kgLW}^{0.73}$ (MAFF, 1984). Tests were conducted using concentrate pellets (12.5MJ/kg/DM: Green keil, NorthEastern Farmers, Rosehall, Turriff, Scotland), previously established as a highly preferred feed for Blackface sheep (Chapter 3). The sheep were familiar with feeding from the bins used in the test and to the concentrate pellets. Continuous access to drinking water in the home pens was available.

The sheep had been in this social group for over a year, and had been mainly kept in a field dominated by perennial ryegrass (*Lolium perenne*). Given this time period the sheep were assumed to have a well-established social group.

Data Collection

All trials were recorded on video and behavioural observations scored from video analysis at the end of the trial. This ensured that the human observer did not interfere with the behaviour of the sheep and that scores were unbiased. The camera was set up over the arena to give a plan view.

Training

To familiarise the subjects with the test procedure, training took place in the experimental arena for four days prior to the experiment. The arena measured 4.5m x 4.5m with walls 2m high. Sheep were introduced individually into the test arena, and permitted 10 minutes of free access to feeding bins containing the pellets.

Food competition trials

The food competition trials took place in the same arena as the training, but during the test, only one feed bin was available, and hence access to the bin was restricted to one animal only. At the beginning of the test each bin contained 300g of concentrate pellets. Refusals were collected but were negligible. Testing took place in dyads. Each of the 8 group members was tested against every other individual, with one individual competing in one dyad per day (Table 6.1). Within each day the order of the dyads was randomised so that individuals did not appear consistently in one position in the day (for example always tested first). The design was slightly unbalanced due to eight animals being tested over seven days. Testing began four hours after the initial morning feed, at 12:30, as this time period has been shown to give the animals sufficient motivation to compete for a limited resource (H.Erhard, *pers. comm.*). As a result each pair of animals was equally motivated to compete for the resource although the first group on any day had a shorter fasting time than the last group. The tests did not interfere with the daily feeding regime as this could affect the level of motivation (Lankin 1997).

Table 6.1: The order and position of the dyads in one day.

Day	1st	2nd	3rd	4th
1	6-3	5-4	2-7	1-8
2	7-1	4-8	3-5	2-6
3	7-8	5-2	6-1	3-4
4	4-2	6-8	7-3	5-1
5	4-1	2-3	5-8	6-7
6	8-2	1-3	6-4	7-5
7	6-5	7-4	2-1	8-3

Measurements

For a test, the two individual animals were removed from their home pen and taken to the arena. In the test pen only one sheep could access the food bin (18*16*16cm) at any one time. Bins were provisioned with 500g pellets and tests lasted three minutes. A pilot test had shown tests of longer than three minutes resulted in elevated levels of aggression towards weaker animals, as the stronger animals became satiated. Although there was an attempt to minimise this by providing more food than could be consumed within five minutes, consideration of welfare of the animals limited the time of the tests. Refusals were collected and weighed to the nearest gram. Time in control of the bin was measured as a total of the time spent feeding by each individual plus the time spent defending the resource by preventing the head of the other animal entering within 0.5m of the bin. Defence usually took the form of threatening or overtly aggressive behaviour. Behaviour was recorded by focal continuous sampling (Martin & Bateson 1993) and all measurements were scored from analysis of video recording of the trials.

Each animal's rank was based on the proportion of time spent in control of the feed bin. This method was chosen in preference to the "social-tension index", the number of aggressive acts delivered minus the number of aggressive acts each animal received (Craig et al. 1969 in (Craig 1986)) because this method is biased towards aggressive, but not necessarily the most successful animals. Success in the current experiment was considered to be the ability to control the food resource through defence of the feed bin, measured as the time spent in control of the bin.

Analysis

The aim of the analysis was to establish a dominance hierarchy within a group of sheep based on time spent in control of the feeding resource. The proportion of time spent in control of the feed bin as described in *Measurements* was calculated from the video recording. On the basis of these data a win-loss matrix was constructed and hierarchy formed. Using Kendall's co-efficient modified by Appleby (1983) the linearity of the hierarchy was established. The significance of the hierarchy was tested using Appleby's test of significance (Appleby 1983). From these results the sheep were divided into two groups, a dominant group and a subordinate group for the main part of the experiment.

RESULTS

Using the proportion of time spent in control of the bin the following win-loss matrix was constructed (Table 6.2).

Table 6.2: The win-loss matrix. Numbers within the matrix represent the proportion of time spent in control of the feed resource

sheep	1	2	3	4	5	6	7	8	Average control per dyad
1		0.07	0.01	1	0.32	0.27	0.76	0	0.35
2	0.93		0.91	1	1	1	1	0.93	0.97
3	0.99	0.09		1	0.9	1	0.89	0.99	0.84
4	0	0	0		0	0.02	0	0	0.003
5	0.68	0	0.1	1		0.99	0.94	0.3	0.58
6	0.73	0	0	0.98	0.01		0	0	0.25
7	0.24	0	0.11	1	0.06	1		0.23	0.38
8	1	0.07	0.01	1	0.7	1	0.77		0.65

The rows and columns represent the individual sheep across all dyadic interactions. For example in the 2-1 dyad sheep 2 controlled the resource for 0.93 of the total time both animals were engaged with the resource and sheep 1 was in control for only

0.07 of the total time. From these results on proportion of control, a win-loss matrix was formed with the most dominant animal in the top left of the matrix. Sheep 2 was found to be the dominant animal in the group, monopolising the resource against all other individuals (Table 6.3).

The matrix revealed one triad in this group. Sheep 1 was dominant to 7, sheep 6 was dominant to 1 and sheep 7 was dominant to 6. The hierarchy was found to be significant despite the two reversals ($d=1$, $P=0.02$). The degree of linearity of the hierarchy was calculated using Kendall's adaptation to be 0.95 (where 1 represents a completely linear relationship).

Table 6.3: The win-loss matrix arranged by rank. Sheep numbers are on the top row and the first column. Where the row individual is dominant to the column individual this is indicated by "1". Shaded numbers represent the triad.

		Loser								
Winner		2	3	8	5	1	6	7	4	Rank
	2		1	1	1	1	1	1	1	1
	3	0		1	1	1	1	1	1	2
	8	0	0		1	1	1	1	1	3
	5	0	0	0		1	1	1	1	4
	1	0	0	0	0		0	1	1	5
	6	0	0	0	0	1		0	1	5
	7	0	0	0	0	0	1		1	5
	4	0	0	0	0	0	0	0		6

Dominant

Subordinate

From this data the 8 animals were divided into 2 groups, one dominant group, the other subordinate (Table 6.4). The four animals that showed most control of the resource were sheep 2,3,8 and 5. The animals showing least control of the resource were 7,1,6 and 4. Although there are differences in the magnitude of the ranks between animals in each group, the condition of the groups was that all animals in the dominant group were dominant over all animals in the subordinate group.

Table 6.4: The division of the group into dominants and subordinates

dominant	subordinate
2	1
3	6
8	7
5	4

On the establishment of the dominant and subordinate groups, the second and main part of the experiment could take place.

THE EFFECT OF SOCIAL FORAGING ON INFORMATION AND BEHAVIOUR

MATERIALS AND METHODS

Animals and Housing

The second part of the experiment took place under the same housing and feeding conditions as part one. The trials ran in February and March 2000 with the dominant and subordinate animals from the previous section.

Data Collection

All trials were recorded on video by 4 cameras and monitored remotely. The cameras were positioned as for the experiment presented in Chapter 4.

Food Rewards

The food rewards used in this experiment were good quality chopped hay, a food reward of intermediate preference, and concentrate pellets (12.5Mj/kj/DM: Green Keil, NorthEastern Farmers, Rosehall, Turriff, Scotland), a highly preferred reward (Chapter 3).

Initial training

Animals were released into the experimental arena (Figure 6.1) to gain familiarity with the environment, feeding regime and to foraging individually. This training period took place over five days. Initially sheep were allowed 30s in the arena when foraging alone, but this was increased to five minutes, as the sheep became accustomed to the procedure. Initial training runs took place four times per day.

Experimental Set-up

An arena was built to simulate a foraging environment within the same building as the animals' housing and replicated the set-up used in Chapter 4. The arena measured 11m by 6m and was divided by a partition 9.5m long (Figure 6.1). There was one entry gate and one exit gate both at the top of the arena. At the bottom of the arena a third gate could be closed to divide the arena in two. On entering the arena, the sheep were confronted with the stable hay patch. This patch contained good quality hay from which two sheep could feed without interference. By moving around the arena the sheep encountered the variable pellet patch. Pellets were only available according to treatment and delivered in a bin accessible by only one sheep at any time.

Experimental Design

Training Period

The experiment consisted of two parts. The first part was a training period during which the sheep foraged individually in the arena to gain knowledge of patch conditions. Two environment types were simulated; high quality and low quality generated by adjusting the probability at which a 50g pellet reward was available from the variable patch. In the "high" environment the variable patch was provisioned on 0.75 of the runs in the arena. In the "low" treatment the pellets patch was provisioned on only 0.25 of the runs. Each sheep had 12 individual runs in the arena. A run consisted of the introduction of an animal into the arena where it was permitted up to five minutes feeding time on the stable hay patch. If the sheep chose to move to the variable patch within the five minute period a gate at the bottom end of the arena (Figure 6.1) was closed behind the sheep. This ensured that the decision to move to the variable patch entailed some risk for the forager. If the variable patch

was empty the sheep incurred a cost of “lost opportunity” (Stephens & Krebs 1986) to feed at the stable hay patch.

Training and Tests – 4 Periods.

Overall the experiment consisted of four training periods, each three-day training period followed by a three-day test period. On each day, each sheep had four runs. Over the four periods, each dominant sheep was paired with each subordinate in different combinations of training and test environment. The environments were balanced across sheep and periods (Table 6.5).

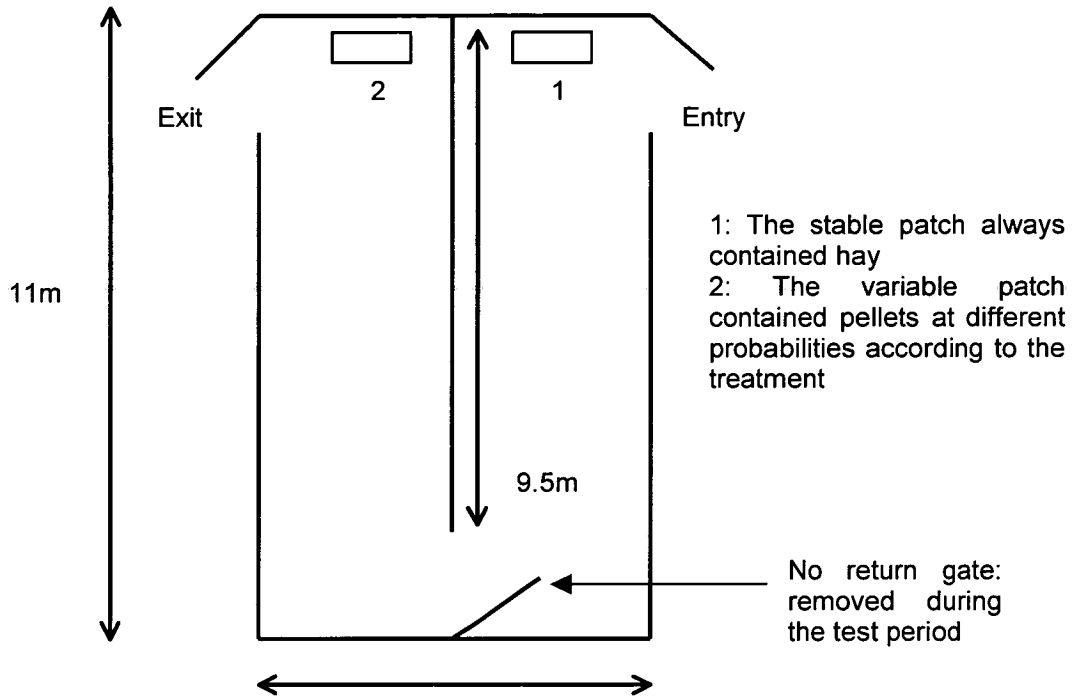


Figure 6.1: The experimental arena

Test Period

For the test period, the quality of the variable patch was balanced across treatments (Table 6.5). Therefore, the quality of the variable patch during the test for some individuals was the same as the training (in which case they had accurate knowledge about patch quality) and for others it differed (in which case they had inaccurate information). During the test period sheep were introduced into the arena in pairs. Pairing one animal from the dominant group with one animal from the subordinate group formed the dyads. As described above, the environment was assigned low or high quality and this was again generated by provisioning the variable patch with pellets on 0.25 of runs for the low quality or 0.75 of runs for the high quality

environment. During this phase of the experiment the gate was not closed behind the sheep as they moved from the stable to the variable patch. This allowed both sheep to explore the variable patch at any time over the 5-minute period. In consequence, the previous risk of lost opportunity was eliminated.

Table 6.5: The experimental design

Period	Dyad: Dominant * Subordinate	Training environment for dominant	Training environment for subordinate	Test environment for pair trials
1	3*4	High	High	Low
1	2*6	High	Low	High
1	5*1	Low	High	High
1	8*7	Low	Low	Low
2	3*7	High	Low	Low
2	2*1	High	High	High
2	5*6	Low	Low	High
2	8*4	Low	High	Low
3	8*1	High	Low	High
3	5*7	High	High	Low
3	2*4	Low	Low	Low
3	3*6	Low	High	High
4	5*4	High	Low	Low
4	3*1	Low	Low	High
4	2*7	Low	High	Low
4	8*6	High	High	High

Analysis

Training period

This analysis was carried out to examine the effect of the alternative patch quality on the behaviour of individual foraging sheep. The response variable was “leave time”, the time at which the sheep left the first stable patch for the second variable patch, recorded as sheep crossed from the stable side of the arena to the variable. Leave time was used as the response variable in preference to the volume of hay eaten due to daily time limitations. In a previous experiment using the same experimental set-up (Chapter 4) both leave time and hay eaten were recorded. A highly significant correlation (0.92) was found between these variates. This indicated that leave time was a suitable variable to measure.

The data used in this part of the analysis was taken from day three of the three day training run. By using only this data, it was assumed that the sheep had built an expectation of variable patch quality. Analysis was made using the REML (REsidual Maximum Likelihood) technique in Genstat (Genstat 1998). This technique was used, despite the experiment being balanced, because the data had a strong bimodal distribution. With response variate as “leave time”, the fixed model terms were; treatment, previous state, previous treatment and status. Individual sheep, experimental period and their interaction, and run number within a day were included as random model terms (Table 6.6).

Table 6.6: Definition of terms in fixed model

Fixed model terms	Definition
Treatment	Overall quality of the environment (high or low)
Previous state	The condition of the variable patch on the most recent run
Previous treatment	The quality of the alternative patch during the last period (high or low)
Status	The ranking of individual sheep as dominant or subordinate

Significance levels were determined using the Wald statistic (Elston 1998). The Wald statistic has an asymptotic chi-squared distribution with degrees of freedom equal to those of the fixed model term. The statistic determines the change in fit of the model when a new term is added to the current model containing all the previous terms.

Test Period

This part of the analysis was carried out to examine the patch leaving behaviour of sheep in the presence of a conspecific. The first analysis explored the factors governing which animal, dominant or subordinate, was likely to move to the variable patch first. The effects of the dominant training environment, subordinate training environment, test environment, the difference in rank between animals, individual differences and their interactions, plus effects and interactions of time (explanatory

variables) on the status of the animal first to move to the variable patch (response variable) were analysed by generalised linear modelling. This was implemented with a binomial distribution and a log link function (McCullagh & Nelder, 1989). Significance of effects was analysed by analysis of deviance. All procedures were carried out in Genstat 5, Release 4.1 (Genstat, 1998). Approximated F-statistics were constructed by dividing the mean deviance of each factor in the initial analysis by the mean deviance for unexplained random variation. Where the deviance ratios for the factors were still significant after additional random variation at the level of individual sheep had been accounted for; this factor was included in the model. Factors that were non-significant after accounting for random variation within the factor were dropped from the model.

The response variable was then sub-divided into two further response variables for analysis (1) the first to move during the first four runs of the trial (2) the first to move during the last four runs of the trial and the analysis repeated. The proportion of dominants and subordinates moving first were compared between the first and last runs using a Chi-squared test for comparison of proportions. The components could not be treated as independent (Martin & Bateson 1993) and, therefore, proportions of dominant and subordinate animals were corrected for the number of non-movers in each comparison.

The second analysis examined the likelihood of the first animal to move being followed. The analysis was carried out with the same explanatory variables as above, plus the variable “first to move”, which describes the dominance status of the first animal to move to the variable patch. The response variable again had a binomial distribution, indicating whether the first sheep was followed. This response variable

was sub-divided for further analysis: (1) following behaviour in during the first four runs of the trial and (2) following behaviour in the last four runs of the trial. Chi-squared analysis of proportions was carried out to identify if the proportions of following behaviour of dominant and subordinate behaviour changed over the trial. Trial was defined as the 12 test runs of a period.

RESULTS

Training

Treatment, referring to the quality of the variable patch as high or low, had a highly significant effect on the leave time of the sheep ($W_1=83.86$, $P<0.001$). Sheep left the stable patch earlier when the quality of the variable patch was estimated to be high. Sheep were also more likely to have a shorter leaving time from the stable patch when their most recent experience in the variable patch had been positive ($W_1=33.05$, $P<0.001$), once treatment effect had been accounted for. These results are in agreement with a previous experiment that specifically examined the patch leaving behaviour of foraging sheep in response to unpredictability in the quality of the variable patch (Chapter 4). The fixed model terms found to be non-significant were previous treatment i.e. the treatment probability in the previous period ($P=0.231$) and the effect of individual dominance status ($P=0.596$) i.e. dominant sheep showed no more tendency to leave early than subordinate sheep.

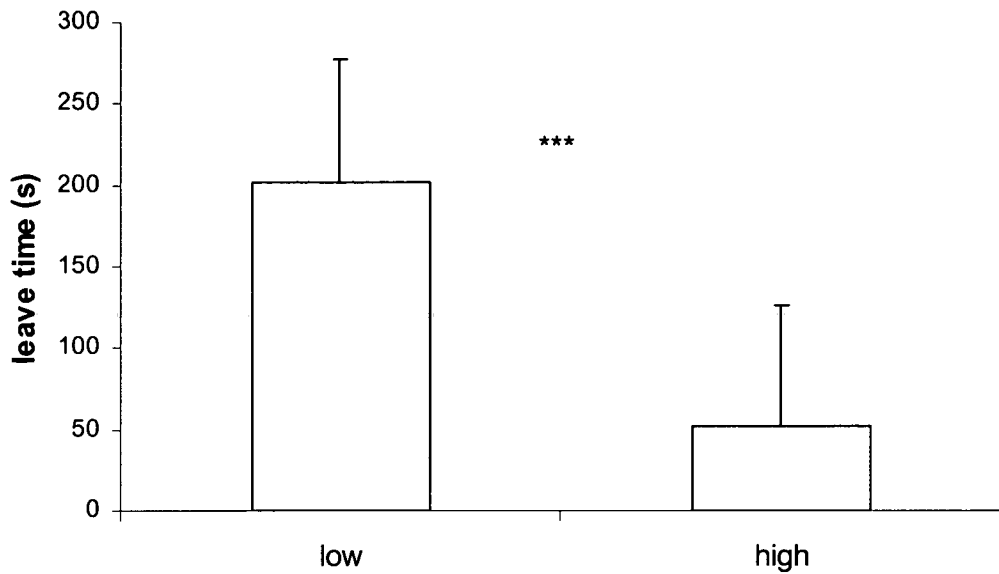


Figure 6.2: Mean leaving time (s) with standard error bars. At the low treatment, sheep stayed longer at the stable patch (***)=P<0.001)

Test Period

The first sheep to move during a trial

This analysis was carried out to determine the factors influencing the first sheep to move when sheep foraged in pairs in a variable environment. Across trials, the previous training environments of both individuals was important in explaining which animal was the first to move (subordinates: $F_{1,4}=19.08$, $P<0.01$, dominants: $F_{1,4}=11.93$, $P<0.05$; Figure 6.3, Table 6.7).

Overall, subordinate animals successfully monopolised the variable patch and consumed all pellets on only 4% of runs. Despite the strong effects of training environment on the first sheep to move, the quality of the test environment during the trial did not influence the status of the first sheep to move ($F_{1,4}=0.03$, NS). Where there was a large difference between pairs on the dominance hierarchy (Table 6.7) the dominant sheep was most likely to move first ($F_{4,4}=5.63$, $P<0.05$). As the

difference between pairs in the dominance hierarchy increased, subordinates became less likely to move first.

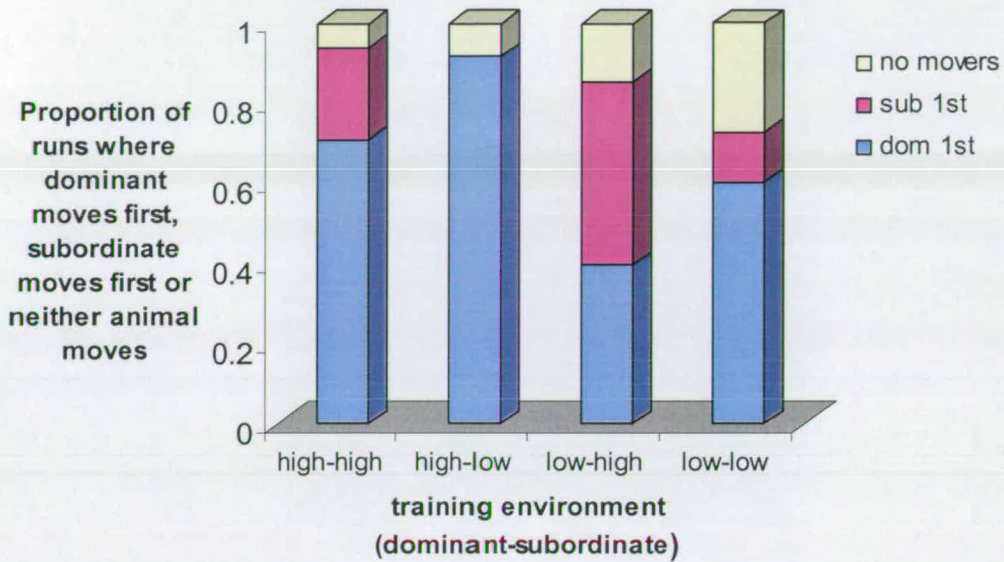


Figure 6.3: The likelihood of a dominant or subordinate being first to move, according to their previous treatment in the training environment. Dom = dominant animal moved first; sub = subordinate animal moved first; no movers = no animal went to the variable patch

Individual differences within the dominant group played an influential role in determining which animal moved first ($F_{3,4}=8.04, P<0.05$). Sheep 2 was the most likely of the dominant animals to move first and sheep 8 least likely. However, this pattern was not observed in the subordinate animals. No subordinate animal showed a greater tendency to move first than any other ($F_{3,4}=2.26, NS$). Neither the period in which the experiment took place ($F_{3,4}=2.16, NS$), nor the state of the variable patch on the previous run ($F_{1,4}=0.00, NS$) influenced the tendency of dominants or subordinates to move first.

Within a trial, the status of the first moving animal was influenced by run number ($F_{1,9}=12.68, P<0.05$). Individual animals, both dominant and subordinate, responded in the same way within a trial i.e. there was no tendency for one animal to respond to

change in environmental quality or aspects of social foraging any more than another (dominants; $F_{3,9}=4.3$, NS, subordinates; $F_{3,9}=3.13$, NS).

Table 6.7: Results of Generalised Linear Model for the analysis of first to move

Explanatory factor	Degrees of freedom	Corrected F-value	Probability
Subordinate training environment	1,4	19.08	<0.05
Dominant training environment	1,4	11.93	<0.05
Test environment	1,4	0.83	NS
Difference in hierarchy	4,4	5.63	<0.05
Dominant individual	3,4	8.04	<0.05
Subordinate individual	3,4	2.26	NS
Period	3,4	2.16	NS
Run	1,9	12.68	<0.05

Effect of run number

As run number had a significant effect on the first moving animal, the trial was broken down into (1) the first four runs and (2) the last four runs of the trial. The first section considered the early stages of the trial when sheep were first introduced to the paired foraging set-up. The training environment of the subordinate sheep in the early stage of the test had a strong influence on the status of the first sheep to move ($F_{1,3}=18.28$, $P<0.05$). However, in the early stages of the trial, the training environment of the dominant animal did not affect the first animal status ($F_{1,3}=3.07$, NS). Individual differences in dominant animals played an important role, with sheep 2 most likely to move first and sheep 8 least likely ($F_{3,3}=25.35$, $P<0.05$). However, there was no evidence that subordinate animal differences ($F_{2,3}=1.0$, NS), or the quality of the test environment influenced the status of the first moving sheep ($F_{3,3}=0.00$, NS).

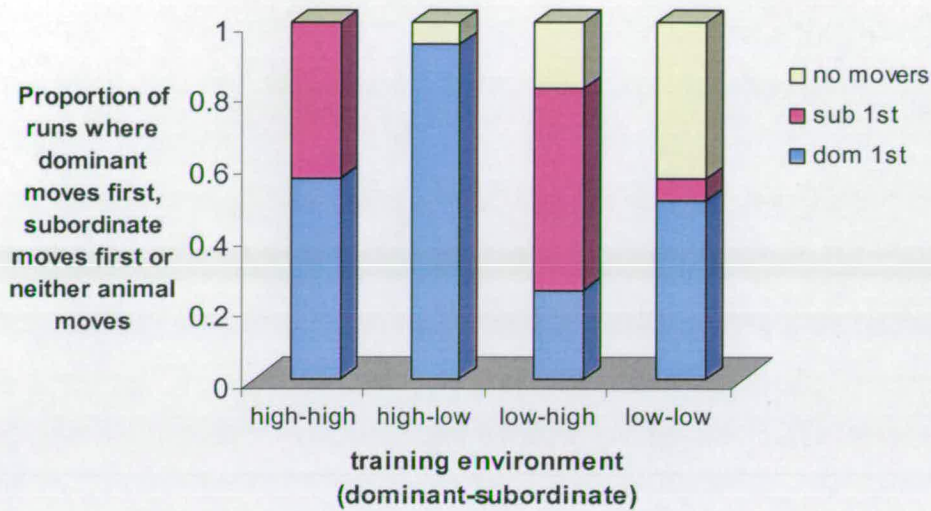


Figure 6.4: The likelihood of being first to move during the first four runs of the test.

These results were compared with last four runs of the trial. At this stage, the training environment of the subordinate animal no longer had an effect on the first animal status ($F_{1,4}=0.88$, NS). Despite playing no part in the early stages of the trial dominant sheep used information from their training environment during the last four runs ($F_{1,4}=10.04$, $P=0.002$). Sheep did not respond to the quality of the test environment in the latter stages of the trial ($F_{1,4}=0.45$, NS). Individual differences in both dominant ($F_{3,4}=4.42$, $P=0.004$) and subordinate ($F_{2,4}=3.12$, $P=0.044$) animals were influential with some animals showing an increased tendency to move first compared to others. In comparing the proportion of dominants and subordinates moving first at early and later stages of the trial, a significant change in proportions was found for treatment High-High ($\chi^2_{0.05,1}=7.607$, $P=0.03$; Figure 6.4 & 6.5). Dominant and subordinate animals were equally likely to move at the early stages of the test, but in later stages, the subordinate never moved first. Across the other

treatments, however, there was no change in proportion of dominants or subordinates moving first.

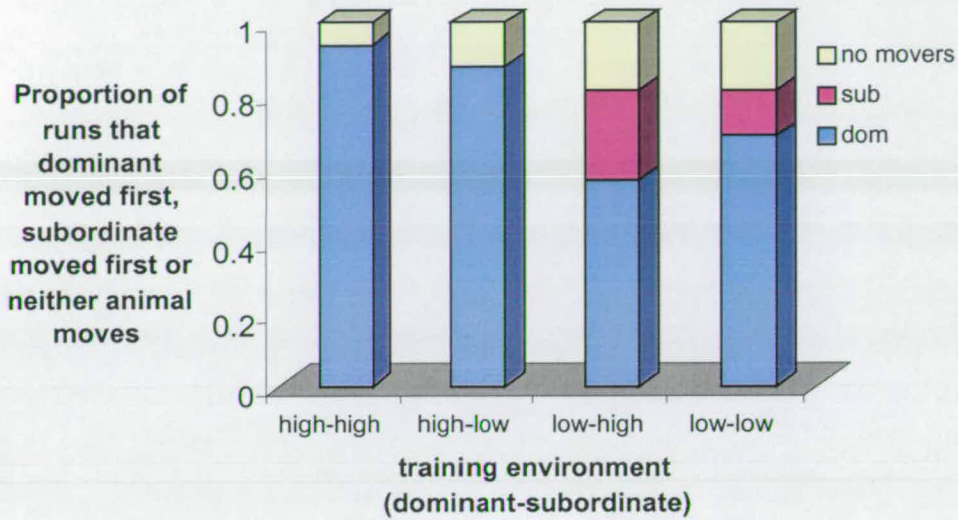


Figure 6.5: The likelihood of being first to move during the last four runs of the test.

Following behaviour

Once one animal had moved, what was the response of the second animal? The likelihood of the second sheep following the first sheep to move to the variable patch was dependent on the status of the first sheep, with dominants following significantly more than subordinates ($F_{1,4}=28.08$, $P<0.001$). Following was more common when the test environment was high than when the test environment was low ($F_{1,4}=57.19$, $P<0.001$). This was true for both dominant and subordinate animals. As the difference between pairs in the dominance hierarchy increased the incidence of following declined ($F_{4,4}=3.17$, $P=0.013$). Following was not explained by training environment for the dominant animal ($F_{1,4}=2.54$, NS), however, where subordinates had a high training environment, they were more likely to follow than after a low training environment ($F_{1,4}=7.53$, $P=0.006$). Following was not explained by

individual differences between animals (dominants ($F_{1,4}=0.86$, NS); subordinates ($F_{1,4}=1.76$, NS)). During the course of the trial run number within the trial explained a decrease in the incidence of following for both dominant and subordinate animals, suggesting that animals were still learning the test environment at later stages of the trial ($F_{1,7}=9.15$, $P=0.002$).

Effect of run number

Given the significance of this factor, the trial was sub-divided into (1) the first four runs and (2) the last four runs. During the first four runs following was explained by the status of the first animal to move. Subordinate animals were significantly more likely to be followed than dominant animals ($F_{1,3}=9.44$, $P<0.002$; Figure 6.6). The quality of the test environment also had a strong effect on the likelihood of following occurring for both dominant and subordinate animals. Where the test environment was low, there was less following than where the test environment was high ($F_{1,3}=17.62$, $P<0.001$; Figure 6.6).

This same pattern was observed during the last four runs of the trial, with following only explained by the status of the first animal to move ($F_{1,3}=9.94$, $P=0.002$; Figure 6.7) and quality of the test environment ($F_{1,3}=22.69$, $P<0.001$; Figure 6.7). In the high test environment, where dominants moved first they were followed by subordinates on 87% of runs. However, in the low test environment where dominants moved first they were only followed by subordinates on 14% of runs. When subordinates moved first in the high environment the dominant individual always followed. Comparing the early and late stages of the test, the proportion of runs where subordinates followed dominants was significantly greater in the early stages of the test ($\chi^2_{0.05,1}=22.6$, $P<0.001$; Figure 6.6 & 6.7).

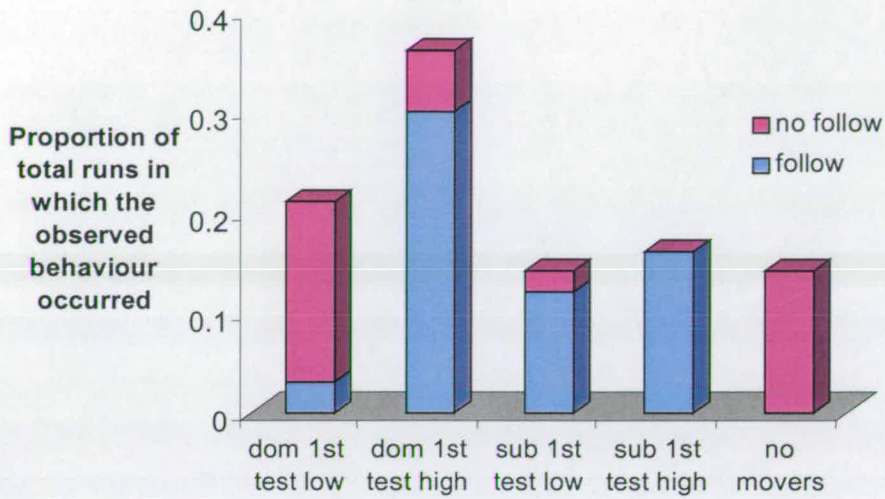


Figure 6.6. Following behaviour during the first 4 runs of the pair trials. dom 1st =, the dominant animal was first to move round. follow = the first animal to move was followed, no follow = the first animal to move was not followed

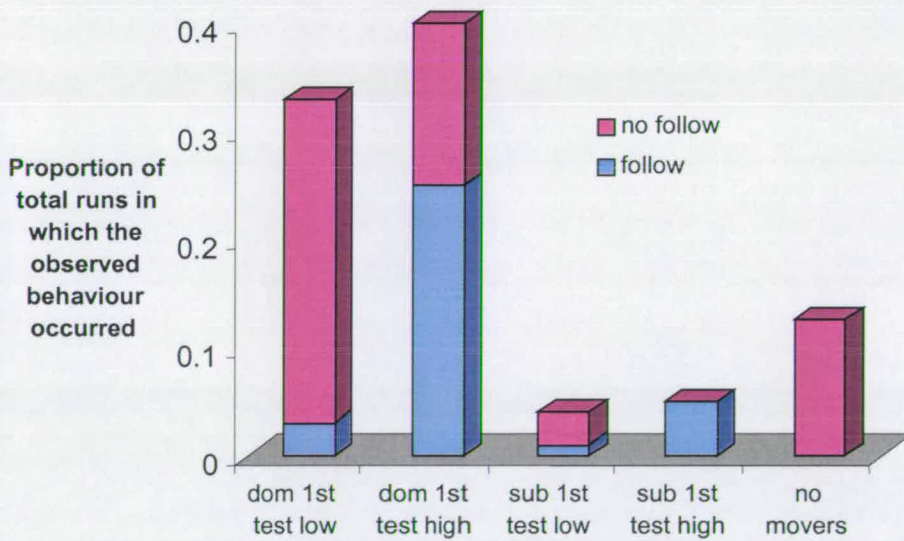


Figure 6.7: Following behaviour during the last 4 runs of the pair trials. The y-axis represents the proportion of total runs in which the observed behaviour, described in the x-axis occurred.

DISCUSSION

Summary of results

Where the trial is considered as a whole, both training environments of the dominant and subordinate animals explain the status of the first sheep to move. The test environment had no effect. The greater the relative difference in rank between the pairs, the less likely the subordinate was to move first. Individual dominant animals differed in their tendency to move first, but subordinates did not. Run number across the trial was significant and so separate analyses were made of the beginning and end of the trial. In the early stages of the trial subordinates training environment and individual dominant animal explained the variation in status of the first moving animal. In the latter stages of the trial dominant training environment, and both individual dominant and subordinate animals explained the variation in status of the first moving animal. Dominant sheep were more likely to follow than subordinates and sheep of both status followed more when the test environment was high. Subordinates used information from previous training to determine whether to follow and were more likely to follow when the difference in rank was less.

First to move

During this pair trial, dominant animals tended to be first to investigate a variable patch when they held a high expectation of reward based on previous experience. Although dominants were more likely to move first, the training environment of the subordinates explained significant variation in the first animal to move. This suggests that during the early stages of the pair trials dominant animals, although being first to move to the variable patch, may have been basing their cue to move on some aspect of the behaviour of the subordinates. This does not imply however, that they were

incapable of using their own information from the previous training environment. Subordinate animals were observed moving from the stable patch but being overtaken by the dominant animal, at the point where “first round” was measured. Results from the training period show that the sheep were capable of learning about the environment. Why was the test environment not influential in the moving behaviour of the sheep? It is possible that the removal of the gate, and therefore, the removal of risk of moving to the variable patch, reduced the need to learn about the environment. There was no penalty to a wrong decision as the sheep could return to the stable hay patch without the cost of lost opportunity to feed. Alternatively, learning about the quality of the environment could have been impaired by social interference (Dumont & Hill 2001).

Following behaviour

Although animals were not responding as if they had knowledge of the test environment conditions, they were learning about the state of the environment, as shown in the results of the following behaviour. Here, the quality of the test environment had a significant effect on the likelihood of following occurring. Where the test environment was high, subordinates were more likely to follow the dominants and dominants always followed when subordinates moved first. Under the high quality environment conditions the subordinates appeared willing to risk an aggressive encounter to gain access to the pellets, despite the results showing that this was rarely achieved. Subordinates, though not dominants, based following decisions on their previous expectation of patch quality, from the training runs. This emphasises that retaining information on which to base foraging decisions may be more important for subordinate animals. Where there might be confrontation for a

food resource that the subordinate is likely to lose, as shown in this experiment, taking the risk to follow must be based on the likelihood of accessing the food.

Producer-scrounger roles

The idea that dominant animals exploit the findings of subordinate conspecifics stems from the producer-scrounger hypothesis. Barnard & Sibly (1981) developed a model for foraging strategies of different individuals within a group of house sparrows (*Passer domesticus*). The scrounger strategy relied on explorative subordinate producers to find food patches. Subordinate animals in a group tend to occupy unfavourable and exposed leading positions in the group, whereas dominant animals occupy preferred central positions (Hall & Fedigan 1997). This gives the subordinate animals a finder's advantage, being first to come across higher quality food patches. However, dominant scroungers displace the subordinates, and monopolise the patch (Stahl et al. 2001). The qualitative predictions on following are supported in this study, with dominants following and displacing subordinates. On no run did subordinates follow and successfully displace dominant animals from the patch when pellets were present. However, dominant animals in this trial also played a finder's role, by moving first to the variable patch on most runs. The results here differ from the traditional producer-scrounger model in the information held by dominant and subordinate animals in the pair trial. In the producer-scrounger scenario, neither animal has a previous expectation of patch quality. Scroungers get all their information from the producer. In the current experiment, the subordinate animal only moved first where she had an expectation of a high quality patch. However, by the end of the test, as a result of constant displacement, the subordinates were reluctant to move and stayed on the low quality patch for the duration of the

test. In this situation, subordinates were aware of the test conditions, as shown in the results of the following, but chose not to respond. Because the subordinate did not respond, the dominant also lost that information.

Difference in rank

The experiment was designed to ensure that between the dominant and subordinate groups, all dominant animals were dominant over all subordinate animals, as it was considered that sheep might not be capable of identifying relative differences. Wiley & Hartnett (1980) found that juncos (*Junco hyemalis*) in the middle of the dominance hierarchy behaved differently towards dominant and subordinate individuals, but did not differentiate according to differences in the magnitude of rank. This was also observed in female bighorn sheep, where low ranking females did not show discriminatory avoidance behaviour according to the ranks of more dominant females (Eccles & Shackleton 1986). However, Seyfarth (1981) found in a group of primates that females ranked one another according to their exact positions in the hierarchy, prejudicing responses towards grooming solicitations from the highest ranking females. In the current experiment there is evidence that this group of sheep were capable of identifying relative differences in dominance, when foraging in pairs. Evidence of this has also been found in dairy cows where Manson & Appleby (1990) found that cows closest in rank tended to feed closest together.

The larger the difference in rank between pairs of sheep in the current experiment, the less competition for the variable patch occurred, as dominants moved round first and were less likely to be followed. If dominance hierarchies exist to reduce the costs of intraspecific interactions (Gauthreaux 1978) then it is possible that subordinate sheep avoided moving to the variable patch where the risk of interaction and,

therefore, escalated aggression was greater, i.e. where the dominant animal was significantly higher in the hierarchy. Where sheep were closer in the hierarchy there was an increased possibility for the subordinate of accessing the pellets.

Sociability

Although following behaviour might be explained by the likelihood of accessing the variable patch according to dominance status, it is possible that social considerations affected behaviour. Subordinates may have followed dominants and vice versa in an attempt to retain social contact, as the experimental set-up prevented the animals seeing each other when foraging from different patches. Sociability, the tendency of individual animals to be close to others (Sibbald et al. 1998), was not measured in this group; however, its influence was minimised by ensuring the sheep were unstressed while foraging individually in the arena before beginning pair trials.

Comparing natural with restricted foraging

In natural environments, there is little escalation of agonistic encounters, as the subordinate is free to move away in an encounter with a dominant conspecific. In a study of group living red deer (*Cervus elephus*) Thouless & Guinness (1986) noted,

“the stability of dominance hierarchies is a result of weak and low-ranking individuals accepting their position in preference to fighting for access to resources and losing”.

This situation occurs where the costs of defending a resource and fighting are high in comparison to the predicted benefits. Therefore, in foraging herbivores, where resources are generally low quality and relatively continuously distributed, subordinates will not challenge for access and give up quickly when conflict escalates. In the current experiment, where movement between patches was restricted, subordinates forgo patch quality information, allowing the dominant

animal almost complete access to the variable patch. By remaining at the stable patch, the subordinate can maximise intake of hay, without the cost of moving to the variable patch. The dominant pays the cost of moving to the variable patch but with the benefit of exploiting the patch when it contained pellets.

Modifications to the experimental set-up

To examine the level of information obtained by the foragers during the pair trial, it would be interesting to re-run individual trials immediately following the pair trials, and record the patch leaving behaviour of the sheep. If no information on patch quality had been retained over the test period, as a result of no reinforcement, or interference in retention of memory then we would expect sheep to behave as in their previous individual runs. If information had been obtained during the test, it would be reflected in the next set of individual runs. Alternatively, a third patch could be introduced in the series, to separate the effects of following for social reasons from patch exploitation. Allowing animals to see each other at any position within the arena would also control for social effects.

The results from this Chapter have shown that both dominant and subordinate animals altered their behaviour when foraging in pairs compared to foraging alone. However, as described above the limitations of the experimental set-up prevented the sheep from exhibiting natural behaviour. In the experiment described in Chapter 8 an attempt is made to overcome this as behaviour in response to a spatially and temporally variable environment is studied under more natural conditions.

SUMMARY

In socially foraging herbivores, shared information about patchy or limited food sources can reduce the variability associated with finding food. However, information and resources may not be distributed evenly between all group members. The foraging strategies of pairs of sheep with known dominance status were investigated in a two-patch environment. Patches were presented in series, with the second patch of variable quality manipulated to produce a high or low quality environment. Analysis considered the movement of pairs of sheep towards the second variable patch across the trial. Dominant animals appeared to use information from subordinates and tended to move first to the variable patch in the early stages of the trial. Subordinates were consistently displaced at the variable patch and disregarded previous patch information to avoid confrontation. Following behaviour was highly dependent on the status of the animal, with dominants following more than subordinates ($P < 0.001$). Dominants followed regardless of previous patch information, however, subordinates were more likely to follow when previous information indicated a high quality environment ($P = 0.006$). The likelihood of both dominants and subordinates following was greater when foraging in a high quality environment ($P < < 0.001$). When the relative difference between pairs in the hierarchy was greater, subordinates were less likely to challenge for access to the food resource ($P = 0.013$). This experiment showed that the opportunity to learn about the environment could be disrupted when foraging as a group in rapidly depleted patches.

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CHAPTER 7

THE EFFECT OF A TIME DELAY ON THE CHOICE BETWEEN A STABLE AND VARIABLE PATCH

INTRODUCTION

Natural systems are typically unpredictable in the resources available to a foraging animal. In order to forage efficiently animals must integrate information from previous patch experiences and knowledge of environmental variability to guide foraging decisions (Kamil & Roitblat 1985). This was shown in Chapter 4 where foraging sheep responded to average patch conditions, as well as most recent experiences within the patch. Tracking environmental variability allows the forager to integrate information from recent foraging bouts with information from the past to build up an expectation of future patch quality (Stephens, 1987; Tamm 1987). How far back the forager should consider while tracking is dependent on the rate of change of the environment. Several models considering the devaluation of information with time have been developed (Cowie, 1977; Devenport & Devenport, 1994; Hirvonen, et al 1999) and arrived at similar conclusions. These models are based on the assumption that information from the recent past is more valuable than information from the distant past. Devenport & Devenport (1994) found that chipmunks (*Tamias minimus*) relied less on recent patch experience as the time between patch experiences grew, instead reverting to a choice based on an average of the patches. Where environmental conditions rapidly changed, this reversion to an average happened more quickly than where the environment was

slow changing. These results reflect the loss of information value over time (Beauchamp et al. 1997). This hypothesis does not suggest that animals are forgetting information about patch quality, instead weighting the information according to recency related to environmental conditions. Should the animal be forgetting information and therefore approaching the patches as if with no previous experience, it is predicted that their behaviour would be based on lateral preference, olfactory or visual cues, or some other aspect of the environment.

By altering properties of memory in a flexible manner foraging animals can account for change in more or less variable environments. In the type of model discussed above animals are confronted with two patches that change at the same rate. However, in a natural system this is unlikely to be the case. Patches will be unevenly exploited by competing foragers and may vary in the quantity and quality of resources available. How does an animal respond to a situation where two patches are available but differ in stability? This problem has been explored through risk sensitivity theory, the response of foraging animals to variance in reward. In general terms risk sensitivity models predict that a forager operating on a positive energy budget should always choose the less variable patch. However, where the forager is operating on a negative energy budget, choosing a variable patch may be its only route to survival (Caraco, 1980; for review see Bateson & Kacelnik, 1998).

In the current experiment these two aspects of foraging are considered. Firstly, the effect of the passage of time on patch choice in variable environments (i.e. a time discounting effect) and secondly the choice between two patches where patches differ in the reliability of reward and rate of change of patch conditions (i.e. a risk sensitive choice).

To test this using Scottish Blackface sheep as subjects, a foraging environment was simulated offering a two-patch choice. One patch was variable in quality, the other stable and always containing the same reward. Both patches had the same mean reward. Using this set-up the effect of a time delay on patch choice, where one patch was more predictable than the other, coupled with the influence of environmental rate of change was investigated.

For the foraging sheep operating on a neutral energy budget, it is hypothesised that, if responding to the variance in reward, they would choose the stable patch. This is based on the predictions of risk sensitivity theory for preference for stability. As the length of time since the last patch experience increased it was predicted that the sheep would respond to the average of two patches and choose at random. The time at which the patch choice of the sheep reverted to random would be based on the rate of change of the environment.

MATERIALS AND METHODS

Animals, Housing and Care

The experiment was carried out at Glensaugh research farm, Scotland (56°N, 2°W). It ran over July and August 2000 with 12 non-pregnant, non-lactating Scottish Blackface ewes (mean live weight at the start of the study \pm SD=46.2 \pm 5.5kg). Throughout the study the animals were housed in individual strawed pens, under natural light conditions. During the experiment the animals were fed to maintenance via a morning feed and any food eaten during the training and experimental period, with the remainder fed in the

evening. The maintenance ration was calculated according to the equation $0.435\text{MJ/kgLW}^{0.73}$ (MAFF, 1984). Tests were conducted using concentrate pellets (12.5MJ/kg/DM: Green keil, NorthEastern Farmers, Rosehall, Turriff, Scotland), previously established as a highly preferred feed for Blackface sheep (Chapter 3).

Experimental Set-up

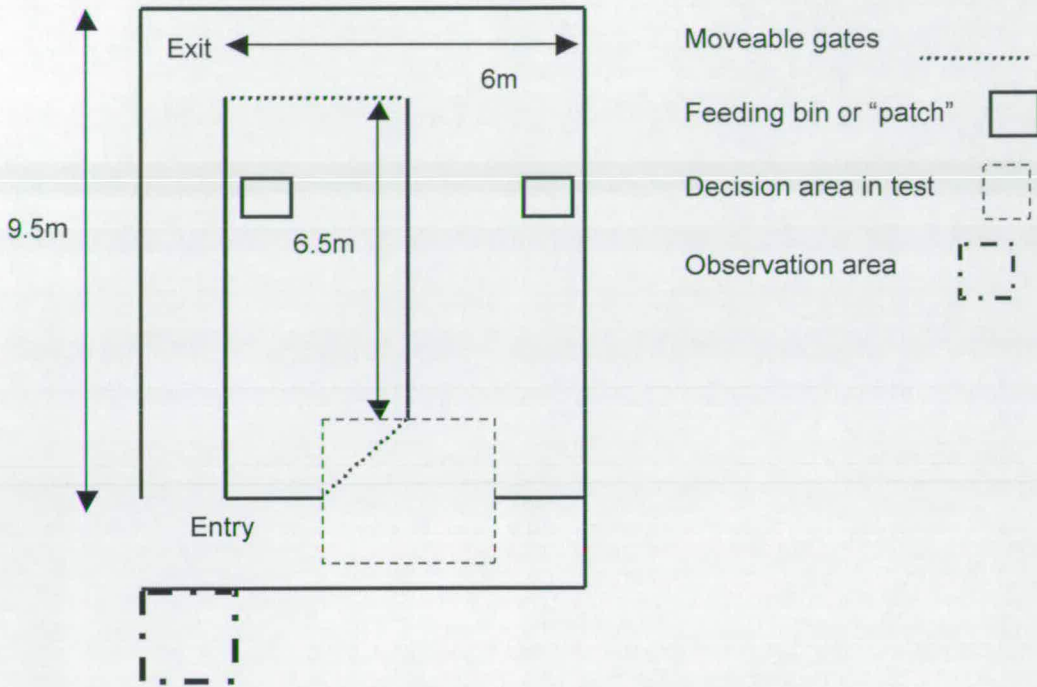


Figure 7.1. Plan of the foraging arena. The observation area is shown on the bottom left and the 2 bins with gates closing off access to one bin

Foraging runs were carried out in an arena close to the home pens (Figure 7.1). The arena measured 9.5m by 6m and was divided down the middle by a fence 6.5m in length. Feeding bins (50cm*18cm*18cm) were placed as artificial patches 20cm in from the edge of the arena and pellets were placed outside the arena at these points to minimise the possibility of the animal identifying the presence of pellets through olfaction. Moveable gates were positioned to restrict entry to one side or the other according to the treatment. The sheep could not see the pellets until they had made the patch choice and were within 1m of the bin.

Habituation to the procedure

The first five days of the experiment allowed habituation of the animals to their individual pens and to foraging while socially isolated. Animals were removed from the pens and released into the arena where they were permitted up to five minutes of exploration time. At this point access was possible to both sides of the arena and the sheep was free to leave through the exit gate at any point during the training. In the early stages of the test all sheep were observed to go to the right hand bin first. This was probably as a consequence of the arena set-up where sheep were introduced in the bottom left corner of the arena and followed initially by the observer. In response to this the sheep had a tendency to run to the opposite corner of the arena. At this stage of the training all sheep chose the right hand side of the arena. Bins were provisioned with good quality hay to inform the sheep of the role of the bin as a food patch. The sheep quickly adapted to the foraging set-up and after 5 days were foraging individually and from both sides of the arena in a calm manner.

Assignment to the treatments and initial training

The 12 animals were divided into three groups of four. Patch types were allocated to the bins; one bin designated "stable" and the other "variable". For half the group the stable bin was on the left of the arena, for the other half of the group it was on the right hand side of the arena. Each sheep had 24 individual runs in the arena. A run consisted of the movement of an individual sheep from her home pen through to the decision area in the arena. The sheep was free to spend up to five minutes in the arena exploring and investigating the available patches before returning to the home pen.

Experimental design

Each sheep received 24 runs in the arena, with three runs per day over an eight-day period. Of the 24 individual runs in the arena, 12 were on the stable side and 12 on the variable side. Using gates to restrict access to one side enforced and standardised patch experiences on the sheep. The sequence of patch visits was alternated with the first patch visit randomly assigned for each animal. Once the sheep had finished eating from the patch she was free to return to the home pen by leaving the arena through the exit gate.

Each group of four sheep was assigned to one of the following treatments:

Fast changing environment: In this treatment the stable patch always contained 50g of pellets and the variable patch contained either 0g or 100g of pellets. The sequence of provisioning to the variable bin was random on the condition that no more than two “high” (bin containing 100g pellets) or two “low” (empty, 0g pellets) were concurrent. The total volume of pellets offered in the variable patch was the same as that offered in the stable patch.

Slow down environment: Of the 12 runs experienced in the variable patch, the first six were “high”, containing 100g of pellets on every run and the following six were “low”, the patch was empty. This represented a slow changing patch, i.e. a relatively stable environment. The stable patch was provisioned with 50g pellets on every run.

Slow up environment: Of the 12 runs experienced in the variable patch the first six were “low” and the following six were “high”. This set-up also represented a slow changing patch. The stable patch was provisioned with 50g pellets on every run.

Testing procedure

At the end of the 24 run training period each sheep was tested five times for patch choice representing five delay periods. In these free choice trials the gates were removed and the sheep was considered to have made a patch choice after leaving the decision area. The delays tested were: 1 hour after the last run of the training block (or the “immediate test”), 2 days, 5 days, 9 days and 21 days after the last run of the training block. The delay tests composed of one test per sheep for each delay period.

During the tests the bins were provisioned as for the treatments to ensure that the sheep were not penalised as a result of their choice. The stable bin contained 50g of pellets and the contents of the variable bin were dependent on the previous treatment of each individual. For example, the fast group variable bin was provisioned with at random. The provisioning for the variable bin for the slow down group was low (0g) and for the slow up group was high (100g). As a consequence of this set-up, the delay from the most recent run in the foraging arena run was shorter than the delay from the last run of the training block.

Once the sheep had selected the bin from which to feed and consumed the pellets if the bin was provisioned, she was pushed out of the arena to prevent her investigating the other patch. Between the 9-day test and the 21-day test the sheep were moved from their home pens and re-housed in a group pen, before being returned to the individual pens for the final test.

Measurements

All trials were recorded on video. Details of sheep number, treatment, time of day, and patch state were recorded. During the trial the time of entry and exit to the arena, time taken to approach the patches, time spent feeding under different patch conditions, and any other non-feeding activities were recorded. Feed weights before and after each trial were recorded to the nearest gram.

Analysis

The experiment was divided into two parts. The first part of the analysis considered the behaviour of the sheep during the training period where the sheep could learn the patch conditions. The second part concerned the patch choice of the sheep in the free choice trial and the influence of a time delay on this choice.

Learning the patch conditions

This analysis was carried out to investigate the response of sheep to variability in patch quality over a short time period. The behaviour of the sheep during the training phase can reveal their learning and hence expectation about the patch quality. This was reflected in their running speed to the bin and in this experiment was recorded as the time taken to travel from the decision area to the feed bin. Crespi (1942) used this measure of expectation on rats in a running maze, finding that rats ran faster towards a higher reward. Travel time was compared between animals moving towards the variable bin after the different training regimes: treatment group slow down and treatment group slow up. Only these data were considered because sheep in the fast treatment had no opportunity to build up an expectation of patch quality due to the unpredictable nature of

the patch. In addition the group size of four animals was too small to reliably compare with the combined data from the other two treatment groups. The data were analysed as two sets. Firstly, the time taken to reach the variable patch on the sixth run after a period of five successive “highs” and secondly, after a period of five successive “lows”. These analyses were carried out to examine the differences in “time to bin”, a measure that represented the speed at which animals approached each patch. Where variances between groups were equal, as determined by a variance ratio test, a paired t-test was carried out. When variances were not equal, the non-parametric Wilcoxon paired sample test was used.

To determine if sheep took significantly longer to consume 100g of pellets compared with 50g of pellets, the data were normalised through log-transformation and analysed using a t-test. All analyses were carried out using the Genstat 5 package, Release 4.1 (Genstat 1998).

Patch choice in free choice trials

The second part of the analysis considered the results of the time delay test. Patch choice was examined firstly for the test immediately after the training period (“immediate test”). To assess patch choice, results were compared with a chance performance of 50% (half of all patch choices to the stable patch). The results of the immediate test were then compared to the combined results of the longer delay tests. This was to identify evidence of a change in patch choice over the longer delay periods. A one-tailed Fishers exact test was used to compare between treatment groups (one-tailed to identify a switch in choice from the first to the final test). Two-tailed Fishers Exact tests were used to determine if

there was a significant difference in the proportions of stable and variable chosen during the delay tests compared to a random choice.

RESULTS

Learning the patch conditions: The behaviour of the sheep during the training period

The expectation that the sheep held of patch quality was compared for the two sets in the slow changing environment. Data for each sheep on the time taken to reach the feed bin was recorded and referred to as “time to bin” (Table 7.1). Only the results from the final run in a group of six runs were analysed as it represented a culmination of knowledge from the previous five runs.

Table 7.1: “time to bin” for sheep after 5 high runs, 5 stable runs and 5 low runs

Individual sheep	Time to bin after 5 high runs (s)	Time to bin after 5 stable runs (s)	Time to bin after 5 low runs (s)
11	5	5	9
12	12	8	41
13	6	6	60
14	4	13	6
21	4	6	30
22	7	10	8
23	4	6	9
24	5	4	19
n	8	8	8
Median	5	6	14
SD	2.39	2.64	17.42

The “time to bin” for sheep after five runs with the variable patch yielding a high reward was faster than after five runs of the variable patch yielding a low reward ($t_7 = 0, P \leq 0.01$)

How did this compare with the expectation the sheep held for the stable patch? The “time to bin” for sheep after a run of five highs in the variable patch (100g) was compared with “time to bin” after five runs in the stable patch. The null hypothesis was accepted. The sheep travelled at the same speed to the stable patch as they did to the variable patch in the high condition ($t_7=1.030$, $P>0.05$)

Although not significant, there was a tendency for sheep to walk more quickly to the stable, and predictable reward bin, than towards the variable bin after five runs on the low treatment ($t_7=5$, $P=0.07$). In summary, sheep walked more slowly to the variable patch when previous experience gave a low expectation of reward. Conversely after experiencing high yielding conditions, sheep moved more quickly to the variable patch (Figure 7.2)

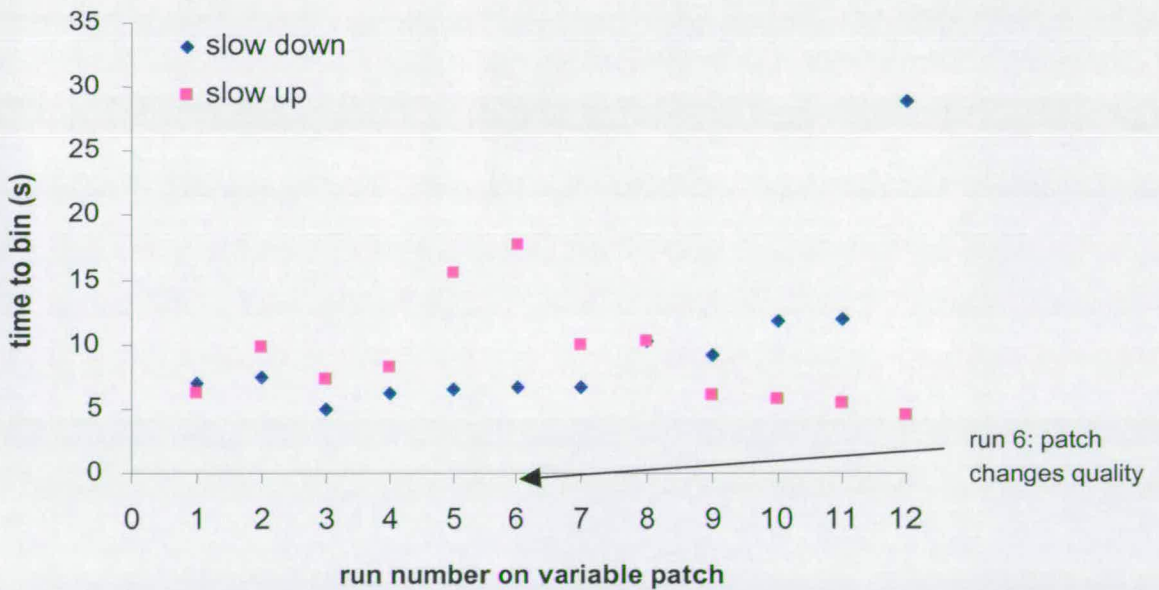


Figure 7.2: The change in walking behaviour for the two slow environment groups. Slow down changed from a high environment quality to a low environment quality. Slow up changed from low to high

Sheep were significantly faster in consuming 50g of pellets than 100g ($t_{11}=-5.94$, $P<0.001$).

Patch choice in the free trials

The second part of the analysis considered the effect of a time delay on patch choice. The first analysis examined the patch choice of the sheep immediately following the last training run. On this run the gates that had previously enforced patch experience were removed and the sheep were presented with a free choice. These results were analysed to determine if patch choice of the sheep was random or based on information gathered from the recent training runs. With 11 of the 12 sheep choosing the stable patch, sheep were not selecting at random ($P=0.006$, 2-tailed test. Table 7.2: immediate test). The sheep were exhibiting a significant preference for the stable patch over the variable patch. It is possible that the sheep were responding to a lateral preference for one side of the arena. In the immediate delay test seven sheep went to the right hand side of the arena and five sheep went to the left. This indicated that the group of sheep as a whole had no significant side preference ($P= 0.774$, 2-tailed test), though individuals may have had distinct preferences.

Was this choice maintained over the course of the delay tests? Patch choices from the 2-day until the 21-day tests were combined to identify any “switches” after the immediate test. A value of 0 indicates no switch, and a value of 1 indicates that there had been at least one switch. After the 21-day test, it can be seen that four animals made a switch in patch choice but eight animals did not. A one-tailed test was used to determine if a significant number of animals had maintained their patch choice over the course of the

delay tests. This hypothesis was rejected ($P=0.146$, 1-tailed test. Table 7.2: 2 day-21 day test). The switching of patches to random behaviour first occurred at the 2-day test (Table 7.2). At 2 days the proportion of animals choosing the variable patch had risen and there was no longer a significant preference ($P=0.193$).

Table 7.2: Results of the patch choice tests after varying delays. The tests occurred immediately ("immediate test"), 2, 5, 9 or 21 days after the last training session. (S = animal chooses the stable patch; V = animal chooses the variable patch)

Treatment	Sheep	Position of stable patch	Immediate test	2 day	5 day	9 day	21 day	Switch?
Slow down	2	Right	S	S	S	S	S	0
Slow down	7	Left	S	S	S	S	S	0
Slow down	12	Right	S	S	S	S	S	0
Slow down	10	Left	S	S	S	S	S	0
Slow up	11	Right	S	V	V	V	S	1
Slow up	6	Left	S	S	S	S	S	0
Slow up	5	Right	S	V	V	V	V	1
Slow up	3	Left	S	S	S	S	V	1
Fast	1	Right	S	S	S	S	S	0
Fast	8	Right	V	V	V	V	V	0
Fast	4	Right	S	V	S	S	S	1
Fast	9	Left	S	S	S	S	S	0
P-value			P=0.006	P=0.193	P=0.146	P=0.146	P=0.146	

Was there a significant difference in switching rate between the treatment groups slow down, who ended the training period with a run of six "lows" and the treatment group slow up, ending their training period with a run of six "highs"? All four sheep in group slow down chose the stable patch on the immediate test, and retained this choice over all subsequent tests. Of the four sheep in slow up, three animals switched their patch choice after choosing stable on the immediate test. Of these three, one animal switched back to stable again for the 21-day test. The difference in switching rate between group slow down and slow up, while not significant at the 5% level ($P=0.07$, 1-tailed Fishers Exact test), suggests the sheep in slow down may have held and used information about patch

quality for longer than sheep in slow up. In addition there was no difference in switching behaviour between slow up and fast groups ($P=0.244$, 1-tailed Fishers Exact test).

Consideration of group size effect.

To determine the effect of group size on the likelihood of observing an effect, a power analysis was carried out specifically examining the difference between groups slow up and slow down in the occurrence of a patch switch over the course of the experiment. The probability of 1 switch occurring was found to be 0.75 ($P(1)=0.75$). However, power analyses cannot be based solely on the observations made during the experiment, so here I present a power analysis for group sizes of up to 6 and over a range of values of $P(1)$.

Table 7.3: Power analysis over range of different effects and group sizes

Group size	P(1)					
	0.5	0.6	0.75	0.8	0.9	1.0
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	0.125	0.216	0.42	0.51	0.729	1
4	0.0625	0.13	0.31	0.41	0.66	1
5	0.186	0.337	0.63	0.73	0.91	1
6	0.336	0.546	0.76	0.89	0.98	1

This analysis shows that with a group size of 4 and a probability of observing a score 1 within the group of 0.75 (as was observed), the chance of identifying a difference was only 0.31. If the group size had been increased by only one animal, the probability of observing a significant difference increases to 0.63, and with 6 animals to 0.76. In

addition, if a stronger effect had been observed (e.g. 0.9) increasing group size by one animal results in a much stronger probability of observing a significant difference between groups.

DISCUSSION

The results from the training period support other studies that suggest foraging animals use information obtained from previous foraging bouts to exploit current patch conditions (Stephens & Krebs 1986; Tamm 1987; Laca 1998; Hirvonen et al. 1999). When the sheep had been trained to expect a high reward from the patch they moved quickly towards it. However, when the patch had been empty over the previous five runs, there was no expectation of the patch containing a reward and the sheep responded by moving only slowly towards the patch, and engaging in exploratory behaviour before returning to the home pen. This gradual decline in walking behaviour is in response to a persistently unrewarded stimulus, i.e. the patch in “low” condition.

There was also a tendency for sheep to move more quickly to the variable patch after a run of five “high” than they did to the stable patch. The significant difference in the time taken to consume the different volumes of pellets may have acted as a stimulus upon which sheep based their expectation. A stronger effect might have been observed if there had been a longer runway between the decision area and the patches. This may explain the lack of difference between the “time to bin” after a run of five “low” in the variable bin and the “time to bin” for the stable patch. Here, I would have expected the sheep to approach the stable bin more quickly, however, due to the short distance between the

decision area and the bin, and large variation in the “time to bin” for the “low” group, no significant differences were identified.

The training phase of the experiment established that sheep could respond to the “all or nothing” conditions of the variable patch, and showed a tendency to differentiate between the reward from the stable patch and the reward from the variable patch in “high” conditions. Despite both the stable and the variable patch having the same overall mean value at the end of the training period, the results of the immediate test, with 11 of the 12 animals choosing the stable patch, strongly suggests that the sheep were responding to variability in patches by being risk averse. This is in accordance with risk sensitivity theory, which predicts risk aversion in mammals on a positive energy budget for food amount (Caraco 1980; Bateson & Kacelnik 1998). This result would match a prediction for the treatment group “fast”. The sheep in this group would have received the same mean output from both patches, but by choosing the stable patch, avoid the risk of getting nothing. On the basis of previous experience the slow down group have a low expectation of reward from the variable patch and, therefore, would also be expected to choose the stable patch. Group slow up, with final 6 runs of positive experience on the variable patch, would be expected to select the variable patch. However, with 11 of the 12 animals selecting the stable patch, preference for predictability over variability appears the stronger influence.

The level of the mean reward and variability can strongly influence the tendency of animals to be risk averse. Increasing the mean expected reward from the variable patch can alter preference. Real (1991) showed that foraging bumblebees (*Bombus pennsylvanicus*) chose equally between variable and predictable flowers once the mean

reward in the variable flowers had reached a threshold level. The same titration procedure could have been used in the current experiment to obtain the threshold value at which sheep were indifferent to the stable and variable patches. For both groups in the slow changing environment, one might expect the rate of memory decay to be the same. However, the results suggest that while slow up reverted to random foraging, slow down appeared to retain information over the 21-day period.

There is evidence that sheep (Edwards et al. 1996; Dumont & Petit 1998), deer (Gillingham & Bunnell 1989) and cattle (Bailey et al. 1989a) have accurate memories for food resources over space and time. Bailey et al (1989a) reported that cattle used short-term memory or working memory to associate particular arms of a radial maze with differing food amounts. The animals were capable of returning to these patches in relative order of quality within a period of 24 hours. In addition cattle could remember food availability over longer time periods, using a form of memory known as reference memory (Bailey et al. 1989b). For example, Bailey et al. (1995) found that cattle could avoid the poorest of three patches for 21 consecutive days and Edwards et al. (1996) showed that performance of memory in sheep did not decline after a 72-hour interruption.

If large herbivores are capable of remembering patches over a long period, why should the two slow-changing environment groups differ in their patch choices? For group slow up, their final training runs were always successful, regardless of which patch was selected. The stable patch contained 50g of pellets, the variable patch 100g. As shown above, the expectation the sheep held for each patch type was the same, suggesting that animals were referring to the average of path quality rather than their most recent

experience. On average both groups slow up and slow down experienced the same patch conditions the only difference being that slow down ended on a bad run. There is evidence to suggest that foraging animals respond more strongly to losing than to winning streaks. Hosoi et al (1995a,b) found that goats and cattle tended to adopt a “lose-shift” strategy by switching patches when the previous patch visit had been unsuccessful. Animals can store and retrieve memories over long time periods more easily if they were stressed or aroused at the time of the event. Negative experiences are, therefore, more likely to be recalled than neutral experiences (Fulop & Menzel 2000). In the current experiment the variable patch offered either 100g of pellets or 0g. The negative effect of consistently encountering an empty patch may have been strong enough to force the sheep into adopting a “lose-shift” strategy and choosing the stable patch in the free patch choice tests. Indeed the negative effect of the empty patches could have been strong enough to persist over the 21-day period. For slow up the consequences of the patch choice were less significant. Therefore no information, other than that both patches contain pellets, was retained.

This biasing of memory in response to negative experience may influence the output of the type of foraging models described in Chapter 2. Based on the output of these models memory is predicted to devalue quickly in a fast changing environment. This was observed in the current experiment with the “fast” group reverting to random behaviour on the second day of the test. It would also be predicted that both groups in the slow changing environment treatments would retain memory of patch conditions, through a low devaluation rate. However, these data, though limited by small sample size, suggest that sheep having recently experienced a low quality environment retain information for

longer than sheep with previous high quality experience. This should be considered in further development of foraging models that refer to memory by considering that negative experiences are devalued at a lesser rate than positive experiences.

One sheep in the fast group (Sheep 8; Table 7.2) did not appear to be selecting patches according to information but perhaps basing choice solely on a lateral preference within the arena. During the habituation period all sheep showed a preference for the right hand side of the arena, probably because the entrance to the arena was not central but positioned to the bottom left. It appeared that by the end of the training period, all sheep had overcome this, but it is possible that sheep 8 maintained a preference. Lateral biases have been identified in goats (Illius et al. 1999) and Grandin et al (1994) found after the position of the negative stimulus had been switched that cattle appeared unable to change a learned preference. Where memory is disrupted through fear or interference, simple tasks can become confounded (Mendl et al. 1997). The small number of animals in the current experiment results in an over-riding influence of individual variation in response to trials.

Limitations of the experimental design

A problem with the experimental design resulted in a confounding of the time delay between patch visits with the last experience in that patch. During the tests bins were provisioned according to the states of the stable and variable bins on the last run of the training period. The analysis, however, did not consider the effect of the intervening test runs on the behaviour on the test run in question, instead always referring back to the training period. Because the animals were only permitted to visit one patch during the

test run, their experience in subsequent tests would have been skewed towards this patch. In consequence the average volume of food obtained from the stable and variable patch was not equal, breaching a condition of risk sensitivity tests.

To overcome this problem and improve the power of the analysis, this experiment would be redesigned with the same treatments, however, different groups of sheep would be exposed to each time delay. This would allow separation of the effects of training and of most recent patch experience.

This chapter has shown, supporting the conclusions of Chapter 4, that information from previous foraging bouts is used to help the forager make patch choice decisions when environmental conditions are uncertain. Foraging sheep showed a strong tendency to select for patch stability, emphasising the value of information for the sheep, but as the time since the last patch experience increased the patch choice reverted to a random choice representing an average for the environment. However, where negative consequences of choice existed for the forager there was a higher tendency for memory of patch conditions to persist.

SUMMARY

In an unpredictable environment information gathered whilst feeding may aid future foraging decisions. I investigated the use of information in a two-patch environment after several time delays and the effect of rate of patch change on the use of information. Sheep were trained to forage individually from two patches. One patch yielded a constant, intermediate value reward. The second patch yielded rewards that varied

between high and zero, but with the same mean value as the stable patch. Sheep were then given the choice between the two patches after five delay periods: immediate, 2 days, 5 days, 9 days and 21 days. Sheep ran faster towards patches when they had a high expectation of reward. With a short delay between the last training run and the test, sheep responded in a risk-sensitive manner, choosing the stable patch. Sheep that experienced a long losing run in the variable patch showed a tendency to stay with the stable patch choice at the longest time delay ($P=0.07$). However, sheep that experienced a fast changing or winning run environment chose patches at random at the longest time delay ($P=0.146$). The importance of negative experience in future foraging bouts was demonstrated.

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CHAPTER 8

THE EFFECT OF SPATIAL AND TEMPORAL VARIATION IN PATCH QUALITY ON THE FORAGING BEHAVIOUR OF SHEEP.

INTRODUCTION

In a heterogeneous environment optimal foraging models predict that animals should move between resource patches in such a way as to maximise their food intake rate (Charnov 1976; for review see Pyke, 1984). Implicit in these models is the assumption that the forager has complete knowledge of its instantaneous rate of intake and the optimal rate of intake achievable in the environment, and that this knowledge is obtained at no cost (Orians, 1981). Under natural conditions, where resources vary in time and space, this assumption is unrealistic (Nishimura 1992). To overcome the uncertainty associated with limited knowledge of the resources available for exploitation, the forager can obtain information through learning about resource distribution and reliability. The better informed an individual; the better it can exploit the natural heterogeneity of the environment (Stephens & Krebs 1986).

Previous chapters in this thesis have emphasised the importance of tracking variation in patch quality over time and the effect of conspecific foragers on the information available to individuals. In this current experiment the question of uncertainty focuses on the ability of foraging sheep to overcome spatial and temporal variability in patch quality in an experimental set-up replicating a more natural system. The use of spatial memory has been shown in herbivorous species and allows foragers to exploit predictable patchy resources in a heterogeneous environment (Bailey et al.

1996; Dumont & Petit, 1998). Evidence for spatial memory has been found in herbivorous species such as deer (Gillingham & Bunnell 1989), cattle (Bailey et al. 1989a, b; Laca, 1998) and sheep (Edwards et al. 1996; Dumont & Petit 1998). Foraging efficiency in Black-tailed deer was greater than expected by chance when food items were predictably distributed in a 0.5-hectare enclosure. The deer were seen to repeat previously successful search paths to relocate patches (Gillingham & Bunnell 1989). Bailey et al (1989a; 1989b) found that cattle used spatial memory to return to previously rewarded arms of parallel and radial arm mazes. In addition, the cattle returned first to the arms of the maze that had contained the highest volume of food before investigating other arms. Sheep have also been shown to use spatial memory to relocate patches constructed in pasture using flat-bottomed bowls and a pelleted feed concentrate. Sheep responded flexibly to change in distribution and used visual cues where available to aid spatial memory (Edwards et al. 1996). Dumont & Petit (1998) increased the complexity of the system, creating high quality resource sites, again with pellets in bowls within a pasture. Sheep visited more sites and consumed more pellets with increased experience of resource distribution. In addition, search paths were repeated and area concentrated searching, particularly within dense resource sites increased site exploitation.

Spatial memory is, however, only useful where the environment is highly stable. In a heterogeneous environment, patch quality can vary as a consequence of foraging by intra and interspecific competitors, spatial and temporal variation in vegetation and fluctuating weather conditions. In the face of such unpredictability, remembering the exact location and the previous quality of patches may be of little informative value (Illius & Gordon 1990). Instead, investing time in exploring patches to determine

their quality may reduce the cost of feeding on a low quality patch where a high quality alternative is available. Such sampling behaviour helps the forager overcome the problem of “incomplete information” (Stephens & Krebs 1986) by tracking environmental fluctuations and thereby increasing foraging efficiency.

The aim of this experiment was to explore the trade-off between the use of spatial memory and tracking of variation in patch conditions under competitive pressure. The following hypotheses were tested: (1) that foraging efficiency increases as resource distribution becomes more stable in space and time, (2) that sampling behaviour, measured here as the total number of patch visits in a trial, will increase in response to a decrease in predictability of resource distribution and (3) that search paths will be followed by the sheep where the environment is stable and more importantly, where resources of high quality are clumped in distribution. Additionally, memory for resources will be considered at within site level (which could be compared with feeding station scale) and between site level (which could be compared with a patch scale).

MATERIALS AND METHODS

Animals and the pasture

The experiment took place in June and July 2001 at the INRA farm of Saint Genes Champanelle in central France (43°N, 3°E). The subjects were 18 yearling or 2 year old non-pregnant ewes (mean live weight \pm SD=44.5 \pm 8kg) with grazing experience. Animals were tested on a cocksfoot sward (*Dactylis glomerata*) maintained at a constant height (5.9 \pm 0.5cm) by mowing every three to four days. A sample of sward was taken and analysed for crude protein (31.58 mg/gDM (Kjeldahl)), organic matter digestibility (0.729 (pepsin cellulase method; Aufrère & Michalet-Doreau, 1983)) and NDF (46.7%DM (Van Soest & Goering, 1970)).

Creation of resource sites

The experimental plot measured 100m*100m within which seven resource sites were created (Figure 8.1). Each site consisted of 21 flat-bottomed bowls (15cm*3cm) dug into holes with rims at ground level. Sites were formed in a hexagon to ensure each site was equally accessible from the central patch and consisted of bowls in a 12m*12m square, minus the corner bowls. Therefore, the distance to any other two sites from the current site was always the same. Within a site, bowls were placed 3m apart so that sheep were unable to see from the current bowl into the next bowl. Sites were 10m in from the edge of the plot, and spaced 22m apart.

Bowls were provisioned with concentrate pellets (25% barley, 25% wheat, 15% beet pulp, 10% soya and sunflower meal). The volume of pellets in each bowl and each site was dependent on the treatment. However, a total of 882g of pellets were always available in the experimental plot regardless of the treatment. Every bowl in the plot

was designated with a number. Plot maps were created to allow observers to accurately track the movement of animals between patches and between bowls within the site.

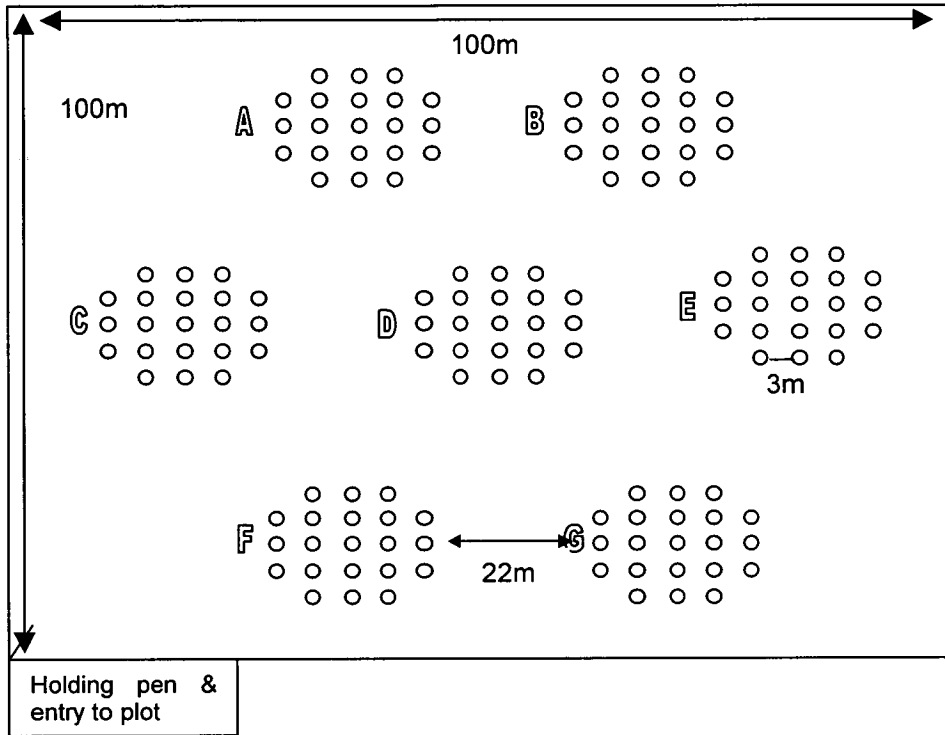


Figure 8.1: Plan of the pasture showing the position of the 7 sites (bowl size not to scale).

Treatments

To test the hypotheses relating to spatial memory, level of sampling and the use of search paths with increasing unpredictability in the environment, 4 treatments were implemented in a two by two factorial design representing different combinations of within and between site variability (Table 8.1).

Table 8.1: Structure of the treatments

		Between site variability	
Within site variability	treatment	no	yes
	no	<i>stable</i>	<i>variable</i>
	yes	<i>intermediate</i>	<i>high</i>



Plate 8.1: Close up of a bowl within the sward



Plate 8.2: View of a resource site.

Definitions

“Experiment” refers to the four weeks over which all groups of sheep experienced all treatments. Each five day period, during which each group experienced one treatment within the experiment is referred to as a “trial”, and each occasion that the sheep experienced the treatment in the experimental plot, and within a trial is referred to as a “run”. There were four trials for each group in the experiment and each group had five runs per trial. Plot refers to the experimental site, within which were created seven resource sites.

Stable (Figure 8.2a)

Seven bowls within a site were provisioned at random with three bowls containing 27g pellets; one bowl containing 18g and three bowls containing 9g of pellets, resulting in 126g of pellets within a site and a total of 49 bowls provisioned with 882g pellets over the site. The position of the provisioned bowls and the volume within each bowl was randomised at the start of each trial then remained constant throughout the trial. All sites were identical.

Intermediate (Figure 8.2b (I)-(V))

Seven bowls within a site were provisioned at random with three bowls containing 27g pellets; one bowl containing 18g and three bowls containing 9g of pellets. The position and pellet volume in each bowl was randomly assigned (in a balanced design) and changed on every run. Again this pattern is imposed on every site so that we see variability in bowl position and volume between runs within sites but not variation between sites between runs (see Table 8.1).

Variable (Figure 8.2c)




882g of pellets were available across the plot, distributed in 21 bowls containing 27g, seven bowls containing 18g and 21 bowls containing 9g of pellets. seven bowls were provisioned in every site, however in this treatment three sites were designated 'high' (seven bowls in the site will contain 27g pellets), one site as 'intermediate' (seven bowls will contain 18g pellets) and three sites as 'low' (seven bowls will contain 9g pellets) (Table 2). Site quality remained constant for the trial once the state of the site had been allocated. Position of the bowls within the sites was constant over the trial, and identical between sites.

High (Figure 8.2d (I)-(V))

882g pellets were available across the plot, distributed in the same way as in "Variable" to give three 'high' sites, one 'intermediate' site and three 'low' sites. In this treatment however, the position of the high, intermediate and low sites was not constant but varied on every run within a trial. Initially each site was designated with a different bowl pattern that was maintained for each individual site quality over the runs (Figure 2d (I-V)). If sites had not differed in bowl position this would have strongly reduce the within site variability, as each site of 9 or 27g appears three times within the plot. This set-up therefore gave variation within sites (seven different bowl patterns) as well as variation between sites (high, intermediate and low quality sites) between runs within a trial.

The patterns shown in Figure 8.2 a-d were consistently used across all groups of sheep.

Figure 8.2a: Stable distribution:
Days 1-5

-  Low - 9g
-  Intermediate - 18g
-  High - 27g

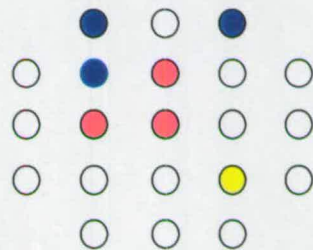
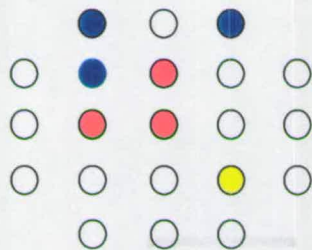
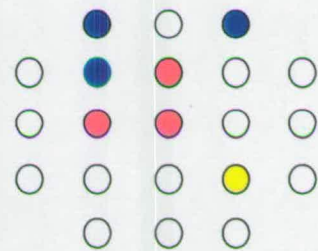
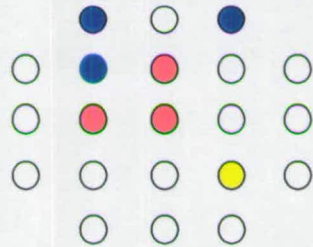
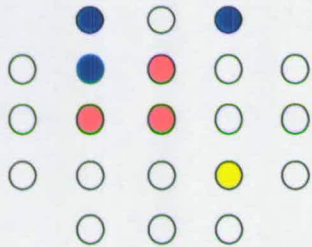
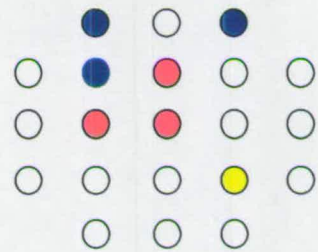
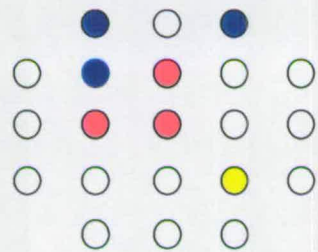


Figure 8.2b(l) Intermediate: Day 1

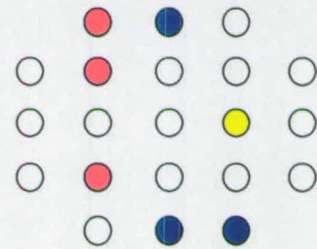
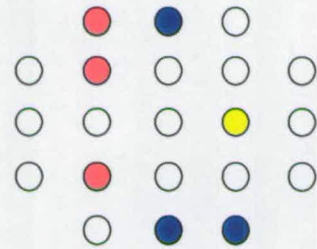
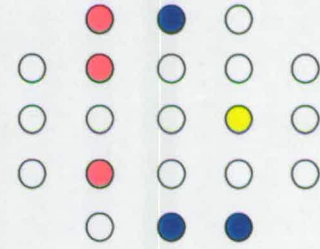
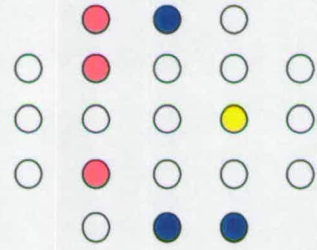
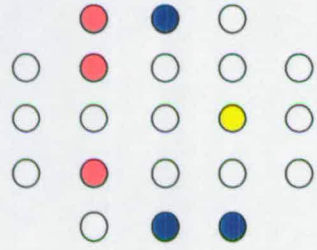
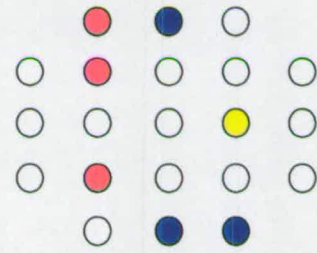
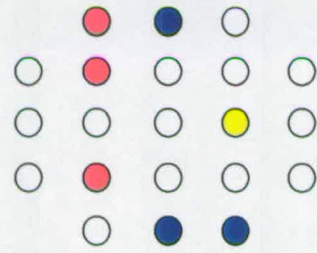


Figure 8.2b (II) Intermediate:
Day 2

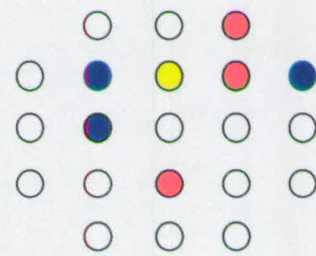
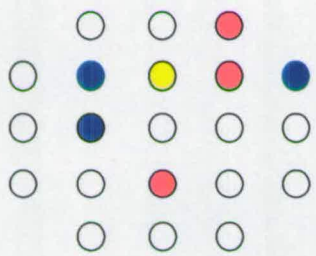
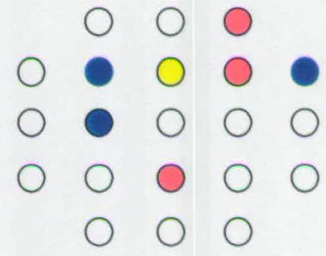
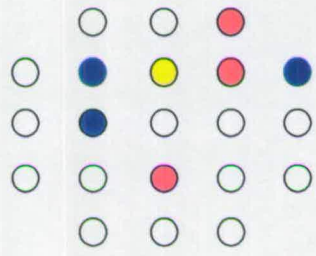
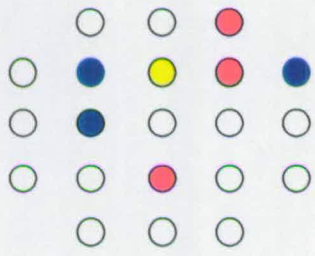
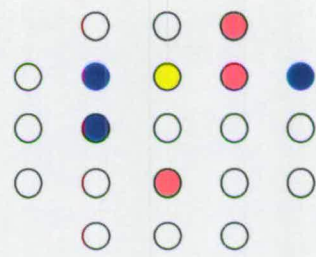
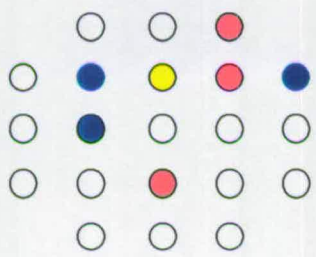


Figure 8.2b (III) Intermediate:
Day 3

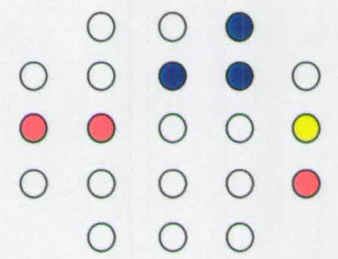
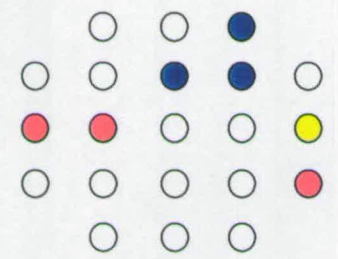
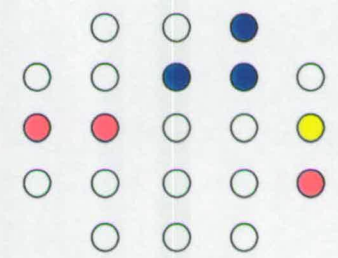
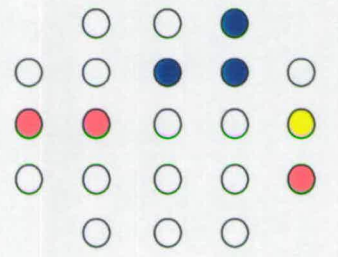
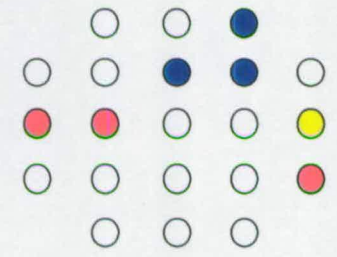
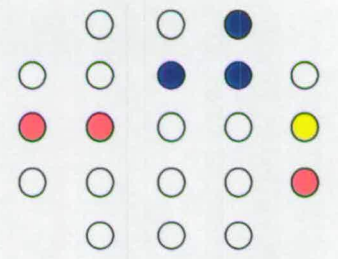
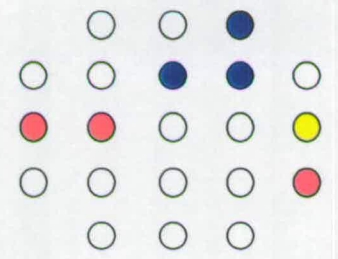


Figure 8.2b (IV) Intermediate:
Day 4

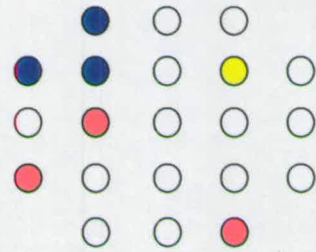
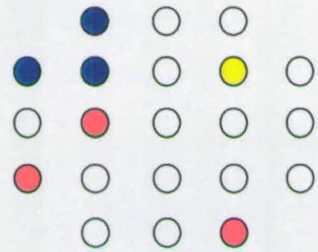
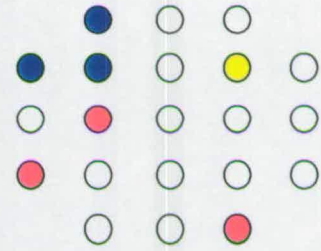
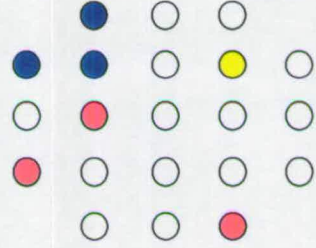
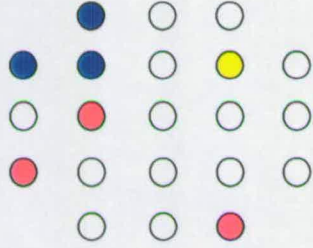
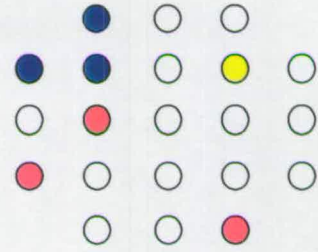
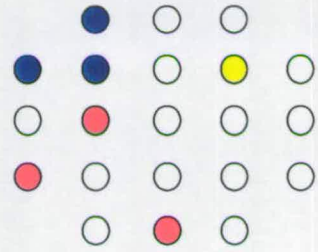


Figure 8.2b (V) Intermediate:
Day 5

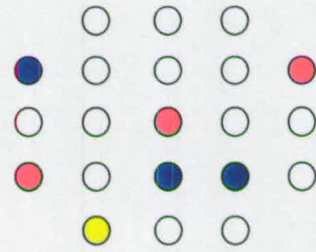
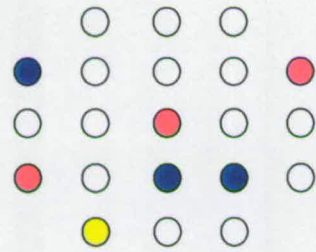
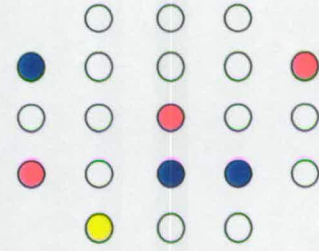
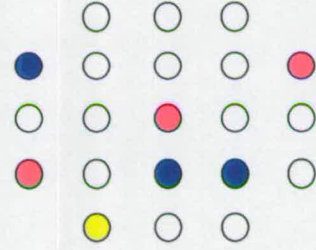
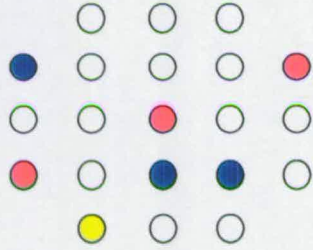
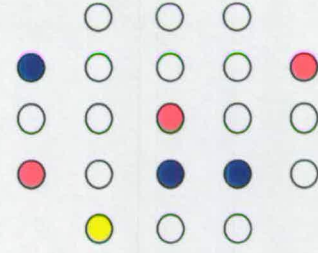
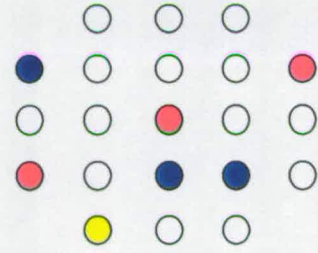


Figure 8.2c Variable: Day 1-5

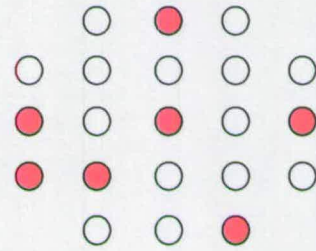
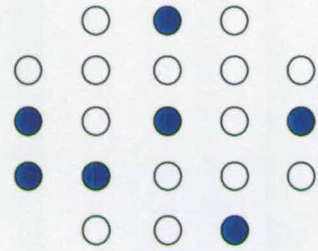
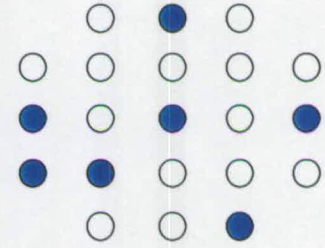
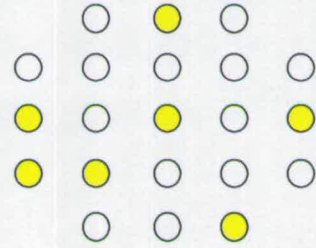
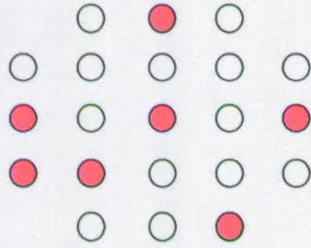
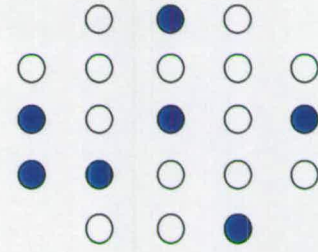
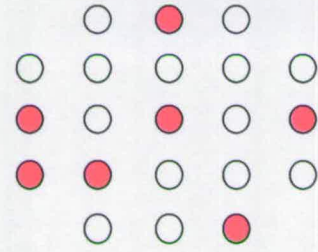


Figure 8.2d (I) High: Day 1

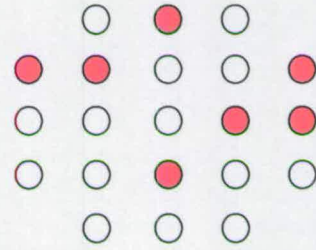
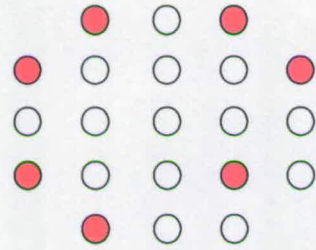
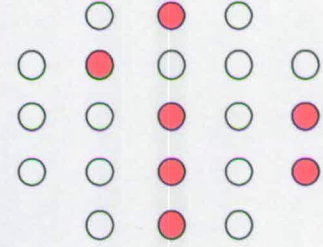
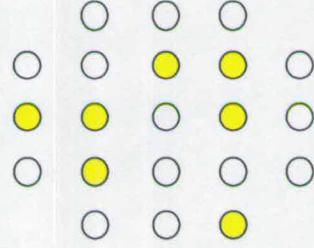
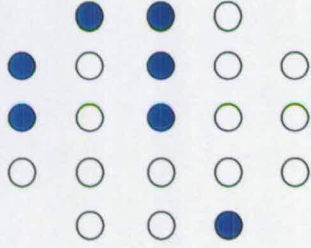
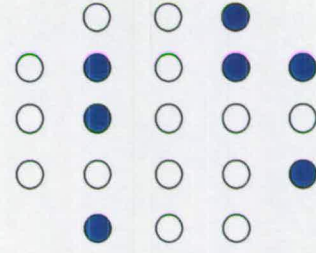
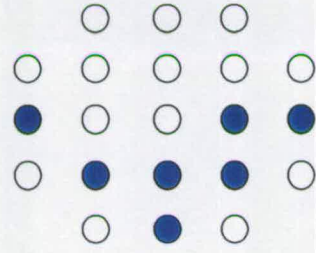


Figure 8.2d (II) High: Day 2

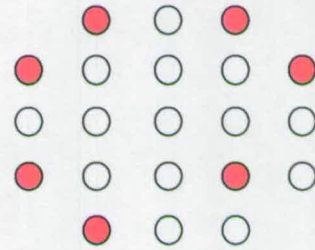
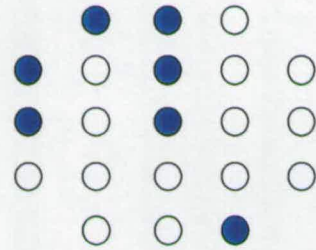
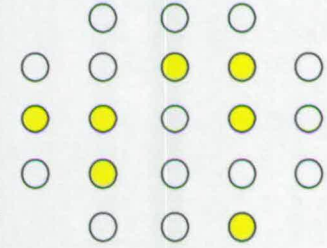
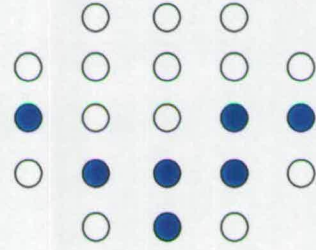
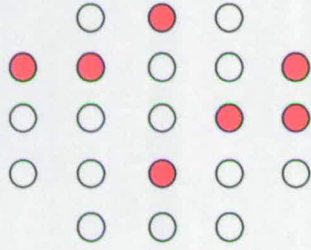
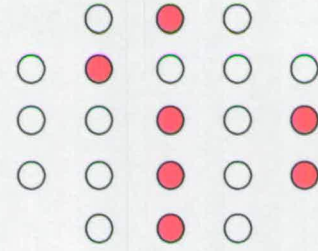
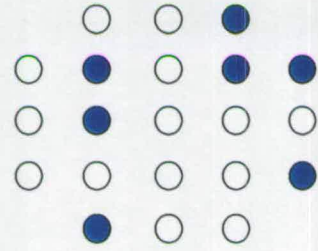


Figure 8.2d (III) High: Day 3

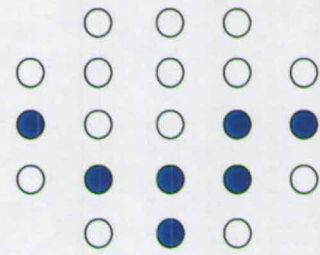
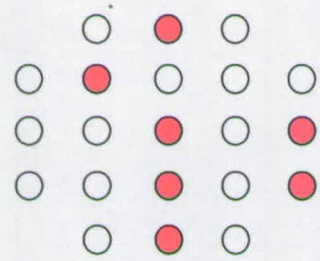
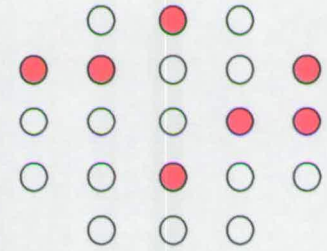
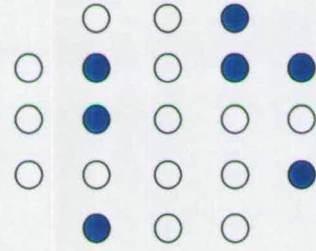
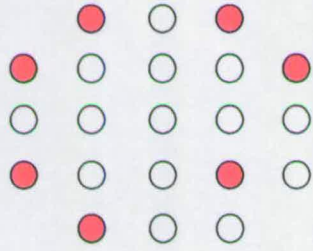
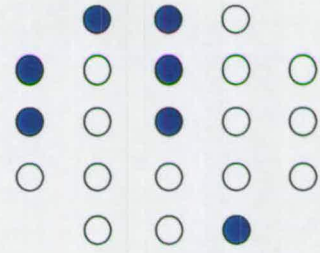
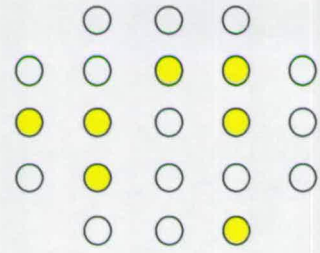


Figure 8.2d (IV) High: Day 4

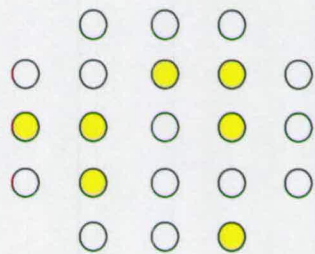
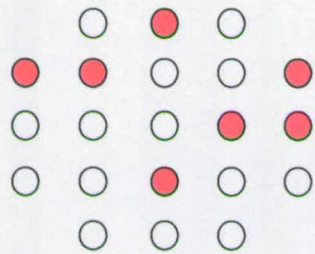
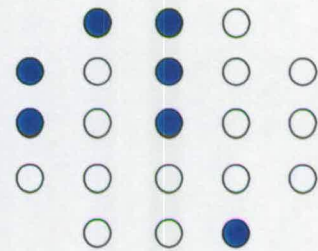
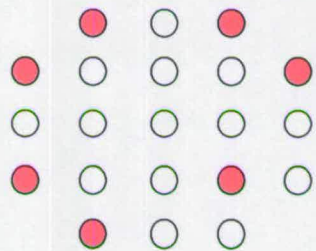
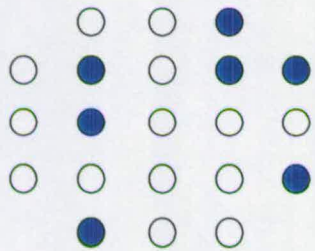
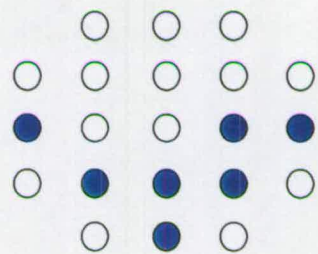
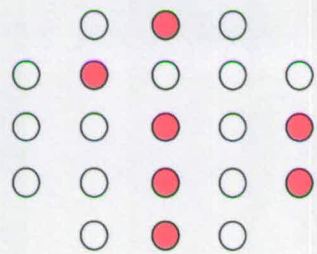
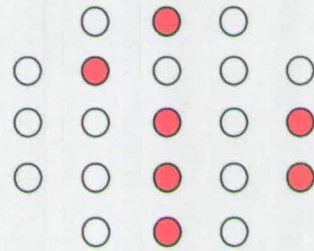
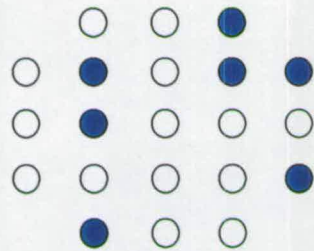
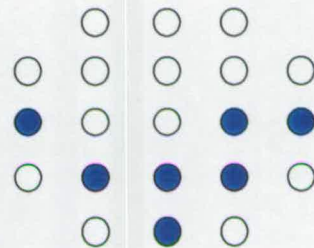
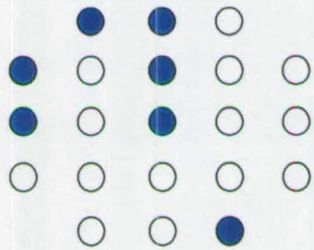
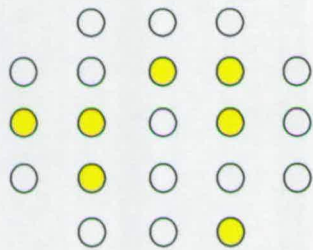
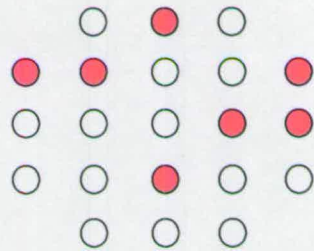
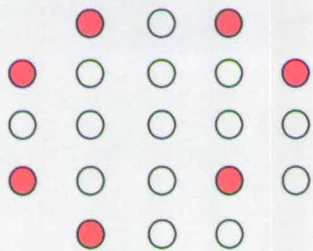


Figure 8.2d (V) High: Day 5



Formation of groups

The sheep were assigned at random into six groups of three animals, with each group experiencing each treatment over the experiment. Three animals were selected for each group as this number represents the minimum number of animals that will behave as a group, in terms of grazing time. Where group size is less than three, sheep have been observed to reduce meal length and may not gain weight as quickly as individuals within larger groups (Penning et al. 1993).

Timing

The experiment lasted for five weeks, with one week of training and four weeks of trials. One trial lasted for five days. Each group of sheep was tested in a balanced order for 20 minutes per day.

Training

To familiarise the sheep with the spatial distribution of sites, a training period of five days took place before the treatments. During this period a random selection of 14 of the 21 bowls in each site was provisioned with 9g of pellets. The same pattern applied to all sites. Overall 98 bowls were provisioned with a total of 882g pellets.

Groups of three sheep were released from the holding pen into the pasture and permitted to feed and explore for 20 minutes. Data was collected during this period to assess the extent of learning about the experimental set up before the test periods began. Focal animals were also selected during the training period for high activity in searching for pellets.

Testing Procedure

The testing procedure consisted of releasing the group of sheep into the pasture and allowing them to forage for 20 minutes. The sheep were then removed and the

remaining pellets recovered and recorded. Pellets and empty bowls were checked in a random order by both observers to prevent the following group using human scent tracks to locate provisioned bowls.

Measurements

The experimental plan aimed for one run per group on each day of the five day trial. However, on some days we were forced to do two runs on each group due to inclement weather conditions on preceding days. Trials took place between 0800h and 1700h. Outwith these times the sheep were released to graze on an adjacent pasture. The observation order of the groups was balanced to ensure that each group did not consistently appear in the same order every day. Two observers recorded the behaviour of the animals during the trials. The first observer scored the activity of the group every 20 seconds as moving, feeding from a bowl, grazing or inactive. Moving was defined as goal directed fast walking or running between sites or between bowls within sites. Grazing was defined as the animal moving more slowly, with head close to the sward, or standing and chewing grass. The second observer followed the movements of a focal animal within the group. All bowl visits and the time spent within each site were recorded. At the end of the trial the remaining pellets were collected for weighing and the bowls refilled for the next group.

Analysis

Training

This analysis was carried out to investigate the learning behaviour of the sheep over the six day training period. The number of sites visited and the total volume of pellets consumed over time were assessed using single factor analysis of variance (ANOVA). Day was considered as a fixed effect in the model and group, a random

effect. Differences between days were identified using least significant differences (LSD) at the 5% level (Snedecor & Cochran 1980).

Use of data

The data used in the analysis was taken from an average of days 4 and 5 of the treatments. Dumont & Petit (1998) showed that the behaviour of sheep in a 12 day trial, sheep reached an asymptote at day 5/6. The average of days 4 and 5 as taken in the current experiment to account for individual day effects.

Across all treatments, the 20-minute trials usually consisted of a period of searching and exploitation followed by grazing, during which sites were opportunistically revisited. To assess efficiency during the early searching stages of the trial, the 20-minute period was truncated at the point where variance in number of sites visited between treatments was greatest.

Efficiency

These analyses were carried out to test the hypotheses that foraging efficiency should increase when resources become more predictably distributed across spatial and temporal scales. Efficiency was measured for the group over the 20-minute trial period, following Dumont & Petit (1998). This was calculated as the ratio of the volume of pellets consumed to the time devoted to pellet exploitation (time spent walking and feeding from the bowls). A further measure of efficiency was considered for the focal animal within the truncated time period: the number of bowls containing pellets visited as a ratio of the total number of bowl visits (including revisits). To determine if more efficient bowl searching led to the consumption of more pellets, the volume of pellets consumed in this time was calculated.

Sampling behaviour

To test the hypothesis that sampling behaviour increased as site predictability decreased the following analyses were carried out. Using group data the number of site visits over the 20 minute trial period and the number of site visits within the truncated period were calculated. The average site residence time and time to first grazing were then calculated for each treatment from the focal animal data to compare with the results of the scan sampling data, within the truncated period. A “giving up” threshold was calculated as the number of empty bowls visited before leaving a site, measured within the truncated period.

Path similarity

The third hypothesis considered the search paths of the sheep, proposing that as predictability of resources increases, following a previously successful search path would be valuable in relocating high quality sites. Search paths were defined here as visits to sites in the same order as the previous day. Following Dumont & Petit (1998) a path similarity index was calculated. The value of this index was equal to n when the focal animal visits the first n sites in the same order as the previous run, entering a new site on the $n+1$ th trial. In this analysis treatments were not grouped as within and between patch variability, but analysed individually. Data from only days 4 and 5 were compared as it was assumed that sheep had established the treatment conditions by this point. It was predicted that (1) there would be no value in following similar paths in the stable and intermediate treatments as all sites were of equal quality, (2) there would be an advantage in following a search path in the variable treatment to account for the difference in site quality, and (3) in the high

treatment, it would in fact be more beneficial to switch paths on every run to take advantage of the changing site quality.

As six groups of sheep experienced the treatments over only four weeks the experimental design could not be fully balanced. Therefore analysis of the above data was carried out using the REML (Residual Maximum Likelihood) procedure to test the effect of treatment on the behavioural parameters described above (Patterson & Thompson 1971). As the treatments represented a two by two factorial design, fixed factors were considered: within site variability (stable and variable versus intermediate and high) and between site variability (stable and intermediate versus variable and high) and the interaction, which is equivalent to individual treatments (Table 8.1). Group and week were fitted into the fixed model before treatment effects to ensure these factors were accounted for before significance of treatments. The significance of fixed effects was determined by the Wald statistic produced by REML. The Wald statistic has an asymptotic chi-squared distribution with degrees of freedom equal to the degrees of freedom of the terms in the fixed model. Differences between treatments were identified using least significant differences (LSD) at the 5% level (Snedecor & Cochran 1980). All procedures were implemented in Genstat 5, Release 4.1 (Genstat 1998).

RESULTS

Training

Over the six day training period, the groups discovered more sites ($F_{5,30}=14.3$, $P<0.001$; Figure 8.3) and consumed more pellets ($F_{5,30}=36.32$, $P<0.001$; Figure 8.4)

as the trial progressed. All groups but one successfully located and fed from the seven sites in the set-up during the six-day training period.

Test

Truncation of the data

To measure efficiency in the focal animal, the data from the test phase were truncated at the point where variance in site visits between treatments was greatest. This occurred 180s into the trial. Analysis of focal animal behaviour was determined from data collected within this truncated period.

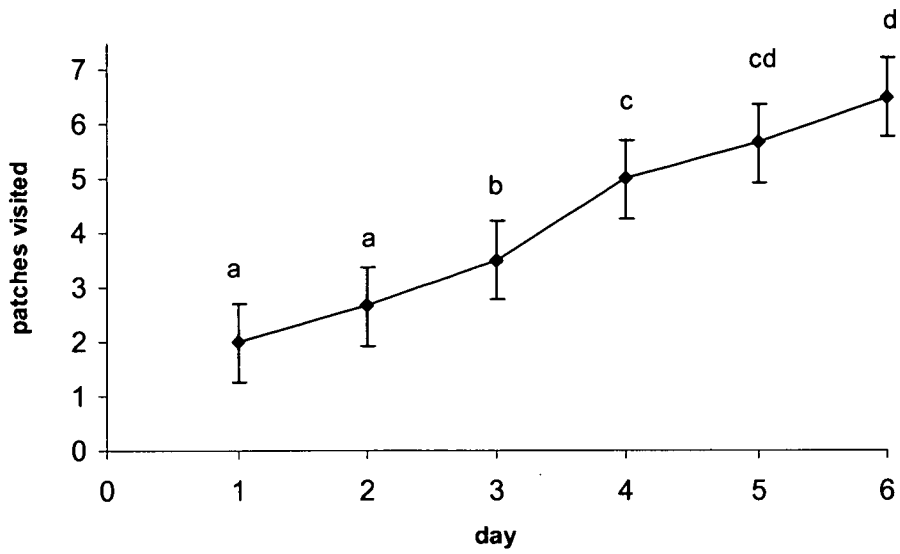


Figure 8.3: Increase in sites visited over the 6-day training period. Means with different superscripts are significantly different ($P < 0.05$).

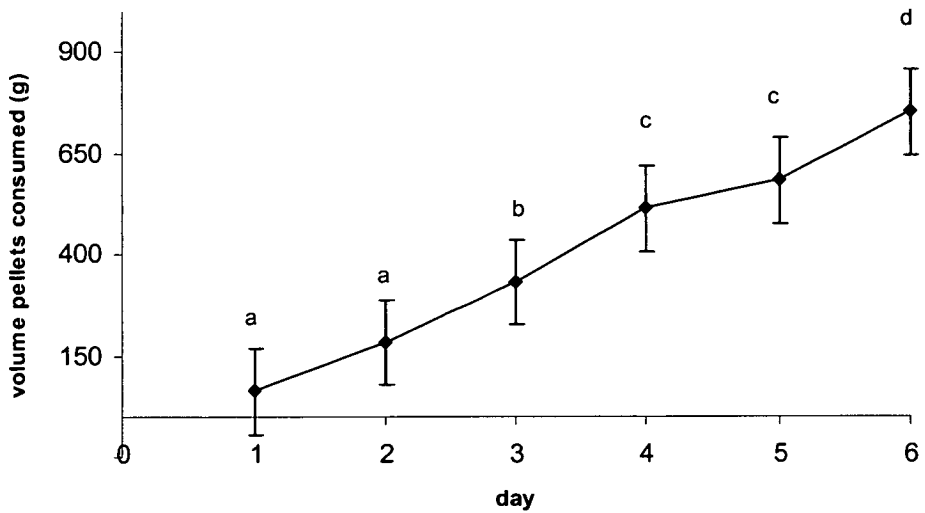


Figure 8.4: Increase in the volume of pellets consumed over the 6-day training period. Means with different superscripts are significantly different ($P < 0.05$).

Group efficiency

The groups exploited the pellet resource more efficiently in the stable and variable treatments by reducing the amount of time devoted to pellet exploitation in relation to the total volume of pellets consumed over the 20-minute period ($W_3=5.58$; $P=0.018$; Figure 8.5. Table 8.2.). Therefore sheep were more efficient when the bowl position within a site was held constant within a trial (stable and variable) than where bowl position within a site varied on every run (high and intermediate).

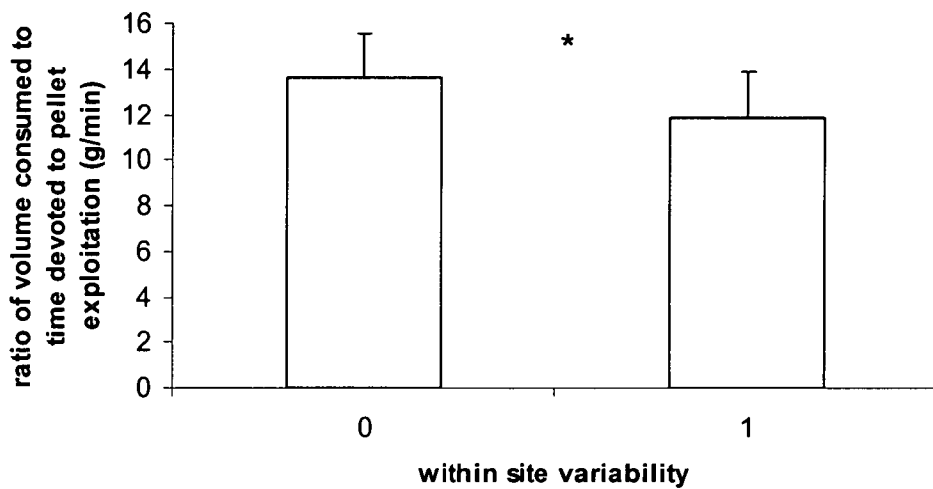


Figure 8.5: Variation in group efficiency across treatments. (* = $P < 0.05$).

- 0= no within site variability (Stable & Variable)
- 1= within site variability (High & Intermediate)

Between site variability did not significantly affect efficiency. Both group ($W_5=19.57$; $P=0.002$; Table 8.2.), and week within the experiment ($W_3=8.42$; $P=0.038$; Table 8.2.) had a significant effect on efficiency, with some groups more efficient than others and overall efficiency improving over the experiment before decreasing again on week four. Residual information resulting from individual treatments did not significantly influence efficiency ($W_1=3.04$; $P=0.081$; Table 8.2).

To look in more detail at the early stages of the test, data from the truncated period examined efficiency in the focal animal. A strong correlation between the behaviour of the focal animal and the group as a whole ($r^2=0.908$) justified the use of focal animal data. The measure of efficiency here was the ratio of full bowl visits to the total number of bowl visits, including revisits. As for the group efficiency data the constraining factor was within site variability. Sheep on the stable and variable treatments were significantly more efficient in finding pellet bowls than sheep on the high and intermediate treatments ($W_1=12.43$; $P<0.001$: Figure 8.6. Table 8.2).

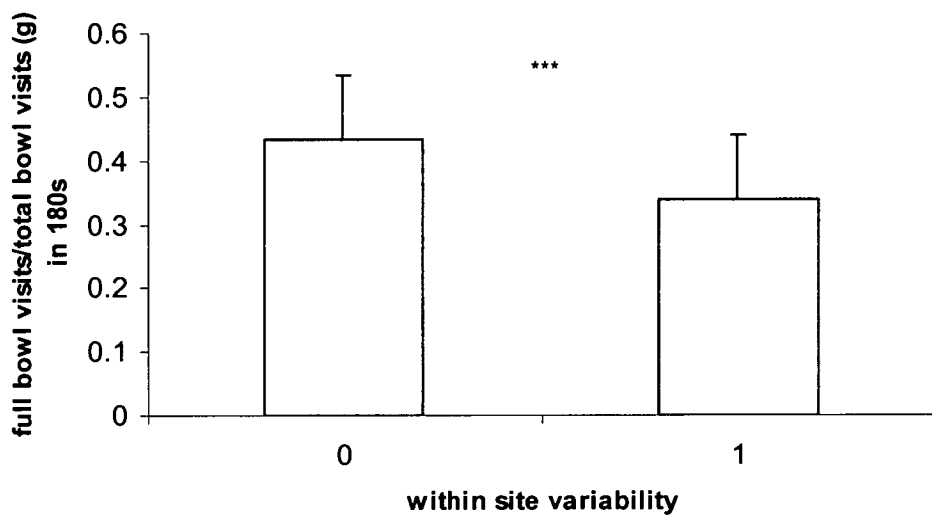


Figure 8.6: Variation in focal animal efficiency across treatments. These data were taken from the truncated period. (** $P<0.001$).

How does this translate into the volume of pellets actually consumed? Again, within site variation was the constraining factor, with sheep on the stable-variable treatments consuming more pellets than those on high-intermediate treatments ($W_1=10.45$; $P=0.001$: Figure 8.7. Table 8.2).

Focal animals did not return preferentially to the highest quality bowls within the sites across the treatments (within site variability: $W_1=0.95$; $P=0.329$; between site variability: $W_1=1.09$; $P=0.297$).

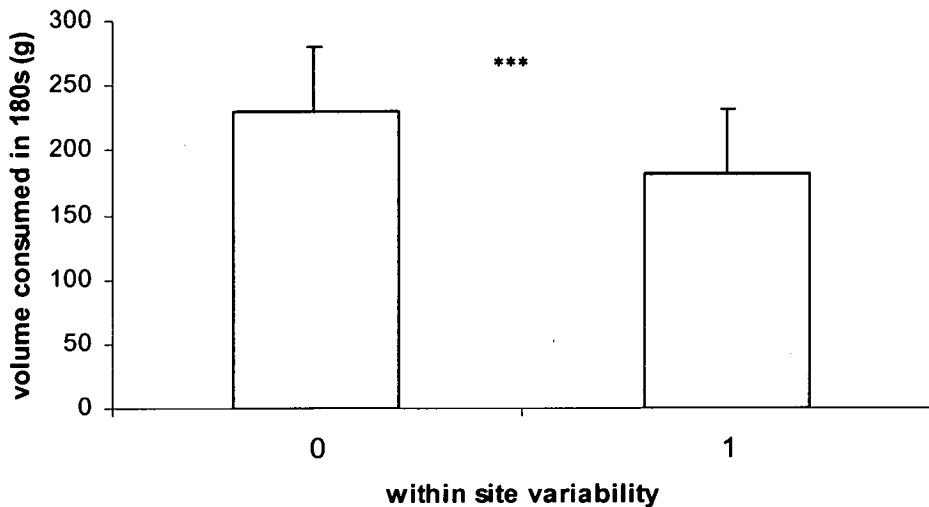


Figure 8.7: Variation in the total volume of pellets consumed by the focal animal within the truncated period. (***)= $P \leq 0.001$

Table 8.2: REML results for the comparison of efficiency measures across treatments

Fixed term	Wald Statistic	df	χ^2 Probability
<i>Group Efficiency (20 min)</i>			
Group	19.57	5	0.002
Week	8.42	3	0.038
High-intermediate/variable-stable	5.58	1	0.018
High-variable/intermediate-stable	1.31	1	0.252
Interaction	3.04	1	0.081
<i>Focal Animal efficiency (180s)</i>			
High-intermediate/variable-stable	12.43	1	<0.001
High-variable/intermediate-stable	0.66	1	0.416
Interaction	1.55	1	0.213
<i>Volume pellets consumed (180s)</i>			
High-intermediate/variable-stable	10.45	1	0.001
High-variable/intermediate-stable	0.57	1	0.449
Interaction	0.65	1	0.422

Sampling behaviour

Sheep on the stable and variable treatments made fewer site visits during the 20 minute period than those on high and intermediate ($W_1=4.44$; $P=0.035$. Figure 8.8.

Table 8.3). No effects were accounted for by between site variability or residual

differences across individual treatments. However, the week of the experiment had a strong effect on the number of site visits ($W_2=16.54$; $P<0.001$) with a general decrease in total site visits as the experiment progressed. Focal animal results for site visits within the 180s truncated period found no significant differences in the number of site visits across any fixed effects. In addition, no significant differences were identified in time spent in individual sites in the truncated period. Time spent in individual sites was not analysed over the 20-minute trial period as this was distorted towards the end of the trial while sheep grazed within site boundaries.

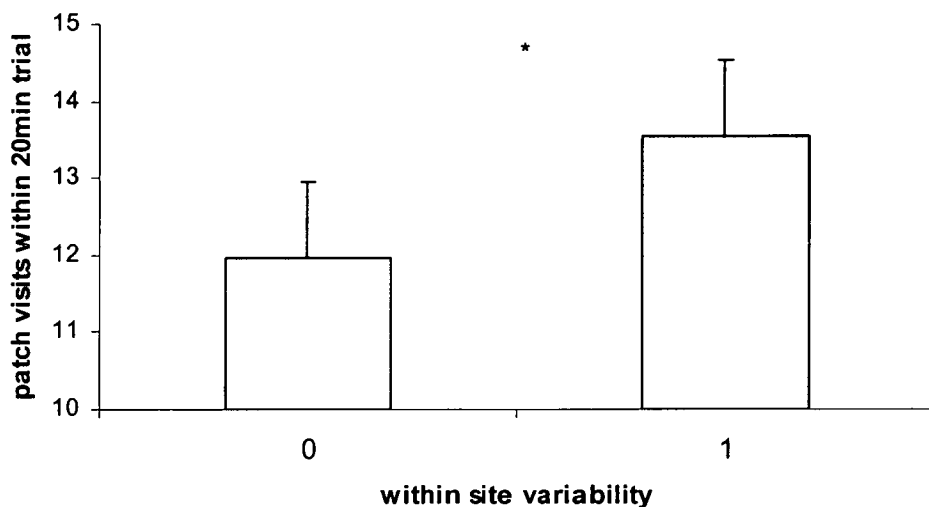


Figure 8.8: Sheep on treatments where within site variability was held constant made fewer site visits over the 20 minute trial period. (*= $P<0.05$)

Sheep on the high and variable treatments searched for bowls for longer before grazing than sheep on the stable and intermediate treatments. This represented an effect of between site variability ($W_1=8.96$; $P=0.003$; Figure 8.9. Table 8.3). There was no effect of within site variability ($W_1=0.15$; $P=0.696$), and interaction effect was not significant, suggesting that individual treatments did not have an effect above that accounted for by within and between patch variability ($W_1=0.02$; $P=887$).

However, there was a difference in behaviour between groups of sheep ($W_5=59.04$; $P<0.001$: Table 8.3).

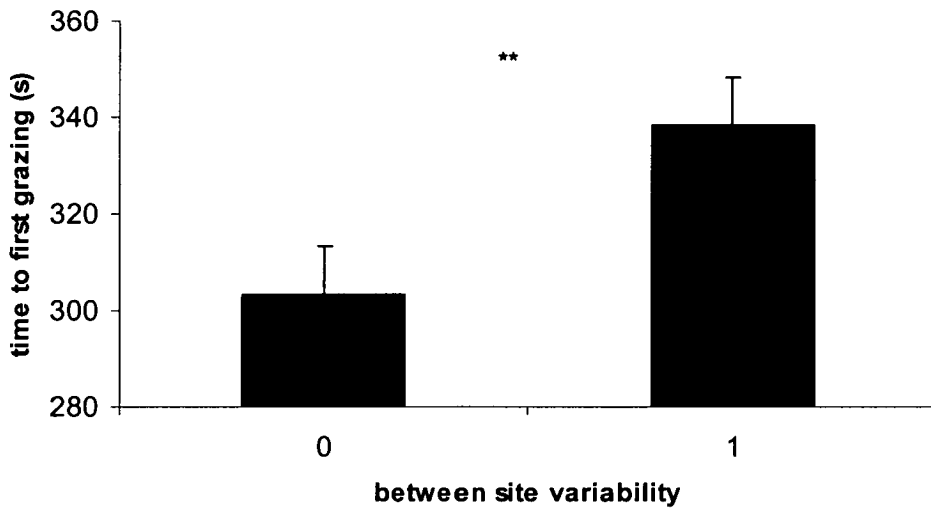


Figure 8.9: Variation in the time until the first grazing across treatments. These data originate from group scan sampling. (**= $P<0.01$)

0=no between site variability (Stable & Intermediate)
 1=between site variability (High & Variable)

Analysis of the time to first grazing considered the overall time at which sheep stopped actively searching for pellets over the whole plot. How did this compare with leaving rules within sites? Sheep on the stable and variable treatments checked fewer empty bowls before leaving an individual site, i.e. they had a lower “giving up” threshold ($W_1=12.82$; $P<0.001$, Figure 8.10. Table 8.3) compared to the high and intermediate treatments. Again the differences lay in within site variability. No other fixed effects explained a significant amount of variation.

Sheep spent the same time foraging in individual sites across treatments (Within site variability: $W_1=0.21$; $P=0.648$; Between site variability: $W_1=0.62$; $P=0.430$) and took the same time to travel between sites across treatments (Within site variability: $W_1=0.30$; $P=0.587$; Between site variability: $W_1=2.57$; $P=0.109$).

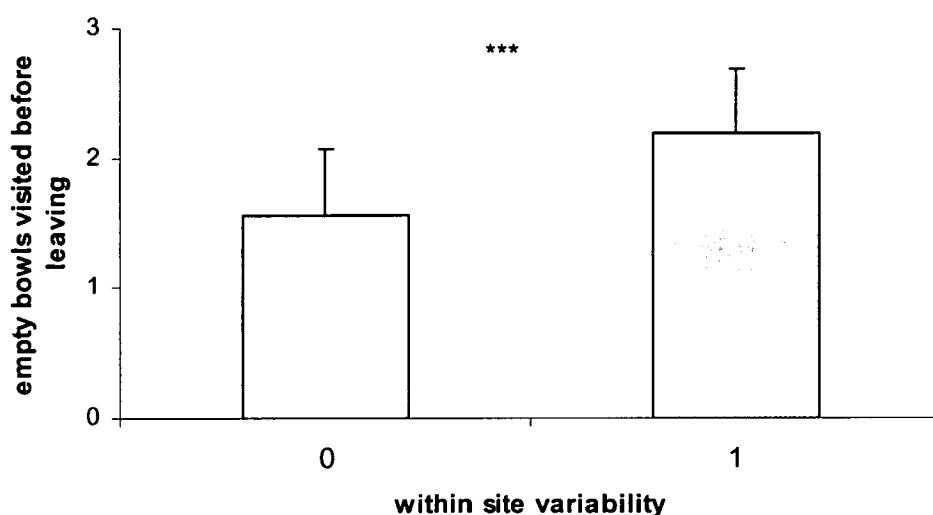


Figure 8.10: Variation in the number of bowls checked before leaving the site. (***)= $P < 0.001$)

Table 8.3: Summary of means for efficiency measures across treatments. Means with different superscripts differ ($P < 0.05$)

Effect	Within site variability		Between site variability		SE
	High-intermediate	Variable-stable	High-variable	Intermediate-stable	
Site visits within 20m	13.54 ^a	11.96 ^b	12.17	13.33	0.7517
Site visits within 180s	4.699	4.796	4.550	4.945	0.2799
Time spent in site within 180s (s)	36.36	35.18	37.23	34.64	3.294
Time to graze (s)	323.2	318.6	338.5 ^a	303.3 ^b	11.74
Bowls before leaving	2.190 ^a	1.567 ^b	1.852	1.905	0.1738

Search Paths.

Comparison of search paths between day 4 and day 5 showed that all focal animals began their search path with the first site visited on the previous day (Figure 8.11). There was no significant difference between treatments in the loyalty to search path ($W_3=6.35$; $P=0.096$; Figure 8.12). However, one group of sheep differed

significantly from the others, showing high search path fidelity and relying on the same search path regardless of treatment ($W_5=24.49$; $P=0.017$).

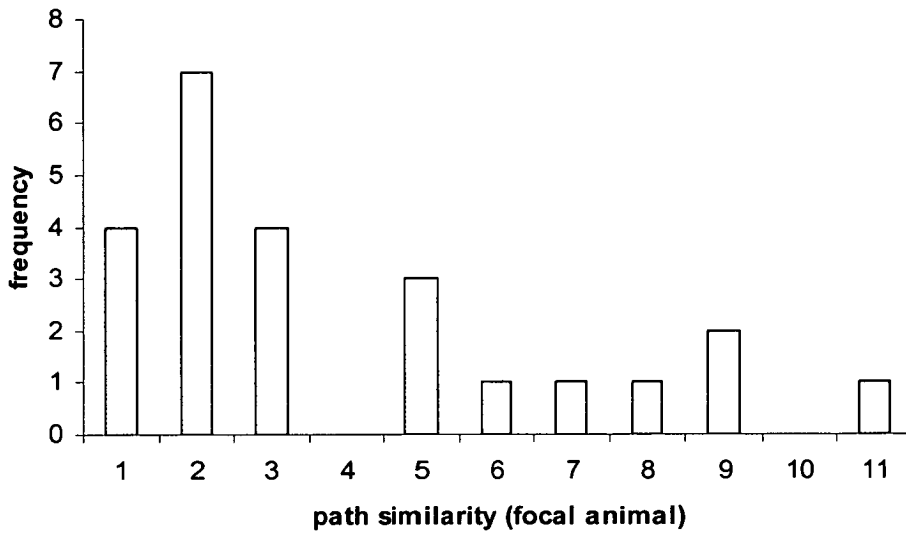


Figure 8.11: Path similarity across all treatments between days 4 and 5.

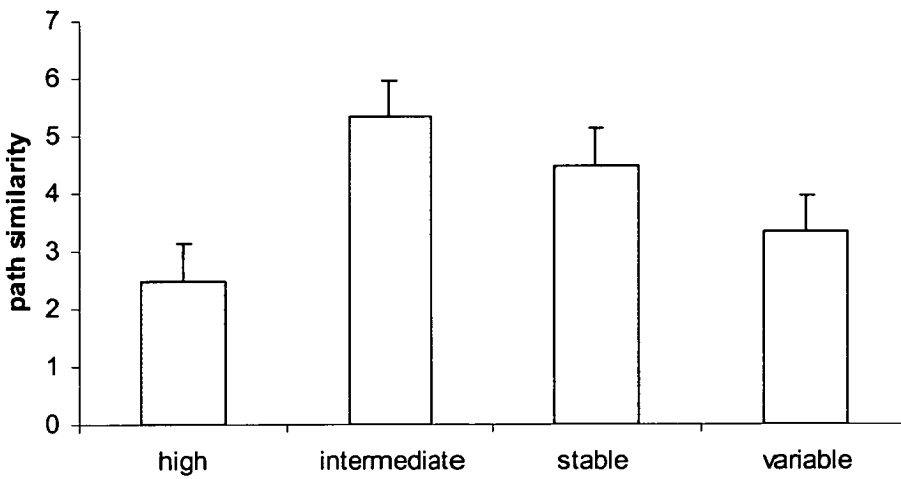


Figure 8.12: There was no significant difference between treatment groups in search path similarity

DISCUSSION

Training

During the training period sheep returned to previously found sites on consecutive days, on each day of the trial increasing the number of sites discovered and the total quantity of feed consumed. This agrees with previous studies examining the use of spatial memory in herbivores where resources were distributed in a stable and predictable manner (Edwards et al. 1996; Dumont & Petit 1998). Laca (1998) found that cattle increased their intake rates with increasing experience of a site. In the current set-up all groups but one located all sites in the plot and returned to each site on the succeeding day. This supports Edwards et al. (1996), where sheep were observed to remember patch locations after only one previous visit. This ability allows foraging sheep to utilise consistent high quality resources more efficiently within the environment (Dumont & Petit 1998).

The training period ensured that all sheep were familiar with the location of the resource sites. As a result, the effects of resource variation within and between sites could be reliably assessed during the experimental treatment.

Efficiency

The aim of this experiment was to investigate the strategies of foraging sheep under more natural conditions where resources were variable over space and time. The first measure of efficiency concerned the behaviour of the group of sheep over the 20 minute trial period. Efficiency, the ratio of time devoted to pellet exploitation to the volume of pellets consumed, was highest in the stable and variable treatments where the distribution of resources within sites was held constant across days. This measure of efficiency implies that sheep moved around the environment less to obtain the

same volume of pellets where there was no within site variability in bowl position between runs. The effect of individual treatments once within and between site variability had been accounted for was not significant, suggesting that changing the bowl position within sites had as disruptive an effect as changing the location of the higher quality sites within the plot. This confirms the use of spatial memory at a scale below the patch level.

Similar results were obtained with focal animal data. Sheep on the variable and stable sites visited fewer empty bowls to find the pellet bowls, and consumed more pellets as a result, again showing that the constraint in pellet exploitation was the varying distribution of pellet bowls within sites.

Sampling

Sampling within sites

Once sheep entered sites they used a form of “area-concentrated” searching to discover full bowls (Benhamou 1994). Area concentrated searching is characterised by an increase in searching effort around sites where food had been recently found or is a predictable resource. This behaviour has been recorded in many species. Desert gazelles (*Gazella dorcas*) concentrated their feeding efforts in areas of high plant density and made shorter move lengths after discovering food (Ward & Saltz 1994). Benhamou (1994) concluded that area-concentrated search based around a spatial memory related search mechanism was very efficient in a continuous patchy environment. A model forager harvested around 1.6 times the number of prey than a forager using the same strategy without reference to spatial memory. Where the distribution of resources is not known at the within site scale, area concentrated searching represents a simple and low cost rule for systematic searching (Laca 1998).

However, in the current experiment, treatments stable and variable offered the opportunity for the sheep to relocate bowls within sites using spatial memory, and the results suggest that this was the case. Within sites the sheep visited more empty bowls and stayed for longer when the bowl distribution was variable between runs, in the high and intermediate treatments. However, there was no evidence that sheep returned to bowls of higher quality within the sites, suggesting that while the sheep were capable of relocating bowls within sites, they could not or did not remember specific volumes within bowls. The ability of foragers to respond to within patch variability in resources is important in determining diet choice and predicting optimal foraging strategy (Dall & Cuthill 1997). However for herbivores, the use of spatial memory at such low scale is expected to be too costly in terms of time and accuracy to permit storage in the forager's reference memory (Senft et al. 1987). This study suggests that this may not always be the case.

Sampling between sites

Sheep made more site visits in the less predictable treatments. This supports the prediction of increased sampling in stochastic environments. Under conditions of unpredictability, sampling among sites can provide information about resource distribution at small cost to short term intake rate (Illius & Gordon 1990). The observed reduction in efficiency in less predictable environments is due, therefore, to increased time devoted to visiting alternative sites in order to assess quality. This analysis was repeated within the truncated period but no differences between treatments were identified. At this stage of the trial, the lack of difference may be attributed to social and the resultant competitive effects of group foraging. Sheep entered and departed sites dependent on the movement of the other animals in the

group, biasing site exploitation behaviour. In a simulation of foraging in a patchy environment Dumont & Hill (2001) predicted a negative relationship between foraging efficiency and the degree of social attraction. Where there is a strong attraction between conspecifics, foragers became aggregated in rapidly depleted food patches and as a result it became difficult for individuals to learn the quality of the resource (Beauchamp et al. 1997)

Time to first grazing was predicted to reflect site knowledge. The shorter the time to first grazing the less expectation of pellets remaining in the site. However, the results showed that the difference in time to first grazing occurred at the level of between site variability. Sheep reverted to grazing earlier on the stable and intermediate treatments compared with the high and variable treatments. Where there are some sites of much greater quality in the environment it is worth investing more time in identifying all high quality sites. This is particularly true for the “high” treatment where the occurrence of high quality sites could not be predicted from previous experience but must be identified through site sampling. It is possible that this result arose as a consequence of the increased time taken by the sheep to consume 27g pellets over 9g pellets. However, as the plot contained an equal number of 27g bowls and 9g bowls, it was expected that overall consumption time was equalised over the plot.

Search Path

By days 4 and 5 of each treatment all sheep began their foraging bouts at the same site within the plot. This tended to be a function of the position of the holding pen in relation to the plot, with site “F” visited most frequently on entry (see Figure 8.1). The results of the search path analysis showed no difference in loyalty to search

paths across treatments. Although not significant the high treatment showed the lowest search path similarity; however, the variable treatment did not show the greatest level of path similarity. This is not the predicted result, as the treatments where there was between site variability offered the opportunity to preferentially exploit rich sites. In the variable treatment the position of the rich sites remained constant over the trial period, which would have permitted the use of spatial memory to return to and exploit the higher quality sites. However, the high treatment offered little opportunity to respond with spatial memory as site quality and bowl location within sites changed on every run.

Why was no difference observed between path similarities? This question might be answered by considering the extent of lost opportunity cost (Stephens & Krebs 1986) in the current experimental set-up. All sites within the plot were essentially rich sites, as they all contained some highly preferred food items. As such, any search path followed by the sheep would be rewarded. Animals were not time-limited in the current experiment, and therefore could visit all sites during the trial. Where resources were highly clumped as in the current experiment, sheep may have compensated for this by increasing their walking speed between sites (Dumont et al. 2000) however the data collected here does not support this idea.

In all treatments there was little cost of lost opportunity to feed at the best sites and perhaps, therefore, little pressure to remember the location of highly rewarded sites. Had these costs been increased, for example, through introducing a time limit on foraging or greater variability between high and low quality sites there would be more value in gathering information through sampling, and remembering

information on site quality (Kohlmann & Risenhoover 1998; Bednekoff & Balda 1997).

Social influence on foraging efficiency

Within sites, sheep were remembering the location of bowls and by doing so increasing their foraging efficiency. As discussed above a major cost of within site foraging is competition, as the sheep tended to travel around the site in a group. The ability to relocate bowls within sites is, therefore, a constraint on their foraging efficiency in the presence of conspecifics. If sheep had been foraging alone, the use of spatial memory to relocate bowls would probably have less value, as area-concentrated searching and an increase in turning frequency after locating a full bowl would allow bowl relocation (Senft et al. 1987). A further experiment to investigate this would be of interest; however, the aim of the current experiment was to approach a more realistic foraging scenario. The effect of social interactions on foraging behaviour in sheep was considered in an earlier chapter (Chapter 6).

This experiment has shown that predictability of resources within sites can have an important effect on foraging efficiency in a group of sheep. Increased efficiency was found where sites provided a stable and predictable food source, suggesting the use of spatial memory to relocate resources at the feeding station level. The ability to use within-patch information can have important consequences for foraging decisions (Dall & Cuthill 1997) and in this study allowed foragers to return to areas within patches of high food concentration. It has previously been suggested that reference spatial memory for foraging herbivores would not be useful (WallisDeVries et al. 1999) and in fact be costly at this scale (Laca & Ortega 1995; Laca 1998). This is due to the large memory capacity required to store information on frequent events

such as feeding station visits (Senft et al. 1987). However, this experiment has shown that under competitive pressure the costs may be high enough to warrant investment in spatial memory at this scale.

In conclusion, this Chapter has shown that foraging sheep were able to exploit resource heterogeneity at the scale of feeding stations within a site. Hobbs (1999) suggests that foraging responses are determined by the spatial and nutritional qualities of the environment, for example, a large contrast in feed value at the feeding station level compared with the patch level would be highlighted by a stronger foraging response. This may have been the case in the current experiment. Further work is required to examine the effects of increasing costs on foraging behaviour in herbivores, the relevant definition of patches for sheep and the effects of competitors on the ability of these animals to exploit heterogeneous environments.

SUMMARY

Spatial memory has been shown to improve foraging efficiency in stable and predictable environments. However, most natural systems are characterised by unpredictability in the distribution of resources and under these conditions it is proposed that spatial memory becomes less reliable. The aim of this study was to explore the foraging efficiency of sheep in relation to the predictability in spatial distribution of resources. Resource distribution was manipulated within a plot by using bowls of preferred food to represent resource sites. The provision of bowls with pellets and the volume of pellets therein were altered to create treatments representing differences in within and between patch variability. Strong effects were observed of both within and between patch variability on measures of foraging

efficiency. Where variability within sites was held constant, sheep improved foraging efficiency, in time devoted to pellet exploitation ($P < 0.05$) and in the number of bowl visits made ($P < 0.001$). Sheep showed increased sampling in more unpredictable environments ($P < 0.05$), again constrained by within patch variation in pellet distribution. It was shown that sheep could use spatial memory at the feeding station level to improve foraging efficiency.

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CHAPTER 9

GENERAL DISCUSSION

INTRODUCTION

The aim of this thesis was to investigate the foraging behaviour of sheep in response to environmental uncertainty. The experiments focused on the short-term decisions made by foraging sheep at the feeding station and patch scales. Initially three aspects of uncertainty were considered: the probability of reward in an alternative patch (Chapter 4), the social environment (Chapter 6) and the effect of the passage of time since the patch was last visited (Chapter 7). These experiments were carried out in indoor arenas. The three factors were then incorporated into a final experiment in an attempt to replicate more natural conditions (Chapter 8). The focus of this discussion chapter is to consider the implications of uncertainty for foraging herbivores through assessment of the methodology with particular emphasis on the associated costs and the effect of social constraints on obtaining and using environmental information.

SUMMARY OF RESULTS

Sheep were found to respond to probability of reward from a variable environment by basing patch-leaving decisions on previous information gained while foraging. In a high quality environment sheep were able to trade-off the time spent in the first patch against the cost of lost opportunity if a second patch was empty. No relationship could be

identified between the propensity to take risky decisions and the behaviour of the sheep in the trial.

The information used in making patch-leaving decisions when foraging in pairs differed between animals according to dominance status. Dominant animals exploited subordinates by following and displacing them at the resource patch, regardless of patch conditions. Conversely, subordinates based patch decisions on the possibility of accessing food and on minimising the risk of aggression, achieving this by disregarding their own patch information. Sheep preferred a stable patch to a variable patch, but as information degraded over time, their choice reverted to random. Negative previous experiences persisted in the memory of the sheep for longer than neutral or positive experiences.

In the final experiment, sheep foraged socially in environments that varied on both spatial and temporal scale. Sheep improved their foraging efficiency when resource distribution was predictable at the feeding station level.

IMPLICATIONS FOR FORAGING IN AN UNCERTAIN ENVIRONMENT

Throughout the experiments presented here, foraging sheep exhibited a tendency to return to high quality patches within a heterogeneous environment. This behaviour persisted despite the patches being completely depleted on a previous run. This is known as a “win-stay” strategy.

Win-stay vs. win-shift strategies for foraging

Olten et al (1981) proposed a set of strategies to determine where a new foraging bout should begin: “win-stay”, to return to a previously rewarded patch or “win-shift”, to search for food in a different site than the previous foraging bout. Both types of behaviour have been tested in radial arm mazes on a number of species (Hosoi et al. 1995a; Hosoi et al. 1995b; Laughlin & Mendl 2000). Win-stay is predicted to occur where foragers have evolved to exploit high quality and clumped resources. Win-shift is predicted where resources are unevenly distributed throughout the environment, for example in grazed systems, or fully depleted in previous foraging bouts, as in the experimental procedures presented here. It has also been proposed that win-shift tasks are simpler for a forager to learn due to a natural tendency to explore their environment and sample different patch options (Bednekoff & Balda 1997). Despite these predictions, evidence suggests that sheep, goats (*Capra hircus*) and cattle (Hosoi et al. 1995a; Hosoi et al. 1995b) tend to adopt win-stay strategies. In the experiments presented here, sheep showed evidence of a win-stay strategy by returning to previously rewarded patches, for example, previous experience on a patch had a strongly significant effect (Chapter 4) and following similar search paths between patches on successive days (Chapter 8). In addition, a lose-shift effect was observed in Chapter 7 where the sensitivity of sheep to recent negative experience was observed. In this case, the memory of negative patch experiences appeared to persist for longer than memory of positive patch experience.

In all the experiments in this study, the expectation that patches would be replenished may have occurred in response to the feeding regimes imposed by indoor housing where

animals were fed in the same bins at regular times. This does not, however, explain the behaviour of the sheep in the outdoor experiment (Chapter 8) where animals had little experience of indoor housing procedures and no previous experience with the bowls used in that experiment. The outdoor experiment (Chapter 8) presented here suggests that sheep have the capacity to adopt a win-stay strategy and can learn quickly (within one run) that patches will be replenished. This flexibility in behaviour allows the foraging sheep to respond to changing environmental conditions, an adaptation that has also been exhibited in other species living in unpredictable environments (Hughes & Blight 2000).

THE COST OF INFORMATION

The win-stay strategy adopted by the foragers in these experiments emphasises the tendency of sheep to show risk averse type behaviour where the consequences of foraging decisions are uncertain. The preference of sheep for predictability in foraging choice (Chapter 7) stressed the value of environmental information. How did the cost of obtaining information as a result of the experimental set-up influence the foraging behaviour of the sheep?

Cost of information in the indoor experiments

The arena set-up used in experiments in Chapter 4 and the first part of Chapter 6 presented two patches in series, with the variable patch second in the series. This set-up was based on that of Dumont & Petit (1995) where animals had to travel to reach a second patch initially out of sight of the animal. However, in the experiments presented

here, a gate was positioned half way between the patches. When the sheep moved from the stable to the variable patch the gate was closed behind it. This procedure was carried out to enforce learning upon the animals by imposing a cost of missed opportunity (Stephens & Krebs 1986) to feed on the stable patch if the wrong decision was made i.e. the decision to move when the variable patch was empty. In Chapter 4 and the first part of Chapter 6, sheep responded as predicted by adjusting their patch leaving according to their expectation of reward. Where the risk of incurring a cost of lost opportunity was high, in the low quality environments, the sheep compensated for this by staying longer in the stable patch. It is interesting to note the effect of the removal of the gate in the main section of Chapter 6. In this case the sheep were free to move between the patches, with the only cost being time and energy spent walking. It was observed that sheep did not respond to the test environment during the pair trials when the gate was removed. Dominant animals showed a tendency to move quickly to investigate the variable patch regardless of expected quality. This inefficient behaviour was probably a result of the reduced cost of sampling (Krebs & Inman 1992; Bednekoff & Balda 1997). Without the gate to prevent a return to the stable patch, the costs of lost opportunity decreased, and it is probable that the value of information also fell, reducing the need for animals to perform accurately whilst foraging (Kohlmann & Risenhoover 1998; Laughlin & Mendl 2000). In a model of diet selection Murray (1991) found that the level of selection was dependent on both the difference between metabolisable energy concentration of the high and low quality foods and the cost of locomotion. Therefore, the cost incurred by the subordinate individual in avoiding the variable patch and hence choosing a lower

quality diet was negated by the benefits of staying at the stable patch, in terms of movement costs and the avoidance of aggressive interaction.

The experiment in Chapter 7 differed from the experiments described in Chapters 4 and 6 by presentation of the patches in parallel rather than in series. The cost of lost opportunity in Chapter 7 only occurred at the decision point in the arena, but due to the all or nothing output from the patches this imposed a heavy penalty on the wrong decision. Where this risk was high, for example where there had been a long run of negative experience in the variable patch, sheep were more likely to retain memory for patch choice than where the risk of a negative patch experience was low.

Costs of information in the pasture experiment

In the final experiment (Chapter 8) movement between patches was not restricted and animals were free to sample and return to patches at will. Penalties of suboptimal decisions in this experiment were, therefore, considered less severe than in previous experiments (Chapters 4 and 7). In Chapter 8 the “poorest” resource sites continued to offer sheep a preferred reward. As the sheep were aware of the position of all sites in the plot, it is possible that information on the quality of individual sites was of less value, given that individual resource sites were of equal quality in two treatments and unpredictable in a fourth treatment. Alternatively, sheep may have been unable to discriminate between the volume of pellets offered and as seven bowls were always offered in each site, the sites were considered equal. The differences discovered between treatments in this experiment were, therefore, attributed to competitive pressure from

conspecifics. As sheep tended to travel round the sites as a group the pressure was not to relocate sites but to be first to relocate bowls within sites.

Spatial memory at the feeding station scale

The importance of decision making at a scale appropriate to current environmental conditions i.e. that decisions at some spatial scales are more beneficial than at others, was emphasised in this study where sheep were observed to adapt their behaviour to respond to the most relevant scale (Illius & Hodgson, 1996). An important finding in the study presented in Chapter 8 was the ability of sheep to relocate feeding stations within a patch. It has been shown that hummingbirds (*Selasphorus rufus*) use spatial memory to return to artificial rewarded “flowers” among unrewarded flowers when clumped to create an area of high resource density (Hurly 1996). In addition, the hummingbirds appeared to remember non-rewarded sites and directed sampling behaviour towards flowers that had not previously been checked. In herbivores however, the cost of storing information about feeding station quality may not outweigh the benefits of obtaining that bite (Laca & Ortega 1995). Illius et al. (1992) found that sheep did not exploit clover (*Trifolium repens*) at small scale within a ryegrass patch however, they were capable of choosing patches where clover was present in different proportion, suggesting overall selection at the patch level, but not at the level of bite (Bailey et al. 1996). Wallis De Vries et al (1999) suggested that selectivity in fine-grained environments, i.e. at small scale, was less effective than in coarse or larger scale environments. The results obtained here reflect the costs associated with selection of feeding stations. Under normal grazing conditions selection of feeding stations is a low cost activity, with few consequences of a

wrong choice. However, in the experiment presented here, artificially created feeding stations offered a high return and equally a high cost if feeding stations could not be relocated by an individual before being exploited by competitors. Essentially, where information is valuable at lower spatial scales foraging sheep are capable of using that information to exploit the resource. Evidence of a lack of discrimination at lower spatial scales reflects does not imply that animals are incapable of learning, only that the cost of storing and using that information does not exceed the benefits.

SOCIAL COMPLEXITY AND INFORMATION

An important thread in the experiments presented here was the development from examination of the behaviour of individual animals to behaviour while foraging in a social group. Sheep are a sociable species and, therefore, have become adapted through natural selection to respond to the behaviour of conspecifics, whether this is through learning about food resources (Provenza & Burritt 1991), or strategies to avoid aggressive interaction (Eccles & Shackleton 1986; Thouless & Guinness 1986).

The first experiments in this study were designed to minimise this complexity and look specifically at the ability of individual sheep to gather information in a variable environment. In addition to physical interference from conspecifics, the learning and memory recall of foragers can also be influenced by the mere presence of other foragers (Laughlin et al. 1999). In a spatial memory relocation task, pigs that had been exposed to another animal between foraging bouts showed decreased performance, even though the second animal did not enter the experimental arena (Laughlin et al. 1999). Even without

aggressive interference and competitive effects, there is evidence that learning in groups can have detrimental effects. Naïve zebra finches (*Taeniopygia guttata*) learned about a food source more slowly when paired with a knowledgeable partner compared with a non-knowledgeable partner, an observation in the opposite direction to that normally predicted when considering the social facilitation of foraging (Beauchamp & Kacelnik 1991).

Chapters 4, 7 and the first part of Chapter 6 were concerned with the ability of an animal to make foraging decisions under minimum of interference. To achieve this, the first task in the indoor experiments was to habituate the sheep with foraging individually in the arena. Stress associated with experimental treatments has been shown to interfere with the learning abilities of cattle (Grandin et al. 1994). In this study, the calmest animals made the most accurate choice. In the experiments presented here, stress appeared to be minimal. The sheep quickly adapted to foraging individually in the arenas, which were always built adjacent to the home pens. As sheep learned the test procedure, familiarity with handling, and the domestic activities around the home pen ensured that the sheep were given the greatest opportunity to learn.

A crucial aspect of the “social” experiment described in Chapter 6 was the preliminary individual training to treatment. Dominants and subordinates did not differ in their tendency to move. Firstly, this emphasises that dominance is an attribute of an individual that can only be considered in a social context. Secondly, it showed that all animals in the group were capable of learning the experimental treatment, replicating the results of

Chapter 4. However, the introduction of another animal into the arena required more complex decision making for both animals. The results showed that the foraging strategy of the dominant and subordinate animals diverged over the course of the trial. Dominant animals tended to exploit the variable patch without reference to patch conditions. Subordinate animals tended to relinquish information held about patch quality to avoid confrontation with the dominant animal at the variable patch. In an environment with an information deficit, it has been shown that subordinate animals shift preferences but dominants do not (Sandlin 2000). In this experiment with high competitor density, subordinate hummingbirds switched from foraging selectively to foraging opportunistically and the extent of this shift was dependent on the difference in level of dominance. This was reflected in the current study. As shown in Chapter 6, the further apart in rank the sheep were, the less the subordinate animal attempted to exploit the variable patch, indicating the costs of group foraging for subordinates increases the lower the individual is ranked within the group (Ranta et al. 1993).

Dominance and information

An increase in the number of competitive interactions may also have interfered with the ability of both animals in the pair to track the conditions of the variable patch. However, competitive interactions were not equally distributed over the group. If the number of competitive interactions decreases with increasing dominance then the animals highest in the dominance hierarchy may be better able to track change in an unpredictable environment (Dall et al. 1999). Dominant animals experience a two-fold benefit of group foraging. Dominance affords the benefit of a central position in the group through

protection by peripheral group members (Hall & Fedigan 1997). Subordinate animals forced onto the group edges frequently show higher levels of vigilance behaviour as a predator avoidance strategy, reducing the need for dominants to be vigilant (Keys & Dugatkin 2002). In consequence, dominant animals have more time to devote to tracking resources and become more informed about patch conditions than subordinates (Dall et al. 1999). In the context of Chapter 6 subordinates may not have shown vigilance behaviour to avoid predation, but instead to avoid aggression from the dominant animal (Thouless & Guinness 1986).

On this basis, it is possible that subordinate animals operate in a more complex medium than dominant animals. The experiment in Chapter 6 showed that subordinate animals used more information to make foraging decisions than dominant animals. Learning about patch resources was impaired for subordinates due to a lack of reinforcement and aggressive interactions. Therefore, the subordinate's foraging environment became more uncertain than that of the dominants, reflecting the larger costs associated with group foraging for subordinate animals.

Comparing the results from Chapter 4 and Chapter 6 support this argument. In Chapter 4 no difference was found between the observed results and those predicted from conditions of complete knowledge, with run number only having an effect, i.e. learning still taking place, at treatment 0.5. In this experiment animals responded to the average probability of receiving a reward by leaving the certain patch after consuming a volume of hay proportional to the reward probability. The results of Chapter 4 can be compared

with those of Chapter 6 where the dominance status of individual animals was known, and animals foraged in pairs.

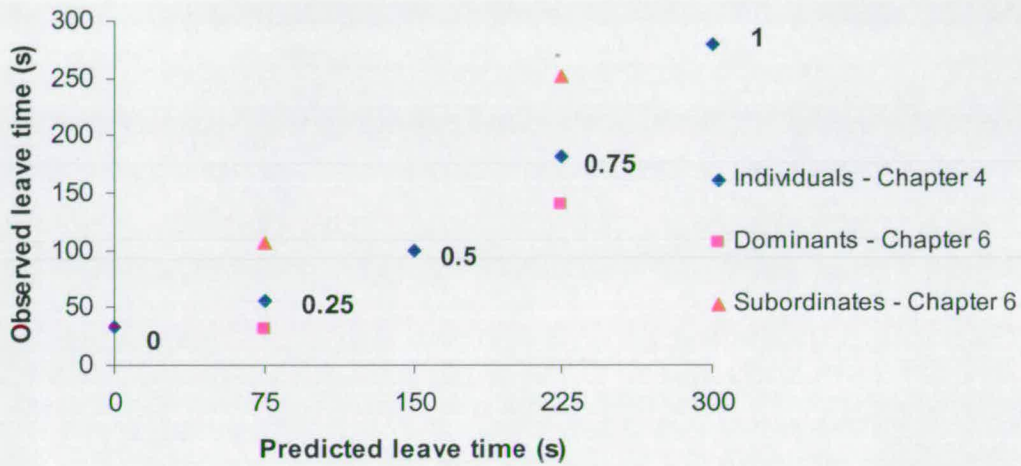


Figure 9.1. Comparison of leaving times across experiments in Chapter 4 and Chapter 6.

Figure 9.1 shows the average patch leaving times (equivalent to volume of hay consumed) for individuals in Chapters 4 and 6. Predicted leaving times for each probability treatment were calculated as a proportion of the time available for feeding during one experimental run (300s). Figure 9.1 compares the leaving times of dominant and subordinate animals at treatments 0.25 and 0.75 (Chapter 6) with individuals foraging alone (Chapter 4). Both dominant and subordinate animals show behaviour skewed away from that of the average response of an individual. This comparison suggests a decrease in efficiency as paired individuals diverged in behaviour as a result

of the increased uncertainty imposed by a social environment. The dominance status of the individual influenced the behavioural strategy adopted. Without full knowledge of patch conditions sheep, when given a choice between patches, preferred the most predictable option (Chapter 7) which in this case (Chapter 6) was the certain hay patch. Subordinate animals appeared to behave more risk aversely by spending longer than the dominants in the certain patch. This behaviour suggests that subordinates had less information about the environment, therefore greater uncertainty than the dominant animals.

Social effects at pasture

In Chapter 8 animals were free to move to alternative patches without excessive aggression in interactions, more akin to a natural system. Groups consisting of three animals were chosen as the minimum number of sheep that can be considered to approximate normal group behaviour (Penning et al. 1993). However, no measures of sociability or dominance status were made for this group of sheep. In the experimental set-up in Chapter 8 dominant animals may have experienced reduced information in comparison with the social experiment in Chapter 6. In the experiment described in Chapter 8 subordinates were able to learn about the environment by consuming resources without the risk of aggressive interactions from dominant animals. Dominants could continue to use the strategy of following subordinates but in most cases the first animal to arrive at a patch consumed all the pellets. At the beginning of the experiment, focal animals were chosen from within the 6 groups because of their propensity to actively search for pellets in a preliminary training run. Although there were differences

in activity between groups in some of the variables measured in this experiment, all groups showed the same pattern of response. If focal animals had been randomly selected from dominant and subordinate animals it can be assumed that they were responding in the same way. However, it may have been that dominant or subordinate animals had a higher propensity towards activity and, therefore, were selected as focal animals. Unfortunately there were too few interactions between animals, and groups were too small to permit a reliable hierarchy to be established to verify this argument.

Effect of dominance status on performance

It has been shown that subordinate red deer hinds have reduced breeding success in comparison with dominants (Clutton-Brock et al. 1982), and that subordinate hinds under high stocking densities suffer reduced growth rates (Blanc & Theriez 1998). At artificially high density, or close inter neighbour distances, subordinate animals avoid conflict by stopping feeding and moving away (Thouless 1990) or showing increased vigilance behaviour (Blanc & Theriez 1998). In the experiment presented in Chapter 6 subordinate animals were highly restricted in their access to an alternative patch and as a result this patch was monopolised by the dominant animals. Under more natural conditions, where density between neighbours was not restricted, studies of groups of bighorn sheep (*Ovis canadensis*) have revealed no difference between quality of diet, activity costs or productivity between high and low ranking females (Eccles & Shackleton 1986; Festa-Bianchet 1991). In the experimental set-up in Chapter 8 the reduced ability of dominant animals to monopolise the food sites meant that resources were distributed more evenly among group members. Subordinate animals, therefore,

had the chance to exploit resource sites without interference. This was particularly true in treatments where resource sites were unpredictable in bowl distribution or overall quality. Despite food resources being more evenly distributed across the group, sheep still appeared capable of learning environmental conditions, and responded in such a way as to maximise their foraging efficiency. As this experiment was an attempt to approach more natural conditions, giving individuals the opportunity to exploit alternative resources and move away from conspecifics to feed, it appears that subordinate animals are not the victims of the high costs suggested by the results of Chapter 6.

Sociability

Although sheep were capable of foraging alone in an experimental arena, as shown in chapter 4, 5, 6 and 7, the introduction of another sheep may have influenced their behaviour beyond an adaptation of foraging strategy. Where levels of conspecific attraction are high, the foraging success of individuals is predicted to fall, as individuals become concentrated in poor and rapidly depleting resource sites (Beauchamp et al. 1997). It is possible that highly sociable sheep sacrificed patch expectations to be near the other sheep. This might have been avoided in Chapter 6 if transparent partitions, while still restricting a view of the variable patch, had been used in the arena in place of wooden partitions. Further work could be carried out to look at sociability and dominance ranking in relation to exploitation of a variable environment. This could be achieved by considering a third patch in an experiment analogous to Chapter 6, either in series to permit the subordinate sheep to move away when the dominant sheep

approached, or in parallel. A third patch in parallel could be assigned a food resource of intermediate quality to the hay and pellet patches. It is predicted that the subordinate animal, to minimise the risk of aggressive interaction would stay at the hay patch, as in Chapter 6, or would move to the patch of intermediate quality. The dominant animal would be predicted to stay at the hay patch to maintain social contact (Caraco et al. 1989), move to the preferred patch, or follow the subordinate sheep to the intermediate patch. This would determine if the primary motivating force for the dominant animal was to exploit the information of the subordinate, maintain social contact, or reaffirm its dominant status by supplanting the subordinate where food resources offered were only marginally beneficial compared to that offered in the best quality patch. The effects of the restriction in Chapter 6 were eliminated by the extensification of the experimental set-up in Chapter 8. For the experiment described in Chapter 8 a record of dominance status, sociability and further to this, focal animal data for all animals in the group would permit a more thorough examination of the constraints on social foraging in a variable environment.

SUMMARY

Foraging sheep have the capacity to react rapidly and consistently to changes in their environment. Like many herbivore species sheep adopt a win-stay strategy to foraging decisions, and are generally risk averse, preferring the predictable option where a choice is available (Chapter 7). The comparison of behaviour in Chapters 4 and 6 highlights the alternative strategies adopted by animals as uncertainty in the environment increases. Strategy is dependent on the individual characteristics of the animal, for example

dominance status (Chapter 6) or personality trait (Chapter 5). As the cost of obtaining and storing information increases, animals are more likely to choose the most reliable option (Chapter 7) or revert to a random choice (Chapter 7, Chapter 8). Further, foragers may alter their search strategy to account for reduced information (for example more time devoted to searching in variable environments – Chapter 8), reflecting a flexible behavioural strategy responsive to minor changes in resource distribution (a memory for feeding stations – Chapter 8) or general environmental conditions (the removal of the gate between training and test – Chapter 6).

FUTURE DIRECTION

This series of experiments considered only a fraction of the field of herbivore foraging strategy affected by information and uncertainty. While this study did not set out to explicitly test particular foraging models, it has emphasised the value of information and behavioural rules in variable environments to make foraging decisions. The preference of sheep for predictability (Chapter 7) stressed the value of environmental information to foraging sheep. The cost of obtaining that information was highlighted under different conditions and this should be investigated in more depth, particularly at low spatial scales and under more complex conditions than presented here (Illius et al 1992). In conjunction with this should come more experimental work to examine the rules used for making within and between patch decisions, as well as comprehending the definition of a patch for a forager. Though this is not a new problem (Laca & Demment 1991; Hobbs 1999) it remains unresolved. A deeper understanding of social interaction,

individual differences and the trade-offs between obtaining using information for herbivores is necessary to develop herbivore foraging theory.

CONCLUDING REMARKS

This series of experiments set out to explore the response of foraging herbivores to uncertainty in the environment. If uncertainty is measured in terms of probability then a “*reduction in uncertainty*” can be achieved through the gathering and use of information (Shannon & Weaver 1949). Acquisition of information and the consequent reduction in uncertainty is important because informed decision making improves foraging efficiency (Ljungberg & Enquist 1986). This study has emphasised not only the complexity of decision making for group living herbivores but also the importance of gaining reliable information in unpredictable environments.

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APPENDIX I

Table I.I: The order of pellet presentation in the variable patch. The orders were balanced across days and treatments. 0=no pellets; 1= 50g pellets

treatment	pattern			
0	0,0,0,0	0,0,0,0	0,0,0,0	0,0,0,0
0.25	0,0,0,1	0,0,1,0	0,1,0,0	1,0,0,0
0.5	0,10,1	1,0,0,1	0,1,1,0	1,0,1,0
0.75	1,1,1,0	1,1,0,1	1,0,1,1	0,1,1,1
1	1,1,1,1	1,1,1,1	1,1,1,1	1,1,1,1