

Thesis submitted for the degree of
Doctor of Philosophy
at the University of Leicester

by

Husni Ibrahim
Department of Biology
University of Leicester

2008

UMI Number: U495707

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI U495707

Published by ProQuest LLC 2013. Copyright in the Dissertation held by the Author.
Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against
unauthorized copying under Title 17, United States Code.



ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

In Loving Memory...

**To my late father; Hj. Ibrahim Puteh
(1933 – 2007)**

Declaration

I hereby declare that no part of this thesis has been previously submitted to this or other University as part of the requirements for a higher degree. The content of this thesis is the result of my own work unless otherwise acknowledged in the text or by reference.

The work was conducted in the Department of Biology, University of Leicester during the period July 2004 to January 2008.

Signed.....

Husni Ibrahim, May 2008.

The Role of Migration in the Distribution of the Brown Rat in the UK Agricultural Landscape

**By
Husni Ibrahim**

Abstract

The brown rat (*Rattus norvegicus*) is an important agricultural pest in the UK. To enable more effective measures for controlling rat populations a better understanding is required of the distribution and movements of rats in the agricultural landscape. The aims of this study were to understand the extent and causes of movements between local rat populations in an agricultural environment. This aim was achieved by examining the movement of rats between farm buildings and fields using trapping, tracking plates and video surveillance. In addition, the spatial distribution of rats and small mammal populations in farm buildings and agricultural land was investigated, and whether rat distributions are affected by food availability. Finally, morphological differences in skull shape were investigated to examine whether they reflected geographical isolation. It was shown that the siting of traps had a significant effect on the numbers of rats caught. There were temporal variations in rat captures; with more rats caught in autumn than in other seasons. Rats in reproductive condition were caught throughout the year, suggesting that individuals in the study populations breed continuously throughout the year. There was a significant differences between the weight of male and female rats, with males heavier than females, and body fat levels were demonstrated to increase with age. Rats were predominantly caught moving from farm buildings towards the fields during the spring and predominantly moved from fields into farm buildings during autumn. More fecund males moved into the farm during autumn accompanied by non-breeding females. Video monitoring of a single trap system provided evidence that rats are active during both day and night. The level of activity was relatively low in this study with an average of 5 sightings per day. Their direction of movement was not consistent and trapping appeared not to change rat behaviour. It appeared that farm buildings provided the most suitable habitat for brown rats all year round and their density remained constant if no control measures were taken. Small mammals dominated the Field habitat and there was little spatial overlap between brown rats and small mammals around farm buildings. In summer brown rats increased in the Field and in autumn small mammals showed their highest abundance in the Farm habitat. However, there was some potential for small mammals to compete for resources with brown rats in open field areas during summer. Farm sites contained more food than agricultural land. Food was available throughout the year at both sites, but was most abundant during winter at farm sites and during autumn in field sites. At the farm site supplemental feeding attracted rats and small mammals, but was less effective when alternative food was abundant. In field sites supplemental feeding appeared not to attract rats or small mammals. An examination of skull morphology among three rat populations showed significant differences, though there was no evidence of a strong geographical component to variation. There was no significant difference in skull morphology between the sexes, though there was a significant interaction between sex and population. Variation in skull morphology among populations was probably linked to diet type, and food availability as well as genetic drift arising through reproductive isolation of the study populations.

Acknowledgements

I would like to thank my supervisor, Dr Carl Smith for his invaluable advice, guidance and support that enabled me to complete this project and thesis writing and my sincere thanks to Prof. Robert Smith, for all his help and the opportunity for me to start this project.

I would also like to thank the Ministry of Higher Education Malaysia for the sponsorship and Universiti Pendidikan Sultan Idris for approving my study leave. My deepest gratitude to Dr Malcolm Brown for his help with some of the field work and many thanks to Dr Mark Lambert of Central Science Laboratory, York, for some of the rat samples and some of the information shared.

Sincere thanks to the members of the Department of Biology; Donna, Yvonne, Penny Butler, Penny Chamberlain, Sue, Judy, Leslie, Steve, Jean, Maurice and Elaine for their assistance. Many thanks to Akram, Chris, Carolyn and Muna who made my day with laughter. Special thanks must go to all the farmers, who allowed me with unrestricted access to their land and buildings.

Thank you to all my Malaysian friends in Leicester; especially to Rahmat, Masrah, Azmir, Muna, Azhar, Tuah, Sadiyah, and many more who always cheer me up and for their support. Finally to my beloved wife Dr Haniza Hanim Mohd Zain, for the caring, support and encouragement, my children; Anis, Imran, Aiman and Farhan for the joy and their sacrifice and my parents and families in Malaysia for their support and encouragement.

Table of Contents

Dedication	ii
Declaration	iii
Abstract	iv
Acknowledgement	v
Table of contents	vi
Lists of figures	ix
Lists of tables	xi
 Chapter 1 – Introduction	 1
1.1 General introduction	1
1.2 Population ecology of brown rats	4
1.3 Rat movements in an agricultural landscape	8
1.4 Aims and objectives of the study	13
 Chapter 2 – Population biology, rat movement and activity along migratory routes in leicestershire: trapping and video surveillance	 14
2.1 Introduction	14
2.2 Materials and Methods	18
2.2.1 Trap system (TS)	18
2.2.2 Rat trapping	21
2.2.3 Video monitoring of rat activity	23
2.3 Results	24
2.3.1 Rat population structure	24
2.3.2 Reproduction	30
2.3.3 Movement direction of trapped rats	33
2.3.4 Video monitoring of rat activity	34
2.4 Discussion	38
2.4.1 Rat population structure	38
2.4.2 Direction of movement into or out of farms	43
2.4.3 Rat activity by video surveillance	44

2.4.4	Implications of rat behaviour for control measures	46
2.5	Summary	48
Chapter 3 – Seasonal changes and distribution of brown rats in leicestershire: interactions with small mammal populations		50
3.1	Introduction	50
3.2	Materials and Methods	55
3.2.1	Study site and duration of study	55
3.2.2	Sampling design	56
3.3	Results	59
3.3.1	Levels of activity and animal distribution	59
3.3.2	Population estimation	68
3.3.3	Linking of tracking score with small mammal trapping	71
3.4	Discussion	76
3.4.1	Species distributions	76
3.4.2	Rat and small mammal interactions	82
3.5	Summary	85
Chapter 4 – The effect of food availability on the distribution and abundance of brown rats		87
4.1	Introduction	87
4.2	Materials and Methods	93
4.2.1	Food availability assessment	93
4.2.2	Effect of food availability on distribution	94
4.3	Results	95
4.3.1	Food assessment	95
4.3.2	Effects of supplemental food on animals distribution	99
4.3.3	Food intake	103
4.4	Discussion	108
4.5	Summary	112
Chapter 5 – Population variation in skull morphology		113
5.1	Introduction	113

5.2	Materials and Methods	116
5.2.1	Skull preparation	116
5.2.2	Skull parameters	118
5.3	Results	123
5.4	Discussion	127
5.5	Summary	132
Chapter 6	– General discussion	133
6.1	General discussion	133
References		141

List of Figures

2.1	Example of trap system built in a gap along a hedgerow at Farm C	19
2.2	Map of study area	20
2.3	Total number of rats caught from each trap system for both trapping occasions	26
2.4	Monthly changes of mean body weight of rats caught from three farms	27
2.5	Monthly proportion of rat body weight classes on three farms	28
2.6	Monthly median fat index of trapped rats	30
2.7	Monthly number of scrotal and non-scrotal rats caught from three farms	31
2.8	Monthly proportion of reproductive condition of female rats from three farms	33
2.9	The total number of rats that can be spotted through screen monitor in observation area	35
2.10	Mean total rats sightings	36
2.11	Mean rate of rat sightings	37
2.12	Temporal variation in rat activity	37
2.13	The rate of rats using or avoiding the TS when Fenn traps were set and not set	38
3.1	Rat footprints on carbon-coated tracking plate	58
3.2	Mean (+ s.e.) daily activity score for tracking plates by brown rats laid in Farm and Field sites over four seasons	61
3.3	Mean (+ s.e.) daily activity score for tracking plates by small mammals laid in Farm and Field sites over four seasons	61
3.4	Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in spring	64
3.5	Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in summer	65
3.6	Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in autumn	66
3.7	Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in winter	67
3.8	Comparison of the total numbers of small mammals caught in both study sites	69
3.9	Proportion of each small mammal species caught at the Field site over the entire study period	70

3.10	Correlation between estimated rat abundance from tracking plates and small mammal abundances from Longworth traps at Field and Farm sites in all seasons	71
3.11	Correlation between tracking plates score and the number of all small mammals caught using Longworth traps at the Farm site	72
3.12	Correlation between tracking plates score and the number of small mammals caught at the Field site	73
3.13	The total numbers of all small mammals caught next to unmarked tracking plates and those marked by rats at the Farm site	74
3.14	The total numbers of all small mammals caught next to unmarked tracking plates and those marked by rats at the Field site	74
4.1	Bait box used in present study	95
4.2	Food sample from the Farm site	96
4.3	Comparison of the total food index in the farm buildings and in the fields throughout the study period	97
4.4	Comparison of the mean biomass of food (gm^{-2}) availability from the Farm and the Field study sites throughout the year	98
4.5	The most dominant fruit during autumn in the Field	99
4.6	Mean supplemental food intakes per visit by rats and small mammals at both study sites	104
4.7	Proportion of food taken by rats, small mammals or both in the Farm and Field	105
4.8	Mean amount of food intake per visit by rats, small mammals or both during study period on both study sites	106
4.9	Correlation between tracking plate score and amount of bait taken per visit for brown rats	107
4.10	Correlation between tracking plate score and amount of bait taken per visit for small mammals	107
5.1	Brown rat skulls ready for measurement	118
5.2	Schematic drawing of adult brown rat skull in lateral view, mandibular, dorsoventral view and dorsal view	122
5.3	Plot of values for the first and second canonical variates generated from standardization of skull measurements from three populations of brown rats	126
5.4	Interaction plot among populations and sexes for the first canonical variate	127

List of Tables

2.1	The distance between trap systems and farm buildings	21
2.2	The direction taken by rats as determined through video observation	24
2.3	Sex of rats caught in different seasons during trapping sessions	25
2.4	Percentage of male and female rats from three farms in body weight and head and body length classes	29
2.5	Percentage of rats caught by fat class and by body weight class from three farms	29
2.6	Proportion (%) of sexually mature males by fat class and body weight class from three farms	31
2.7	Proportion (%) of sexually mature females by fat class and body weight class from three farms	32
2.8	Total number of rats caught in TS in relation their direction of movement and season	34
3.1	Dates covered by four different sampling sessions	56
3.2	Seasonal numbers and proportion of tracking plates marked by rats and small mammals and by both in the Farm	62
3.3	Seasonal numbers and proportion of tracking plates marked by rats and small mammals and by both in the Field	62
3.4	The estimated numbers of small mammals (Longworth trapping) and brown rats (tracking plate) at the Farm site for all seasons	69
3.5	The estimated numbers of small mammals (Longworth trapping) and brown rats (tracking plate) at the Farm site for all seasons	70
3.6	The relationship between the distribution of rats and the probability of capture of small mammal species at the Farm and Field sites	75
4.1	The total numbers of sub-blocks visited by the brown rats on the Farm and the Field in summer and winter	101
4.2	Total footprint index for brown rats on the Farm and the Field for both seasons	101
4.3	The total numbers of sub-blocks visited by the small mammals in the Farm and the Field for both seasons	102
4.4	The total numbers of foot print index by the small mammal on the Farm and the Field for both seasons	103
5.1	Rat skull parameter measurement	119

5.2	Mean values of the proportion indices in each skull measurements among populations	124
5.3	First two canonical discriminant functions	125
5.4	Character loading factors searched from canonical variate analysis	125
5.5	Predicted and observed population group for LE, YO1 and YO2	126

Chapter 1: Introduction

1.1 General Introduction

The brown rat (*Rattus norvegicus*) is believed to have been introduced to the UK in the 1720s on shipping from Russia, though it originates from the steppes of Central Asia (Yalden, 1999). Since then the brown rat (hitherto simply referred to as the rat unless specified otherwise) has rapidly established populations throughout the UK. This species is also known as the common rat or Norway rat and represents a major rodent pest in the UK agricultural landscape. They can be considered obligate pests because across all or part of their geographical range their distribution is closely associated with human agricultural production (Aplin *et al.*, 2003). The term 'commensal' is not appropriate to use for the rat since it infers no damage to the host (Macdonald & Fenn, 1994). The rat is a pest in terms of both economic damage and health problems, and represents a continued threat to human health and food production as human population size grows exponentially, with the impact of the rat perhaps greatest in those areas which are least able to cope (Meyer, 1999). Numerous measures have been taken to control rat populations, including trapping, shooting, using dogs and ferrets to kill or flush rats from their burrows. However, probably the most effective measure used against rats is poisonous baits; particularly anticoagulant rodenticides which act by blocking the vitamin K cycle in the liver. Despite their initial efficiency, rats have quickly evolved anticoagulant resistance (Greaves, 1994). New, more powerful anticoagulants have been developed, which now pose a risk to non-target mammals as well as birds through secondary poisoning (MacVicker, 1998; Brakes, 2003; Hoare & Hare, 2006).

There are two species of rat in the UK, in addition the brown rat there is also the black rat (*Rattus rattus*). The black rat is also known as the ship or roof rat and originates in the Far East, the southeast Asian mainland, the islands of Indonesia and the Philippines (Aplin *et al.*, 2003). There are pronounced differences in appearance and biology of brown and black rats. Black rats have been present in UK for at least 2000 years and were once common throughout the British Isles and their distribution is now limited to a few small populations. Brown rats have a coarse fur and are usually dark brown or dark grey; the underparts are lighter grey or brown, though fur colour is not a reliable means of identification since black rats can be much lighter in colour than brown rats. The tail of the brown rat is shorter than the head and body length, is hairless, and dark coloured above and paler on the underside. Its nose is blunt and its ears and eyes are small. The average weight of an adult brown rat is about 350 g. It is believed that the brown rats have excluded black rats from the UK because they are better adapted to temperate conditions (Lambert, 2003) and the UK population of brown rats currently appears to be healthy (Langton *et al.*, 2001).

Whenever suitable food, water and shelter are available there is a chance for the establishment of rat populations. These requirements are met in rural areas all over the world, as well as in urban areas (Lund, 1994). The presence of rats is characterised by well used pathways or runs. Runs may appear as slight linear depressions in grass or other low vegetation or as well-worn trails of bare earth. A network of runs is maintained by the deposition of residual cues such as rat urine or food (Galef & Buckley, 1996). They are usually 50 – 100 mm wide and continuous; distinguishable from those made by rabbits which are discontinuous (Taylor, 1977). Runs in buildings show as dark, greasy smears on wood or brickwork. Droppings are another sign of the

presence of rats. Rat droppings are approximately 12 mm long and often tapering to a point at one or both ends. Footprints or tail marks are evident on soft surfaces such as mud or in snow. Another method to determine the presence of rats is the use of ultraviolet light; rat urine, both wet and dry, fluoresces under ultraviolet light. In highly infested areas gnawing may also be visible on doors, ledges, or stored materials (Lund, 1994). Rats usually form burrows in outdoor areas for nesting. Burrows are generally 65 – 90 mm in diameter and rarely exceed 0.5 m depth. Burrows are often situated on sloping ground, such as banks or the sides of ditches, or beneath some form of cover such as flat stones, logs or tree roots. In urban areas the occurrence of rats is often correlated with the presence of water. In the city of Salzburg the density of rats can reach 113 individuals/km along river banks. The distribution of rats was strongly influenced by vegetation, habitat modification and man-made impact in the area (Traweger *et al.*, 2006).

Rats are robust animals and are able to tolerate wide variations in their physical environment. They are agile and fast (Recht, 1988), and accomplished swimmers. Russell *et al.* (2005) reported that a single adult male rat swam 400 km across open water between Motuhoropapa Island and Otata Island in New Zealand. With an ample supply of food and adequate shelter, about 5% of wild brown rats in rural environments can live for 1 year, with female rats living slightly longer than males (Davis, 1948). Under certain conditions, brown rats can survive outdoors during the winter, but it is believed that an indoor migration increases as temperatures get cooler and food and water sources outdoors decrease. Migratory behaviour, therefore, is an important ecological process for population dynamics.

1.2 Population ecology of brown rats

The rat is believed to have originated from the steppes of Central Asia. From their centre of origin, they have slowly spread throughout the globe, facilitated by the growth of human populations and international trade. The availability of refuges as well as food appears crucial to the establishment of rat populations. For example, Lambert (2003) showed that population size on farms could be reduced by up to 41% if potential refuges were removed, where repeated use of toxicants did not give lasting control. In a constant environment, rat populations are likely to increase to their carrying capacity and remain relatively stable. A stable population size arises through a balance between birth and death and immigration and emigration. Pocock *et al.* (2004) showed that in the house mice (*Mus musculus*), birth and death had more influence on the overall population dynamics than migration. In contrast, Stickel (1979) concluded that migration was a primary mechanism of population regulation in mice inhabiting a cropfield mosaic.

In general, the physical environment plays a key role in limiting the population size of rats. Orgain & Schein (1953) correlated the physical environment with a rat population in Baltimore. Environmental factors, including building structure, fencing, as well as sanitary conditions and food supply were investigated. It was shown that food supply, the extent of paved areas and building structure were positively correlated with population size. The rate of recovery of reduced rat populations varies in nature. Populations that were moderately reduced (between 50% and 90%), showed rapid signs of recovery and increased at rates of about 4% of the capacity level each month; as they approached capacity they slowed down to a rate of about 2% per month or less (Emlen *et al.*, 1948). Populations reduced by more than 90% were

shown to recovered at a slower rate of between 1 and 3% per month (Emlen *et al.*, 1948).

In open fields, wild rats live in underground burrows. They dig burrows usually less than 18 inches deep, usually within approximately 30 m of food and water sources. Harper *et al.* (2005) found that on Stewart Island, New Zealand brown rats were most commonly found around vegetation associated with water, in contrast to black rats and Pacific rats. They believed that the differences in habitat use may represent different physiological adaptations to cold and wet, the avoidance of predation, inter-specific competition or complex vegetation types. Similarly, Hartley & Bishop (1979) linked rat infestation of hedges to access to streams.

Population estimates of rats have been carried using several different methods. Tracking plates can be used to estimate the population size (Quy *et al.*, 1993). Brakes (2003) used tracking plates scores to estimate population size on two farms before and after bait application. Tracking plates are based on a principle of quantifying the coverage of rat paw prints on randomly placed plates. The initial population size in one population was 85, with the post-bait population reduced to 44. In the second population, the initial size was 49 and this was reduced to 1. Taylor *et al.* (1981) used a capture-mark-recapture (CMR) method to estimate the population size of rats on three refuse tips. For Tip 1, the population estimate varied from 30 – 947; Tip 2 from 15 – 126 and Tip 3 varied from 0 – 95. They compared the estimation method with visual counts and bait consumption and found that the latter two methods led to underestimation of the real population. Venables & Leslie (1942) observed a rat population in the corn ricks (62% occupied by rats) and showed that the mean number

of active rats varied seasonally. In November 1939, the mean number of active rats per rick was around 16 and increased to 57 active rats per rick in April 1940. Butler & Whelan (1994) noted that there was a bimodal abundance in the rat population on two pig farms in Ireland over a period of 12 months. Rat captures peaked in July/August and in October/November and declined to minimum numbers in January. McGuire *et al.* (2006) captured and marked 297 rats at the University of Illinois Biological Research Area over a period of 13 months. Seventeen rats were recaptured >20 times. At the start of trapping in April 1986, the population contained just 10 adult females, nine of which were lactating or pregnant and three adult males. Juveniles began to appear in traps in the first week of May and the number increased to 102 by late June. They also observed a bimodal pattern in rat abundance; one in late June and again in late October, which declined to a minimum in March 1987. Gomez Villafane & Busch (2007) studied rat populations in 55 poultry farms near Buenos Aires and showed relatively low abundance on the farms (149 individuals comprising 4,382 trap-nights), though rats were detected on 70% (48 farms) of the total farms surveyed. In their study, they found no significant difference in rat abundance among seasons or between years. Surprisingly, they did not find differences in rat abundance between farms where rodenticides were applied and farms where poison was not used. According to Gomez Villafane & Busch (2007), the absence of temporal fluctuations in abundance was probably a consequence of the year-round breeding because of a constant supply of food and water resources and moderate environmental conditions throughout the year.

Poultry rearing is often associated with rat infestations. A study by Gomez Villafane *et al.* (2003) showed that high infestation rates were related to higher

chicken densities. Sheds located between other sheds of the same farm showed a lower infestation by rats than sheds located beside the perimeter of the farm. Farms that were properly managed, with a better control of vegetation growth (< 20 cm in height) at both the perimeter and within the internal area and a high maintenance of poultry sheds showed reduced infestations by rats (Gomez Villafane *et al.*, 2001). In contrast, Gomez Villafane & Busch (2007) found that rat abundance was not significantly related to plant cover, days since the chicken were brought to the farm, presence of pigpens, litter, car bodies, garbage or discarded tyres. This discrepancy among studies suggests relatively complex responses of rat populations to environmental variables.

Many researchers have classified rat maturity based on body weight. Davis (1948) stated that adult rats weighing more than 175 g and female rats weighing more than 150 g were adults. Butler & Whelan (1994) categorised rats <100 g body weight as juvenile. McGuire *et al.* (2006) subdivided age classes based on body mass as follows: juvenile (<80 g for males and females); subadult (80 – 200 g for males; 80 - 180 g for females) and adult (>200 g for males; >180 g for females).

Reproduction in rats appears to be seasonal, but shows substantial variability. Venables & Leslie (1942) observed a peak in female pregnancy during March to April. They found that heavier females tended to be more frequently pregnant than lighter females, and at the same time had a greater average number of embryos per pregnancy. Davis (1951a) compared pregnancy rates in three rat populations and observed that decreasing populations had the highest percent of pregnancy (30.9%), followed by increasing population (29.8%) and stationary populations (18.6%). Davis

(1951b) noted that there were seasonal changes in pregnancy and lactation in rural and urban populations. In farm rats there was a sharp increase in pregnancies during March – April. Urban rats had peaks in June, July and October. He also found that the mean number of embryos was significantly higher in urban environments (10.1%) than rural (8.2%). Allowing for a 20% mortality at and after birth, he estimated that urban females weaned an average 35 young per year while rural females weaned 13.6 young. Butler & Whelan (1994) noted that breeding peaks occurred in March, August and in the following February. McGuire *et al.* (2006) showed that the effective breeding season began in mid March and continued through to mid November and that breeding did not occur throughout the year.

1.3 Rat movements in an agricultural landscape

Migration represents regular movements, sometimes annual and often for the purpose of breeding, from one area to another, which may involve return movements to the original starting point (Frisch, 1969). In the context of the present study, the change in distribution of rats does not strictly represent migration in the sense of Frisch (1969), but instead small-scale movements, probably in relation to the availability of resources. However, these movements may be seasonal and the term migration is retained here and used in its broader sense of predictable seasonal movement. Rat migration in this study can be described as movements between alternate areas in response to ecological, physiological or environmental factors. Therefore, migration rate, which is the difference between immigration and emigration, may be a factor regulating population size.

Movement from the natal site or current home range and immigration to a permanent territory or home range area that will be the adult breeding site can be referred to as dispersal and usually involves juveniles or young adults (Wolff, 2003). Dispersal is distinct from migration in that it infers no return movement and is an additional movement to consider in relation to the spatial ecology of a species. Lidicker (1975) identified two basic forms of dispersal. Saturation dispersal occurs when the population has reached the carrying capacity, whereas presaturation dispersal occurs before the population reaches its carrying capacity. Dispersal range may be restricted by interactions with predators, parasites or competition. Dispersal and migration may operate simultaneously in rats, both with consequences for population change.

Four main reasons for rats to migrate and occupy farms are to obtain access to food, water, shelter or mates (Meehan, 1984). The extent to which rat movements are determined by their immediate requirements, and what stimuli, external and internal, provoke and direct these movements are poorly understood (Barnett, 1963). According to Halliday (1966) fear may play a role in the motivation of exploratory behaviour in rats and careless management of the farm environment can increase this type of movement. Often there is abundant food for rats on farms, and disused machinery, scattered rubbish and debris provide shelter from predators. These factors tend to increase the carrying capacity for local populations (Lambert, 2003). A radio-tracking study showed that 56% of rats remained in an uncleared area in contrast to only 8% rats that occupied farm buildings where the ground cover was kept permanently clear. Rats in the cleared area were exposed to a greater risk of predators and significantly reduced their home range area (Lambert, 2003). Brodie (1981)

observed changes in rat movements in relation to farming practice. Harvesting of barley crops resulted in an immediate increase in rat activity in oat fields, and rats began to invade refuse tips and farm buildings. Removal of oat crops resulted in further increases in the number of rats invading farm buildings suggesting that rats were affected by the loss of cover. This movement pattern reflected the results of a study by Bishop & Hartley (1976) who found that their estimates of the population size in hedgerow tended to peak at the time of crops harvest, due to the arrival of young and unmarked adults.

It is believed that rats tend to move from fields into farm buildings in early winter and move back to the field during spring (Huson & Rennison, 1981). A study showed that during autumn and winter rats in more distant localities tended to move towards farm buildings, but there was no suggestion of an orderly migration (Hartley & Bishop, 1979). Observations by Errington (1935) also showed that rat populations are sporadically distributed away from farm buildings during summer and as winter progressed, rats in field areas reduced in number. These movement patterns are believed to be associated with food availability. In an agricultural landscape pheasant feeders, which represent a high value food resource, can also influence rat movement patterns and distribution (Brown, 2007). Around farm buildings livestock sheds and grain barns appear to particularly attract rats (Brown, 2007). A study by Bishop & Hartley (1978) indicated that there was a constant movement of sub-mature or mature rats into and out of field populations and more males than females were involved in movements. However, a radio tracking study by Fenn *et al.* (1987) has shown that brown rats may regularly make nightly movements from nest sites outside a farm to farm buildings to access resources, even during colder periods, though some

individuals remained close to their home site. Differences in movements by rats within populations may arise from aggressive behaviour by dominant or resident individuals forcing others to forage over a wider area, although antagonistic encounters are difficult to observe. Hartley & Bishop (1979) suggested that rats established in buildings may exclude rats immigrating from hedges; none of rats they released in buildings were recaptured in hedges. The social behaviour of rats is complex; older male rats fight more frequently than older female rats, while younger rats play more often than they fight (Hart, 1973).

Rats living in open fields usually occupy larger home ranges than rats living in farm buildings. Davies (1953) found that only 8.9% of rats moved among four buildings, and in a day, less than 0.1% of the population went to another building. Notably, Byrom (2003) showed that rats that moved longer distance were more likely to be killed by a predator. In general, movement rates appear low in constant environments but can be high in more disturbed environments. Lambert (2003) found that rats living in field margins occupied larger home ranges than rats living near farm buildings and the distance travelled between consecutive observations was up to 650 m. Brown (2007) also showed that rats in farm buildings covered a smaller area (408 m²) and moved shorter distances (41.4 m) compared to rats in fields, which covered an area of up to 12,171 m² and moved a maximum distance of 210 m. However, there was no significant difference in home range size between male and female rats, suggesting high variability in mean ranges and movements among and within habitat types. The study by Brown (2007) also indicated that rats tended to shift their home ranges. Rats significantly reduced their home range area (74%) in response to a

reduction of harbourage. Brown rats are often active at night and show a preference for dark and covered environments (Whishaw *et al.*, 1992).

Male rats generally move greater distances and change their home sites more frequently than females; on average, males changed their home site every seven days, compared to females who changed every 14 days (Taylor, 1978). However rats living near to a food source rarely moved more than 30 m from their home sites. Taylor (1978) artificially provided a food source near to a hedgerow rat population and when the food was removed, rats expanded their range considerably. A male brown rat has been recorded in a radio-tracking study moving up to 3.3 km in one night (Taylor & Quay, 1978), though the average distance travelled in one night on arable land by rats was 660 m by males and 340 m by females. A study by Hartley & Bishop (1979) examined the movement of rats by the capture-recapture method on two farms in mid-Wales. Their estimate of mean home range for males was 66.1 m and for females was 54.8 m. The longest recorded distances travelled were 850 m for a female and 954 m for a male; there were no significant differences between the distances travelled by the sexes or by different age groups. Moors (1985) found that males tended to travel much further than females on island habitats. The average distance recorded by trapping showed 113 m for males and 49 m for females and the longest movement recorded was 330 m. These results may reflect the different mating strategies between the two sexes, where males are highly promiscuous and probably move further than females to search for mates. Breeding females are usually restricted to ranges close to their nest site. A radiotracking study by Lambert (2003) showed that the home-range size of rats on Yorkshire farms varied from 19.5 m² to 14,571 m² for males and from 38.5 m² to

1,695 m² in females; home range size and shape appeared to be determined by habitat microstructure.

1.4. Aims and objectives of the study

The aims of this study were to understand the extent and causes of movements between local rat populations in the UK agricultural landscape. Specifically, the objectives were to:

1. Investigate the population biology of brown rat in three selected farms in Leicestershire.
2. Study the movement pattern of rats between farm buildings and fields using trapping in a funnel trap system, tracking plates and monitor the activity of rats using video surveillance.
3. Investigate the relationship between the spatial distribution of rats and small mammal populations in farm buildings and agricultural land.
4. Determine whether rat distribution is influence by food availability in farm buildings and agricultural land.
5. Investigate whether geographical variation in skull morphology of rat populations reflects geographical isolation.

Chapter 2: Population Biology, Rat Movement and Activity along Migratory Routes in Leicestershire: Trapping and Video Surveillance

2.1. Introduction

Little is known about the behaviour and ecology of free-ranging brown rats. In the laboratory, many studies have been conducted on laboratory rat strains but it is clear that there are significant differences between wild and laboratory rats (Hart, 1973; Klemann & Pelz, 2005). Therefore, any conclusions about wild rat behaviour and their ecology cannot be derived solely from studies of laboratory rats.

In the wild, rats live in colonies with one to six females sharing a small burrow system in which they may raise their young together. Usually one or a few males are associated with the group and their social organization and mating system depend on population density. At low densities, males defend a territory from intruders and the mating system is polygynous. At high densities, males do not defend a territory and the mating system is promiscuous (Moore, 1999).

Like other animals, rat population dynamics are likely to be influenced by the local environmental conditions (availability of food, refuges and seasonal variations in these), the rate of predation, the extent of inter-specific and intra-specific competition for food and refuges, the birth rate and rates of immigration and emigration. Studies of their reproductive rates in particular provide data that help in understanding population change, dispersal and mortality rates (Davis, 1951b). Under ideal

conditions, rats are capable of high rates of population increase over short periods of time. Brown rat tends to conform to an r-selected life-history strategy (Macdonald & Fenn, 1994), and are extremely prolific breeders, reproducing throughout the year (Butler & Whelan, 1994). Under normal conditions, the gestation period for females is 20 to 23 days. Litter sizes are usually about 7 to 9 young. Davies (1951b) estimated that a single female farm rat weaned about 14 young per year with a peak in breeding from March – April and in September. Others studies also support these findings (Butler & Whelan, 1994).

The Brown rat is associated with farm buildings in rural areas. A survey conducted by Langton *et al.* (2001) estimated that 3.8% of farms had a problem with rat infestations that occurred inside farm buildings, while 38.3% had infestations that were outside. Rates of infestation vary; e.g. 94% of the farms in Hampshire were shown to be infested by rats (Greaves *et al.*, 1982). Rat infestations are a particularly serious problem when there is careless management of the farm environment; abundant food, rubbish and debris that provides shelter from predators. Rats can damage farm buildings and equipment as a result of their gnawing behaviour. According to Huson & Rennison (1981), deep litter poultry houses were the most frequently infested type of farm facility by rats. Rats consume animal feed and can damage stored and standing crops. Damage to stored grain and animal feed in the UK has been estimated to be £10 – 20 million per year (Lund, 1994). They can also destroy and contaminate food and are a potential source of disease (Buckle & Smith, 1994), posing a serious hazard to public health. At least 13 zoonotic parasitic species, including *Cryptosporidium parvum*, *Coxiella burnetii* and *Listeria* spp. were found in brown rats (Webster & MacDonald, 1995). Rats also represent a significant risk of

disease for farm workers and livestock (Quy, *et al.*, 1999; Daniels & Hutchings, 2001).

Due to economic losses and concerns for public health, effective control programmes are required in order to reduce the damage caused by rats. Poison baits have been the most popular method used to control rats in the UK (Buckle, 1994). However, there are several options available for non-chemical control of rats on farms; chemical control by poisoning does not have long-term effects on rat populations because rats are believed to move quickly into areas where population size is reduced by poisoning from other populations (Smith, 1994). Furthermore, there are individuals could recover from bleeding. Recently the awareness among public of anticoagulant used had increased. Anticoagulant poisons generally take several days to kill, during which time they cause distress, disability and pain and sub-lethally affected animals are also likely to experience haemorrhages. Most believed that this method is inhumane in terms of their speed and mode of action, the appearance and behaviour of affected animals, experiences of human victims, and long-term effects on animals that survive exposure and welfare risks to non-target animals (Mason & Littin, 2003). Compared to a well-designed snap traps, this method emerge as relatively humane because usually it kills swiftly and with little distress.

The extent to which rats move from one farm to another or from fields into farm buildings is poorly understood. Such movements might have a significant impact on population dynamics by linking local populations to a larger-scale metapopulation structure (Smith, 1999). One suggestion has been that rats rely on landscape features for movement, particularly hedgerows, which thereby act as corridors for movement.

Therefore, rat -control programmes may need to focus on larger-scale population dynamics and recognise the possible role of environmental features, such as hedgerows, as routes of movement.

In order to take a metapopulation approach to rat population management it is important to understand and to obtain a greater understanding about their ecology and behaviour, particularly movements among populations. These data could then contribute to more ecologically based rat management systems.

In this study, trapping and video monitoring were used to identify features of rat population structure, movement and activity levels. Trapping was used systematically along hedgerows to determine population structure and movement patterns. A video monitoring system was used to observe rat daily activity near a trap system on a farm site. The use of video monitoring equipment may be a valuable tool to understand the behaviour of rats; observations can be run continuously, day and night, and in all weather conditions. The aims of the current study were to 1) investigate the population biology of brown rats in three selected farms in Leicestershire; 2) study the movement pattern of rats between farm buildings and fields using trapping in a funnel trap system; and 3) monitor the activity of brown rats by video surveillance.

2.2. Materials and Methods

2.2.1. Trap System (TS)

The TS used was based on the concept of the Trap Barrier System (TBS), developed in Southeast Asia by Singleton *et al.* (1998). In a modification of the TBS system, an “attractive” refuge was constructed along a hedgerow using locally available materials to funnel rats into a covered trapping area where their activity can be monitored or they can be trapped. The TS were constructed from four straw bales. Each straw bale was approximately 1.5 m long, and 0.75 m high and 0.3 m wide. Traps were sited in gaps in hedges with bales arranged in parallel lines, with two bales on each side (Figure 2.1). Wire netting was fitted along both side of the bales and served as a funnel at both ends for channelling rats through the trap. Wire netting was fitted to a pole at both ends, adjacent to the hedge. The tunnel was covered with plastic sheeting to ensure it remained dry. Wire mesh (‘weld mesh’) was fitted at both entrances with 5 cm gaps to prevent access from larger non-target animals. In order to evaluate the attractiveness of different width tunnels to rats and other small mammals, tunnels were prepared with two different widths, either 30 cm or 50 cm.



Figure 2.1 Example of trap system built in a gap along a hedgerow at Farm C.

Eleven trap systems were set up on three different farm sites located near Loddington, Leicestershire. Four-trap system were set at Farm B and Farm C and three trap system at Farm A. The distance between Farm B and Farm C is approximately 1.6 km and between Farm A and Farm B 2.4 km (Figure 2.2). Each trap system was numbered from 1 to 11. TS numbers 1 - 3 were located on Farm A, TS numbers 4 - 7 on Farm B and TS numbers 8 - 11 on Farm C. Their distance from farm buildings varied from less than 50 m to more than 200 m (Table 2.1).

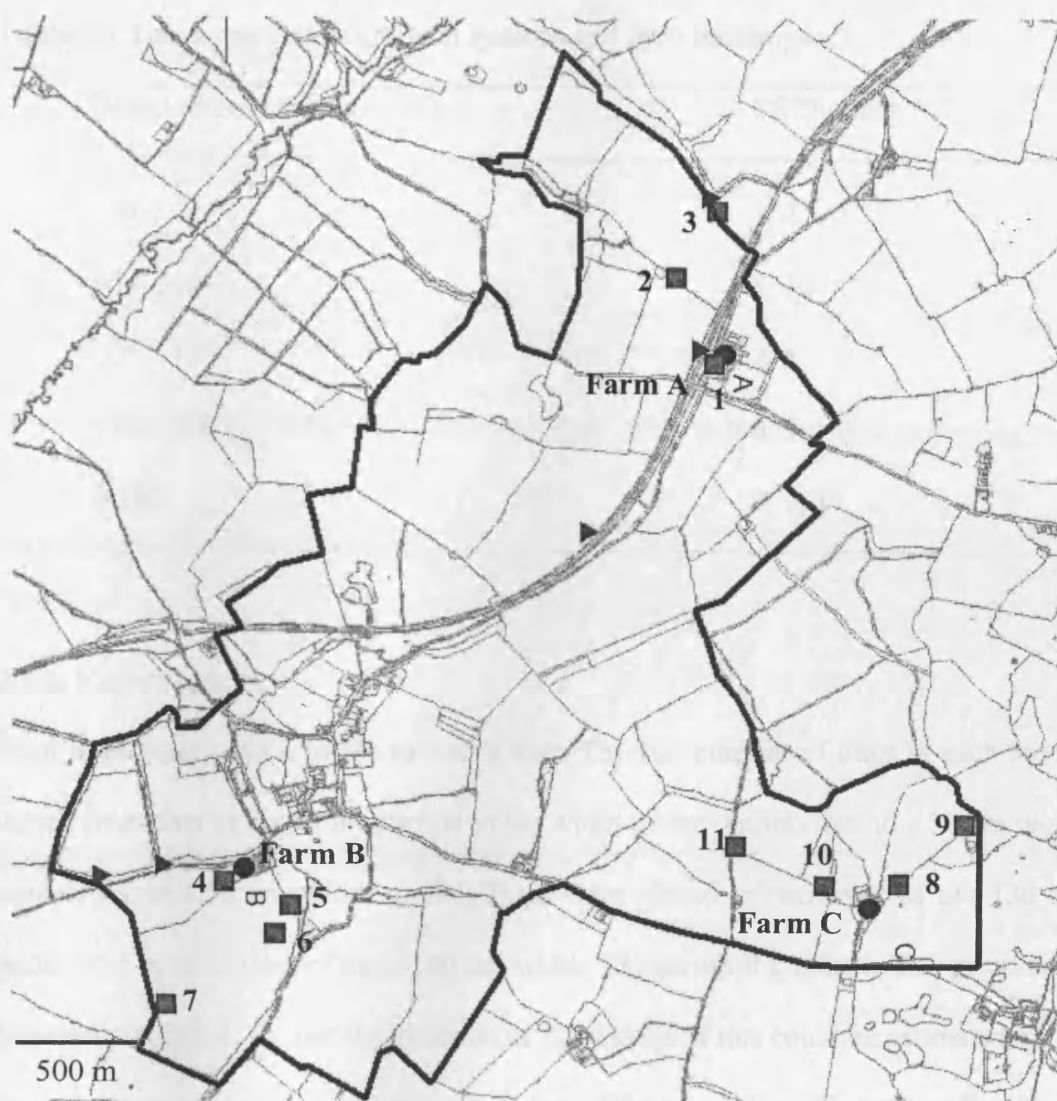


Figure 2.2 Map of study area. Numbers indicate the traps systems.

TS 1 was sited in a hedgerow between the road side and a cattle barn. TS 3 was sited along a small rill between grazing fields and a crop of wheat. TS 2, 4 and 5 were sited between grazing land and fields of wheat. TS 6 and 7 were placed in a beetle bank between fields of wheat and rape seed, while TS 8, 9, 10 and 11 were sited in hedgerows between grazing fields.

Table 2.1 The distance between trap systems and farm buildings.

Distance from the farm (m)	TS Number
< 50	1, 4
50 – 100	8, 10
100 – 150	2, 5
150 – 200	6, 9
> 200	3, 7, 11

2.2.2. Rat trapping

Fenn traps were placed in the tunnel of each TS. The number of traps in each tunnel varied from four to six in proportion to the width of the tunnel; four in a 30 cm width tunnel, six in a 50 cm width tunnel. Traps were placed in two rows of two (30 cm width TS) or two rows of three (50 cm width TS) across the tunnel. The position of traps was recorded, so that the direction of movement of rats could be estimated based on which trap was sprung and the orientation of the trapped rat. Traps were laid three weeks before trapping began, to allow rats to become familiar with them. Small amounts of grain were spread throughout the tunnel to increase their attractiveness to rats. All traps were set at the same level of the ground and lightly covered with grass.

Trapping was carried out on two different occasions. The first trapping period was conducted during spring 2005 for 10 weeks (04/04/2005 – 10/06/05). The second trapping period was conducted in autumn 2005 for 11 weeks (12/09/2005 – 25/11/2005). All traps were set on four consecutive nights each week. Traps were checked on the morning following setting.

In the event that rats were caught in tunnels, the following information was recorded: i) date of capture; ii) funnel and trap number; iii) sex – determined by visual inspection of external genitalia; iv) body weight; and v) orientation in the tunnel. In the latter category IN indicated that the rat was moving towards the farm when trapped and OUT that the rat was moving away from the farm.

Trapped rats were brought back to the lab for further inspection and were subsequently frozen for skull morphological studies (Chapter 5). Body morphological parameters were recorded including head and body length (i.e. nose to anus). Tail and hind foot length were also measured for species confirmation.

The body cavity of every trapped rat was opened and the amount of fat on the kidneys and attached to the abdominal wall was assessed by visual inspection using the following ordinal scale: 0 = no fat; 0.5 = traces of fat on body wall; 1 = fat on body wall and attached to kidney; 2 = up to $\frac{1}{4}$ kidney surface covered with fat and 3 = more than $\frac{1}{4}$ kidney surface covered with fat (Butler & Whelan, 1994).

For male rats, their testes were described as abdominal or scrotal. The left testis was weighed to the nearest 0.01g using an electronic balance (Sartorius®) after fat removal. The reproductive condition of females was determined by visual inspection. Females were classified into three different categories: a) non-breeding (NB); b) lactating (LCT) and c) pregnant (PGT). Pregnancy in rats can be determined by the presence of a swollen uterus or embryos in the uterus. The number of embryos was recorded if present.

2.2.3. Video monitoring of rat activity

The study was conducted at Farm B, Loddington, Leicestershire, a mixed arable, dairy and sheep farm. A funnel trap system (described in 2.2.1.) was used. The site chosen for video monitoring showed a high level of rat activity and was close to a power source. Numerous rat runs were evident linking surrounding hedgerows to the farm yard and along a ditch. Existing rat trails were used as criteria for setting the video camera because rats often follow the trails deposited used by other rats (Galef & Buckley, 1996).

The video camera was sited to enable a record of the direction that rats moved around the trap system. The camera was a monochrome video camera (Model: NCL 1100 "Ultimate" low light, 0.02 lux) with wide angle lens sensitive to infra red light. A time-lapse video cassette recorder (Model: Hitachi 480 Lr VTL 2000E) was connected to the video camera and set at a recording resolution of 2 frames per second, giving 96 hours of continuous recording time from a 4-hour video cassette. A weatherproof infra red floodlight lamp was used to illuminate the area with 'black' light allowing observation of rat activity during darkness. The lamp was controlled by a photocell, which turned the light off and on automatically at dawn and dusk.

Video monitoring was carried out continuously from 17/08/05 – 12/10/05, representing 1,368 hours of recording time. The direction of rat movement was recorded from video recordings, along with the time and date and weather conditions observed via the camera. The direction of rat movements was scored in a series of seven categories (Table 2.2). During 57 days of observation, rat trapping was carried

out on 21 randomly selected days using a Fenn trap. Any rats caught were removed from the tunnel on the following morning. A comparison of rat activity during periods of trapping and non-trapping was made.

Table 2.2 The direction taken by rats as determined through video observation.

Direction	Description
D1	The rat moved out from the trap system and went to the right toward the farm yard.
D2	The rat moved out from the trap system and went to the left toward the ditch.
D3	The rat moved into the trap system from the right.
D4	The rat moved into the trap system from the left.
D5	The rat moved from the right to the left without entering the trap system.
D6	The rat moved from the right to the left without entering the trap system.
D7	Other than D1 – D6 above.

2.3. Results

2.3.1. Rat population structure

A total of 125 rats were trapped in the TS. There was a marked difference in the numbers of rats trapped in spring and autumn. A total of 20 rats were trapped during spring and 105 in autumn, with an average catch of 2.0 and 9.5 rats per week

respectively. On both occasions, the number of males outnumbered females (Table 2.3) though there was no significant difference in the numbers of each sex caught among months (ANOVA, $F_{1,13} = 0.17$, $p = 0.683$). There was a significant difference in the mean number of rats caught among farms (ANOVA square-root transformed data, $F_{2,10} = 7.09$, $p = 0.017$) (Figure 2.3).

Table 2.3 Sex of rats caught in different seasons during trapping sessions.

Trapping Session	Sex	
	Male	Female
Spring	13	7
Autumn*	54	47

* Four samples are missing

There was no significant correlation between the distance a TS was sited from a farm and the total rats caught (Pearson's correlation, $r_{10} = -0.292$, $p = 0.383$). A comparison between the two tunnel widths used also shows there was no significant difference in total number of rats caught (ANOVA, $F_{1,10} = 0.68$, $p = 0.429$).

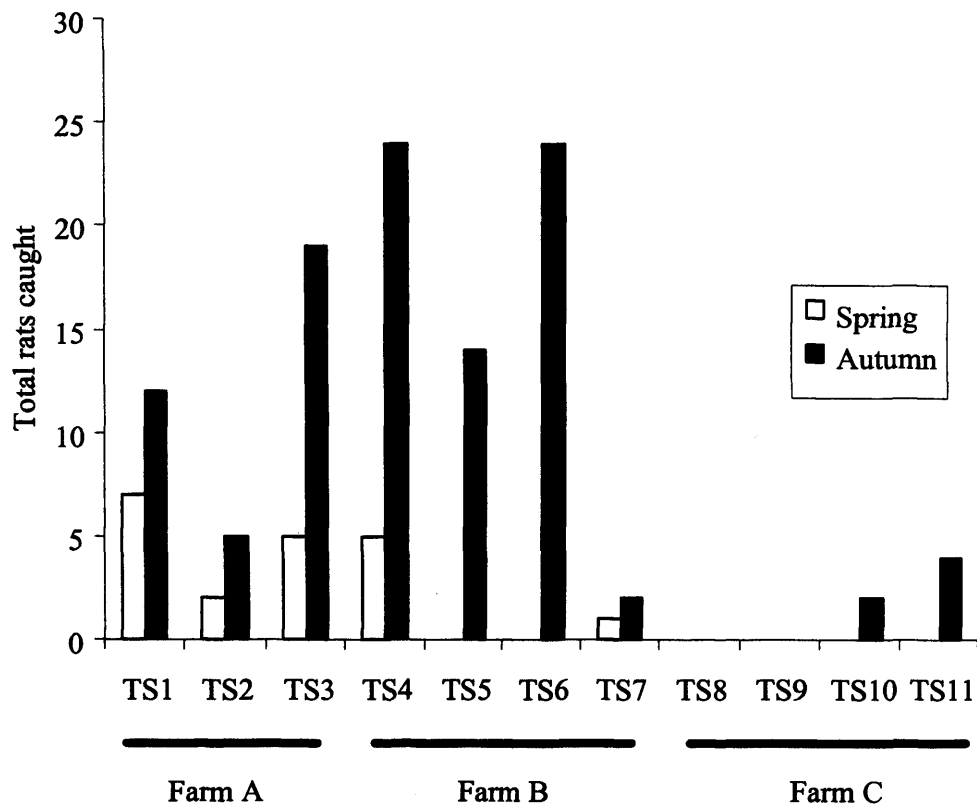


Figure 2.3 Total number of rats caught from each trap system for both trapping occasions.

There was no significant difference in the mean weight of rats among farms (ANOVA, $F_{2,124} = 1.97$, $p = 0.144$). However, rat body weight varied significantly among trapping periods (ANOVA, $F_{6,124} = 3.23$, $p = 0.006$) (Figure 2.4). Male rats were significantly heavier than female rats; mean body weights were 307.12 ± 12.81 g and 233.06 ± 12.87 g for males and females respectively (ANOVA, $F_{1,119} = 16.33$, $p < 0.001$). Mean body weight was highest in April - August and was lowest from September - November (Figure 2.4). Several young rats were trapped in the trap system, which contributed to lower mean body weight from September - November, reflecting the seasonality of breeding and/or movements.

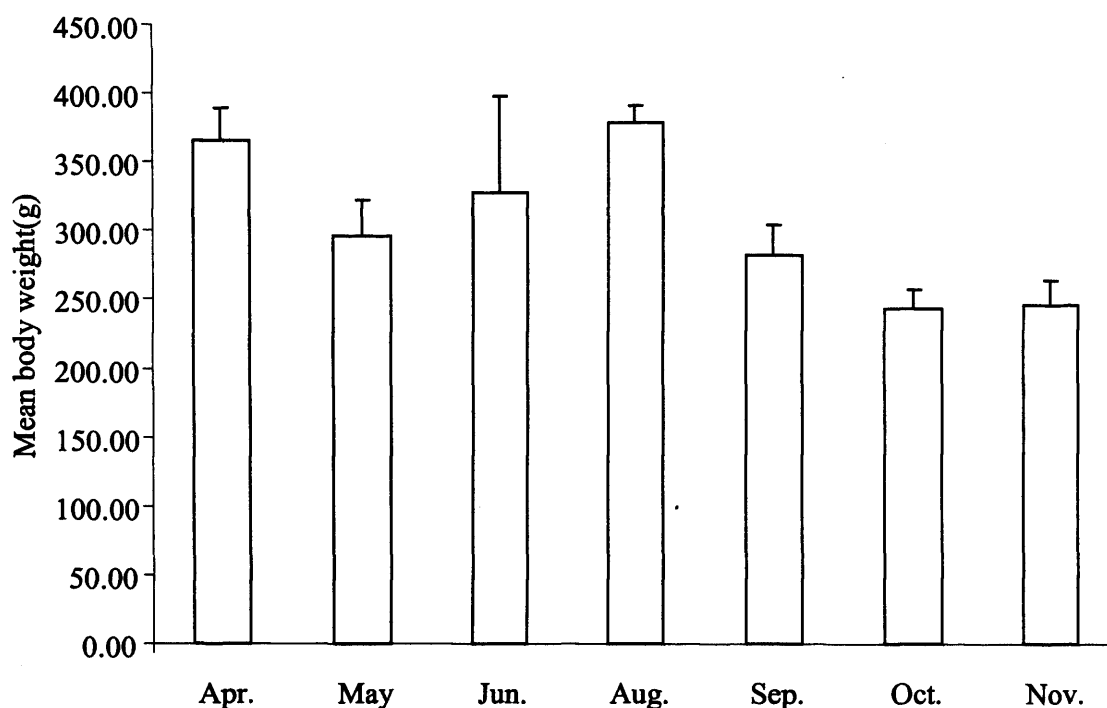


Figure 2.4 Monthly changes of mean body weight of rats caught from three farms. Error bars are 1 sem.

Rats were assigned to 100 g weight classes for analysis. During the trapping session, rats in the weight class of 200 – 299 g were most abundant, making up to 35.2% of the catch for the whole trapping period followed by rats in the weight class 300 – 399 g (25.6%). Rats in the weight class of <100 g constituted the lowest proportion of all weight classes (1.6%). The proportion of each weight class contributing to the population varied among months (Figure 2.5). Rats with a body weight < 200 g were only caught from September to November, probably reflecting the appearance of new recruits at the end of the summer. Rats in the weight class of 200 – 299 g were the most abundant in June and November, and August was the only month in which they were not caught. They showed a bimodal trend of population increase, from April to June and from September to November, suggesting reproduction took place throughout the year. The largest weight group (> 399 g)

peaked abundance in June and were found in all months during the trapping period except May.

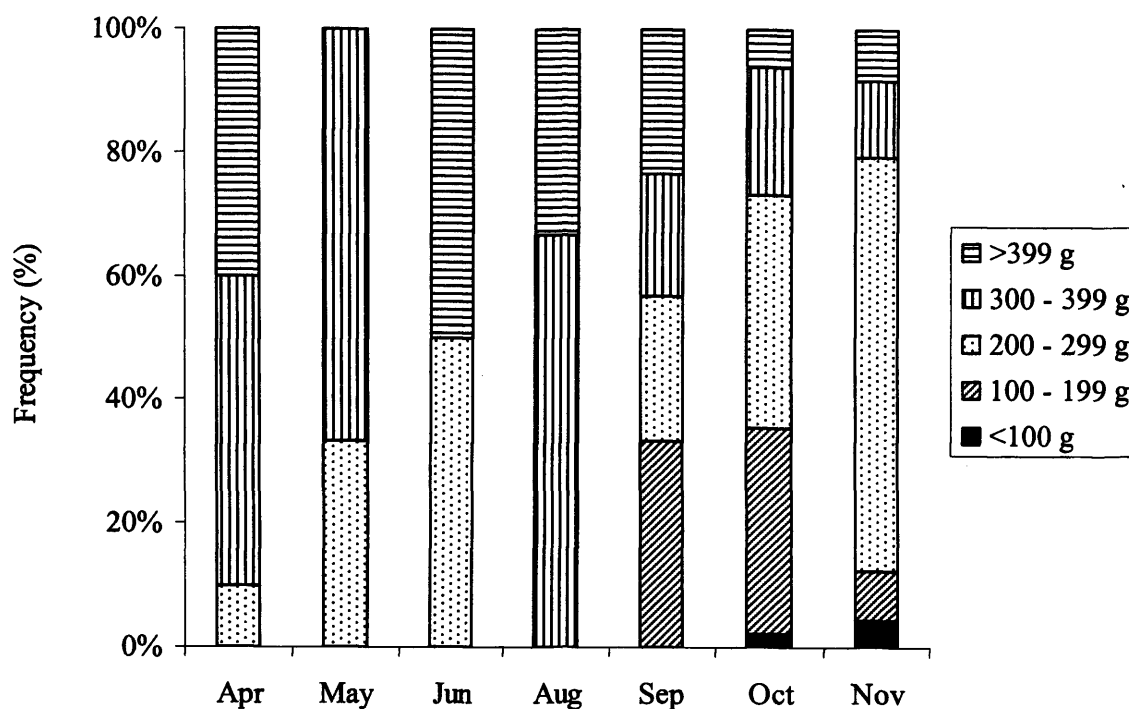


Figure 2.5 Monthly proportion of rat body weight classes on three farms.

There was a significant difference in the proportion of male and female rats in body weight classes and head and body length classes (Table 2.4). There were more males in body weight classes of 300 – 399 g and >399g. For head and body size classes, the same pattern occurred with males tending to be bigger than females, which were predominantly in the head and body length class of 175 – 199 mm.

Males and females were evenly distributed among fat classes ($\chi^2 = 3.306$, $d.f. = 4$, $p = 0.508$). Rats in the larger body weight classes predominated in the higher fat classes (Table 2.5). Rats in the lower body weight classes did not show a consistent pattern, though there was a positive correlation between body weight class and fat class for the whole population (Spearman's correlation, $r_{1,119} = 0.262$, $p < 0.004$).

There was a significant difference in fat classes among months, showing that the body condition of rats varied over the trapping period (ANOVA, $F_{6,119} = 6.12$, $p < 0.001$) (Figure 2.6).

Table 2.4 Percentage of male and female rats from three farms in body weight and head and body length classes.

Body weight classes (g)*	% male	% female	Head and body length classes (mm)**	% male	% female
<100	0.00	3.70	100 – 124	0.00	1.85
100 – 199	14.92	33.33	125 – 149	3.03	3.70
200 – 299	29.85	37.04	150 – 174	12.12	14.81
300 – 399	34.33	16.67	175 – 199	16.67	48.15
>399	20.90	9.26	200 – 224	46.97	18.52
			225 – 249	21.21	12.96

* $\chi^2 = 21.948$, $d.f. = 4$, $p < 0.01$

** $\chi^2 = 34.833$, $d.f. = 5$, $p < 0.01$

Table 2.5 Percentage of rats caught by fat class and by body weight class from three farms.

Body weight class (g)	0	0.5	Fat class 1	2	3
<100	0.0%	0.0%	0.0%	1.6%	0.0%
100 – 199	0.0%	2.5%	8.4%	7.5%	5.0%
200 – 299	0.8%	2.5%	5.8%	8.4%	15.8%
300 – 399	2.5%	0.8%	5.8%	8.4%	9.2%
>399	0.0%	0.0%	2.5%	5.0%	7.5%

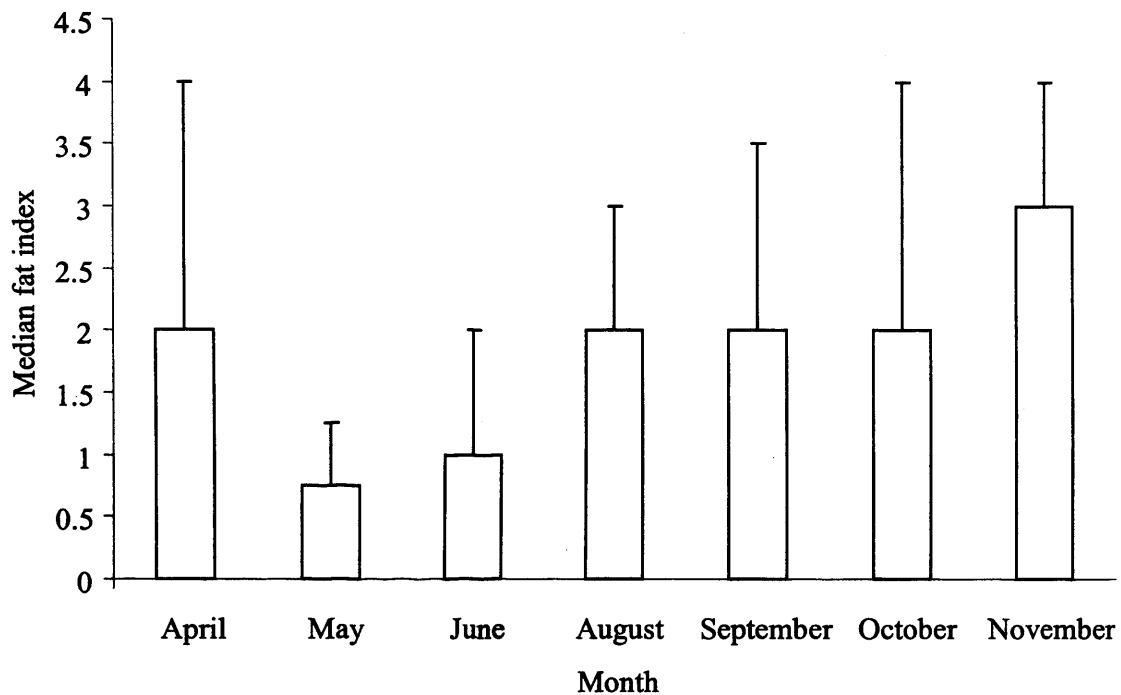


Figure 2.6 Monthly median fat index of trapped rats. Error bars are inter-quartile range.

2.3.2. Reproduction

Based on visual inspection, sexually mature (scrotal) males were caught during every month of the trapping period, though the frequency varied seasonally, with peaks in April and September. Immature males (non-scrotal) appeared from June and gradually increased towards the end of the trapping period, while at the same time the number of mature males decreased (Figure 2.7), reflecting the peak of breeding during the summer. The highest proportion of males were in the high body weight classes and in the high fat categories (Table 2.6). Males were not observed to mature until they were in the size range of 200 – 299 g.

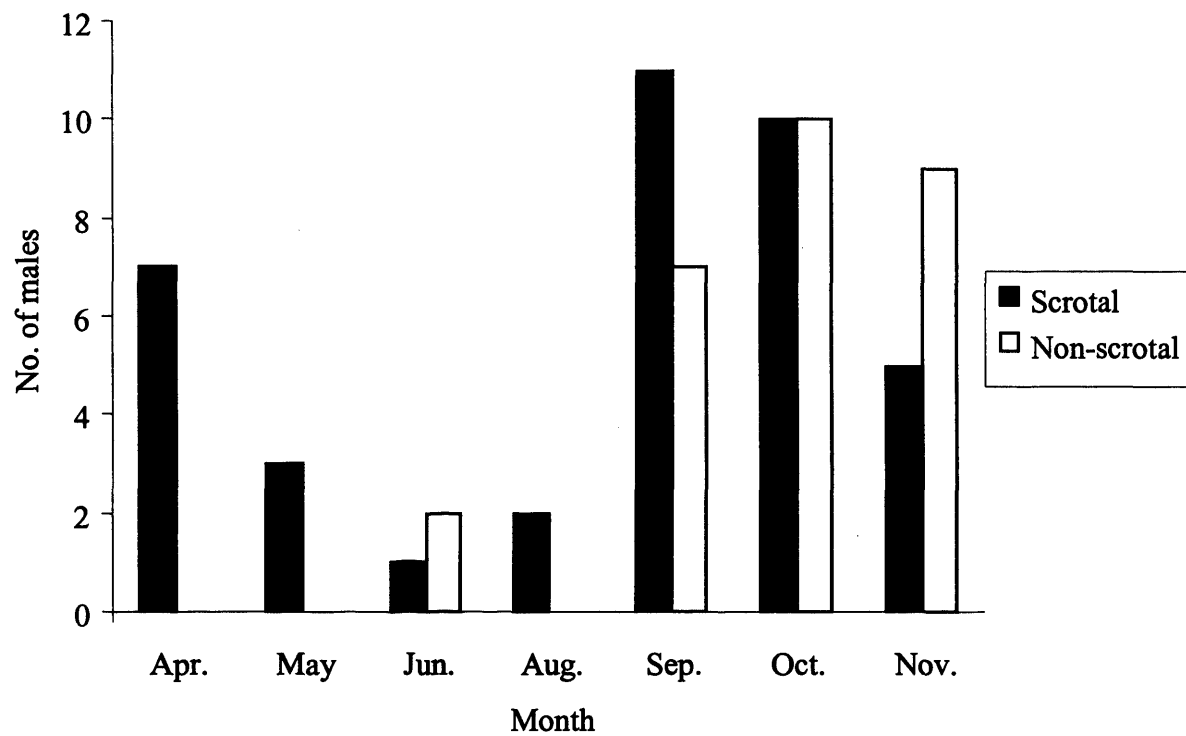


Figure 2.7 Monthly number of scrotal and non-scrotal rats caught from three farms.

Table 2.6 Proportion (%) of sexually mature males by fat class and body weight class from three farms.

Body weight class (g)	Fat class				
	0	0.5	1	2	3
<100	0	0	0	0	0
100 – 199	0	0	0	0	0
200 – 299	0	0	25	43	17
300 – 399	100	0	100	100	63
>399	0	0	100	100	100

Table 2.7 Proportion (%) of sexually mature females by fat class and by body weight group from three farms.

Body weight class (g)	Fat class				
	0	0.5	1	2	3
<100	0	0	0	0	0
100 – 199	0	0	0	0	0
200 – 299	0	100	33	33	25
300 – 399	0	0	67	100	67
>399	0	0	100	100	100

Overall males had a mean testicular weight of 1.24 ± 0.08 g. There was a significant positive correlation between testis weight and body weight (Pearson's correlation, $r_{62} = 0.858$, $p < 0.001$). Males less than 200 g in body weight had testicular weights of <0.6 g and were sexually immature.

Fecund females (i.e. pregnant or lactating) were encountered in all months where females were trapped, but with peaks of 50% in April and June (Figure 2.8), the proportion decreasing as more non-fecund individuals appeared in the population (Figures 2.7 and 2.8). Fecund females showed the same pattern as males, with more fecund females found in higher body weight and fat categories. Sexual maturity in females was observed in the 200 – 299 g class and greater, with no sexually immature females >399 g in body weight (Table 2.7). In contrast to male rats, immature or non-fecund females were found in all months, where females were caught.

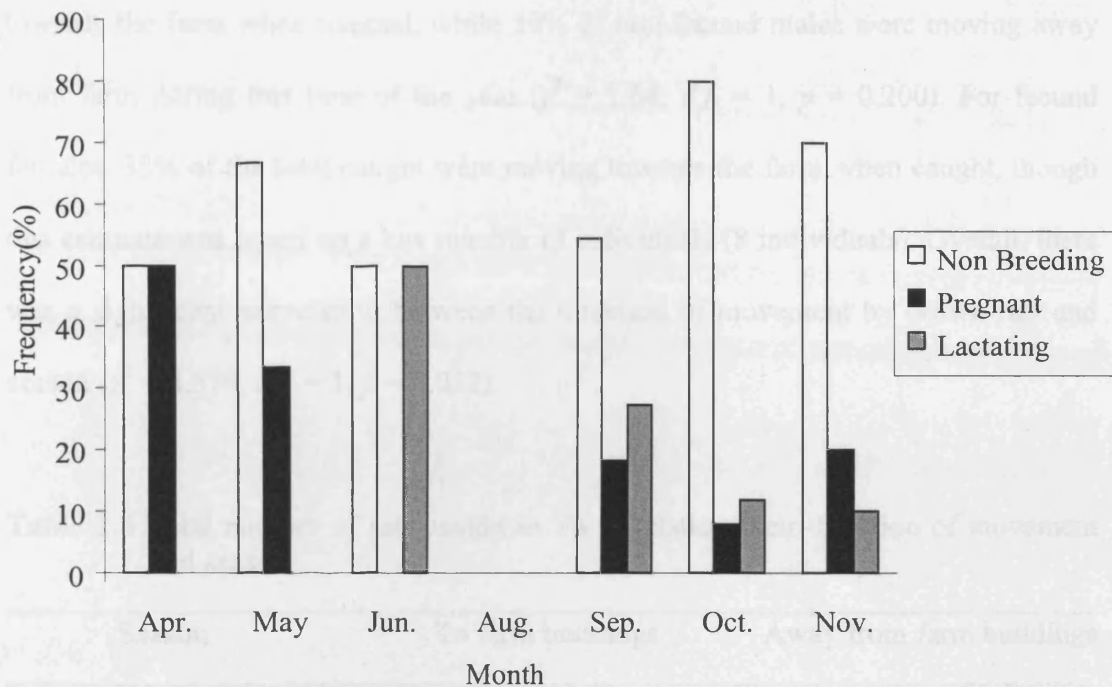


Figure 2.8 Monthly proportion of reproductive condition of female rats from three farms.

2.3.3. Movement direction of trapped rats

The direction of movement of trapped rats could be estimated based on their head and body position. Rats showed a seasonal difference in direction of movement. In spring, rats predominantly moved away from farm buildings (70%), whilst 30% moved towards farm buildings. In autumn, rats predominantly moved towards farm buildings (57%) (Table 2.8). During spring trapping, 79% of males were moving away from farm buildings when trapped. In female rats, their movement direction was equivalent, with 50% moved into the farm and 50% moved out from the farm.

During autumn trapping, 54% of males were moving into farm buildings, compared to 61% of females. The majority of mature males (67%) ($\chi^2 = 11.6$, $d.f. = 1$,

$p = 0.001$) and non-fecund females (68%) ($\chi^2 = 13.0$, $d.f. = 1$, $p < 0.001$) were moving towards the farm when trapped, while 59% of non-fecund males were moving away from farm during this time of the year ($\chi^2 = 1.64$, $d.f. = 1$, $p = 0.200$). For fecund females, 38% of the total caught were moving towards the farm when caught, though this estimate was based on a low number of individuals (8 individuals). Overall, there was a significant association between the direction of movement by brown rats and season ($\chi^2 = 4.574$, $d.f. = 1$, $p = 0.032$).

Table 2.8 Total number of rats caught in TS in relation their direction of movement and season.

Season	To farm buildings	Away from farm buildings
spring	6	14
autumn	47	36

2.3.4. Video monitoring of rat activity

Overall rat activity was relatively low. The total number of rats sighted each day using continuous surveillance ranged from 0 to 31 with a mean (sem) of 5.1 (0.81) sightings per day (Figure 2.9). There was no significance difference (ANOVA, $F_{2,54} = 0.14$, $p = 0.865$) in rat level of activity in August, September and October.

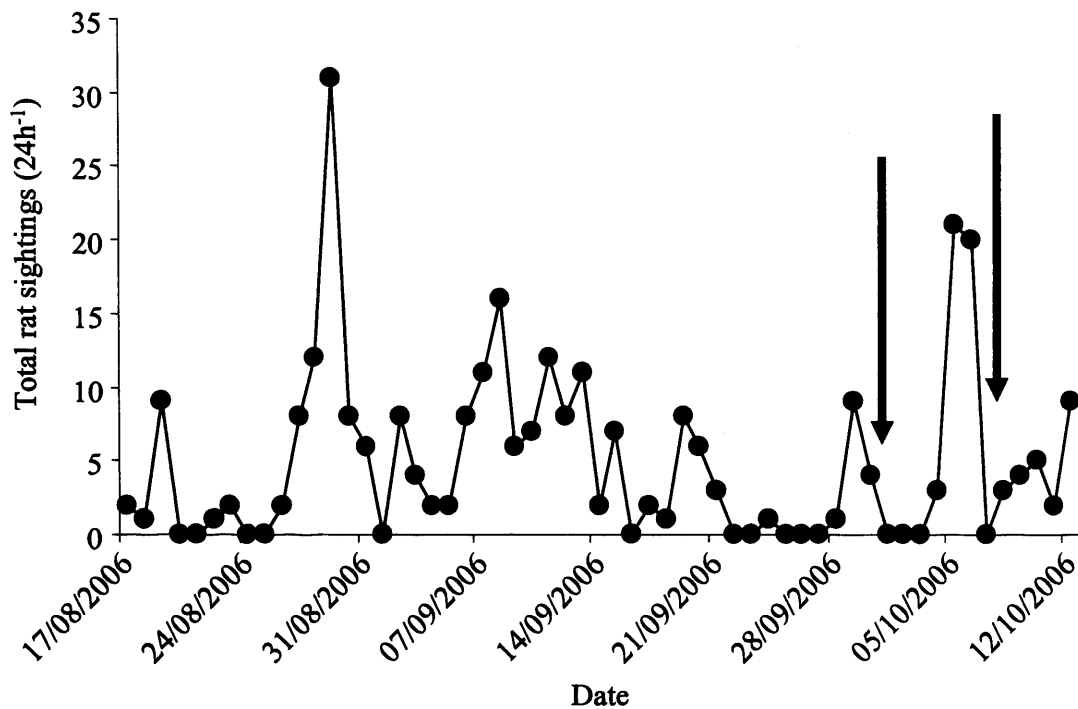


Figure 2.9 The total number of rats that can be spotted through screen monitor in observation area. Arrows indicate the day that a cat was spotted.

Weather conditions did not have a significant impact on rat activity. A comparison between still and windy conditions showed no significant difference in the number of rat sightings (ANOVA, $F_{1,61} = 0.01$, $p = 0.909$).

Total rat activity varied significantly at different times of the day (ANOVA, $F_{3,164} = 11.32$, $p = 0.01$). Rat activity was greater during daylight (between one hour after sunrise and one hour before sunset) and night (between one hour after sunset and one hour before sunrise) compared with dusk (between one hour before sunset and one hour after sunset) and dawn (between one hour before sunrise and one hour after sunrise) (Figure 2.10). However, a comparison of the rate of rat activity based on number of rat sightings per hour (rate), showed there was no significant difference among time periods (ANOVA, $F_{3,164} = 2.20$, $p = 0.09$) (Figure 2.11).

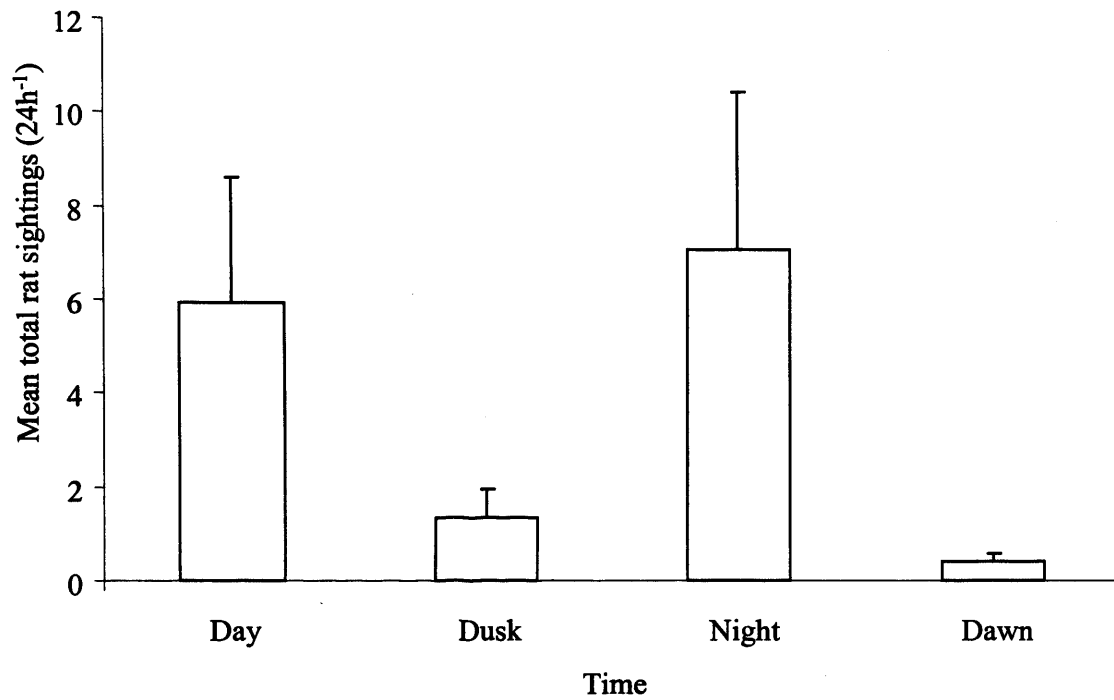


Figure 2.10 Mean total rats sightings. Error bars are 1 sem.

The level of rat activity varied temporally (ANOVA, $F_{23,984} = 2.31$, $p < 0.001$; Figure 2.12). There were two peaks of diel activity. One was around midnight and another at early dusk. The lowest activity level was recorded at dawn.

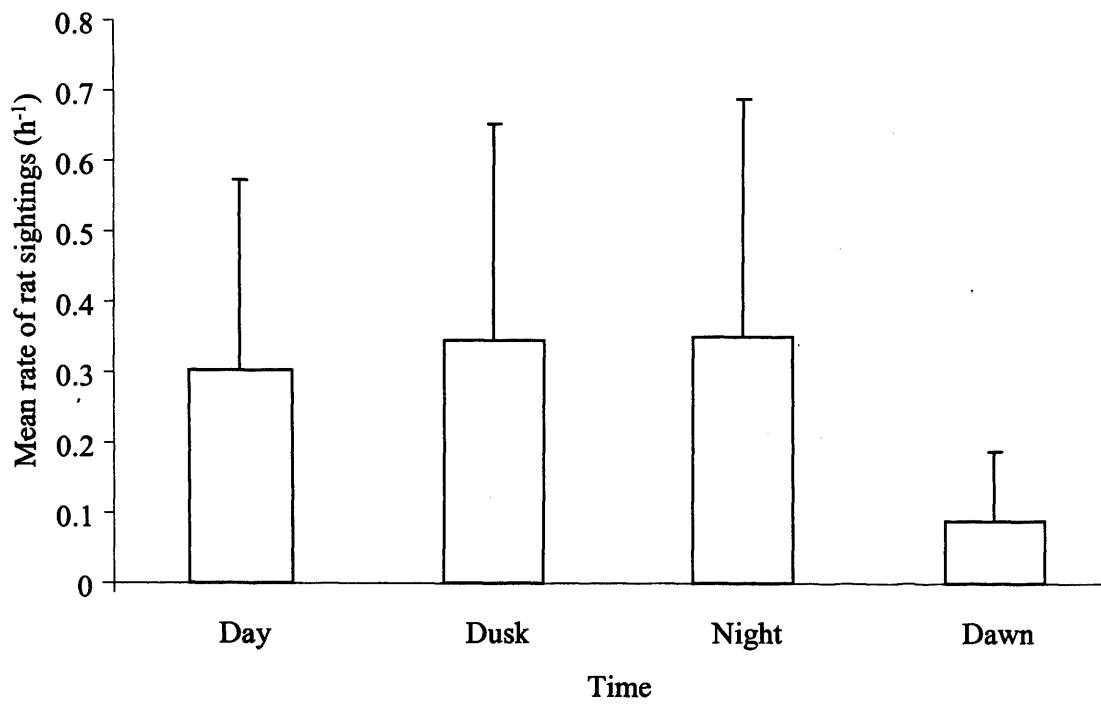


Figure 2.11 Mean rate of rat sightings. Error bars are 1 sem.

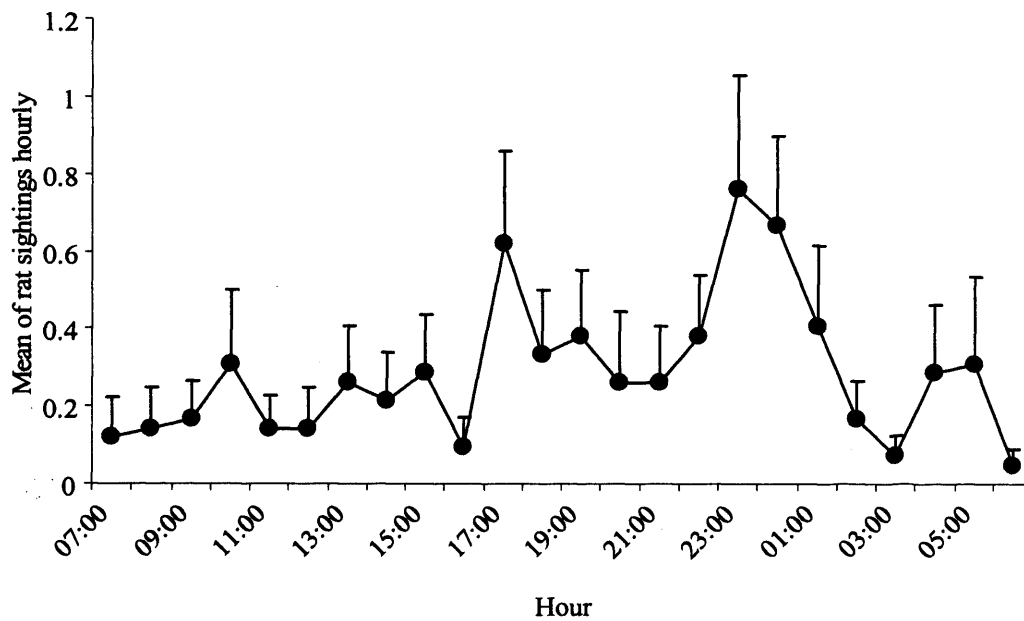


Figure 2.12 Temporal variation in rat activity. Error bars are 1 sem.

The direction of movement of rats based on video observations showed no significant difference among direction categories (D1 to D6) (ANOVA, $F_{5,257} = 1.45$, $p = 0.206$). There was no significant difference in the rate at which rats entered or left (D1 – D4) or avoided (D5 – D7) the TS whether the trap was set or not (unpaired t-test, $t_{29} = 0.042$, $p = 0.649$) (Figure 2.13).

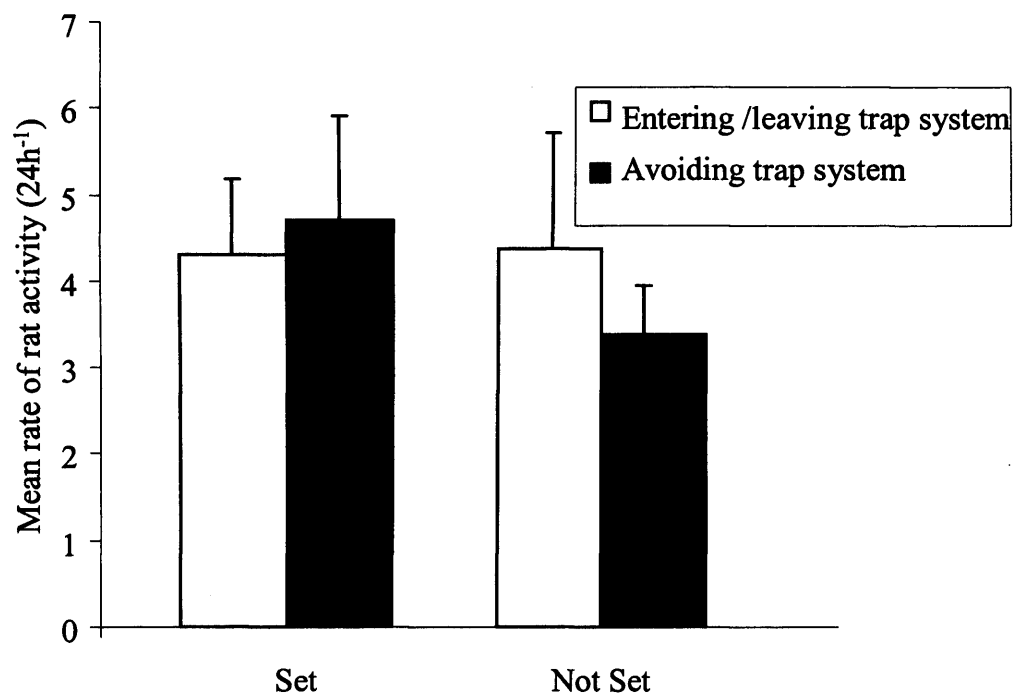


Figure 2.13 The rate of rats using or avoiding the TS when Fenn traps were set and not set. Error bars are 1 sem.

2.4. DISCUSSION

2.4.1 Population structure

The farm sites chosen selected for this study were not heavily infested with rats. The differences in population abundance may be related to farm-management practices and the surrounding environment. From this study, there was a significant correlation

between the number of rats and some features of the landscape. Trap systems at Farm A and Farm B were sited between planted crops or farm buildings. In contrast, those at Farm C were sited between grazing fields and the trap catch was significantly lower compared with the catches from Farm A and B. Many studies have shown that the abundance of rodent communities is strongly associated with plant growth form and foliage density (Rosenzweig & Winakur, 1969; Dueser & Porter, 1986; Vernes, 2003; Alain *et al.*, 2006) and the same appears to be the case with rats. A study by Fitzgibbon (1997) on wood mice and bank voles showed that their populations were strongly influenced by the landscape, especially the types of crops grown in surrounding fields. In this study, grain crops appear to enhance rat population size. However, only three sites were investigated in the present study and greater replication would be needed to confirm this finding.

Kendall (1984) reported that the sex ratio of brown rats trapped in his study was female biased overall. The sex ratio tended to be male biased in winter and to be more female biased in summer. His observation was explained by the argument that the sex ratio was controlled by dominant males, which forced subordinates out of favourable into less favourable habitats. Consequently, male rats tended to be the more numerous in less favourable habitats, such as hedgerows (Bishop & Hartley, 1976), leaving the females rats to occupy more favourable habitats, such as farm buildings and refuse dumps.

In this study there was no significant difference in the sex ratio of rats caught during the trapping period. Davis (1951c) showed that there were more males in an increasing population compared to a stationary or decreasing population, though these

slight differences were not significant. According to Bishop & Hartley (1976), females are caught less frequently than males, perhaps because they are less active and therefore less likely to enter traps when they are pregnant or lactating. Differences in sex ratio may also arise because of differential mortality rates between the sexes. Aars & Ims (2002) studied tundra voles (*Microtus oeconomus*), and found that the population tended to be female biased in the spring. They attributed this result to the survival rate of males being lower than that of females, due to their larger body mass. During the present study, no extreme weather was experienced. Variation in seasonal abundance of rats was probably mainly due to the appearance of young rats (based on their body weight and non-reproductive condition). Therefore, population change in this study was probably due to reproduction rather than large scale migration. The study populations may have been centered around the hedge base (Bishop & Hartley, 1976). The pronounced increase in rats caught in autumn might also be due to the timing of the cereal harvest, when rats are forced into the hedgrows by the reduction in the amount of shelter when crops are harvested (Brodie, 1981).

Body condition can be indicated by fat level and body mass. Bishop & Hartley (1976) demonstrated that body size and age are correlated. The same relationship has been shown in *Rattus rattus* and *Mus musculus* (Miller & Miller, 1995). In the present study, the appearance of young rats was clearly shown in Figure 2.5. Rats in the body weight group <100g were trapped only in October and November, and the number of rats in body weight group of 200 – 299 g increased progressively from September to November. Young rats have little stored fat compared to older individuals. From this study, it appears that males and females matured at a greater weight, as evidenced by the high proportion of males and females in the largest weight class (Table 2.6 & 2.7).

More non-fecund individuals emerged during October and November (Figure 2.7 & 2.8), but the median body fat index remained high at this time of the year. This result was due to a large number of females in the body weight category of 200 – 299 g being caught and they displayed a relatively high fat content. The trend seen in body condition over the study period was correlated with body weight, therefore the accumulation of fat was not only seasonal but also increased with age. Males and females rats followed the same pattern of increase in body weight and fat. It is possible that most females refrain from breeding during October and November in order to maintain good body condition and to enhance survival during unpredictable periods of cold weather.

It is not uncommon for male rats to have a larger body size than females. Overall mean body weight for male rats was 307 g and for females 233 g. There is evidence that growth slows and weight stabilizes when rats reach a weight of 300 g (Bishop & Hartley, 1976). Sexual dimorphism in body size is widespread in the animal kingdom. Usually dominant males show the largest body size. Larger body size is an advantage in intra-sexual competition but can be energetically costly (Scantlebury *et al.*, 2006). Male rats in this study did not exhibit maturity until relatively late in life. A median body weight of mature males was 360 g. This corresponds approximately to an age of seven months (Bishop & Hartley, 1976). Testis weight showed a strong correlation with male body weight and is another parameter closely linked to fecundity. The median body weight of breeding females was 300 g and the age at maturity approximately 6.5 months. Therefore, the age at which males and females become mature appears not differ greatly. This age estimate is much greater than the age of 8 to 12 weeks proposed by Meehan (1984). Bishop &

Hartley (1976) found that the median weight of rats that were pregnant or had been pregnant was 235g. According to Butler & Whelan (1994), the differences that can occur between populations may be attributed to several factors, including population density, position in social hierarchy and quality of available food, and are a reflection of genetic heterogeneity or phenotypic variation in growth rates resulting from local conditions (Glass *et al.*, 1988). Previous studies have shown that rat body weight and size varies among populations in different habitats. Davies (1951a) found that city rats were heavier than farm rats and Glass *et al.* (1988) also showed that urban rats were significantly heavier than parkland rats. In this study fecund rats were found to be in the heavier body weight and fat classes, suggesting that reproductive maturity may depend on body condition as is common in other mammals.

Data on the reproduction of females indicated the potential rates of population increase. In this study, pregnant and lactating females were trapped in every month of trapping except August, when no females were caught. It appears that breeding occurs in every month of the year although it is less common in the winter months. Young rats were not trapped in April, May, June and August but the presence of lactating females in the population during June and September indicates that births took place from May to August. The appearance of young, low body weight rats (100 – 199 g) during September supports this pattern of reproduction. Relatively low numbers of breeding females in the study populations suggests that female reproduction may have been constrained to some extent. According to Bishop & Hartley (1976) hedgerow rat populations are less productive compared to farm populations, which may reflect the quality of their habitat and food availability.

2.4.2 Direction of movement into or out of farms

Huson & Rennison (1981) demonstrated that food supplies were the main factors that influenced rat movements and their infestation of farm buildings. Evidence from the present study supports their finding; rats appeared to move into the immediate vicinity of farm buildings during autumn but moved back into field areas in spring. Though the method used here was relatively crude, it gave a broad picture of rat movements in an agricultural landscape. A study of food availability in relation to farm buildings and field habitats is addressed in more detail Chapter 4.

The direction of movement by male rats was more seasonal than that of females. One notable pattern was that a high proportion of fecund males and non-fecund females that moved towards farm buildings during autumn. At the same time, a high proportion of non-fecund males moved away from farm buildings. One possible explanation is that during autumn more rats are searching for better quality habitats for breeding purposes and mature males (usually more dominant) drive out young and non-fecund males from farm buildings to less favourable habitats. Observations by Klemann & Pelz (2006) showed that male rats tend to be more aggressive when resources are limited. Arakawa (2006) showed that an increase in the rate of active exploratory behaviour is inhibited by the establishment of social relationship among adult rats, while a decrease in activity is primarily an effect of subordination. In complex dominance hierarchies, fighting is reduced and avoidance is preferred (Scott, 1966). The pattern of breeding in females was less clear. However, pregnant and lactating females are usually restricted in their range of movement (Bishop & Hartley, 1976).

2.4.3. Rat activity by video surveillance

In this study, data for rat activity are potentially pseudoreplicated since it was impossible to identify rats individually from video footage. The measurement of activity is used as an index of activity for the population only, and is not an estimate of population size. Recordings showed no sign of neophobia towards the trap system by rats. The trap system was built six months before video surveillance study began thus recordings were likely to provide an unbiased view of the normal daily activity.

Still and windy weather had no effect on rat activity in the study area. However, there was no sign of rat activity during rain, even though this species is commonly associated with water. Recht (1988) also noted that brown rats usually ceased their activity above ground during rain. The overall level of rat activity based on video monitoring was relatively low (Brakes, 2003). This situation may be related to a small population inhabiting the area. Based on trapping results, the trap system monitored by video yielded the highest number of rats caught in spring and autumn; i.e. 30% and 22.9% of the total catch respectively, thus the number of rats in the immediate vicinity of where recording took place did not appear to have been low. Another factor that might have affected their activity could be associated with the activity of farm cats in the area. The monitoring area was less than 50 m from farm buildings and several domestic cats lived in the farm area. Video images showed two incidences of cats trying to enter the tunnel system. A study by Bramley *et al.* (2000) demonstrated that rats showed strong aversion to predator odour. Field and laboratory studies also show that predator odours have distinctive behavioural effects that include (1) inhibition of activity; (2) suppression of non-defensive behaviours such as foraging, feeding and grooming; and (3) shifts to habitats or secure locations where

such odours are not present (Apfelbach *et al.*, 2005). Thus, although rats were clearly present in the area, their level of activity may have been constrained due to the presence of potential predators.

The activity of brown rats outside burrows is generally nocturnal and normal activity is at a minimum during daylight hours, with feeding in particular a mainly night-time activity (Meehan, 1984). In this study, there were two main peaks in activity from 17:00 – 18:00 and 23:00 – 24:00 hours. However, rat activity was not confined to darkness; 44.7% of rat activity was observed during the day and dusk (1 hour before sunset). Brown rats can change their behaviour to a diurnal phase to avoid competition (Recht, 1988). Changes in food availability, risk of predation and seasonal changes can cause shifts in the timing of animal activity (Alcock, 2005). Webster (2001) reviewed the effect of *Toxoplasma gondii* infection on behavioural changes in brown rats and showed that the pathological condition causes an increase in rat activity. Infection also reduced the normal aversion to cat odour, which instead became a mild attractant (Berdoy *et al.*, 2000; Vyas *et al.*, 2007). A study of the feeding patterns of brown rats on a farm by Klemann & Pelz (2006) also showed that rats frequently forage during the day.

The direction of rat movements based on video observations showed no consistent pattern. In this respect video monitoring at a single trap system was less informative than trapping, which gave broad patterns of seasonal movements. Video monitoring of rat activity was on a relatively small scale and data derived in this way probably only gives an indication of local exploratory movements. Brown rats live in a relatively small home range and their exploratory behaviour is usually confined to

their nest or breeding area so, their movement patterns are localized (Davies, 1953). Lambert (2003) and Brown (2007), however, have shown occasional long-distance movements using radio telemetry, which cannot be detected using the video monitoring system adopted here.

2.4.4. Implications of rat behaviour for control measures

Rapid learning about their habitat and surroundings has been key to the success of the brown rat. In this study trapping was conducted at the same time as video monitoring. Brown rats can learn from observation to avoid contact with potentially dangerous objects that threaten conspecifics (White & Galef Jr., 1998). In this study rats were able to observe their conspecifics trapped in a tunnel system. Video footage showed that some rats appeared to avoid entering the tunnel when another rat was already caught in a Fenn trap. Unfortunately, a direct correlation between the time rats were caught and avoidance behaviour by conspecifics cannot be made. However, there was no significant difference in the direction of rat movement when traps were set and not set. These results indicate that trapping did not significantly change rat behaviour, suggesting that the presence of already trapped rats in a funnel system may not strongly affect subsequent catch success.

Many control programmes have failed due to a lack of knowledge of rat behaviour. For example, rats are known for their avoidance of novel objects in natural conditions (Inglis *et al.*, 1996; Priyambodo & Pelz, 2003). Rats frequently reject poison baits newly introduced to them because their sense of smell is good and they tend to avoid new objects in their environment. Baits may also not be palatable because of the taste and odour. Shumake & Hakim (2000) found that carbon

disulphide at 10 ppm had a potential attractant effect on rats. Consumption levels were significantly different between control baits and treated baits, thus improving baiting efficacy for acute doses. Inglis *et al.* (1996) investigated the foraging behaviour towards novel foods and food containers. They found that rats were more neophobic to new food containers rather than to new foods, suggesting that bait containers should be left in place as a permanent part of the environment for poisoning. In contrast to the usual assumption, Pisula *et al.* (2006) showed that, under low stress conditions, rats demonstrate a positive response towards novelty.

Brown rats are social animals and they can obtain information from conspecifics through observation and communication. Adult rats emit ultrasonic calls (22-kHz), which may serve as alarm calls, and are used in situations associated with threats or distress (Brudzynski, 2001). However, the relationship between alarm call duration and the magnitude of risk needs further investigation (Brudzynski, 2005). More research and understanding of rat behaviour is crucial because misinterpretation of their natural behaviour could delay the impacts of rat-control programs. For now, correct placement of baits (Endepols *et al.*, 2003) in suitable amounts, proofing, use of traps and good housekeeping (removing harbourage and spilled food) are likely to remain fundamentals of effective rodent control.

2.5. SUMMARY

1. The distance of trap systems from farm buildings and tunnel width did not affect trapping success. There was a positive correlation between the number of rats caught and where the trap systems were sited.
2. Brown rats were not evenly distributed among farms in the study area. More rats were trapped during autumn than spring, a total of 125 rats were trapped during both trapping sessions.
3. Fecund individuals were caught in every month during the trapping period, suggesting that individuals in the study populations breed continuously throughout the year. There was a significant difference between the weight of male and female rats, with males heavier than females. The median body weight of sexually mature males was 360g and the median body weight of fecund females was 300 g.
4. Body fat levels increased with age. Young rats predominated in the low-fat groups while older rats predominated in the higher fat groups. Fecund females (pregnant or lactating) were found in heavier weight and fat classes.
5. Rats were predominantly caught moving from farm buildings towards the fields during the spring and predominantly moved from fields into farm buildings during autumn. More fecund males moved into the farm during spring accompanied by non-breeding females.

6. Video monitoring of a single trap system provided evidence that rats are active during both day and night. The level of activity was relatively low in this study with an average of 5 sightings per day. Their direction of movement was not consistent.

7. Trapping appeared not to change rat behaviour.

Chapter 3: Seasonal Changes and Distribution of Brown Rats in Leicestershire:

Interactions with Small Mammal Populations

3.1. Introduction

Small mammals include small rodents and insectivores with an adult live body weight of up to about 120 g (Delany, 1974). Because of their size, these animals can conceal themselves from predators and have ready access to a wide number of food sources. They are able to take full advantage of microclimates in their environment and show a polyestrous pattern of reproduction. However, they also face high energy costs, especially in cooler regions and high energetic costs of locomotion; the cost of running a given distance is higher for small mammals than for large one. For example a horse can move one gram of its body weight over one kilometre more cheaply than a mouse (Bourliere, 1975).

The ecological role of small mammals in temperate forests, grasslands and cultivated fields had been discussed in detail by Golley *et al.* (1975). They grouped the impacts of small mammals into four main categories: (1) those concerned with destruction of an ecosystem component by mammals; (2) those concerned with movement of materials or components by mammals; (3) those concerned with alteration of the environment; and (4) those concerned with other consumers, especially predators.

Small mammals are often considered as pests on agricultural land. The damage they inflict can occur at all stages of crop development; by digging up newly planted

seeds, cutting tillers, destroying roots, direct grazing or consuming developing grain as the crop matures and reducing seed regeneration. In temperate regions small mammal pests can be divided into two main groups; those occurring mainly in woodland and those in grassland, and there are particular concerns about the impact to the latter (Wood, 1994). For example, the house mouse can cause severe damage to crops. According to Brown *et al.* (2007), the majority of damage by mice occurred around the time of emergence of the crop when mouse densities were >100 mice ha^{-1} with 12.4 % of the crop damaged. In Australia, outbreaks occur approximately every four years with as high as >800 mice ha^{-1} , which can have significant impact on the livelihoods of farmers (Singleton *et al.*, 2005). Their reproduction appears not to be strongly density dependent and one mouse population was recorded to exceed 70,000 ha^{-1} in a chicken barn (Berry, 1981).

Small mammals serve as a food resource for higher trophic level animals and play a significant role in regulating the population size of their predators (King, 1985). Microtine rodents were the main prey group of foxes (Dell'Arte *et al.*, 2007), weasels (McDonald *et al.*, 2000; Lanszki & Heltai, 2007), stoats and stone martens (Lanszki *et al.*, 1999). Avian predators, such as owls, chiefly rely on small mammal as their prey (Petty, 1999; Bond *et al.*, 2004). These predators also affect the population size of small mammals, though the effects of predators are unpredictable and may not be long lasting (Brown, 1966).

Agricultural land makes up a high proportion of the UK's countryside, comprising approximately 75 % of the land area. Consequently, competition for space among woodland species is high and they are likely to enter grassland and arable

systems. Gurnell (1985) reviewed the interrelationships among woodland rodent communities, specifically the wood mouse (*Apodemus sylvaticus*), yellow-necked mouse (*A. flavicollis*) and bank vole (*Clethrionomys glareolus*). He concluded that both species of mouse coexist with the bank vole with niche overlap limited by microhabitat, food and time partitioning. However, all three species may compete with each other when animal densities are high, and food and space can become limiting (Solomon, 1949). This interspecific competition can negatively affect the fecundity, growth or survival of competing individuals (Rosenzweig, 1981). Under conditions of high competition some animals might travel beyond their normal range and dispersal might be unavoidable (Davies, 1953). There is evidence that wood mice migrate from woodland to arable environments (Kikkawa, 1964; Green, 1979). This species is particularly mobile, especially during the breeding season, and factors that are thought to influence their home range size include season, sexual maturity, age, population density and habitat quality (Wolton & Flowerdew, 1985).

In natural habitats the brown rat has a relatively restricted distribution, though they are still responsible for the ecological degradation of natural ecosystems (Nogales *et al.*, 2006). On the granitic islands of the Seychelles, the brown rat was only caught on 1 of 9 islands surveyed (Hill *et al.*, 2003). On the other islands, the black rat (*Rattus rattus*) was trapped, and only one *Rattus* species occurred on each island probably as a result of competitive exclusion. Moors (1985) believed that potential factors that constrained rat numbers on the islands were limited food availability and cover; compared to urban and agricultural environments there was less buffering of climatic extremes and shortages of fresh water. Lack of a protein-rich diet and fresh water would lead to low reproductive output in rats. Harper *et al.*,

(2005) reported that there was a negative correlation between the abundance of brown rats and black rats on Stewart Island, New Zealand. It appeared that black rats had excluded brown rats even though brown rats have an advantage in terms of size and physiology. In the forests of south-eastern Nigeria, the brown rat is known as a ground-dwelling rodent with their distribution restricted to one of six habitat types. In this region they can only be trapped in suburbia; a strongly altered habitat type found near roads with mature trees and grassy fields (Angelici & Luiselli, 2005).

The interaction between small mammals and rats in agricultural environments is poorly documented and little is known about the way brown rats interact with small mammals, particularly in their use of farm buildings. Interspecific interactions may lead to competition if both species show similarities in foraging behaviour, especially when food is not abundant. In these circumstances competition could reduce the fitness of either one or both species. In addition, they might compete for space, particularly at high densities or at certain times of the year. If small mammal populations have the capacity to exclude brown rats through competition, this fact might be used in attempts to control rat populations. For example, small mammals may reduce the overall productivity or rate of population increase of a rat colony, thereby reducing its capacity to recover from trapping or poisoning (Lambert, 2003). This approach to rat control reflects the recognition that competition is a major ecological interaction that can effect population regulation (Begon *et al.*, 1990). Conversely, Huitu *et al.* (2004) concluded that interspecific competition in small mammal communities may not play a strong role in structuring communities compared to predation and food availability. However, in their study, conducted in western Finland, they found that field vole densities peaked at least two months earlier

than bank voles and the growth rate of bank vole populations was negatively related to increasing densities of field voles.

The effect of inter-specific interactions among rodents had been investigated previously. Wasserberg *et al.* (2006) showed that temporal partitioning occurred in the activity times of two gerbil species; *Gerbillus pyramidum* altered the time of activity of *G. andersoni* and this change in activity was the result of interference competition by *G. pyramidum*. Temporal partitioning also occurs among the desert rodents; *Acomys cahirinus* and *A. russatus*. In this case partitioning was not related to aggressive interference, instead other factors, including foraging success, predator avoidance, water conservation and productivity shifted *A. russatus* into diurnal activity (Pinter-Wollman *et al.*, 2006).

A negative interaction between an ungulate and field voles has also been observed. Steen *et al.* (2005) found that the summer population growth rate and autumn density of the field vole was lower at high sheep densities; sheep density may alter the pattern of population synchrony among voles. Merritt *et al.* (2001) showed that there were negative effects on population growth rate among six small mammals in an assemblage in the Appalachian Plateau, USA. The results were due to strong interspecific competition for food, breeding sites or for predator-free space. In another study the abundance of *Mus domesticus* was found to increase when a dominant competitor (*Akodon azarae*) was removed from crop field in central Argentina (Busch *et al.*, 2005). The study showed that the appearance of *A. azarae* could suppress *M. domesticus* productivity. Under competitive conditions, survival of female bank voles was low, the total number of breeding females was reduced, and territory size also

decreased. This study is an example of indirect exploitation competition; a decrease in fitness occurred in females bank voles when a dominant competitor, the field vole, was present (Eccard & Ylonen, 2002).

In this study the principal aim was to investigate the relationship between the spatial distribution of brown rats and small mammal populations in farm buildings and agricultural land. More specifically the questions addressed were:

1. Is the distribution of brown rats and other small mammal species the same in agricultural buildings and adjacent farmland?
2. Is there an interaction between brown rats and other small mammals species that results in a spatial separation between these two groups?

To address these questions tracking plates were used to monitor brown rat and small mammal distributions and activity. In addition, Longworth traps were used to determine small mammal assemblage composition and abundance.

3.2. Materials and Methods

3.2.1. Study site and duration of study

The study was conducted on Farm A, Leicestershire, a mixed arable and beef/dairy farm. The location of the farm and description of the study site are given in Chapter 2. An experiment was carried out in two experimental blocks simultaneously. The first experimental block was in the farm building area (termed Farm) and the second along

a network of hedgerows adjacent to an arable crop, grazing land and a disused railway track (termed Field). For the Farm and Field sites a map of each respective area was divided into a series of 100 10 x 10 m² squares (sub-blocks). For each site sub-blocks were assigned a different number to facilitate a randomised sampling design. Data collection was carried out on four different occasions, covering all seasons of the year (Table 3.1).

Anticoagulant poison (Difenacoum 0.005% w/w, Jaguar Blox[®]) was laid by farmers during the winter sampling period at the Farm site. No poison bait or traps were set during spring, summer or autumn at any time at the Field site.

Table 3.1. Dates covered by four different sampling sessions.

Season	Dates
Spring	2 nd May, 2006 – 22 nd May, 2006
Summer	6 th July, 2006 – 26 th July, 2006
Autumn	6 th November, 2006 – 26 th November, 2006
Winter	3 rd January, 2007 – 23 rd January, 2007

3.2.2. Sampling design

Fifty sub-blocks were randomly selected for sampling for each season in the Farm and Field sites. Sub-blocks were assigned to 5 groups, with sampling taking place in 10 sub-blocks simultaneously over the sampling period. In each sub-block two Longworth traps were placed randomly within the area approximately 1-2 m apart. Traps were set in the safe mode for two nights prior to trapping to overcome any neophobic reaction by small mammals. On the third day, all traps were set to live

mode. Traps were baited with grain with hay provided as bedding. Traps were checked on the following morning at approximately 0900 over two consecutive nights. Traps with a closed door were placed in a large, clear polythene bag. The trap was carefully opened and the contents inspected. All trapped animals were identified to species and their sex and location of capture recorded. Any shrews that were trapped were released immediately after identification without handling to avoid undue stress. Some of the Longworth traps have a small hole at one side allowing the shrews to escape in case of being trapped. Every small mammal was marked individually by fur clipping. The trap then was reset and returned to its original position. For wood mice, bank voles, field voles and house mice, an estimation of population size was performed using the minimum number alive (MNA) method. The figures were calculated by dividing the number of unmarked individuals captured during the trapping session by the length of area surveyed (0.5 km), giving MNA km^{-1} for every trapping session.

At the same time that Longworth traps were set in live mode, four small mammal tracking plates were also placed in each of the 10 randomly selected sub-blocks in use. Plates were placed randomly along walls or in narrow gaps where small mammals were likely to pass within 1-2 m of Longworth traps. Tracking plates comprised a white vinyl floor tile cut to a size of 100 x 200 mm and covered with adhesive book binding film. The surface had been lightly scrubbed with a sponge to prevent air bubbles being trapped between the tile and binding film and to make the surface rough. An activated carbon powder (Norit®) suspended in industrial methylated spirits (approximately $2.5\text{g } 100\text{ ml}^{-1}$) was brushed onto the plastic coated

surface. As the spirit evaporated, a thin coated carbon powder remained, which was dislodged on contact leaving highly visible footprints (Figure 3.1).



Figure 3.1: Rat footprints on carbon-coated tracking plate (Brakes, 2003).

Each plate was checked every morning and scored based on a 4-point system according to the extent it was covered by footprints, as follows: '0' = no prints, '1' = 1 – 25% of the plate covered with prints, '2' = 26 – 95% covered and '3' = 96 – 100% covered (Quy *et al.*, 1993). It is easy to distinguish between the marks made by rats and other small mammals, therefore for each plate a separate score was recorded for each group. After scoring, plates were replaced. Summation of plate scores provided a daily measure of rat and small mammal activity, from which the mean was taken for the ten days of data collection. Estimates of brown rat population size were made using the function:

$$y = 1.56x$$

Where; y is the number of brown rats, and x is the index of activity based on tracking plate scores (Lambert, 2003). Because tracking plates were placed near Longworth traps the probability of capture next to marked plates (with rat footprints) was calculated from:

$$p(m) = \frac{n}{r}$$

Where n is the number of captures next to marked tracking plates and r is the number of tracking plates marked by rats. The probability of capture next to unmarked tracking plate was then calculated as:

$$p(u) = \frac{N}{U}$$

Where N is the number of captures next to unmarked tracking plates and U is the number of unmarked tracking plates.

After two nights, all traps were moved to the next 10 randomly selected sub-blocks and the procedure was repeated as above. The traps were moved on four occasions to cover all 50 randomly selected sub-blocks. In every season, a total of 200 trap nights were completed for small mammal trapping and 400 tracking plates were examined for each block.

3.3. Results

3.3.1. Levels of activity and animal distribution

A total of 1,600 tracking plates were deployed in the Farm site and 1,520 in the Field. In the Farm, 376 (23.5%) were marked by rats and small mammals, while 1,021 (67.2%) tracking plates in the Field were marked. Of the marked plates in the Farm

site, 90.4% (340 plates) were scored as category 1, 9.3% (35 plates) as category 2 and 0.3% (one plate) as category 3. In the Field site, 83.5% (852 plates) were scored as category 1, 16.3% (166 plates) as category 2 and 0.3% (three plates) as category 3.

Based on tracking plate scores there was a highly significant difference in rat activity between Farm and Field (ANOVA, $F_{1,70} = 24.59$, $p < 0.001$), with more rat activity detected overall at the Farm site than Field (Figure 3.2). There was also a highly significant difference in rat activity among seasons (ANOVA, $F_{3,70} = 11.98$, $p < 0.001$). A Tukey's *post-hoc* test showed a higher level of activity in summer than autumn or spring (Tukey's test $p < 0.05$). There was also a significant interaction between site and season (ANOVA, $F_{3,70} = 11.90$, $p < 0.001$); rat activity levels were higher in the Farm site for all seasons except for autumn when they were higher in the Field sites.

There was a significant difference in small mammal activity levels based on tracking plate data between sites (ANOVA, $F_{1,70} = 397.34$, $p < 0.001$) and among seasons (ANOVA, $F_{3,70} = 13.11$, $p < 0.001$). However there was no interaction between sites and season (ANOVA, $F_{3,70} = 0.94$, $p = 0.428$). Activity levels were consistently higher in the Field site compared to Farm, with the highest levels of activity during autumn and winter (Tukey's test $p < 0.05$; Figure 3.3).

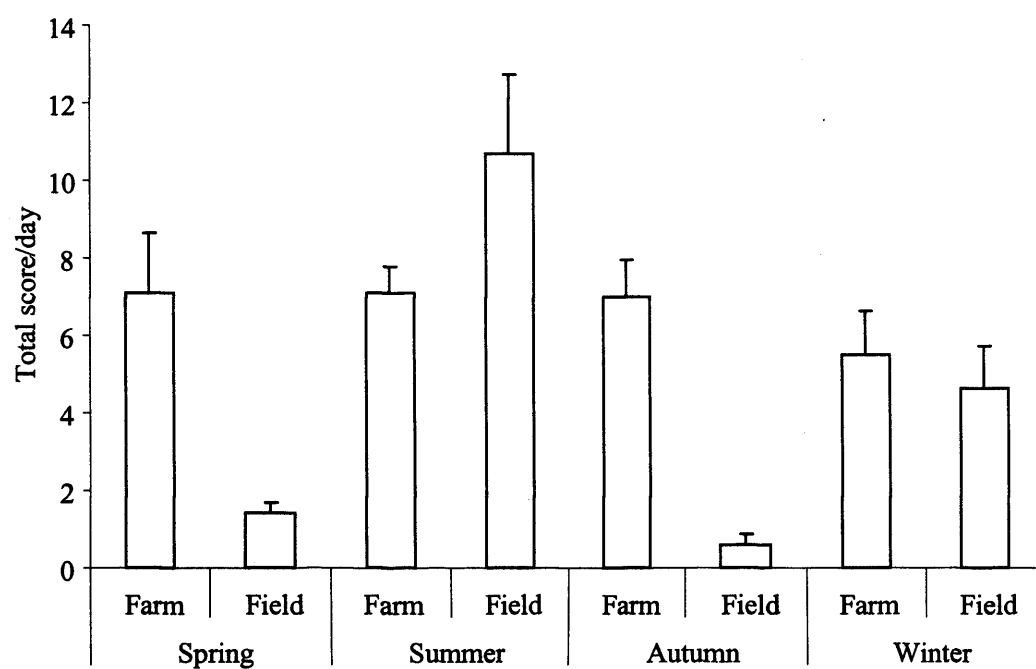


Figure 3.2 Mean (+ s.e.) daily activity score for tracking plates by brown rats laid in Farm and Field sites over four seasons. Error bars are one sem.

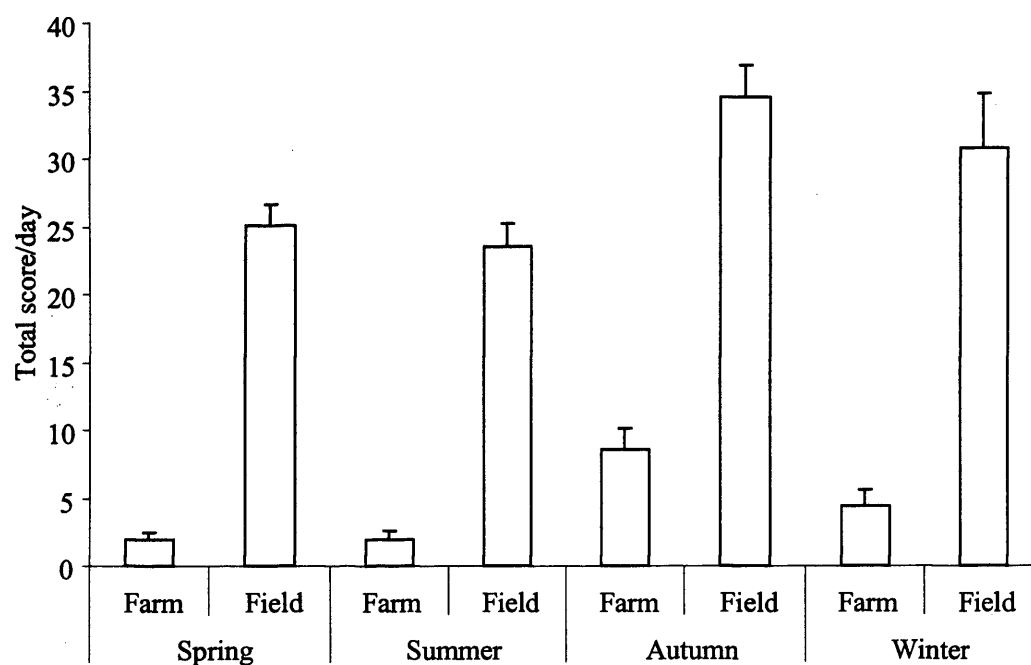


Figure 3.3 Mean (= s.e.) daily activity score for tracking plates by small mammals laid in Farm and Field sites over four seasons. Error bars are one sem.

There was a highly significant association between the number of tracking plates marked by rats and small mammals at the Farm ($\chi^2 = 41.3$, $d.f. = 3$, $p < 0.001$; Table 3.2) and Field study sites ($\chi^2 = 137.4$, $d.f. = 3$, $p < 0.001$; Table 3.3). At each site a lower than expected number of tracking plates showed rat and small mammal tracks on the same tracking plate.

Table 3.2 Seasonal numbers and proportion of tracking plates marked by rats and small mammals and by both in the Farm.

Season	Not marked	Rat only	Small mammal only	Rat + small mammal
Spring	321 (80.25%)	59 (14.75%)	18 (4.5%)	2 (0.5%)
Summer	326 (81.5%)	55 (13.75%)	14 (3.5%)	5 (1.25%)
Autumn	262 (65.5%)	52 (13%)	76 (19%)	10 (2.5%)
Winter	315 (78.75%)	41 (10.25%)	37 (9.25%)	7 (1.75%)

Table 3.3 Seasonal numbers and proportion of tracking plates marked by rats and small mammals and by both in the Field.

Season	Not marked	Rat only	Small mammal only	Rat + small mammal
Spring	162 (40.5%)	4 (1%)	226 (56.5%)	8 (2%)
Summer	140 (35%)	62 (15.5%)	177 (44.25%)	21 (5.25%)
Autumn	97 (24.25%)	2 (0.5%)	297 (74.25%)	4 (1%)
Winter*	100 (31.25%)	11 (3.44%)	187 (58.44%)	22 (6.87%)

* A total of 320 tracking plates were laid during Winter.

The results of tracking plate surveys in the Field site gave a different result from the Farm. In the Field, the majority of the sub-blocks were dominated by small mammals, where more than 90% of the sub-blocks were marked by small mammals in all seasons.

Figures 3.4 – 3.7 illustrate the sub-blocks at the Farm site where tracking plates were marked by rats, small mammals or both. More than 50% of Farm site sub-blocks had were marked in each season, except in summer when 46% of the sub-blocks yielded marked tracking plates.

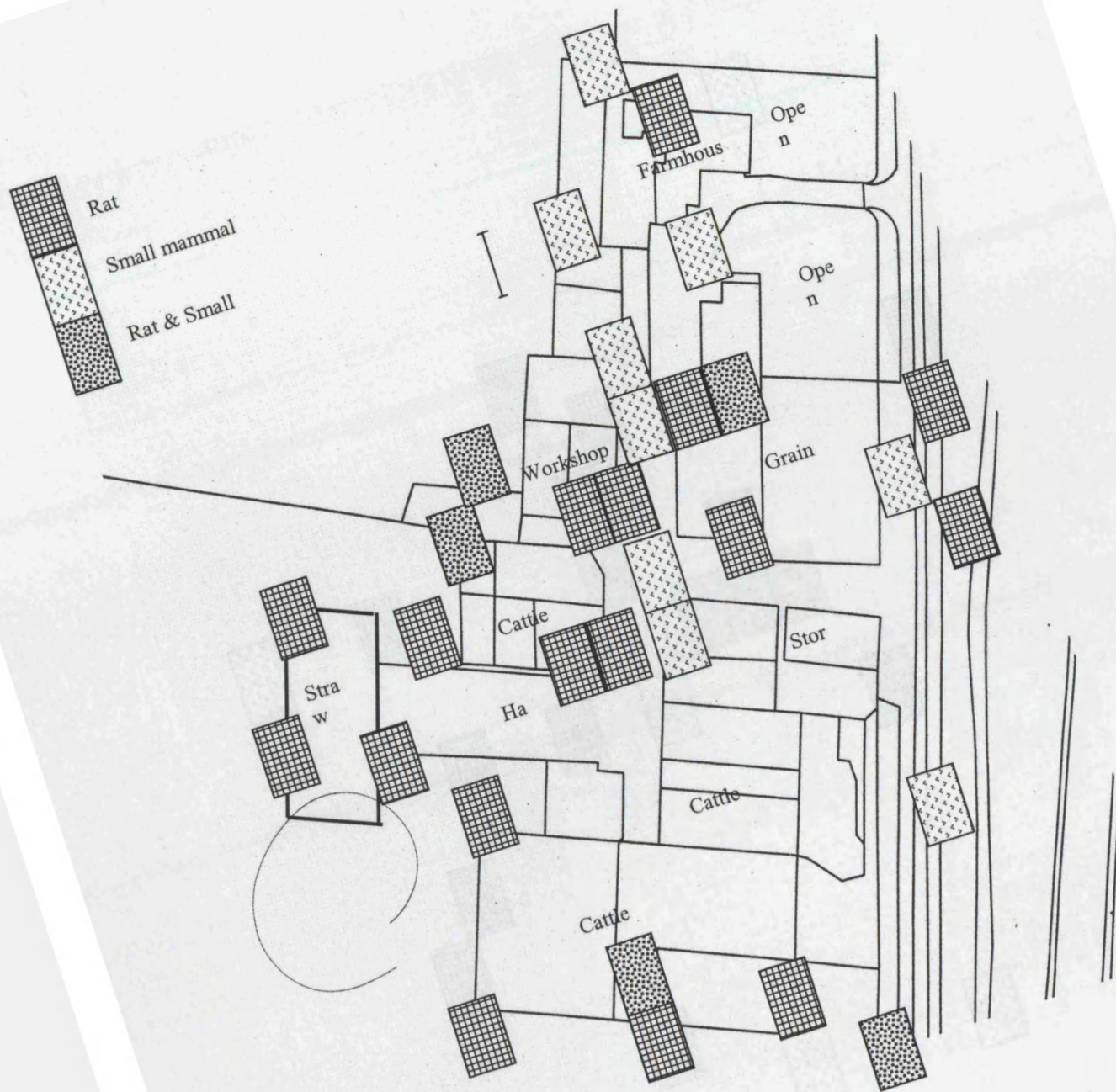


Figure 3.4 Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in spring.

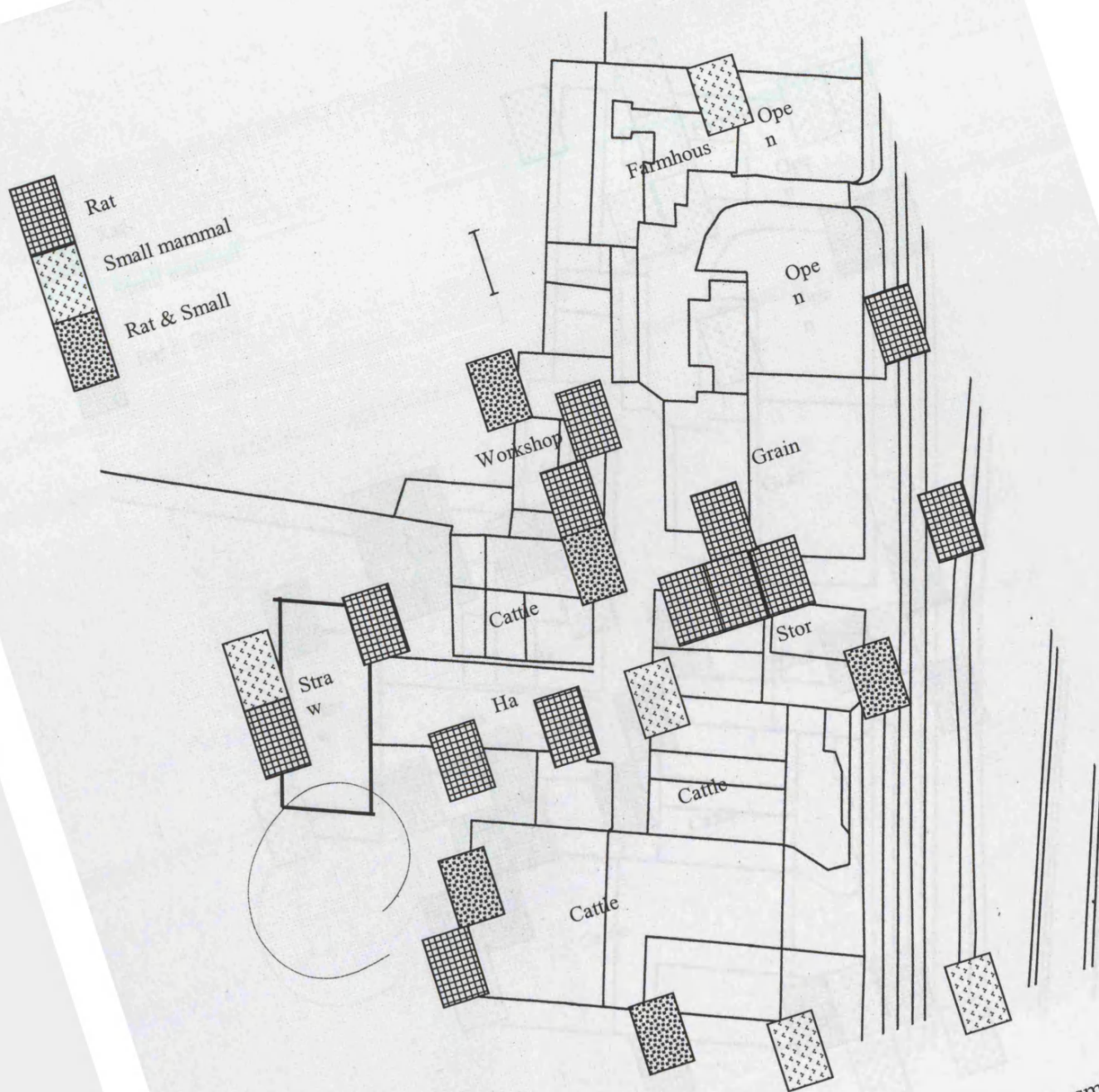


Figure 3.5 Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in summer.

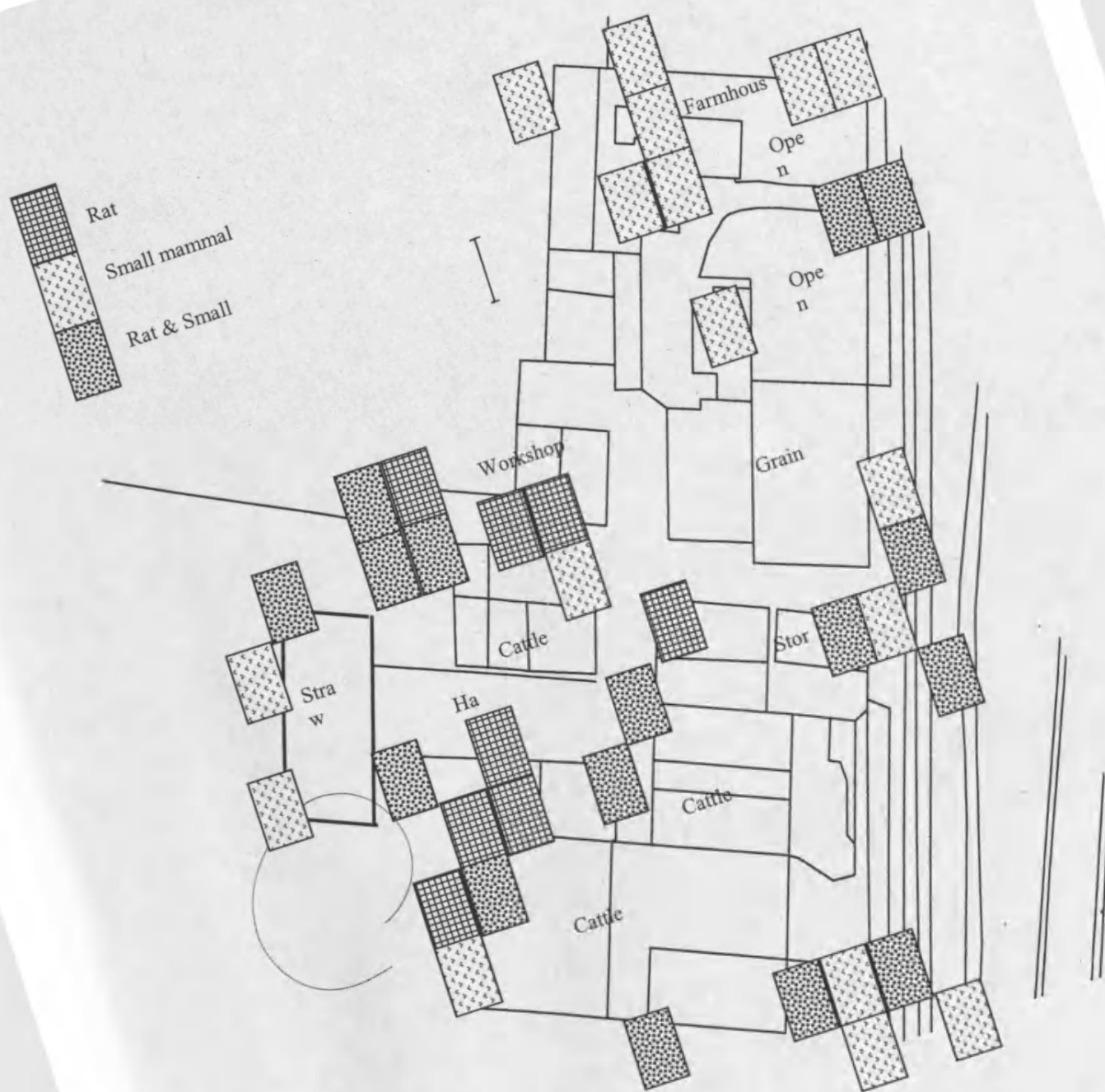


Figure 3.6 Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in autumn.



Figure 3.7 Plan of Farm site showing the sub-blocks marked by rats, small mammals or both in winter.

3.3.2 Population estimation

A total of 28 small mammals were caught at the Farm site resulting from 800 trap-nights. These captures gave an overall trap success of 3.5%. Recaptures accounted for 10.7% (3 recaptures) of the total, giving an estimate of 25 individuals from five species of small mammal: namely *M. musculus* (MM) - house mouse, *A. sylvaticus* (AS) – wood mice, *C. glareolus* (CG) – bank vole, *M. agrestis* (MA) – field vole and *S. araneus* (SA) – common shrew. *M. musculus* was the most abundant species at the Farm site.

Small mammal trapping at the Field site yielded 325 catches from 800 trap-nights. An overall trap success of 40.6%, with recaptures of 26.2% (85 recaptures) individuals. Wood mice dominated the catches of trapping sessions during spring, autumn and winter, whereas bank voles were the most abundant species in the summer (Figure 3.8). The proportion of field voles in the catch increased from Summer – winter. Table 3.4 and 3.5 show the numbers of small mammals caught in each season and the estimated numbers of brown rats (RN). The same species were trapped in the Field as the Farm except for the house mouse, which was not present in catches from the Field site. The total numbers of small mammals caught (excluding recaptures) from both study sites is illustrated in Figure 3.9.

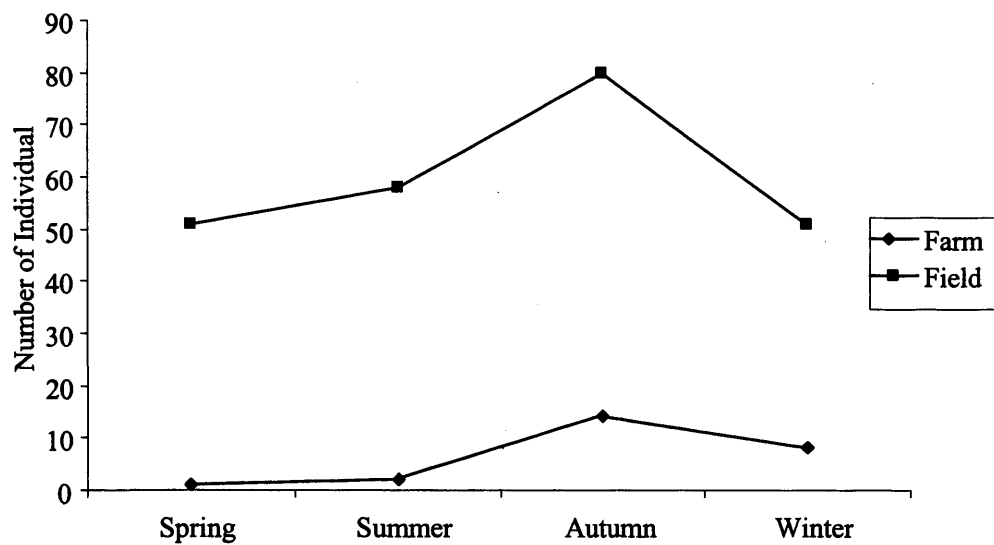


Figure 3.8 Comparison of the total numbers of small mammals caught in both study sites.

Table 3.4 The estimated numbers of small mammals (Longworth trapping) and brown rats (tracking plate) at the Farm site for all seasons. *M. musculus* (MM) house mouse, *A. sylvaticus* (AS) wood mice, *C. glareolus* (CG) bank vole, *M. agrestis* (MA) field vole and *S. araneus* (SA) common shrew.

Season	Species					RN
	MM	AS	CG	MA	SA	
Spring	2	0	0	0	0	11
Summer	2	0	0	0	2	11
Autumn	18	4	2	2	2	11
Winter	8	0	6	0	2	9

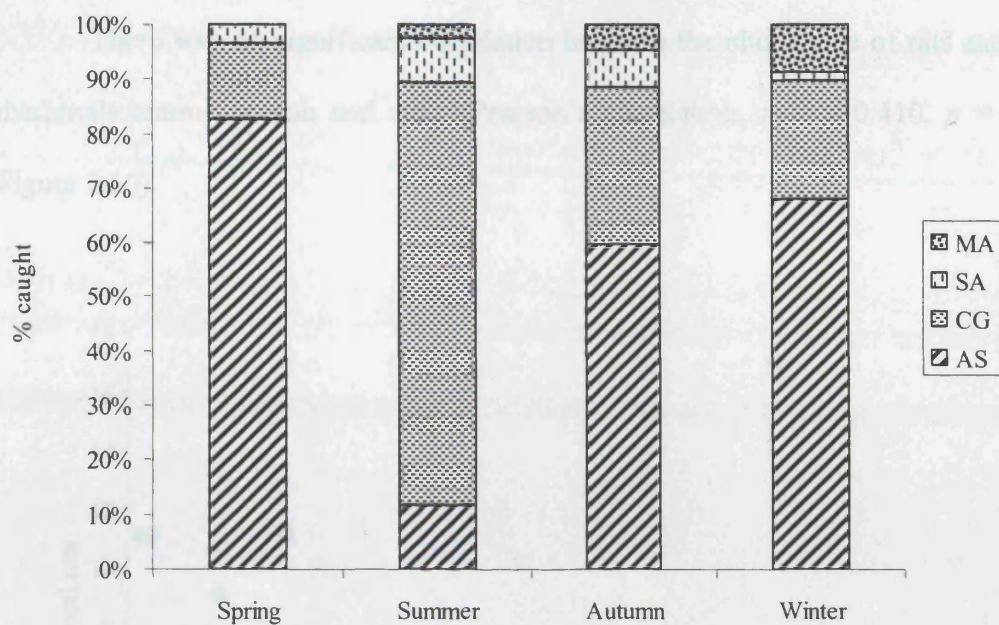


Figure 3.9 Proportion of each small mammal species caught at the Field site over the entire study period. *A. sylvaticus* (AS) wood mice, *C. glareolus* (CG) bank vole, *M. agrestis* (MA) field vole and *S. araneus* (SA) common shrew.

Table 3.5 The estimated numbers of small mammals (Longworth trapping) and brown rats (tracking plate) at the Field site for all seasons. *M. musculus* (MM) house mouse, *A. sylvaticus* (AS) wood mice, *C. glareolus* (CG) bank vole, *M. agrestis* (MA) field vole and *S. araneus* (SA) common shrew.

Season	Species				
	AS	CG	MA	SA	RN
Spring	78	18	0	6	2
Summer	14	86	4	12	17
Autumn	72	48	8	12	1
Winter	62	28	10	2	7

There was no significant correlation between the abundance of rats and small mammals among season and sites (Pearson's correlation, $r_7 = -0.410$, $p = 0.313$; Figure 3.10).

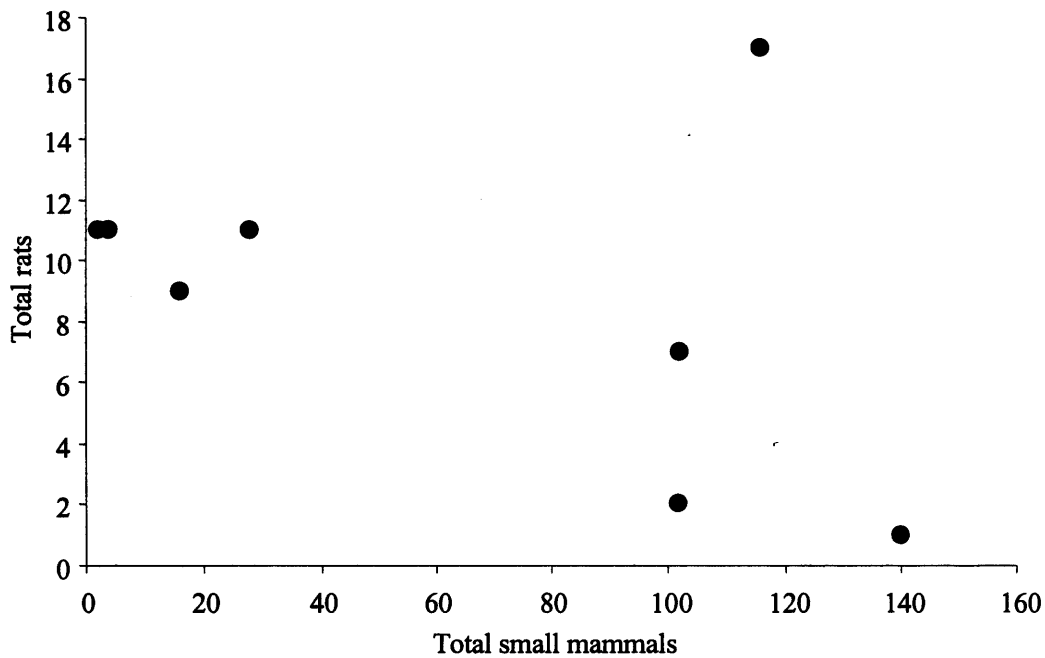


Figure 3.10 Correlation between estimated rat abundance from tracking plates and small mammal abundances from Longworth traps at Field and Farm sites in all seasons.

3.3.3 Linking of tracking score with small mammal trapping

For small mammals there was a highly significant positive correlation between tracking plate score and numbers in the Longworth traps (Figure 3.11) at the Farm site (Pearson correlation, $r_{39} = 0.736$, $p < 0.001$). However, there was no significant correlation in the Field site (Pearson's correlation, $r_{37} = 0.283$, $p = 0.086$; Figure

3.12). These results were based on data derived from 760 trap-nights and 1520 tracking plates.

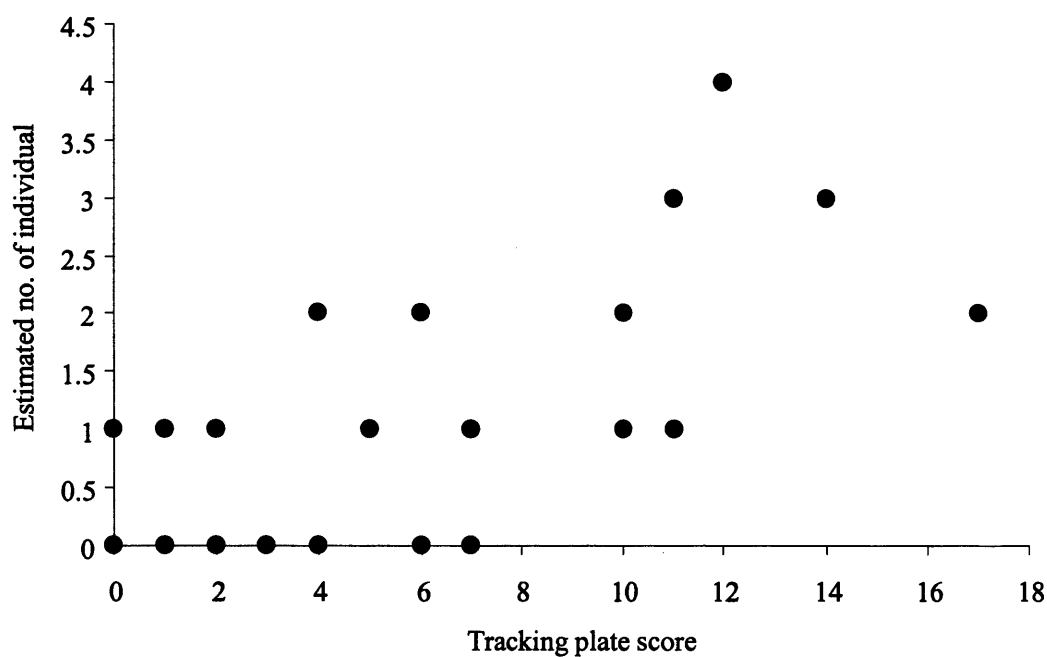


Figure 3.11 Correlation between tracking plates score and the number of all small mammals caught using Longworth traps at the Farm site.

A total of five captures (17.9%) of small mammals were associated with marked tracking plates at the Farm site giving a probability of capture of $p(m) = 0.022$. The probability of capture next to an unmarked tracking plates was 0.017. In the Field the probability of capture next to marked tracking plates was 0.381 and next to unmarked tracking plates was 0.192. There were 51 captures of small mammals next to marked tracking plates, comprising 16.1% of the total catch at the Field site.

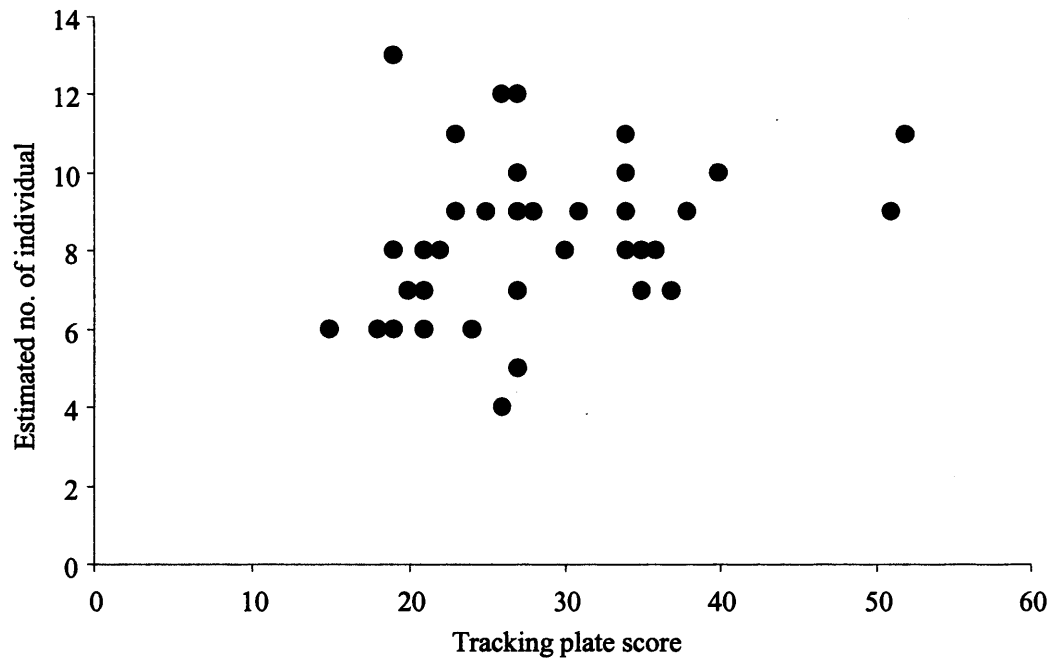


Figure 3.12 Correlation between tracking plates score and the number of small mammals caught at the Field site.

There was a significant association between the total number of small mammals caught in Longworth traps that were adjacent to tracking plates that were unmarked by rats compared with plates marked by rats at the Field ($\chi^2 = 111.4$, $d.f. = 1$, $p < 0.001$) and Farm sites ($\chi^2 = 11.57$, $d.f. = 1$, $p < 0.001$) with more small mammals trapped where plates were unmarked by rats than expected by chance. The total numbers of small mammals caught next to unmarked tracking plates and those marked by rats are shown in Figures 3.13 and 3.14.

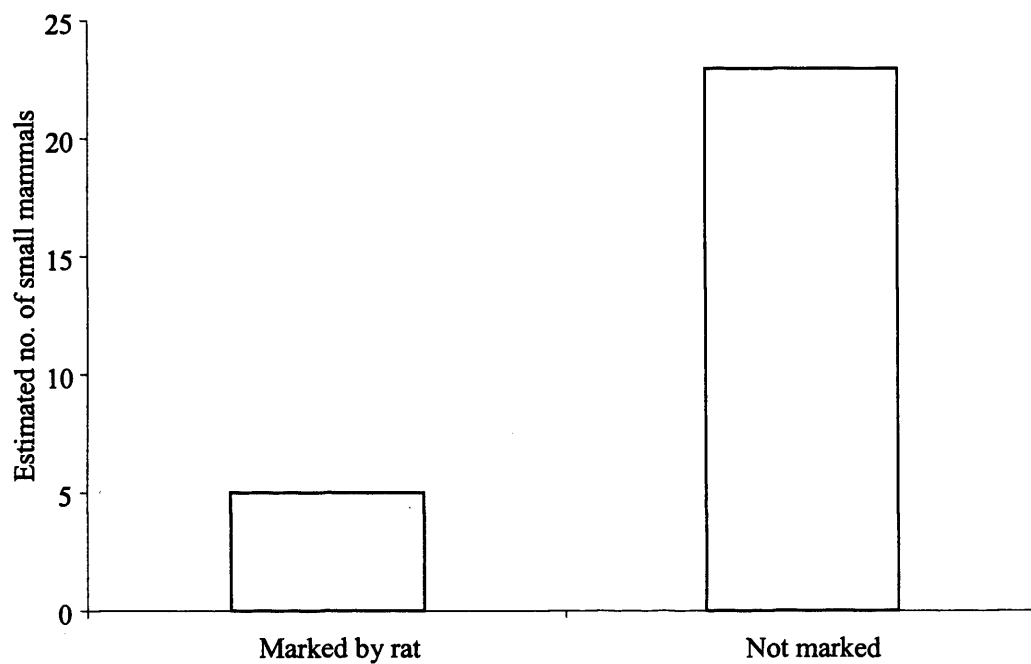


Figure 3.13 The total numbers of all small mammals caught next to unmarked tracking plates and those marked by rats at the Farm site.

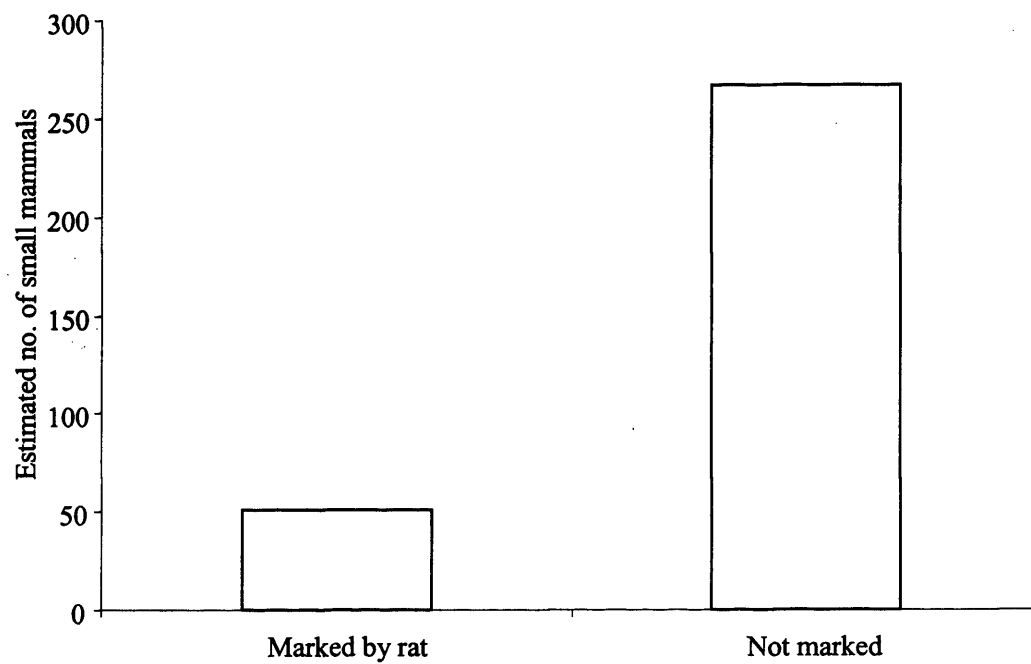


Figure 3.14 The total numbers of all small mammals caught next to unmarked tracking plates and those marked by rats at the Field site.

Based on these results, the probability of capture was calculated for both study sites (Table 3.6). Capture results from the Farm do not show any pattern of interaction between small mammals and rats, possibly because estimates were low. In the Field, the probability of capture adjacent to unmarked tracking plates by wood mice was the highest among all small mammals caught. For marked tracking plates, the bank vole scored the highest.

Table 3.6 The relationship between the distribution of rats and the probability of capture of small mammal species at the Farm and Field sites. *M. musculus* (MM) house mouse, *A. sylvaticus* (AS) wood mice, *C. glareolus* (CG) bank vole, *M. agrestis* (MA) field vole and *S. araneus* (SA) common shrew.

	Species				
	MM	AS	CG	MA	SA
$p(m)$	Farm: 0.013	Farm: 0.004	Farm: 0	Farm: 0	Farm: 0.004
		Field: 0.172	Field: 0.179	Field: 0	Field: 0.03
$p(u)$	Farm: 0.011	Farm:<0.001	Farm: 0.003	Farm:<0.001	Farm: 0.001
		Field: 0.113	Field: 0.063	Field: 0.007	Field: 0.009

$p(m)$ = probability of capture next to tracking plates marked by rat

$p(u)$ = probability of capture next to unmarked tracking plates.

3.4 Discussion

In this study the aim was to use a combination of trapping and tracking plate data to assess the distribution of brown rats and other small mammal species in agricultural buildings and adjacent farmland. In addition, these data were used to assess the degree of interaction between brown rats and other small mammals species.

3.4.1 Species distributions

Small mammals dominated the Field sites, while brown rats were predominantly confined to the Farm site except in autumn when they also occurred in the Field sites. This spatial separation may reflect differences in the habitat preferences of both groups. Bellamy *et al.* (2000) showed that road verges are suitable for small mammals and their abundance was positively associated with the dimensions of hedges and width of tall grass areas, and negatively correlated with ditch width. It is known that hedgerows support large numbers of small mammals, and hedgerow features, such as ground cover, gaps and a permanent water supply, can influence the size of small mammals populations (Kotzageorgis & Mason, 1997). Hedgerows provide a network of connectivity in the agricultural landscape and can influence the abundance of mammal species (Butet *et al.*, 2006). A study by Moore *et al.* (2003) showed that wood mice and bank voles are most abundant in farm woodlands followed by hedgerows and to a lesser extent farmland itself. Wood mice tend to be found in open areas, whereas bank voles prefer situations with good ground cover (Delany, 1974). Wood mice are generalists and do not appear favour habitat heterogeneity (Tew *et al.*, 2000). They show a high degree of space use in their ranges within cropped areas

before harvest, and shift to hedgerows at post-harvest (Tattersall *et al.*, 2001). These observations may explain why there were so many bank voles caught during summer (Figure 3.9), when the grass was tall, but more wood mice during autumn when there were no standing crops. The distribution pattern of small mammals in the fields were associated with vegetation cover, possibly as refuges from predators or linked to food availability.

Small mammal abundance was also observed to vary seasonally. The decrease in small mammal activity level in winter before recording the highest activity levels in autumn cannot solely related to the bait poisoning event because the number of small mammals caught in the Field during the winter trapping session also decreased (Figure 3.8). Alternatively the decrease may have been due to the elimination of house mice by poison baits. There were significant differences in small mammal activity levels between Farm and Field among all seasons, indicating that small mammal activity levels were constantly high in the fields throughout the year. Butet *et al.*, (2006) found that four species (*A. sylvaticus*, *C. glareolus*, *Crocidura russula* and *Sorex coronatus*) showed marked fluctuations in abundance over time. *A. sylvaticus* peaked in abundance from late autumn to the end of winter, while *C. glareolus* and *S. coronatus* predominated in the community during spring and summer and *C. russula* during October – November. Other researchers found that wood mice were the most abundant in hedgerows throughout the year (Todd, *et al.*, 2000; Tattersall *et al.*, 2002; Michel *et al.*, 2006) while bank voles peaked during spring and summer (Fitzgibbon, 1997). However, fluctuation in the abundance of small mammals may differ in different regions in response to local farm management practices (Jacob, 2003; Flowerdew *et al.*, 2004).

House mice were only caught in farm buildings and never in the Field sites. Their restricted distribution reflects their high dependency on habitats associated with man. In general, mice live in a landscape that can be classified into four habitat types; farm buildings, cropland, natural woodland and natural vegetation along water courses (Singleton *et al.*, 2007). Like the brown rat, house mice are common in poultry houses, piggeries, calf pens and dairy units (Rowe, 1981), and they appear to show little dispersal between these areas (Pocock *et al.*, 2004). Compared to feral mice, house mice migration was the primary mechanism for population regulation in response to habitat changes (Stickel, 1979). It was reported that this species lives mainly near agricultural fields closely related to human habitats (Pocock *et al.*, 2004; Singleton *et al.*, 2007). In the present study 77% of house mice were caught in traps laid near farm buildings. For other small mammal species 80% were caught in hedges adjacent to farm buildings, where the rest of the trapped house mice (23%) were also caught.

Farm buildings appear to offer the most suitable habitat for rats; the results showed that their levels of activity were constant among seasons. This result contrasts with those reported by Huson & Rennison (1981) who showed a decline in the prevalence of infested buildings from April to July. The difference between these studies may be due to the area surveyed. In the present study, the entire farm area was included, while that of Huson & Rennison (1981) concentrated on cow houses, piggeries, poultry houses, Dutch barns, fodder lofts, food stores and granaries. Some brown rats may build their nests in hedgerows or adjacent fields and use farm buildings only for foraging. Their frequent movements every night from various entry points may contribute to a constant activity level over an entire farm area. Fenn *et al.*

(1987) recorded rats commuting between hedgerow breeding sites and farm buildings while others were permanent residents of farm buildings. Cowan *et al.* (2003) also noted that the average size of rat populations around farm buildings was not significantly different among seasons, even though changes in rat population size are believed to be closely linked to the seasonal agricultural cycle. McGuire *et al.* (2006) studied a population of brown rats inhabiting a barn in east-central Illinois and their data indicated that migration does not contribute to population fluctuations but seasonal breeding by residents can exhibit dramatic changes in overall numbers.

The decline of rat activity levels in winter in farm buildings was most likely due to the use of poison baits by the farm owner. The rodenticide may have eliminated the resident rat population entirely, with signs of rat activity due to reinvasion by new groups. Another possibility was that the rats at this site may display difenacoum resistance and that a proportion of the population was unaffected by poisoning. Greaves *et al.* (1982) reported that 14% of trapped rats in Hampshire show resistance to difenacoum. In addition, low winter temperatures may have reduced rat activity levels. Brown rats are less active on cold nights (Fenn *et al.*, 1987) and the frozen ground during this time may have made alternative food less accessible. Rat activity was unchanged at the same sites throughout the year where they were active around cattle barns, straw bales stores and near grain barns (Figure 3.5 – 3.8).

Even though the farm environment frequently changed it did not influence the overall levels of rat activity estimated by tracking plates. For example, the barns were cleared during summer and a pile of hay bales were brought in during early autumn. A grain barn was full with harvested grain in September and remained there until March.

Farm machinery may also create a complex environment with numerous shelters. Genaro & Schmidek (2000) reported that brown rats exhibit high exploratory performance in a complex environment with refuges but avoided open field habitats. Most of the space used by rats in this study showed they occupied a complex environment, with less activity in open areas, showing that harbourage may play a major role in rat infestations (Table 3.3), a consideration in rat control programs (Endepols & Klemann, 2004). In particular, for economic and time constraint purposes, less attention should be given to “unused” areas because rats tend to use the same area repeatedly and follow the trails used by conspecifics. Spatial behaviour studies in the laboratory has shown that rats follow odour trails left by other rats or by themselves (Galef & Buckley, 1996; Gheusi *et al.*, 1997; Wallace *et al.*, 2002).

In this study, the estimated number of brown rats in the Field areas increased during summer (Table 3.5). This result followed the same pattern described by previous researchers (Bishop & Hartley, 1976; Huson & Rennison, 1981). However, the source of rats may not have been from farm buildings because their estimated numbers remained constant around farm buildings until autumn, even though their movement pattern was predominantly from farm buildings to the field during spring (Table 2.3, Chapter 2). The source of the increased rat activity may have been from movements along hedgerows, which can serve as a corridor for migration (Meehan, 1984). Another likely explanation for higher abundance estimates was through increased recruitment of young rats to the population; pregnant females were most frequently encountered during spring (Figure 2.8, Chapter 2).

From the present study, the use of tracking plates to determine small mammal distribution and abundance appeared only to be reliable on the Farm study site (Figure 3.11 & 3.12). Here the habitat structure is simpler and it is easier to predict the route taken by the small mammals. At Field sites the habitat is more complex and it is difficult to predict small mammal routes of movement. Small mammals may move under vegetation and litter and thereby avoid tracking plates. Furthermore animals in the Farm are habituated to human presence compared to the Field. Tracking plates, which had been handled by a researcher, might be more strongly repellant to animals in a Field environment than around farm buildings.

3.4.2 Rat and small mammal interactions

Small mammal species composition trapped along hedgerows was similar to that reported by previous researchers, with wood mice and bank voles the most abundant species (Moore *et al.*, 2003; Flowerdew *et al.*, 2004). Around farm buildings house mice was most abundant. Consequently, interactions between rats and small mammals in farm buildings in present study was restricted largely to house mice, and in the fields wood mice or bank voles.

Small mammal activity levels were constantly high in the Field with a peak in autumn, when rat activity levels were lowest, and lowest in summer when rat activity levels were highest. It was shown that activity levels of rats (tracking plates) and small mammals (Longworth traps) were negatively associated. It was further shown that small mammals were significantly less likely to be caught in Longworth traps adjacent to sites where rats were active. Though not conclusive, these data hint at a negative relationship between rats and small mammals. This may simply be a consequence of

different habitat preferences, but might also reflect competitive exclusion by one group of the other. Competitive exclusion may arise because one group is better at foraging than the other. Alternatively, one group may aggressively exclude the other.

Most small mammal activity was recorded near the farmhouse where there was little sign of rat activity (Figures 3.4 – 3.7). This result suggests that the two groups used different microhabitats, though there is potential niche overlap where both groups showed an overlapping foraging area, but in a small proportion of the area used. The exception was in autumn where their degree of overlap reached 32% (Figure 3.6). When small mammal density increased, their foraging behaviour changed and they explored beyond their absolute niche. From personal observations, the farmhouse area was not a favourable habitat due to less alternative food sources and cover. Thus, this separation may be due to habitat quality rather than direct interference competition; i.e. this area may have been avoided by brown rats and consequently occupied by small mammals.

Rat and small mammal distributions in the Farm in spring showed that their centre of activity was in the middle of the farm buildings within the grain barn, cattle barn and workshops (Figure 3.4). Only rat activity was recorded around sites where straw bales and hay were stored. Small mammal signs were more obvious around the farmhouse. Evidence of activity by rats and small mammals was also recorded in the hedgerow along the road. In summer, no rat activity was recorded around the farmhouse and their activities were centered more around the grain barn, cattle barn, straw bales area and workshops. Small mammal activity was also recorded in the

straw bale area, but their activity appeared more restricted to the fringe of the farm buildings (Figure 3.5).

In autumn, small mammal activity was more dispersed. Signs of activity were recorded at all sampling sites, including the centre of the farm buildings, which were rarely used in spring and summer. The pattern of rat distribution in the autumn was almost the same as in spring and summer. These data clearly showed that rats avoided the farmhouse area. The distribution of small mammals in winter showed that they used almost the entire area of the Farm site, while rat activity was confined to the same area they used at other times, suggesting that rats may permanently inhabit the farm buildings.

Direct aggressive interactions between rats and small mammals are difficult to observe, though Davies (1979) saw brown rats kill house mice. Delong (1966) reported that house mice were more passive compared to meadow mice, and meadow mice caused severe reductions in a house mouse population. These studies suggest that brown rats may exclude house mice through direct competition.

In the Field site there was a significant negative correlation between the abundance of brown rats and wood mice. During summer the numbers of wood mice dropped drastically when the numbers of brown rats increased. Brown rats moved into the Field areas during summer and the increases of their number may have directly affected the wood mouse population. However, at the same time the numbers of bank vole increased (Table 3.5). Thus, wood mice may face two competitors at the same time which might suppress their productivity. Selas *et al.* (2002) found a difference

between wood mice and bank voles in food and habitat selection. Bank voles responded significantly to a high production of bilberries, whereas acorns significantly influenced wood mice populations. A removal experiments between these two species was conducted by Fasola & Canova (2000) in a forested area of Central Europe. They found that the removal of wood mice strongly affected the population density of bank voles, but the removal of bank voles did not significantly affect the density of wood mice showing that wood mice may be more dominant compared to bank voles. According to Gurnell (1985), aggressive encounters between these two species may be reduced by temporal partitioning as wood mice are absolutely nocturnal whereas bank voles are most active during the day.

In the present study, there was no strong pattern of association between the numbers of brown rats and bank voles, field voles or common shrews. The low captures of these species make comparisons impossible to interpret. Lambert (2003) found that there was no evidence that brown rats showed any aversion towards field vole or wood mice odours. Therefore, there is no evidence to support the use of these species to exclude brown rats. No strong pattern was observed in the Farm suggesting that population regulation of brown rats was not influenced by the appearance of small mammal in the same area. However, in the Field the appearance of wood mice was negatively associated with brown rat numbers; rat numbers were constantly low in spring, autumn and winter, while during this period the number of wood mice was relatively high. In summer, when the number of bank voles increased and wood mice decreased there was a pronounced increase in brown rat abundance. This relationship warrants further investigation.

Although the probability of catching small mammals during the trapping period was not influenced by the appearance of brown rats, if small mammals were allowed to establish at certain densities in field habitats, they might affect rats during summer through competition for food. Table 3.6 shows that wood mice and bank voles do not entirely avoid brown rat where they forage in the same area and they appear to share the same resource. The data presented in this study shows that small mammals were well established in the field habitat and may compete with brown rats during summer when control measures around the farm buildings during this time are usually neglected.

3.5 Summary

1. The Farm site was the most suitable habitat for brown rats all year round and their density remained constant if no control measures were taken. In contrast, small mammals dominated the Field habitat. In summer brown rats increased in the Field and in autumn small mammals showed their highest abundance in the Farm habitat.
2. Tracking plates were used successfully to determine small mammal abundances and distributions in the Farm but not in Field habitats.
3. Spatial overlap between brown rats and small mammals was low in the Farm site.
4. Wood mice and bank voles were the most common species caught in the Field areas, whereas house mice dominated in the Farm area.

5. The potential of small mammal for competing for resources with brown rats in
Field areas during summer should be investigated further.

Chapter 4: The Effect of Food Availability on the Distribution and Abundance of Brown Rats

4.1 Introduction

One of the most important extrinsic factors that may affect animal population size and growth is food availability. Food is believed to be a major factor in rat infestations of agricultural premises. Large rat populations that can cause significant damage often occur on working farms with abundant stored or discarded food items, itself a reflection of farm type (Cowan *et al.*, 2003). Notably Husson & Rennison (1981) proposed that a shortage of food in farm buildings during late spring and summer may cause the dispersal of rats to surrounding fields. It was evident from their study that the high frequencies of infestation in farm buildings was related to food availability. Similarly, Orgain & Schein (1953) demonstrated that food supply was positively correlated with rat population size in a residential area, proposing that food was the limiting environment factor to population size. Despite the link between rat abundance and food availability it is often difficult to exclude rats from buildings where food is stored. A study by Belmain *et al.* (2003) showed that rats were trapped in every house in which food was stored in a rural area of Mozambique.

The study of food distribution, abundance and intake by rats may have an important role in the control of rat population size. Bait preference tests and studies of foraging behaviour may permit improvement of methods for rodent monitoring and control (Macdonald & Fenn, 1994; Weihong *et al.* 1999; Shumake & Hakim, 2000).

For example, Gentle *et al.* (2006) suggested that rats living in an environment with low food diversity showed greater persistence of conditioned taste aversion to particular food types compared to rats exposed to a more diverse number of foods, which may have implications for bait use. Food intake in brown rats can also be influenced by interactions with conspecifics. For example, naive rats that interacted with conspecifics that had been trained to eat protein-rich diets developed a strong preference for that diet (Galef, 1986; Beck & Galef, 1989; Galef & Whiskin, 1995). Conversely, rats may learn to associate new food types with distress in other individuals, with the results that they will develop an aversion to the new food without eating it (Lavin *et al.*, 1980). A study by Gillies *et al.*, (2003) on black rats demonstrated a seasonal effect on the amount of bait consumed, with consumption of bait during winter and spring greater than autumn and spring.

Many rodent pests are omnivorous, feeding on plant material, including seeds, leaves, roots, whole young plants, fruit, grain and tree bark. Food items of animal origin are also consumed, including insects, snails, other invertebrates and the bodies of vertebrates (Wood, 1994). According to Berdoy & Macdonald (1991) the brown rat is an omnivorous generalist, and as such makes many more decisions about diet choice than more specialist species, though diet is tailored to availability. In the laboratory, it is known that rats are efficient foragers (Foti *et al.*, 2007). On islands, rats were also recognised as seabird predators and eradication of rats is often attempted for conservation reasons (Taylor *et al.*, 2000; Thorsen *et al.*, 2000; Towns *et al.*, 2006). Predation of birds, especially eggs and chicks, is not confined to islands and control of rats has also been undertaken in forest habitats for bird conservation (Gillies *et al.*, 2003). Moors (1985) observed that the most common food items of

brown rats on the Noises island off New Zealand were insects, seeds, fruit and other plant material. A population of rats also fed chiefly on invertebrates on Rangitoto Island off New Zealand (Miller & Miller, 1995). A survey by Drummond (1960) on Bridgemark Island indicated that grasses belonged to genus *Spartina* were eaten throughout the year, supplemented with the seeds of dicotyledons in autumn, and insects and crustaceans during winter. A dietary study of rats by Major *et al.* (2007) using stable isotope analysis on Kiska Island, Alaska showed that diet composition was dependent on location. Rats at Sirius Point foraged at the highest trophic level (invertebrates), whereas at East Kiska Lake they fed mainly on terrestrial vegetation, while the major component of the diet of rats at Christine Lake was marine invertebrates and freshwater algae.

An early study by Emlen *et al.* (1948) showed that rats in Baltimore ate an average of about 25 g of ground corn per day, and Leslie & Ranson (1954) obtained an average value of about 24 g of wheat per rat per day. Inglis *et al.* (1996) determined no differences in the amount consumed between male and female rats, though there was variation in individual feeding patterns. The mean total amount of food taken per day by males and females was $28.9 \text{ g} \pm 3.8$ and $28.5 \text{ g} \pm 5.9$ respectively. Several studies have indicated that female brown rats forage in numerous short visits whilst males make fewer but longer feeding visits (Inglis *et al.*, 1996; Klemann & Pelz, 2006). Rogers (1979) listed the dietary requirements of laboratory rats, which are probably similar to those of wild rats, while McCoy (1949) discussed typical deficiency symptoms. Laboratory tests of food preference indicated that wheat was the most preferred grain and the method of presentation also affected acceptance

(Meehan, 1984). In contrast to the house mouse, the study showed that rats preferred oats rather than wheat (Ward, 1981).

Differences in the timing of food availability may also affect growth patterns of rat populations, which may alter their population structure in different environments (Glass *et al.*, 1988). On the Noises Islands shortages of protein-rich food was a potential factor that limited rat numbers (Moors, 1985). Shortages of protein in rats can induce resorption of embryos, high infant mortality, permanent growth stunting and delayed development (Widdoson & Cowen, 1972; Chow & Rider, 1973). The effect of undernutrition was shown in brain development of rats where it increased the concentrations of total solids, nitrogen, total phospholipid and reduction of whole brain cholesterol (Dobbing & Widdowson, 1965). Increasing levels of iron deficiency among rats also affects memory for taste aversion and reduces activity levels (Williamson & Ng, 1980). In grey squirrels (*Sciurus carolinensis*) Gurnell (1996) showed that food availability was more important to breeding females than breeding males. In this species breeding usually starts in December, but when food supplies were poor, the start of breeding was deferred until spring. The same relationship may occur in rats. In the face of food limitation the energetic costs of growth must be balanced against reproduction (Doonan & Slade, 1995). The response to increased food availability may occur in several ways: increased individual growth rates, resulting in more rapid maturation and higher abundance of adults; increased reproductive effort per adult; or increased survivorship. All responses are likely to lead to increased population densities.

Murphy (1992) showed that house mouse populations increased dramatically in density during a hard beech (*Nothofagus truncata*) mast year. This increase was due to an increase in breeding as a consequence of the greater abundance of food by both young and old females and by recruitment of their young. Murphy (1992) also reported that a delay in sexual maturation by young mice was not observed which is normally seen in autumn. In the cotton rat (*Sigmodon hispidus*) supplemental feeding also increased population densities (Doonan & Slade, 1995). In southern Norway, population growth of bank voles was significantly influenced by mast seeding of bilberry (*Vaccinium myrtillus*) and spruce seed (*Picea abies*), which are important food items for this species during winter (Selas *et al.*, 2002). Wood mouse microhabitat preference was greatly influenced by the dispersion of food plants which differed markedly between months and between sexes; related to the energetic and nutritional demands incurred by the contrasting reproductive tactics of males and females (Tew *et al.*, 2000). High resource availability may enhance the ability of young female wood mice to reach sexual maturity early (Montgomery *et al.*, 1991).

Some food supplement studies have shown that food supply is a density-dependent factor. Adler, (1998) showed that populations of spiny rats (*Proechimys semispinosus*) provisioned with extra food increased their densities. He suggested that the food-provisioning response was due to an increased female reproductive effort. Taitt (1981) showed that populations of deermice (*Peromyscus maniculatus*) were similarly increased by supplemented food. In a predator-free environment, cyclical changes in the density of populations of the California vole (*Microtus californicus*) delayed their decline (relative to controls) when supplied with supplemental food (Ford & Pitelka, 1984).

Food depletion can have a powerful effect on changing animal behaviour. Ylonen *et al.* (2002) proposed that at increased densities and food competition the distribution patterns of animals across habitats will vary, possibly through territoriality and despotic control of good quality habitats and of dispersers in unfavourable habitats. In their study they found that mice ignored the risk of predation to maximise foraging at high population densities and low food supply. Mice became more opportunistic in their habitat use when high numbers of mice were exploiting a poor habitat. The same pattern was also seen in a Eurasian red squirrel (*Sciurus vulgaris*) population (Wauters *et al.*, 2001). A comparison of the feeding pattern of the brown rat on a farm showed that bait stations with frequent disturbance and limited food supply increase individual food consumption (bait per 100 g body weight) and increase the number of visits, with the total time spent at the bait station approximately 2.5 times longer than at a site with low disturbance and a stable food supply (Klemann & Pelz, 2006). Klemann & Pelz (2006) also found that in a habitat with a limited food supply, rats were active during daytime and encounters with conspecifics tended to be more aggressive, while in habitats with a stable food supply defensive behaviours prevailed.

It is clear that food availability has an important impact on patterns of growth and reproduction, distribution and behaviour. However, the relationship between food availability and life history traits may vary among species. Indeed, Taylor *et al.* (2005) suggested that some life history traits may be fixed and may be relatively unaffected by food availability.

The aim of this study was to determine brown rat distributions and bait intake in two different environments; i.e. Farm and Field. Comparison was also made between summer and winter in food abundance, with the prediction that food would be relatively scarce in the Farm site during summer but most abundant during winter, with the converse true of the Field site. The distribution of brown rats was determined using tracking plates and food availability was estimated from quadrat surveys. The same procedures were also implemented with small mammals population for comparison.

4.2 Materials and Methods

This study was conducted during the summer and winter of 2006 on Farm A, Loddington, Leicestershire. The work was carried out simultaneously with a study of small mammal abundance at the same site.

4.2.1 Food availability assessment

Ten sub-blocks were selected randomly at each study site; i.e. in the Farm and in the Field. On the selected sub-block, any potential food for rats or small mammals was surveyed in a 2 x 10 m area. Potential food items included any grain, fruits, seeds and shoots; insects and molluscs were excluded from the survey. The index of food availability range from 0 to 4, where no food observed was recorded as 0. If there was less than 10% of coverage of food items within the surveyed area, the score was 1. '2' if there was 10 to 50%, '3' when the food abundance was from 50 to 75% and '4' if the food was more than 75%. Samples of all potential food items were collected from

two randomly selected 1 m² quadrats in each block. Food was weighed and identified in the laboratory. The survey was carried out for all 4 seasons.

4.2.2 Effect of food availability on distribution

Five randomly chosen sub-blocks at both study sites were selected and a bait box was placed within the area with 100 g of grain inside. The bait box used measured 340 (L) x 240 (W) x 130 (H) mm. The box was made from plywood and fitted with a galvanised steel lid (Figure 4.1). It had a large bait holding area with two entrances. The two entrances facilitate subordinate individuals escaping if a dominant enters. One tracking plate was placed at each entrance to monitoring the activity of target animals (rats and small mammals). Each box was checked the morning following placing and the remaining grain was weighed then replaced with another 100g. Tracking plates were replaced when necessary. The tracking plates were scored according to the scoring system used in 3.2.2 (Chapter 3).

Bait boxes were laid out in the selected sub-blocks for two consecutive nights and then removed to another randomly selected sub-block. Two nights enabled animals to familiarise themselves with the box and tracking plates, but avoided repeated resampling of the same location (and animals). All together there were 50 bait box nights on each study site for each season.



Figure 4.1 Bait box used in present study.

4.3 Results

4.3.1 Food assessment

Data for food availability in each season were calculated as a total index in each sub-block surveyed (Figure 4.2). In the Farm, 50% of the sub-blocks surveyed showed the availability of food in all seasons. The availability of food in the Field site sub-blocks varied throughout the year, reflecting food availability changes according to season. In spring 80% of sub-blocks surveyed showed some food availability. During summer and autumn all sub-blocks (100%) were scored as 1 – 4. During the winter 50% of the sub-blocks surveyed recorded “0”.

Natural food in the Field study site showed a peak during summer and autumn, with winter showing the lowest levels. The only food items regularly scored in surveys were seeds and fruits. In the Farm site, food resources were predominantly grain and cow pellets (Figure 4.2).



Figure 4.2 Food sample from the Farm site – grain (left) and cow pellets (right).

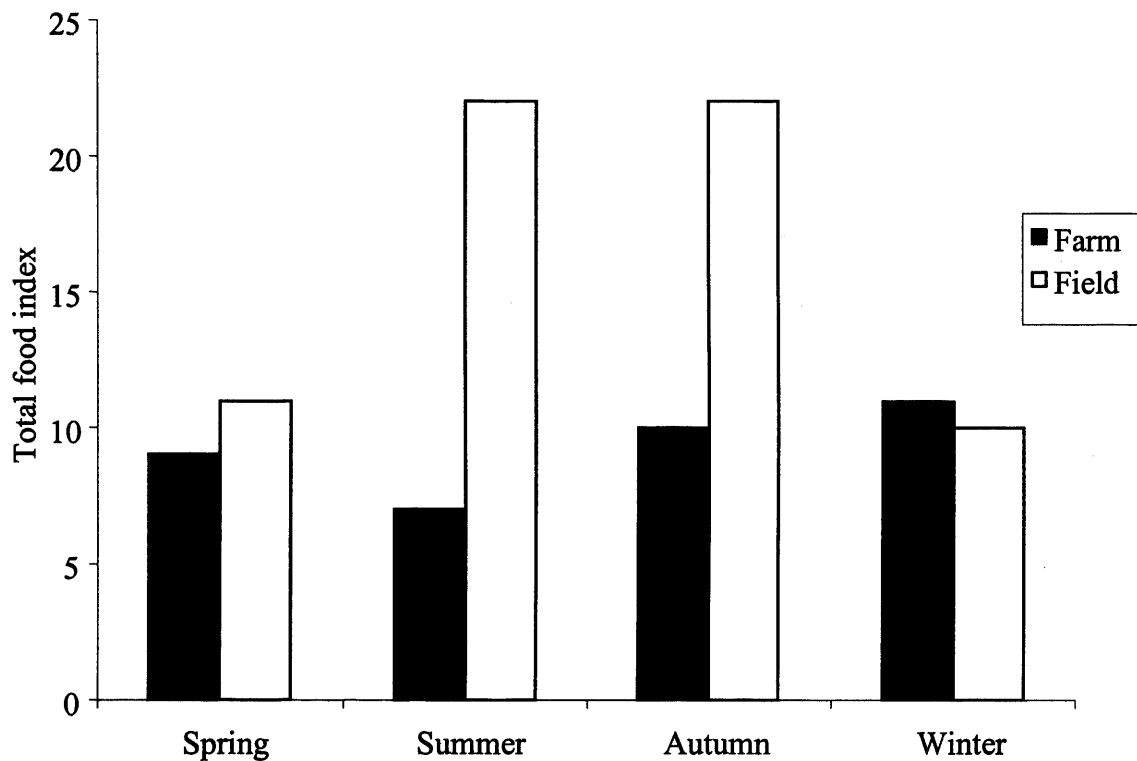


Figure 4.3 Comparison of the total food index in the farm buildings and in the fields throughout the study period.

The biomass of food available showed a different pattern from the total food index (Figure 4.3). Figure 4.4 shows that food biomass in the Farm site increased gradually from spring to winter. There was no significance difference in food biomass among seasons (rank transformed data, ANOVA, $F_{3,39} = 2.07$, $p = 0.122$). However, food biomass in the Farm site was significantly greater compared to the Field (ANOVA, $F_{1,72} = 9.63$, $p = 0.003$). There was no interaction between study site and season (ANOVA, $F_{3,72} = 1.52$, $p = 0.217$).

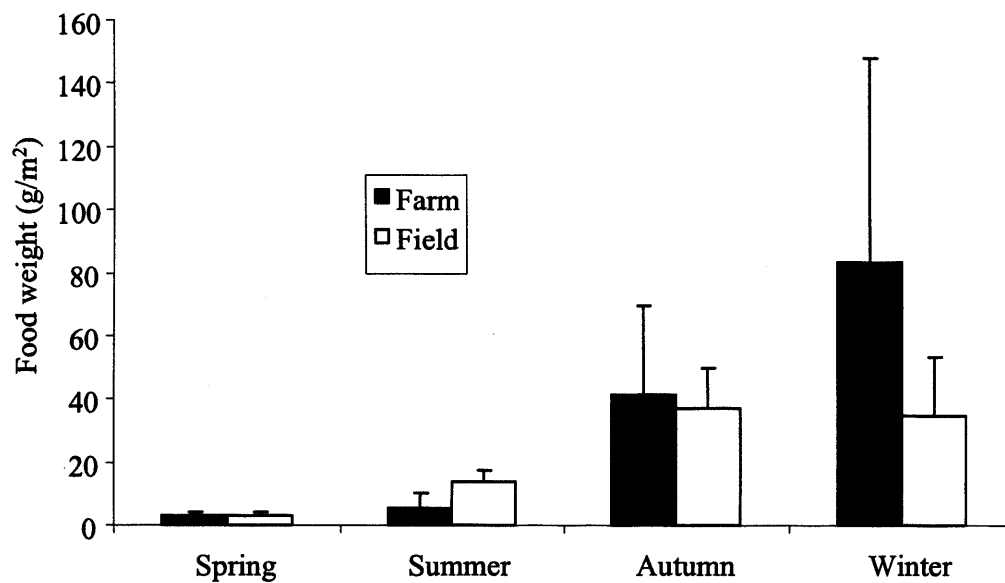


Figure 4.4 Comparison of the mean biomass of food (g m^{-2}) availability from the Farm and the Field study sites throughout the year. Error bars are one sem.

Quadrat surveys in the Field showed that during autumn food resources were dominated by hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*) berries (Figure 4.5). Common weeds found in the Field during spring and summer were soft-brome (*Bromus hordeaceus*), black-grass (*Alopecurus myosuroides*), wild-oat (*Avena fatua*), giant hogweed (*Heracleum sphondylium*) and common couch (*Elytrigia repens*). Their seeds are a potential food for rats and other small mammal species.



Figure 4.5 The most dominant fruit during autumn in the Field. The berries of hawthorn (left) and blackthorn (right).

4.3.2 Effects of supplemental food on animals distribution

During summer 32% (16) of bait box nights in the Farm site were visited by animals. Footprint marks indicated that most of the bait boxes were visited by rats, comprising 75% (12) of the total bait box nights that were visited. Visit rates by small mammals were low, with only 6% (1) visited solely by small mammals and 19% (3) shared by the brown rats and small mammals.

In the Field study site, 39 bait box nights showed visits by animals, representing 78% of the total bait box nights with visits. Tracking plate data showed that 21% (8) bait box nights were visited by rats, 51% (20) bait box nights visited by the small mammals and 28% (11) bait box nights by both.

During the winter session there was a slight drop in the number of bait box nights visited in the Farm but an increase in the Field study site. In the Farm the

proportion of bait box nights visited dropped to 28% (14). Bait box nights visited by rats dropped to 36% (5) while bait box nights visited by small mammals increased to 28% (4). Bait box nights visited by both brown rats and the small mammals also increased to 36% (5).

In the Field study site the percentage increased to 84% (42) but the proportion of visited was dominated by small mammal, representing 78% (29) and only 1 (3%) was visited by brown rats. Seven bait box nights were visited by both. Data on 22 and 23 of January were not recorded because all the tracking plates were covered with snow. There were 5 bait boxes that showed signs of bait being taken.

Data from tracking plates revealed the distribution of animals within sub-blocks that were supplied with food were compared with those that were not supplied with food. The total number of sub-blocks with food and without supplemental food visited by rats in summer and winter is presented in Table 4.1. In the Farm sub-blocks that were provided with additional food attracted more rats compared with those without additional food. In the Field, the result also showed that sub-blocks with additional food attracted more rats. However, there was no significant association between visitation rates with food or without food by rats between summer and winter in the Farm (Chi-squared test, $\chi^2 = 0.003$, $d.f. = 1$, $p = 0.955$) and Field (Chi-squared test, $\chi^2 = 0.027$, $d.f. = 1$, $p = 0.869$).

Table 4.1 The total numbers of sub-blocks visited by the brown rats on the Farm and the Field in summer and winter.

	Farm		Field	
	With Food	Without Food	With Food	Without Food
Summer	18	12	20	12
Winter*	16	11	9	6

* During winter only 40 sub-blocks were surveyed in the fields study site.

Table 4.2 shows that the score for the brown rat foot print index was highest during summer within the sub-blocks with food in the fields because the number of brown rats was greater compared in the farm buildings during this season (Figure 3.3, Chapter 3).

Table 4.2 Total footprint index for brown rats on the Farm and the Field for both seasons.

	Farm		Field	
	With Food	Without Food	With Food	Without Food
Summer	44	27	82	24
Winter*	42	13	26	11

* During winter only 40 sub-blocks were surveyed in the fields study site.

There was also no association in tracking plates score between visited sub-blocks with food or without food by rats between summer and winter in the Farm site (Chi-squared test, $\chi^2 = 2.963$, $d.f. = 1$, $p = 0.085$) and Field (Chi-squared test, $\chi^2 = 0.745$, $d.f. = 1$, $p = 0.388$).

Table 4.3 shows the total number of sub-blocks visited by small mammals in the Farm and in the Field for both sampling seasons. The effect of food supply on their distributions showed no significant association between visited sub-blocks with food or without food between summer and winter in the Farm (Chi-squared test, $\chi^2 = 1.657$, $d.f. = 1$, $p = 0.198$) and Field sites (Chi-squared test, $\chi^2 = 0.057$, $d.f. = 1$, $p = 0.811$).

Table 4.3 The total numbers of sub-blocks visited by the small mammals in the Farm and the Field for both seasons.

	Farm		Field	
	With Food	Without Food	With Food	Without Food
Summer	6	5	39	41
Winter*	19	6	37	36

* During winter only 40 sub-blocks were surveyed in the fields study site.

Table 4.4 shows the results of the total tracking plate score in this study for small mammals. There was no association between tracking plates scores for sub-blocks with food or without food for small mammals between summer and winter in Farm (Chi-squared test, $\chi^2 = 0.905$, $d.f. = 1$, $p = 0.341$) and Field (Chi-squared test, $\chi^2 = 0.799$, $d.f. = 1$, $p = 0.372$). There was no significant correlation between food biomass and food print score for rats (Pearson's correlation, $r = -0.543$, $p = 0.457$) or small mammals (Pearson's correlation, $r = -0.039$, $p = 0.961$) based on tracking plate data.

Table 4.4 The total numbers of foot print index by the small mammal on the Farm and the Field for both seasons.

	Farm		Field	
	With Food	Without Food	With Food	Without Food
Summer	13	6	144	95
Winter*	35	9	156	87

* During winter only 40 sub-blocks were surveyed in the fields study site.

4.3.3 Food intake

The amount of food consumed during the summer study period was greater than in winter. The total biomass of grain consumed during summer and winter was 1995 g and 1510 g respectively. Mean food intake per visit was also higher in summer compared to winter (Figure 4.6). Food intake per visit in this study refers to the total weight of food eaten or taken from the bait box in 1 night. There was no significant difference in the amount of food taken per visit between summer and winter (ANOVA, $F_{1,110} = 2.8$, $p = 0.097$). However, there was a significantly higher food intake per visit in the Field compared to the Farm (ANOVA, $F_{1,110} = 4.02$, $p = 0.047$).

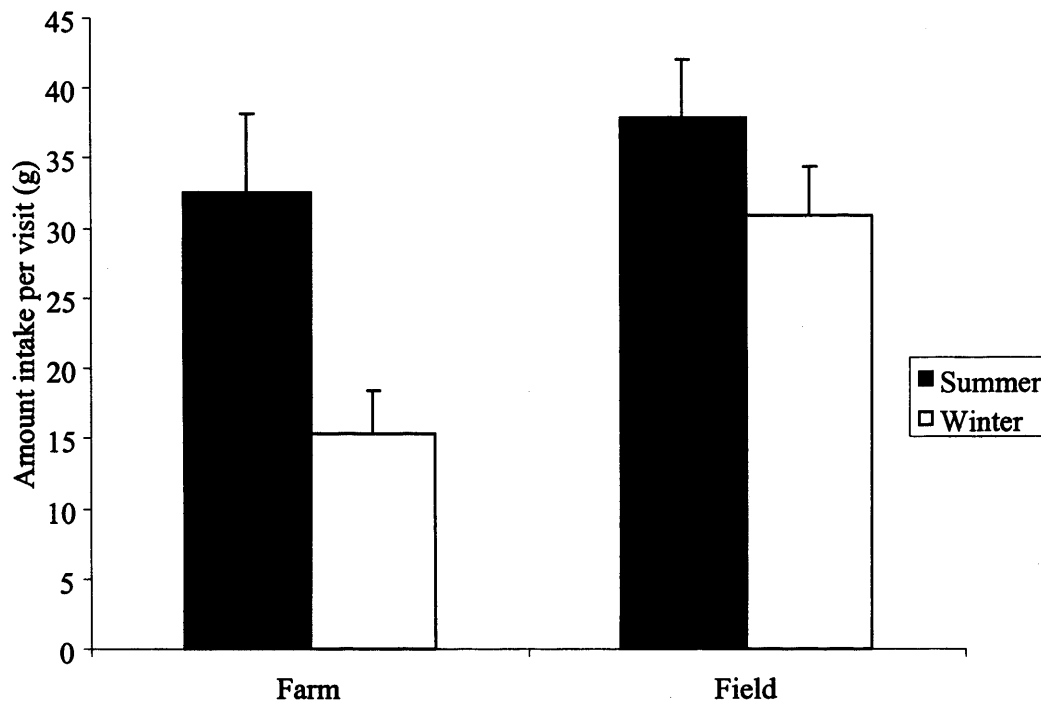


Figure 4.6 Mean supplemental food intakes per visit by rats and small mammals at both study sites. Error bars are 1 sem.

On the Farm study site, most of the food taken from the bait boxes was by rats only (64.5%) followed by both rats and small mammals (30.5%). Small mammals alone consumed only 5% of the total food taken. In contrast, 48.5% of the food taken from bait boxes in the Field was by small mammals, with rats consuming only 15.8% (Figure 4.7). In both study sites, whenever the bait boxes were visited by both groups, the amount of food taken was less compared to the amount taken by one of the groups alone. There was no significant difference in the average food intake by small mammals only (24.3 g) compared to rats only (33.5 g) (ANOVA $\log_{10}$ transformed data, $F_{1,79} = 3.3$, $p = 0.073$; Figure 4.8).

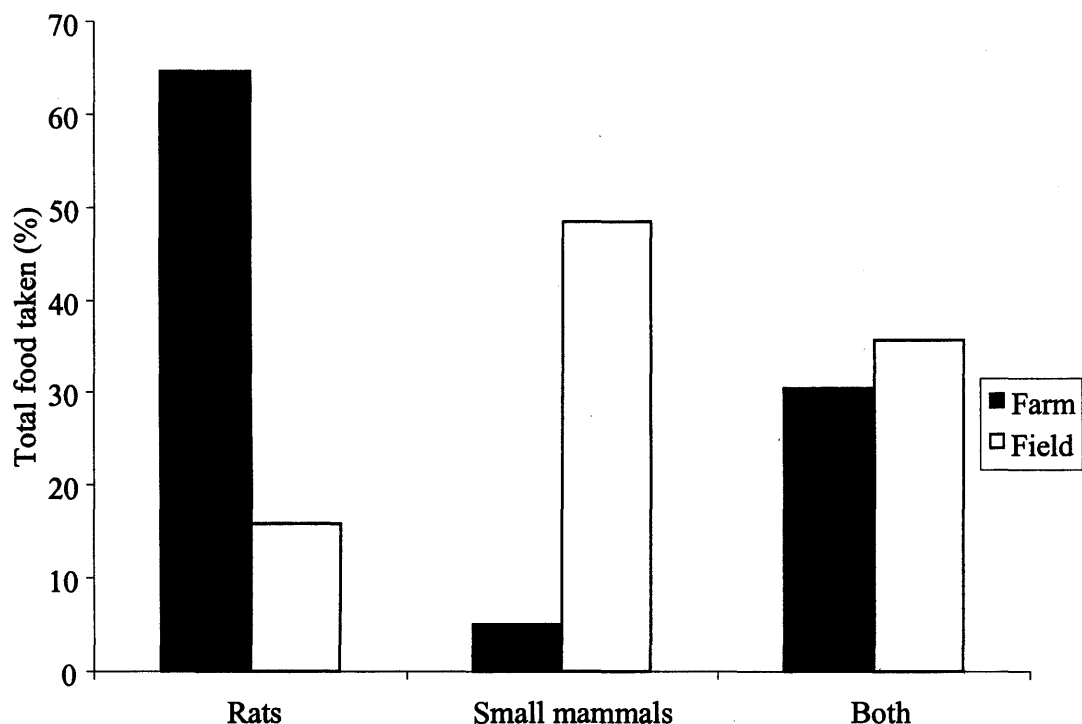


Figure 4.7 Proportion of food taken by rats, small mammals or both in the Farm and Field.

The mean food intake per visit by rats on the Farm during Summer was 30.8 g, which decreased during winter to 17 g. For small mammals the mean intake was 5 g (based on only a single observation) during summer but increased to 7.5 g per visit during winter. In the Field, the mean intake per visit by rats was 45.6 g during summer and 50 g during winter (based on a single observation). For small mammals the mean amount was similar between seasons; 26.2 g in summer and 25.9 g in winter. However, there was no significant difference of the mean intake between rats and small mammals (ANOVA, $F_{1,79} = 3.30$, $P = 0.073$). On all occasions, the mean food intake was highest if the bait box was visited by both rats and small mammals.

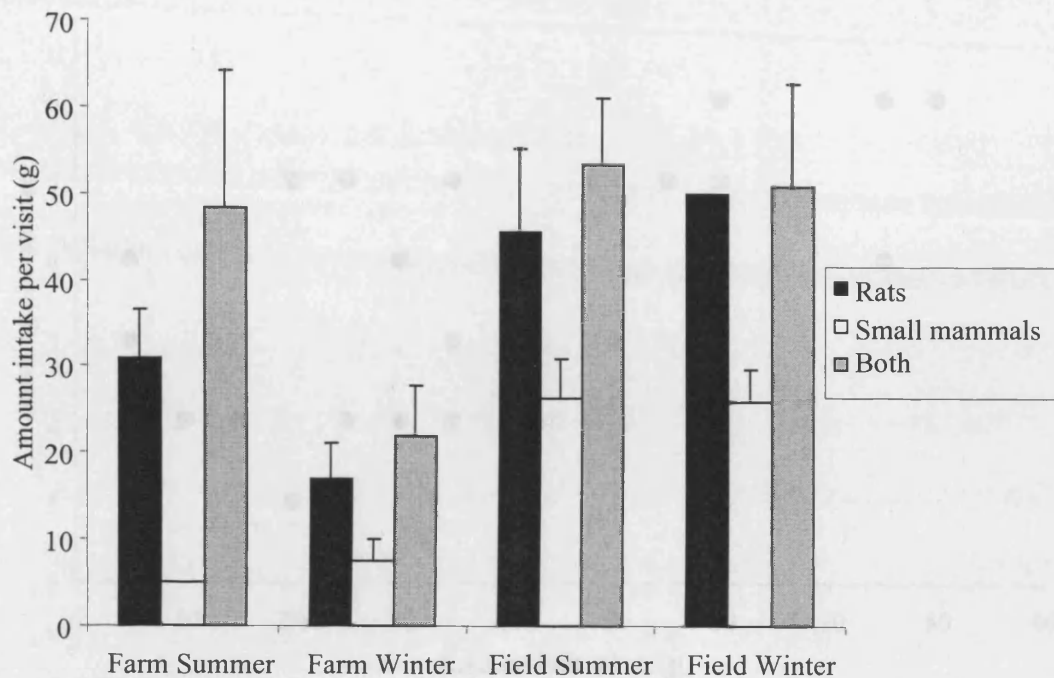


Figure 4.8 Mean amount of food intake per visit by rats, small mammals or both during study period on both study sites. Error bars are 1 sem.

There was a significant positive correlation between the tracking plate score and amount of bait taken per visit for rats (Pearson's correlation, $r_{25} = 0.639$, $p < 0.001$; Figure 4.9) and small mammals (Pearson's correlation, $r_{53} = 0.431$, $p = 0.001$; Figure 4.10).

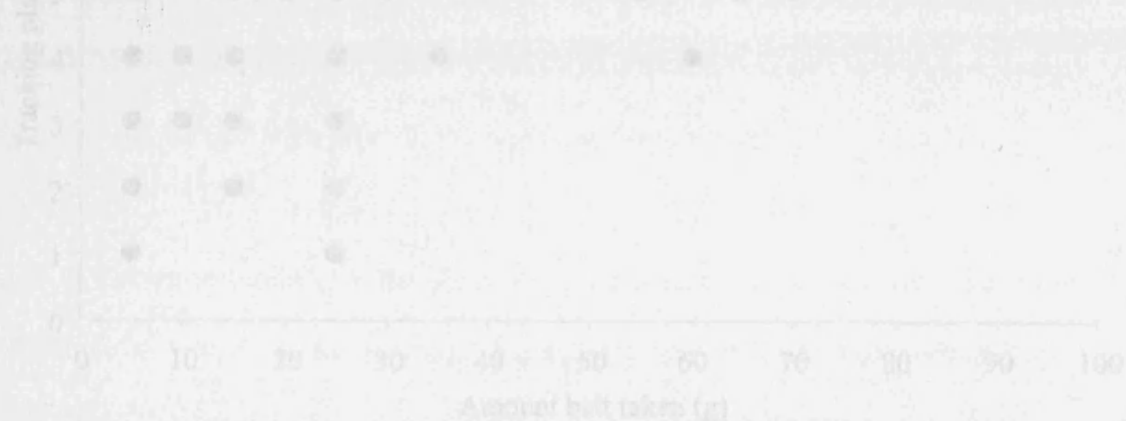


Figure 4.10 Correlation between tracking plate score and amount of bait taken per visit for small mammals. Data for summer and winter pooled. Data for bait boxes that were visited by both rats and small mammals were excluded.

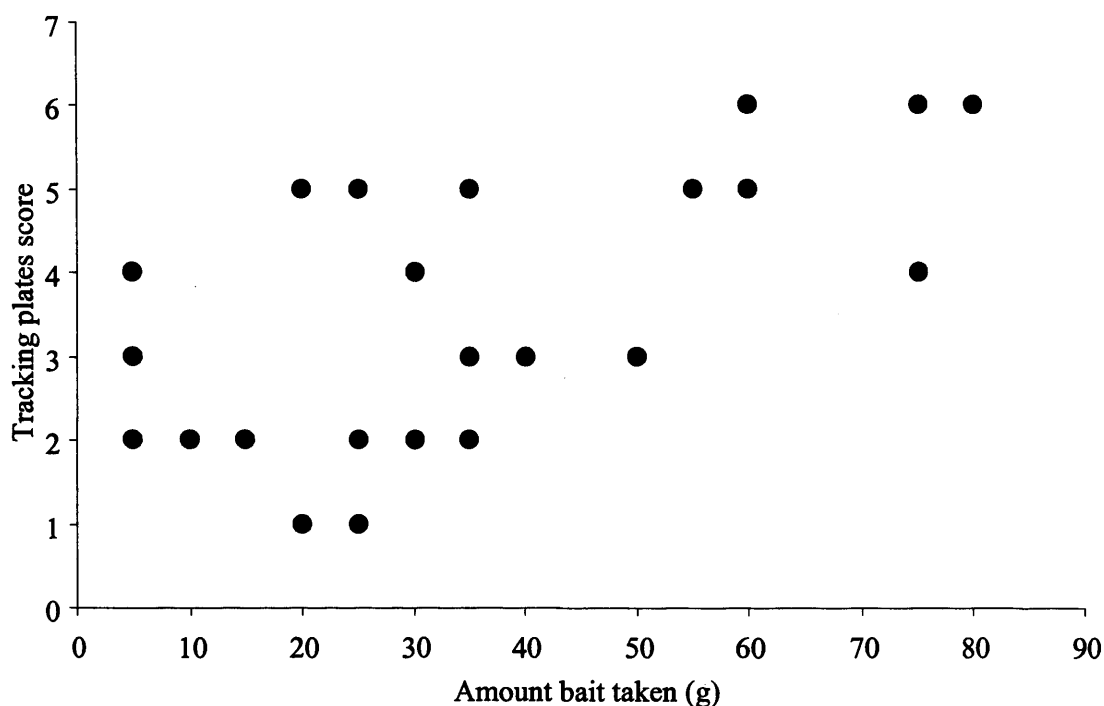


Figure 4.9 Correlation between tracking plate score and amount of bait taken per visit for brown rats. Data for summer and winter pooled. Data for bait boxes that were visited by both rats and small mammals were excluded.

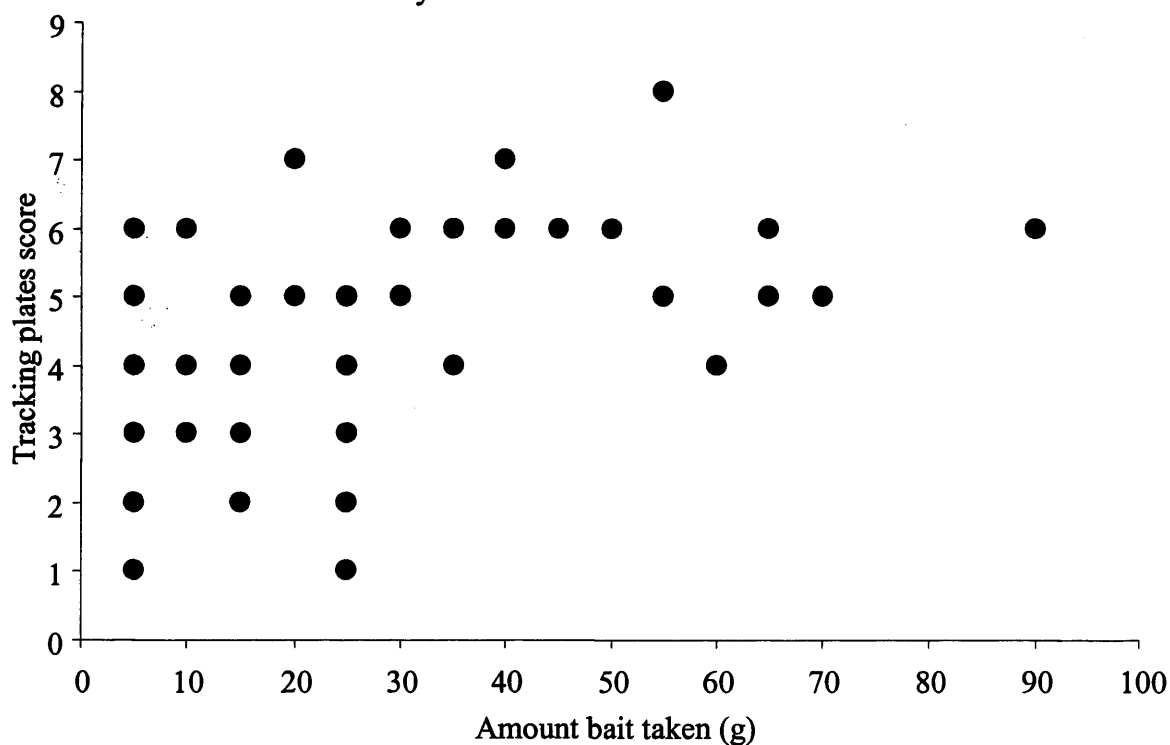


Figure 4.10 Correlation between tracking plate score and amount of bait taken per visit for small mammals. Data for summer and winter pooled. Data for bait boxes that were visited by both rats and small mammals were excluded.

4.4 Discussion

The present study indicates that food was available in the Farm site throughout the year and in greater abundance than in the Field, particularly during autumn and winter (Figure 4.3). This situation may make Farm habitats more attractive to rats (Meehan, 1984). Estimates of food abundance support the results from Chapter 3, which showed that rat abundances were almost constant in the Farm site for the entire year. A constant and predictable food availability in the Farm may make this site favourable for rats, promoting population growth (Macdonald & Fenn, 1994). An average of food availability as low as 2.87 g m^{-2} (during spring) supported an estimated 110 rats ha^{-1} (total area surveyed each day was 0.1 ha). In general, brown rats eat approximately one tenth of their body weight each day (Chitty, 1954). Even though food is crucial to their growth and is known as an important limiting factor to population growth, brown rats do not necessarily need excessive amounts of food. Meehan (1984) believed that rats only eat what is necessary for maintenance; if offered the constituent parts of a diet individually they will only eat enough of each dietary component necessary to ensure good health; a phenomenon known as 'dietary self selection'. An implication of this behaviour may result in low poison bait intake if the rats already have enough dietary components from other food sources available to them.

Food availability on the Farm followed a seasonal pattern, with the lowest food index scored in the summer. During this time a cattle barn, which was a significant source of food, was cleared while cattle were moved to the fields. The grain store was also almost empty and the entire hay barn cleared. In contrast, in winter the index was the highest. During this time all the cattle were kept in the barn

and food was supplied to them continuously. The grain store was full and loose grain was heaped around a drying machine. The hay barn was almost full with straw and hay bales. The average biomass value does not reflect the food availability index in the Field study site because seeds and fruit abundance varied according to season. There was a considerable contrast between the food availability index and food biomass in food size, type and weight. Most of the hedgerow vegetation produced fruit during autumn, which remained until mid winter. Seeds from grasses and weeds were abundant during late spring and summer, reflecting a high index of food availability but relatively low overall food biomass.

Tracking plate scores reflects rat activity and also, it is assumed, the number of rats foraging in a particular area. From this study the total tracking plate score was greater in the sub-blocks containing food (Tables 4.2 & 4.4). However, based on a comparison between the number of visited sub-blocks supplemented with food and without food, food supply seems not to affect small mammal distribution in the Field and during summer in the Farm (Table 4.3). For brown rats the supply of food similarly did not appear to strongly affect their distribution (Table 4.1). One explanation for the lack of a significant effect may be due to the distribution of natural food in the habitat. The food availability assessment study showed that food in the Farm was highly clumped while in the Field, natural foods were more evenly distributed throughout the habitat. In these conditions, animals in the field may have reliable access to food and, therefore, are not influenced by supplemental food. The distribution of small mammals also indicates that they were widely distributed in the Field and their numbers were high compared to rats.

The overall proportion of sub-blocks visited by brown rats in both Farm and Field study sites was relatively low; not more than 40%. The highest score was during summer in the Field study site when the number of brown rats was highest compared to other occasions. The low percentage was probably due to their neophobic behaviour towards bait boxes; a study by Inglis *et al.* (1996) demonstrated that brown rats show greater neophobic behaviour towards new food containers than to new food. If this is the case, the low result recorded in the present study may be due to rats that were reluctant to approach the bait box. Empty bait boxes are best left out several days in advance in each sub-block, though this can be time consuming. A study by Priyambodo & Pelz (2003) showed that a neophobic response is a long-lasting feature can be detected in the laboratory even after the rats have been kept in captivity for some time and rats from different populations show different levels of neophobic behaviour. Another explanation for this low result was that the study sites were not highly infested by rats and their distributions were restricted to particular habitats as demonstrated in Chapter 2. The tracking plate data also showed that rats and small mammals visited bait boxes less frequently when food availability was high. Another notable pattern emerging from the study was that the sub-block with supplemented food showed an increase in small mammal activity on the Farm when rats activity was decreasing during winter. This result further suggests an avoidance strategy by small mammals (Chapter 3) which may promote their coexistence with rats.

Food intake by rats and small mammals may be directly associated with the amount of food available at study sites. Both took more supplemented food during summer at both study sites when food availability was low compared to the average intake per visit during winter (Figure 4.6). Consumption of any additional food

offered to rats and small mammals in the wild must compete with natural food available. According to Pelz & Klemann (2004) the behaviour of rat populations plays a significant role in determining bait uptake. Three behavioural parameters may be involved in this process; dietary preferences, neophobia and social interactions. Klemann & Pelz (2006) showed that habitat characteristics also influenced bait uptake behaviour in rats where disturbance and a limited food supply would influence rats to visit a bait station more frequently, spent more time and took more bait. However, in the present study at the Farm site, categorized as a more disturbed but stable food supply, the rats took more bait compared to the Field where there may be less disturbance but a lower food supply. This finding indicates that food availability may be more important than disturbance in influencing the feeding behaviour of brown rats. Rats in the Farm were more habituated to human activity compared to rats in the Field (personal observation). Low bait intake will directly affect the efficacy of any control program for rats. A major challenge is how to make poisonous baits more attractive to rats when abundant alternative food is available. It may be best to offer familiar baits that match food sources in the local area (Kamal & Hossain, 2003; Klemann & Pelz, 2005), or to investigate baits that elicit a feeding response by rats.

A positive correlation between tracking plate score and the amount of bait taken indicates that more damage to food stocks are likely to be incurred when rats achieve high abundances and/or levels of activity. In Figure 4.7 it is shown that rats could cause a major problem in the Farm area, whereas in the Field, more bait was taken by small mammals. On some occasions rats and small mammals shared food resources in both study sites, indicating that any marks or odours left by the other group may not adversely affect the other group's use of food resources. Montgomery

et al. (1991) found a positive correlation between the distributions of seed supply and *A. sylvaticus* population size, particularly in years with the highest overall population density and production of deciduous seeds.

4.5 Summary

1. The Farm site contained more food than the Field. Food was available throughout the year at both sites, but was most abundant in winter at the Farm and during autumn in the Field.

2. At the Farm site supplemented food attracted rats and small mammals but was less attractive when alternative food was abundant. In the Field supplemental feeding appeared not to attract rats or small mammals.

3. Rats took more supplemented food in the Farm and small mammals dominated in the Field which reflect their abundance in these different habitats. The amount of food intake per visit was lower when the amount of natural or alternative food was high.

4. Rats and small mammals shared the same food resources.

Chapter 5: Population Variation in Skull Morphology

5.1 Introduction

Morphometrics is the quantitative analysis of the phenotypic traits of an organism. Apart from being an important facet of evolutionary and systematic studies, morphometrics also impinge on a wide range of other disciplines including genetics, biometry, gerontology, developmental and experimental biology (Thorpe, 1981). Morphological variation among organisms can usually be associated with geographical location, which can vary among habitat patches to entire continents. Geographical variation in body size may be related to several factors, including climate, inter- and intraspecific competition and predation (Yom-Tov *et al.*, 1999). In particular, skull morphometrics is an important phenotypic trait for taxonomists and systematists who use physical characteristics to describe species and their relationships with other taxa (Denys *et al.*, 2003; Lee & Mill, 2004) or distinguishing variation within species (Wojcik *et al.*, 2006; Hayashida *et al.*, 2007); the shape of the skull can reflect phylogeny and function, representing a phenotypic response to the environment and genetically-based variation. Omland (1997) maintained that the rate of molecular and morphological evolution is usually coupled. However, Renaud *et al.* (2007) showed that ecological specialization can trigger an uncoupling of molecular and phenotypic evolution, with natural selection forcing morphological evolution away from this expected correlation through phenotypic plasticity. Notwithstanding debate over the significance of phenotypic variation, Denys *et al.* (2003) urged that the combination of different techniques for understanding interpopulation variation is

necessary in order to better understand the significance of population variation and the extent of population isolation.

Endo *et al.* (2003) demonstrated geographical variation in the skull morphology of the red-cheeked squirrel (*Dremomys rufigenis*). Their results indicated that the mean values of some measurements, such as profile length, maximum length, condylobasal length and zygomatic width, were significantly larger in a Malaysian population than in two from Vietnam and Laos. The populations were separated on the basis of their adaptive strategies related to locomotion and diet; the Malaysian population was adapted for a terrestrial-insectivorous life, rather than an arboreal fruit eating life seen in the other populations. Hayashida *et al.* (2007) found the same pattern in the gray-bellied squirrel (*Callosciurus caniceps*). Differences in flora reflected morphological variations in the skulls of *C. caniceps* between northern and southern groups. Another factor reinforcing differences was the geographical barrier of the Isthmus of Kra, which hindered northern and southern population from mixing.

Recently it has been claimed that global warming has affected body size in mammals which is also reflected in skull sizes. Patterns of body size variation in response to climate change may also be detected at the community level (Millien *et al.*, 2006). In general, the global warming in recent decades appears to have affected ecological organization, including population and life-history parameters, shifts in geographical range, species composition of communities and changes in structure and function of ecosystem (McCarthy, 2001). Yom-Tov & Yom-Tov (2004) found that the greatest length of the skull and zygomatic breadth were significantly increased in the Japanese field mouse (*Apodemus speciosus*) as a reaction to warmer autumn, summer

and winter, but with no effect on the vole, *Eothenomys smithii*. Elevated temperatures enhance plant growth, thereby prolonging the growing period and increasing food availability for herbivorous animals, which may have consequences for morphological variation.

In island populations of mammals, several selective forces are thought to affect body size and many favour the evolution of larger body size, especially on small islands. In particular, lower predation risk, reduced interspecific competition or both may contribute to this phenomenon (Dayan & Simberloff, 1998; Millien & Damuth, 2004). The body size of the mammals varies significantly with the characteristics of the island itself; i.e. degree of isolation and island area influence rates of immigration, resources limitation and intra- and interspecific interactions (Lomolino, 2005). Studies on wood mouse populations by Renaud & Michaux (2007) showed that mandible shape diverged mostly on islands of intermediate remoteness and competition levels, whereas molars exhibited the greatest shape differentiation on small islands though remained similar to mainland populations. On small islands, the numbers of competitor and predator species are often reduced and resources are more limited with predictable changes in body size, with large mammals growing progressively smaller (Meiri *et al.*, 2005). Researchers have also shown that skull variation can be determined by rainfall, which reflects habitat primary productivity (Yom-Tov & Geffen, 2006; Capellini & Gosling, 2007; Cardini *et al.*, 2007).

The skull of the rat comprises the nasal, premaxillaries, maxillaries, zygomas, palatine, vomer, lacrimals, ethmoid, frontals, basisphenoid, presphenoid, parietals, occipital, interparietal, squamosals, periotic capsules, tympanic bullae, auditory

ossicles, turbinates, hyoid and mandibles (Greene, 1949). The skull evolved as several distinct functional units rather than a single unit. For example, the viscerocranium is associated with breathing and feeding (Lightfoot & German, 1998). The skull is relatively narrow and enables even adult animals to squeeze through small openings since their bodies are highly flexible (Smith, 1994). The description and conformity of skull shape is a valuable technique for assessing variation in natural populations, and to attribute ecological and evolutionary explanations for variation. Yom-Tov *et al.* (1999) concluded that skull size especially skull length was a reliable indicator of body size.

The aim of this study is to investigate geographical variation in skull morphology of three brown rat populations from farm sites in Leicestershire and Yorkshire. The hypothesis addressed was that with limited migration, geographically isolated rat populations would show significant morphological differences in skull shape that reflected degree of isolation. Morphological differences may represent genetic differences arising through genetic drift, or through selection leading to functional changes in skull shape. Alternatively, or additionally, variation in skull shape may reflect phenotypic plasticity in response to variation, for example, diet.

5.2 Materials and Methods

5.2.1 Skull preparation

Samples of brown rats were obtained from three adjacent farms in Leicestershire (Leicester) using Fenn traps prior to the population structure study (Chapter 2) and were pooled together as one population. Samples from York (York 1) were obtained

from Dr Mark Lambert at the Central Science Laboratory (CSL). The York 1 population was obtained from north-east Yorkshire. The location of trapping sites was described in detail by Brown (2007). Another set of samples were obtained from York (York 2) at a different location in north Yorkshire, again from Dr Mark Lambert. Both sets of samples from Yorkshire were trapped using Fenn traps. Only individuals with a body weight >200 g were used; i.e. adults. After the measurement of body morphological parameters, the head was separated from the body. Heads were stored at -20°C wrapped in a transparent plastic bag and individually labelled with sex, body weight, locality and date of capture.

For cleaning, the samples were thawed at room temperature for 30 min. A scalpel was used to remove as much skin and flesh as possible from the skull. Other organs such as the eyes and tongue were also removed using a scalpel and sharp scissors. Finally the brain was removed from the skull using a brain hook under running warm water. All tissue and organs were bagged and refrozen for disposal.

The skull was simmered for 30 min and boiled for a further 15 min. Boiling made it easier to remove the remaining flesh. The mandible (lower jaw) was separated from the skull after boiling. A soft wire brush was used to remove the remaining flesh. The skull was washed and dried with a hair dryer and placed on tissue paper overnight to dry completely. A pair of cleaned skulls are shown in Figure 5.1. Skulls were stored in a plastic bottle at room temperature and individually labelled.

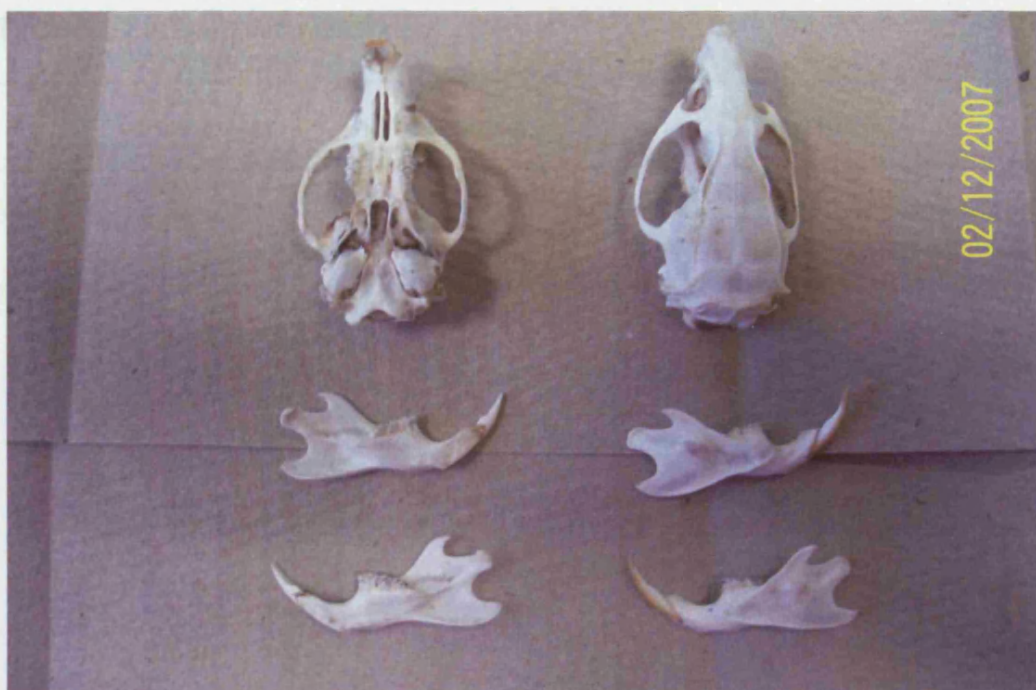


Figure 5.1 A pair of brown rat skulls ready for measurement after cleaning.

5.2.2 Skull parameters

A total of 27 skull parameters were measured. A digital vernier calliper was used to obtain measurements of each parameter to the nearest 0.01 mm. Measurements were all made by one individual, thereby minimizing any measurement error. Quantitative continuous characters were measured. Figure 5.2 presents a schematic drawing of an adult rat skull showing the measurements obtained. Parameter abbreviations are defined in Table 5.1. Points were identified according to descriptions given by Greene (1949), Lightfoot & German (1998) and Lobe *et al.* (2006). Pairs of these points were used to obtain two-dimensional distances in mm. Measurements involved four regions of the skull: total skull, face, mandible and neurocranium.

Table 5.1 Rat skull parameter measurements.

No.	Parameter	Abbreviation	Description
1	Condylobasal length	CB	The length of the skull, measured from the front of the premaxillary bones to the rear surface of the occipital condyles.
2	Skull height	SH	Measured from suture between nasal and frontal bones to anterior point of maxillary tooth row.
3	Maximum palate width	PW	The maximum width across the alveoli of the upper molar.
4	Minimum palate width	MW	The minimum width across the palate, measured behind the incisor.
5	Palate length	PL	Measured from the front of the alveolus of the incisor, to one of the choanae on the same side at the rear of the palate.
6	Hard palate length	HL	Measured from posterior edge of palatine fissure to posterior edge of palatine bone.
7	Facial width	FW	Measured from anterior point of left zygomatic arch to anterior point of right zygomatic arch.
8	Orbit length	OL	Measured from optic canal to suture between frontal bone and maxilla.
9	Foramen magnum diameter	FM	Distance between the occipital condyles.
10	Nasalia length	NL	Overall length of the nasal bones.
11	Nasal width	NW	Distance between nostrils.
12	Interorbital breadth	IB	Minimum distance between the upper edges of the orbits, measured across the top of the skull.

13	Biorbital breadth	BB	The maximum width across both the zygomatic arches, measured across the top of the skull.
14	Cranium length	CL	Measured from occipital condyle to suture at posterior edge of palatine bone.
15	Cranium width	CW	Measured from anterolateral edge of left tympanic bulla to anterolateral edge of right tympanic bulla.
16	Cranium height	CH	Measured from optic canal to edge of frontal bone.
17	Dorsoventral basicranial length	DL	Measured from posterior edge of palatine bone to posterior edge of skull.
18	Distance between tympanic bulla	TB	Measured from anteromedial edge of left tympanic bulla to anteromedial edge of right tympanic bulla.
19	Frontal length	FL	Measured from suture between nasal and frontal bones to lateral ridge of frontal bone.
20	Neurocranial length	RL	Measured from lateral ridge of frontal bone to external occipital condyle.
21	Jaw length	JL	The length of the lower jaw, from the front tip of the dentary bone to the angle.
22	Jaw height	JH	Measured from posterior most point on the angle to superior most point of condyle.
23	Right jaw notch length	JN	Measured from right mandibular condyle to right coronoid process.
24	Molar tooththrow length for lower jaw	JM	Measured between anterior point of first and posterior point of third mandibular tooththrow.

25	Molar toothrow length for maxilla.	MM	Measured between anterior point of first and posterior point of third maxillary toothrow.
26	Length of lower diastema	JD	Measured from the front tip of the dentry bone to the anterior point of lower jaw tooth row.
27	Length of upper diastema	MD	Measured from the tip of upper incisor to the anterior point of maxillary tooth row.

Skull morphometric data were obtained for 147 skulls collected from three populations. The population from Leicester (LE) contributed 71 skulls (46 males and 25 females). York 1 (YO1) contributed 43 skulls (29 males and 14 females) and 34 skulls from York 2 (YO2), (17 males and 17 females). To eliminate a high proportion of character variation on the basis of skull size differences, each measurement value was divided by the geometric mean of all measurement values (Endo *et al.*, 2003). Multivariate canonical variate analysis (CVA) was carried out with all 27 skull parameters using SPSS (version 12). Comparison was made for the first (CAN1) and second canonical discriminant function (CAN2) among populations using ANOVA. Differences in canonical values between sexes within populations were examined using a *t*-test.

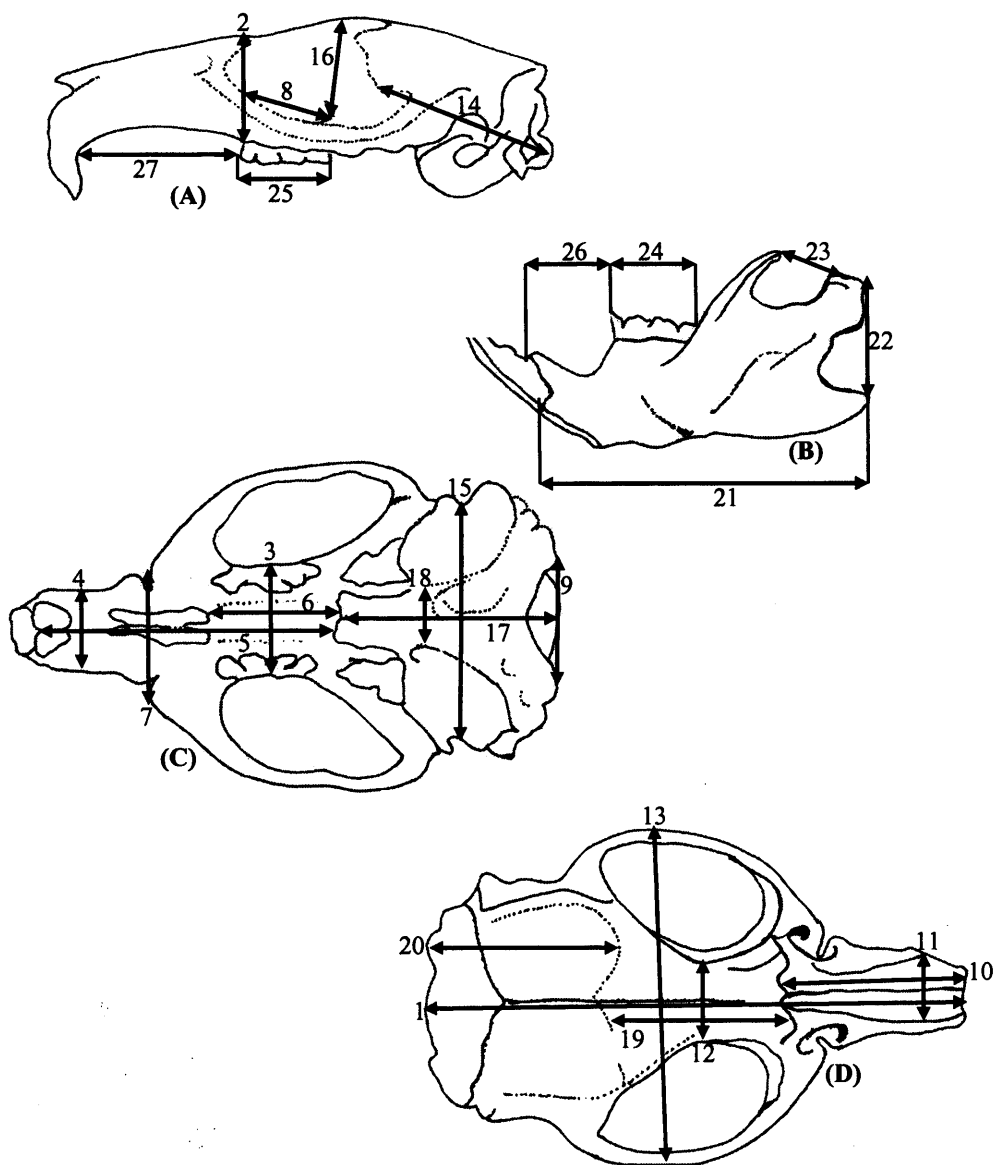


Figure 5.2 Schematic drawing of adult brown rat skull in lateral view (A), mandibular (B), dorsoventral view (C) and dorsal view (D). All of these measurements are numbered in accordance with Table 5.1.

5.3 Results

Mean values of 27 standardized skull measurements are given in Table 5.2. Multivariate canonical variate analysis resulted in two significant canonical axes ($P < 0.001$), that were responsible for 64.9% and 35.1% of variance respectively (Table 5.3). Skull morphologies were separated on the first canonical variate mainly by relative cranium and palate height and width, and the second variate by relative facial width and length (Table 5.4). Discriminant scores differed significantly among populations for the first (ANOVA, $F_{2,141} = 82.4$, $p < 0.001$), and second variate (ANOVA, $F_{2,141} = 41.2$, $p < 0.001$). A Tukey's post-hoc test showed significant differences among all populations for both factors ($p < 0.05$). A plot of the first and second canonical variates (Figure 5.3) showed clear separation of each population from the other along the first variate, and LE and YO2 from YO1 on the second variate. The separation of the three populations was further demonstrated by the fact that almost 80% of individuals were reliably classified into their correct population groups (Table 5.5), indicating that the morphological variables used for analysis were appropriate for distinguishing among populations.

No significant differences were detected between the sexes in skull morphology for the first (ANOVA, $F_{1,141} = 0.87$, $p = 0.353$) or second canonical scores (ANOVA, $F_{1,141} = 0.15$, $p = 0.696$). However, there was a significant interaction between population and sex for the first canonical variate (ANOVA, $F_{2,141} = 3.31$, $p = 0.040$), though not the second (ANOVA, $F_{2,141} = 0.26$, $p = 0.769$). For the first canonical variate skull morphology deviated strongly between the sexes in the YO2 population, but not in either of the other two populations (Figure 5.4).

Table 5.2 Mean values of the proportion indices in each skull measurements among populations.

	Leicester		York 1		York 2	
	Male	Female	Male	Female	Male	Female
CB	3.52	3.52	3.52	3.49	3.53	3.51
SH	0.88	0.88	0.88	0.88	0.89	0.89
PW	0.71	0.72	0.71	0.72	0.70	0.71
MW	0.48	0.47	0.49	0.48	0.50	0.51
PL	1.72	1.72	1.72	1.72	1.72	1.72
HL	0.75	0.75	0.75	0.75	0.76	0.75
FW	0.84	0.83	0.83	0.82	0.84	0.84
OL	0.66	0.66	0.66	0.66	0.66	0.66
FM	0.48	0.47	0.46	0.47	0.45	0.43
NL	1.34	1.34	1.34	1.33	1.36	1.34
NW	0.39	0.39	0.38	0.38	0.39	0.39
IB	0.50	0.49	0.50	0.50	0.48	0.49
BB	1.76	1.76	1.77	1.81	1.79	1.79
CL	1.45	1.45	1.45	1.45	1.45	1.43
CW	1.20	1.21	1.19	1.20	1.17	1.19
CH	0.74	0.74	0.75	0.74	0.72	0.71
DL	1.41	1.40	1.40	1.38	1.39	1.38
TB	0.25	0.25	0.24	0.26	0.26	0.25
FL	1.05	1.04	1.07	1.05	1.06	1.07
RL	1.24	1.27	1.23	1.24	1.24	1.23
JL	2.09	2.10	2.10	2.10	2.11	2.15
JH	0.46	0.46	0.48	0.48	0.48	0.48
JN	0.35	0.34	0.36	0.36	0.36	0.36
JM	0.56	0.56	0.56	0.56	0.54	0.53
MM	0.58	0.58	0.57	0.58	0.56	0.56
JD	0.59	0.58	0.59	0.58	0.60	0.61
MD	1.00	1.00	1.01	1.01	1.02	1.03

Table 5.3 First two canonical discriminant functions that were used in the analysis.

Function	Eigenvalue	% of variance	Cumulative %
CAN1	1.143	64.9	64.9
CAN2	0.618	35.1	100

Table 5.4 Character loading factors searched from canonical variate analysis. Those variables with the high loadings are highlighted in bold.

Variables	CAN1	CAN2
CB	0.158	0.470
SH	0.345	0.459
PW	-0.064	0.523
MW	-0.347	0.037
PL	0.428	0.224
HL	-0.091	0.265
FW	0.235	0.716
OL	0.243	0.179
FM	0.354	0.359
NL	0.007	0.252
NW	0.308	0.699
IB	0.234	-0.129
BB	-0.158	-0.065
CL	0.086	0.413
CW	0.343	0.421
CH	0.312	-0.293
DL	0.444	0.398
TB	0.457	0.346
FL	-0.169	0.141
RL	0.181	0.633
JL	-0.010	0.732
JH	-0.133	0.250
JN	0.203	0.183
JM	0.138	-0.230
MM	0.032	0.021
JD	0.009	0.427
MD	0.295	0.062

Table 5.5 Predicted and observed population group for LE, YO1 and YO2. Percentage for each group was presented in parentheses.

	Population	Predicted group membership			Total
		LE	YO1	YO2	
Observed group membership	LE	55 (77)	11 (16)	5 (7)	71
	YO1	5 (12)	31 (74)	6 (14)	42
	YO2	2 (6)	3 (9)	29 (85)	34

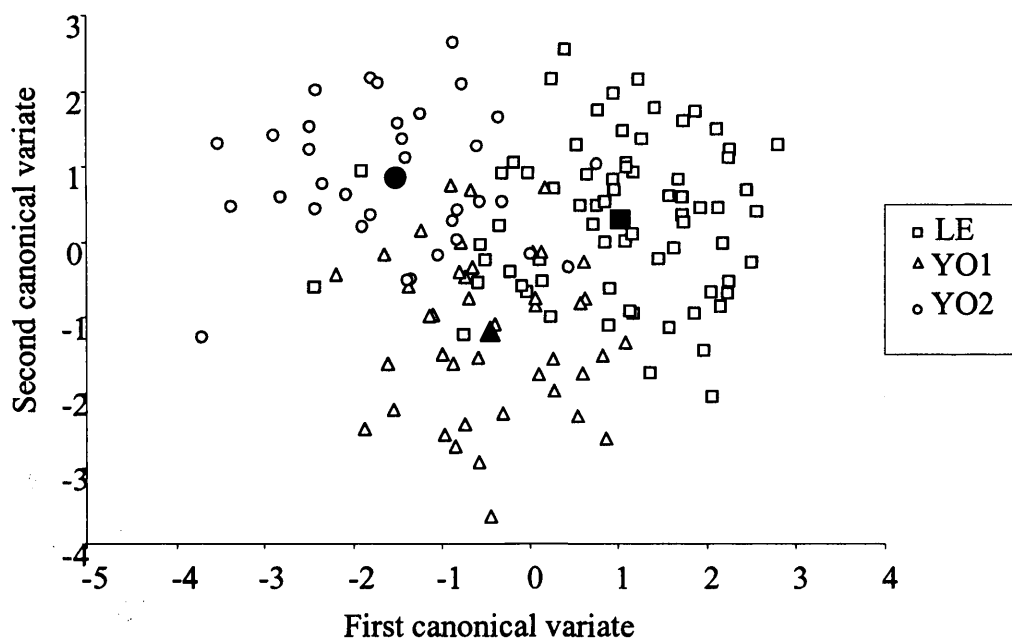


Figure 5.3 Plot of values for the first and second canonical variates generated from standardization of skull measurements from three populations (LE, YO1, YO2) of brown rats. Filled symbols (■, ▲ and ●) indicate the centroids of the respective populations.

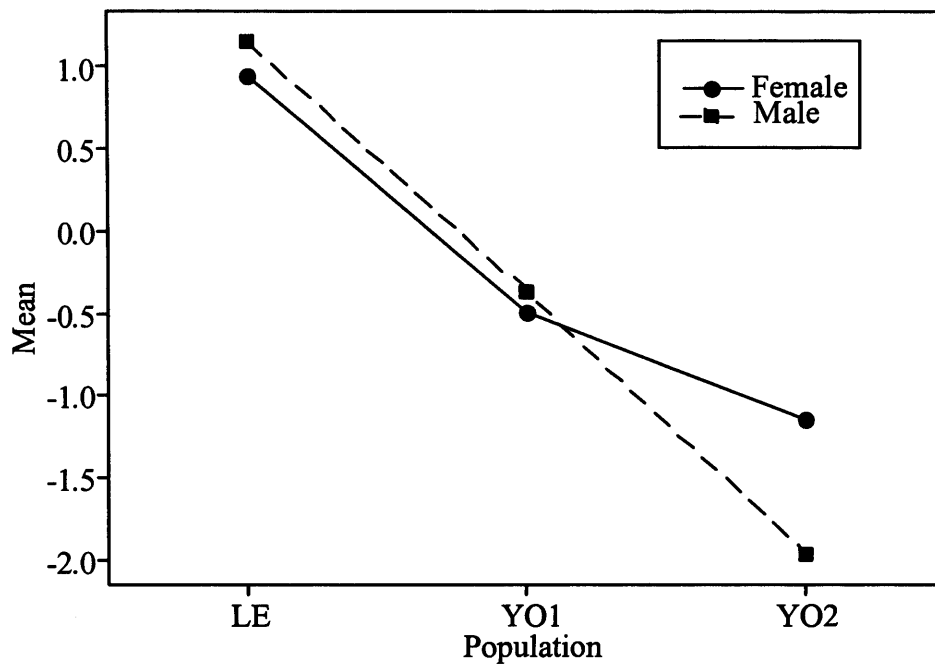


Figure 5.4 Interaction plot among populations and sexes for the first canonical variate.

5.4 Discussion

The present study demonstrated that skull morphology among three farm populations of brown rats are highly significantly different. There was no evidence of a geographical pattern to these differences; both YO1 and YO2 were as different to each other as they were to the Leicester population. The difference in latitude between Leicester (52.37') and York (54.30') is too small for the population differences to follow Bergmann's rule, which predicts that individuals in populations occurring in warmer climates should be smaller than conspecifics that occur in colder climates. These results may be a reflection that each population has undergone divergent evolution separately. The pattern of variation within and among populations may due

to a response to environmental and/or genealogic determinants (Thorpe, 1976). According to Capellini & Gosling (2007), local adaptation is a key process in the evolution of biological diversity. Monteiro *et al.* (2003) investigated five local environmental variables, i.e. altitude, mean temperature, rainfall, human population density and vegetation type; and correlated these variables with variation in skull and mandible shape in the punare rat (*Thrichomys apereoides*). They found that the three morphological landmarks of the skull (dorsal, lateral and ventral) and the mandible were significantly associated (positively) with a latitude, longitude, altitude and rainfall, and negatively correlated with mean temperature, human density and vegetation type. Environmental variables may similarly vary among the three study populations, which have driven the rats to adapt locally, which is reflected in the size and the shape of their skulls. Notably Yom-Tov *et al.* (1999) reported that rats showed adaptations in body size to local habitats within a few decades.

One of the most important variables that determined variation among the populations in this study was jaw length, which can reflect functional adaptations to diet. Rats from YO2 had a greater jaw length compared to rats from LE and YO1. Rats from YO2 were obtained from a pig farm, where they have access to a high protein diet of pig food (Dr M. Lambert, personal communication). Dietary protein is a limiting factor in mammalian growth, which can significantly affect skeletal growth; limited amino acids must be partitioned between the physiological processes of reproduction and growth. Lobe *et al.* (2006) found that there was a significant impact of life-long protein malnutrition on the pattern of growth of the craniofacial skeleton between malnourished rats and those on a control diet. Similarly Miller & German (1999) showed that rats fed a low protein diet had shorter and relatively wider skulls

compared to a control diet (24% protein). Consequently, the observed differences in skull morphology among populations may relate to diet and feeding conditions during development among populations. Overall body size of rats from YO2 was greater from LE and YO1, which correlates with skull size. According to Dayan *et al.* (1989) an increase in body and skull size are considered to be outcomes of competition. Larger individuals have an advantage to access restricted food resources, physiological advantage under stressful conditions and have greater mobility.

The overall availability of food can play an important role in determining skull size in mammals. Yom-Tov *et al.* (2007) found that the skull size of foxes collected in agricultural areas was significantly larger than of those from non-agricultural areas, and suggested that the increased food availability derived from animal husbandry was the cause for the observed difference in skull size. Yom-Tov (2003) demonstrated that improved nutrition may cause an increase in body size in mammals which ultimately affects skull morphology. He found that an increase in body length over 50 years of commensal mammals in Israel appeared to be related to improved nutrition owing to a substantial increase in the amount of garbage and agricultural crops available. Animals specializing on feeding on food items imposing different mechanical demands show clear patterns of morphological specialization in their cranial morphology. True herbivores feed on a diet of fibrous and tough foliage and usually have taller skulls and a shorter snout (Metzger & Herrel, 2005). In the present study, a comparison of food availability and diet quality at each study location was not carried out, and this would be needed to test this hypothesis.

Sexual dimorphism is not uncommon in skull morphology. Yom-Tov *et al.* (1999) found no significant difference between males and females skull measurements of brown rats from New Zealand and other Pacific islands in a study in which they investigated the relationship between skull size and latitude, island size and the presence of other rodent species. No significant differences were observed in the yellow-necked mouse (Wojcik *et al.*, 2006), and Japanese field mouse in the incisors of both living and fossil populations (Millien & Damuth, 2004). However, Yom-Tov *et al.* (2007) found that skull measurements varied between males and females in red fox (*Vulpes vulpes*), with males being larger. The same pattern was also observed in the Eurasian badger (*Meles meles*) by Lee & Mill (2004) and in the house mouse by Lightfoot & German (1998). Sexual dimorphism was also observed in the western green lizard (*Lacerta bidineata*) (Bruner *et al.*, 2005).

In present study, there was no significant difference in skull morphology between sexes, but there was an interaction between population and sex because in population YO2, the females showed a divergent pattern in skull shape, with females also larger than males which contrasted with the other two populations. This result suggests that females in this population may have developed differently due to the quality and quantity of food available. The differences may be genetically determined and/or through the direct impact of environmental effects; the pattern of morphological differentiation is the result of a complex interplay between environmental and genetic differences (Renaud & Michaux, 2007). Dayan *et al.* (1989) viewed each sex as a separate morphospecies; the rationale was that each sex must be competing against the other, as well as against both sexes of other species. Miller & German (1999) found that skull growth rates between the sexes were

different. Female rats reached a significantly higher maximum rate of growth, but after reaching that maximum rate, their growth slowed more quickly than that of male rats, indicating that male rats grew for a longer period of time.

The significant differences in skull shape among the populations suggested that all three populations were isolated, with the differences in skull morphology possibly arising through genetic drift due to isolation. When several separate populations are undergoing the effects of drift, differences in allele frequencies gradually increase as chance loss and fixation occur in the separate populations (Krohne, 2001). Skull growth may also have differed from one population to another; according to VanderBerg *et al.* (2004), the growth potential of the craniofacial part of the skull in rats can be highly variable. Conditions experienced during early development would affect growth and ultimately skull size which is usually used as a proxy to body size. It is known that variation in skull morphology is not likely to be due to adaptation of a few characters to a single environmental variable, but is more probably a multidimensional process involving the adaptation of many characters to a variety of interdependent environmental factors whose gradients and range probably overlap in a rather complex fashion (Sokal & Rinkel, 1963 in Yom-Tov *et al.*, 1999). The study of skull morphometrics in wild brown rats is limited. The present study suggests significant flexibility in skull morphology in rats that may reflect variation in habitat, especially diet. A better understanding of skull variation and its functionality in rats will require further research.

5.5 Summary

1. Skull morphology was significantly different among populations, though there was no evidence of a strong geographical component to variation.
2. There was no significant difference in skull morphology between the sexes, though there was a significant interaction between sex and population.
3. Variation in skull morphology was probably linked to diet type, and food availability as well as genetic drift arising through reproductive isolation of the study populations.

Chapter 6: General Discussion

The aim of this study was to develop an understanding of the pattern of movement of brown rats in an agricultural landscape with a view to better designing measures for controlling their population size. The population structure, distribution and pattern of activity of rats was studied on farms in Leicestershire. Two factors were specifically addressed: the interaction of rats with small mammal populations, and the role of food availability on the pattern of rat movements and distribution. In addition, variation in brown rat skull morphology was investigated in three populations as a measure of the degree of morphological similarity among discrete populations, which could serve as an index of the degree of movement or migration among populations.

Understanding the population structure and behaviour of brown rats is crucial to successful control programs. In the UK the brown rat is a major rodent pest in agriculture. A successful approach to the control of rats needs to incorporate an understanding of the scale of rat movements so that efforts to control rats can be directed at the appropriate spatial scale.

The capability of rats to reproduce at high rates throughout the year (result from Chapter 2) is a significant contributor to their potential rates of population increase. Breeding males and females were found during every month of trapping. Results from Chapter 2 indicated that brown rats populations were not equally distributed across the agricultural landscape suggesting that environmental structure could shape their distribution.

Trapping using the Trap System showed that there was a seasonal movement pattern of rats. Rats predominantly moved away from farm buildings and towards the field areas in spring and predominantly moved into the farm buildings from the field in autumn. The result gave a broad picture of rat movements in an agricultural landscape and these movement patterns could be associated with breeding, where a high proportion of fecund males and non-fecund females moved towards farm buildings during autumn. At the same time, more non-fecund males moved away from farm buildings. This result suggests that farm buildings are a suitable breeding site because they represent better quality habitats and are also linked to food availability. These results suggest that farm and field sites are not discrete and that control measures in either site needs to accommodate movements from the other. Video monitoring observations showed that rats were active during the day and night during the study period, and appeared insensitive to the presence of already trapped rats. According to Krebs (2003), dispersal may have evolved as an inbreeding avoidance mechanism, but the demographic consequences of dispersal may play some role in population limitation, if only by increasing the probability that predators or disease or bad weather will kill dispersing individuals. Data from the present study suggest mixing of rats, at least on a local scale, supporting the view that local populations may be linked in a metapopulation structure with potential consequences for population dynamics (Smith, 1999).

Tracking plate data (Chapter 3) showed that the relative abundance of brown rats remained almost constant throughout the year around farm buildings. An exception was in winter, when a slight decrease in abundance was probably due to the use of poisonous baits. Around farm buildings tracking plates appeared to be a reliable

measure of rat abundance. In contrast, estimates from field sites using tracking plates were unreliable, probably due to habitat structure. Data from Chapters 2 and 3 showed that the studied population did not experience large changes in numbers, suggesting their population fluctuate around a carrying capacity and that populations were relatively stable.

In general there was a difference in the habitat preference of small mammals (with the exception of the house mouse) and the brown rat, with small mammals more concentrated in field habitats and the farm buildings appearing to be more suited to brown rats. Brown rats were encountered in field sites during winter, though their numbers were low compared to summer. Notably fewer small mammals were caught in areas where there were signs of rat activity. However, tracking plates were marked by both rats and small mammals especially at high densities, showing that these two groups have the potential to co-occur. Some differences in their ecological requirements may enable their coexistence though interference competition between the two cannot be excluded. Overall, it appeared that small mammal populations did not significantly affect the distribution and movement of brown rats. Consequently the proposal to use small mammal populations to exclude brown rats appears not to be a practical option.

In Chapter 4 the results showed that food has the potential to influence the distribution of rats although this was not clear cut. Rats tended to forage in areas with supplemental food compared to non-supplemented areas. However, the amount of supplemented food eaten was reduced when alternative food was available showing that artificial food items, including poisonous baits, must compete with natural food in

the environment which can interfere with attempts to control rats using poisonous baits. Food availability on the study farms was always high, especially in the mixed arable farms, creating a suitable habitat for the rats. Meyer (1994) stated that the shortage of food supply can limit rodent populations if not available in sufficient quantity; not available on a consistent basis; and its availability changes on a seasonal or other less predictable basis. Thus, food availability in favourable habitats can be manipulated for rodent control purposes. During the season of peak alternative food availability, rat control must be planned carefully because the usage of rodenticide will be less effective and during periods of low alternative food availability, the use of rodenticide, for example during summer, should be increased. The effectiveness of bait consumption will depend on the availability of food in the farm buildings. In addition, the acceptance of poison bait can be due to other factors, including environmental variables, such availability of cover, amount of disturbance, efficiency of materials and methods employed in control and intrinsic variables such as rat behaviour, speed of feeding, conditioning to sites and baits, distraction and diet and hunger (Rzoska, 1954).

Assessment of the amount of food available in farm and field sites was aimed at understanding whether the pattern of movements of brown rats was affected by food availability. It appears that food did shape the movement pattern of brown rats in an agricultural landscape and was a major factor in rat infestations in farm buildings. Consequently, to reduce high infestations of rats better management and handling of food in farm buildings is required. Spilled grain and cow pellets were commonly found in farm yards. Reducing access to food of this sort could reduce the number of rats. Food-rich areas around farm buildings were the most likely places to encounter

rats, but were the most difficult places to trap them; alternative food sources meant that rats rarely consumed food placed as bait. Changing the location of sites of food storage might also make food less predictable and could discourage rats. Although this method might be impossible within farm building with permanent grain stores and barns, changing the food environment might make poison baits more likely to be consumed by rats, especially those with small home ranges (Cowan *et al.*, 2003).

Based on skull morphology variation (Chapter 5) all three study populations were readily separated suggesting that they were isolated from each other. The basis to these differences is unclear, but may be due to dietary differences, genetic differences arising from genetic drift due to isolation, or both. Quality and quantity of food during the growth period is correlated with growth rate and body mass of juveniles thereby affecting skull shape (Yom-Tov *et al.*, 2007). This result indicates that rats in the UK do not migrate long (>100 km) distances, though evidence from Chapter 2 suggests that rats do make regular or seasonal smaller-scale movements in an agricultural landscape; from farm buildings to adjacent fields or neighbouring farm. Movements of this sort have direct implications for rat control programs since any attempts to eliminate rats from one farm is likely to result in rapid replacement from adjacent areas. Clinchy *et al.* (2001) showed that areas from which rats were removed were filled by neighbouring residents that expanded their home ranges into the area. Many removal experiments have shown that when removing breeding adult rodents from an area, a flood of 'surplus' individuals quickly colonise the removal site, and in many cases bring the population density of the removal site back to the pre-control density (Krebs, 2003). The most widely used technique for controlling rats is rodenticides, and their application should not be restricted to a single site or farm, but must be

implemented on a larger scale to have an impact on all connecting sub-populations in that area. This 'metapopulation' approach to rat population control is likely to be effective for rats in rural environments. Whether the same pattern of movements and population connectivity also applies in urban environments is unclear and will require further research.

A disadvantage of the metapopulation approach to rat control is that the application on a large scale of rodenticide would expose the environment to a hazardous toxin with a greater potential risk to non-target species, particularly through secondary poisoning (McDonald & Harris, 2000; Brakes & Smith, 2005). Furthermore, repeated use of rodenticide will encourage resistance in rats. Neophobic responses to poison is an adaptive behaviour that would need to be overcome. Rats may learn to be reluctant to enter bait containers (Inglis *et al.*, 1996) or refuse to eat baits because they are sensitive to bait quality (Priyambodo & Pelz, 2003). Continued long-term application of the same control technique may lead to selection for avoidance mechanisms (Meyer, 1999).

More ecologically-based rodent pest management should be applied simultaneously with initial control by rodenticides. The aim of control is to reduce numbers of rats to a minimum density below which their damage is negligible. According to Cowan *et al.* (2003), populations reduced to low levels may take two years or more to recover to their previous levels if there are no reservoir colonies nearby. Ecologically-based rodent management must tackle the movement patterns of the rats by breaking links between sub-populations. This can be done by intercepting rats along their potential migration routes, such as hedgerows and ditches, by trapping.

This approach is one in which the trap system used in this study may be valuable, similar to the trap-barrier system proposed by Singleton *et al.* (1998).

Additional measures to assist with rat control are to reduce available cover around farm buildings in order to expose rats to predators (including domestic cats and dogs). Other measures, including techniques such as diversionary feeding, fertility control and outbreak forecasting, might help to reduce damage incurred by the rats. However, the precise approach to be used is likely to be highly site specific. Leirs (2003) argued that ecologically-based rat management is a generic approach but its application is site and species specific.

Future studies in this field might focus more on the free ranging behaviour of rats, especially their foraging behaviour and pattern of movement between food-rich patches and the degree of association with their physical environment. Routine censusing of wild rat population change are particularly valuable in order to monitor levels of infestation, especially in high risk sites such as pig and cattle farms. At the same time, food preference tests, including the use of flavours and odours to mask rodenticides, should be continued in laboratory trials as an attempt to develop effective methods for the use of rodenticides.

In this study, skull collections were limited to three populations only. Data derived from these skulls were highly informative and future collections across the UK might be informative in understanding genetic and phenotypic adaptations of rats. Such data may also provide a fuller picture of rat population structure in the UK

which might be associated with their pattern of movement or migration on a larger scale. Such studies would complement wholly genetic studies of rat populations.

References

- Aars, J. & Ims, R.A. (2002). Intrinsic and climatic determinants of population demography: the winter dynamics of Tundra Voles. *Ecology*, **83**: 3449 – 3456.
- Adler, G.H. (1998). Impacts of resource abundance on populations of a tropical forest rodent. *Ecology*, **79**: 242 – 254.
- Alain, B., Gilles, P. & Yannick, D. (2006). Factors driving small rodents assemblages from field boundaries in agricultural landscapes of western France. *Landscape Ecology*, **21**: 449 – 461.
- Alcock, J. (2005). *Animal Behavior*. (8th ed.). Sinauer Associates, Inc. Sunderland USA. pp. 564.
- Angelici, F.M. & Luiselli, L. (2005). Patterns of specific diversity and population size in small mammals from arboreal and ground-dwelling guilds of a forest area in southern Nigeria. *Journal of Zoology, London*, **265**: 9 – 16.
- Apfelbach, R., Blanchard, C.D., Blanchard, R.J., Hayes, R.A. & McGregor, I.S. (2005). The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neuroscience and Biobehavioral Reviews*, **29**: 1123 – 1144.
- Aplin, K.P., Chesser, T & Have, J.T. (2003). Evolutionary biology of the genus *Rattus*: profile of an archetypal rodent pest. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 487 – 498. ACIAR Monograph No. 96.
- Arakawa, H. (2006). Changes in the pattern of exploratory behaviour are associated with the emergence of social dominance relationship in male rats. *Developmental Psychobiology*, **48**: 39 – 47.

- Barnett, S.A. (1963). *A Study in Behaviour. Principles of Ethology and Behavioural Physiology, Displayed Mainly in the Rat*. Methuen & Co Ltd, London. pp. 288.
- Beck, M. & Galef, B.G. (1989). Social influences on the selection of a protein-sufficient diet by Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, **103**: 132 – 139.
- Bellamy, P.E., Shore, R.F., Ardesir, D., Treweek, J.R. & Sparks, T.H. (2000). Road verges as habitat for small mammals in Britain. *Mammal Review*, **30**: 131 – 139.
- Belmain, S.R., Meyer, A.N., Timbrine, R. & Penicela, L. (2003). Managing rodent pest in households and food stores through intensive trapping. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 440 – 445. ACIAR Monograph No. 96.
- Berdoy, M. & McDonald, D.W. (1991). Factors affecting feeding in wild rats. *Acta Oecologica*, **12**: 261 – 279.
- Berdoy, M., Webster, J.P. & Macdonald, D.W. (2000). Fatal attraction in rats infected with *Toxoplasma gondii*. *Proceedings of the Royal Society London B*, **267**: 1591 – 1594.
- Berry, R.J. (1981). Population dynamics of the house mouse. (ed. R.J. Berry) *Biology of the House Mouse. Symposium Zoological Society of London*, **47**: 395 – 425.
- Bishop, J.A. & Hartley, D.J. (1976). The size and age structure of rural populations of *Rattus norvegicus* containing individuals resistant to the anticoagulant poison Warfarin. *The Journal of Animal Ecology*, **45**: 623 – 646.

- Bond, G., Burnside, N.G., Metcalfe, D.J., Scott, D.M. & Blamire, J. (2004). The effects of land-use and landscape structure on barn owl (*Tyto alba*) breeding success in southern England, U.K. *Landscape Ecology*, **20**: 555 – 566.
- Bourliere, F. (1975). Mammals, small and large: the ecological implications of size. *Small Mammals: Their Productivity and Population Dynamics* (eds. F.B. Golley, K. Petruszewicz & L. Ryszkowski), pp. 1 – 8. Cambridge University Press, London.
- Brakes, C.R. (2003) The exposure of non-target wildlife to rodenticides, with special reference to the red kite (*Milvus milvus*). *PhD thesis*, University of Leicester.
- Brakes, C.R. & Smith, R.H. (2005). Exposure of non-target small mammals to rodenticides: short-term effects, recovery and implications for secondary poisoning. *Journal of Applied Ecology*, **42**: 118 – 128.
- Bramley, G.N., Waas, J.R. & Henderson, H.V. (2000). Responses of wild Norway rats (*Rattus norvegicus*) to predator odors. *Journal of Chemical Ecology*, **26**: 705 – 719.
- Brodie, J. (1981). Norway rats (*Rattus norvegicus*) on cereal stubble. *Journal of Zoology, London*, **195**: 542 – 546.
- Brown, L.E. (1966). Home range and movement of small mammals. (eds. P.A. Jewell & Caroline Loizos) *Play, Exploration and Territory in Mammals. Symposium Zoological Society of London*, **18**: 111 – 142.
- Brown, M. (2007). Rats in an agricultural landscape: population size, movement and control. *Ph.D Thesis*, University of Leicester.
- Brown, P.R., Huth, N.I., Banks, P.B. & Singleton, G.R. (2007). Relationship between abundance of rodents and damage to agricultural crops. *Agriculture, Ecosystems and Environment*, **120**: 405 – 415.

- Brudzynski, S.M. (2001). Pharmacological and behavioral characteristics of 22 kHz alarm calls in rats. *Neuroscience and Biobehavioral Reviews*, **25**: 611 – 617.
- Brudzynski, S.M. (2005). Principles of rat communication: quantitative parameters of ultrasonic calls in rats. *Behavior Genetics*, **35**: 85 – 92.
- Bruner, E., Costantini, D., Fanfani, A. & Dell’Omo, G. (2005). Morphological variation and sexual dimorphism of the cephalic scales in *Lacerta bilineata*. *Acta Zoologica*, **86**: 245 – 254.
- Buckle, A.P. (1994). Rodent control methods: chemical. In A.P. Buckle & R.H. Smith (eds.) *Rodent Pests and Their Control*. pp: 127 – 160, CAB International, Oxon, UK.
- Buckle, A.P. & Smith, R.H. (1994). *Rodent Pests and Their Control* (eds). CAB International, Oxon, UK.
- Busch, M., Bilenca, D.N., Cittadino, E.A. & Cueto, G.R. (2005). Effect of removing a dominant competitor, *Akodon azarae* (Rodentia, Sigmodontinae) on community and population parameters of small rodent species in Central Argentina. *Austral Ecology*, **30**: 168 – 178.
- Butet, A, Paillat, G. & Delettre, Y. (2006). Seasonal changes in small mammal assemblages from field boundaries in an agricultural landscape of western France. *Agriculture, Ecosystems and Environment*, **113**: 364 – 369.
- Butler, F.T. & Whelan, J. (1994). Population structure and reproduction in brown rats (*Rattus norvegicus*) from pig farms, Co. Kildare, Ireland. *Journal of Zoology, London*, **233**: 277 – 291.
- Byrom, A.E. (2003). Predation risk and behaviour during dispersal: implications for population dynamics of rodents. *Rats, Mice and People: Rodent Biology and*

Management (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 165 – 168. ACIAR Monograph No. 96.

Capellini, I. & Gosling, L.M. (2007). Habitat primary production and the evolution of body size within the hartebeest clade. *Biological Journal of the Linnean Society*, **92**: 431 – 440.

Cardini, A., Jansson, A. & Elton, S. (2007). A geometric morphometric approach to the study of ecogeographical and clinal variation in vervet monkeys. *Journal of Biogeography*, **34**: 1663 – 1678.

Chitty, D. (1954). The study of the brown rat and its control by poison. *Control of Rats and Mice*. Vol. 1 (ed. Dennis Chitty), pp. 160 – 305. Clarendon Press, Oxford.

Chow, B.F. & Rider, A.A. (1973). Implications of the effects of maternal diets in various species. *Journal of Animal Science*, **36**: 167 – 173.

Clinchy, M., Krebs, C.J. and Jarman, P.J. (2001). Dispersal sinks and handling effects: interpreting the role of immigration in common brushtail possum populations. *Journal of Animal Ecology*, **70**: 515 – 526.

Cowan, D.P., Quy, R.J. & Lambert, M.S. (2003). Ecological perspectives on the management of commensal rodents. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 433 – 439. ACIAR Monograph No. 96.

Daniels, M.J. & Hutchings, M.R. (2001). The response of cattle and sheep to feed contaminated with rodent faeces. *The Veterinary Journal*, **162**: 211 – 218.

Davis, D.E. (1948). The survival of wild brown rats on a Maryland farm. *Ecology*, **29**: 437 – 448.

- Davis, D.E. (1951a). The relation between level of population and pregnancy of Norway rats. *Ecology*, **32**: 459 – 461.
- Davis, D.E. (1951b). A comparison of reproductive potential of two rat population. *Ecology*, **32**: 469 – 475.
- Davis, D.E. (1951c). The relation between level of population and size and sex of Norway rats. *Ecology*, **32**: 462 – 464.
- Davies, D.E. (1953). The characteristics of rat populations. *Quarterly Review of Biology*, **28**: 373 – 401.
- Davies, R.A. (1979). Unusual behaviour by *Rattus norvegicus*. *Journal of Zoology*, **188**: 298.
- Dayan, T. & Simberloff, D. (1998). Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review*, **28**: 99 – 124.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1989). Inter and intraspecific character displacement in mustelids. *Ecology*, **70**: 1526 – 1539.
- Delany, M.J. (1974). *The Ecology of Small Mammals*. Edward Arnold Limited. London. pp. 60.
- Dell'Arte, G.L., Laaksonen, T., Norrdahl, K. & Korpimäki, E. (2007). Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecologica*, **31**: 276 – 281.
- Delong, K.T. (1966). Population ecology of feral house mice: interference by *Microtus*. *Ecology*, **47**: 481 – 484.

- Denys, C., Lecompte, E., Granjon, L., Baylac, M., Cordeiro, P., Cornette, R., Dobigny, G., Fichet-Calvet, E., Hugot, J., Meslage, C., Millien-Parra, V., Petrillo, P., Volobouev, V. & Welz, M. (2003). Integrative systematics: the importance of combining techniques for increasing knowledge of African murinae. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 499 – 506. ACIAR Monograph No. 96.
- Dobbing, J. & Widdowson, E.M. (1965). The effect of undernutrition and subsequent rehabilitation on myelination of rat brain as measured by its composition. *Brain*, **88**: 357 – 366.
- Doonan, T.J. & Slade, N.A. (1995). Effects of supplemental food on population dynamics of cotton rats, *Sigmodon hispidus*. *Ecology*, **76**: 814 – 826.
- Drummond, D.C. (1960). The food of *Rattus norvegicus* Berk. in an area of sea wall, saltmarsh and mudflat. *The Journal of Animal Ecology*, **29**: 341 – 347.
- Dueser, R.D. & Porter, J.H. (1986). Habitat use by insular small mammals: relative effects of competition and habitat structure. *Ecology*, **67**: 195 – 201.
- Eccard, J.A. & Ylonen, H. (2002). Direct interference or indirect exploitation?. An experimental study of fitness cost of interspecific competition in voles. *Oikos*, **99**: 580 – 590.
- Emlen, J.T., Stokes, A.W. & Winsor, C.P. (1948). The rate of recovery of decimated populations of brown rats in nature. *Ecology*, **29**: 133 – 145.
- Endepols, S. & Klemann, N. (2004). Rats and the placement of rodenticide baits for their eradication on indoor livestock farms. *NJAS Wageningen Journal of Life Sciences*, **52**: 185 – 193.

- Endepols, S., Klemann, N., Pelz, H.J. & Ziebell, K.L. (2003). A scheme for the placement of rodenticide baits for rat eradication on confinement livestock farms. *Preventive Veterinary Medicine*, **58**: 115 – 123.
- Endo, H., Kimura, J., Oshida, T., Stafford, B.J., Rerkamnuaychoke, W., Nishida, T., Sasaki, M., Hayashida, A. & Hayashi, Y. (2003). Geographical variation of skull morphology and its functional significances in the red-cheeked squirrel. *Journal of Veterinary Medical Science*, **65**(11): 1179 – 1183.
- Errington, P.L. (1935). Wintering of field-living Norway rats in South-Central Wisconsin. *Ecology*, **16**: 122 – 123.
- Fasola, M. & Canova, L. (2000). Asymmetrical competition between the bank vole and the wood mice, a removal experiment. *Acta Theriologica*, **45**: 353 – 365.
- Fenn, M.G.P., Tew, T.E. & Macdonald, D.W. (1987). Rat movements and control on an Oxfordshire farm. *Journal of Zoology, London*, **213**: 745 – 749.
- Fitzgibbon, C.D. (1997). Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. *Journal of Applied Ecology*, **34**: 530 – 539.
- Flowerdew, J.R., Shore, R.F., Poulton, S.M.C. & Sparks, T.H. (2004). Live trapping to monitor small mammals in Britain. *Mammal Review*, **34**: 31 – 50.
- Ford, R.G. & Pitelka, F.A. (1984). Resource limitation in populations of the California vole. *Ecology*, **65**: 122 – 136.
- Foti, F., Spirito, F., Mandolesi, L., Aversano, M. & Petrosini, L. (2007). Effects of spatial food distribution on search behavior in rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, **121**: 290 – 299.
- Frisch, O.V. (1969). *Animal Migration*. Collins Publishers, London. pp. 125.

- Galef, B.G. (1986). Social identification of toxic diets by Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, **100**: 331 – 334.
- Galef, B.G. & Buckley, L.L. (1996). Use of foraging trails by Norway rats. *Animal Behaviour*, **51**: 765 – 771.
- Galef, B.G. & Whiskin, E.E. (1995). Learning socially to eat more of one food than of another. *Journal of Comparative Psychology*, **109**: 99 – 101.
- Genaro, G. & Schmidek, W.R. (2000). Exploratory activity of rats in three different environments. *Ethology*, **106**: 849 – 859.
- Gentle, M., Massei, G. & Quay, R. (2006). Diversity of diet influences the persistence of conditioned taste aversion in rats. *Applied Animal Behaviour Science*, **97**: 303 – 311.
- Gheusi, G., Goodall, G. & Dantzer, R. (1997). Individually distinctive odours represent individual conspecifics in rats. *Animal Behaviour*, **53**: 935 – 944.
- Gillies, C., Campbell, J., Marsh, N. & Gembitsky, M. (2003). Seasonal differences in bait acceptance by forest-dwelling rats following simulated aerial 1080 possum control operations in New Zealand: interim results. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 343 – 345. ACIAR Monograph No. 96.
- Gillies, C.A., Leach, M.R., Coad, N.B., Theobald, S.W., Campbell, J., Herbert, T., Graham, P.J. & Pierce, R.J. (2003). Six years of intensive pest mammal control at Trounson Kauri Park, a department of conservation “mainland island”, June 1996 – July 2002. *New Zealand Journal of Zoology*, **30**: 399 – 420.

- Glass, G.E., Korch, G.W. & Childs, J.E. (1988). Seasonal and habitat differences in growth rates of wild *Rattus norvegicus*. *Journal of Mammology*, **69**: 587 – 592.
- Golley, F.B., Ryszkowski, L. & Sokur, J.T. (1975). The role of small mammals in temperate forests, grasslands and cultivated fields. *Small Mammals: Their Productivity and Population Dynamics* (eds. F.B. Golley, K. Petrusiewicz & L. Ryszkowski), pp. 223 – 241. Cambridge University Press, London.
- Gomez Villafane, I.E., Bilenca, D.N., Cavia, R., Mino, M.H., Cittadino, E.A. & Busch, M. (2001). Environmental factors associated with rodent infestations in Argentine poultry farms. *British Poultry Science*, **42**: 300 – 307.
- Gomez Villafane, I.E. & Busch, M. (2007). Spatial and temporal patterns of brown rat (*Rattus norvegicus*) abundance variation in poultry farms. *Mammalian Biology*, **72**(6): 364 – 371.
- Gomez Villafane, I.E., Cavia, R., Busch, M. & Bilenca, D.N. (2003). Intra-farm variation of rodent infestations on poultry farms of central Argentina. *British Poultry Science*, **44**: 669 – 673.
- Greaves, J.H. (1994) Resistance to anticoagulant rodenticides. In A.P. Buckle & R.H. Smith (eds.) *Rodent Pests and Their Control*. pp: 197 – 217, CAB International, Oxon, UK.
- Greaves, J.H., Shepherd, D.S. & Gill, J.E. (1982). An investigation of difenacoum resistance in Norway rat populations in Hampshire. *Annual Applied Biology*, **100**: 581 – 587.
- Green, R. (1979). The ecology of woodmice (*Apodemus sylvaticus*) on arable farmland. *Journal of Zoology*, **188**: 357 – 377.
- Greene, E.C. (1949). Gross anatomy. *The Rat in Laboratory Investigation*. (eds. Edmond J. Farris & John Q. Griffith). pp. 24 – 50. Hafner Press, New York.

- Gurnell, J. (1985). Woodland rodent communities. (eds. J.R. Flowerdew, J. Gurnell & J.H.W. Gipps). The Ecology of Woodland Rodents Bank Voles and Wood Mice. *Symposia of the Zoological Society of London*, **55**: 377 – 411.
- Gurnell, J. (1996). The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology*, **33**: 325 – 338.
- Halliday, M.S. (1966). Exploration and fear in the rat. (eds. P.A. Jewell & Caroline Loizos) Play, Exploration and Territory in Mammals. *Symposium Zoological Society of London*, **18**: 45 – 59.
- Harper, G.A., Dickinson, K.J.M. & Seddon, P.J. (2005). Habitat use by three rat species (*Rattus* spp.) on Stewart Island/ Rakiura, New Zealand. *New Zealand Journal of Ecology*, **29**: 251 – 260.
- Hart, M. (1973). *Rats*. Allison & Busby, London. pp. 172.
- Hartley, D.J. & Bishop, J.A. (1979). Home range and movement in populations of *Rattus norvegicus* polymorphic for warfarin resistance. *Biological Journal of the Linnean Society*, **12**: 19 – 43.
- Hayashida, A., Endo, H., Sasaki, M., Oshida, T., Kimura, J., Waengsothorn, S., Kitamura, N. Yamada, J. (2007). Geographical variation in skull morphology of gray-bellied squirrel *Callosciurus caniceps*. *Journal of Veterinary Medical Science*, **69**: 149 – 157.
- Hill, M.J., Vel, T. & Shah, N.J. (2003). The morphology, distribution and conservation implications of introduced rats, *Rattus* spp. in the granitic Seychelles. *African Journal of Ecology*, **41**: 179 – 186.

- Hoare, J.M. & Hare, K.M. (2006). The impact of brodifacoum on non-target wildlife: gaps in knowledge. *New Zealand Journal of Ecology*, **30**: 157 – 167.
- Huitu, O., Norrdahl, K. & Korpimäki, E. (2004). Competition, predation and interspecific synchrony in cyclic small mammal communities. *Ecography*, **27**: 197 – 206.
- Huson, L.W. & Rennison, B.D. (1981). Seasonal variability of Norway rat (*Rattus norvegicus*) infestation of agricultural premises. *Journal of Zoology* **194**: 257 – 289.
- Inglis, I.R., Shepherd, D.S., Smith, P., Haynes, P.J., Bull, D.S., Cowan, D.P. & Whitehead, D. (1996). Foraging behaviour of wild rats (*Rattus norvegicus*) towards new foods and bait containers. *Applied Animal Behaviour Science*, **47**: 175 – 190.
- Jacob, J. (2003). Short-term effects of farming practices on populations of common voles. *Agriculture, Ecosystems and Environment*, **95**: 321 – 325.
- Kamal, N.Q. & Hossain, M.M. (2003). Comparison of different baits to attract rats to traps in rice fields in Bangladesh. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 281 – 283. ACIAR Monograph No. 96.
- Kaneko, Y., Maruyama, N. & Macdonald, D.W. (2006). Food habits and habitat selection of suburban badgers (*Meles meles*) in Japan. *Journal of Zoology*, **270**: 78 – 89.
- Kendall, P.B. (1984). Seasonal changes of sex ratio in Norway rat (*Rattus norvegicus*) populations in Wales. *Journal of Zoology*, **203**: 288 – 291.

- Kikkawa, J. (1964). Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* (L). *Journal of Animal Ecology*, **56**: 585 – 596.
- King, C.M. (1985). Interactions between woodland rodents and their predators. (eds. J.R. Flowerdew, J. Gurnell & J.H.W. Gipps). The Ecology of Woodland Rodents Bank Voles and Wood Mice. *Symposia of the Zoological Society of London*, **55**: 219 – 247.
- Klemann, N. & Pelz, H.J. (2005). Studies on food selection behaviour of the Norway rat (*Rattus norvegicus*) on farms. *Journal of Pest Science*, **78**: 45 – 52.
- Klemann, N. & Pelz, H.J. (2006). The feeding pattern of the Norway rat (*Rattus norvegicus*) in two differently structured habitats on a farm. *Applied Animal Behaviour Science*, **97**: 293 – 302.
- Kotzageorgis, G.C. & Mason, C.F. (1997). Small mammal populations in relation to hedgerow structure in an arable landscape. *Journal of Zoology, London*, **242**: 425 – 434.
- Krebs, C.J. (2003). How does rodent behaviour impact on population dynamics?. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 117 – 123. ACIAR Monograph No. 96.
- Krohne, D.T. (2001). *General Ecology* (2nd edition). Brooks/Cole, Thomson Learning, Australia. pp. 459.
- Lambert, M.S. (2003). Control of Norway Rats in the agricultural environment – alternatives to rodenticide use. *Ph.D Thesis*, University of Leicester.

- Langton, S.D., Cowan, D.P. & Meyer, A.N. (2001). The occurrence of commensal rodents in dwellings as revealed by the 1996 English House Condition Survey. *Journal of Applied Ecology*, **38**(4): 699 – 709.
- Lanszki, J. & Heltai, M. (2007). Diet of the weasel in Hungary. *Folia Zoologica*, **56**: 109 – 112.
- Lanszki, J., Kormendi, S., Hancz, C. & Zalewski, A. (1999). Feeding habits and trophic niche overlap in a carnivora community of Hungary. *Acta Theriologica*, **44**: 429 – 442.
- Lavin, M.J., Freise, B. & Combes, S. (1980). Transferred aversions in adult rats. *Behavioral and Neural Biology*, **28**: 15 – 33.
- Lee, S. & Mill, P.J. (2004). Cranial variation in British mustelids. *Journal of Morphology*, **260**: 57 – 64.
- Leirs, H. (2003). Management of rodents in crops: the pied piper and his orchestra. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 183 – 190. ACIAR Monograph No. 96.
- Leslie, P.H. & Ranson, R.M. (1954). The amount of wheat consumed by the brown rat. *Control of Rats And Mice* (ed. Dennis Chitty), pp. 335 – 349. The Clarendon Press, Oxford.
- Lidicker, W.Z., Jr. (1975). The role of dispersal in the demography of small mammals. *Small Mammals: Their Productivity and Population Dynamics*. (eds. F.B. Golley, K. Petrusiewicz & L. Ryszkowski), pp. 101 – 128. Cambridge University Press, London.

- Lightfoot, P.S. & German, R.Z. (1998). The effects of muscular dystrophy on craniofacial growth in mice: a study of heterochrony and ontogenetic allometry. *Journal of Morphology*, **235**: 1 – 16.
- Lindstedt, S.L., Miller, B.J. & Buskirk, S.W. (1986). Home range, time, and body size in mammals. *Ecology*, **67**: 413 – 418.
- Lobe, S.L., Bernstein, M.C. & German, R.Z. (2006). Life-long protein malnutrition in the rat (*Rattus norvegicus*) results in altered patterns of craniofacial growth and smaller individuals. *Journal of Anatomy*, **208**: 795 – 812.
- Lomolino, M.V. (2005). Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, **32**: 1683 – 1699.
- Lund, M. (1994). Commensal rodents. In A.P. Buckle & R.H. Smith (eds.) *Rodent Pests and Their Control*. pp: 23 – 43, CAB International, Oxon, UK.
- Macdonald, D.W. & Fenn, M.G.P. (1994). The natural history of rodents: preadaptations to pestilence. In A.P. Buckle & R.H. Smith (eds.) *Rodent Pests and Their Control*. pp: 1 – 22, CAB International, Oxon, UK.
- MacVicker, H.J. (1998) The ecotoxicology of rodenticide use on farms. *PhD Thesis*, University of Leicester.
- Major, H.L., Jones, I.L., Charette, M.R. & Diamond, A.W. (2007). Variations in the diet of introduced Norway rats (*Rattus norvegicus*) inferred using stable isotope analysis. *Journal of Zoology*, **271**: 463 – 468.
- Mason, G. & Littin, K.E. (2003). The humaneness of rodent pest control. *Animal Welfare*, **12**: 1 – 37.
- McCarthy, J.P. (2001). Ecological consequences of recent climate change. *Conservation Biology*, **15**: 320 – 331.

- McCoy, R.H. (1949). Dietary requirement of the rat. *The Rat in Laboratory Investigation*. (eds. Edmond J. Farris & John Q. Griffith). pp. 68 – 103. Hafner Press, New York.
- McDonald, R.A. & Harris, S. (2000). The use of fumigants and anticoagulant rodenticides on game estates in Great Britain. *Mammal Review*, **30**: 57 – 64.
- McDonald, R.A., Webbon, C. & Harris, S. (2000). The diet of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) in Great Britain. *Journal of Zoology, London*, **252**: 363 – 371.
- McGuire, B., Pizzuto, T., Bemis, W.E. & Getz, L.L. (2006). General ecology of a rural population of Norway rats (*Rattus norvegicus*) based on intensive live trapping. *American Midland Naturalist*, **155**: 221 – 236.
- Meehan, A.P. (1984). *Rats and Mice. Their Biology and Control*. Rentokil Limited. East Grinstead.
- Meiri, S., Dayan, T. & Simberloff, D. (2005). Area, isolation and body size evolution in insular carnivores. *Ecology Letters*, **8**: 1211 – 1217.
- Merritt, J.F., Lima, M. & Bozinovic, F. (2001). Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. *Oikos*, **94**: 505 – 514.
- Metzger, K.A. & Herrel, A. (2005). Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. *Biological Journal of the Linnean Society*, **86**: 433 – 466.
- Meyer, A.N. (1994). Rodent control in practice: Food Stores. In A.P. Buckle & R.H. Smith (eds.) *Rodent Pests and Their Control*. pp: 273 – 290, CAB International, Oxon, UK.

- Meyer, A.N. (1999). Commensal rodent control: challenges for the new millennium. *Proceedings of the 3rd International Conference on Urban Pest.* : 99 – 103.
- Michel, N., Burel, F. & Butet, A. (2006). How does landscape use influence small mammal diversity, abundance and biomass in hedgerow networks of farming landscape?. *Acta Oecologica*, **30**: 11 – 20.
- Miller, C.J. & Miller, T.K. (1995). Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. *New Zealand Journal of Ecology*, **19**: 19 – 27.
- Miller, J.P. & German, R.Z. (1999). Protein malnutrition affects the growth trajectories of the craniofacial skeleton in rats. *Journal of Nutrition*, **129**: 2061 – 2069.
- Millien, V. & Damuth, J. (2004). Climate change and size evolution in an island rodent species: new perspectives on the island rule. *Evolution*, **58**: 1353 – 1360.
- Millien V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**: 853 – 869.
- Monteiro, L.R., Duarte, L.C. & dos Reis, S.F. (2003). Environmental correlates of geographical variation in skull and mandible shape of the punare rat *Thrichomys apereoides* (Rodentia: Echimyidae). *Journal of Zoology*, **261**: 47 – 57.
- Montgomery, W.I., Wilson, W.L., Hamilton, R. & McCartney, P. (1991). Dispersion in the wood mouse, *Apodemus sylvaticus*: variable resources in time and space. *Journal of Animal Ecology*, **60**: 179 – 192.

- Moore, J. (1999). Population density, social pathology and behavioral ecology. *Primates*, **40**: 1 – 22.
- Moore, N.P., Askew, N. & Bishop, J.D. (2003). Small mammals in new farm woodlands. *Mammal Review*, **33**: 101 – 104.
- Moors, P.J. (1985). Norway rats (*Rattus norvegicus*) on the Noises and Motukawao islands, Hauraki Gulf, New Zealand. *New Zealand Journal of Ecology*, **8**: 37 – 54.
- Murphy, E.C. (1992). The effects of a natural increase in food supply on a wild population of house mice. *New Zealand Journal of Ecology*, **16**: 33 – 40.
- Nakagawa, M., Miguchi, H., Sato, K. & Nakashizuka, T. (2007). A preliminary study of two sympatric *Maxomys* rats in Sarawak, Malaysia: spacing patterns and population dynamics. *The Raffles Bulletin of Zoology*, **55**: 381 – 387.
- Nogales, M., Rodriguez-Luengo, J.L. & Marrero, P. (2006). Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review*, **36**: 49 – 65.
- Omland, K.E. (1997). Correlated rates of molecular and morphological evolution. *Evolution*, **51**: 1381 – 1393.
- Orgain, H. & Schein, M.W. (1953). A preliminary analysis of the physical environment of the Norway rat. *Ecology*, **34**: 467 – 473.
- Pelz, H.J. & Klemann, N. (2004). Rat control strategies in organic pig and poultry production with special reference to rodenticide resistance and feeding behaviour. *NJAS Wageningen Journal of Life Sciences*, **52**: 173 – 184.

- Petty, S.J. (1999). Diet of tawny owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *Journal of Zoology*, **248**: 451 – 465.
- Pinter-Wollman, N., Dayan, T., Eilam, D. & Kronfeld-Schor, N. (2006). Can aggression be the force driving temporal separation between competing common and golden spiny mice?. *Journal of Mammalogy*, **87**: 48 – 53.
- Pisula, W., Stryjek, R. & Nalecz-Tolak, A. (2006). Response to novelty of various types in laboratory rats. *Acta Neurobiologiae Experimentalis*, **66**: 235 – 243.
- Pocock, M.J.O., Searle, J.B. & White, P.C.L. (2004). Adaptations of animals to commensal habitats: population dynamics of house mice *Mus musculus domesticus* on farms. *Journal of Animal Ecology*, **73**: 878 – 888.
- Priyambodo, S. & Pelz, H.J. (2003). Studies on neophobic behaviour in Norway rats (*Rattus norvegicus* Berkenhout, 1769) from farms in Germany. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 155 – 158. ACIAR Monograph No. 96.
- Quy, R.J., Cowan, D.P., Haynes, P.J., Sturdee, A.P., Chalmers, R.M., Bodley-Tickell, A.T. & Bull, S.A. (1999). The Norway rat as a reservoir host of *Cryptosporidium parvum*. *Journal of Wildlife Diseases*, **35**: 660 – 670.
- Quy, R.J., Cowan, D.P. & Lambert, M.S. (2003). Adapting baiting tactics to match the foraging behaviour of Norway rats: a balance between efficacy and safety. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 451 – 456. ACIAR Monograph No. 96.

- Quay, R.J., Cowan, D.P. & Swinney, T. (1993). Tracking as an activity index to measure gross changes in Norway rat populations. *Wildlife Society Bulletin*, **21**: 122 – 127.
- Rastogi, A.D., Zanette, L. & Clinchy, M. (2006). Food availability affects diurnal nest predation and adult antipredator behaviour in song sparrows, *Melospiza melodia*. *Animal Behaviour*, **72**: 933 – 940.
- Recht, M.A. (1988). The biology of domestic rats: telemetry yields insights for pest control. *Proceedings of the Thirteenth Vertebrate Pest Conference*. University of Nebraska, Lincoln.: 98 – 100.
- Renaud, S. & Michaux, J.R. (2007). Mandibles and molars of the wood mouse, *Apodemus sylvaticus* (L.): integrated latitudinal pattern and mosaic insular evolution. *Journal of Biogeography*, **34**: 339 – 355.
- Rogers, A.E. (1979). Nutrition in the laboratory rat. *The Laboratory Rat. Vol. 1. Biology and Disease*. (eds. Baker, H.J., Lindsey, J.R. & Weisbrothy, S.H.) pp 123 – 152. Academic Press, London.
- Rosenzweig, M.L. (1981). A theory of habitat selection. *Ecology*, **62**: 327 – 335.
- Rosenzweig, M.L. & Winakur, J. (1969). Population ecology of desert rodent communities: habitat and environmental complexity. *Ecology*, **50**(4): 558 – 572.
- Rowe, F.P. (1981). Wild house mouse biology and control. (ed. R.J. Berry) *Biology of the House Mouse. Symposium Zoological Society of London*, **47**: 575 – 589.
- Russell, J.C., Towns, D.R., Anderson, S.H. & Clout, M.N. (2005). Intercepting the first rat ashore. *Nature*, **437**: 1107.

- Rutz, C. & Bijlsma, R.G. (2006). Food-limitation in a generalist predator. *Proceedings of The Royal Society B*, **273**: 2069 – 2076.
- Rzoska, J. (1954). Stomach analysis of brown rats poisoned in the field. In *Control of Rats and Mice* (ed. Dennis Chitty). pp. 395 – 413. Clarendon Press, Oxford.
- Scantlebury, M., Speakman, J.R. & Bennett, N.C. (2006). The energy costs of sexual dimorphism in mole-rats are morphological not behavioural. *Proceeding of the Royal Society B: Biological Sciences*, **273**: 57 – 63.
- Schoener, T.W. (1968). Sizes of feeding territories among birds. *Ecology*, **49**: 123 – 141.
- Scott, J.P. (1966). Agonistic behaviour of mice and rats: a review. *American Zoologist*, **6**: 683 – 701.
- Selas, V., Framstad, E. & Spidso, T.K. (2002). Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. *Journal of Zoology, London*, **258**: 459 – 468.
- Sheard, J.B. (2007). National Rodent Survey Report 2006. National Pest Technicians Association, Nottingham, UK.
- Shumake, S.A. & Hakim, A.A. (2000). Evaluating Norway rat response to attractant and repellent odors to improve rodenticide baiting effectiveness. *Proceedings of Wildlife Damage Management Conferences*. pp.: 103 – 110. University of Nebraska, Lincoln.
- Silva, J.D., Woodroffe, R. & Macdonald, D.W. (1993). Habitat, food availability and group territoriality in the European badger, *Meles meles*. *Oecologia*, **95**: 558 – 564.

- Singleton, G.R., Brown, P.R., Pech, R.P., Jacob, J., Mutze, G.J. & Krebs, C.J. (2005). One hundred years of eruptions of house mice in Australia – a natural biological curio. *Biological Journal of the Linnean Society*, **84**: 617 – 627.
- Singleton, G.R., Sudarmaji & Suriapermana, S. (1998). An experimental field study to evaluate a trap-barrier system and fumigation for controlling the rice field rat, *Rattus argentiventer*, in rice crops in West Java. *Crop Protection*, **17**: 55 – 64.
- Singleton, G.R., Tann, C.R. & Krebs, C.J. (2007). Landscape ecology of house mouse outbreaks in south-eastern Australia. *Journal of Applied Ecology*, **44**: 644 – 652.
- Smith, R.H. (1994) Rodent control methods: non-chemical and non-lethal chemical. In A.P. Buckle & R.H. Smith (eds.) *Rodent Pests and Their Control*. pp: 109 – 125, CAB International, Oxon, UK.
- Smith, R.H. (1999) Population biology and non-target effects of rodenticides: trying to put the eco into ecotoxicology. *Advances in vertebrate pest management* (eds D.P. Cowan & C.J. Feare), pp.331-346. Vilander Verlag, Fürth.
- Solomon, M.E. (1949). The natural control of animal populations. *Journal of Animal Ecology*, **18**: 1 – 35.
- Southwood, T.R.E. & Henderson, P.A. (2000). *Ecological Methods* (3rd ed.). Blackwell Science Ltd., Oxford. pp. 575.
- Steen, H., Mysterud, A. & Austrheim, G. (2005). Sheep grazing and rodent populations: evidence of negative interactions from a landscape scale experiment. *Oecologia*, **143**: 357 – 364.
- Stensland, E., Angerbjorn, A. & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, **33**: 205 – 223.

- Stickel, L.F. (1979). Population ecology of house mice in unstable habitats. *Journal of Animal Ecology*, **48**: 871 – 887.
- Taitt, M.J. (1981). The effect of extra food on small rodent populations: 1. Deermice (*Peromyscus maniculatus*). *The Journal of Animal Ecology*, **50**: 111 – 124.
- Tattersall, F.H., Macdonald, D.W., Hart, B.J., Johnson, P., Manley, W. & Feber, R. (2002). Is habitat linearity important for small mammal communities on farmland?. *Journal of Applied Ecology*, **39**: 643 – 652.
- Tattersall, F.H., Macdonald, D.W., Hart, B.J., Manley, W.J. & Feber, R.E. (2001). Habitat use by wood mice (*Apodemus sylvaticus*) in a changeable arable landscape. *Journal of Zoology*, **255**: 487 – 494.
- Taylor, E.N., Malawy, M.A., Browning, D.M., Lemar, S.V. & DeNardo, D.F. (2005). Effects of food supplementation on the physiological ecology of female western diamond-backed rattlesnakes (*Crotalus atrox*). *Oecologia*, **144**: 206 – 213.
- Taylor, K.D. (1977). Common rat *Rattus norvegicus*. *The Handbook of British Mammals*. (eds. G.B. Corbet & H.N. Southern), p.p. 240 – 247. Blackwell Scientific Publications, Oxford.
- Taylor, K.D. (1978). Range of movement and activity of Common rats (*Rattus norvegicus*) on agricultural land. *Journal of Applied Ecology*, **15**: 663 – 677.
- Taylor, K.D. & Quay, R.J. (1978). Long distance movements of a common rats (*Rattus norvegicus*) revealed by radio tracking. *Mammalia*, **42**: 63 – 71.
- Taylor, K.D., Quay, R.J. & Gurnell, J. (1981). Comparison of three methods for estimating the number of common rats (*Rattus norvegicus*). *Mammalia*, **45**: 403 – 413.

- Taylor, R.H., Kaiser, G.W. & Drever, M.C. (2000). Eradication of Norway rats for recovery of seabird habitat on Langara Island, British Columbia. *Restoration Ecology*, **8**: 151 – 160.
- Tew, T.E., Todd, I.A. & Macdonald, D.W. (2000). Arable habitat use by wood mice (*Apodemus sylvaticus*). 2. Microhabitat. *Journal of Zoology*, **250**: 305 – 311.
- Thorpe, R.S. (1976). Biometric analysis of geographic variation and racial affinities. *Biology Review*, **51**: 407 – 452.
- Thorpe, R.S. (1981). The morphometrics of the mouse: a review. (ed. R.J. Berry) *Biology of the House Mouse. Symposium Zoological Society of London*, **47**: 85 – 125.
- Thorsen, M., Shorten, R., Lucking, R. & Lucking, V. (2000). Norway rats (*Rattus norvegicus*) on Fregate Island, Seychelles: the invasion; subsequent eradication attempts and implications for the island's fauna. *Biological Conservation*, **96**: 133 – 138.
- Todd, I.A., Tew, T.E. & Macdonald, D.W. (2000). Arable habitat use by wood mice (*Apodemus sylvaticus*). 1. Macrohabitat. *Journal of Zoology*, **250**: 299 – 303.
- Towns, D.R., Atkinson, I.A.E. & Daugherty, C.H. (2006). Have the harmful effects of introduced rats on islands been exaggerated?. *Biological Invasions*, **8**: 863 – 891.
- Traweger, D., Travnitzky, R., Moser, C., Walzer, C. & Bernatzky, G. (2006). Habitat preferences and distribution of the brown rat (*Rattus norvegicus* Berk.) in the city of Salzburg (Austria): implications for an urban rat management. *Journal of Pest Science*, **79**: 113 – 125.
- VandeBerg, J.R., Buschang, P.H. & Hinton, R.J. (2004). Absolute and relative growth of the rat craniofacial skeleton. *Archives of Oral Biology*, **49**: 477 – 484.

- Venables, L.S.V. & Leslie, P.H. (1942). The rat and mouse populations of corn ricks. *The Journal of Animal Ecology*, **11**: 44 – 68.
- Vernes, K. (2003). Fine-scale habitat preferences and habitat partitioning by three mycophagous mammals in tropical wet sclerophyll forest, north-eastern Australia. *Austral Ecology*, **28**: 471 – 479.
- Village, A. (1982). The home range and density of kestrels in relation to vole abundance. *Journal of Animal Ecology*, **51**: 413 – 428.
- Vyas, A., Kim, S.K., Giacomini, N., Boothroyd, J.C. & Sapolsky, R.M. (2007). Behavioral changes induced by *Toxoplasma* infection of rodents are highly specific to aversion of cat odors. *Proceedings of the National Academy of Sciences of the United States of America*, **104**: 6442 – 6447.
- Wallace, D.G., Gorny, B. & Whishaw, I.Q. (2002). Rats can track odors, other rats, and themselves: implications for the study of spatial bahavior. *Behavioural Brain Research*, **131**: 185 – 192.
- Ward, R.J. (1981). Diet and nutrition. (ed. R.J. Berry) *Biology of the House Mouse. Symposium Zoological Society of London*, **47**: 255 – 266.
- Wasserberg, G., Kotler, B.P. & Abramsky, Z. (2006). The role of site, habitat, seasonality and competition in determining the nightly activity patterns of psammophilic gerbils in a centrifugally organized community. *Oikos*, **112**: 573 – 579.
- Wauters, L.A., Gurnell, J., Preatoni, D. & Tosi, G. (2001). Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. *Ecography*, **24**: 525 – 538.

- Webbon, C.C., Baker, P.J., Cole, N.C. & Harris, S. (2006). Macroscopic prey remains in the winter diet of foxes *Vulpes vulpes* in rural Britain. *Mammal Review*, **36**: 85 – 97.
- Webster, J.P. (2001). Rats, cats, people and parasites: the impact of latent toxoplasmosis on behaviour. *Microbes and Infection*, **3**: 1037 – 1045.
- Webster, J.P. & Macdonald, D.W. (1995). Parasites of wild brown rats (*Rattus norvegicus*) on UK farms. *Parasitology*, **111**: 247 – 255.
- Weihong, J.I., Veitch, C.R. & Craig, J.L. (1999). An evaluation of the efficiency of rodent trapping methods: the effect of trap arrangement, cover type, and bait. *New Zealand Journal of Ecology*, **23**: 45 – 51.
- Whishaw, I.Q., Dringenberg, H.C. & Comery, T.A. (1992). Rats (*Rattus norvegicus*) modulate eating speed and vigilance to optimize food consumption: effects of cover, circadian rhythm, food deprivation, and individual differences. *Journal of Comparative Psychology*, **106**: 411 – 419.
- White, D.J. & Galef Jr., B.G. (1998). Social influence on avoidance of dangerous stimuli by rats. *Animal Learning & Behavior*, **26**(4): 433 – 438.
- Widdowson, E.M. & Cowen, J. (1972). The effect of protein deficiency and calorie deficiency on the reproduction of rats. *British Journal of Nutrition*, **27**: 85 – 95.
- Williamson, A.M. & Ng, K.T. (1980). Behavioral effects of iron deficiency in the adult rat. *Physiology and Behavior*, **24**: 561 – 567.
- Wojcik, A.M., Polly, P.D., Sikorski, M.D. & Wojcik, J.M. (2006). Selection in a cycling population: differential response among skeletal traits. *Evolution*, **60**: 1925 – 1935.

- Wolff, J.O. (2003). Density-dependence and the socioecology of space use in rodents. *Rats, Mice and People: Rodent Biology and Management* (eds Grant R. Singleton, Lyn A. Hinds, Charles J. Krebs & Dave M. Spratt), pp. 124 – 130. ACIAR Monograph No. 96.
- Wolton, R.J. & Flowerdew, J.R. (1985). Spatial distribution and movements of wood mice, yellow-necked mice and bank voles. (eds J.R. Flowerdew, J. Gurnell & J.H.W. Gipps). *The Ecology of Woodland Rodents Bank Voles and Wood Mice. Symposia of the Zoological Society of London*. **55**: 249 – 275.
- Wood, B.J. (1994). Rodents in agriculture and forestry. In A.P. Buckle & R.H. Smith (eds.) *Rodent Pests and Their Control*. pp: 45 – 83, CAB International, Oxon, UK.
- Yalden, D. (1999). *The History of British Mammals*. T & AD Poyser Ltd, London. pp. 305.
- Ylonen, H., Jacob, J., Davies, M.J. & Singleton, G.R. (2002). Predation risk and habitat selection of Australian house mice *Mus domesticus* during an incipient plague: desperate behaviour due to food depletion. *Oikos*, **99**(2): 284 – 289.
- Yom-Tov, Y. (2003). Body sizes of carnivores commensal with humans have increased over the past 50 years. *Functional Ecology*, **17**: 323 – 327.
- Yom-Tov, Y. & Geffen, E. (2006). Geographic variation in bodysize: the effects of ambient temperature and precipitation. *Oecologia*, **148**: 213 – 218.
- Yom-Tov, Y. & Yom-Tov, S. (2004). Climatic change and body size in two species of Japanese rodents. *Biological Journal of the Linnean Society*, **82**: 263 – 267.
- Yom-Tov, Y., Yom-Tov, S., Barreiro, J. & Blanco, J.C. (2007). Body size of the red fox *Vulpes vulpes* in Spain: the effect of agriculture. *Biological Journal of the Linnean Society*, **90**: 729 – 734.

- Yom-Tov, Y., Yom-Tov, S., MacDonald, D. & Yom-Tov, E. (2007). Population cycles and changes in body size of the lynx in Alaska. *Oecologia*, **152**: 239 – 244.
- Yom-Tov, Y., Yom-Tov, S. & Moller, H. (1999). Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *Journal of Biogeography*, **26**: 947 – 958.
- Zanette, L., Clinchy, M. & Smith, J.N.M. (2006). Combined food and predator effects on songbird nest survival and annual reproductive success: results from a bi-factorial experiment. *Oecologia*, **147**: 632 – 640.
- Zhou, Q., Huang, C., Li, Y. & Cai, X. (2007). Ranging behaviour of the Francois' langur (*Trachypithecus francoisi*) in the Fusui Nature Reserve, China. *Primates*, **48**: 320 – 323.