UNIVERSITY OF SOUTHAMPTON

BEHAVIOURAL ASPECTS DEFINING MALE DOMINANCE IN FERAL FARM CATS (*Felis silvestris catus*)

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Declaration

This thesis is the result of work done wholly while in registered postgraduate candidature. The work recorded in this thesis has been carried out by myself and the thesis written by myself.

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ABSTRACT

FACULTY OF SCIENCE

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BEHAVIOURAL ASPECTS DEFINING MALE DOMINANCE IN FERAL FARM CATS *Felis silvestris catus*

by Candida Anne d'Sa

Male dominance in group-living animals is traditionally assessed by observations of physical differences between individuals and their assumed priority of access to resources based on behavioural observations. This study of feral farm cats (*Felis silvestris catus*) attempted to qualify and quantify these aspects of dominance and thus determine the dynamics and strategies of the mating system of the cat.

Free-ranging adult males at two United Kingdom farms were radiotracked to determine home ranges. Home ranges were overlapping, although some contained exclusive sections, and all overlapped with female ranges. Core areas remained similar for all males, and were centred around the main human-mediated resource areas of the farms. Ranges and activity levels were affected by time of day. The size of the home range also correlated positively with body weight and age of the individual. At both farms, an older and heavier male was identified as having a significantly larger range than the other males. One of these males frequently travelled beyond radiotracking range and appeared to engage in aggressive bouts during these trips, suggesting the occurrence of resource defence.

At both farms, behavioural interactions between the cats were studied and analysed, and indicated the existence of a social hierarchy or ranking order among the males. This hierarchy may have been determined prior to this study, as no active defence of ranks (or resources) was observed among the study animals. The wider-ranging males identified from the home range study were recognised as being higher-ranking than their male conspecifics, based on their socially interactive behaviour within the colony.

Microsatellite analysis of the cats was carried out using DNA obtained from hair samples, in order to measure reproductive success of the individual males. It was found that the older, heavier, wider-ranging and higher-ranking males achieved the greatest rates of reproductive success, but genetic variability was low and some inbreeding was suspected. These males, although now classed as dominant, did not, however, completely monopolise mating opportunities; subordinate males from the farms and unknown males were also found to be fathering kittens in both study areas, suggesting a mating strategy whereby all males maximised their own reproductive success, but this remained relative to their rank within their home colony. Dominant males seeking resources outside their home colony most likely suffered a loss in rank in achieving mating success.

Such a successful mating system for relatively few males should be considered in the context of the domestic pet cat population, which is subject to heavy neutering rates yet continues to escalate, and the potential problems of a reduced gene pool must be addressed.

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CHAPTER 1: AN INTRODUCTION TO THE BEHAVIOUR AND ECOLOGY OF THE FERAL CAT

Traditional approaches to the study of male dominance in animals have focused on the individual's ability to achieve priority of access to all or any resources which enhance that individual's fitness. This involves the acquisition, defence and exploitation of these resources, ultimately to optimise and maximise reproductive success. For the most part, studies of male dominance have been largely based on observational research alone, and dominant individuals identified accordingly.

Among the Felidae, or cat family, truly social behaviour (outside the breeding season) is only exhibited by the lion (*Panthera leo*) and domestic cat (*Felis silvestris catus*), although coalitions may occasionally be formed by the cheetah (*Acinonyx jubatus*); males of the other, more solitary family members therefore play very different roles from their social relatives.

In this study of a group-living carnivore, the feral farm cat, dominance in males was measured by (a) quantifying seasonal home range (both in and out of the breeding seasons) and exploring the possible link between home range and an individual's age, size and body condition, (b) qualifying the ranks of individuals within the group by quantifying behavioural interactions of group members, thus searching for evidence of a social hierarchy, and (c) calculating male reproductive success using microsatellite analysis to establish paternity. Social systems can have profound effects on genetic structure, and by assessing the results of the home range study and relating them to analyses of the socially interactive and genetic relationships within the group, dominance may then be accurately defined and quantitative answers to the questions surrounding the mating system of *Felis silvestris catus* may be answered.

Despite domestication, the cat appears to have retained much of its ancestral behaviour. There are two main schools of thought for the reasons for this. First, although the cat has been domesticated for several thousand generations, man did not attempt to manipulate or control its breeding until relatively recently. The second factor to consider is the nutritional requirements of the cat. Cats are obligate carnivores and have lost the ability to synthesise certain key elements such as taurine, niacin, vitamin A and arachidonic acid; these days nutritionally complete catfoods are commercially available, but until relatively recently cats

would have had to rely on their own predatory skills in order to fulfil their dietary needs (Bradshaw, Horsfield, Allen and Robinson, 1999).

The feral cat, unlike other domesticated species, can be thought of as an intermediate between a wild and truly domestic species, due to its highly variable degree of dependence on man. Usually, it benefits from both shelter and supplementary feeding. Although man has little or no direct influence on its reproductive or ranging behaviour, indirectly, its social behaviour is determined largely by the resources afforded by man. Therefore, the feral cat maintains its commensal relationship with man and profits from his managed, domestic environment. Little research has been carried out on the reproductive behavioural ecology of the feral cat in terms of quantifying its mating strategies. Information such as this could be used to determine how dominant individuals may affect the population (both feral and domestic) as a whole, and may raise questions of the possible consequences of widespread neutering among domestic pet cat populations.

With the domestic cat now the most popular companion animal in the developed world (Anon., 1995), the need for a greater understanding of its ecology and social behaviour is evident and will aid the long-term management of the population.

1.1 Overview

The following sections aim to provide a detailed and comprehensive introduction to the study species, *Felis silvestris catus*, in terms of its evolution, history, ecology and social behaviour, based on a thorough review of published literature.

1.1.1 Evolution

All modern members of the Order Carnivora are linked by common descent from the miacids, the first true carnivores of 60 million years ago (mya). The palaeosabres, thought to represent the earliest cat-like carnivores, inhabited the North American jungles 40 mya (Macdonald, 1992). Another possible ancestor for the first true felid is *Proailurus*, a European species of 30 mya. However, the first definite member of the Felidae, or cat family was *Pseudaelurus*, classified on the basis of its bones, and dating from 20 mya (Macdonald, 1992). It crossed to North America and Asia via the Bering land-bridge between 20 and 16 mya.

The Felidae evolved alongside the Viverridae (civets and genets), Hyaenidae (hyenas) and Herpestidae (mongooses) from the Old World Viverravine lineage of the miacids, approximately 20 mya. The New World Vulpavines formed the sister branch stemming from the miacids, from which arose the Canidae (dogs), Ursidae (bears), Procyonidae (racoons and coatis) and Mustelidae (weasels) (Macdonald, 1992).

Recent molecular research has confirmed the presence of at least three felid lineages (Masuda, Lopez, Slattery, Yuhki and O'Brien, 1996). First, the **ocelot lineage** which represents the oldest surviving cat lineage, evolving 12 mya and consisting of small cats from South and Central America: the ocelot (*Felis pardalis*), tigrina (*F. tigrina*), margay (*F. wiedii*), pampas cat (*F. colocolo*), Geoffroy's cat (*F. geoffroyi*), kodkod (*F. guigna*) and mountain cat (*F. jacobita*). Second, the **wildcat lineage** which split off 8-10 mya and consists of the European wildcat (*F. silvestris*), African wildcat (*F. lybica*), jungle cat (*F. chaus*), sand cat (*F. margarita*), blackfooted cat (*F. nigripes*) and Pallas' cat (*F. manul*). About 4-6 mya a gradual divergence of mid-sized and large cats began, due to a dramatic change in the world's climate which severely affected the Carnivora; many older members of the cat family became extinct as forests were replaced with open scrub and savannah. These catastrophic changes remain unexplained: 13% of mammalian families and 73% of genera became extinct over a period of one million years (Macdonald, 1992). The most recent divergence of the Felidae (1.8-3.8 mya) produced a split of the lynxes and the big cats [Eurasian lynx (*Lynx lynx*), Canada lynx (*L. canadensis*), Iberian lynx (*L. pardinus*), bobcat (*L. rufus*), marbled cat (*Pardofelis marmorata*), clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), tiger (*P. tigris*), leopard (*P. pardus*), jaguar (*P. onca*), lion (*P. leo*)] of the **Panthera lineage** [puma (*F. concolor*), cheetah, Temminck's golden cat (*F. temminckii*), Bornean bay cat (*F. badia*), African golden cat *(F. aurata*), flat-headed cat (*F. planiceps*), leopard cat (*F. bengalensis*), rusty-spotted cat (*F. rubiginosa*), fishing cat (*F. viverrina*), Iriomote cat (*F. iriomotensis*), serval (*F. serval*), caracal (*F. caracal*), jaguarundi (*F. yaguarondi*)] (Kitchener, 1991; O'Brien, 1996).

It is from the wildcat lineage that the domestic cat (*Felis silvestris catus*) arose. The African wildcat is the species most likely to represent the ancestor of the domestic cat (see Ragni and Randi, 1986); the more northern species of wildcat shows both extreme timidity and extreme aggression, thus making it an unsuitable candidate for domestication (Wayne and Koepfli, 1996).

1.1.2 History of the domestic cat

In its very early stages, the domestication of the wildcat probably occurred in a similar manner to that of the wolf (*Canis lupus*) (family Canidae). Wolves were most likely attracted to human settlements 15,000 years ago by the lure of scraps to be scavenged from the remains of meals, and from this association with man arose the domestication process to the dog (*Canis familiaris*) (Clutton-Brock, 1995). Wildcats were attracted to human settlements by the ample source of prey in the form of ever-present commensal rodent pests. The widely held view is that the domestication of the wildcat originated in Egypt (Serpell, 1988; Macdonald, 1992; Bradshaw, 1993; Daniels, Balharry, Hirst, Kitchener and Aspinall, 1998). Early Egyptian civilisations of 5,000 years ago were wholly agronomic and relied on the cultivation of grain. Stored grain encouraged rodent pests.

The fundamental difference between the two domestication processes of dog and cat undoubtedly lies in the sociality of the species. Wolves are highly gregarious with a social system mirroring that of man; the evolution of the domestic dog therefore represents a process of true domestication. Wildcats, on the other hand, are solitary; their domestication occurred through commensalism (Clutton-Brock, 1996).

The Egyptians would have tolerated and even appreciated the cat for its pest control qualities. In this way the cat remained in the company of humans, gradually being recognised not only for its utilitarian attributes, but also as a companion animal: thus the domestic cat evolved.

The cat soon became an important symbol of Egyptian reverence and veneration. The male cat[1] was worshipped as it was believed to be sacred to the sun god Ra. Cats and lionesses were associated with the warlike goddess Sekhmet, and most importantly, the cat was seen as a representative of the cat goddess Bastet. Later, the Greeks and Romans introduced the cat to other regions of their empires, with the Romans taking the species to northern Europe and beyond. However, the demise of pagan worship in favour of Christianity in Europe between the twelfth and fourteenth centuries saw a complete reversal in attitudes to cats, which then became the symbol of the Antichrist for many centuries, suffering extreme religious persecution (Serpell, 1988, 2000).

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[1] The male and female cat are commonly referred to as "tom" and "queen" respectively. However, throughout this thesis, the terms "male" and "female" will be used.

Today however, the domestic cat outshines the domestic dog as the developed world's most popular pet (Anon., 1995).

1.1.3 The feral cat

The cat's tremendous adaptability, flexibility and fecundity have given it a world-wide distribution. Despite its importance as a pet and companion animal in many of today's societies and cultures, the vast numbers of domestic cats on every populated continent means that the potential for feralisation is very great. Feralisation is often considered to be a reversal of domestication, involving changes to both the genotype and the phenotype (Price, 1984, 1999). However, Daniels and Bekoff (1989) discussed feralisation from an ontogenetic viewpoint and defined it as a developmental process by which individual domestic animals either become de-socialised from humans, or never become socialised, and thus behave as untamed, non-domestic animals. The authors emphasised the behavioural changes affecting the individual and not necessarily the whole population. Feralisation varies among species depending mainly on their history of socialisation to humans.

Remfry (1996) defined feral cats as "domestic cats that have adopted or been born into a free-living lifestyle". Patronek (1998) described feral cats as "having been born in the wild and essentially having no human contact". However, he went on to explain how the status of individual cats can change from owned to un-owned, and house-dwelling to free-roaming, during short periods. A more concise definition of feral cats was given by Page, Ross and Bennett (1992) as simply "un-owned, unwanted and unconfined". Similarly Barratt (1997) classed feral cats as "domestic cats not attached to a particular household". The term *feral* should not be confused with *stray*; stray cats are previously-owned cats that have been abandoned or lost by their owners (Mahlow and Slater, 1996). In time, stray cats can become feral if they reduce and often eventually cease their dependence on, and socialisation to humans. Bradshaw *et al.* (1999) stated that the term *feral cat* refers to individuals or populations whose relationship with man may be described as partially commensal. This definition would therefore not include the populations found on remote, uninhabited islands (see Section 1.2.2).

The feral farm cat, the focus of this thesis, can be thought to represent an intermediate between the true feral cat and the true domestic cat[2]. It generally

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[2] The domestic cat may be feral, stray or pet. For the purpose of this study, I refer to the term "domestic" to describe the fully domesticated pet house cat; ferals and strays are named as such. The term "cat" refers to *Felis silvestris catus* and not to the wild Felidae.

shows a highly variable degree of dependence on humans, seeking both shelter and supplementary feeding (Niewold, 1986). However, unlike the domestic cat, man has little or no direct influence on its reproductive or ranging behaviour, and for this reason it is considered to be feral. Indirectly, the farm usually serves to provide shelter and nest sites, and a ready food source; thus the farm area will be encompassed into the farm cat's home range. Farm cats usually avoid direct physical contact with humans and are not generally considered to be tame.

1.1.4 Legislation

As a domestic species, cats, including feral cats are protected in the United Kingdom under the Cruelty to Animals Act 1876, the Protection of Animals Act 1911, the Abandonment of Animals Act 1960 and the Animals Act 1971. This latter legislation, which imposes a duty of care on owners of domestic dogs and livestock to take what is considered to be reasonable care to prevent their animals from straying onto roads, does not extend to cat owners.

Consequently, cats are free to roam and owners are not liable for damage caused by them except in extreme circumstances. However, this also means that there is no legal requirement under the Road Traffic Act 1988 for drivers to report road traffic accidents involving cats. Cat owners can, however, be prosecuted under the Public Health Act 1936 or the Environmental Protection Act 1990 if their cats are considered a nuisance or a health risk (information supplied by Cats Protection, 2002).

1.2 Feral cat control

Feral cats have been targeted for persecution and intensively controlled world-wide for three main reasons which shall be discussed below. Applied ecological techniques of studying feral cats have been employed for decades, mainly as methods of controlling populations (summarised by Gunther and Terkel, 2002).

1.2.1 Disease

The first reason prompting control of feral cats is their ability to spread disease. The incidence of transmission of most zoonotic diseases from feral cats to humans

is unknown, because, with the exception of rabies (see Nicholson, 1981; Krebs, Noll, Rupprecht and Childs, 2002) and plague (Eidson, Tierney and Rollag, 1988), few diseases are reportable at the national level (Patronek, 1998). Feral populations of cats are likely to harbour and transmit diseases more readily than pet cats (Yamaguchi, Macdonald, Passanisi, Harbour and Hopper, 1996), which benefit from veterinary care, higher-quality food and a relatively stress-free lifestyle. Disease spreads quickly through colonies of feral cats where interaction rates are high, and every cat, regardless of age, sex or status becomes vulnerable to infection through within-group transmission (Macdonald, Yamaguchi and Passanisi, 1998).

Feral cats are recognised as a source of toxoplasmosis (Frenkel, 1973) and other parasitic infections (see McColm, Hutchinson and Siim, 1981; Nichol, Ball and Snow, 1981; Patton, Johnson, Loeffler, Wright and Jensen, 1986; Bennett, Lloyd, Jones, Brown, Trees, McCracken, Smyth, Gaskell and Gaskell, 1990; Mtambo, Nash, Blewett, Smith and Wright, 1991; Yamaguchi *et al.*, 1996), and are also known to be susceptible to *Mycobacterium bovis* infection, which causes bovine tuberculosis (see Ragg, Moller and Waldrup, 1995; Wynne Jones and Jenkins, 1995; Gunn-Moore, Jenkins and Lucke, 1996; Monies, Cranwell, Palmer, Inwald, Hewinson and Rule, 2000). Wall, Threlfall, Ward and Rowe (1996) found feral cats in England were carrying and consequently shedding in their faeces a multidrug-resistant strain of *Salmonella typhimurium*. It is also thought that feral cats are linked to the spread of Lyme's disease in humans, possibly by dispersing infected ticks in the environment (Magnarelli, Anderson, Levine and Levy, 1990).

1.2.2 Predation

The second reason prompting feral cat control concerns their predatory impact on native fauna. Cats are obligate carnivores and generalist predators, relying on nutrients in animal tissues to meet their specific nutritional requirements (Bradshaw, 1992; Zoran, 2002). Although in many instances the prey choice of feral cats has been found to be similar to that of domestic cats, feral cats survive almost completely on natural prey and their absolute intake was calculated to be four times that of an average domestic cat (Liberg, 1984; Ruxton, Thomas and Wright, 2002). Furthermore, although opportunistic, feral cats may continue to feed on a species disproportionately to its abundance (Konecny, 1987b).

The feral cat has been the subject of intensive eradication and control programmes world-wide for the past three decades, particularly on southern oceanic islands. Cats are considered a direct predation threat to native wildlife (Clarke and Pacin, 2002), and in particular are held responsible for the decline of many avian and mammalian populations world-wide (see Boitani, 2001; Macdonald and Thom, 2001; Courchamp, Chapuis and Pascal, 2003; Woods, McDonald and Harris, 2003). Of all the species which are known to have become extinct on islands due to introduced predators, 26% have done so as a result of cat predation (King, 1985; see also Courchamp *et al.*, 2003). To achieve successful management of this predator, it has been necessary to study its ecology and behaviour, as well as that of its prey. With the protection of the prey populations considered a priority, conservation of the feline predators has, on the whole, been ignored and feral cats have been labelled pests and culled rather indiscriminately. Control techniques have largely been developed on islands (e.g. Van Aarde, 1978, 1980, 1983; Jones and Coman, 1981; Karl and Best, 1982; Apps, 1983, 1986; Brothers, Skira and Copson, 1985; Fitzgerald and Veitch, 1985; Kirkpatrick and Rauzon, 1986; Konecny, 1987a, 1987b; Van Rensburg, Skinner and Van Aarde, 1987; Van Rensburg and Bester, 1988; Bloomer and Bester, 1990, 1991; Seabrook, 1990; Eason and Frampton, 1991; Fitzgerald, Karl and Veitch, 1991; Nogales, Rodriguez, Delgado, Quilis and Trujillo, 1992; Clapperton, Eason, Weston, Woolhouse and Morgan, 1994; Tidemann, Yorkston and Russack, 1994; Martin, Twigg and Robinson, 1996; Nogales and Medina, 1996; Edwards, Piddington and Paltridge, 1997; Paltridge, Gibson and Edwards, 1997; Risbey, Calver and Short, 1997, 1999; Short, Turner, Risbey and Carnamah, 1997; Moller and Alterio, 1999; Molsher, Newsome and Dickman, 1999; Bester, Bloomer, Bartlett, Muller, Van Rooyen and Büchner, 2000; Edwards, DePreu, Shakeshaft and Crealy, 2000; Risbey, Calver, Short, Bradley and Wright, 2000; Wiseman, O'Ryan and Harley, 2000; Read and Bowen, 2001; Bester, Bloomer, Van Aarde, Erasmus, Van Rensburg, Skinner, Howell and Naude, 2002; Burbidge and Manly, 2002; Paltridge, 2002; Pontier, Say, Debias, Bried, Thioulouse, Micol and Natoli 2002; Say, Gaillard and Pontier, 2002; Short, Turner and Risbey, 2002). These include the artificial introduction of disease, shooting, trapping, hunting with dogs and poisoning.

1.2.3 Urban pest status

A third reason for the control of feral cats applies mainly to urban populations. Although cats are valued for their ability to control rodents and other pests near rural communities, where urbanisation encroaches on these areas, the cats

themselves are often considered pests (see Hilsenroth, 1999; Griffin, 2001; Gunther and Terkel, 2002). Feral cats are generally regarded as a nuisance because of their noisy courtship, territorial behaviour, fecundity and urine spraying by males (Zaunbrecher and Smith, 1993; Natoli, Ferrari, Bolletti and Pontier, 1999). Feral cats are known to form colonies in both urban and rural environments such as dockyards (Dards, 1978, 1983; Dards and Robinson, 1983), hospitals and factories (Nichol *et al.*, 1981; Southam, 1981), farms (Macdonald, Apps, Carr and Kerby, 1987), archaeological ruins (Natoli, 1983, 1984, 1985a, 1985b, 1989, 1990; Natoli and DeVito, 1987, 1988, 1991; Natoli *et al.*, 1999) and rubbish tips (Izawa, Doi and Ono, 1982; Calhoon and Haspel, 1989; Haspel and Calhoon, 1989; Denny, Yakovlevich, Eldridge and Dickman, 2002). There is evidence to suggest that females in feral populations have higher fecundity than their domestic counterparts (Hilsenroth, 1999).

Whilst they are mostly perceived as pests, there are documented instances when even feral cats have fulfilled the need for the human-animal bond (Wells, Rosen and Walshaw, 1997), particularly those colonies regularly fed by caring individuals (Natoli *et al.*, 1999; Centonze and Levy, 2002).

1.2.4 Surgical and hormonal control

In addition to the various control methods detailed above for the reduction in feral cat numbers, some rather more humane methods have been developed.

Trap-neuter-release programmes were initiated in the United Kingdom and still constitute the major part of the work of various cat welfare charities. Many studies have concentrated on the long and short-term effects of neutering cat colonies. Hart and Barrett (1973) found that life expectancy increases in neutered cats, particularly males. Rees (1981) detected no observable changes in the behaviour of the cats after neutering, and even found that groups became more stable and better defined. Remfry (1982, 1996) investigated the long-term success of such neutering programmes, and found survival rates of 70% on the cats' original site for up to five years after neutering, provided that the cats continued to receive supplementary feeding. Neville and Remfry (1984) studied the behaviour of individuals and groups of cats before and after a neutering programme had taken place and concluded that the methods used were both humane and effective (see also Smith and Shane, 1986; Tabor, 1989; Zaunbrecher and Smith, 1993; Inserro, 1997; Anon., 1999; Gibson, Keizer and Golding, 2002). However, trap-neuter-

release programmes do not provide the ultimate solution to the problem of feral cats, as other (un-neutered) cats tend to migrate in if food and shelter are available (Hilsenroth, 1999). Further opposition to these programmes has been expressed by Gross, Hoida and Sadeh, 1996.

Trapping and euthanasia of feral cats with placement of kittens and docile elderly cats in homes, is widely carried out in the United States (Mahlow and Slater, 1996). Other methods of control include the use of vasectomy (Mahlow and Slater, 1996; Hilsenroth, 1999), prolactin inhibitors (Jöchle and Jöchle, 1993), contraceptives in the form of progestational steroids (Remfry, 1996), and other immunocontraceptive methods (Anon., 1998; Gorman, Levy, Hampton, Collante, Harris and Brown, 2002).

1.3 Social behaviour

1.3.1 Carnivore social behaviour

The common classification of a carnivore species as either group-living or solitary, social or asocial, monogamous or polygynous, often fails to recognise a high level of intraspecific behavioural variability (Gompper and Wayne, 1996). Some essentially group-living species may adopt a solitary lifestyle when performing certain behaviours such as foraging (e.g. Ethiopian wolf (*Canis simensis*): Sillero Zubiri and Gottelli, 1995). Other species previously perceived as solitary may show spatial variability in degrees of sociality (e.g. red fox (*Vulpes vulpes*): Doncaster and Macdonald, 1991). In contrast to some other mammalian orders, members of the Carnivora do not commonly live in groups; only about 10-15% of all species aggregate at some period outside of the breeding season (Gittleman, 1989). Creel and Macdonald (1995) found that the majority of species (85-90%) are solitary outside of mating periods (not including temporary associations between mothers and offspring).

1.3.2 The Resource Dispersion Hypothesis (RDH)

Carnivores were previously thought to live in groups for three main reasons: cooperative hunting of larger prey, communal defence and cooperative reproduction including alloparental behaviour. Certainly, group-living carnivores do benefit from one or all or these attributes (Packer, Scheel and Pusey, 1990). Corbett (1979)

suggested that grouping allows the animal to make maximum use of clumped food resources. However, Macdonald's (1983) Resource Dispersion Hypothesis (RDH) has become the most popular theory on group-living. He suggested that carnivore society may in fact be influenced by the dispersion and abundance of available resources, particularly food. It is possible to apply the RDH to all social systems. In an environment where food is patchily available, the RDH predicts that group sizes are determined by the dispersion of these patches (Kruuk and Macdonald, 1985; Johnson, Kays, Blackwell and Macdonald, 2002; Valenzuela and Macdonald, 2002). At rich and abundant food patches, high densities of animals are found and territorial behaviour is rare or absent (see Section 1.3.4). It is thought that in such cases, the presence of surplus food may alleviate the need to maintain a feeding territory – it may also be impossible for a single animal to defend a territory where many others come to feed (Macdonald, Courtenay, Forbes and Mathews, 1999). A minimal home range will be of a size that allows an animal assurance of finding sufficient resources within its range (Carr and Macdonald, 1986; Creel and Macdonald, 1995). The spacing pattern of individuals within a population is therefore a consequence of the reactions of each individual to one another and the environment (White and Harris, 1994). Ultimately, the spacing pattern in a population will be the result of the tactics chosen by the individual animals in their attempts to survive and maximise reproductive success (Sandell, 1989).

1.3.3 Cat sociality

Cats live under a large diversity of socio-ecological conditions on every inhabited continent. Their social behaviour is, not surprisingly, extremely variable, ranging from relatively solitary (Page *et al.*, 1992; Genovesi, Besa and Toso, 1995) to gregarious and cooperative (Macdonald *et al.*, 1987) and in varying associations with humans.

Their closest relative, the African wildcat, is a solitary species, as are all the other members of the wildcat lineage. Among the wild Felidae, the lion is the only true social species (Packer *et al.*, 1990) with the cheetah sometimes forming variable coalitions and Temminck's golden cat loosely forming pairs (Ortolani and Caro, 1996). Creel and Macdonald (1995) mention lions and farm cats as examples of social species within predominantly solitary families, which sometimes breed in large groups.

Among the other Viverravine families, the Viverridae exhibit variable sociality; most genets and civets (subfamily Viverrinae) and palm civets (subfamilies Paradoxurinae and Hemigalinae) are solitary foragers but some form short-lived family associations. Of the Hyaenidae, hyenas (spotted hyena (*Crocuta crocuta*), brown hyena (*Hyaena brunnea*), striped hyena (*H. hyaena*)) have complex social relationships; aardwolves (*Proteles cristatus*) usually form pairs. In the Herpestidae, the majority of species are solitary. A few form pairs for variable lengths of time; at least eight species are highly social (Kingdon, 1997).

It was suggested by Liberg (1980) that the process of domestication in cats increased the selection for grouping around human settlements, which supplied ample food and shelter. With the exception of the solitary-living feral cats inhabiting sub-Antarctic oceanic islands, most other cats studied to date have received some degree of supplementary feeding and usually in the form of an abundant and predictable source, either directly or indirectly, from humans. In fact, group-living has never been clearly documented in cat populations surviving solely on natural prey (Liberg and Sandell, 1988). Cats may be fed in the household, as with true domestic cats (e.g. Barratt, 1997); urban feral cats may be fed regularly by caring individuals (e.g. Dards, 1978; Natoli, 1985b, Natoli *et al.*, 1999); farm cats are either fed by the farmer or else scavenge from human table scraps and animal foodstuffs usually readily available (Macdonald *et al.*, 1987); other feral cats may feed from rubbish tips (Izawa *et al.*, 1982; Calhoon and Haspel, 1989; Haspel and Calhoon, 1989; Denny *et al.*, 2002).

Returning to the RDH, the resources at stake for the domestic or feral cat differ according to gender. Many studies of home range and spatial organisation in cats have led to similar conclusions: female range size is determined by food abundance and distribution as well as shelter sites; male ranges are determined by the density and distribution of females (Macdonald *et al.*, 1987; Kerby and Macdonald, 1988; Liberg and Sandell, 1988; Yamane, Ono and Doi, 1994; Macdonald, Yamaguchi and Kerby, 2000). Alternatively, in terms of reproduction it is clear that female reproductive success is linked to an ability to exploit resources in order to successfully produce and raise kittens, whilst male reproductive success depends only on an ability to secure females (Gehrt and Fritzell, 1998).

1.3.4 Home range

The concept of a "home range" or "territory" has been defined and redefined many times (for reviews see Burt, 1943; Jewell, 1966; Kaufmann, 1983; Maher and Lott, 1995). Most authors do not distinguish between home range and territory, but the latter is more commonly considered to involve some element of defence associated with priority of access to one or more resources within the territory; territory may be defined as a defended space, so this would imply that some form of territorial behaviour is required to be exhibited by the territory-holder. Territoriality is undoubtedly linked to the acquisition of resources (Kaufmann, 1983). Powell (2000) did, however, link home range and territory in his definition: "A territory is an area within an animal's home range over which the animal has exclusive use, or perhaps priority use". Home range however, may be defined more simply as "a more or less restricted area within which an animal moves when performing its normal activities" (Harris, Cresswell, Forde, Trewhella, Woollard and Wray, 1990). Home ranges or territories cannot be constructed or established at random, because resources (such as food, water, dens and mates) do not occur randomly in space (Johnson *et al.*, 2002). Furthermore, animals may not have free and equal access to all areas when establishing their home range. Garshelis (2000) postulated that home ranges may be established near the natal area simply due to familiarity with resources or neighbouring animals and not because of habitat composition.

Roper, Shepherdson and Davies (1986) considered territory on the basis of reproductive success as the defining resource, and males exhibiting territoriality were doing so in order to control mate access. The authors suggested that territory size, therefore, was determined by the spacing behaviour of dominant males.

In terms of food as the resource, a home range contains a finite potential energy resource which is proportional to its area (Lindstedt, Miller and Buskirk, 1986); home range can therefore be thought of as a measure of energy availability. The same authors stated that in carnivore species, home range size scales linearly to body mass. Home range size correlates directly to prey availability for many carnivore species (see Fuller and Sievert, 2001).

1.3.5 Home range in cats

Most studies of spatial organisation in cats have involved the use of radiotracking (or radiotelemetry) in order to determine home ranges (e.g. Macdonald and Apps, 1978; Corbett, 1979; Liberg, 1980; Schär and Tschanz, 1981, 1982; Izawa *et al.*, 1982; Jones and Coman, 1982b; Warner, 1985; Apps, 1986; Fitzgerald and Karl, 1986; Niewold, 1986; Turner and Mertens, 1986; Konecny, 1987a; Macdonald *et al.*, 1987; Calhoon and Haspel, 1989; Haspel and Calhoon, 1989; Langham and Porter, 1991; Langham, 1992; Page *et al.*, 1992; Genovesi *et al.*, 1995; Mirmovitch, 1995; Barratt, 1997; Norbury, Norbury and Heyward, 1998; Weber and Dailly, 1998; Moller and Alterio, 1999; Hall, Kasparian, Van Vuren and Kelt, 2000; Edwards, DePreu, Shakeshaft, Crealy and Paltridge, 2001; Naidenko and Hupe, 2002). Say *et al.* (2002b) used the walked-line transect method for estimating the density of cats; other studies relied solely on observation to determine home ranges (e.g. Dards, 1978; Panaman, 1981).

Home range has varied tremendously, from as small as 0.72ha for adult males (Izawa *et al.*, 1982; Yamane *et al.*, 1994) to as large as 2,210.5ha (Edwards *et al.*, 2001). Nocturnal home range, where measured, has been found to be larger than diurnal (Langham and Porter; 1991; Barratt, 1997) and dominant[3] individuals generally had larger home ranges than subordinate individuals (Corbett, 1979; Fitzgerald and Karl, 1986; Niewold, 1986; Turner and Mertens, 1986; Langham, 1992; Barratt, 1997).

1.3.6 Spatial organisation in cats

Solitary carnivores are expected to form spatial groups when heterogeneity of resources is high and competition for these resources is low. For a species previously considered to be solitary (e.g. Leyhausen, 1979), feral cats spend more time together than would be expected by chance (Macdonald *et al.*, 1987). Liberg and Sandell (1988) suggested that for cats, group formation occurs when a concentrated and stable food resource large enough to support more than one individual is available. As with most group-living carnivores, a certain degree of hierarchical organisation exists in cat societies, which serves to reduce aggressive encounters (and probably inbreeding – see Section 1.4.2).

[3] For an explanation of dominant and subordinate behaviour, see Section 1.5.

Cat society is generally centripetally organised around a core, or Central Resource Area, CRA (Macdonald *et al.*, 1987). Where these more uniform, homogeneous and richer resources occur, cats have smaller home ranges with greater degrees of overlap; densities of cats are high (Izawa *et al.*, 1982; Natoli, 1985b; Apps, 1986; Turner and Mertens, 1986; Konecny, 1987a; Langham and Porter, 1991; Mirmovitch, 1995; Ishida and Shimizu, 1998; Weber and Dailly, 1998). Patchy, heterogeneous and more sparse resources attract lower densities of cats which in turn have larger home ranges (Macdonald and Apps, 1978; Konecny, 1987a; Cromwell-Davis, Barry and Wolfe, 1997).

At high resource levels, cats exhibit little or no territoriality and ranges overlap considerably (Laundré, 1977; Dards, 1978; Panaman, 1981; Izawa *et al.*, 1982; Natoli, 1985b; Warner, 1985; Apps, 1986; Konecny, 1987a; Cromwell-Davis *et al.*, 1997; Norbury *et al.*, 1998; Weber and Dailly, 1998); at low resource levels cats are found at lower densities and are generally territorial. These cats are asocial and adopt a lifestyle more akin to their wildcat relatives (Dards, 1978; Corbett, 1979; Page *et al.*, 1992; Genovesi *et al.*, 1997). In Genovesi *et al.*'s (1997) study, the solitary feral cats even exhibited annual parturition, unlike domestic cats which are usually seasonally polyoestrous. At very low resource levels, territories are too energetically expensive to maintain (Konecny, 1987a).

At clumped and abundant food resources, females form stable, philopatric, matrilineal groups (Laundré, 1977; Dards, 1978; Fagen, 1978; Macdonald and Apps, 1978; Liberg, 1980; Panaman, 1981; Izawa *et al.*, 1982; Schär and Tschanz, 1982; Natoli, 1983, 1985b; Fitzgerald and Karl, 1986; Turner and Mertens, 1986; Macdonald *et al.*, 1987; Kerby and Macdonald, 1988; Liberg and Sandell, 1988; Genovesi *et al.*, 1995; Mirmovitch, 1995; Cromwell-Davis *et al.*, 1997; Yamane, Emoto and Ota, 1997). Among lions, the only other truly social felid, females are also strongly philopatric (Packer *et al.*, 1991; Spong, Stone, Creel and Björklund, 2002). Natal philopatry appears to be at the base of sociality in all carnivore groups (Waser, 1996).

Synchronised breeding results in cooperative reproduction including communal nest sites and allosuckling of the young (Macdonald *et al.*, 1987). Female home ranges show less overlap than males, and females are considered to be philopatric. Although females generally have significantly smaller home ranges than males (Dards, 1978; Corbett, 1979; Liberg, 1980; Schär and Tschanz, 1981; Natoli, 1984; Fitzgerald and Karl, 1986; Macdonald *et al.*, 1987; Langham, 1992;

Mirmovitch, 1995; Cromwell-Davis *et al.*, 1997), they often have high energy requirements, for example during pregnancy and lactation. Therefore they need to select areas of high productivity and be intrasexually more exclusive (Turner and Mertens, 1986; Konecny, 1987a).

However, the degree of overlap is thought to be determined by kinship (Langham and Porter, 1991; Barratt, 1997). This can also be seen in pet cats; females from separate houses (assumed to be unrelated) do not have overlapping home ranges (Schär and Tschanz, 1981; Barratt, 1997; Cromwell-Davis *et al.*, 1997). Males however, do have home ranges which overlap with males from other households (Barratt, 1997; Horsfield, 1998) but in many cases they avoid each other both spatially and temporally. Creel and Macdonald (1995) distinguished between shared and encompassing home ranges, with the former including only those cases in which individuals have similar, essentially identical ranges. The authors also stated that with encompassing home ranges, not all individuals are considered to have come from a single breeding group.

Males move between the various groups of females. Consequently, as stated above, male home ranges can be overlapping and include those of several groups of females (Laundré, 1977; Dards, 1978, 1983; Liberg, 1980; Natoli, 1985b; Warner, 1985; Fitzgerald and Karl, 1986; Niewold, 1986; Konecny, 1987a; Liberg and Sandell, 1988; Langham and Porter, 1991; Langham, 1992; Mirmovitch, 1995; Cromwell-Davis *et al.*, 1997; Weber and Dailly, 1998). In the presence of an oestrous female, males are not thought to avoid each other but instead appear to form aggregations in the courtship areas (Liberg, 1980).

1.4 Reproductive behaviour

The basic reproductive biology of the cat has been studied intensively as the domestic cat has risen in popularity as a pet and companion animal. In fact, the cat has become an important model system for developing artificial technologies (e.g. semen cryopreservation, artificial insemination and *in vitro* fertilisation) to promote captive management and breeding of wild and often endangered felids (Goodrowe, 1992; Goodrowe, Walker, Ryckman, Mastromonaco, Hay, Bateman and Waddell, 2000).

At a molecular level, the full resolution of the cat's genome sequence is currently underway, which, when complete, will hold considerable value for human genome annotation, for veterinary medicine, and for insight into the evolution of genome organisation among mammals (O'Brien, Menotti-Raymond, Murphy and Yuhki, 2002).

1.4.1 The cat mating system

The mating system of the cat ranges from promiscuity to polygyny, according to environmental conditions (Say, Devillard, Natoli and Pontier, 2002. For a review of mammalian mating systems, see also Clutton-Brock, 1989). Females are seasonally polyoestrous (Sanchez and Silva, 2002) and may produce up to three litters per year; oestrus is thought to be influenced by length of daylight (Jones and Coman, 1982a). In one period of oestrus, the female is attracted to males for six to eight days, during which time she permits and, in fact, actively seeks copulations for the last four to six days (Bradshaw, 1992). Cats are induced ovulators (females must copulate several times with the same or different males in order for intromission to induce ovulation (Hunter, Petrie, Otronen, Birkhead and Møller, 1993; Lawler, Johnston, Hegstad, Keltner and Owens, 1993; Schramm, Briggs and Reeves, 1994), with ovulations occurring 24-50 hours after copulation (Liberg, 1983); successive copulations are much more likely to induce ovulation than only one. Therefore, females would be expected to actively seek repeated copulations. The concept of induced ovulation is thought to be unique to mammals (Hunter *et al.*, 1993).

1.4.2 Inbreeding avoidance

There are several theories attempting to explain the adaptive significance of females copulating with multiple males (for a review, see Hosken and Blanckenhorn, 1999; also Jennions and Petrie, 2000; Zeh and Zeh, 2001; Stockley, 2003), but that of inbreeding avoidance appears to be the strongest. Breeding between close relatives maximises the likelihood of genetic incompatibility (Tregenza and Wedell, 2002; Stockley, 2003), often with deleterious consequences (Cooney and Bennett, 2000). Inbreeding is typically associated with low fitness (e.g. Wildt, Bush, Goodrowe, Packer, Pusey, Brown, Joslin and O'Brien, 1987; Amos, Worthington Wilmer, Fullard, Burg, Croxall, Bloch and Coulson, 2001).

However, a study by Natoli, DeVito and Pontier (2000) found that female cats did not choose mates among the different males available. In contrast, Ishida, Yahara, Kasuya and Yamane (2001) found that feral female cats did not accept all mounting or copulation attempts by males during their oestrous period, and suggested that the females controlled paternity of their offspring during copulation; females avoided breeding with close relatives. It has been suggested that because subordinate individuals often lack access to unrelated mates, they limit their reproduction as a means of avoiding inbreeding (Cooney and Bennett, 2000).

Interestingly, a population of cats studied by Devillard, Say and Pontier (2003) were found to be highly inbred, but the authors did not observe any decrease of litter size, survival probabilities or body weight of the offspring, suggesting there are low costs of inbreeding in cats.

Gestation in cats lasts approximately 63 days and litters consist of an average of four to five kittens in the wild (Bradshaw, 1992). There is no paternal care; this stands to reason given that a male is unlikely to invest paternal care in a female's offspring if he cannot be "sure" that he is the father of those offspring (Hunter *et al.*, 1993; Jennions and Petrie, 2000), and oestrous female cats mate repeatedly with many different males. It has been suggested that males are not expected to provide care if they can enhance their reproductive success to a greater extent by seeking other matings (Woodroffe and Vincent, 1994; Neff, 2003). As with all mammals, the sole source of nutrition for newborn kittens is lactation, so female cats are obligated to provide a certain minimum amount of care to their offspring (Bales, French and Dietz, 2002).

1.4.3 Cooperative breeding

In feral cats, generally one to two litters are produced per year, one in the spring and another in late summer/early autumn. Dards (1983) however, observed sexual behaviour throughout the year, with peaks in the spring and autumn; this is consistent with observations by breeders of domestic cats (V. Anderson, pers. comm.). Among group-living feral cats, oestrus is usually synchronised (Liberg, 1983), although asynchrony has also been recorded in large groups (Natoli and DeVito, 1988). Synchronised periods of oestrus are thought to occur in order to procure the benefits of communal nursing and defence of the young. Such cooperative breeding is common in cats and is thought to be associated with the reduced dispersal of female offspring when cats have clumped and abundant food

resources (Deag, Manning and Lawrence, 2000). Cooperative behaviour has not been documented in feral cats living more solitary lifestyles without resources provided by man. For a more detailed study on cooperative breeding, see Clutton-Brock, 2002.

Communal rearing, and more specifically non-offspring nursing (or allosuckling behaviour) has also been studied extensively in lions (e.g. Packer, Lewis and Pusey, 1992), and is thought to be most common when the costs to the lactating female are low. For example, lionesses with smaller litters (with presumably more milk to spare) allosuckle more than those with larger litters. Allosuckling occurs more with closely related kin. Furthermore, lionesses give more milk to non-offspring as their own cubs grow older and need less milk themselves (Pusey and Packer, 1994).

Of the social felids, reproductive suppression (the tendency of females to curtail reproductive functioning of another female) of subordinate females by dominant females within a colony has not been reported in feral cats or lions (Jennions and Macdonald, 1994; Creel and Macdonald, 1995) but occurs in varying degrees in other carnivores, e.g. Ethiopian wolves (Sillero Zubiri, Gottelli and Macdonald, 1996).

1.4.4 Dispersal

Dispersal is generally thought to have evolved to minimise inbreeding and/or competition among relatives (Spong *et al.*, 2002). As discussed above, the majority of literature relating to dispersal in cats states that this behaviour is male-biased and depends on environmental conditions. Where promiscuous, high-density colonies exist, such as in urban habitats, the lack of, or reduction in resource defence by male cats means that male dispersal is rare. However, for polygynous cats living under low densities, where the males actively defend the resources available, male dispersal is usual (Liberg, 1980; Say, Pontier and Natoli, 1999; Liberg, Sandell, Pontier and Natoli, 2000). Male dispersal is also seen in the lion, the other social felid (Packer and Pusey, 1982), and generally in polygynous and promiscuous mammals (Waser, 1996).

However, in a recent study by Devillard *et al.* (2003), the authors found that in a promiscuous, high-density urban population of feral cats, it was the adult females (between one and two years of age) that dispersed. Prior to dispersal, these females had enjoyed reproductive success equalling that of the non-dispersing

females. It was concluded that under such conditions, the females were competing for suitable den sites, leading to breeding dispersal (in contrast to natal dispersal which occurs before the first reproduction) of the less competitive females.

1.5 Dominance

Traditionally, the term "dominance" has been defined and redefined many times in terms of either one of the following two factors, or a combination of both. The first of these factors is priority of access to resources. It is usually assumed that a dominant animal has priority of access to all resources, which, in animal behaviour, account for food, mating opportunities and dens. A dominant animal may also have a greater home range than a subordinate animal, because a wider-ranging male should, in theory, have the highest encounter rates with females. Fisher and Lara (1999) suggested that for solitary species, wide-ranging males are more likely to find uncontested females. However, these authors, in their study of bridled nailtail wallabies (*Onychogalea fraenata*), discovered that even the smaller males achieved a degree of reproductive success by increasing their home ranges, which enabled them to encounter the more solitary of the females.

The second factor defining dominance is overt agonistic interaction. It should be noted that a dominant animal is not necessarily the most aggressive *per se*, but the one that generally prevails in agonistic encounters when they occur.

In some populations where natural selection may have favoured dominant individuals to the extreme, virtually all genes conducive to subordination may have been eliminated from the population, and individual ranks are only altered due to chance events such as changing environmental circumstances (Ellis, 1995).

Many definitions of dominance are given in reviews by Dewsbury (1982), Kaufmann (1983), Drews (1993) and Ellis (1995). Other factors commonly considered to influence dominance, particularly among males, are age and body size (the latter can surely be positively correlated to the outcome of aggressive encounters). Male body weight may influence priority of access to oestrous females (larger males gain a competitive advantage), and is often related to the age of the animal (e.g. Fisher and Lara, 1999).

A biochemical, rather than physical difference distinguishing dominant and subordinate animals may also exist. Several studies of male rats and mice (e.g. by Hardy, Sottas, Ge, McKittrick, Tamashiro, McEwan, Haider, Markham, Blanchard, Blanchard and Sakai, 2002) found that subordinate males had higher levels of corticosterone (a steroid hormone produced in the adrenal cortex during times of stress) than dominant males – dominance being defined according to the outcome of agonistic encounters. Whilst generally this finding is consistent with many other studies relating dominance and corticosterone levels, there are some exceptions. Littin and Cockrem (2001) found no correlation between social rank and corticosterone concentrations in laying hens (*Gallus domesticus*). However, it has been found that in dogs and humans, stress hormones are produced in conjunction with both the fight and flight mechanism, i.e. stress may be experienced by both dominant and subordinate individuals and therefore glucocorticoid levels alone should not be taken as a measure of dominant or subordinate behaviour (T. Barlow, pers. comm.).

In some species, a dominance hierarchy forms, whereby the animals arrange themselves into a priority order for access to the available resources (Broom, 2002). This hierarchy sometimes takes a linear form, with a dominant alpha animal at the top of the hierarchy. For group-living males, it is thought that pre-determined dominance hierarchies evolved. In such social species, animals in the hierarchy have constant individual knowledge of each other's competitive ability (Leyhausen, 1979; Fisher and Lara, 1999). In solitary species, dominance is not pre-determined but instead established at each mating because males are unaware of any physical changes in their conspecifics males between the breeding seasons.

Leyhausen (1979) maintained that dominant and subordinate behaviour in cats, on the basis of the outcome of aggressive encounters, depended on the two animals' relationship to their surroundings: "relative hierarchies" were formed where rank was determined only in relation to the place and time of the encounter (territorial fighting), in contrast to "absolute hierarchies" where the strongest animal in the group enjoyed uncontested top rank (following fighting between rivals on neutral ground). This is consistent with Kaufmann (1983), who postulated that dominance hierarchies were representative of absolute dominance, and territorial behaviour was representative of relative dominance.

1.5.1 Dominance and reproductive success

An animal's priority of access to resources includes its priority of access to mating opportunities. Dominant males are assumed to accomplish greater reproductive success than subordinate males. The males fathering the most offspring are assumed to have exerted some form of dominance over the other competing males. In many species, most notably birds, this dominance may take the form of excessively elaborate adornments and displays by the males (e.g. peacocks (*Pavo cristatus*) and bower birds (*Ptilonorhynchus violaceus*) (Krebs and Davies, 1993), which influence female choice. A recent study of lions by West and Packer (2002) found that the shade of the male's mane also influenced female choice, with darker manes correlating to higher levels of nutrition and testosterone. Similarly, Hirotani (1994) found that the size and complexity of reindeer (*Rangifer tarandus*) antlers influenced dominance rank and hence reproductive success.

There is no published literature suggesting that any sexually-related dimorphisms exist in male cats. From personal observation, older, heavier male cats have larger jowls, but there is no evidence to suggest that this on its own is a reason for greater reproductive success. However, Utami, Goossens, Bruford, DeRuiter and Van Hooff's (2002) study of reproductive success in male Sumatran orang-utans (*Pongo pygmaeus abelii*), found that males with full secondary sexual characteristics such as cheek flanges, actively prevented unflanged males from copulating with females.

On the basis of a lack of evidence to suggest otherwise, it is assumed that reproductive success in male cats is determined only by social dominance and may be influenced by female choice. Say, Pontier and Natoli (2001) found that male reproductive success was far greater when females bred asynchronously, with dominant males fathering the highest proportion of offspring. This may be explained by the theory that synchronously-breeding females cannot easily be monopolised by a single male, even a dominant one. The relationship between male dominance and reproductive success has been a subject for exploration for some years now, in cats (see Section 1.5.2 below) and in other species (see also Dewsbury, 1982; Hirotani, 1994; Ellis, 1995; Bartmann and Gerlach, 2001; Røed, Holand, Smith, Gjøstein, Kumpula and Nieminen, 2002). Studies have been greatly enhanced by the relatively recent development of molecular techniques (see Section 1.6.2) enabling reproductive success to be quantified and not simply

estimated, thereby determining whether male dominance does, in fact, equate to reproductive success.

1.5.2 Male mating tactics in cats

For the domestic cat, Liberg (1983) described a mating system whereby a dominant or "central" male monopolised matings and remained physically closer to the female in oestrus than the subordinate "peripheral" males. Central males were generally older and larger than peripheral males. The central male remained with the female whilst she was receptive and then often moved off to another group of females in oestrus, leaving the subordinate males to copulate with any other females coming into oestrus. Pontier and Natoli (1996) described one instance when one individual feral male cat almost completely monopolised all the females in the study area, siring 95.5% of kittens in one year. However, as the authors correctly pointed out, the mating system of feral cats cannot by considered polygynous on the basis of a single study.

Natoli and DeVito (1987) found that urban feral male cats securing the most matings were not necessarily those considered to be dominant on the basis of the results of agonistic encounters, and their second study (Natoli and DeVito, 1988) failed to identify a central or peripheral male (Liberg, 1983). Instead, several males simultaneously courted the same female during a single oestrous period and remained equidistant to her. They appeared to hold equal status in terms of access to the female, with no evident hierarchies. The authors found no positive correlation between the amount of time spent in close proximity to the female in oestrus and percentage of successful (with intromission) mounts. These "occasional" males may be leaning towards the more successful strategy. All males copulated with the oestrous females, although not always achieving intromission.

However, they did identify two types of male: those that remained with the female constantly while she was receptive, and those that did not. The latter males appeared for a short while and then left. These findings were supported by a later reassessment of the data by the same authors (Natoli and DeVito, 1991), emphasising that a long-stay, central position close to the female is not necessarily a better reproductive strategy for the male cat. However, these regular males were thought to be dominant, based on observations of the body language of the cats (see Bradshaw, 1993). This assumed dominance did not manifest itself with more frequent access to the female or more successful copulations, and aggressive

behaviour among the courting males was rare. Males that were considered dominant on the basis of winning fights again did not secure more successful matings. In Dards' (1983) study, tolerance between adult males was also observed and it was hypothesised that a dominance hierarchy must have already been established by means of aggressive encounter outcomes. Similarly, Natoli, Baggio and Pontier (2001) found a dominance hierarchy based on the outcome of agonistic encounters among male and female farm cats. They found amicable relationships existing between adult females, whereas adult males showed reciprocal tolerance.

The subject of dominance in male cats remains enigmatic; other factors thought to contribute to social ranking include urinary and faecal scent-marking (Corbett, 1979; Natoli, 1984, 1985a, 1989), although Leyhausen (1979) maintained that urine spraying was not indicative of territoriality as it was not found to cause an intimidating effect. Ishida and Shimizu (1998) found that larger males (which they considered to be more dominant) buried their faeces at higher frequencies at sites closer to their core areas and thus suggested that dominance ranking was related to scent-marking in males. Yamane (1999) observed male-male mounting behaviour during the breeding season, with the larger, older and more dominant males mounting the lighter, younger and sexually immature subordinate males. He suggested that this behaviour was simply the result of "sexual tension".

It would appear that the role of the "occasional" male has been under-estimated by Natoli and DeVito (1987, 1988, 1991). In a recent study of mating systems in urban cats, four litters in the study area were found to have been fathered by unknown males and not the resident males (Horsfield, 1998).

In the above studies it is clear that the subject of dominance in male cats has yet to be explored fully. It would appear that dominant males in the form of larger, more powerful animals that emerge as victors from aggressive interactions on their home ground, are not necessarily dominant in terms of monopolising mating opportunities; subordinate males may be achieving reproductive success through surreptitious fertilisation or kleptogamy.

Most of Natoli and DeVito's (1987, 1988, 1991) findings have been contradicted in more recent work by Yamane, Doi and Ono (1996). They observed competition between males during the breeding season, with fighting a frequent occurrence. Larger, heavier males predictably won over smaller, lighter males, and a dominance hierarchy was evident. Younger males usually won over older males. The mean

courtship distance (i.e. distance to female in oestrus) was found to be positively correlated with body weight, indicating that the more dominant (heavier) males had greater access to the females and hence better mating success than the subordinate lighter males. Indeed, copulation rates correlated with body weight.

These results relate to males within their own groups. Some males do not remain permanently with their own groups but visit females of other groups; the "occasional" males of Natoli and DeVito's (1991) studies. Males are known to extend their home range during the breeding season to find females (Liberg, 1980). Yamane *et al.* (1996) found that "occasional" males, despite being dominant within their own groups, were sometimes subordinate when outside their group and even lost fights to lighter males. The authors suggested that male courtship rank is influenced not only by physical factors such as body weight, but also by the local factor (either inside or outside their own group). This is in keeping with Leyhausen (1979), who maintained that superiority or dominance is firmly associated with the place at which the encounter occurred.

However, Yamane *et al.* (1996) also found that the majority of observed copulations were conducted by pairs within the same groups. Dards (1983) also suggested that females were more likely to mate with "familiar" males.

In a follow-up to Yamane *et al.*'s (1996) study, Yamane (1998) found two mating strategies employed by male cats. Firstly, heavier, more dominant males sought copulations both with females of their own groups as well as outside; secondly, lighter, subordinate males courted and copulated with females only in their own group. However, as documented in the first study (Yamane *et al.*, 1996), dominant males, once outside their own group, lost rank and became subordinate, and were observed to achieve fewer copulations. Yamane (1998) postulated that these dominant males should seek extra-group copulations (despite having a lower chance of success there) before and after the oestrous period of their own group, in which they would surely monopolise matings. He found that this was the most successful mating strategy for the male cat; in addition to monopolising breeding in their own groups, it was revealed that these males had also sired more than half of the kittens in outside groups.

In feral horses (*Equus caballus*), which are social, herd-forming animals, the alternative male strategies are to remain alone, with other bachelors, or, less commonly, to accept subordinate status within a harem. However, a study by Asa

(1999) found that in terms of reproductive success, bachelors were less successful than subordinates within a harem, and the dominant harem stallion achieved highest reproductive success.

In Soay sheep (*Ovis aries*), rams usually consort with individual oestrous ewes sequentially (Coltman, Bancroft, Robertson, Smith, Clutton-Brock and Pemberton, 1999). However, it was found that most lambs were not actually sired by a ram seen in consort with the oestrous mother, and even juvenile and yearling rams rarely observed near the females achieved a degree of reproductive success. In a similar way to cats, it would appear that alternative mating strategies, that do not involve forming consorts with many females during the breeding season [Liberg's (1983) "occasional" males], also confer reproductive success.

In complete contrast to the above studies, Denny *et al.* (2002) found no evidence of dominance in the feral cats inhabiting a rubbish tip in rural Australia, and paternity of the juveniles and subadults was shared between resident and non-resident males.

1.5.3 Multiple paternity

In Liberg's (1983) study, the females did not only seek copulations with the dominant male; multiple paternity (the fathering of individuals within a single litter by more than one male) is possible in cats and thought to be constrained by environmental conditions. Where cats are found at lower densities (e.g. in rural areas), a few males are able to control access to receptive females and monopolise mating opportunities (Say *et al.*, 1999; Say *et al.*, 2002a). Contrastingly, in high density areas (e.g. urban areas), dominant males cannot monopolise the receptive females; the mating system is more promiscuous and multiple paternities among litters are more common. This would also encourage competition among males and give females the opportunity to assess potential male vigour (Krebs and Davies, 1993). Multiple paternity is thought to be strongly influenced by female choice, with females selecting males on the basis of fitness benefits to their offspring – there is a greater benefit in mating with multiple males when male genetic quality is variable (DeYoung, Demarais, Gonzales, Honeycutt and Gee, 2002). It has also been suggested that by creating uncertainties among males regarding paternity, the risk of infanticide is reduced (Eaton, 1978). However, there have been very few documented instances of infanticide occurring in cats (Macdonald *et al.*, 1987; Pontier and Natoli, 1999); although it occurs frequently in lions (Packer and Pusey,

1982; West and Packer, 2002). It is not considered a successful strategy in cats (Natoli, 1990), which would perhaps explain the rarity of this phenomenon, and is thought to be more of a behavioural tactic in response to environmental conditions (Pontier and Natoli, 1999).

1.6 Genetics

1.6.1 Population genetics

The genetic structure of cat populations, based on the observation of allele frequencies of morphological characteristics such as coat colour (see Wright and Walters, 1981), has been the subject of study for nearly three decades (e.g. Clark, 1975; Van Aarde, Erasmus and Blumenberg, 1981; Dards and Robinson, 1983; Ragni and Possenti, 1996; Vinogradov, 1997; Ruiz-Garcia, 1999; Say, Bonhomme, Desmarais and Pontier, 2003). Our understanding and knowledge has been enhanced by recent advances in molecular techniques.

1.6.2 Molecular genetics

Microsatellites are a powerful tool for investigating population genetic issues, parentage, extra-pair copulations, structure and relationships between and within social groups, and for identifying individuals (Taberlet, Luikart and Geffen, 2001). Analysis of mitochondrial DNA (mtDNA) polymorphisms provides a detailed resolution of within-population relatedness. Individuals with different genotypes may appear genetically dissimilar but have the same or related fathers. Thus, analysis of mtDNA polymorphisms is most useful when variability of genotypes is high within populations, and when it is used in conjunction with biparentally inherited markers to determine the genetic contribution of males (Gompper and Wayne, 1996). The loci used are hypervariable and consist of tandem repeats of short DNA sequences that can be assayed through hybridisation with DNA probes or amplified by the polymerase chain reaction (PCR), enabling even trace quantities of DNA to be obtained in amounts appropriate for sequencing or other qualitative analyses (Harley and Baumgarten, 2000). The first studies using these tandem-repeat loci provided phenotypes which could be used to determine paternity (Packer, Gilbert, Pusey and O'Brien, 1991). More recent studies have used a single-locus approach allowing a more precise quantification of relatedness, even in small, isolated populations (Gottelli, Sillero Zubiri, Applebaum, Roy, Girman,

Garcia-Moreno, Ostrander and Wayne, 1994). One of the advantages of microsatellites is that only minute quantities of DNA are required for analysis (Gompper and Wayne, 1996; Horsfield, 1998), therefore only very small quantities of tissue are needed. Horsfield (1998), Say *et al.* (1999) and Say *et al.* (2002a) used DNA extracted from cat hair roots; Yamane (1998) extracted venous blood from the cats. Denny *et al.* (2002) used ear tissue samples.

Yamane's (1998) study involved polymorphic microsatellite DNA analysis and highlights the difficulties involved in behavioural observations in the field; without DNA analysis it has proved impossible to distinguish accurately between successful and unsuccessful copulations and hence determine mating success. Until recently, all domestic cat mating studies have involved purely observational data regarding copulatory behaviour (e.g. Liberg, 1983, 2000; Natoli and DeVito, 1987, 1988, 1991): the promiscuous mating system of the domestic cat described in Section 1.4.1 clearly reflects a need for a more accurate and quantitative technique. In many species, significant numbers of copulations do not result in ejaculations, and some males have higher sperm counts than others (Dewsbury, 1982; Ellis, 1995), and differences in fertilising abilities/capacities (Dewsbury, 1982). Paternity studies using microsatellite analysis of Soay sheep (Coltman *et al.*, 1999) showed that rams rarely observed in the presence of an oestrous ewe still conferred some mating success.

Feline microsatellite primers were previously developed by Menotti-Raymond and O'Brien (1995) (see also Menotti-Raymond, David, Lyons, Schaffer, Tomlin, Hutton and O'Brien, 1999), and have been used in all domestic cat studies of population genetics to date (Horsfield, 1998; Yamane, 1998; Say *et al.*, 1999; Denny *et al.*, 2002; Say *et al.*, 2002a).

1.7 Objectives of this study

Ultimately, this study aims to define male dominance in feral farm cats in terms of home range, social ranking and reproductive success, exploring existing theories surrounding these three main factors and seeking to find an overall link between them.

In **Chapter 2** I aim to provide an introduction to the animals studied in order to produce this thesis, and include detailed descriptions of the study sites. I also

address the logistical problems encountered, many solutions to which lay outside the scope of this study.

Measuring an animal's home range size, shape and pattern of utilisation is important for most ecological and/or behavioural studies (Harris *et al.*, 1990; Powell, 2000), and by quantifying its home range it becomes possible to gain valuable insight to the animal's cognitive map of its home. In **Chapter 3** I aim to qualify and quantify male home range in the study cats, and determine if an individual's home range is correlated with age, health and body size: further hypothesised attributes of dominance. Also, is this home range affected by climatic conditions, seasonal and/or temporal effects? Furthermore, to what extent is an individual's home range affected by that of another individual? Finally, is home range truly affected by the distribution and abundance of resources?

Single behavioural interactions are the fundamental unit of social structure, and it is the changing nature of repeated interactions, or relationships, that gives social structure its potentially dynamic component (Macdonald, Stewart, Stopka and Yamaguchi, 2000). Kaufmann (1983) suggested that social interaction eventually provides priority of access to resources. In **Chapter 4** I aim to find evidence of social hierarchies within the study cats and thus identify dominant and subordinate individuals. I investigate whether certain individuals exhibit certain behaviours, or is the range of behaviours consistent throughout the species regardless of sex or status? By quantifying and qualifying behavioural interactions between individuals, can evidence of sociality and ranking really be determined? Does this ranking correspond to factors such as age, health, body size and home range size?

In **Chapter 5** I aim to identify paternity among the Glebe and Bryces Farm males from microsatellite analysis. Evidence of dominance does not always equate to mating success of males (DeYoung *et al.*, 2002), and many hypotheses pertaining to reproductive ecology are testable only using genetic techniques. Recent advances in molecular markers and techniques enable parentage to be established and relationships among individuals estimated with a high degree of confidence, providing information on reproductive success, social structure, kinship and fitness. In this chapter, I aim to determine male reproductive success in terms of number of offspring sired by individual males. Are there certain qualities about the more "successful" males, again such as age, health, body size, size of home range and status within the group?

Finally, in **Chapter 6** I link all preceding chapters to summarise and clarify the findings of this study.

1.8 Methods of analysis

For data chapters 3 and 4, the following statistical tests are used.

Chi-squared Goodness of Fit – this test is a variation on the classic Chi-Squared test (the contingency table-based statistical test which explores hypotheses of association between variables, and generates expected values), with the expected values being taken from a particular distribution against which the observed distribution is being compared. For both Glebe Farm and Bryces Farm, Chi-Squared Goodness of Fit was used to analyse the frequencies of interactions between cat dyads. Where appropriate, Yates' Correction for Continuity was applied.

G-test - this is an alternative to the Chi-Squared test. This statistical procedure was used to test for heterogeneity or quality of behavioural interactions between the dyads at both Glebe Farm and Bryces Farm. Where appropriate, the associated correction factor, the Williams' Correction, was used.

Kolmogorov-Smirnov - this is a goodness of fit test that compares two sets of data to determine whether they come from the same distribution. This test was used to look for uniformity (i.e. no deviation from the normal distribution) in the number of behavioural interactions occurring between the Bryces Farm cats during the study period.

Levene's test – a test for heterogeneity of variance, which examines the absolute values of the deviations of every replicate from the mean of its sample.

Two-way Analysis of Variance – used to test for differences among sample means and differences among linear combinations of means. For two-way analysis, the effects of two factors are considered simultaneously.

Dunnett's C test/LSD (Least Significant Difference) – these are post-hoc tests: equal variances not assumed.

Paired t-*test* – paired samples occur when a single individual is tested twice (e.g. before and after an event). The null hypothesis for this parametric test is that there is no difference between the two columns and they could come from the same data set. This test was used to investigate whether interaction rate between the cats changed significantly, following the death and disappearance of two members of the Bryces Farm colony.

Pearson's product-moment correlation - this parametric measure of correlation describes a range of associations between two variables from "perfect negative correlation", through "no correlation" to "perfect positive correlation". This test was used to test the individual cats for indicators of sociality, based on the theory that if the cats were behaving asocially, then they would be interacting randomly as they encountered one another (resulting in a significant correlation between the number of interactions and availability, and a significant positive correlation between the rate of interaction and availability).

For details of the statistical tests used, see Sokal and Rohlf, 1995; Fowler, Cohen and Jarvis, 1998; Dytham, 1999.

CHAPTER 2: STUDY SITES

2.1 Introduction

As reviewed in Chapter 1, feral cats have been studied in a wide variety of locations world-wide and under a great diversity of socio-ecological conditions. For example, feral cats are known to form colonies in a wide range of urban and rural environments such as dockyards (Dards, 1978, 1983; Dards and Robinson, 1983), hospitals and factories (Nichol *et al.*, 1981; Southam, 1981), farms (Macdonald *et al.*, 1987), archaeological ruins (Natoli, 1983, 1984, 1985a, 1985b, 1989, 1990; Natoli and Devito, 1987, 1988, 1991; Natoli *et al.*, 1999) and rubbish tips (Izawa *et al.*, 1982; Calhoon and Haspel, 1989; Haspel and Calhoon, 1989; Denny *et al.*, 2002).

This study focuses on feral farm cats.

2.2 Study site descriptions

2.2.1 Geography

Fieldwork relating to the study was carried out at two farms, Glebe Farm and Bryces Farm, in the southern county of Hampshire in the United Kingdom. Both farms are located in the Test Valley area within the small, rural village of Sherfield English near Romsey, close to the border with Wiltshire (see Appendix 1). Sherfield English lies in the valley of the River Blackwater, four miles from Romsey. The main city of Southampton is situated approximately 15 miles to the south-east, with Salisbury approximately 15 miles to the north-west.

2.2.2 Habitat

In 2002, the percentage of rural land in Hampshire was calculated at 90.8% (http://www.hants.gov.uk), with a significant move from livestock to arable systems. At this time, cereal production was the main farm type found in Hampshire (http://www.farmstats.defra.gov.uk).

Glebe Farm was involved solely in dairy production. Until January 2002, both pigs and dairy cows (and some arable crops) were farmed at Bryces Farm, but the livestock was then reduced to dairy alone. The habitat at both farms was largely pasture/meadow for the livestock, with surrounding woodland. Hedgerows were also a feature of the landscape.

2.2.3 Climate

Temperature and rainfall data for the area, taken when this study was carried out, are given in Appendix 2. During this time, average daily temperatures ranged from a maximum of 19.8°C (67.6°F) in summer, falling to a minimum of −3.5°C (25.7°F) in the winter. The highest rainfall recorded during this time was 25.2mm.

2.3 Glebe Farm

Glebe Farm (429624, 122525) comprised an area of approximately 15ha, bisected by the A27 Salisbury Road lying to the south of the main farm buildings. Most of the surrounding properties were either farms or private houses.

Glebe Farm was a small, family-run dairy farm comprising a herd of approximately 300 milk cattle (*Bos taurus*) and a pair of saddle-back pigs (*Sus scrofa*). The farmer and his wife (the proprietors) lived on-site in the farmhouse. The farmer's elderly mother lived in a separate, smaller house (*Springfields*) on the same site. Milking took place twice daily at dawn and dusk.

Figure 2.1 shows the layout of the farm buildings; these consisted of the main farmhouse and farmyard, and surrounding barns and milking parlour. A well-tended garden area surrounded the farmhouse. A row of greenhouses ran alongside the main driveway, somewhat dilapidated although still in use. There were no buildings belonging to Glebe Farm to the south of the road, but a small garden centre and adjoining house were located slightly to the east.

2.3.1 Prey species

Glebe Farm and its environs hosted a diverse natural prey base for feral cats, typical of most farmland in southern England. Mammalian species included rabbits (*Oryctolagus cuniculus*), occasional hares (*Lepus europaeus*), rats (*Rattus*

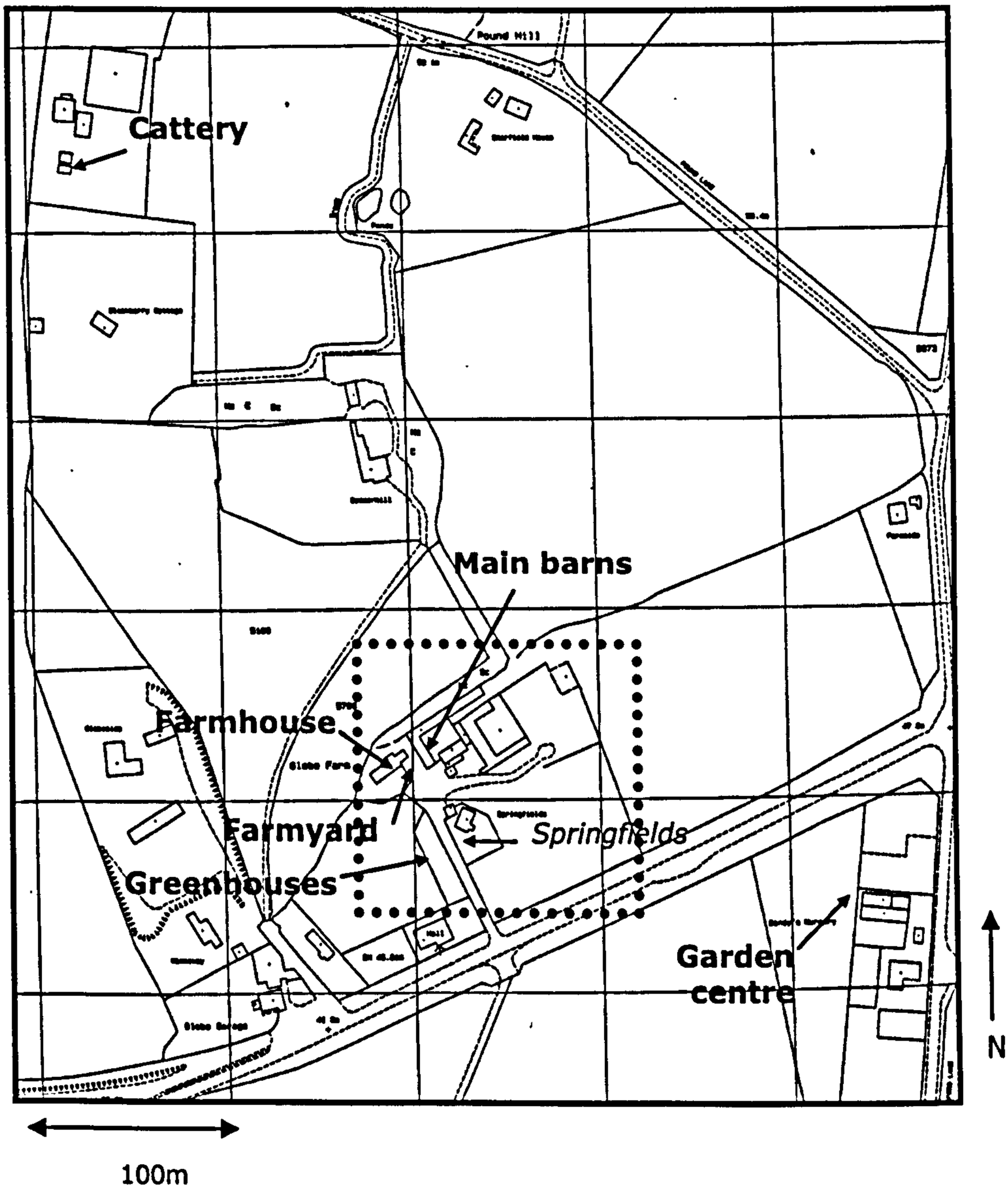


Figure 2.1: Layout of Glebe Farm (dashed area) and environs (refer to text for details)

The dashed area surrounding Glebe Farm does not represent actual farm boundary, as some fields extend beyond map.

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norvegicus), house mice (*Mus musculus*), woodmice (*Apodemus sylvaticus*), harvest mice (*Micromys minutes*), grey squirrels (*Sciurus carolinensis*), bank voles (*Clethrionomys glareolus*), field voles (*Microtus agrestis*), meadow voles (*M. pennsylvanicus*), edible dormice (*Glis glis*) and common shrews (*Sorex araneus*). The more common bird species included pheasants (*Phasianus colchicus*) and wood pigeons (*Columba palumbus*), occasional grey partridges (*Perdix perdix*), and a wide variety of passerine species.

2.3.2 Predatory species

Two dogs were kept as pets on Glebe Farm; an elderly Labrador retriever and a young Jack Russell terrier. Both dogs were generally free to roam throughout the entire property during the day, and also occasionally ventured to neighbouring farms. The terrier was a keen hunter of feral cats, achieving the most success with kittens (see Section 2.7.4).

In addition to the domestic dogs, predatory wildlife species in this area included red foxes, which were commonly sighted, and the occasional weasel (*Mustela nivalis*). Buzzards (*Buteo buteo*) were frequently sighted.

The farmer did not permit hunting on his land but neighbouring farms participated in the annual pheasant shoot; furthermore, the village of Sherfield English lay just inside the New Forest Foxhounds country and slightly to the west of the Hursley Hambledon hunt. Both hunts occasionally passed through farms adjacent to Glebe Farm.

2.3.3 Other species

Other wildlife species commonly sighted in this area included badgers (*Meles meles*), hedgehogs (*Erinaceus europaeus*), fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*).

2.4 Glebe Farm cats

At the time this study was carried out, a colony of feral cats had lived at Glebe Farm, unmanaged, for over 20 years (D. Biddlecombe, pers. comm.). The number of resident cats (defined as cats frequently sighted at Glebe Farm throughout the

year, utilising the farm's food, shelter and nest sites) in October 2000 are given in Table 2.1a. Cats were categorised according to age, as explained in Table 2.1b.

Table 2.1a: Number of cats (Glebe Farm colony), October 2000

	Male	Female	Unknown	Total
Adult	3	5	-	8
Juvenile	3	-	-	3
Kitten	1	-	3	4
Total	**7**	**5**	**3**	**15**

Table 2.1b: Definition of categories

Category	Age
Adult	> 1 year
Juvenile	6 – 12 months
Kitten	< 6 months

Most of the cats congregated frequently in the main farmyard, outside the farmhouse and adjacent to the main barns. The cats were regularly fed there by the farmer's wife with fresh, unprocessed milk and bread twice daily, to coincide with milking times on the farm. In addition they received table scraps and occasionally canned cat or dog food. Most of the cats appeared to obtain the majority of their food by hunting, the exception being an elderly female who was rarely observed away from the vicinity of the farmhouse. From personal observation, the preferred prey choices appeared to be rabbits, mice, voles and sometimes rats, and occasionally birds such as wood pigeon, pheasant and smaller song birds. The cats used the barns, greenhouses and farm buildings for shelter, in particular one livestock barn adjacent to the farmhouse. On the whole, the presence of the feral cats was welcomed by the farmer, and some of the tamer cats occasionally ventured inside the farmhouse.

Mostly, the adult females gave birth to their kittens away from the main farm buildings and farmhouse, but generally moved the litters closer to the farmhouse after a few days. The less experienced mothers made nests at ground level in the

barn adjacent to the house, and their kittens suffered predation by the Jack Russell terrier.

2.5 Bryces Farm

Bryces Farm (428400, 123400) consisted of an area of approximately 30ha. It lay about one and a half kilometres (as the crow flies) from Glebe Farm; by road approximately three kilometres (see Appendix 1). The two brothers who owned Bryces Farm lived with their respective families in farmhouses just outside the gateway to the farm, and were cousins of the owner of Glebe Farm. Within the boundaries of the farm itself there were three inhabited cottages. The lane leading to the farm had houses, cottages and one smallholding along one side.

Figure 2.2 shows the layout of Bryces Farm, extending down the lane to the smallholding *Treeside*. A large pit occupied one side of the pig section; this had been turned into a dump consisting of farm and household waste of all description, including food scraps.

The dairy section of Bryces Farm was the centre of human activity on the farm, with milking carried out twice daily at dawn and dusk.

Prey, predatory and other wildlife species present on this farm were identical to those for Glebe Farm (given in Sections 2.3.1, 2.3.2 and 2.3.3), with the exception of farm dogs. A border collie often accompanied one of the farmers around the farm, but she posed little threat to the feral cats.

2.5.1 *Treeside*

Treeside (Figure 2.2) was a private smallholding close to the main area of Bryces Farm, consisting of a small number of livestock and domestic fowl in enclosures surrounding the main house. During the study, access was not available at all times, particularly during the night. This was heightened due to the presence of two guard dogs on the property, so even observing from a distance outside the property was difficult without causing disturbance to the proprietors, especially at night.

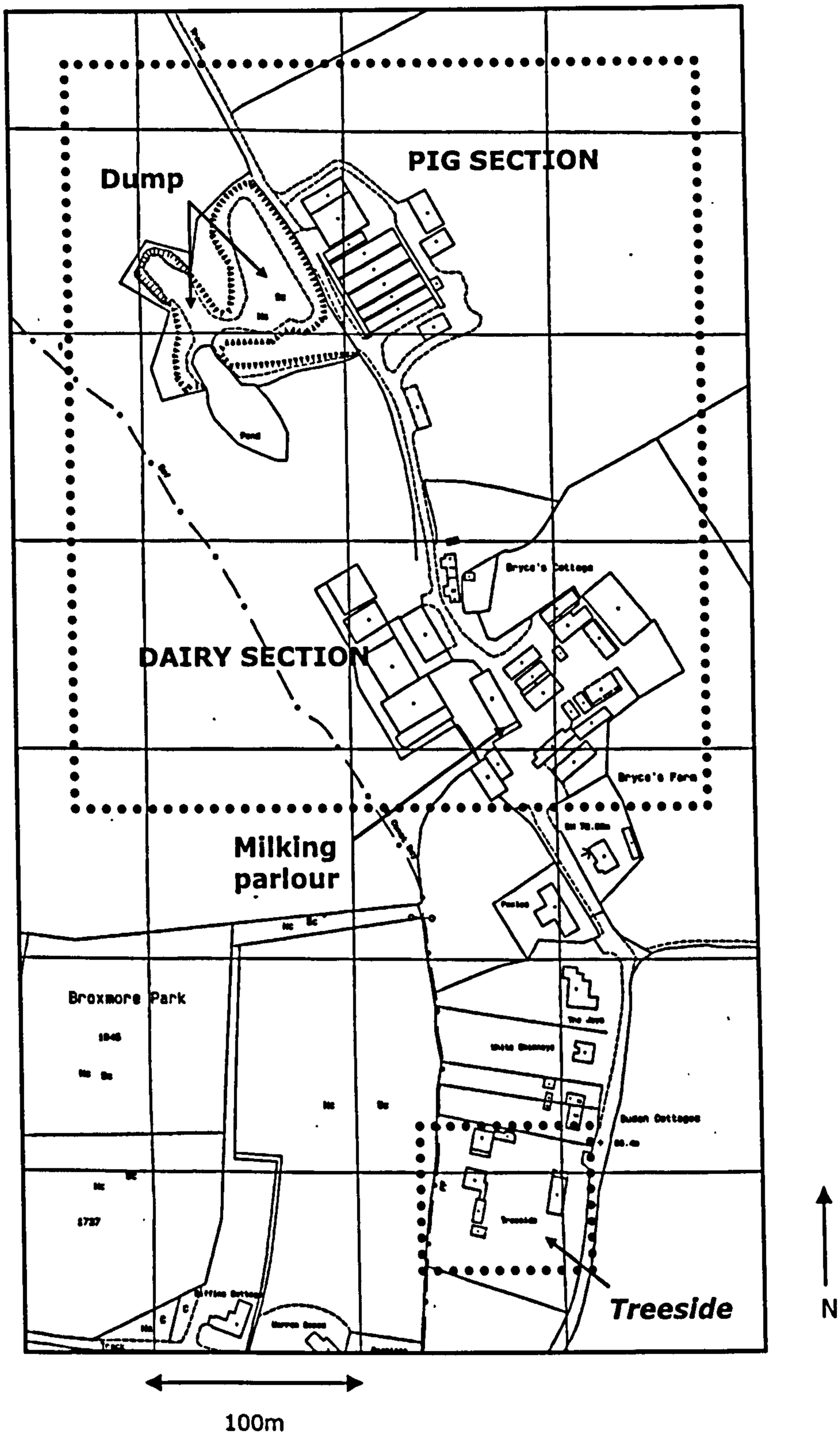


Figure 2.2: Layout of Bryces Farm, *Treeside* (dashed areas) and environs (refer to text for details)

The dashed area surrounding Bryces Farm does not represent actual farm boundary, as some fields extend beyond map.

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2.6 Bryces Farm cats

At the time of writing, farm cats had been present on Bryces Farm for at least 15 years (P. Jewell, pers. comm.). Numbers of cats were regulated naturally and there was no husbandry. When the pig section of the farm was still in operation, the cats could be seen to be divided into two colonies – the northern pig section and the southern dairy section. The females of the former colony remained separate from the females of the latter colony, but most of the males moved freely between the northern and southern areas. The southern colony benefited from fresh milk daily (which they helped themselves to, from buckets left waiting for Bryces Farm residents), and occasional supplementary feeding by the farmer in the form of dry cat biscuits, whereas the northern colony scavenged infrequently on newborn piglet carcasses, thrown into the dump by the farm labourers. With the exception of one cat[4], most of the Bryces Farm cats were not tame, and exhibited fearful behaviour towards humans (although the southern colony was generally more tolerant of humans). Following the closure of the piggery, the numbers of feral cats dropped drastically. The possible reasons for this are dealt with below (Section 2.7).

Two neutered female cats lived as pets in one of the Bryces Farm cottages. These cats did not interact with the feral farm cats. Their lack of social behaviour towards the other colony members, together with their neuter status, meant that they were not classed as belonging to the Bryces Farm colonies.

In November 2000 the estimated number of resident feral cats at Bryces Farm can be seen in Table 2.2 (see Table 2.1b for an explanation of categories).

Table 2.2: Number of cats (Bryces Farm colony), November 2000

	Male	Female	Unknown	Total
Adult	9	4	-	**13**
Juvenile	2	-	1	**3**
Kitten	-	-	3	**3**
Total	**11**	**4**	**4**	**19**

[4] This cat had previously been seriously injured by a farm vehicle, resulting in a suspected broken pelvis and tail and accompanying internal injuries, thus most likely rendering her immobile for a considerable period of time. She survived with no veterinary care, and because of her immobility had become much more tolerant of humans until the point of tameness. At the time of this study she had recovered sufficiently to regain almost full mobility, although her speed of walking and running was compromised and it is unlikely that she could successfully produce kittens.

Due to personal injury, followed by a nationwide foot-and-mouth outbreak (see Section 2.7.1) when access to the farms was prohibited, fieldwork ceased between November 2000 and April 2001. By May 2001 the number of resident cats was estimated in Table 2.3:

Table 2.3: Number of cats (Bryces Farm colony), May 2001

	Male	Female	Unknown	Total
Adult	4	4	-	**8**
Juvenile		1	2	**3**
Kitten	1	-	1	**2**
Total	**5**	**5**	**3**	**13**

2.6.1 *Treeside* cats

A colony of all-female feral cats lived at *Treeside*, mostly utilising an old conservatory adjoining the main house (with free access to the outside), for shelter. This room also served as a nursery for kittens, most of which were born in cardboard boxes provided by the owner. This colony of females exhibited communal reproductive behaviour (see Section 1.4.3).

They were fed regularly by the owner of *Treeside*, with table scraps and canned cat food, and some were reasonably tame towards the owner only.

Continuous access to this area was not possible. Tables 2.4 and 2.5 show numbers of cats present before and after the foot-and-mouth outbreak.

Table 2.4: Numbers of cats (*Treeside* colony), May 2001

	Male	Female	Unknown	Total
Adult	-	7	-	**7**
Juvenile	-	-	2	**2**
Kitten	-	-	5	**5**
Total	**-**	**7**	**7**	**14**

Table 2.5: Numbers of cats (*Treeside* colony), May 2002

	Male	Female	Unknown	Total
Adult	-	7	-	**7**
Juvenile	-	-	-	**0**
Kitten	-	-	12	**12**
Total	**-**	**7**	**12**	**19**

2.7 Adverse factors affecting the study cats

2.7.1 Foot-and-mouth disease

A nationwide outbreak of foot-and-mouth disease (FMD) occurred in the United Kingdom in 2001. FMD is a highly infectious viral disease in which fever is followed by the development of vesicles or blisters, mainly in the mouth or on the feet. The disease is spread mechanically by the movement of animals, people, vehicles or anything contaminated by the virus. Cats are not directly at risk from FMD; animals most susceptible are livestock such as domestic cattle, sheep and goats (all family Bovidae), and pigs, although some wild animals may also be affected, e.g. hedgehogs, coypu (*Myocastor coypus*), rats, deer (Cervidae) and zoo animals such as elephants (Elephantidae).

The 2001 outbreak severely affected the farming economy in the United Kingdom and resulted in the slaughter of 4,207,000 animals (583,000 cattle, 3,474,000 sheep, 145,000 pigs, 3,000 goats, 1,000 deer, 1,000 other) (DEFRA Disease Control System database, 2002). Although there was no outbreak of FMD on any farms in Hampshire, the disease still had a knock-on effect to the Hampshire area, with the movement restrictions causing a large impact particularly on the beef and pig industries, and forcing most sheep farmers into a loss-making situation.

The study farms were not infected but the outbreak resulted in serious restrictions on the movement of livestock and people within and around Glebe and Bryces Farms, and an increase in veterinary and government personnel carrying out inspections on the farms. Although fieldwork was not permitted for several months during this time, it is envisaged that normal routines on the farms were disrupted. This, together with the presence of more strangers on the farms than is usual, may have had a serious effect on the feral farm cats. Once the FMD outbreak was

declared over and access to the farms was resumed, it was found that many previously identified cats had disappeared altogether.

2.7.2 Non-target or secondary poisoning

Rats are a major problem on farms and the most commonly used method of controlling them in the United Kingdom is by laying baits containing an anticoagulant rodenticide. Warfarin previously had widespread use, but resistance to this anticoagulant is now common. Since the mid-1970s, second generation anticoagulant rodenticides have been developed, namely difenacoum, bromadiolone, brodifacoum and flocoumafen (P. Herritty, pers. comm.). However, one of the problems associated with using rodenticide baits is the non-target effect on non-rodent wildlife, in particular, predators of rodents (see Kaukeinen, 1982).

During the spring of 2002, several Bryces Farm cats disappeared from the study area. The bodies of two of these cats were recovered. A preliminary investigation found no signs of injury either from cats and other predators, or as a result of a road traffic accident. Blood was present around the mouths of both cats, a sign indicative of poisoning (E. Cronin, pers. comm.).

Due to the increasing rat problem on Bryces Farm, rodenticide bait levels had been increased early in 2002 (P. Jewell, pers. comm.). Although personal observations suggested that rats were not the preferred prey species, a dying rat or a fresh carcass would certainly provide a ready meal for a feral cat. Leyhausen (1979) noted that cats generally will not opt to fight with an attacking, adult rat; even cats that are keen rat hunters for the most part catch only rats that are half-grown or even smaller, and which do not yet switch from defence to attack. However, it is thought that the disappearance of several cats from the study area, and the discovery of the two dead cats assumed to have died from non-target rodenticide ingestion, is directly linked to the increase in bait levels on Bryces Farm. This is also assumed to be the cause of death of the other missing cats, although the possibility of dispersal (see Section 1.4.4) should not be rejected.

2.7.3 Problems with radiocollars

A new batch of radiocollars was manufactured for the Bryces Farm study (see Chapter 3, Section 3.2.4). Despite applying the same fitting principles as successfully used on the Glebe Farm cats, these new collars became too tight and

had to be removed before the planned radiotracking study time had elapsed. It is thought that there was a manufacturing fault, perhaps resulting from a different quality of nylon used for this second batch of collars, which caused the collars to stiffen and shrink when damp.

2.7.4 Farm dogs

Glebe Farm kept a Jack Russell terrier as a pet. Generally, his movements were not restricted in any way, and he developed the habit of chasing the feral cats for the benefit of any visitors arriving at the farm. On the whole the adult cats, although threatened, were not in any real danger from him. However, the kittens, particularly when very young, often had difficulty in escaping. He was responsible for the deaths of at least three kittens during this study and was a particular threat to the kittens of inexperienced mothers who made their nests at ground level in the barn, often in fairly exposed places.

2.7.5 Road traffic accidents

Another cause of mortality to farm cats was road traffic. The male cats in particular, frequently crossed roads in the course of traversing their territories, and cat deaths due to road accidents are not uncommon. At least two cats were also killed by vehicles in the farmyards. Furthermore, Glebe Farm cats often entered empty vehicles out of curiosity or when playing, and may have then been unable to escape once the vehicle left the farm. During the winter some Glebe Farm cats occasionally even jumped up into the engines of recently-parked cars in the farmyard, seeking warmth. The disappearance of several young cats may well be due to these factors.

2.7.6 Disease

The more responsible of domestic pet cat owners in the United Kingdom have their cats vaccinated annually against feline panleucopaenia (infectious enteritis), feline calicivirus (flu), feline viral rhinotracheitis, feline leukaemia virus (FeLV) and often feline chlamydiosis. Since United Kingdom quarantine laws were changed in February 2000 with the introduction of the Pet Travel Scheme, those travelling abroad and back into the United Kingdom are now also vaccinated against rabies. In addition, pet cats are routinely treated against tapeworm (*Dipylidium caninum*) and roundworm (*Toxocara cati*), and against flea infestations (caused by

Ctenocephalides spp.). Other parasites for which preventative treatment is available include heartworm (*Dirofilaria immitis*), ear mites (*Otodectes cynotis*) and intestinal hookworm (*Ancylostoma tubaeforme*).

With the exception of rabies, which has been absent from the United Kingdom since the 1930s, feral cats, receiving no veterinary care, are susceptible to all the above problems (see Section 1.3.1; also Yamaguchi *et al.*, 1996). In addition, they may suffer from Feline Immunodeficiency Virus (FIV), for which there is no preventative vaccination. FIV has a worldwide distribution among feral and domestic cats and in many cases induces immunodeficiency disease analogous to that of human Acquired Immune Deficiency Syndrome (AIDS) (Carpenter, Brown, Macdonald and O'Brien, 1998). Like Human Immunodeficiency Virus (HIV), FIV in cats has three main stages. First, the initial or acute stage, usually characterised by swollen lymph nodes, fever and susceptibility to skin or intestinal infections. Second, the latent or subclinical stage of infection. No symptoms are visible, but the immune system may slowly be destroyed. When this occurs, the third or final stage of infection arises, and the cat is prone to chronic opportunistic infections such as upper respiratory tract infections, intestinal infections, skin/ear diseases and cancers, usually resulting in death (http://www.peteducation.com).

2.8 Local surveys

2.8.1 Glebe Farm surveys

In order to estimate the number and territory sizes of un-neutered domestic cats and feral cats in the vicinity of Glebe Farm, a questionnaire, prepaid reply envelope and explanatory letter was sent to all surrounding properties. The questionnaire enquired as to the number, gender and status (i.e. neutered or intact) of domestic cats per household, and also asked if the occupier was aware of any feral or stray cats visiting their homes and gardens. The questionnaire also asked for a description of the pet cats for identification purposes.

Questionnaires were sent to ten properties; nine of these (90%) responded. Answers to the questions were clarified by telephoning where necessary, and two of the properties were visited.

In the nine properties, there were a total of 20 domestic cats. Of these, 14 were neutered (70%). The remaining six un-neutered cats (30%) were pedigree Exotic Shorthair cats, kept in secure enclosures. The pedigree females were allowed to range freely during the day, except when in oestrus; the stud males were confined all the time.

Of the nine properties, three had no pet cats and were unaware of any other cats around their property. However, it should be noted that the territory of one Glebe Farm male (GM2) regularly encompassed the gardens and adjacent field of one of these properties, but his presence had never been observed by the home owner, who was adamant that cats would not cross his property because of the presence of his dogs. Table 2.6 summarises the results.

Table 2.6: Summary of local cat survey (Glebe Farm)

	Male	**Female**	**Total**
No. of neutered cats	6	8	**14**
No. of un-neutered cats	2	4	**6**
Total	**8**	**12**	**20**

2.8.2 Bryces Farm surveys

A similar survey was carried out in the vicinity of Bryces Farm, excluding *Treeside*. Out of 12 properties, responses were received from seven households (58%). A total of six pet cats was identified, all of them neutered females. Two households mentioned the presence of feral cats – these were all identified as being Bryces Farm feral cats. Table 2.7 summarises the results.

Table 2.7: Summary of local cat survey (Bryces Farm)

	Male	**Female**	**Total**
No. of neutered cats	0	6	**6**
No. of un-neutered cats	0	0	**0**
Total	**0**	**6**	**6**

CHAPTER 3: HOME RANGE STUDY

3.1 Introduction

The Resource Dispersion Hypothesis (RDH; Macdonald, 1983), reviewed in Chapter 1, Section 1.3.2, is a hypothetical model which proposes that, in spatially and temporally heterogeneous environments, the dispersion of patches of limited resources determines home range size and shape, whereas group size is determined by the abundance of these resources (Johnson *et al.*, 2002; Valenzuela and Macdonald, 2002). According to the RDH, an animal's minimal home range will be of a size that allows it assurance of finding sufficient productive patches (resources) within its range (Carr and Macdonald, 1986). Female home range tends to be determined by food and nest site availability during the most critical periods; male range size is determined by food outside the mating season and receptive females during the mating season (Sandell, 1989). Defending a home range against conspecifics (I.e. territoriality) is often costly, and the costs may outweigh the benefits. For this reason, home ranges are kept to the minimum size necessary to meet the requirements of the occupants (see Kruuk and Macdonald, 1985) and in order to ensure survival during biologically critical periods (Lindstedt *et al.*, 1986; Sandell, 1989).

During the mating season, males of many carnivore species roam over large areas, and their mating home ranges overlap with other males' ranges, whereas in a population of philopatric staying males, ranges would be exclusive (Sandell, 1989). In other words, a system with exclusive home ranges is possible only when it is the best tactic for all reproductively dominant males. In that situation, there would be a mutual interest in exclusivity among all male contestants and no reproductive advantage would be gained by roaming. Cats' spatial tactics have been discussed in Chapter 1, Section 1.3.6.

3.1.1 Measuring home range by radiotracking

Since the 1960s, radiotracking (or radiotelemetry) has been frequently used by biologists as a favoured method of providing data on the location, movement and behaviour of animals.

There are two basic components in a traditional radiotracking system. Firstly, a transmitting subsystem consisting of a radio transmitter, a power source and a propagating antenna, and secondly, a receiving subsystem including a "pick-up" antenna, a signal receiver with reception indicator and a power source. Most radiotracking systems involve transmitters tuned to different frequencies (analogous to different AM/FM radio stations) that allow individual identification (Mech and Barber, 2002).

Three distinct types of radiotracking are in use today. The first of these is conventional, very-high-frequency (VHF) radiotracking; second, satellite tracking, and third, Global Positioning System (GPS). VHF radiotracking is the standard, most cost-effective technique.

Radio transmitters are attached to the animal by a variety of different methods, depending on its size and environment. These include tailmounts, necklaces, legmounts (all especially useful for radiotracking birds) and backpacks (for radiotracking mammals as well as birds). Radio transmitters are attached to collars for most terrestrial and arboreal mammal species, and in reptiles, amphibians and fish the transmitter is usually kept dry and functioning by means of implantation (http://www.biotrack.co.uk).

3.1.2 Analysis of radiotracking data

There are several comprehensive reviews outlining methods of calculating home ranges from radiotracking data (e.g. Kenward, 1987; Worton, 1987; Harris *et al.*, 1990; Doncaster, 1990; White and Garrott, 1990; Powell, 2000). It was decided to use the Minimum Convex Polygon (MCP) after Mohr, 1947. Despite being one of the earliest and relatively simplest techniques, the MCP remains one of the most frequently used; therefore it facilitates comparison with other datasets (Harris *et al.*, 1990; Macdonald *et al.*, 1999).

A convex polygon representing the minimum area is constructed by connecting the outer locations taken from radiotracked fixes. The area of the polygon is then calculated as the home range. However, one of the main disadvantages of the MCP is that all locations are encompassed to make up the home range, regardless of frequency of visitation. In other words, peripheral or outlying fixes representing locations visited very infrequently still fall under the category as being within the animal's home range, and by including these locations when connecting the fixes to

construct the polygon, the range area can contain areas which are never actually visited. A solution to this problem is to exclude these outliers and include only the 95% of fixes that result in the smallest overall range (White and Garrott, 1990). The choice of a 95% parameter is arbitrary but this figure is the most frequently used (P. Doncaster, pers. comm., also see Powell, 2000).

The MCP method and, in fact, most home range analysis methods are based on the assumption of an even distribution of spatial use of the home range. However, there are suggestions of a non-random use of a home range, where some locations or activities may be clumped instead of even (Horner and Powell, 1990). This would have obvious repercussions on the use of the MCP method of analysis. Further possible problems with analysis have been reviewed by Harris *et al.* (1990).

Programmes for calculating MCPs and other techniques can be downloaded from the internet (http://www.detritus.inhs.uiuc.edu/wes/homerange; http://www.soton.ac.uk/~cpd/interact.htm) and have been reviewed (e.g. by White and Garrott, 1990). For the purposes of this study, Michael Stüwe's programme *Micro-computer Programs for the Analysis of Animal Locations* (McPAAL) was used for home range estimates. It was necessary to convert tracking data into a format recognised by McPAAL in order to calculate MCPs. This was facilitated by use of a programme *Convert*, written by T.J. Carter.

3.1.3 Measuring home range in cats

Most studies of spatial organisation in cats have involved the use of radiotracking in order to determine home ranges (e.g. Macdonald and Apps, 1978; Corbett, 1979; Liberg, 1980; Schär and Tschanz, 1981, 1982; Izawa *et al.*, 1982; Jones and Coman, 1982b; Warner, 1985; Apps, 1986; Fitzgerald and Karl, 1986; Niewold, 1986; Turner and Mertens, 1986; Konecny, 1987a; Macdonald *et al.*, 1987; Calhoon and Haspel, 1989; Haspel and Calhoon, 1989; Langham and Porter, 1991; Langham, 1992; Page *et al.*, 1992; Genovesi *et al.*, 1995; Mirmovitch, 1995; Barratt, 1997; Norbury *et al.*, 1998; Weber and Dailly, 1998; Moller and Alterio, 1999; Hall *et al.*, 2000; Edwards *et al.*, 2001; Naidenko and Hupe, 2002).

Say *et al.* (2002) used the walked-line transect method for estimating the density of cats, while other studies relied solely on observation to determine home ranges (e.g. Dards, 1978; Panaman, 1981).

Table 3.1 summarises the results of previous home range studies in cats. Among the wild felids, average male home ranges range from 800-1,000km^2 (tiger), 826km^2 (puma), 275-450km^2 (Eurasian lynx), 50-76km^2 (jaguar), 39-95km^2 (bobcat – California), 9.0 km^2 (Amur leopard cat), to 3.7km^2 (ocelot). This list is taken from Kitchener, 1991, and is by no means exhaustive.

3.2 Methods

3.2.1 Trapping

Whilst investigating choice of bait in order to maximise trapping efficiency, it was found that the Glebe Farm cats ate canned cat food in preference to raw meat (liver, minced beef and beef steak), followed in order of preference by cooked meat (minced beef), and finally, the least preferred food, dry cat food. These findings are in keeping with those of Bradshaw, Healey, Thorne, Macdonald and Arden-Clarke (2000), and reflect the cats' abilities to select their preferences in response to the nutritional composition of their food (Church, Allen and Bradshaw, 1996). The lack of enthusiasm for the dry cat food, although nutritionally complete, may be explained by its unfamiliar texture. Bradshaw *et al*. (2000) suggested that such food may be difficult for cats to ingest due to potential mouth problems. Feral cats, which do not benefit from veterinary attention, commonly suffer from both acute and chronic dental problems including gingivitis and stomatitis (E. Abraham, pers. comm.).

Bryces Farm cats, however, proved much more difficult to trap in terms of bait selection. Being un-tamed and for the most part, rarely fed by humans (see Chapter 2, Section 2.6), they were neophobic and initially highly suspicious of the traps and bait. They had probably never experienced commercial canned cat food before and thus showed no interest in it for at least one month. Furthermore, they would not eat raw meat (beef steak, minced beef, chicken, rabbit) regardless of whether or not it was left near the traps. However, after several weeks of leaving various baits both away from the traps and in open traps (traps fixed open which could not spring shut when activated), the cats began to eat most flavours of commercial canned cat food and raw meat quite readily, and some also ventured inside the traps to eat. The traps were then set.

Table 3.1: Summary of feral cat home range studies where information is available. Based on Liberg *et al.* (2000).

Study ref.[Ψ]	Location	Study area size (km^2)	Habitat	Food			Cat status	Group/ solitary	Highest pop. dens. (n/km^2)	Male mean home range ha (m^2)	Female mean home range ha (m^2)
				Type	Rel. abund.	Distrib.					
1	Dassen Is., South Africa	2.20	Subtropical scrub	Natural prey	Medium	Dispersed	Feral	S	50.00	44.00 (440,000)	19.00 (190,000)
2	Canberra, Australia	0.10	Farmland	House scraps, natural prey	High	Clumped	Feral farm	G	High	3.03 (30,300)	2.34 (23,400)
3	Canberra, Australia	1.00	Edge suburb/rural	House scraps	High	Clumped	Pets	G/S	200.00	3.03 (30,300)	2.34 (23,400)
4	New York, USA	0.33	Urban residential	Rubbish bins	High	Mod. clumped	Feral/pet	S?	500.00	2.62 (26,200)	1.77 (17,700)
5	Monach Is., Scotland	2.40	Dunes, heath	Natural prey	Low	Dispersed	Feral	S	4.00	N/A	42.00 (420,000)
6	Portsmouth, UK	1.00	Dockyard	Handouts	High	Mod. clumped	Feral	G	300.00	8.40 (84,000)	0.84 (8,400)
7	N. Territory, Australia	550.00	Semi-arid woodland	Natural prey	Low	Dispersed	Feral	S	0.10	2,210.50 (22,105,000)	N/A
8	Orongorongo, New Zealand	15.00	Grassland, bush	Natural prey	Low	Dispersed	Feral	S	1.00	140.00 (1,400,000)	80.00 (800,000)
9	Po Delta, Italy	42.00	Reclaimed, cropland	House scraps, natural prey	Med/low	Mixed	Mixed	S	1.40	394.00 (3,940,000)	147.00 (1,470,000)
10	California, USA	0.10	Riparian, farmland	Natural prey	High	Dispersed	Feral	G/S		35.30 (353,000)	26.80 (268,000)
11	Ainoshima Is., Japan	0.10	Fishing village	Fish dumps	High	Clumped	Feral	G	2,350.00	0.72 (7,200)	0.51 (5,100)
12	Victoria, Australia	190.00	Subtropical grassland	Natural prey	Low	Dispersed	Feral	S	1.57	620.00 (6,200,000)	170.00 (1,700,000)

[Ψ] 1. Apps (1983, 1986); 2/3. Barratt (1997); 4.Calhoon and Haspel (1989); Haspel and Calhoon (1989); 5. Corbett (1979); 6. Dards (1978, 1983); 7. Edwards *et al.* (2001); 8. Fitzgerald and Karl (1986); 9. Genovesi *et al.* (1995); 10. Hall *et al.* (2000); 11. Izawa *et al.* (1982); Yamane *et al.* (1994); 12. Jones and Coman (1982).

Table 3.1 continued: Summary of feral cat home range studies where information is available. Based on Liberg *et al.* (2000).

Study ref.[Ξ]	Location	Study area size (km^2)	Habitat	Food			Cat status	Group/ solitary	Highest pop. dens. (n/km^2)	Male mean home range ha (m^2)	Female mean home range ha (m^2)
				Type	Rel. abund.	Distrib.					
13	Galapagos Is.	10/15.00	Tropical scrub	Natural prey	Low	Dispersed	Feral	S	2.35	304.00 (3,040,000)	82.00 (820,000)
14	Hastings, New Zealand	5.20	Farmland	Natural prey	Low	Dispersed	Feral	G/S	3.50	86.00 (860,000)	57.00 (570,000)
15	Revinge, Sweden	20.00	Ranch land	House scraps, natural prey	Medium	Mixed	Mixed	G/S	3.30	370.00 (3,700,000)	50.00 (500,000)
16	Devon, UK	0.60	Dairy farm	Milk, natural prey	Medium	Clumped	Feral farm	G	6.30	83.00 (830,000)	13.10 (131,000)
17	Jerusalem, Israel	0.03	Urban residential	Rubbish bins	High	Clumped	Feral	G	2,800.00	0.75 (7,500)	0.27 (2,700)
18	Otago Peninsula, New Zealand		Coastal grassland	Natural prey	High	Dispersed	Feral	S		207.00 (2,070,000)	148.00 (1,480,000)
19	Avonmouth, UK	1.80	Dockyard	Handouts, rubbish	Medium	Mixed	Feral	S	12.50	15.00 (150,000)	10.30 (103,000)
20	Cornwall, UK	0.16	Dairy farm	Milk, some natural prey	Medium	Clumped	Feral farm	G	30.00		4.04 (40,400)
21	Zurich, Switzerland	1.30	Farmland	Natural prey	Medium	Clumped	Feral farm	G	14.00	7.20 (72,000)	6.00 (60,000)
22	Illinois, USA	52.00	Farmland	Natural prey	Medium	Clumped	Pets	G	6.30	228.00 (2,280,000)	112.00 (1,120,000)
23	Jura Mountains, Switzerland	30.00	Farmland, woodland	House scraps, natural prey	High	Clumped	Feral farm	G	18.00	6.50 (65,000)	50.60 (506,000)

[Ξ] 13. Konecny (1983, 1987); 14. Langham (1992); Langham and Porter (1991).15. Liberg (1980, 1983, 1984); 16. Macdonald and Apps (1978); Macdonald *et al.* (1987); 17. Mirmovitch (1995); 18. Moller and Alterio (1999); 19. Page *et al.* (1992); 20. Panaman (1981); 21. Turner and Mertens (1986); 22. Warner (1985); 23. Weber and Dailly (1998).

Trapping took place over several days, and for some cats, several weeks. The cats were caught using lightweight, self-actuating traps measuring 760 x 280 x 320mm (MDC Exports Ltd, Luton, Beds.), which were baited as described above. On Glebe Farm, trapping was carried out to coincide with the dawn milking session on the farm, as this was when the cats congregated for the milk and bread usually left by the farmer's wife. Here, traps were constantly monitored and cats did not remain inside for longer than 15 minutes. It was not possible to isolate cat GM3 from the other cats in order for trapping to be effective; therefore this animal was caught in a humane catch net (MDC Exports Ltd, Luton, Beds.). Some adult females and kittens were caught by hand.

On Bryces Farm, attempts were made to trap the cats at both dawn and dusk but it was found that more success was achieved if the traps were set late at night. Here, efforts were made in the timing of the trapping sessions to avoid the capture of lactating females unless the traps could be monitored hourly. Some adult females, and most kittens were caught by hand; others needed to be trapped.

Other animals caught in the traps included several rats and a juvenile red fox.

Traps were re-set periodically over several months to try to trap every cat.

3.2.2 Restraint and sedation

Once trapped, the cats were transferred to a wire trap transfer restrainer (MDC Exports Ltd, Luton, Beds.), more commonly referred to as a "crush cage". Once restrained in the crush cage, a sedative (Domitor®, Pfizer Animal Health, Sandwich, Kent) was given (50µg/kg [0.05ml/kg] depending on degree of sedation required, plus 0.4mg/kg butorphanol [0.04ml/kg of 10mg/ml solution]) by intramuscular injection by a veterinary surgeon where necessary for the animal to be treated for fleas and worms (Frontline® Top Spot™ [Rhone Merieux, Lyon, France] and Droncit® [Bayer, Newbury, Berkshire] respectively). After the experimental procedure had been carried out (detailed below), the action of the sedative was reversed with an α_2-adrenoceptor antagonist (Antisedan®, Pfizer Animal Health, Sandwich, Kent) (reversal with half the volume of Antisedan® to that of the previously administered Domitor® i.e. 125µg/kg [0.125ml/5kg][5]). The cat was kept warm to guard against the possibility of hypothermia, and released

[5] For GM3: Domitor® 80µg/kg (0.08ml/kg), butorphanol 0.4mg/kg (0.04ml/kg of 10mg/ml solution) and ketamine 5mg/kg (0.05ml/kg of 100mg/ml solution). Reversal with Antisedan® 200µg/kg (0.04ml/kg).

from the crush cage into a sheltered area inside the farm buildings which was familiar to the respective cat, once fully conscious and considered to have made a full recovery.

Adult females were not sedated for fear of pregnancy; the safety of these drugs on pregnant or lactating cats has not been documented. In fact, once restrained, most of the females could be handled sufficiently well for the purposes of this project without the need for sedation. Kittens were not sedated.

3.2.3 Sampling

The adult cats were weighed, sexed and their general body condition noted, as well as any defining features such as scars or distinctive colour spots. The results can be seen in Appendix 3. For the purposes of this study, Glebe Farm cats were assigned identification numbers using the prefix G and Bryces Farm cats were identified by the prefix B, both followed by either M for male, or F for female, and then an individual number. *Treeside* cats were also given B prefixes due to their proximity to Bryces Farm.

Age was estimated from dentition. Several hairs were plucked from the base of the tail, taking care to ensure the whole follicle was removed for DNA extraction (see Chapter 5). The plucked hairs were placed in labelled clean plastic envelopes and later frozen at –20°C. Kittens and juveniles were sexed, and hair samples taken.

Blood was taken from the jugular vein of the sedated adult males. This procedure was not attempted on non-sedated cats, although may be carried out successfully on tame restrained animals. The blood was stored in EDTA (an anticoagulant) vials and later tested in a veterinary laboratory for the presence of FIV and FeLV (see Chapter 2, Section 2.7.6).

3.2.4 Radiotracking procedures

For the adult males, a radiocollar (Biotrack, Wareham, Dorset) was fitted and secured, such that the tag was positioned under the cat's chin. Female GF2 was also radiocollared for a short period to investigate the concept of philopatry in domestic cats, as discussed in the literature. For the first two days following the fitting of the radiocollar, fixes were not recorded and the animal was disturbed as little as possible in order for it to become habituated to the collar. For the next few

days, fixes were not recorded but the animal was tracked, in order for it to become accustomed to the presence of the radiotracker. Throughout the study, the radiocollared cat was visually monitored for any signs of discomfort associated with the wearing of the collar.

The radiocollar weighed approximately 20g, amounting to approximately 0.67% of the cat's body weight. It consisted of a TW-3 transmitter mounted on a nylon collar with a buckle and a 30cm whip antenna, and transmitting on 138-230MHz. An activity-sensor circuit was added to the transmitter, consisting of a mercury tilt-switch which switched between two distinctly different pulse rates. The tilt-switch was mounted horizontally within the tag. The tags outputted 20ms pulses at a rate of 44 per minute on slow and 69 per minute on fast. When the cat was moving and therefore active, a more irregular output was detected. When at rest, the tag pulsed on either of its two pulse rates.

The receiver used was the M-57 (Mariner Radar Ltd., Lowestoft, Suffolk) with a three-element flexible Yagi antenna (Lintec Antennas Ltd., Worthing, West Sussex).

3.2.5 Data collection

Radiotracking was carried out using a time sampling method whereby home range was determined by periodic sampling (see Martin and Bateson, 1998). A home range must be defined for a specific interval (e.g. a season, a year, or possibly a lifetime). The longer the interval, the more data can be used to quantify a home range, but the more likely that the animal has changed its cognitive map since the first data were collected (Powell, 2000). In this study, the location of the cat to the nearest ten metres was recorded every five minutes throughout the tracking session, using an adapted Ordnance Survey map of the area with a superimposed grid system to record x-y coordinates, and a hand-held dictaphone (Sony). Actual sightings of the cat were also noted, as well as the behaviour of the cat at each fix (whether active or at rest[6]). Tracking periods were in the region of four hours per session from a 24-hour period, giving 48 sample points per four hour sampling session. The timing of radiotracking sessions was allocated equally to ensure even coverage of the 24-hour period. All radiotracking was carried out on foot.

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[6] Behaviours such as grooming, generally performed with the cat in one location and in a relaxed state, were classed as "active" because the head movement involved in grooming produced a similar output from the radio tag as walking or running. Therefore, unless the cat was in sight, it was not always possible to make distinctions between such behaviours. It should be noted that "rest" categories therefore also included situations in which the cat was motionless but very much awake, such as when watching prey or another cat.

Whilst most of the published literature relating to feral cat home ranges obtained by radiotracking gives an overall home range, some authors have calculated both diurnal and nocturnal home ranges. However, from personal observation it became obvious that these are not clearly defined periods for feral cats. Initial observations showed that the cats were more active at dawn and dusk, which also corresponded to milking times on the farms and hence increased disturbance of the cats by human and mechanical activity. Mucking-out and feeding of livestock was also carried out at these times, although with more emphasis on the morning period. As described in Chapter 2, supplementary feeding of the feral cats, where provided, was also carried out around milking times. Prey species of feral cats such as small rodents and birds were also more active at dawn and dusk.

Therefore, three time periods were drawn up with dawn and dusk categorised into one period (Table 3.2).

Table 3.2: Radiotracking time periods

Period	Time
Crepuscular	0400-0800hrs *and* 1600-1900hrs
Diurnal	0800-1600hrs
Nocturnal	1900-0400hrs

For cats GM2 and BM1 which were radiotracked over a longer period of time, data were further divided into seasonal periods, as shown in Table 3.3.

Table 3.3: Radiotracking seasons

Season	Month (inclusive)
Winter	October - January
Spring	February - April
Summer	May - September

3.2.6 Sighting data

In addition to locations obtained by radiotracking, sightings of cats at other times during field visits to the study site were also noted, and included in the overall calculation of home ranges.

On Bryces Farm, BM4, having been trapped and sedated, escaped before a radiocollar could be fitted or a hair sample taken. Despite efforts spanning the following months, he was never re-captured. Therefore, location data (and hence home range) was calculated solely from occasional sightings. Activity data was not collected.

3.2.7 Central resource (core) areas

As discussed in Chapter 1, Section 1.3.6, core areas of importance, or Central Resource Areas (CRAs) are established within an animal's home range. The CRA must be used more than expected by random use (Powell, 2000). For Glebe Farm, the CRA included the vicinity of the farmhouse, farm garden and adjacent barns. Here, the cats were fed and spent much of their time. Many of the Glebe Farm kittens were either born in these barns or were moved there by their mothers very soon after birth.

On Bryces Farm, the CRA was not so easy to identify as the farm was divided into two sections. In the dairy area, the central yard outside the milking parlour and adjacent barns could be described as the CRA, and in the pig section the CRA could be said to encompass the dump as well as the main barn.

3.2.8 Correlates of home range

The literature suggests a correlation between size of home range and an individual's age-size-health characteristics (e.g. Fisher and Lara, 1999). In this study, health was measured qualitatively based on both the results of blood sampling (for FIV/FeLV) and outward appearance (general body condition); health was also considered to be related to the cats' ability to win fights. Age was estimated (based on dentition) for all cats, except those born during the study period for whom dates of birth were known. Due to the small sample sizes involved, quantitative correlations were not calculated but Figure 3.1 illustrates

hypothetical correlations based on published literature and the findings of this study.

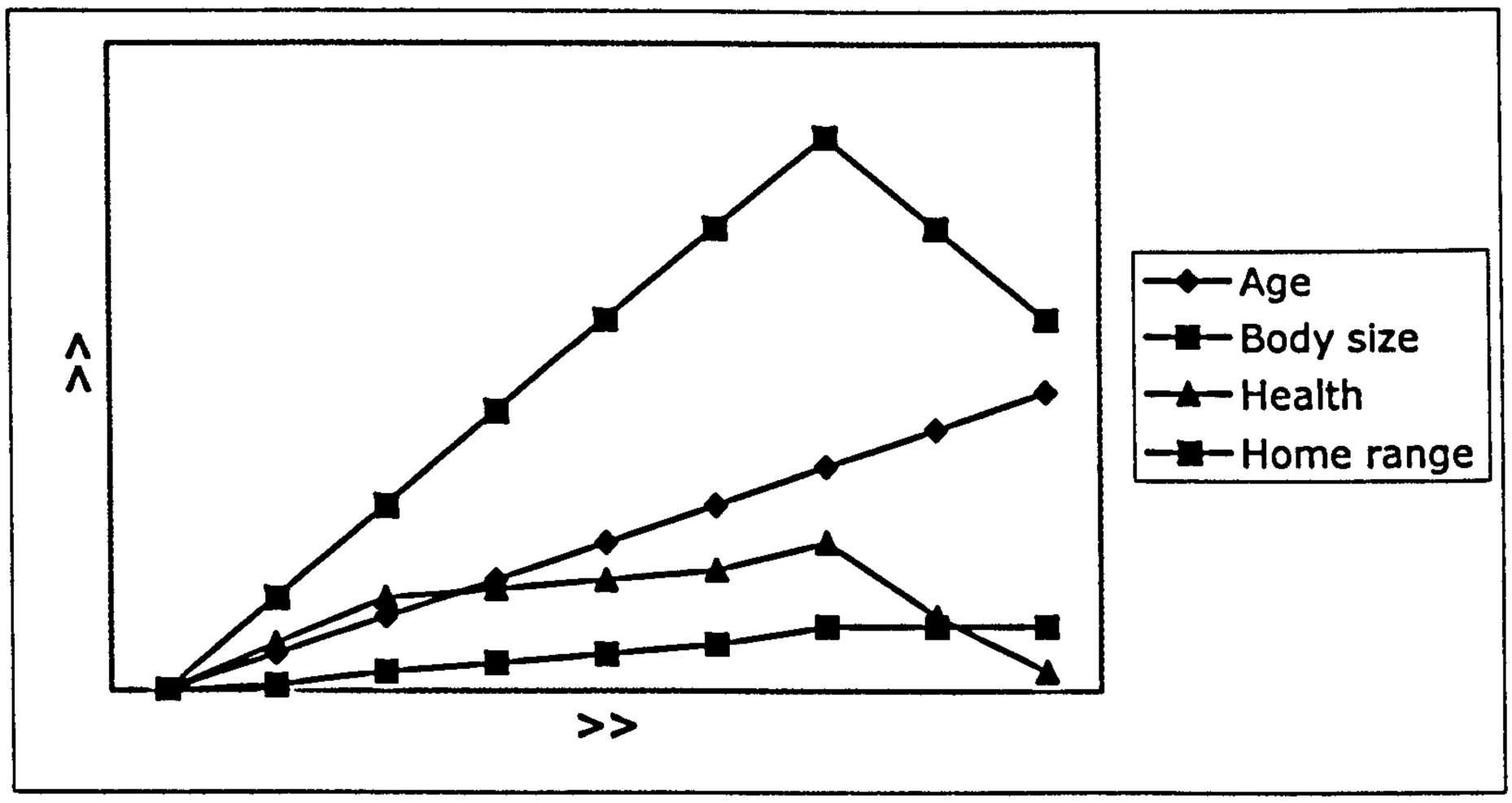


Figure 3.1: Relationship between home range, and age-size-health characteristics

This shows a steady increase in home range until it reaches a maximum value and then falls as the animal ages. The maximum home range corresponds to the animal's peak health condition and body size. Health and body size are not represented exponentially, as the animal may suffer illness (and perhaps an accompanying reduction in body size) and then recover at any point during its life, and finally enter senescence.

3.3 Results: Glebe Farm

3.3.1 Home range

Overall comparative male home ranges

Figure 3.2 illustrates the overall maximum home ranges of the Glebe Farm male cats, in the form of 95% MCPs based on radiotracked fixes and occasional sightings when not being tracked. Range schematics (Figure 3.3a-c) further illustrate the data, identifying every radiotracked fix and/or sighting of each cat (in other words, the 100% MCP).

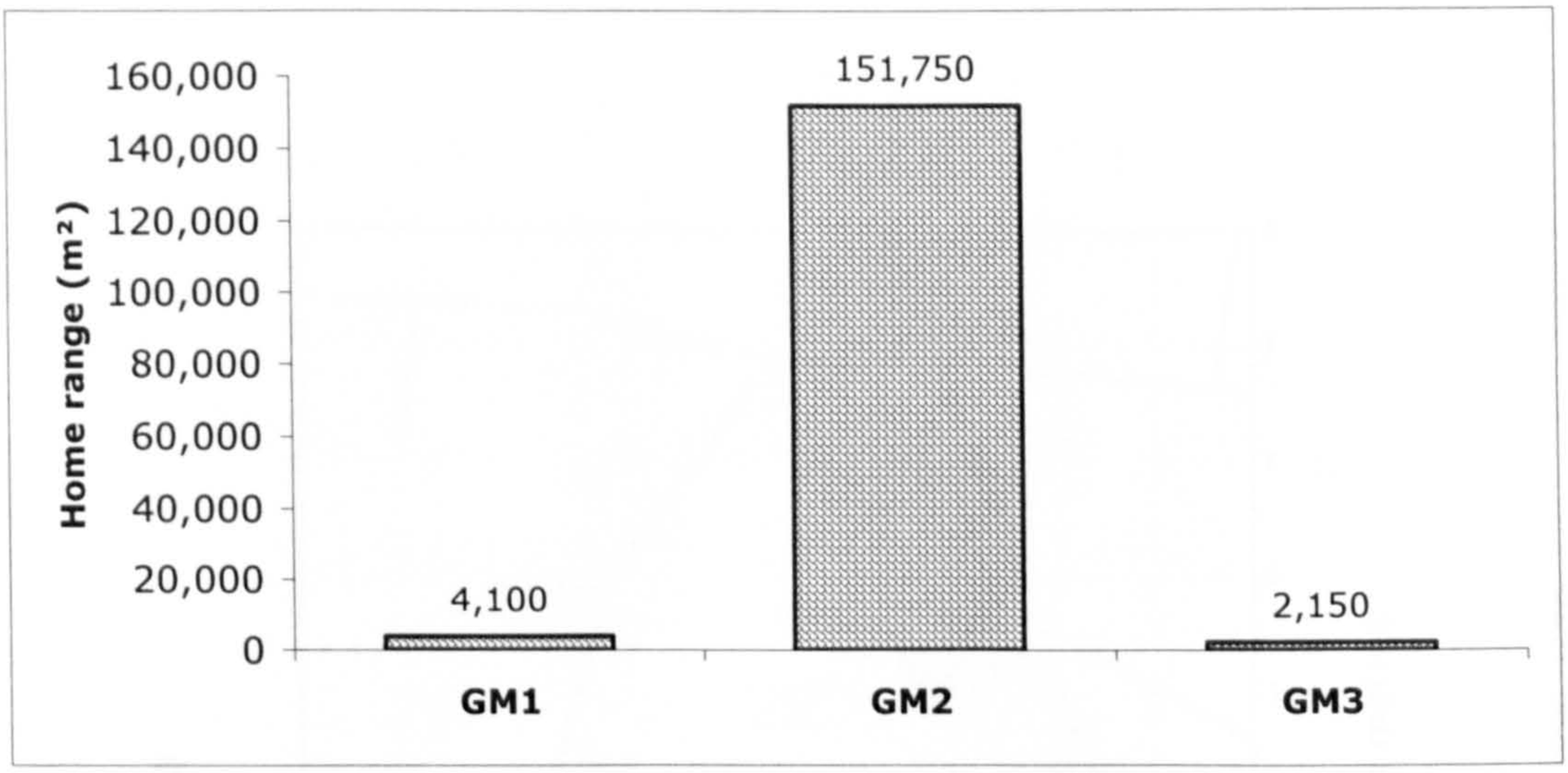


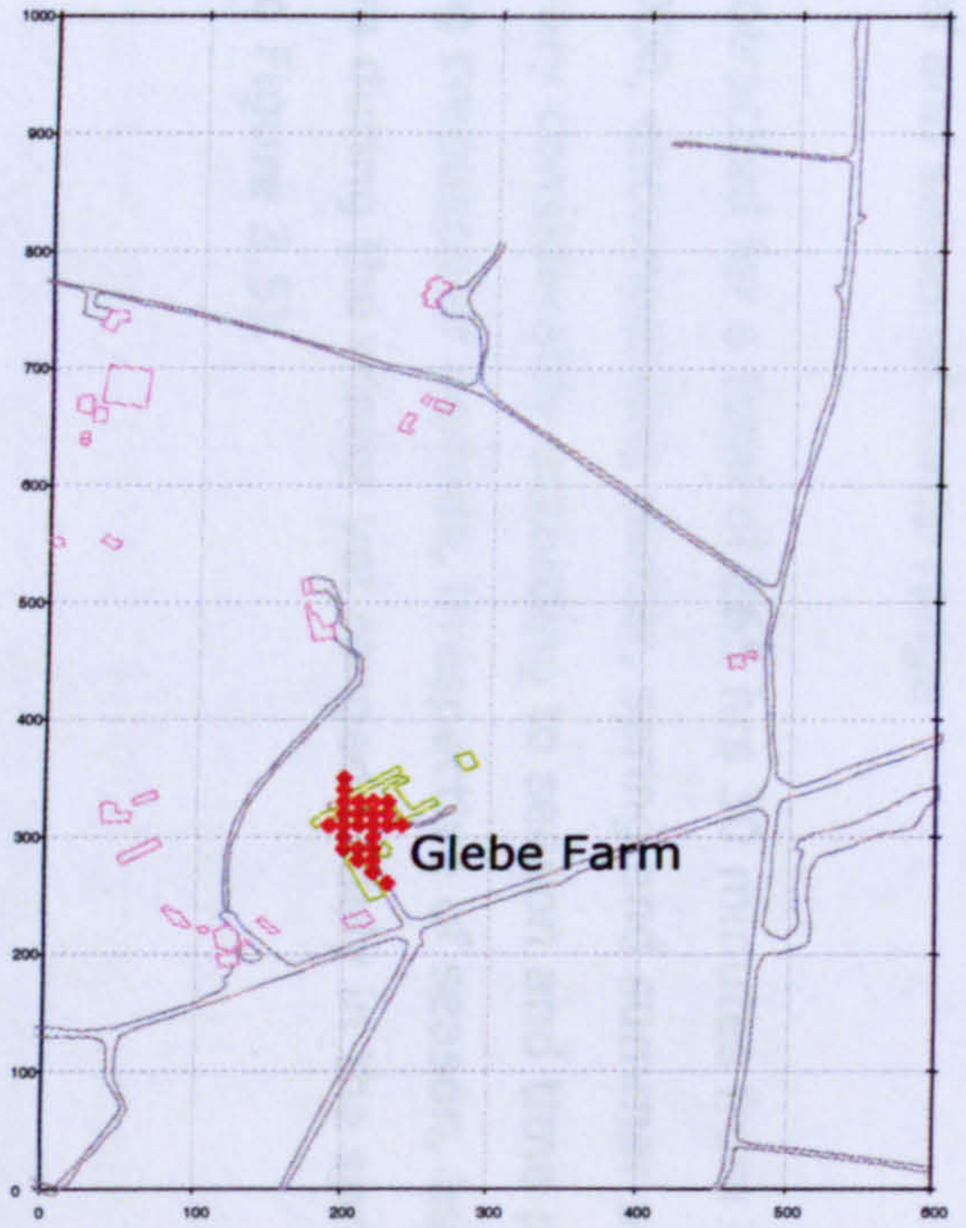
Figure 3.2: Overall home ranges recorded (95% MCPs) for the Glebe Farm males

GM1: temporal home range

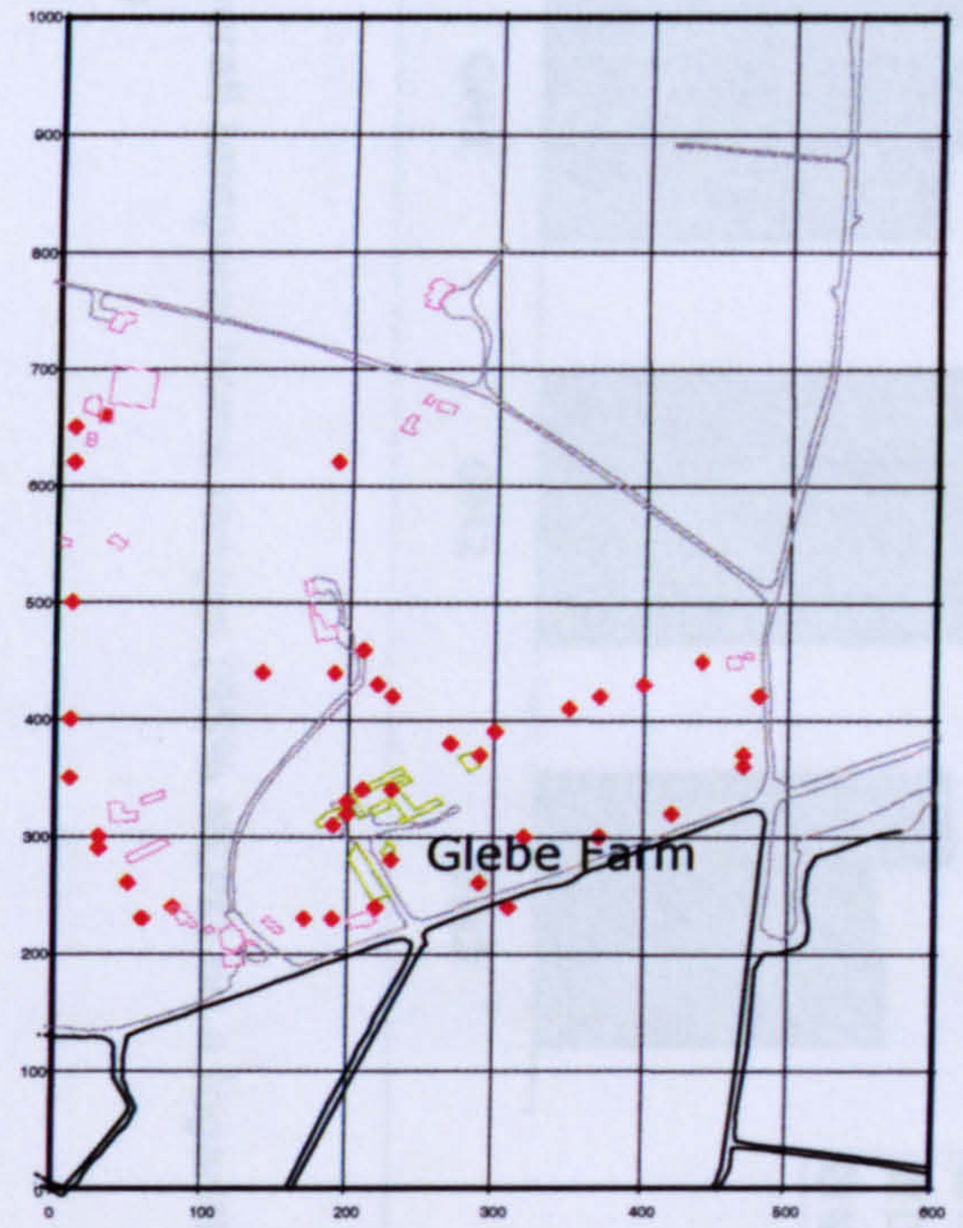
GM1 was radiotracked for a total of 124 hours 30 minutes, over the winter period October 1999 to January 2000. The results, in the form of 95% MCPs based on radiotracked fixes and occasional sightings when not being tracked, are summarised in Table 3.4 and Figure 3.4.

There was little variation in location or range covered by GM1 during crepuscular, diurnal and nocturnal radiotracking sessions. He did not, in fact, venture away from the Central Resource Area (CRA) of Glebe Farm whilst being tracked, nor was he ever sighted away from the CRA at any other time.

(a) GM1



(b) GM2



(c) GM3

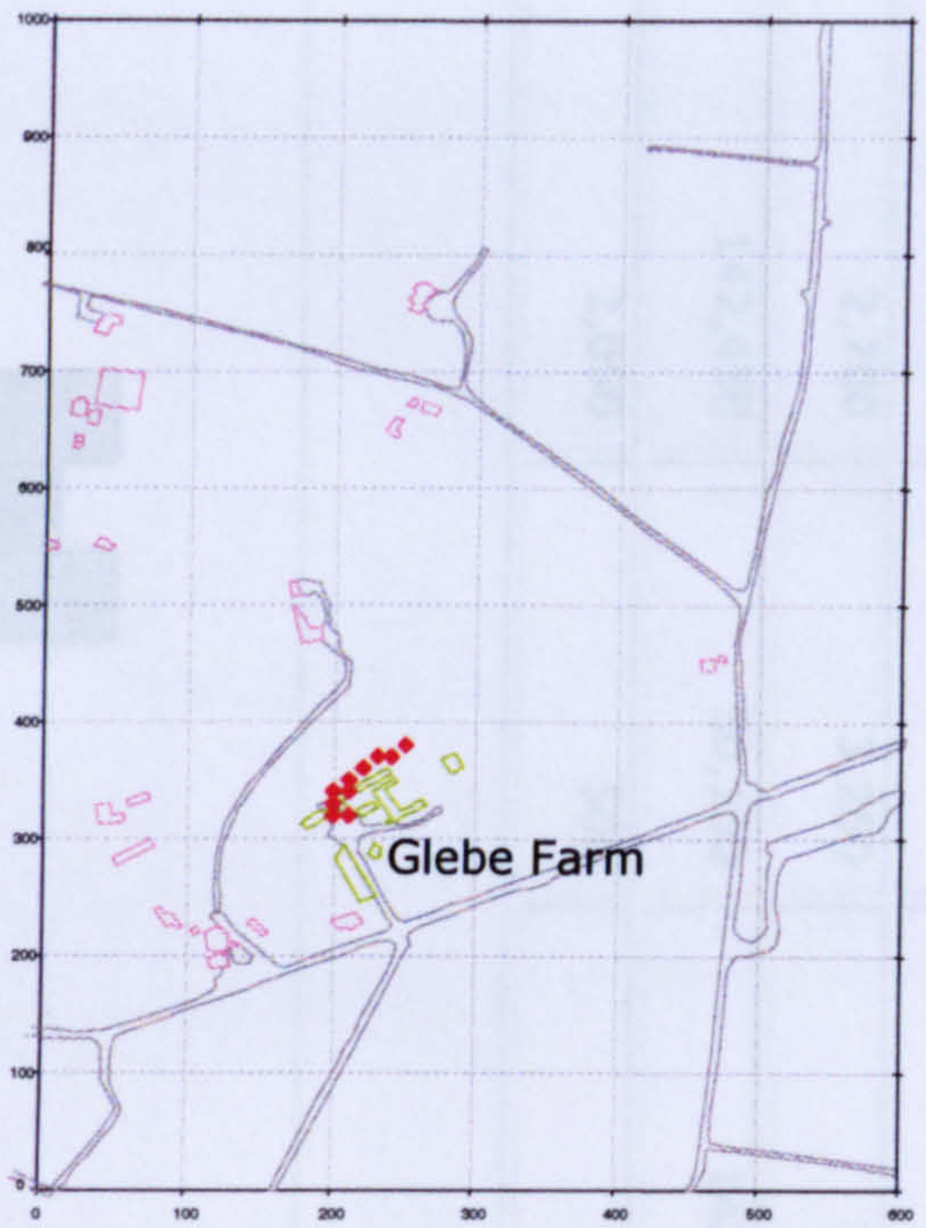


Figure 3.3a-c: Overall range schematics of the Glebe Farm male cats. Grid squares measured in metres.

Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP

Glebe Farm buildings Other properties

Table 3.4: Overall temporal home ranges (95% MCPs) for the Glebe Farm male cats (m^2)

	Crepuscular	Diurnal	Nocturnal
GM1	2,700	3,250	1,700
GM2	142,450	50,100	142,450
GM3	2,050	500	600

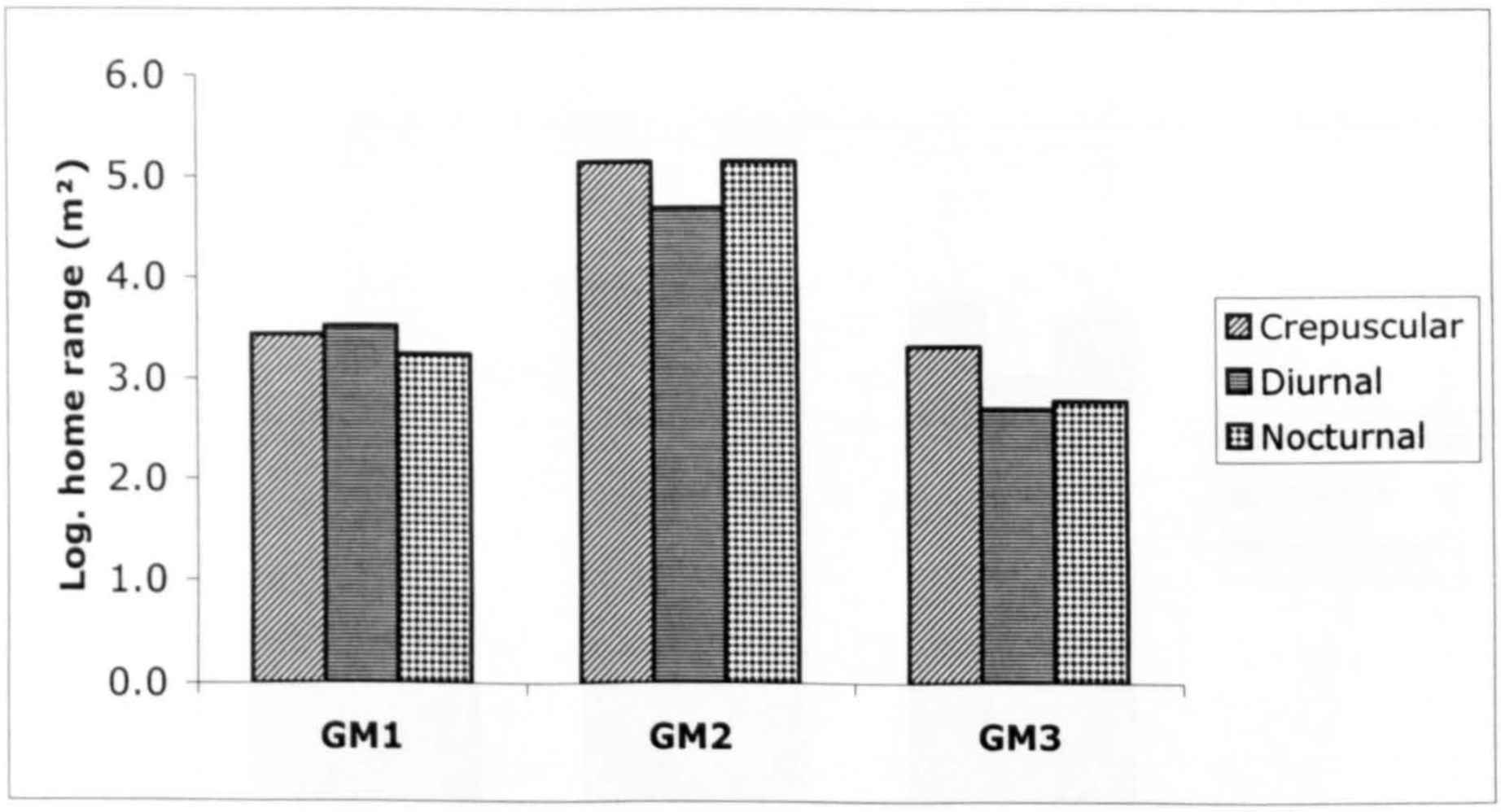


Figure 3.4: Overall temporal home ranges (95% MCPs) on a logarithmic scale for the Glebe Farm male cats

GM2: temporal and seasonal home range

GM2 was radiotracked for a total of 265 hrs 30 minutes from December 1999 to September 2000, encompassing winter, spring and summer seasons. His range appeared to vary considerably according to season and time period; he ranged the furthest during crepuscular periods, irrespective of season, but at night he was almost inactive during the winter yet ranged widely in the spring and summer (Table 3.5 and Figure 3.5).

Table 3.5: Overall seasonal and temporal home ranges (95% MCPs) for GM2 (m^2)

	Crepuscular	Diurnal	Nocturnal	Overall
Winter	9,200	8,100	100	8,600
Spring	116,100	15,250	114,700	119,300
Summer	73,750	14,500	53,100	80,750
Overall	142,450	50,100	142,450	151,750

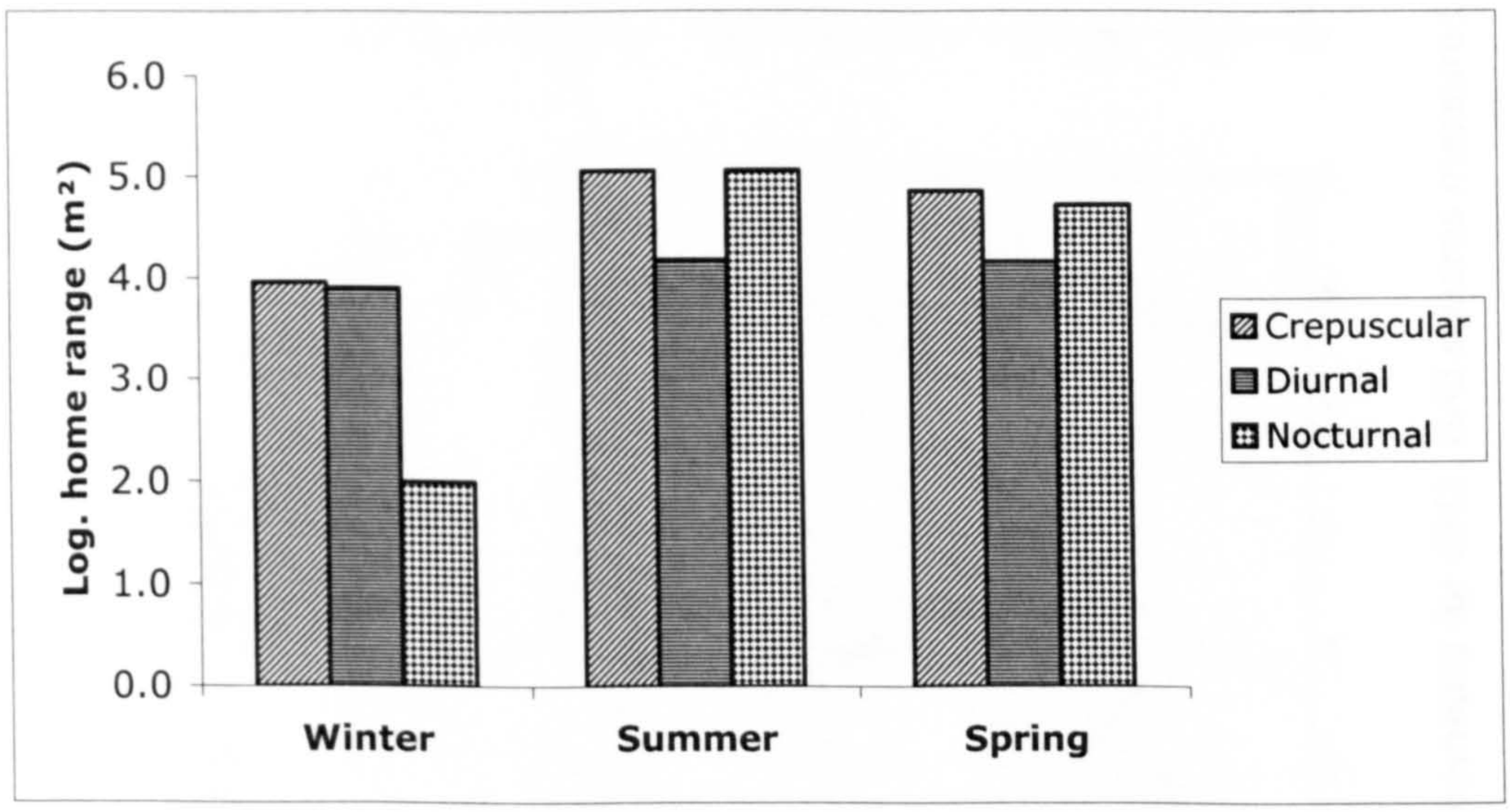


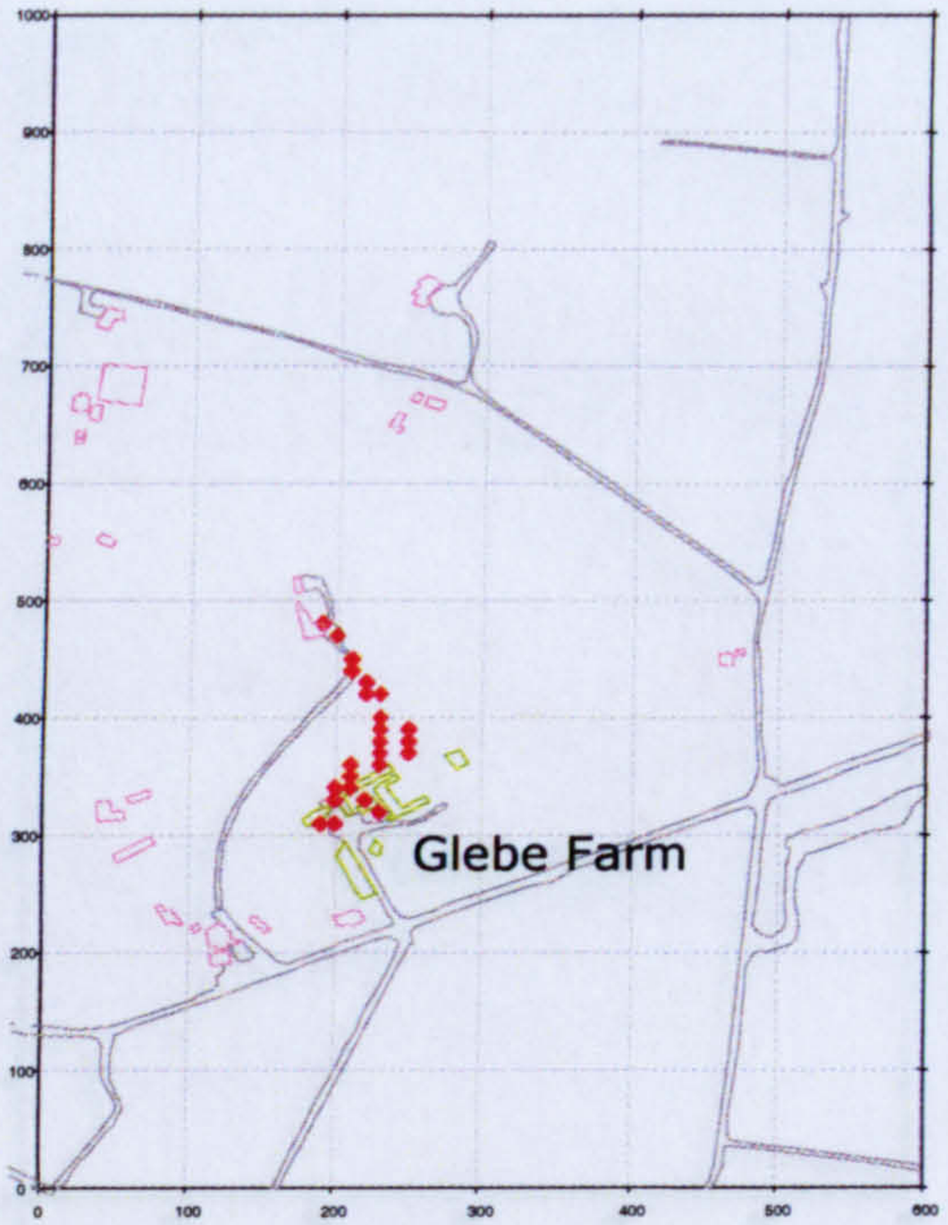
Figure 3.5: Overall seasonal and temporal home ranges (95% MCPs) on a logarithmic scale for GM2

Figures 3.6a-i show overall seasonal and temporal range schematics for GM2, based on radiotracked fixes and occasional sightings when not being tracked.

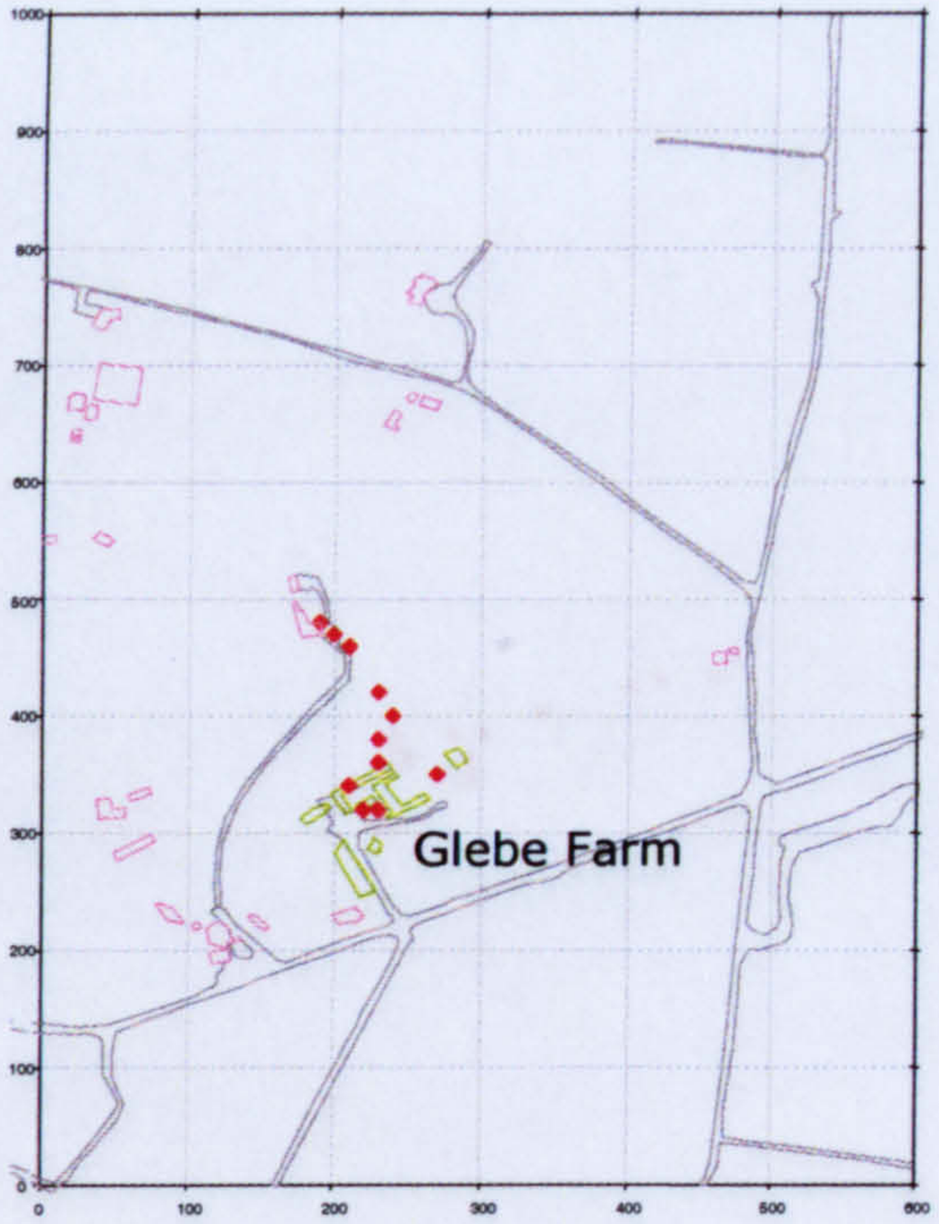
GM3: temporal home range

GM3 was radiotracked for a total of 55 hours during the spring of 2000 (March and April). The results can be seen in Table 3.4 and Figure 3.4. There was little variation in location or range covered by GM3 during crepuscular, diurnal and nocturnal radiotracking sessions, and range almost completely overlapped with that of GM1. As with GM1, GM3 did not venture away from the CRA of Glebe Farm whilst being tracked, nor was he ever sighted away from the CRA at any other time.

(a) Winter crepuscular



(b) Winter diurnal



(c) Winter nocturnal

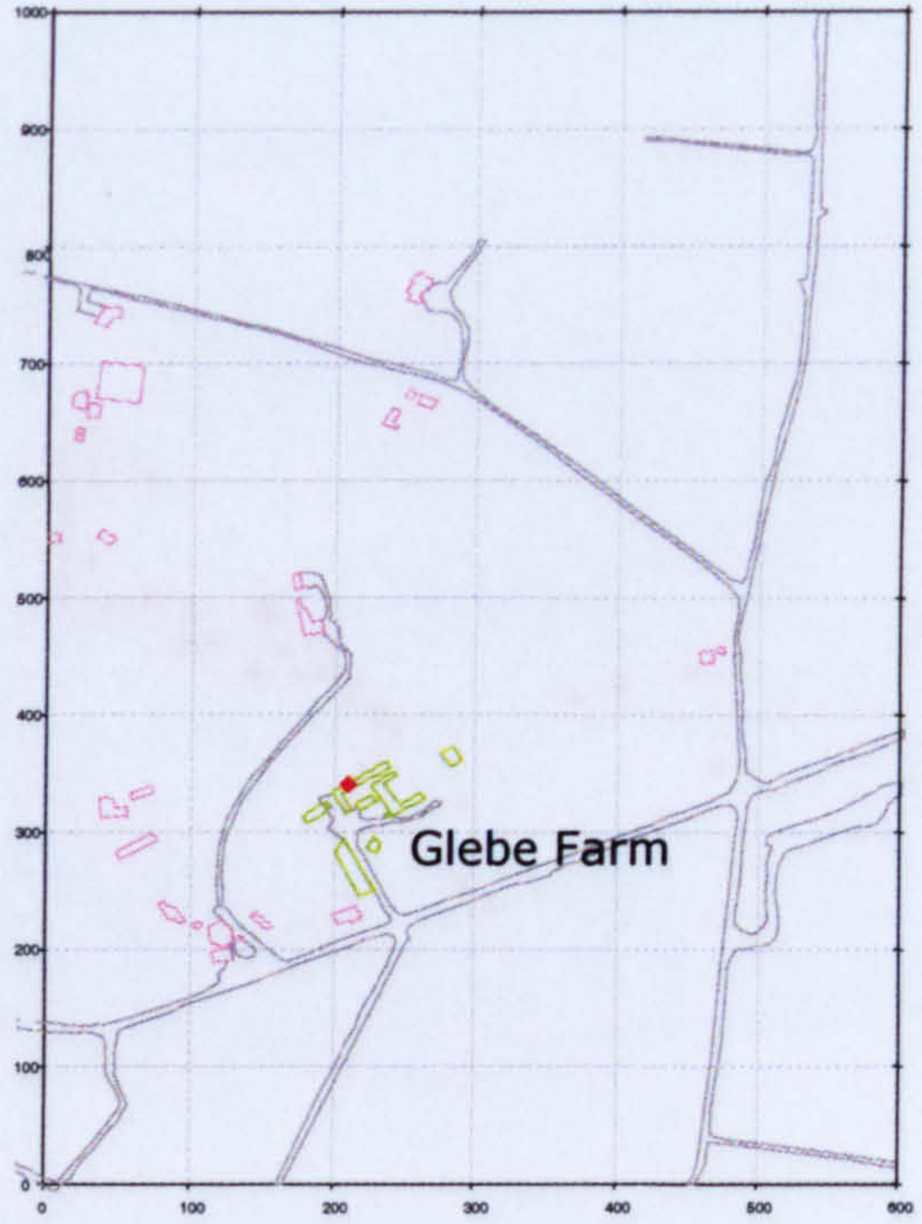
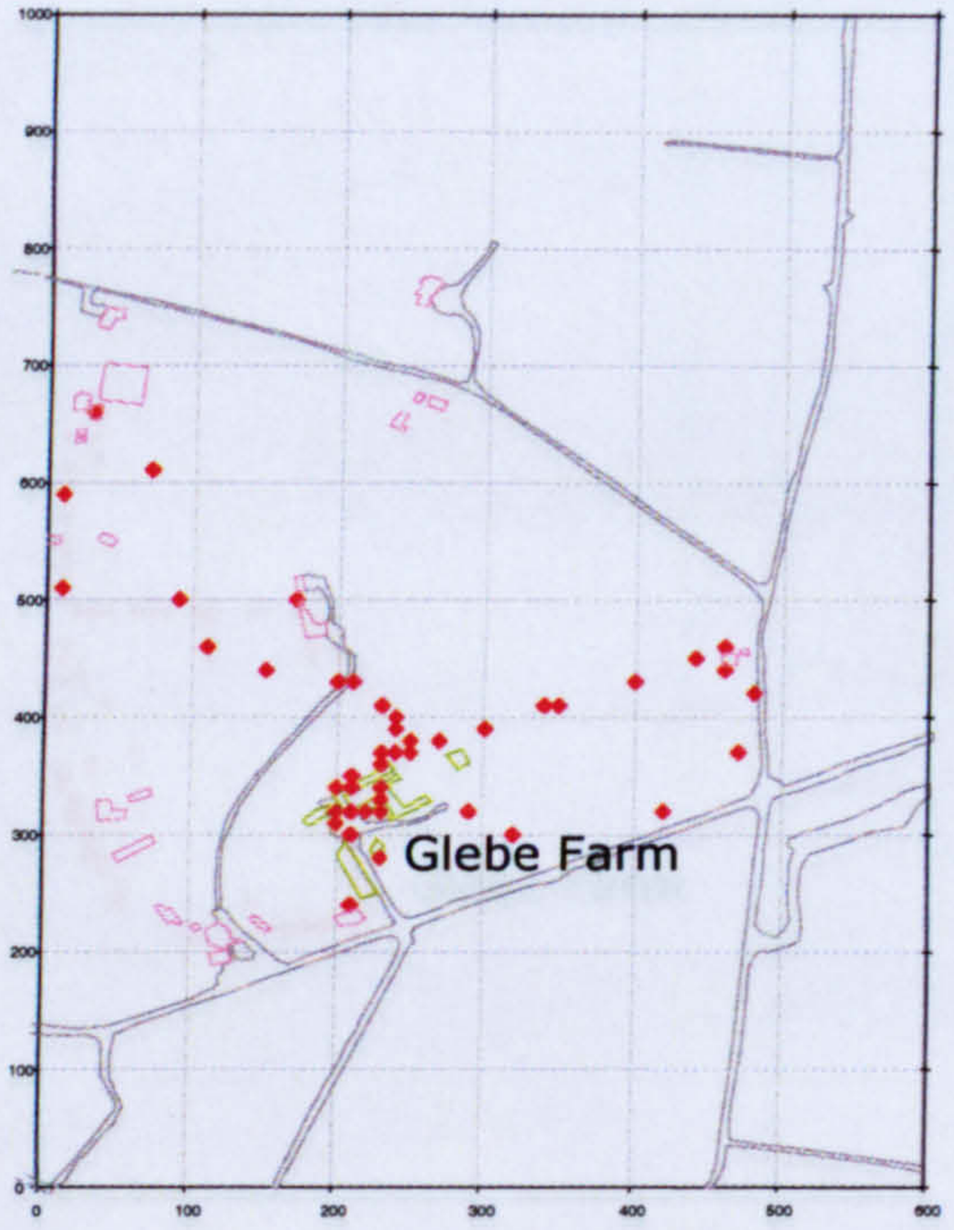


Figure 3.6a-c: Overall winter temporal range schematics for GM2. Grid squares measured in metres.

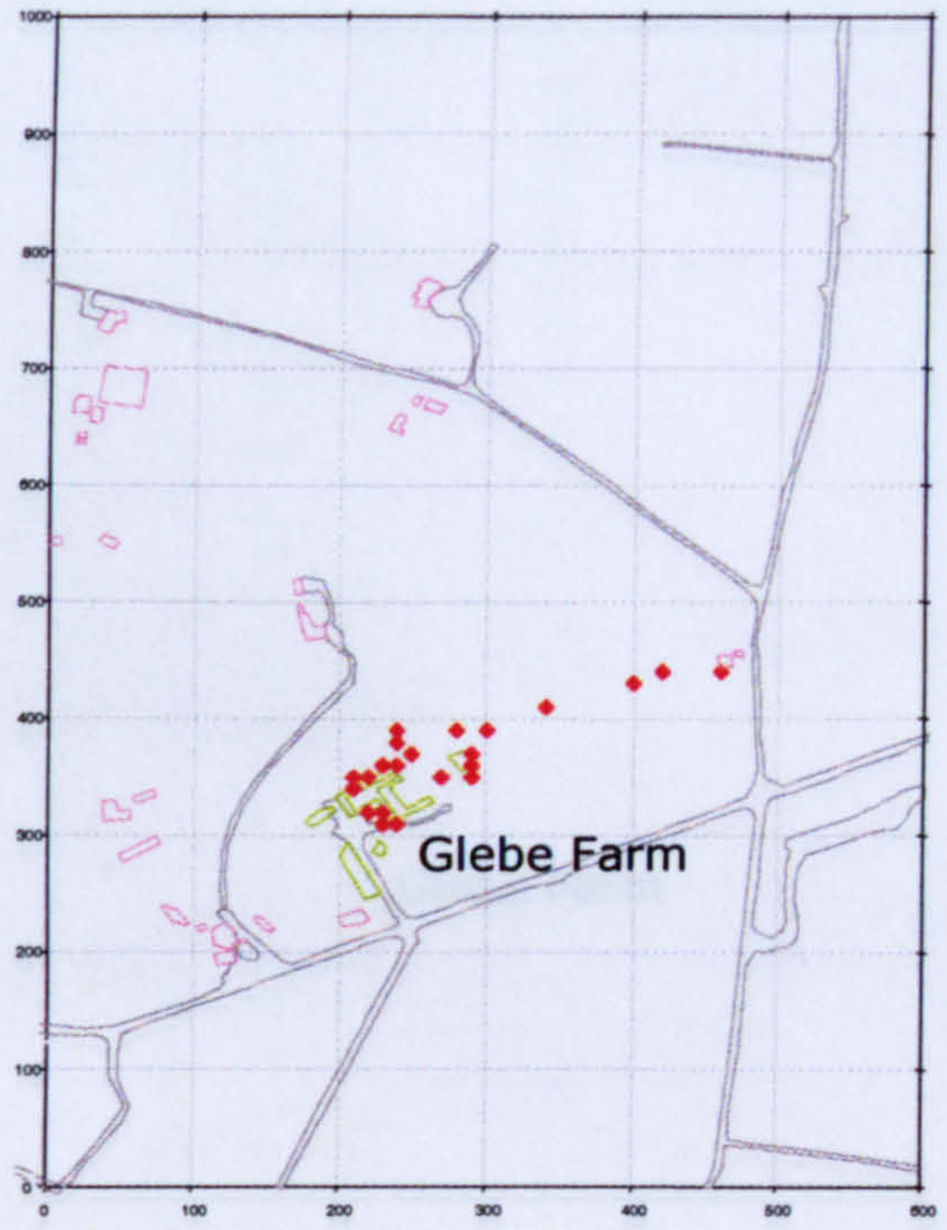
Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP

Glebe Farm buildings Other properties

(d) Spring crepuscular



(e) Spring diurnal



(f) Spring nocturnal

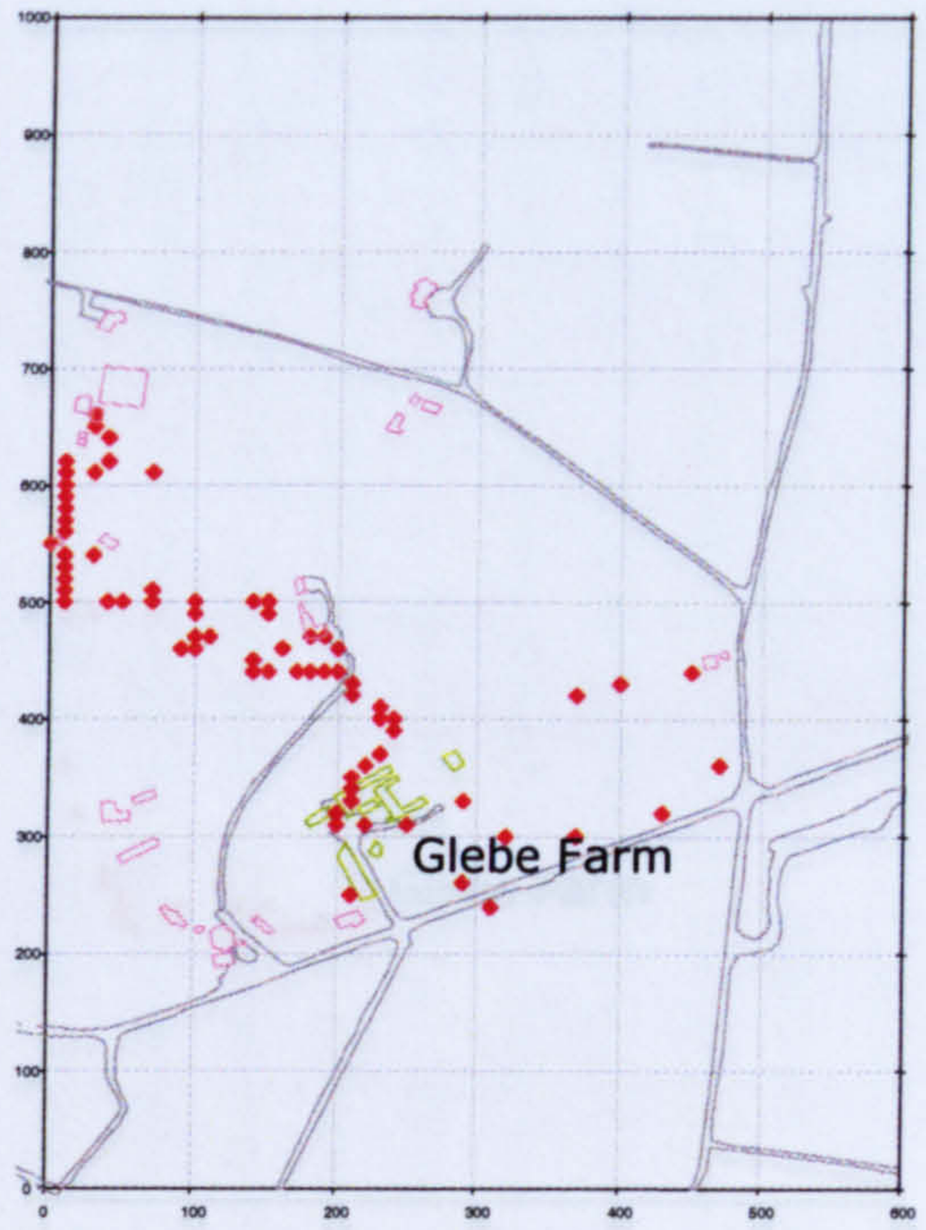
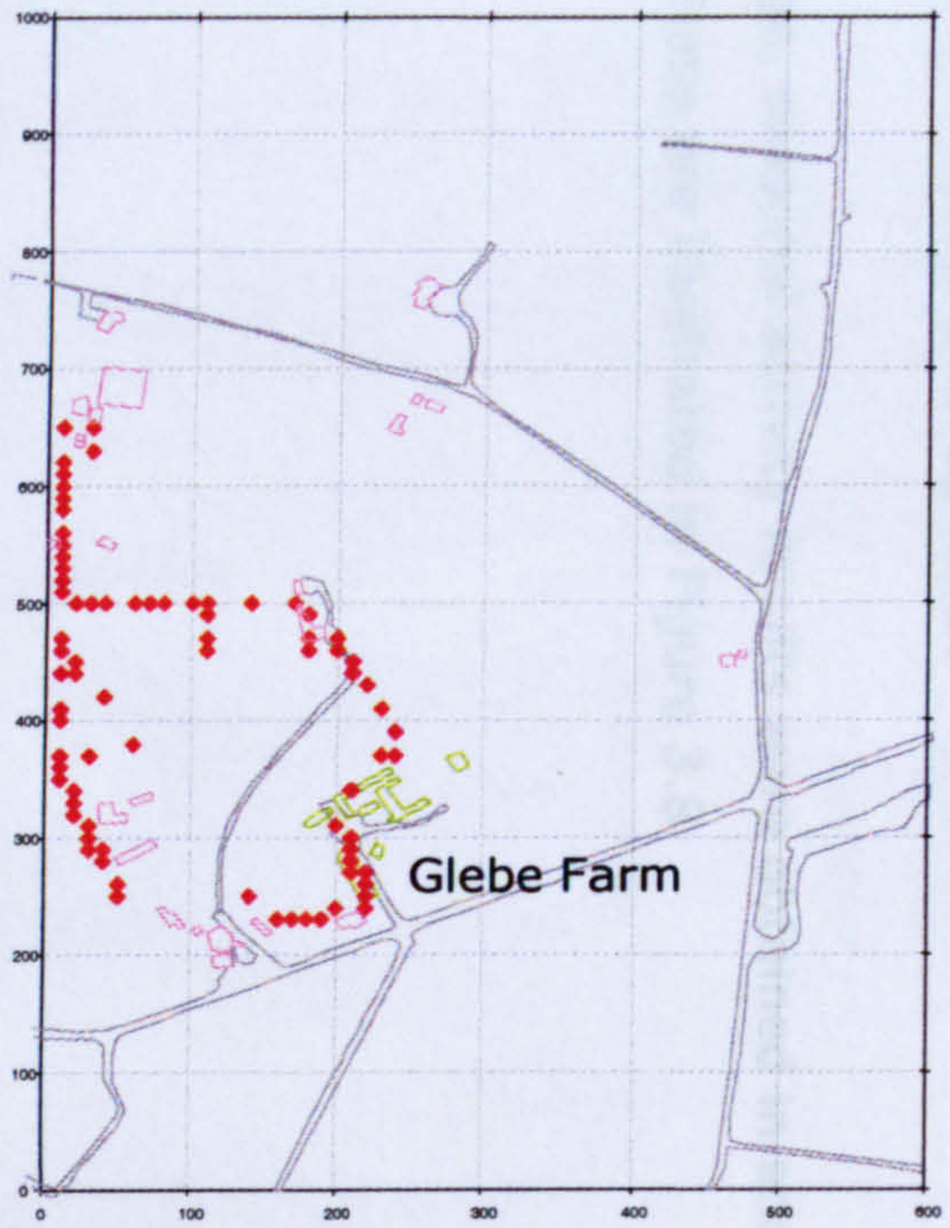


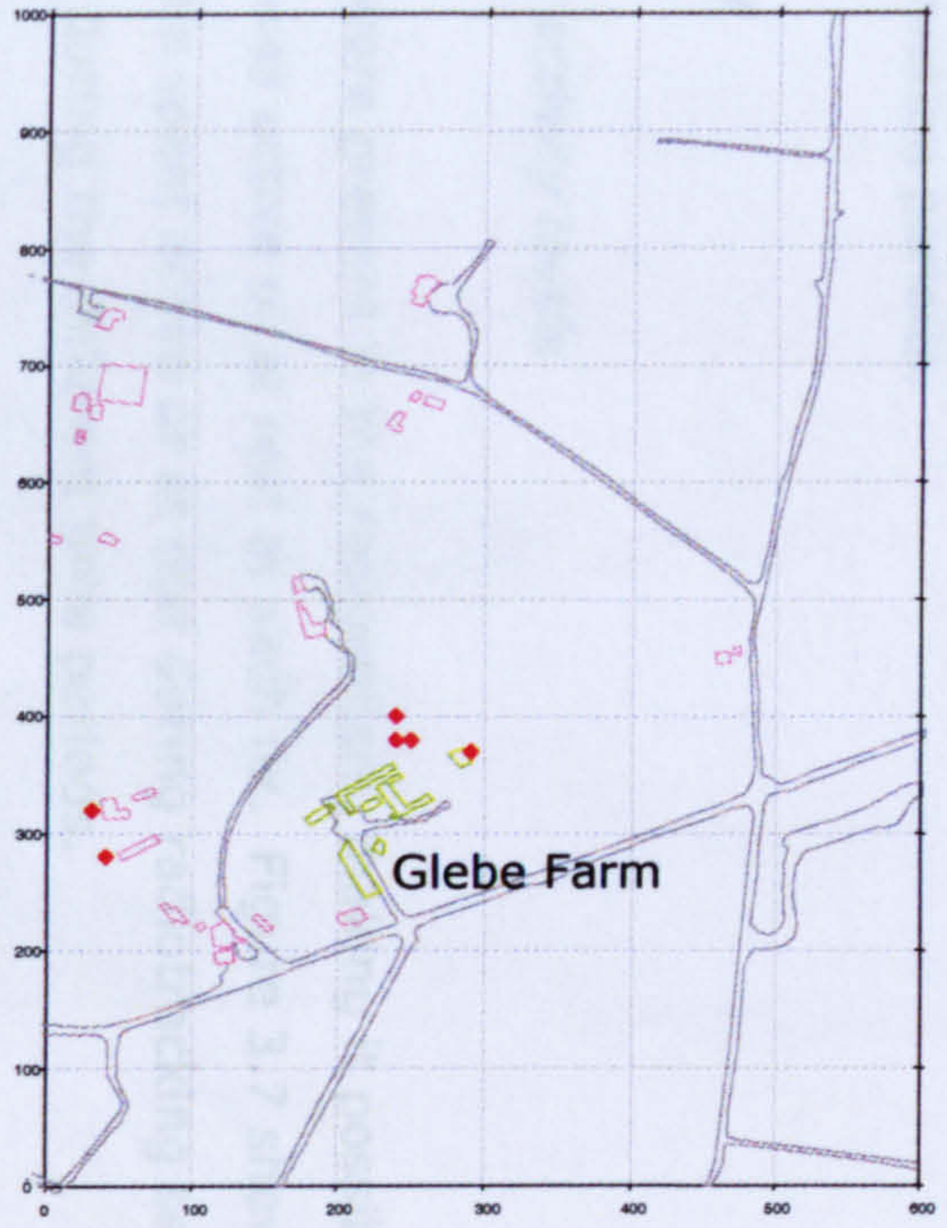
Figure 3.6d-f: Overall spring temporal range schematics for GM2. Grid squares measured in metres.

- Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP
- Glebe Farm buildings
- Other properties

(g) Summer crepuscular



(h) Summer diurnal



(i) Summer nocturnal

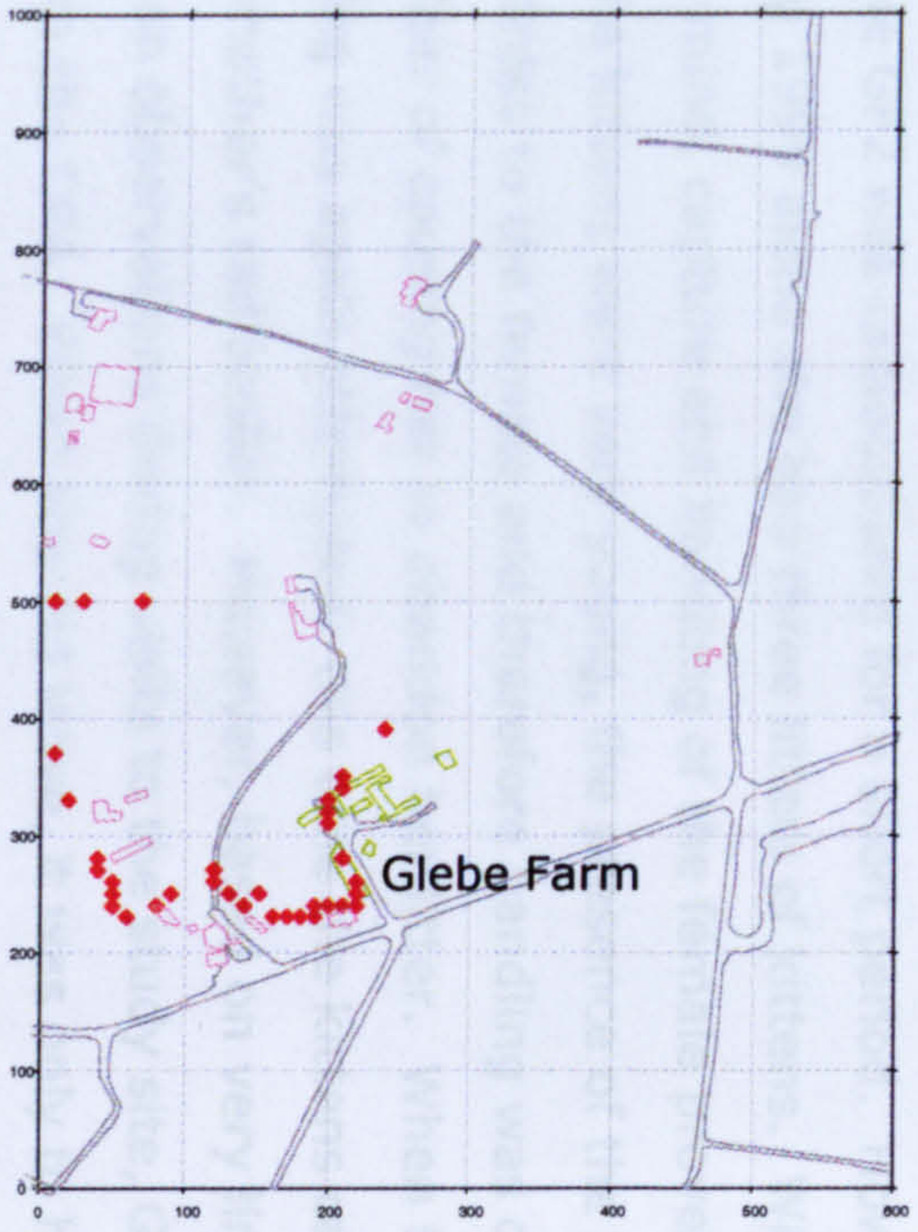


Figure 3.6g-i: Overall summer temporal range schematics for GM2. Grid squares measured in metres.

Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP

Glebe Farm buildings Other properties

Female home range

Glebe Farm female GF2 was radiocollared for a short period. However, this was not successful; during 1999 alone she had three litters of kittens. With welfare considerations in mind, capture and handling of the female proved extremely difficult. When the kittens were very young, the presence of the radiotracker caused obvious stress to the female and therefore handling was ceased immediately for fear of causing her to abandon her litter. When the kittens were older, radiotracking was again attempted: this time the kittens caused considerable damage to their mother's radiocollar. However, based on very limited radiotracking data and mainly on observations during visits to the study site, GF2 was rarely sighted away from the CRA. When she did leave, it was only to hunt in the hedgerow of an adjacent field. In fact, all Glebe Farm females remained within the CRA during observation periods.

3.3.2 Activity

Overall temporal activity levels

Activity sensors were present in the radiocollars, making it possible to determine whether the cat was active or at rest at each fix. Figure 3.7 shows the overall percentage of time spent active or at rest during radiotracking sessions for the three male cats, during the different time periods.

GM2: temporal and seasonal activity levels

As for home range, seasonal activity results were obtained in addition to temporal data for GM2. These are illustrated in Figure 3.8.

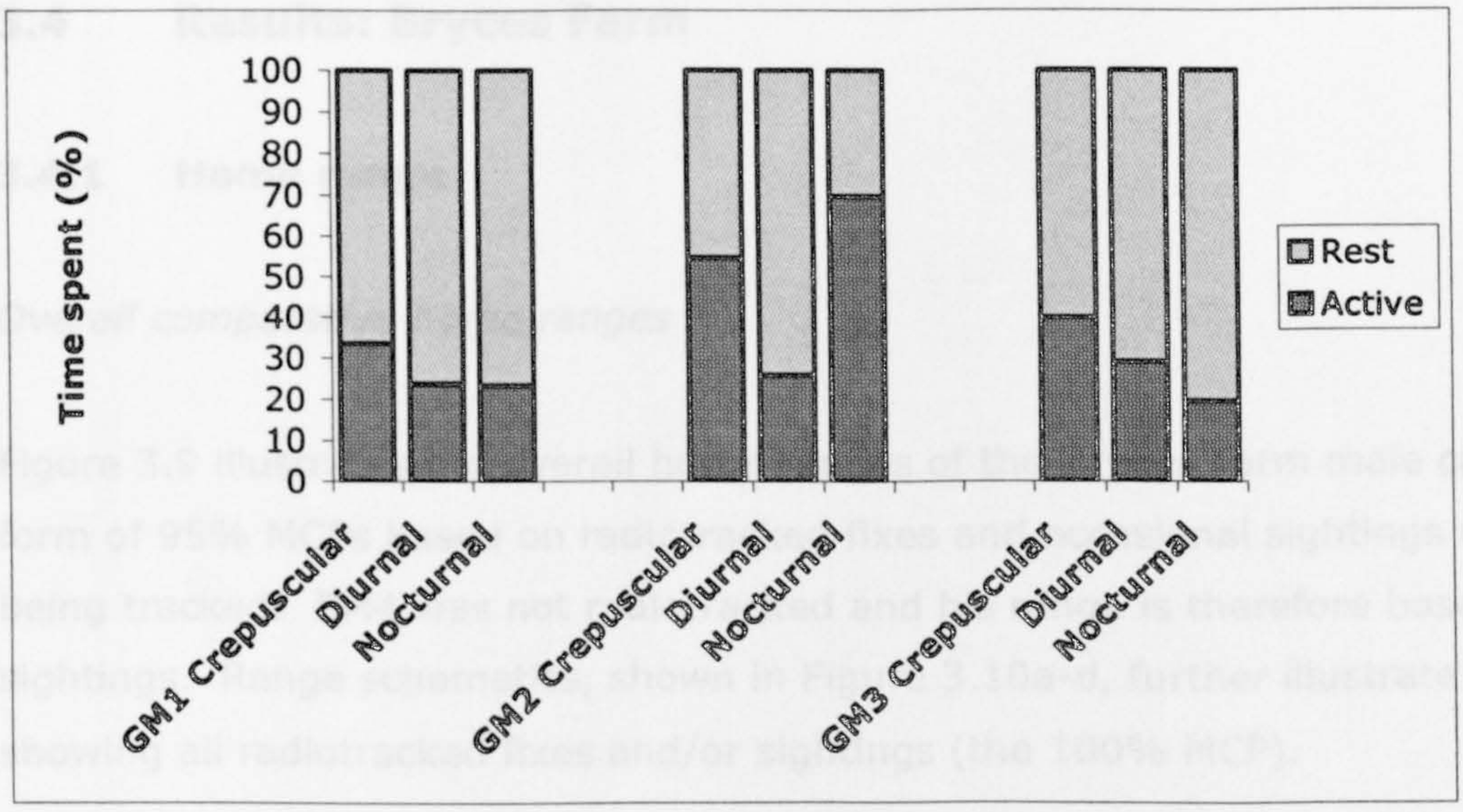


Figure 3.7: Temporal activity data for the Glebe Farm male cats

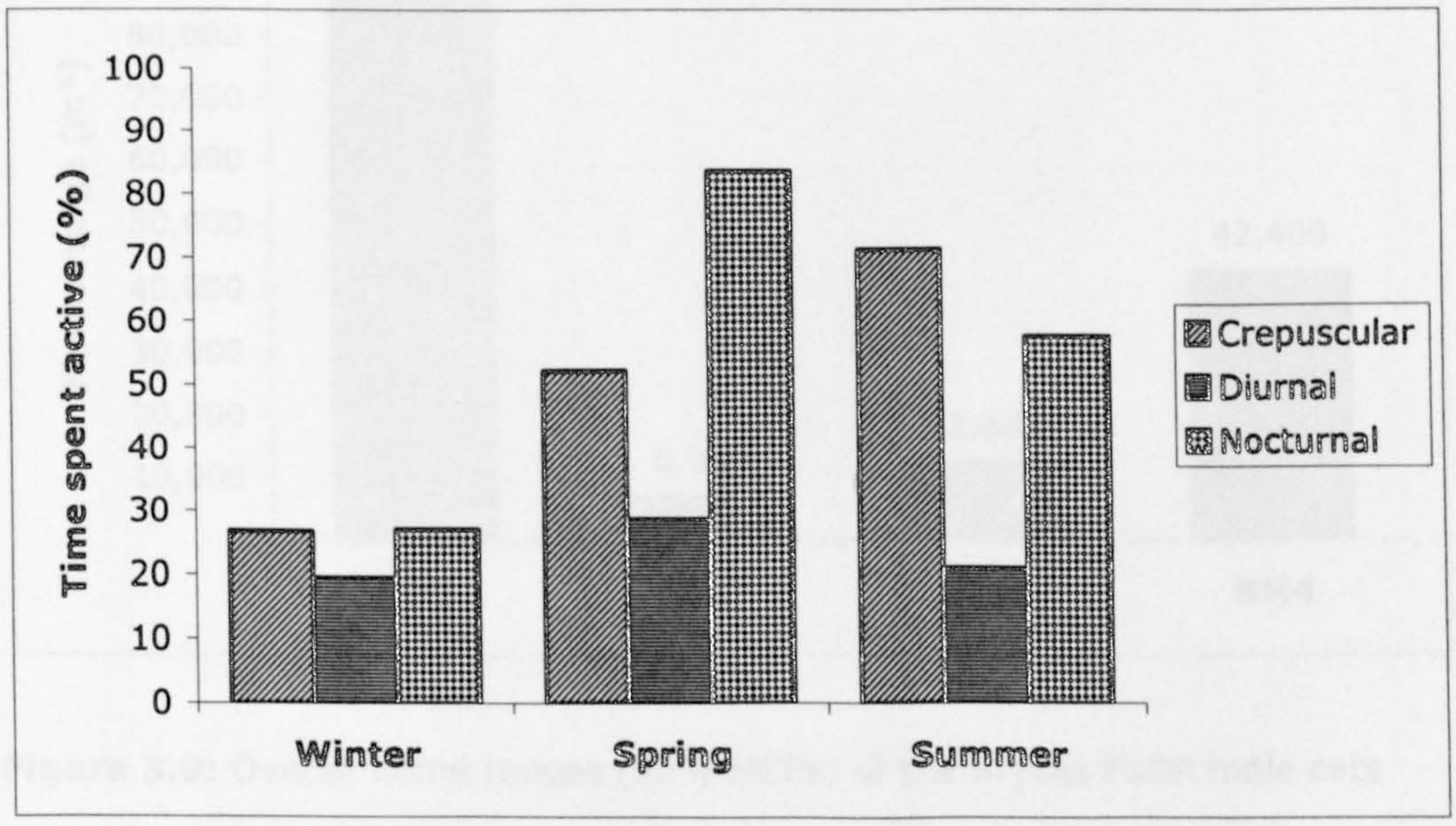


Figure 3.8: Seasonal and temporal activity data for GM2

3.4 Results: Bryces Farm

3.4.1 Home range

Overall comparative home ranges

Figure 3.9 illustrates the overall home ranges of the Bryces Farm male cats, in the form of 95% MCPs based on radiotracked fixes and occasional sightings when not being tracked. BM4 was not radiotracked and his range is therefore based only on sightings. Range schematics, shown in Figure 3.10a-d, further illustrate the data, showing all radiotracked fixes and/or sightings (the 100% MCP).

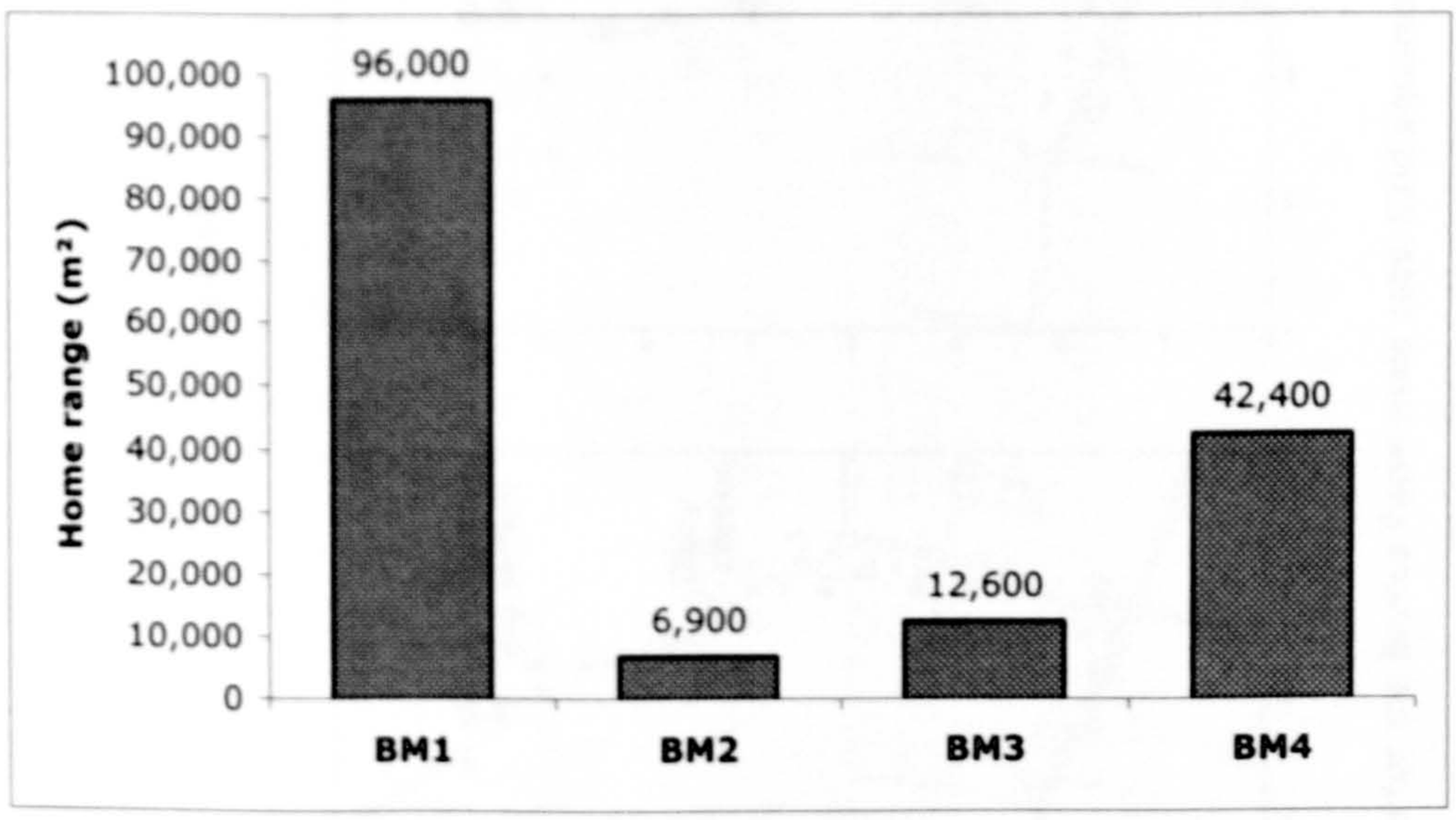


Figure 3.9: Overall home ranges (95% MCPs) of the Bryces Farm male cats

BM1: temporal and seasonal home range

BM1 was radiotracked for a total of 321 hours 25 minutes from October 2001 to July 2002 inclusive, thereby encompassing winter, spring and summer seasons in the study period. Overall, he ranged the furthest during spring crepuscular periods. Winter ranges were the smallest of the year. During the winter he ranged furthest during crepuscular periods and least during the nocturnal hours. In the spring however, he ranged further by night. Summer crepuscular ranges were smaller than diurnal or nocturnal (Table 3.6 and Figure 3.11).

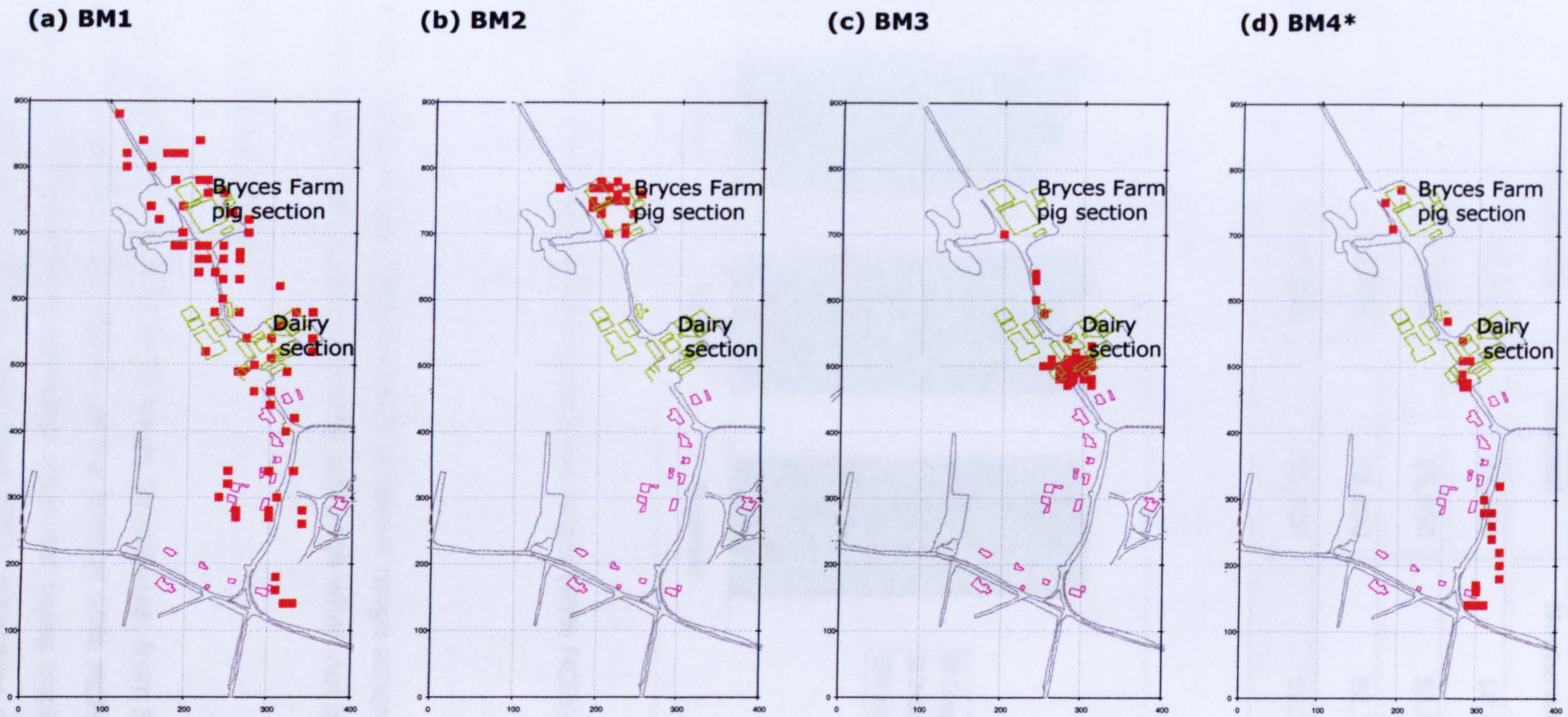


Figure 3.10a-d: Overall range schematics for the Bryces Farm male cats. Grid squares measured in metres.

Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP

Bryces Farm buildings Other properties

*BM4's home range calculated solely on occasional sightings (no radiotracked fixes)

Table 3.6: Overall seasonal and temporal home ranges (95% MCPs) for BM1 (m^2)

	Crepuscular	Diurnal	Nocturnal	Overall
Winter	43,150	23,350	10,700	48,550
Spring	51,450	25,950	53,850	69,800
Summer	42,550	53,100	52,350	58,200
Overall	67,050	55,700	59,150	96,000

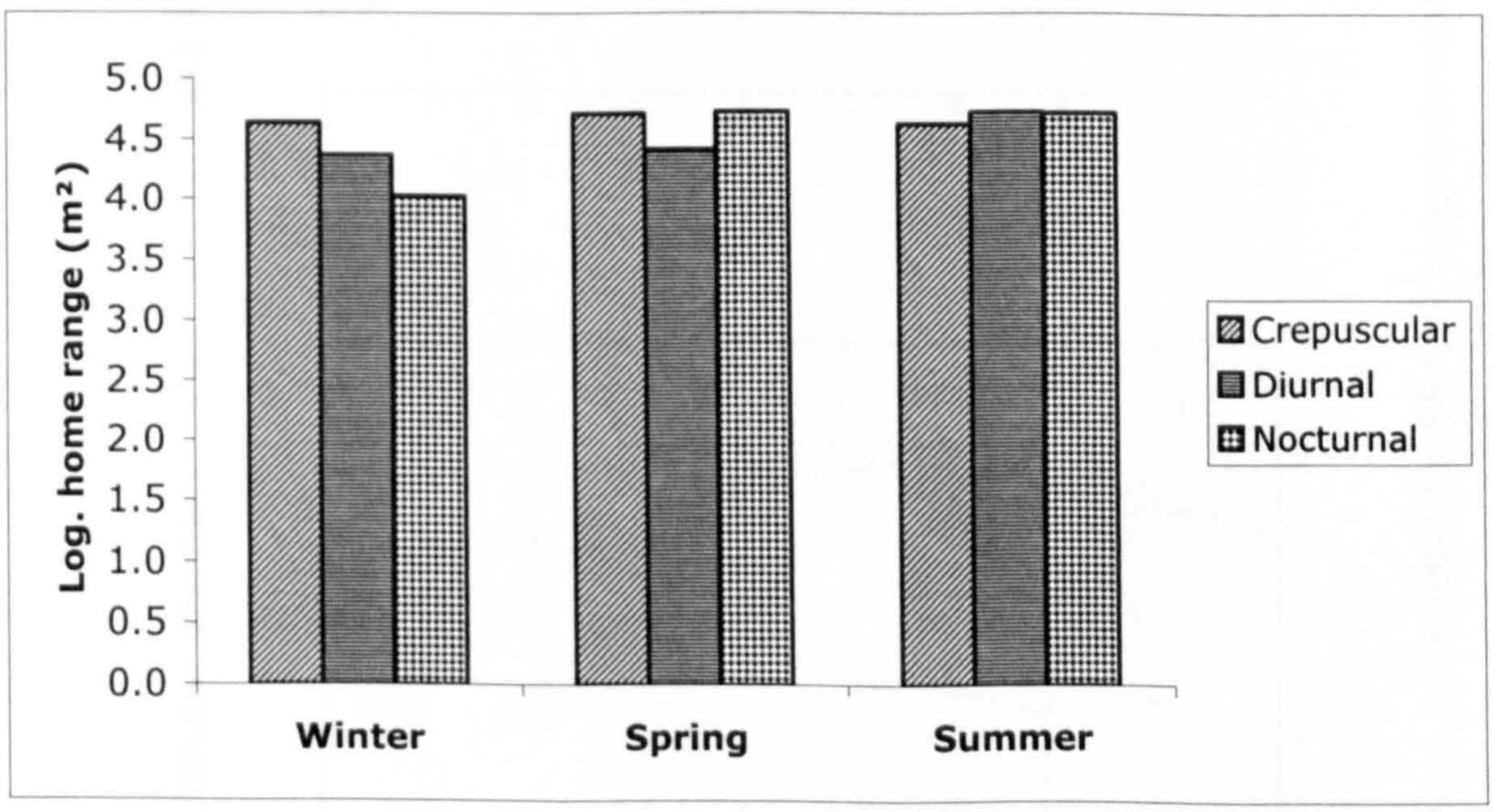


Figure 3.11: Overall seasonal and temporal home ranges (95% MCPs) on a logarithmic scale for BM1

Figures 3.12a-i show overall seasonal and temporal range schematics for BM1, based on radiotracked fixes and occasional sightings when not being tracked.

BM2: temporal home range

BM2 was radiotracked for a total of 59 hours 50 minutes, from September 2001 to November 2002 inclusive. The results, in the form of 95% MCPs based on radiotracked fixes and occasional sightings when not being tracked, can be seen in Table 3.7 and Figure 3.13. During November 2002, it became necessary to remove his collar, for reasons explained in Chapter 2, Section 2.7.3. Before he could be re-

(a) Winter crepuscular



(b) Winter diurnal



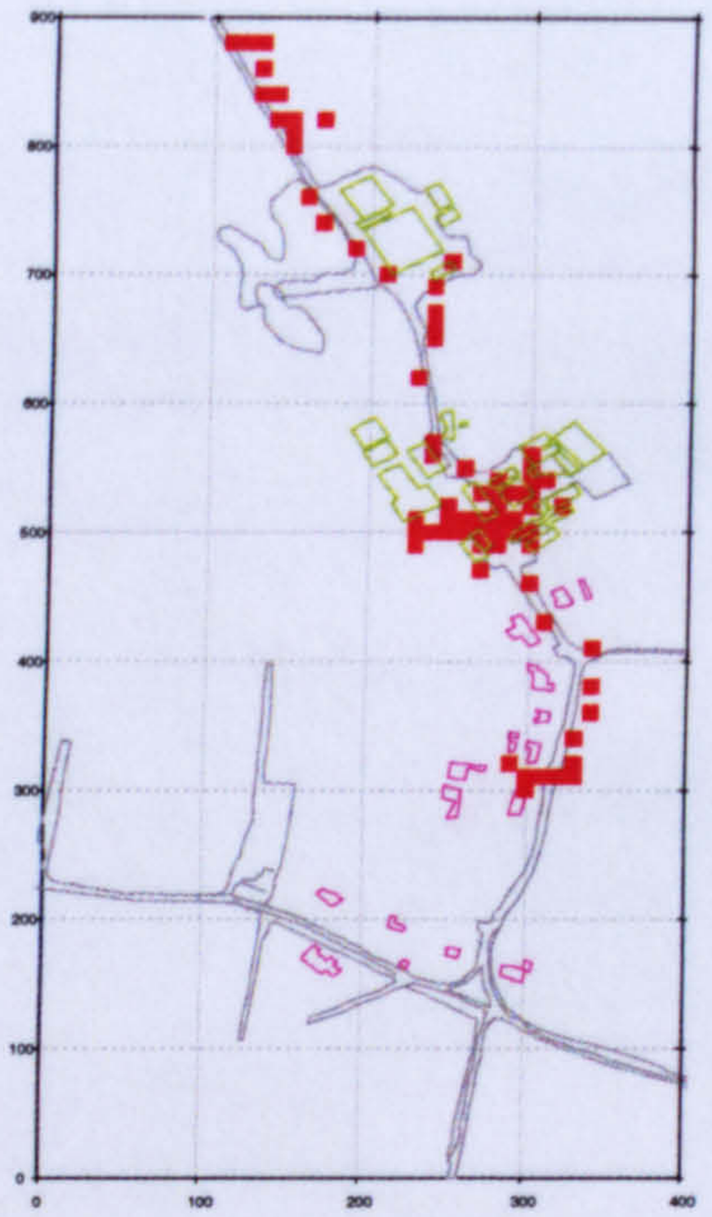
(c) Winter nocturnal



Figure 3.12a-c: Overall winter temporal range schematics for BM1. Grid squares measured in metres.

- Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP
- Bryces Farm buildings
- Other properties

(d) Spring crepuscular



(e) Spring diurnal



(f) Spring nocturnal



Figure 3.12d-f: Overall spring temporal range schematics for BM1. Grid squares measured in metres.

- Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP
- Bryces Farm buildings
- Other properties

(g) Summer crepuscular



(h) Summer diurnal



(i) Summer nocturnal



Figure 3.12g-i: Overall summer temporal range schematics for BM1. Grid squares measured in metres.

- Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP
- Bryces Farm buildings
- Other properties

collared, BM2 died from suspected ingestion of rat poison in February 2002 (see Chapter 2, Section 2.7.2).

There was little variation in location or range covered by BM2 during crepuscular, diurnal and nocturnal radiotracking sessions. He remained at the northern (piggery) section of the farm and did not venture towards other areas of the farm during radiotracking or observation sessions.

Table 3.7: Overall temporal home ranges (95% MCPs) for the Bryces Farm male cats (m^2)

	Crepuscular	Diurnal	Nocturnal
BM1	67,050	55,700	59,150
BM2	4,000	950	5,250
BM3	2,100	850	11,900

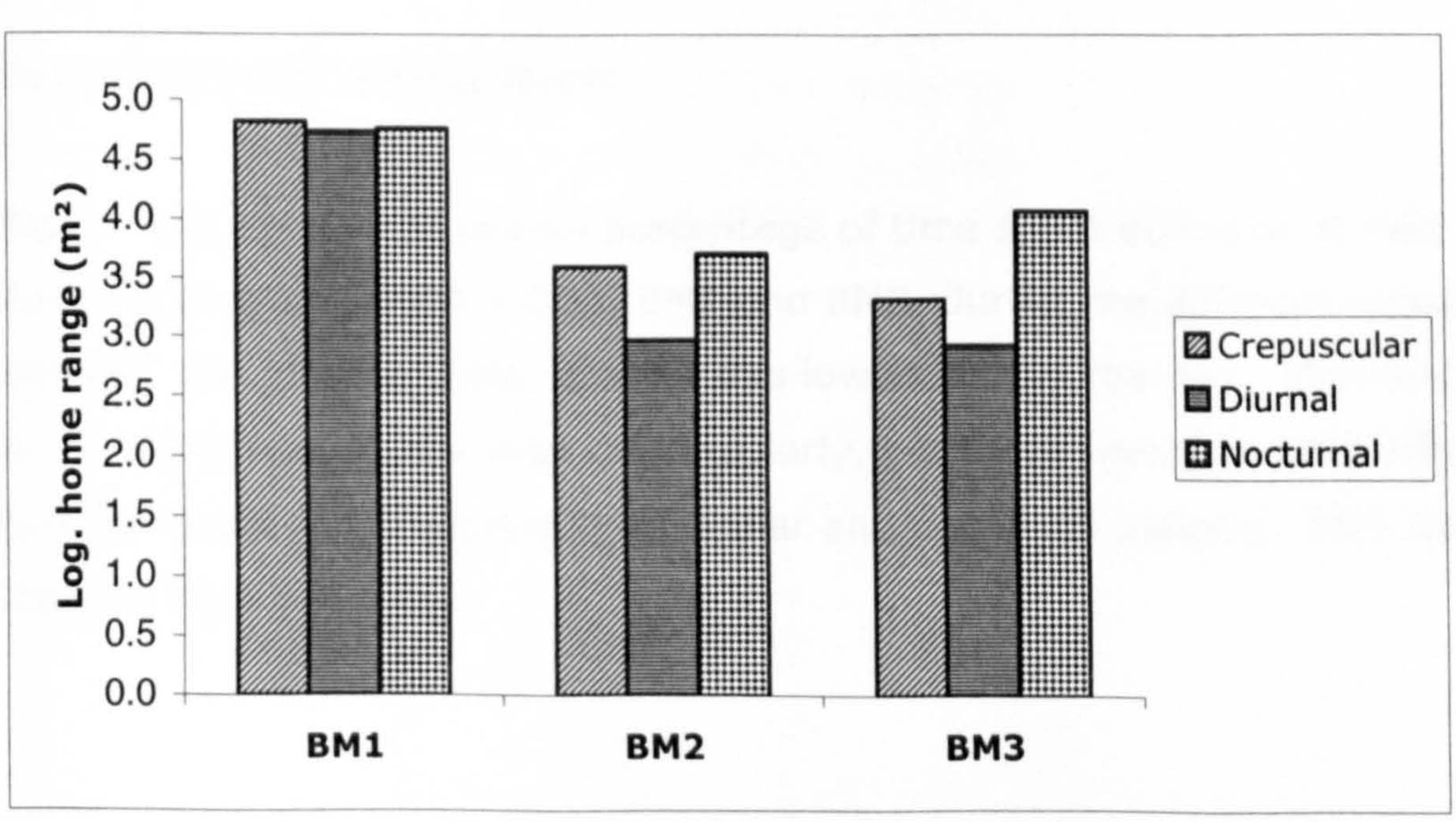


Figure 3.13: Overall temporal home ranges (95% MCPs) on a logarithmic scale for the Bryces Farm male cats

BM3: temporal home range

BM3 was radiotracked for a total of 108 hours 20 minutes, from September 2001 to December 2001 inclusive. He ranged the furthest during nocturnal hours but was

relatively inactive during the day, spending many hours sleeping in the rafters of the milking parlour (Table 3.7 and Figure 3.13). As with BM2, it then became necessary to remove his radiocollar (see Chapter 2, Section 2.7.3).

BM3 spent the majority of his time whilst being radiotracked in the southern dairy section of the farm, and rarely ventured towards the piggery section.

BM4: home range

BM4 escaped whilst sedated, and before a radiocollar had been fitted. Home range data is therefore sparse, and consists only of occasional sightings. These sightings are not categorised by temporal period, but it should be noted that it was rarely possible to get a positive sighting during periods of darkness or low light. Activity data was not collected. As measured, his home range was between that of BM1 and BM3 (Figure 3.9), but this may be an underestimate due to the smaller number of sample points.

3.4.2 Activity

Overall temporal activity levels

Figure 3.14 shows the overall percentage of time spent active or at rest during radiotracking sessions for BM1, BM2 and BM3, during the different temporal periods. For all three cats, activity was lowest during the day. BM2 and BM3 were more active nocturnally than crepuscularly, but there was very little difference in activity levels of BM1 during crepuscular and nocturnal periods. BM3 was very inactive during the day.

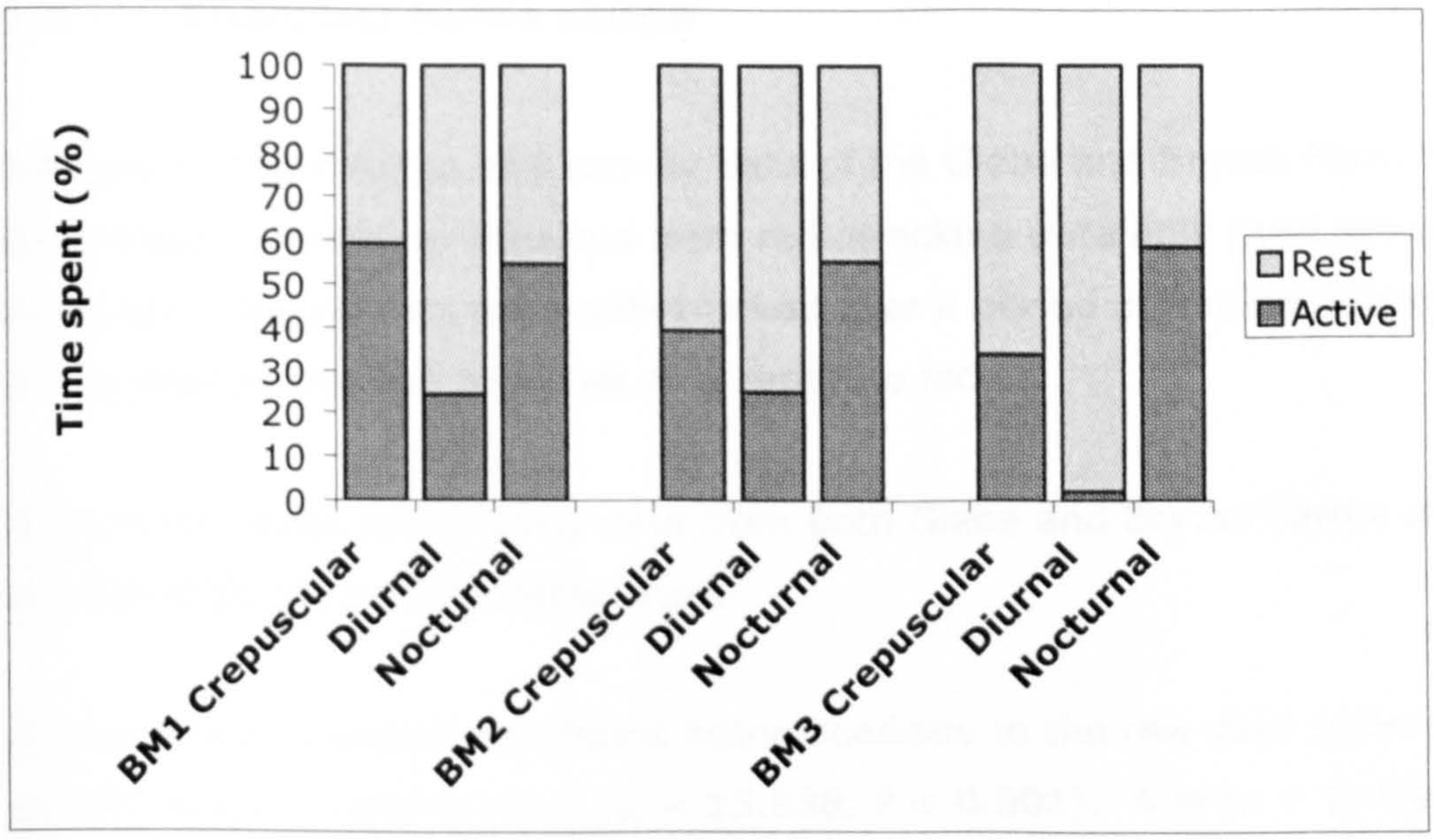


Figure 3.14: Temporal activity data for the Bryces Farm male cats

BM1: temporal and seasonal activity levels

As for home range, seasonal activity levels were obtained in addition to temporal for BM1. Activity was lowest during diurnal periods for all seasons. Crepuscular activity was higher than nocturnal during the winter and spring; however, during the summer, BM1 was more active by night (Figure 3.15).

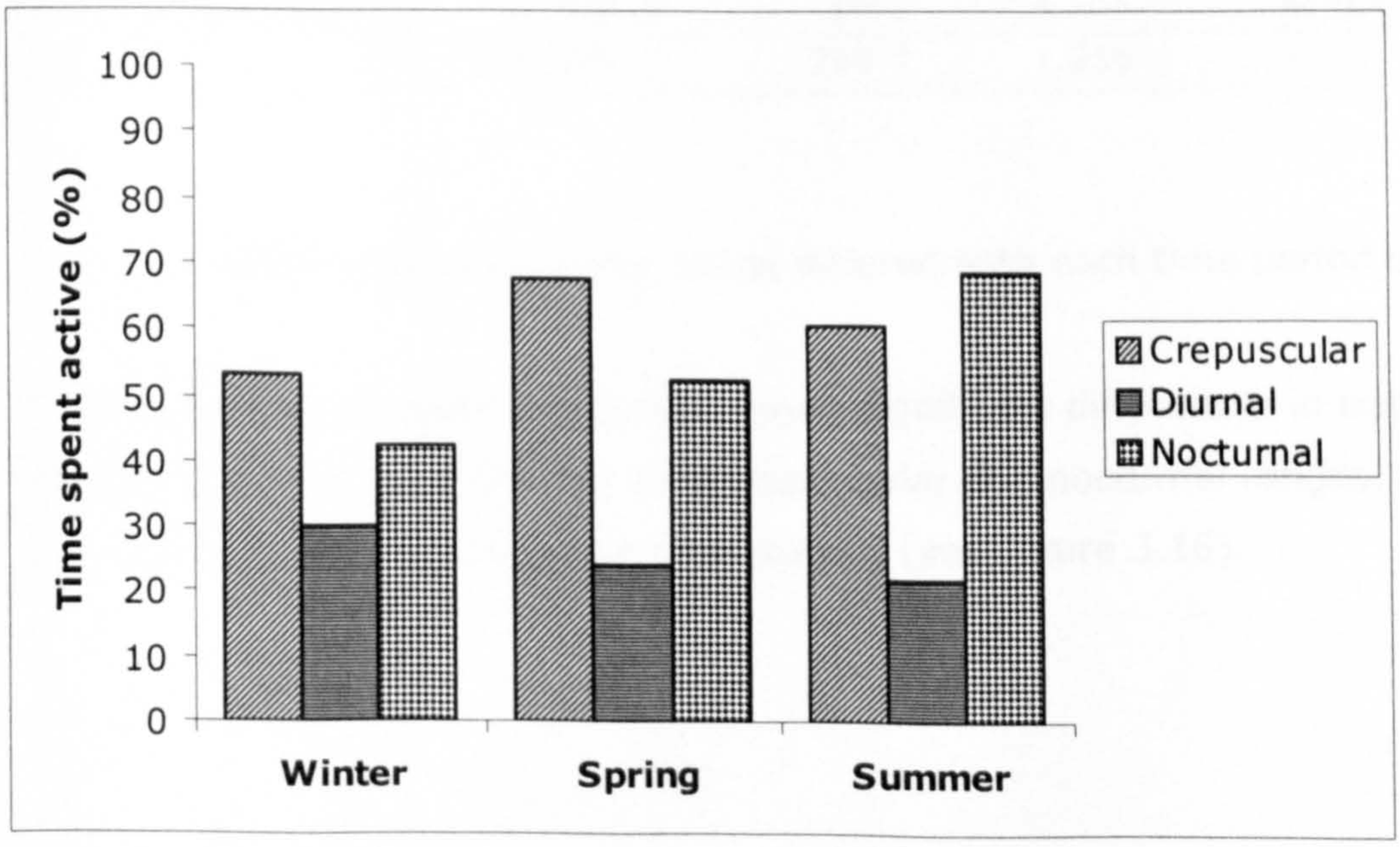


Figure 3.15: Seasonal and temporal activity data for BM1

3.5 Analysis: home range

Analysis of home range and activity data of the Glebe and Bryces Farm cats was performed on locations obtained from radiotracking data only (and not occasional sightings). As the cats were radiotracked over a period of months rather than years, season was not analysed as a separate factor.

Male home range and activity data from both Glebe and Bryces Farms were combined due to small sample sizes.

Levene's Test revealed significant heteroscadisity in the raw data (prior to transformation, Levene's $F_{17, 249} = 15.838$, $P < 0.001$). A ln (x + 1) transformation (Sokal and Rohlf, 1995) was then applied to the data. This reduced, but did not eliminate the issue of heteroscadisity (after transformation, Levene's $F_{17, 249} = 4.582$, $P < 0.001$)[7]. An ANOVA was then carried out on the transformed data. Results are given in Table 3.8.

Table 3.8: Analysis of variance of ln (x + 1) home ranges of the six male cats in different temporal periods

Source	SS	df	MS	F	Sig.
Period	25.862	2	12.931	3.327	NS
Individual	92.367	5	18.473	4.026	P < 0.05
Period*Individual	47.378	10	4.738	2.473	P < 0.01
Error	476.674	249	1.916		

This showed that individual home range differed with each time period observed.

Post-hoc testing (Dunnett's C test) showed significant differences in size of home range of cats GM2 and BM1 for both crepuscular and nocturnal ranges, and to a lesser extent, BM3 for the same time periods (see Figure 3.16).

[7] Levene's Test is unduly sensitive, and if the degrees of freedom > 1 then heteroscadisity may not be a problem (Sokal and Rohlf, 1995).

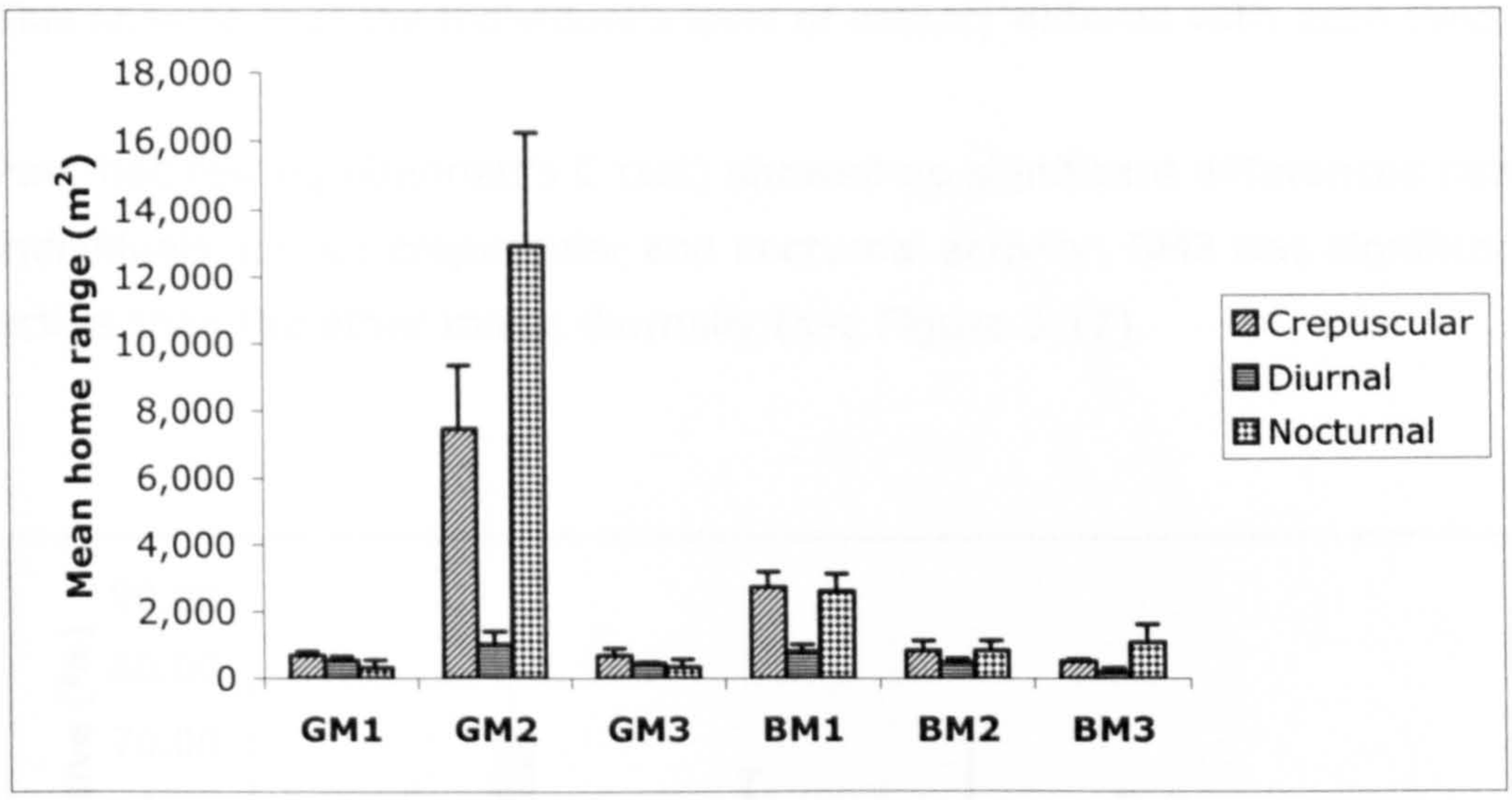


Figure 3.16: Mean home ranges of the male cats for the different temporal periods
Error bars represent Standard Error.

3.6 Analysis: activity

Male activity data from both Glebe and Bryces Farms were also combined. Again, as the cats were radiotracked over a period of months rather than years, season was not analysed as a separate factor.

Levene's Test revealed significant heteroscadisity in the raw data (prior to transformation, Levene's $F_{17, 300} = 2.374$, $P < 0.001$). A ln (x + 1) transformation (Sokal and Rohlf, 1995) was then applied to the data. This reduced, but did not eliminate the issue of heteroscadisity (after transformation, Levene's $F_{17, 300} = 3.205$, $P < 0.001$). An ANOVA was then carried out on the transformed data. Results are given in Table 3.9.

Table 3.9: Analysis of variance of ln (x + 1) activity of the six male cats in different temporal periods

Source	SS	df	MS	F	Sig.
Individual	11.737	5	2.347	6.584	P < 0.001
Period	6.413	2	3.207	8.993	P < 0.001
Individual*Period	13.346	10	1.335	3.743	P < 0.001
Error	106.962	300	0.357		

This showed that the individual's level of activity differed with each time period.

Post-hoc testing (Dunnett's C test) showed no significant differences between individuals in their crepuscular and nocturnal activity; BM3 was significantly less active than the other males diurnally (see Figure 3.17).

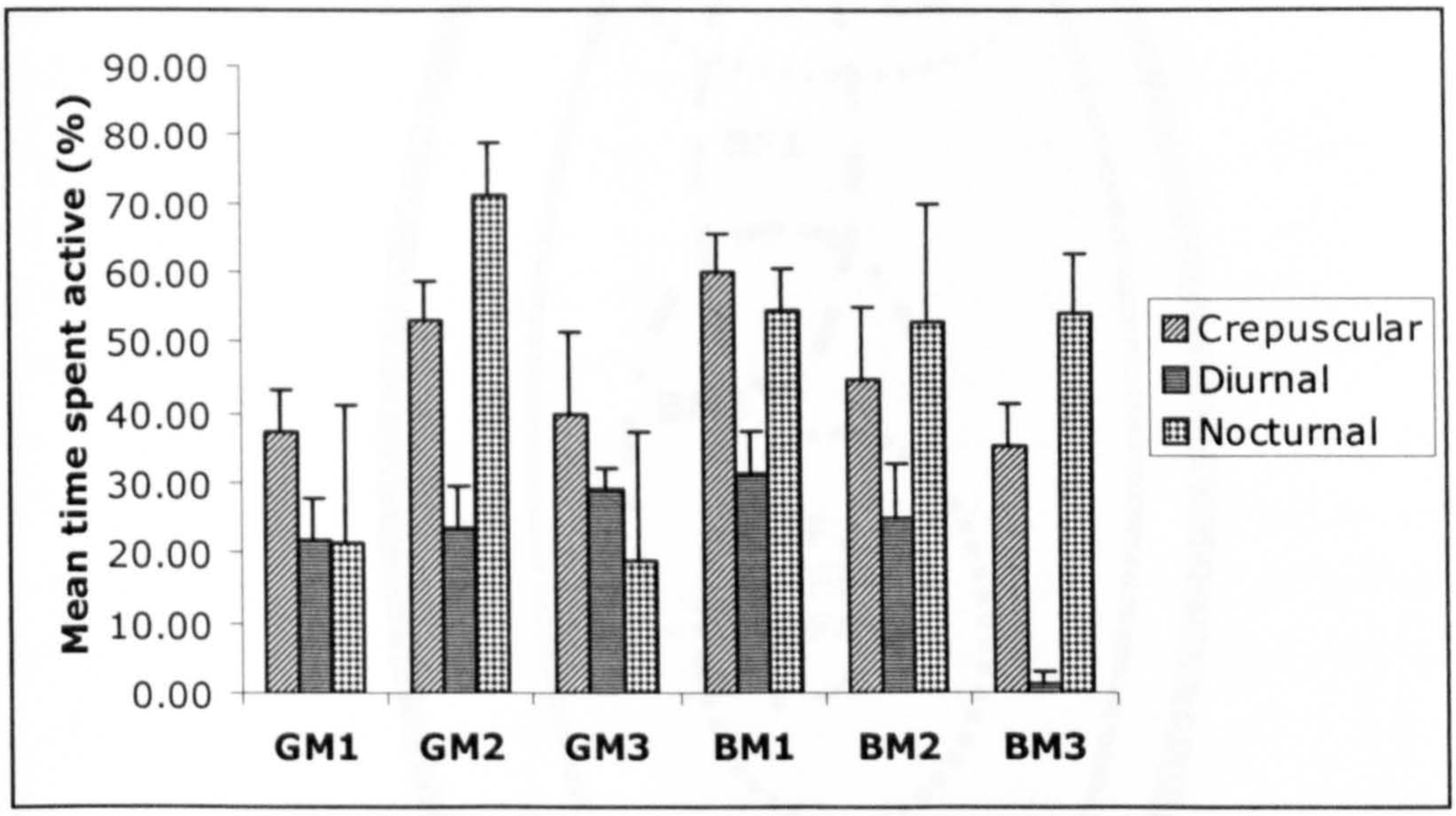


Figure 3.17: Mean activity of the male cats for the different temporal periods
Error bars represent Standard Error.

Figure 3.18 shows a summary graphical representation of the Bryces Farm cats' home ranges (this was not necessary for the Glebe Farm cats; male home ranges are clear from Figure 3.3a-c and females did not leave the CRA (Refer to Chapter 1, Section 1.3.6).

3.6.1 Effect of climate on activity

Activity of the Glebe and Bryces Farm cats did not appear to be affected by temperature or rainfall (results shown in Appendix 4). Also, the solar eclipse on 11 August 1999 had no noticeable effect on activity levels or behaviour of the Glebe Farm cats, under observation at this time.

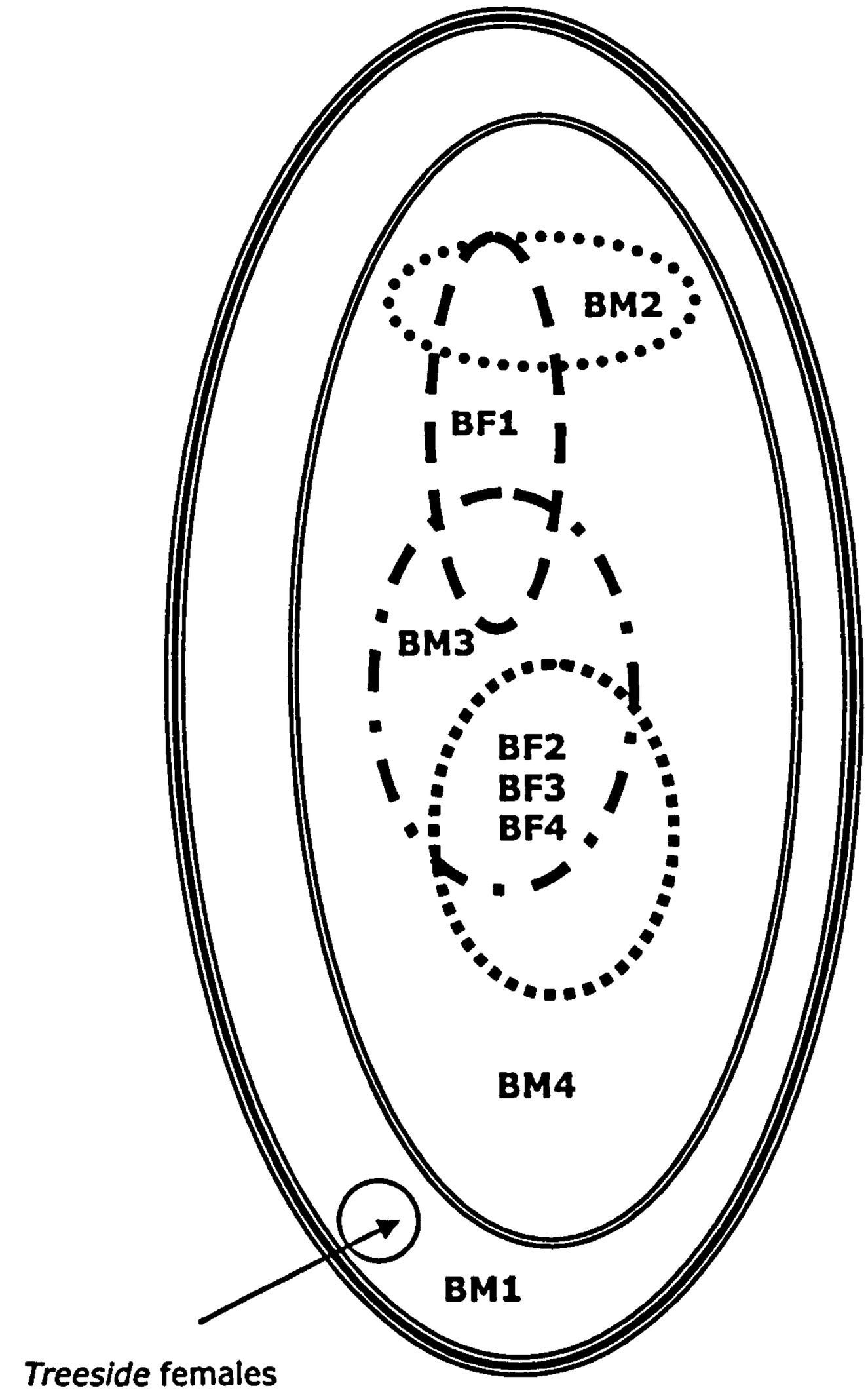


Figure 3.18: Summary of home ranges of the Bryces Farm and *Treeside* cats (not to scale)

3.7 Discussion

It should be noted here that the significant result obtained when temporal period was tested for using an Analysis of Variance of home range data and activity data, *may* indicate a Type I error (false rejection of the null hypothesis).

3.7.1 Glebe Farm

Of the Glebe Farm males, GM2 (the oldest and largest of the Glebe Farm males) ranged considerably further than his conspecific males GM1 and GM3.

During the winter months, the ranges of the three males remained similarly small and philopatric. It is a widely known fact that domestic cats do not like the rain or cold weather, and apparently this is not only a characteristic of household pets. Glebe Farm's feral males spent the majority of their time during the winter months sheltering in the farm buildings, and in the case of GM1 and GM3, sometimes inside the farmhouse itself. During the springtime however, GM2 regularly left the CRA, thereby ranging further than GM3 who did not. Despite this, there was no significant difference in activity levels between the males. A cat is obviously active as he moves physically through his range, but a cat remaining in a small area may also be active in other ways such as feeding, grooming and, importantly, mating. The activity sensors in the radiocollars were also triggered by such behaviours and not only movement over distance.

GM1 and GM3 exhibited very similar, overlapping ranges (see Figures 3.3a and 3.3c) which did not vary according to the time of day. These cats were of approximately equal ages and body weights (Appendix 3), and co-existed in a state of apparent mutual tolerance and affiliativeness (see Chapter 4), sharing a territory and its resources and never observed venturing away from the CRA (either during radiotracking sessions or when sighted at other times).

GM1 spent a considerable amount of time inside the farmhouse sleeping on the kitchen boiler, and, unlike the other males, would tolerate a degree of handling (only by the farmer). However, he was never observed in the main cow barn adjacent to the farmhouse where all the other cats congregated, yet readily engaged in amicable communal feeding with the other cats in the farmyard. GM1 remained less active than GM2 during the same season.

After radiocollaring, GM3 appeared to undergo a behavioural change. He began entering and hiding inside the farmhouse whenever the door was left open, and sometimes exhibited undesirable behaviours such as defecating inside the house. However, he still would not tolerate any human presence near him. At the request of the farmer, GM3's collar was removed after a month. His behaviour returned to normal soon afterwards, and he ceased entering the house completely.

The cats were sedated with Domitor® (medetomidine hydrochloride) and butorphanol/ketamine. Domitor® is a synthetic, non-narcotic α_2-adrenoreceptor agonist with sedative and analgesic properties. Currently, it is the most favoured veterinary sedative available for domestic animals (R. Casey, pers. comm.). Butorphanol (an opioid) is a very potent analgesic; the sedative effects of medetomidine are markedly enhanced when it is given in combination with butorphanol (also fentanyl or pethidine) (Cullen, 1996). Ketamine is a dissociative anaesthetic. Medetomidine, when combined with both butorphanol and ketamine, is widely used for general anaesthesia and has been utilised successfully for some years now, to immobilise a variety of wild animals e.g. lynx (*Lynx lynx*) (Arnemo, Linnell, Wedul, Ranheim, Odden and Andersen, 1999); rhesus macaque (*Macaca mulatta*) (Capuano, Lerche and Valverde, 1999); Sumatran tiger (*Panthera tigris*) (Forsyth, Machon and Walsh, 1999); polar bear (*Ursus maritimus*) (Caulkett, Cattet, Caulkett and Polischuk, 1999); sea lion (*Zalophus californianus*) (Haulena, Gulland, Calkins and Spraker, 2000), as well as for domestic animals in the veterinary environment (Cullen, 1996). An injection of Antisedan® was given after treatment had been completed. Antisedan® (atipamezole), is a potent and selective α_2-adrenoceptor antagonist that reverses the effects of Domitor®, allowing the animal to return to arousal in approximately five to ten minutes.

The only documented side effects of Domitor® and Antisedan® are bradycardia and decreased respiratory rates; vomiting and hypothermia may also occur (Greene, 1999). These are normal physiological responses to medetomidine and other agonists, and are not generally life-threatening. A literature search failed to find any other side-effects, physiological or psychological, associated with the use of these drugs in the domestic cat or any other species (e.g. Vähä-Vahe, 1990; Verstegen, Fargetton, Donnay and Ectors, 1990; Cullen, 1996, 1999; Greene, 1999; Ranheim, Arnemo, Ryeng, Søli and Horsberg, 1999; Moppin and Kerwin, 2000). These findings are supported by conversations with veterinary surgeons and wildlife biologists.

Therefore, no evidence was found to suggest that GM3's abnormal behaviour following radiocollaring was a result of the anaesthesia procedures; furthermore, removal of the radiocollar necessitated further sedation yet the abnormal behaviours ceased. In addition, there is no documented evidence to suggest that the wearing of the radiocollar itself causes a change in behaviour, although it should be noted that GM2's behaviour also changed slightly following radiocollaring, with much less drastic effects (see later). Although not documented, there are however, indications that the effects of the combination of trapping, sedation and radiocollaring on feral cats may indeed induce behavioural changes (G. Kerby, pers. comm.) and the effects of attaching a radiocollar are difficult to quantify in wild animals (Tuyttens, Macdonald and Roddam, 2002).

On the basis of a general lack of published evidence (see Cypher, 1997; Berteaux, Duhamel and Bergeron, 1994; Murray and Fuller, 2000), it was concluded that the behavioural changes affecting GM3 were a result of his FIV infection advancing. Steigerwald, Sarter, March and Podell (1999) demonstrated alterations in behavioural and cognitive function in FIV-infected cats, and neurologic disease including changes in behaviour, loss of house-training and dementia are listed as possible effects of FIV (www.peteducation.com). GM3 was frequently observed with his tongue hanging from his mouth, when at rest and not panting. This is not a normal facial characteristic of cats, and could again be linked to a possible neurological condition. GM3's relatively high activity levels whilst being radiotracked could be explained by the fact that unlike the other cats, he never really became habituated to the presence of the radiotracker, whether observing or tracking. He spent a lot of time fleeing from, or trying to hide from humans, the farm dogs and often other cats. Again, this may be symptomatic of his FIV condition.

GM2 was a larger, heavier and older cat than GM1 and GM3. Observational and radiotracking data suggest that despite his FIV+ status, he was an active and apparently healthy adult male, largely resting during the daylight hours in true domestic cat fashion, and ranging crepuscularly and nocturnally during the spring and summer. GM2 underwent what was perceived as a slight behavioural change after being radiocollared, and seemed to become more sociable towards the other cats and more inclined to interact with kittens and females from the Glebe Farm colony on a regular basis.

It should also be noted that whilst GM2's home ranges must be classed as relative and not absolute (because radiotracking was not carried out continuously for the total time he wore the radiocollar), it was always possible to locate him during radiotracking sessions. His largest mean home range was in the springtime during nocturnal hours (20,210m^2); this corresponds to the period of highest activity. His largest individual range was also recorded in the springtime but during crepuscular hours (45,000m^2). These journeys, resulting in larger ranges, were to two specific locations seen in Figures 3.19a-b: the first was a boarding cattery to the north of Glebe Farm. The cattery owner kept pedigree Exotic Shorthairs for breeding purposes, in addition to the boarding animals. Although the enclosures were all secure (double fencing with a half-metre space between), GM2 periodically visited the cattery, particularly during the spring, and called to the oestrous females (Figure 3.19a). Oestrus in one or more of the pedigree females was confirmed with the cattery owner and found to coincide with GM2's visits. He also visited the cattery during the summer; this was on account of both pedigree females in oestrus (domestic pet cats do not show particularly seasonal oestrous patterns unlike feral and wild animals, but instead produce litters throughout the year), and a higher intake of cats (including un-neutered females) into the cattery during the summer holiday period.

The second location causing GM2 to increase his home range was a large house with extensive grounds to the east of Glebe Farm that was undergoing construction work, and was not inhabited at the time of study. The area was completely sealed off to the observer but not to GM2, who periodically slipped through the fencing and disappeared from sight (Figure 3.19b). Calls could again be heard which were identical to those made by GM2 at the cattery, but no female was ever positively sighted there. However, it is unlikely that GM2 would have been communicating in this fashion with anything other than a female cat in oestrus.

Overall, it can be concluded that in terms of the Resource Dispersion Hypothesis, the Glebe Farm males' home ranges were determined by the distribution of food, shelter and mates. The Glebe Farm females produced kittens more frequently than at Bryces Farm; the females must therefore have been in oestrus more often and observation of litters confirmed that oestrus was not restricted to a spring breeding season. GM1 and GM3 were apparently satisfied by the resources afforded by the CRA, but GM2 ranged much further.

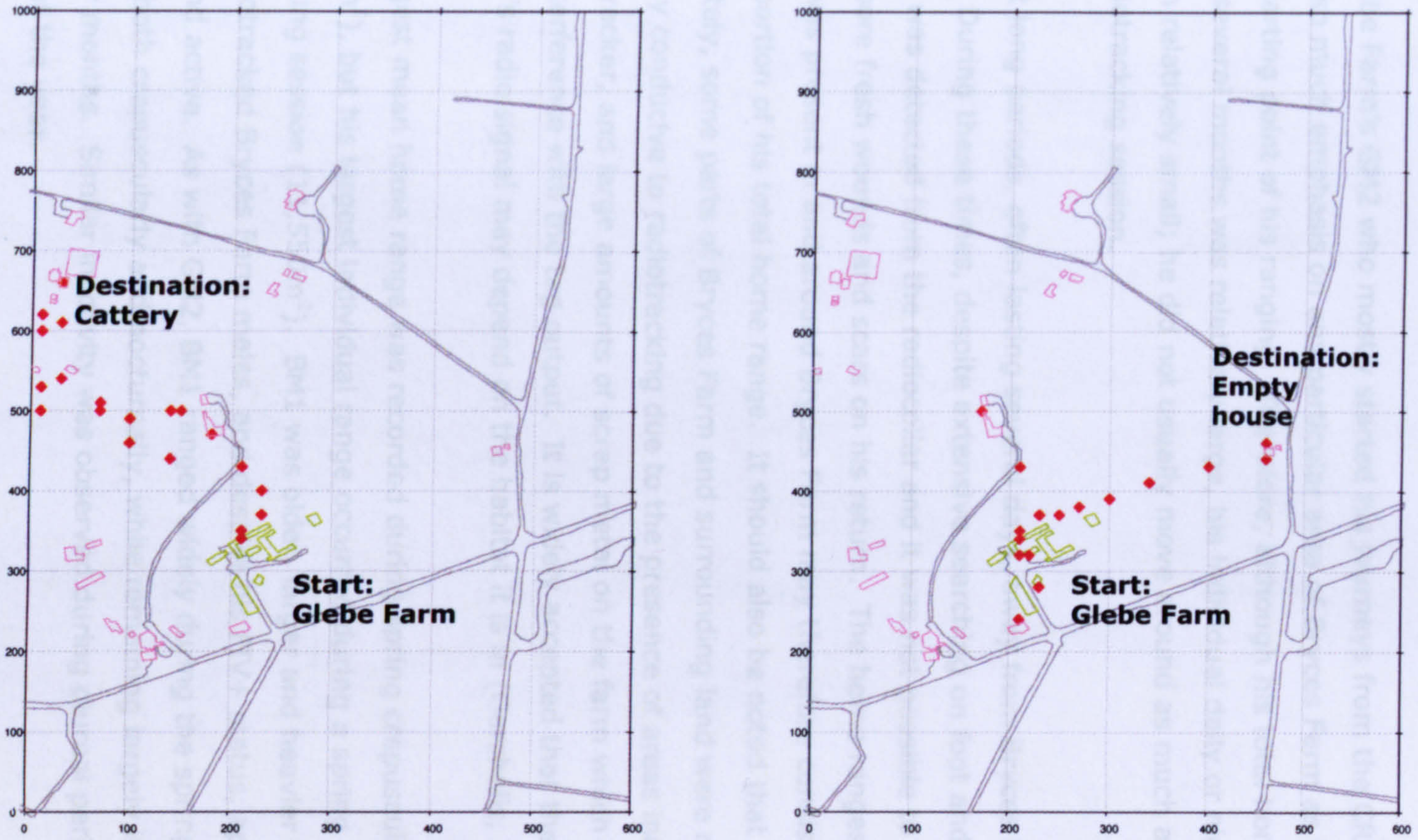


Figure 3.19a-b: Extended ranges of GM2 (a) 95% MCP = 33,750m² (b) 95% MCP = 45,000m². Grid squares measured in metres.

- Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP
- Glebe Farm buildings
- Other properties

3.7.2 Bryces Farm

Analysis indicated that of the Bryces Farm cats, BM1 (the oldest and largest of the radiotracked Bryces Farm males) ranged further than the other radiotracked males.

Unlike Glebe Farm's GM2 who mostly started his journeys from the CRA, BM1 did not place so much emphasis on any particular area of Bryces Farm as being the CRA, or starting point of his ranging. Therefore, although his total home range spanning several months was relatively large, his individual daily or nightly ranges were often relatively small; he did not usually move around as much as GM2 in a single radiotracking session.

BM1 spent long periods, often lasting several days, away from Bryces Farm and its environs. During these times, despite extensive searching on foot and by vehicle, no output was detected from the radiocollar and it was not possible to locate him. He often bore fresh wounds and scars on his return. The home ranges recorded when he was present in and around Bryces Farm may therefore consist of only a small proportion of his total home range. It should also be noted that unfortunately, some parts of Bryces Farm and surrounding land were not particularly conducive to radiotracking due to the presence of areas inaccessible to the radiotracker, and large amounts of scrap metal on the farm which could have caused interference with the tag output. It is widely accepted that the detection of an animal's radio signal may depend on the habitat it is in (Garshelis, 2000).

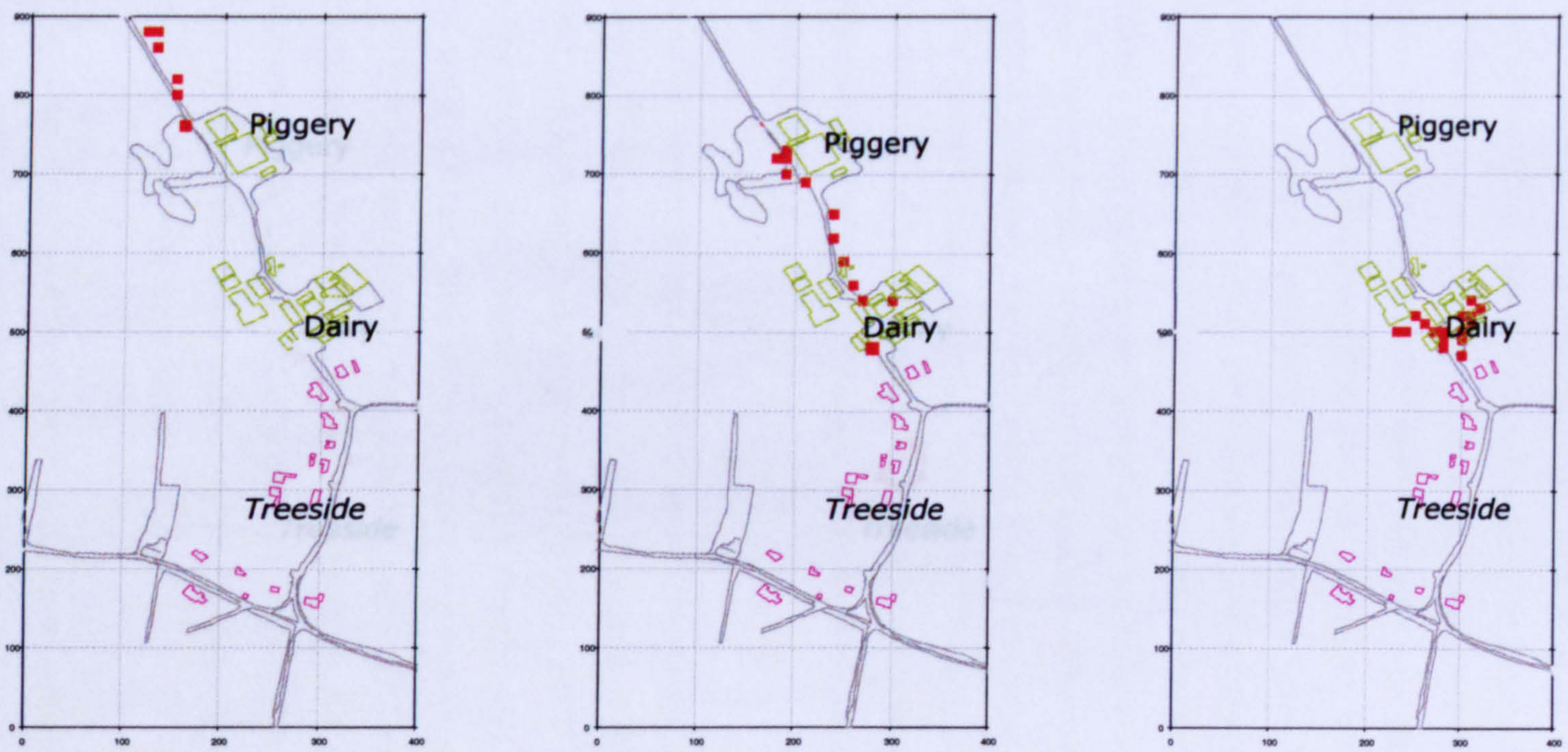
BM1's largest mean home range was recorded during spring crepuscular periods (3,672.7m^2), but his largest individual range occurred during a spring nocturnal radiotracking session (11,550m^2). BM1 was older, larger and heavier than the other radiotracked Bryces Farm males, and despite his FIV+ status, appeared healthy and active. As with GM2, BM1 ranged widely during the spring and summer, both crepuscularly and nocturnally, while remaining largely inactive during the winter months. Similar inactivity was observed during diurnal periods throughout the year.

The range of BM1 covered the whole of Bryces Farm, focusing on the main north-south track running through the farm, and extending down the lane from the farm to the private smallholding *Treeside*. Figures 3.20a-e illustrate the different sections covered by BM1. Six un-neutered adult females (and one neutered) lived at *Treeside*, providing a regular visiting place for BM1. He also often chose this site

(a) Top pig section

(b) Dump and centre section

(c) Bottom dairy section



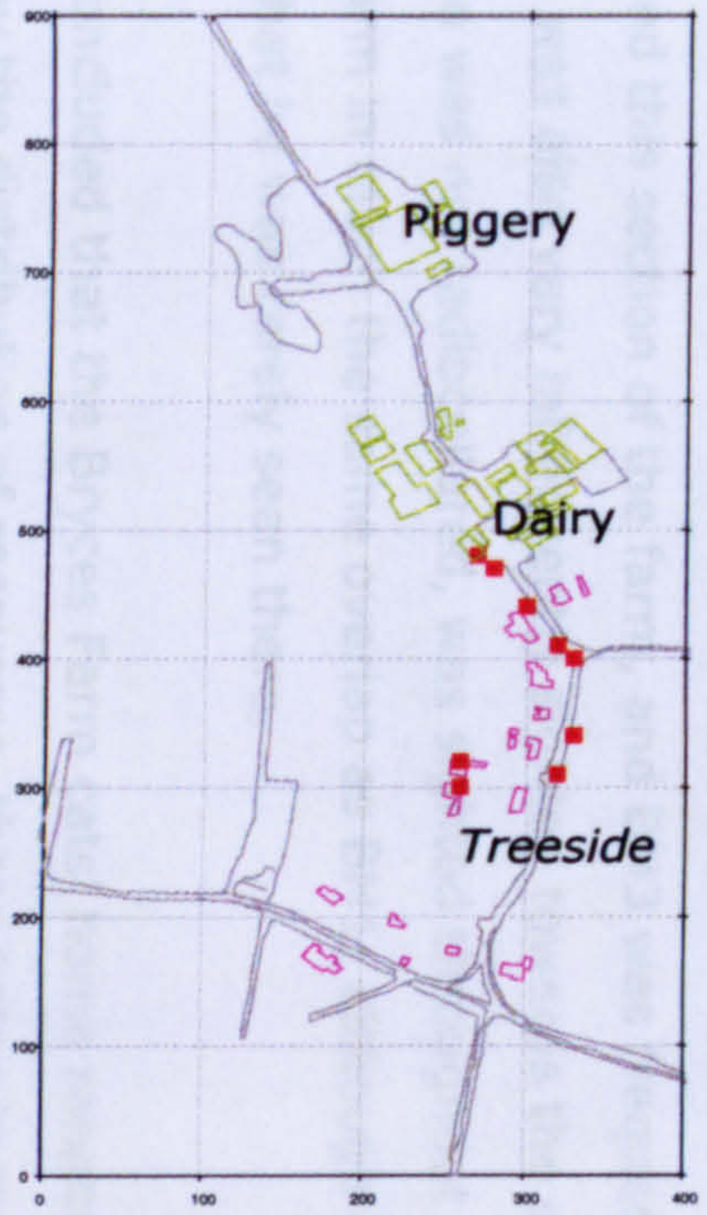
Figures 3.20a-c: Ranges of BM1 (a) 95% MCP = 2,600m² (b) 95% MCP = 7,750m² (c) 5,100m². Grid squares measured in metres.

Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP

Bryces Farm buildings Other properties

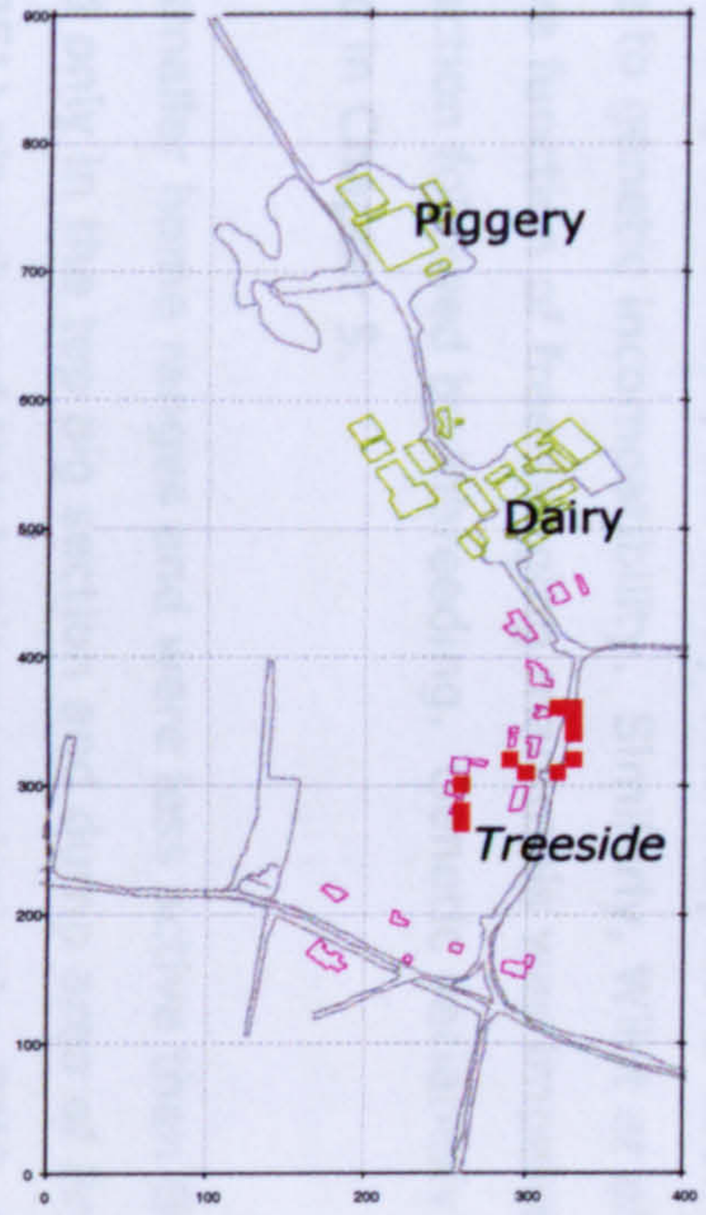
(d) Dairy section to *Treeside*

BM1: 15 Apr02, 1900-2300hrs



(e) *Treeside*

BM1: 24 JuL02, 0200-0600hrs



Figures 3.20d-e: Ranges of BM1 (d) 95% MCP = 11,550m² (e) 95% MCP = 4,550m². Grid squares measured in metres.

Location of radiotracked fixes and/or sightings, the outer points collectively forming the 100% MCP

Bryces Farm buildings Other properties

for a place to sleep during the day, in a shed away from the females who centred their activities close to the house. Several communally-nursed litters of kittens were born at *Treeside* towards the beginning of May 2002, which would have meant their mothers were in oestrus in March (springtime). BM1 was located at *Treeside* particularly towards the latter part of March, although his activity levels were not recorded as having increased at this time. However, access by the radiotracker to this smallholding was very limited. No kittens were seen on Bryces Farm in 2002, although one female (BF3) appeared pregnant in June, indicating an oestrous period in April. In early July she was sighted again but no longer appeared to be pregnant. Her behaviour indicated that either she had not given birth, or the litter had not survived. The low rate of reproduction in the Bryces Farm females during the study (only one surviving kitten) may be a consequence of small colony size and low genetic variability among both females and males; however, Stockley (2003) found significantly lower rates of early reproductive failure in promiscuous female mammals than monogamous or polygynous species. Therefore, despite their promiscuous mating behaviour, the study cats may have been experiencing breeding failure due to genetic incompatibility. Similarly, Wildt *et al.* (1987) found that the reproductive function of free-ranging mammals was impaired as a result of demographic contraction followed by inbreeding. Genetic variability of the study cats will be explored in Chapter 5.

BM2 and BM3 had smaller home ranges and were less active than BM1. BM2, a young male, ranged only in the top pig section and dump area of Bryces Farm. One adult female (BF1) also shared this territory exclusively; BM3, an older cat, mostly remained in the bottom dairy section, spending many hours sleeping in the rafters of the milking parlour itself. The other Bryces Farm females also centred their activities around this section of the farm, and BM3 was frequently sighted in their company. He was also very infrequently sighted towards the centre section of the farm. BM4, who was not radiocollared, was sighted throughout the north-south centre line of the farm in much the same overlap as BM1, although the owner of *Treeside* reported that he was rarely seen there.

Overall, it can be concluded that the Bryces Farm cats' home ranges were very much determined by the distribution of resources, these being in the form of food, shelter and mates. However, BM1, and probably BM4, were apparently not satisfied by the resources afforded by Bryces Farm and neighbouring *Treeside*, and ranged further afield, presumably to seek more females. BM2 and BM3 however, remained for the most part in their respective CRAs, utilising the resources there.

CHAPTER 4: SOCIAL DYNAMICS

4.1 Introduction

The sum of social relationships may be compiled in a matrix of dyadic interactions to produce a social network, and similarly dominance rank (the position of an individual within a hierarchy of social relationships) depends on the social network (see Pearl and Schulman, 1983, also Drews, 1993). In general, the term "dominance" is used to describe predictable aspects of repeated dyadic interactions, and a dominance hierarchy can be produced by ordering the dominance relationships between dyads.

Traditionally, the concept of dominance is related to agonistic behaviour, with dominant status achieved as a corollary of winning agonistic encounters (see Chapter 1, Section 1.5). Drews (1993) defines dominance as "an attribute of the pattern of repeated, agonistic interactions between two individuals, characterised by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation". However, in addition to quantifying and qualifying agonistic behaviour within dyads, affiliative interactions, including non-agonistic physical contact between individuals, are also useful indicators of dominance hierarchies in group-living mammals. Natoli *et al.* (2001), in their studies of farm cats, attempted to determine if it was possible to identify the most dominant male as the one receiving the greatest amount of amicable behaviour from females. Although the results were not wholly conclusive in support of this hypothesis, they were able to show that affiliative behaviour had the role of maintaining a cohesive network of social bonds between the cats. Macdonald *et al.*'s (1987) study of farm cats did show that at least among female cats, affiliative behaviour in the form of rubbing, flowed centripetally towards central dominant individuals.

This chapter consists of a study of interactions among the Glebe Farm and Bryces Farm colonies, to give some insight to the social structure and ranking of the cats which can then be compared to the results of the home range study (Chapter 3) and estimates of reproductive success from microsatellite analysis (Chapter 5).

4.1.1 Identifying behaviours

Body language

The complex social systems of canids and felids rely on effective communication between individuals for their maintenance and the individual's ability to separate group members from unfamiliar individuals (Braastad and Bakken, 2002). In a similar way to that of the dog, the domestic cat expresses its visual signals mainly by body posture, and by the positioning of the tail and ears. During agonistic interactions, cats will attempt to alter their apparent size (Bradshaw and Cameron-Beaumont, 2000) – making oneself appear bigger indicates dominance whereas making oneself appear smaller may be seen as a submissive gesture. In order to achieve the former effect, cats stand tall and piloerect; a submissive cat flattens its ears and crouches close to the ground, hiding its head and tail.

Some of the more easily interpreted body language of cats includes the familiar arching of the back, usually accompanied by piloerection and the tail partly or completely raised. This posture does in fact signal a strong conflict between agonistic and defensive tendencies (Braastad and Bakken, 2002), and is often used when the cat is cornered and flight is not really an option. Also noticeable is the defensive spitting and hissing behaviour, frequently seen together with an arched back. Cats are often seen to rub their heads, tails or flanks against one another or against humans (and even sometimes pet dogs) as an affiliative form of communication (see Macdonald *et al.*, 1987). This behaviour results in the distribution of secretions from skin glands (see Bradshaw and Cameron-Beaumont, 2000). Other uses of body language in non-agonistic encounters include a sequence of rolling postures adopted by oestrous females (see Bradshaw, 1992).

However, there are more subtle aspects of cat communication. The cat's tail is a major signalling device of body language. An affiliative interaction between cats is accompanied by vertically-held tails; usually the cat initiating the friendly interaction approaches the other cat with its tail held up (see Brown, 1993). This behaviour is also frequently seen in domestic cats approaching their human owners. The normal tail position is horizontal or half-lowered; an aggressive cat points its tail at the ground and a submissive cat pulls its tail between its hind legs (Bradshaw, 1992).

During the early stages of agonistic encounters, eye contact between cats is avoided, but staring eyes signal offensive threat. The position of the ears is also significant: submission can be expressed by the ears being folded sideways and downwards, whereas backwards rotation indicates offensive posture. Ear positions can be altered much more quickly than whole-body postures; a cat may alter its facial expression whilst maintaining a fixed body position (Bradshaw, 1992).

Acoustic communication

Cats have a vocal repertoire consisting of four main types: agonistic, sexual, mother-kitten, and cat-human (Bradshaw and Cameron-Beaumont, 2000). Aggressive cats may growl, snarl or yowl; defensive cats may hiss or spit. Miaowing and trilling (also known as "chirruping") are not generally heard between adult cats but instead occur frequently in kittens and between cats and humans. Oestrous females, and often males in the presence of oestrous females, may emit wailing calls indicating willingness for mating. Purring signals a high motivation for contact or solicitation of care (Braastad and Bakken, 2002), and is highly characteristic of the Felidae.

Olfactory communication

Most mammals use urine and faeces for olfactory communication (for a review of the role of odour, see Gorman and Trowbridge, 1989). Urination in cats can be performed either by squatting (by bent hind legs) or by spraying (in an upright position). The spraying of urine, which includes anal gland secretions, is used for scent marking and is performed by both males and females. The function of faeces in scent marking is less well documented: cats tend to bury their faeces within the centres of their territories whereas they often leave them exposed towards the peripheries (Natoli, 1984, 1985a, 1989; Bradshaw, 1992; Ishida and Shimizu, 1998; Bradshaw and Cameron-Beaumont, 2000; Braastad and Bakken, 2002). The sniffing of urine may also induce the Flehmen response in cats, whereby the upper lip is raised and the mouth is held slightly open for a few seconds. It is thought that this behaviour is involved in the transport of fluid-borne materials from the oral cavity to the vomeronasal organ for chemosensory analysis (Hart and Leedy, 1987; Bradshaw, 1992).

4.1.2 The ethogram

An ethogram is a catalogue of descriptions of the discrete, species-typical behaviour patterns that form the basic behavioural repertoire of the species (Lehner, 1987: cited in Martin and Bateson, 1998), or, more simply, a dictionary of the researcher's language (Macdonald *et al.*, 2000).

Macdonald *et al.* (2000) highlighted the dangers of teleology and anthropomorphism when constructing ethograms. For social animals (particularly carnivores), visual communication is essential for the formation and maintenance of social relationships (as are auditory and olfactory communication). In both domestic and wild felids, the nuances of facial expression and body language must be identified and not misinterpreted.

4.2 Methods

4.2.1 Recording interactions

An ethogram was constructed, following Brown (1993) and can be seen in Table 4.1. The behavioural patterns have been abbreviated for ease of recording, and a brief definition is given. It should be noted that the ethogram seen in Table 4.1 is not an exhaustive list of domestic cat behaviours but instead comprises behaviours observed during this study.

During radiotracking and observation sessions, any behavioural interactions between dyads which were directly observed were recorded as they occurred, noting the dyad and the type of interaction (according to the ethogram) each time.

Some behaviour patterns between dyads of cats involve one obvious "initiator" (the cat starting the interaction) and one "recipient" (the cat receiving the behaviour pattern - see Brown, 1993), for example *Chase* and *Flee*. However, other behaviour patterns are not so easy to categorise, and appear to be conducted on a mutual basis, for example *Feed With* and *Sit With Cat* (it should be noted that feeding behaviour refers to food provided by the farmer or the observer, and these cats have always been observed to interact amicably during these feeding times.

Table 4.1: Ethogram (after Brown, 1993)

BEHAVIOUR	ABBREVIATION	DEFINITION
APPROACH	AP	One cat moves towards another cat whilst looking directly at it. Tail not held vertically.
APPROACH RUNNING	AR	As AP but cat moves at speed.
CHASE	CH	One cat races in pursuit of another cat.
CROUCH	CR	Cat crouches on ground.
FEEDING WITH	FW	Cat feeds amicably with other cat. (Food supplied by farmer, not naturally hunted prey.)
FIGHT	FI	Two cats engage in physical combat.
FLEE	FL	One cat runs away from another cat.
FOLLOW	FO	One cat follows another. Tail of the following animal not held vertically.
FREEZE	FR	Cat becomes immobile in response to the behaviour of another cat.
GROOM	GC	One cat grooms another cat.
GROWL	GR	Cat makes low throaty growl at another cat.
MOVE AWAY	MA	Cat moves away from another cat - no raised tail.
RETREAT	RE	One cat backs away from another, maintaining eye contact and without raising tail.
RUB FOREHEAD	HF	One cat rubs its forehead region against another cat.
RUB HEAD	RH	Cat rubs cheek and/or ear against another cat.

Table 4.1 continued: Ethogram (after Brown, 1993)

BEHAVIOUR	ABBREVIATION	DEFINITION
SIT WITH CAT	SW	One cat sits less than one cat's width away from another.
SLEEP WITH CAT	SL	One cat sleeps less than one cat's width away from another.
SNIFF	SN	One cat investigates another cat by sniffing.
SNIFF REAR	SR	One cat sniffs the peri-anal area of another cat.
STARE	ST	Cat stares fixedly at another cat.
TAIL SWISH	TS	Cat moves its tail from side to side rapidly.
TAIL-UP	TU	Cat raises its tail to vertical position.
TAIL-RAISED APPROACH	TA	As AP but tail held in vertical position.
TAIL-RAISED APPROACH RUN	TR	As TA but cat moves at speed.
TAIL-RAISED FOLLOW	TF	As FO but tail held in vertical position.
TAIL-RAISED MOVE AWAY	TM	As MA but tail held in vertical position.
WALK PAST	WP	One cat walks past another, within 1 metre.
WATCH	WA	One cat watches another cat.
YOWL	YO	Cat makes deep whining/wailing noise at another cat.

In contrast, personal observations of laboratory domestic cats at feeding times have shown that interactions are not always amicable, and a dominance hierarchy is evident). With other behaviour patterns, the observer may not arrive in time to determine which animal was the initiator and which the recipient, for example with *Fight*.

Therefore, for the purposes of this study, no initiator or recipient was individually identified but simply a behavioural interaction between two individual cats was recorded. Also, rather than analyse the individual behaviour patterns (many of which were absent or rare), the behaviours were combined and categorised for Glebe Farm into Table 4.2.

Table 4.2: Categories of behaviour for Glebe Farm cats

Category	**Components**
Defensive (Def.)	Flee (FL), Freeze (FR), Move Away (MA)
Aggressive (Agg.)	Chase (CH), Fight (FI), Growl (GR)
Contact (Cont.)	Sit With Cat (SW), Sleep With Cat (SL)
Other	Feed with (FW), Watch (WA)

This categorisation was simplified further for Bryces Farm, as seen in Table 4.3, where although agonistic encounters were not observed, there was a greater diversity of behaviours overall. However, the disadvantage of using different categories of behaviour at Glebe and Bryces Farm was that it became more difficult to compare and contrast between the two sites.

The behaviour *Watch* remains ambiguous. Brown (1993) defined *Watch* simply as "one cat watches another cat". Bradshaw (1992) noted that a submissive cat often deliberately avoids eye contact with its aggressor by pointing its head to the side. In a later study, Bradshaw and Cameron-Beaumont (2000) found that mutual gaze was interpreted as a threat signal. In a non-agonistic situation, the same authors found that mutual gaze was probably not used as a signal. Smith, Durman, Roy and Bradshaw's (1994) study of domestic cats in shelters suggests *Watch* is attributed to defensive behaviour. Avoidance of eye contact was not observed

when recording the *Watch* behaviour pattern of the Glebe Farm colony; often the cat being watched did not appear to know that it was being observed by another cat, while at other times the two interacting cats appeared simply to be watching each other in a mutual gaze with no hint of either defensive or submissive behaviour. Personal observations of laboratory domestic cats and pet cats support this, and for the purpose of this study the term *Watch* will remain neither agonistic nor affiliative in category.

Table 4.3: Categories of behaviour for Bryces Farm cats

Category	Components
Contact (Cont.)	Groom Cat (GC)*, Rub Forehead (HF)$^{\Psi}$, Rub Head (RH)$^{\Psi}$, Sleep With Cat (SL), Sit With Cat (SW)
Affiliative (Aff.)	Sniff (SN)*, Sniff Rear (SR)$^{\Psi}$, Tail-Raised Approach (TA), Tail-Raised Approach Run (TR)$^{\Psi}$,Tail-Raised Follow (TF)$^{\Psi}$, Tail-Raised Move Away (TM), Tail-Up (TU), Walk Past (WP)
Other	Feed With (FW), Watch (WA)

* Not observed between males

Ψ Only observed between males and females

During observation periods including radiotracking sessions, behavioural interactions (behaviours categorised according to the ethogram) between individual cats were recorded, focusing in particular on interactions between male dyads and not necessarily always involving the focal animal being radiotracked. This method differs to the continuous recording method used by Brown (1993), and instead adopts more of a one-zero sampling approach (see Martin and Bateson, 1986; Macdonald *et al.*, 2000).

In a study of the social behaviour of neutered domestic cats, Brown (1993) identified and recorded over 50 different behaviour patterns during intensive continuous recording sessions. Similar studies have been carried out on farm cats (Macdonald *et al.*, 1987, 2000; Kerby and Macdonald, 1988). For this study, observation periods mainly spanned radiotracking sessions, usually with only one focal animal being tracked at a time. Behavioural interactions between cats other than the focal animal could not always be recorded by just one observer. Night

vision equipment was not available and therefore any interactions occurring after dark could not be recorded during nocturnal radiotracking sessions unless they took place in already-illuminated areas (of which there were few) to which the cats had become accustomed, as ordinary sudden torch light caused the cats to flee from the observer.

For Glebe Farm, this study of behavioural interactions represented a pilot study. For Bryces Farm where interactions were recorded more intensively, analysis was carried out on a monthly basis. However, months September to December were grouped, as during these months, behavioural observations were not carried out as intensively or consistently as for the remaining months due to trapping and radiotracking pressures.

4.3 Results

Macdonald *et al.* (1987) suggested that in the absence of social structure, the number of interactions between each possible pair of animals should be in direct proportion to the amount of time they are available to interact. Therefore, overall rates of interaction, irrespective of direction, should be the same between all pairs of cats.

Frequency and type of interactions between dyads at Glebe and Bryces Farm may be seen in Appendix 5.

4.3.1 Glebe Farm male:male dyad analysis

Tables 4.4 and 4.5 show the proportional presence of each male in the Central Resource Area; for GM2 this has been broken down seasonally but for comparison with GM1 and GM3 the overall total has been used in the analysis.

Table 4.4: Proportional presence of Glebe Farm males in CRA

	Total no. of mins. observed	Mins. spent in CRA	% of time spent in CRA
GM1	7470	7470	100
GM2*	15930	9100	57
GM3	3300	3300	100

Table 4.5: Seasonal breakdown of proportional presence of GM2 in CRA

*GM2	Total no. of mins. observed	Mins. spent in CRA	% of time spent in CRA
Winter (Dec-Feb)	5415	4870	89.9
Spring (Mar-May)	5235	3075	58.7
Summer (Jun-Sep)	5280	1155	21.9

A Goodness of Fit test was used to compare the actual distribution of the interactions between dyads with the distribution predicted from random interactions (Table 4.6): interactions between GM1 and GM3 were more abundant than predicted ($\chi^2_1 = 7.35$, $p < 0.01$).

It was necessary to calculate expected frequencies of dyad interactions based on a *ratio* of presence due to the difference in total observation time for each cat (given in Table 4.4).

Table 4.6: Glebe Farm male:male dyad interaction frequency

	Observed frequencies	Ratio of presence	Expected frequencies
GM1:GM2	6	0.57	13.32
GM1:GM3	32	1.00	23.36
GM2:GM3	12	0.57	13.32
Total	50	2.14	50

A G-test was used to detect heterogeneity in the type of interactions within the male dyads in the colony.

This showed highly significant heterogeneity between the male:male dyads (χ^2_8 = 30.04, $p < 0.01$), meaning that one or more dyads of cats differed from the others with regard to behaviours performed or received.

To investigate this further, pairs of dyads were compared (Table 4.7).

Table 4.7: Glebe Farm - pairwise tests of rows

Dyad comparison	Statistical result
GM1:GM2 *vs* GM1:GM3	χ^2_4 = 19.80, $p < 0.01$
GM1:GM2 *vs* GM2:GM3	χ^2_4 = 7.78, $p > 0.05$ (NS)
GM2:GM3 *vs* GM1:GM3	χ^2_4 = 13.94, $p < 0.01$

The above results show that the interactions between the individual males did not occur with the frequencies expected by chance, on the basis of the time spent together in the CRA. Interactions between GM2 and either GM1 or GM3 occurred less frequently than expected, while interactions between GM1 and GM3 occurred more frequently than expected. GM2 was never observed feeding with GM1 or GM3, but GM1 and GM3 often fed together. GM3 sat or slept with both GM1 and GM2, and these two dyads (GM1:GM3, GM2:GM3) also exhibited almost all of the agonistic behaviour observed. GM1 and GM2 appeared to avoid one another; possibly a mechanism for reducing aggression. Agonistic behaviour may therefore not be a good indicator of dominance in this colony.

4.3.2 Glebe Farm male:female dyad analysis

The three males' interaction rates with adult females were also analysed, eliminating categories of behaviour that were absent or rare:

A Goodness of Fit test on the total number of interactions gave a non-significant result (χ^2_1 = 1.3, $p > 0.05$ NS), indicating that the males tended to interact with the females in proportion to the time they were present in the farmyard. However, the type of interaction differed significantly between males (χ^2_1 = 7.35, $p < 0.01$). GM2 rarely fed with females, but was most likely to sit/sleep in contact with them; GM1 was rarely seen in contact with any female.

4.3.3 Glebe Farm male:kitten dyad analysis

The three males' interaction rates with kittens were then analysed, eliminating categories of behaviour that were absent or rare:

In proportion to the time spent in the CRA, GM2 was significantly more likely to interact with kittens than were the other two males (Goodness of Fit test, $\chi^2_1 = 17.65$, $p < 0.01$). His interactions were predominantly sitting/sleeping in contact, whereas GM1 tended to feed with, rather than sit with, the kittens ($\chi^2_2 = 23.29$, $p < 0.01$).

4.3.4 Bryces Farm male:male dyad analysis

Data from months September-December was omitted for this analysis as it was grouped and not consistent with the following months' observation periods. Levene's Test revealed significant heteroscadisity in the raw data (prior to transformation, Levene's $F_{20, 339} = 6.246$, $P < 0.001$). A ln (x + 1) transformation was then applied to the data (after transformation, Levene's $F_{20, 339} = 1.535$, $P = 0.067$). An ANOVA was then carried out on the transformed data. Results are given in Table 4.8.

Table 4.8: Analysis of variance of ln (x + 1) the frequency of interaction of the Bryces Farm males through time

Source	SS	df	MS	F	Sig.
Month	8.08	6.00	1.35	20.76	P < 0.001
Behaviour	3.13	2.00	1.56	24.09	P < 0.001
Month*Behaviour	0.45	12.00	0.04	0.58	NS
Error	21.99	339.00	0.06		
Total	110.62	360.00			

This showed that both month and category of behaviour independently affected frequency of interactions between male:male dyads. The results of post-hoc tests (LSD and Dunnett's C) revealed that the months of January and July were significantly different from the other months with respect to the number of interactions occurring between male:male dyads (see Figure 4.1). Affiliative behaviour was found to be significantly different from both Contact and Other,

again with respect to the frequency of interactions occurring between male:male dyads (Figure 4.2).

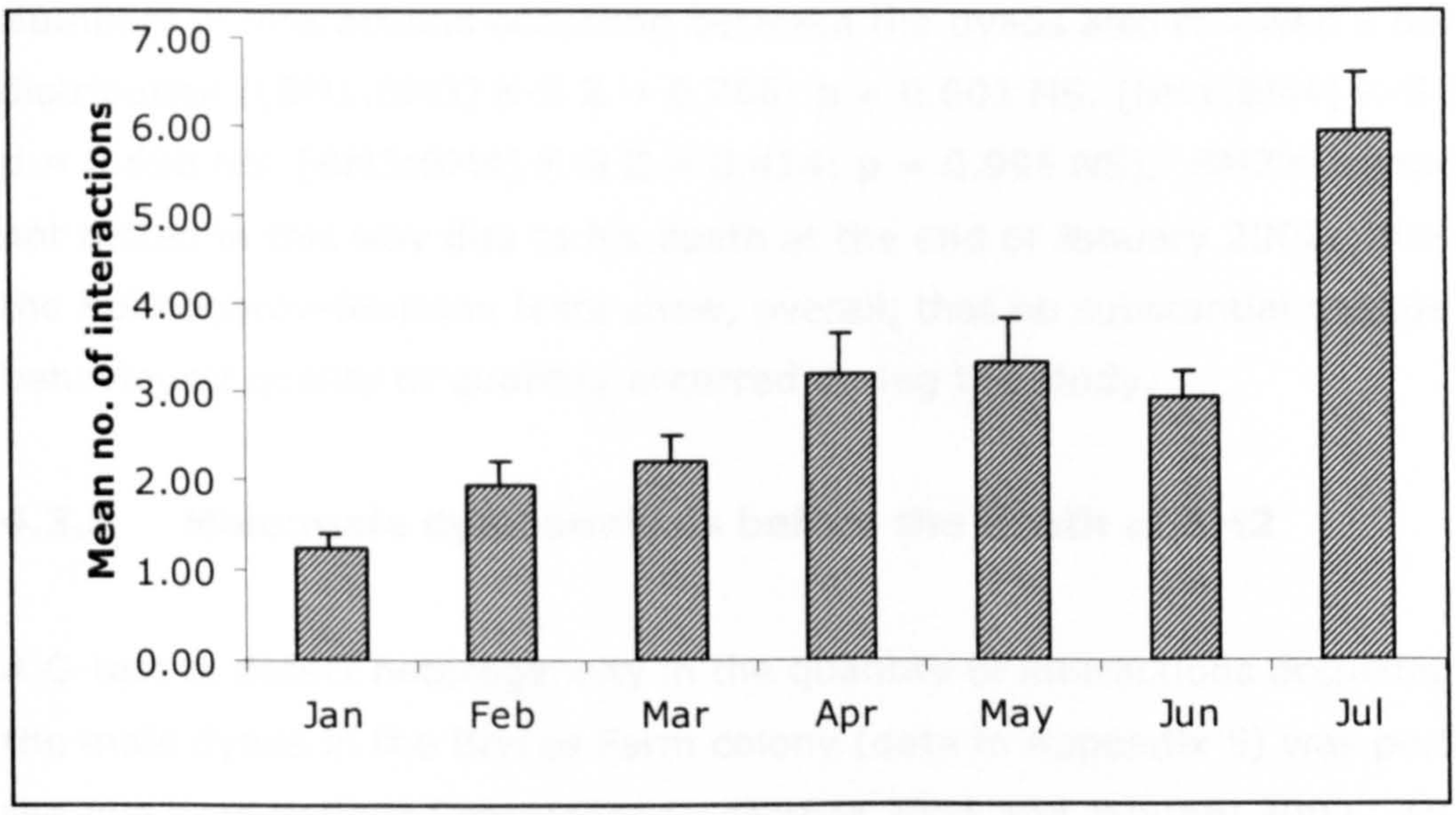


Figure 4.1: Mean number of male:male interactions with respect to month

Error bars represent Standard Error

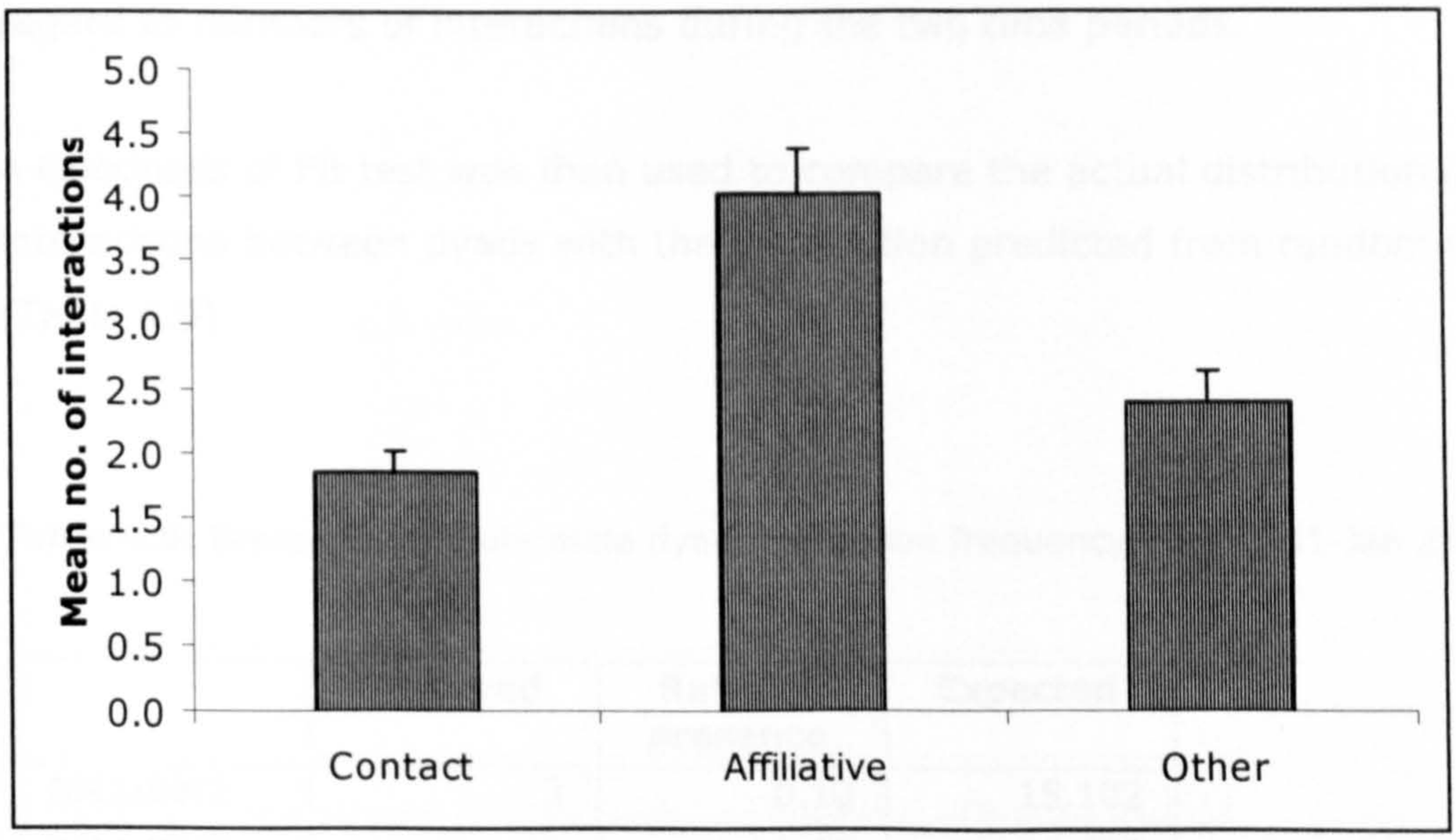


Figure 4.2: Mean number of male:male interactions with respect to behaviour

Error bars represent Standard Error

The overall number of interactions observed occurring between males showed a normal distribution with respect to time (months) (Kolmogorov-Smirnov Z = 0.610; p = 0.851 NS).

Numbers of interactions occurring between the dyads also followed a normal distribution ([BM1:BM3] K-S Z = 0.766; p = 0.601 NS. [BM1:BM4] K-S Z = 0.708; p = 0.698 NS. [BM3:BM4] K-S Z = 0.414; p = 0.995 NS). BM2's interactions were not tested in this way due to his death at the end of January 2002. The results of the Kolmogorov-Smirnov tests show, overall, that no substantial change in behavioural quality or quantity occurred during the study.

4.3.5 Male:male dyad analysis before the death of BM2

A G-test to detect heterogeneity in the quantity of interactions occurring between the male dyads in the Bryces Farm colony (data in Appendix 5) was performed for the two time periods September-December 2001 and January 2002. All male:male dyads were present during this time.

The above test detected no significant heterogeneity between the dyads (χ^2_5 = 4.68; p > 0.25 NS), meaning that no particular dyad differed from the others with regard to numbers of interactions during the two time periods.

A Goodness of Fit test was then used to compare the actual distribution of the interactions between dyads with the distribution predicted from random interactions (Table 4.9).

Table 4.9: Bryces Farm male:male dyad interaction frequency, Sep 2001-Jan 2002

	Observed	Ratio of presence	Expected
BM1:BM2	3	0.10	15.102
BM1:BM3	18	0.16	24.163
BM1:BM4	29	0.12	18.122
BM2:BM3	0	0.29	43.796
BM2:BM4	22	0.12	18.122
BM3:BM4	76	0.19	28.693
TOTAL	**148**	**0.98**	**148**

The very highly significant result ($\chi^2_4 = 140.42$; $p < 0.001$) shows that the observed and expected number of interactions are not in agreement. As there were no interactions between BM2 and BM3, this dyad was omitted and the Goodness of Fit test performed again (Table 4.10):

Table 4.10: Bryces Farm male:male dyad interaction frequency (non-interacting dyads omitted), Sep 2001-Jan 2002

	Observed	Ratio of presence	Expected
BM1:BM2	3	0.10	21.449
BM1:BM3	18	0.16	34.319
BM1:BM4	29	0.12	25.739
BM2:BM4	22	0.12	25.739
BM3:BM4	76	0.19	40.754
TOTAL	**148**	**0.69**	**148**

The result was again very highly significant ($\chi^2_3 = 55.067$; $p < 0.001$). Further Goodness of Fit tests were then carried out to look at the involvement of BM1 (Table 4.11) and BM4 (Table 4.12) in turn.

Table 4.11: Bryces Farm BM1:male dyad interaction frequency, Sep 2001-Jan 2002

BM1	Observed	Ratio of presence	Expected
BM1:BM2	3	0.10	13.158
BM1:BM3	18	0.16	21.053
BM1:BM4	29	0.12	15.789
TOTAL	**50**	**0.38**	**50**

BM1 $\chi^2_1 = 19.339$; $p < 0.001$. BM1 interacted more frequently with BM4 than predicted, and less frequently with BM2.

Table 4.12: Bryces Farm BM4:male dyad interaction frequency, Sep 2001-Jan 2002

BM4	Observed	Ratio of presence	Expected
BM4:BM1	29	0.12	35.442
BM4:BM2	22	0.12	35.442
BM4:BM3	76	0.19	56.116
TOTAL	**127**	**0.43**	**127**

BM4 $\chi^2_1 = 13.315$; $p < 0.001$. BM4's interactions with BM3 were more abundant than predicted, and less abundant with BM2 than predicted.

A G-test was then carried out to test the quality of the interactions, by looking for heterogeneity in the type of interactions (data from Appendix 5). Data from BM2:BM3 were omitted, as there were no interactions between these two cats.

This result showed that one or more dyads differed from the others with regard to behaviours performed or received ($\chi^2_8 = 23.212$; $p < 0.01$). It was noted that unlike the other dyads[8], Contact interactions between BM2 and BM4 occurred more frequently than Affiliative interactions. To investigate this further, BM2:BM4 interactions were tested against the other dyads (data from Appendix 5).

This shows a highly significant difference between BM2:BM4 and the other dyads ($\chi^2_2 = 9.942$; $p < 0.01$).

4.3.6 Male:male dyad analysis after the death of BM2

Analysis was carried out on the male:male interactive data following the death of BM2 at the end of January 2002. The procedure used follows the same pattern as before.

G-test for heterogeneity (data can be seen in Appendix 5):

The non-significant result ($\chi^2_{10} = 10.49$; $p > 0.25$ NS) means that no particular dyad differed from the others with regard to numbers of interactions performed or received.

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[8] BM1:BM2 not included in this observation, as extremely low rates of interaction anyway.

It is possible that the low rate of interaction between BM1 and BM3 during February was a result of the death of BM2 (at the end of January) causing an imbalance within the colony during the following month. To investigate this further, the February data were removed (data can be seen in Appendix 5):

$\chi^2_8 = 3.659$; P> 0.750 NS.

Goodness of Fit to compare the actual distribution of the interactions between dyads with the distribution predicted from random interactions (Table 4.13):

Table 4.13: Bryces Farm male:male dyad interaction frequency, Feb-Jul 2002

	Observed	Ratio of presence	Expected
BM1:BM3	104	0.34	202.328
BM1:BM4	92	0.15	89.262
BM3:BM4	167	0.12	71.410
TOTAL	**363**	**0.61**	**363**

The observed and expected results are not in agreement ($\chi^2_1 = 175.828$; $p < 0.001$). Interactions between BM1 and BM3 were lower than expected, while interactions between BM3 and BM4 were higher than expected.

Involvement of each cat in turn (Tables 4.14-4.16):

Table 4.14: Bryces Farm BM1:male dyad interaction frequency, Feb-Jul 2002

BM1	Observed	Ratio of presence	Expected
BM1:BM3	104	0.34	136
BM1:BM4	92	0.15	60
TOTAL	**196**	**0.49**	**196**

BM1 $\chi^2_1 = 24.305$; $p < 0.001$ (with Yates' Correction for Continuity). BM1's interactions with BM3 were slightly lower in frequency than expected, but slightly higher than expected with BM4.

Table 4.15: Bryces Farm BM3:male dyad interaction frequency, Feb-Jul 2002

BM3	Observed	Ratio of presence	Expected
BM3:BM1	104	0.34	200.304
BM3:BM4	167	0.12	70.696
TOTAL	**271**	**0.46**	**271**

BM3 $\chi^2_1 = 176.613$; $p < 0.001$ (with Yates' Correction for Continuity). BM3's interactions with BM1 were lower in frequency than expected. However, with BM4, they were higher than expected.

Table 4.16: Bryces Farm BM4:male dyad interaction frequency, Feb-Jul 2002

BM4	Observed	Ratio of presence	Expected
BM4:BM1	92	0.15	143.889
BM4:BM3	167	0.12	115.111
TOTAL	**259**	**0.27**	**259**

BM4 $\chi^2_1 = 42.016$; $p < 0.001$ (with Yates' Correction for Continuity). BM3 and BM4 interacted more frequently than expected.

The G-test for heterogeneity (data from Appendix 5) showed that one or more dyads differed from the others with regard to behaviours performed or received ($\chi^2_4 = 14.94$; $p < 0.01$).

At this stage, interactions classed as Other (*Feed With* and *Watch*) appeared to be playing a significant part in the analysis, and it was therefore decided to isolate them from each other (Table 4.17):

Table 4.17: Bryces Farm male:male dyad interaction type (expanded), Feb-Jul 2002

	Contact	Affiliative	Other = FW	Other = WA	TOTAL
BM1:BM3	20	41	21	22	**104**
BM1:BM4	11	39	11	31	**92**
BM3:BM4	40	84	26	17	**167**
TOTAL	**71**	**164**	**58**	**70**	**363**

Again, the test showed that one or more dyads differed from the others with regard to behaviours performed or received ($\chi^2_6 = 25.655$; $p < 0.01$).

Each dyad was then tested against the other two combined (Tables 4.18-4.20):

Table 4.18: Bryces Farm BM1:BM3 interaction type, Feb-Jul 2002

	Contact	Affiliative	FW	WA	TOTAL
BM1:BM3	20	41	21	22	**104**
BM1:BM4 and BM3:BM4	51	123	37	48	**259**
TOTAL	**71**	**164**	**58**	**70**	**363**

BM1:BM3 did not differ from the others ($\chi^2_3 = 2.914$; $p > 0.250$ NS).

Table 4.19: Bryces Farm BM1:BM4 interaction type, Feb-Jul 2002

	Contact	Affiliative	FW	WA	TOTAL
BM1:BM4	11	39	11	31	**92**
BM1:BM3 and BM3:BM4	60	125	47	39	**271**
TOTAL	**71**	**164**	**58**	**70**	**363**

BM1:BM4 however, showed a highly significant difference in their interactive behaviour compared with the other dyads ($\chi^2_3 = 17.365$; $p < 0.01$).

Table 4.20: Bryces Farm BM3:BM4 interaction type, Feb-Jul 2002

	Contact	Affiliative	FW	WA	TOTAL
BM3:BM4	40	84	26	17	**167**
BM1:BM3 and BM1:BM4	31	80	32	53	**196**
TOTAL	**71**	**164**	**58**	**70**	**363**

BM3:BM4 also showed a highly significant difference compared with the other dyads ($\chi^2_3 = 18.975$; $p < 0.01$).

4.3.7 Further effects caused by the death of BM2

Figures 4.3 and 4.4 illustrate, respectively, interaction rates between male:male dyads before and after the death of BM2.

Macdonald *et al.* (2000) pointed out a caveat that when analysing interactive data, recognition must be made of relationships changing within the study period (perhaps following the death of a member of the colony). The paired *t*-test was used to investigate whether interaction rate between the other males changed after the death of BM2. The non-significant result ($t = -2.142$; df = 2; $p = 0.166$ NS) further supports the previous analysis in finding no significant changes in male interactive behaviour following the death of BM2.

4.3.8 Bryces Farm female:female dyad analysis

Data from months September-December was omitted for this analysis as it was grouped and not consistent with the following months' observation periods. Levene's Test revealed significant heteroscadisity in the raw data (prior to transformation, Levene's $F_{20, 51} = 6.630$, $P < 0.001$). A ln $(x + 1)$ transformation was then applied to the data, which very nearly eliminated the heterogeneity of variance problem (after transformation, Levene's $F_{20, 51} = 1.803$, $P = 0.046$). An ANOVA was then carried out on the transformed data. Results are given in Table 4.21.

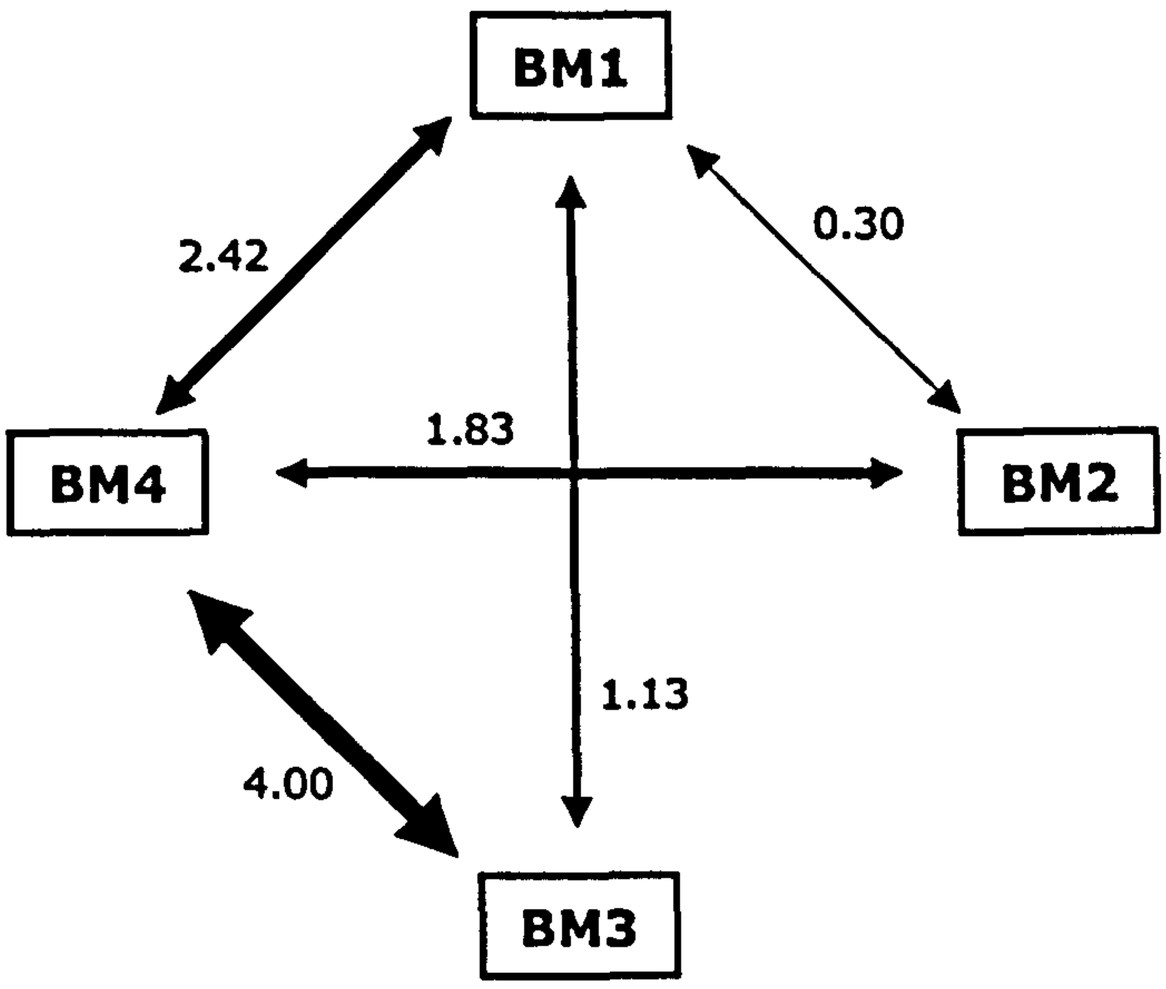


Figure 4.3: Rates of interaction* between male:male dyads before the death of BM2

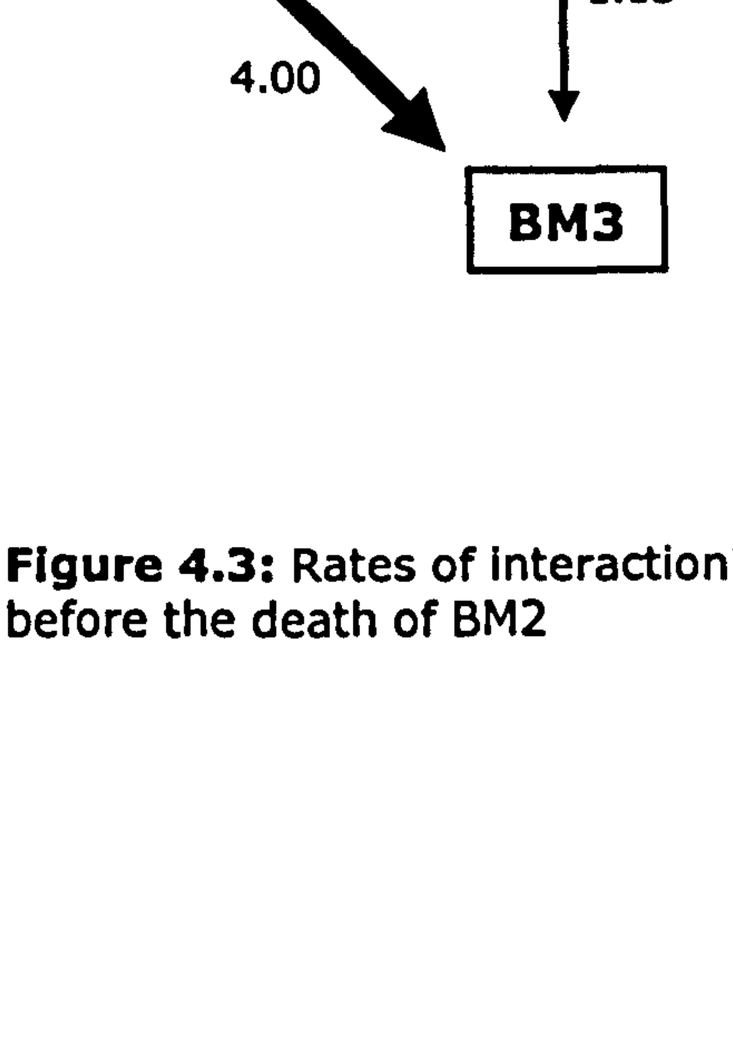


Figure 4.4: Rates of interaction* between male:male dyads after the death of BM2

*Rate of interaction = no. of interactions/availability

Table 4.21: Analysis of variance of ln (x + 1) the frequency of interaction of the Bryces Farm females through time

Source	SS	df	MS	F	Sig.
Month	4.67	6.00	0.78	13.11	P < 0.001
Behaviour	0.17	2.00	0.09	1.47	NS
Month*Behaviour	0.08	12.00	0.01	0.12	NS
Error	3.03	51.00	0.06		
Total	34.97	72.00			

This showed that the month alone affected frequency of interactions between female:female dyads.

The results of post-hoc tests (LSD and Dunnett C) revealed that the months of January/February, and then May/June were significantly different from the other months with respect to the number of interactions occurring between female:female dyads (see Figure 4.5). There were no significant differences in category of behaviour, again with respect to the frequency of interactions occurring between female:female dyads (Figure 4.6).

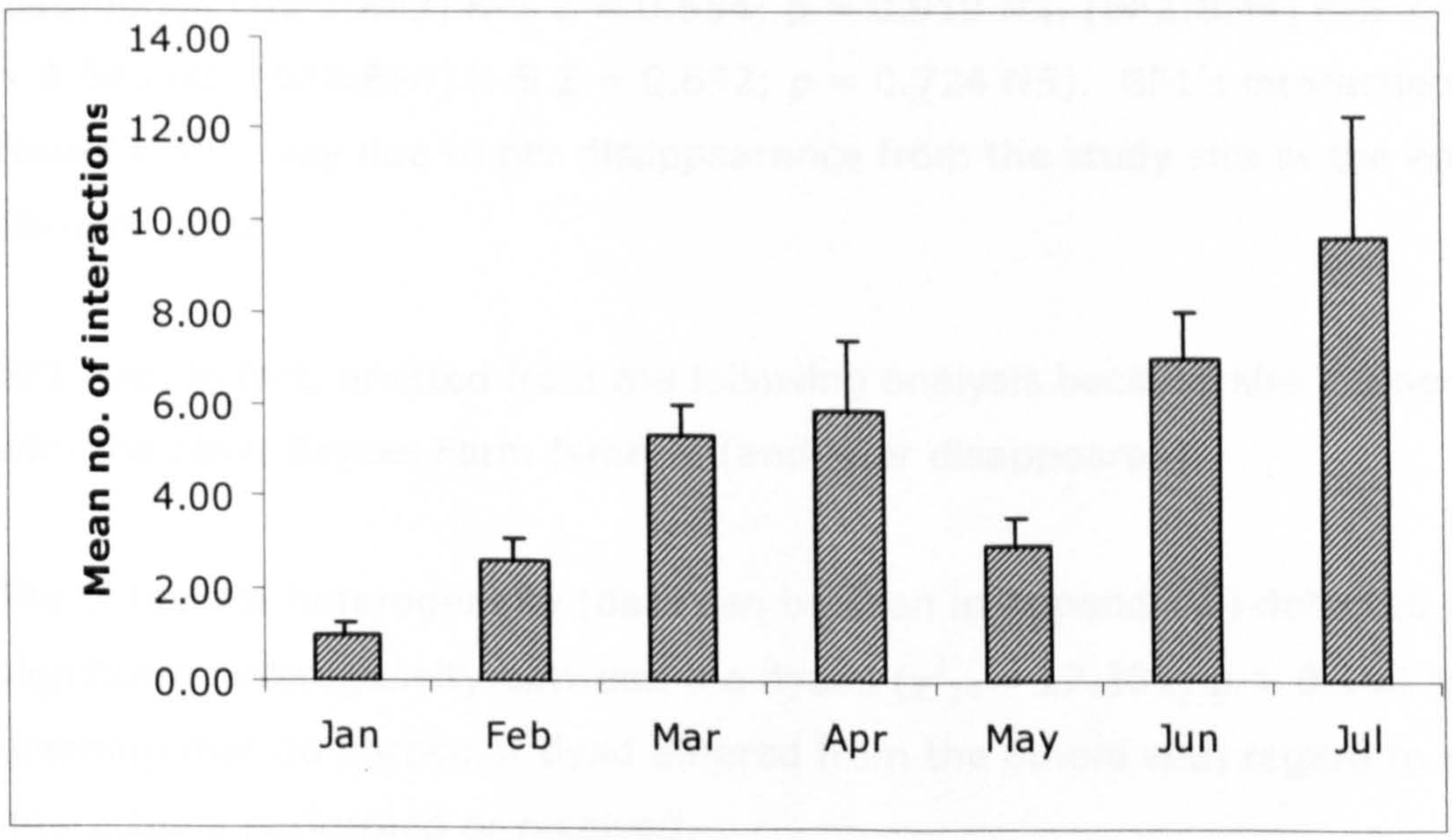


Figure 4.5: Mean number of female:female interactions with respect to month
Error bars represent Standard Error

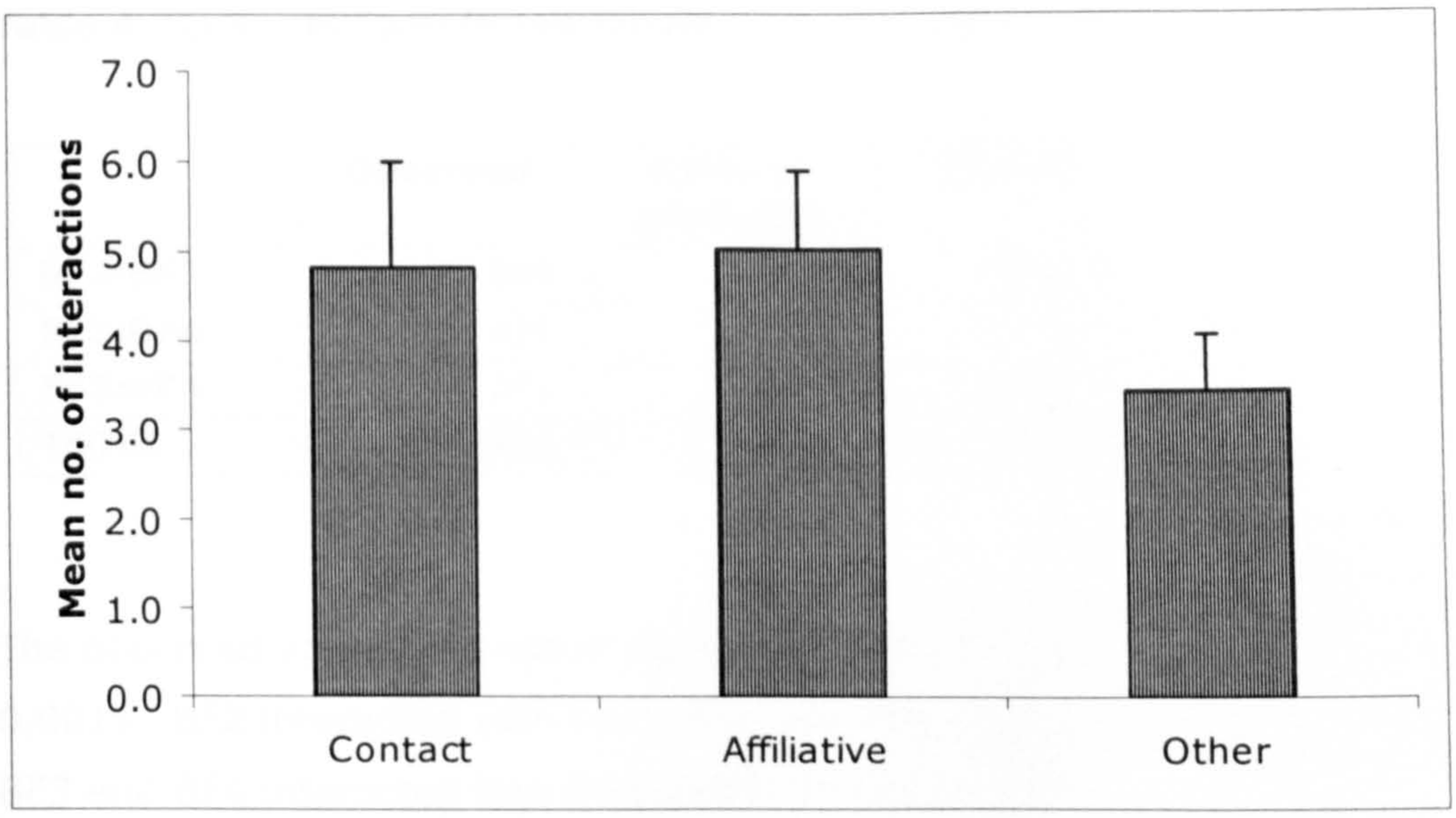


Figure 4.6: Mean number of female:female interactions with respect to behaviour
Error bars represent Standard Error

The overall number of interactions observed occurring between females showed a normal distribution with respect to time (months) (Kolmogorov-Smirnov Z = 0.950; p = 0.328 NS).

Numbers of interactions occurring between the dyads also followed a normal distribution ([BF2:BF3] K-S Z = 0.554; p = 0.919 NS. [BF2:BM4] K-S Z = 0.801; p = 0.543 NS. [BF3:BF4] K-S Z = 0.692; p = 0.724 NS). BF1's interactions were not tested in this way due to her disappearance from the study site at the end of January 2002.

BF1 was, in fact, omitted from the following analysis because she did not interact with the other Bryces Farm females (and later disappeared).

The G-test for heterogeneity (data can be seen in Appendix 5) detected no significant heterogeneity between the dyads ($\chi^2_{14} = 17.301$; $p > 0.100$ NS), meaning that no particular dyad differed from the others with regard to number of interactions performed or received.

Goodness of Fit (Table 4.22):

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Table 4.22: Bryces Farm female:female dyad interaction frequency

	Observed	Ratio of presence	Expected
BF2:BF3	884	0.91	718.632
BF2:BF4	426	0.46	363.265
BF3:BF4	301	0.67	529.103
TOTAL	**1611**	**2.04**	**1611**

The observed values are not in agreement with the expected ($\chi^2_1 = 147.226$; $p < 0.001$). BF2 interacted with the other two females more frequently than expected. BF3 and BF4 interacted less frequently than expected.

Involvement of each cat in turn (Tables 4.23-4.25):

Table 4.23: Bryces Farm BF2:female dyad interaction frequency

BF2	Observed	Ratio of presence	Expected
BF2:BF3	884	0.91	870.146
BF2:BF4	426	0.46	439.854
TOTAL	**1310**	**1.37**	**1310**

BF2 $\chi^2_1 = 0.673$; $p > 0.250$ NS (with Yates' Correction for Continuity).

Table 4.24: Bryces Farm BF3:female dyad interaction frequency

BF3	Observed	Ratio of presence	Expected
BF3:BF2	884	0.91	682.500
BF3:BF4	301	0.67	502.500
TOTAL	**1185**	**1.58**	**1185**

BF3 $\chi^2_1 = 140.398$; $p < 0.001$ (with Yates' Correction for Continuity). BF3 interacted more frequently with BF2 than expected, and less frequently with BF4.

Table 4.25: Bryces Farm BF4:female dyad interaction frequency

BF4	Observed	Ratio of presence	Expected
BF4:BF2	426	0.46	295.947
BF4:BF3	301	0.67	431.053
TOTAL	**727**	**1.13**	**727**

BF4 $\chi^2_1 = 96.254$; $p < 0.001$ (with Yates' Correction for Continuity). BF4 interacted more frequently than expected with BF2. Again, BM3:BM4 interactions were less abundant than expected.

The G-test for heterogeneity (data from Appendix 5) showed that one or more dyads differed from the others with regard to the quality of interactions performed or received ($\chi^2_4 = 20.643$; $p < 0.01$).

Interactions classed as Other (*Feed With* and *Watch*) were then included in the analysis as separate components (Table 4.26).

Table 4.26: Bryces Farm female:female dyad interaction type (expanded)

	Contact	Affiliative	Other = FW	Other = WA	TOTAL
BF2:BF3	287	397	157	43	**884**
BF2:BF4	162	149	78	37	**426**
BF3:BF4	84	121	67	29	**301**
TOTAL	**533**	**667**	**302**	**109**	**1611**

Highly significant differences in the quality of interactions between dyads were found ($\chi^2_6 = 25.809$; $p < 0.01$). Both dyads involving BF3 showed more Affiliative interactions than Contact; BF2:BF4 exhibited more Contact interactions than Affiliative. BF2 and BF3 were observed feeding together more frequently than the other dyads. BF3 and BF4 interacted much less frequently with each other across all behavioural categories compared with the other dyads.

Each dyad was then tested against the other two combined (Tables 4.27-4.29):

Table 4.27: Bryces Farm BF2:BF3 interaction type

	Contact	Affiliative	FW	WA	TOTAL
BF2:BF3	287	397	157	43	**884**
BF2:BF4 and BF3:BF4	246	270	145	66	**727**
TOTAL	**533**	**667**	**302**	**109**	**1611**

$\chi^2_3 = 17.529$; $p < 0.01$

Table 4.28: Bryces Farm BF2:BF4 interaction type

	Contact	Affiliative	FW	WA	TOTAL
BF2:BF4	162	149	78	37	**426**
BF2:BF3 and BF3:BF4	371	518	224	72	**1185**
TOTAL	**533**	**667**	**302**	**109**	**1611**

$\chi^2_3 = 13.190$; $p < 0.01$

Table 4.29: Bryces Farm BF3:BF4 interaction type

	Contact	Affiliative	FW	WA	TOTAL
BF3:BF4	84	121	67	29	**301**
BF2:BF3 and BF2:BF4	449	546	235	80	**1310**
TOTAL	**533**	**667**	**302**	**109**	**1611**

$\chi^2_3 = 9.693$; $p < 0.025$

The above three results show that each individual female dyad was significantly different to the other two combined, in their quality of interactions.

4.3.9 Further effects caused by the disappearance of BF1

Figures 4.7 and 4.8 illustrate, respectively, interaction rates between female:female dyads before and after the disappearance of BF1.

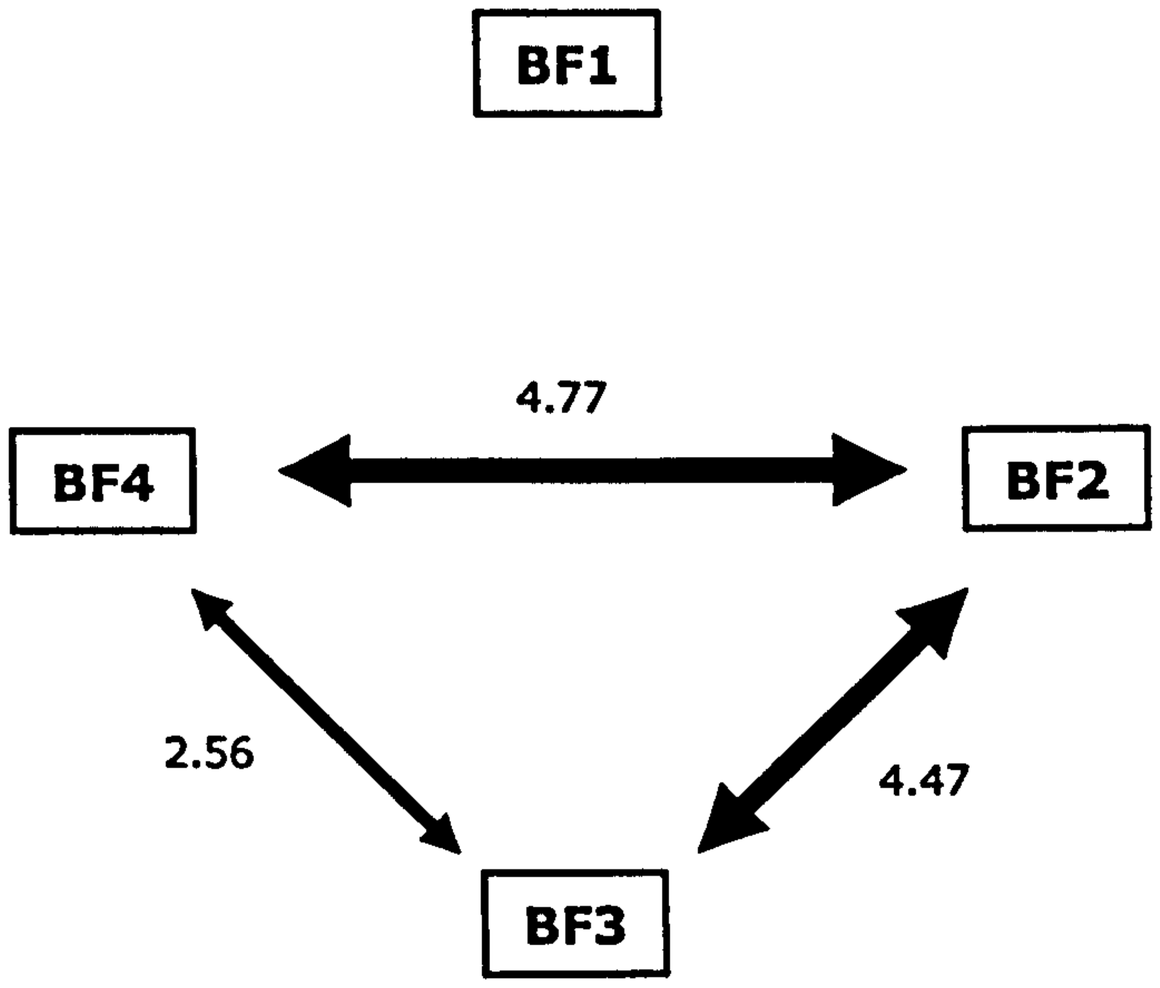


Figure 4.7: Rates of interaction* between female:female dyads before the disappearance of BF1

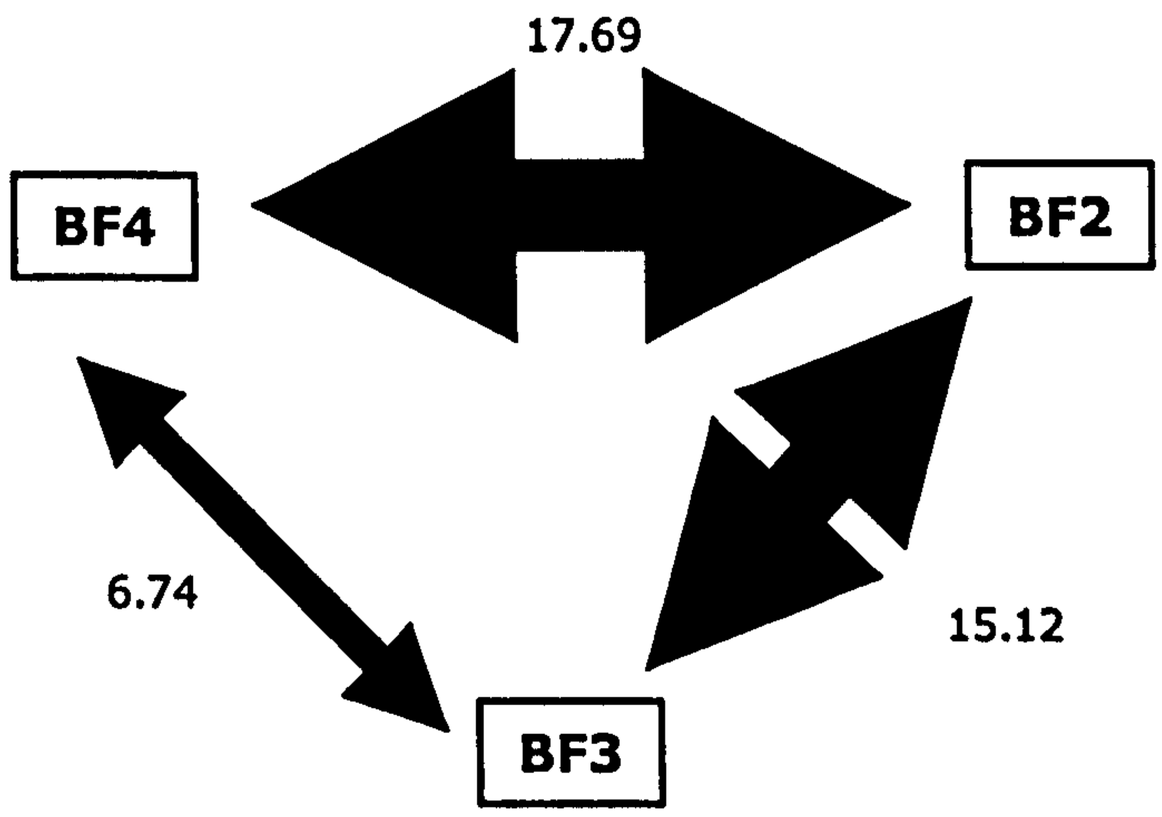


Figure 4.8: Rates of interaction* between female:female dyads after the disappearance of BF1

*Rate of interaction = no. of interactions/availability

The paired *t*-test was used to investigate whether interaction rate between the other females changed after the disappearance of BF1. The non-significant result (t = -3.533; df = 2; p = 0.072 NS) further supports the previous analysis in finding no significant changes in female interactive behaviour following the disappearance of BF1 (although the result is almost significant).

4.3.10 Bryces Farm male:female dyad analysis

Data from months September-December was omitted for this analysis as it was grouped and not consistent with the following months' observation periods. Levene's Test revealed significant heteroscadisity in the raw data (prior to transformation, Levene's $F_{20, 189} = 3.284$, $P < 0.001$). A ln (x + 1) transformation was then applied to the data, which eliminated the heterogeneity of variance problem (after transformation, Levene's $F_{20, 189} = 0.683$, $P = 0.840$). An ANOVA was then carried out on the transformed data. Results are given in Table 4.30.

Table 4.30: Analysis of variance of ln (x + 1) the frequency of interaction of the Bryces Farm males and females through time

Source	SS	df	MS	F	Sig.
Month	5.39	6.00	0.90	14.29	P < 0.001
Behaviour	1.99	2.00	1.00	15.85	P < 0.001
Month*Behaviour	0.29	12.00	0.02	0.38	P = 0.97 NS
Error	11.88	189.00	0.06		
Total	66.96	210.00			

This showed that both month and category of behaviour independently affected frequency of interactions between male:female dyads.

The results of post-hoc tests (LSD and Dunnett C) revealed a pattern showing that the colder months of January, February and March were significantly different from the other months with respect to the number of interactions occurring between male:female dyads (see Figure 4.9). Affiliative behaviour was found to be significantly different from both Contact and Other, again with respect to the frequency of interactions occurring between male:female dyads (Figure 4.10).

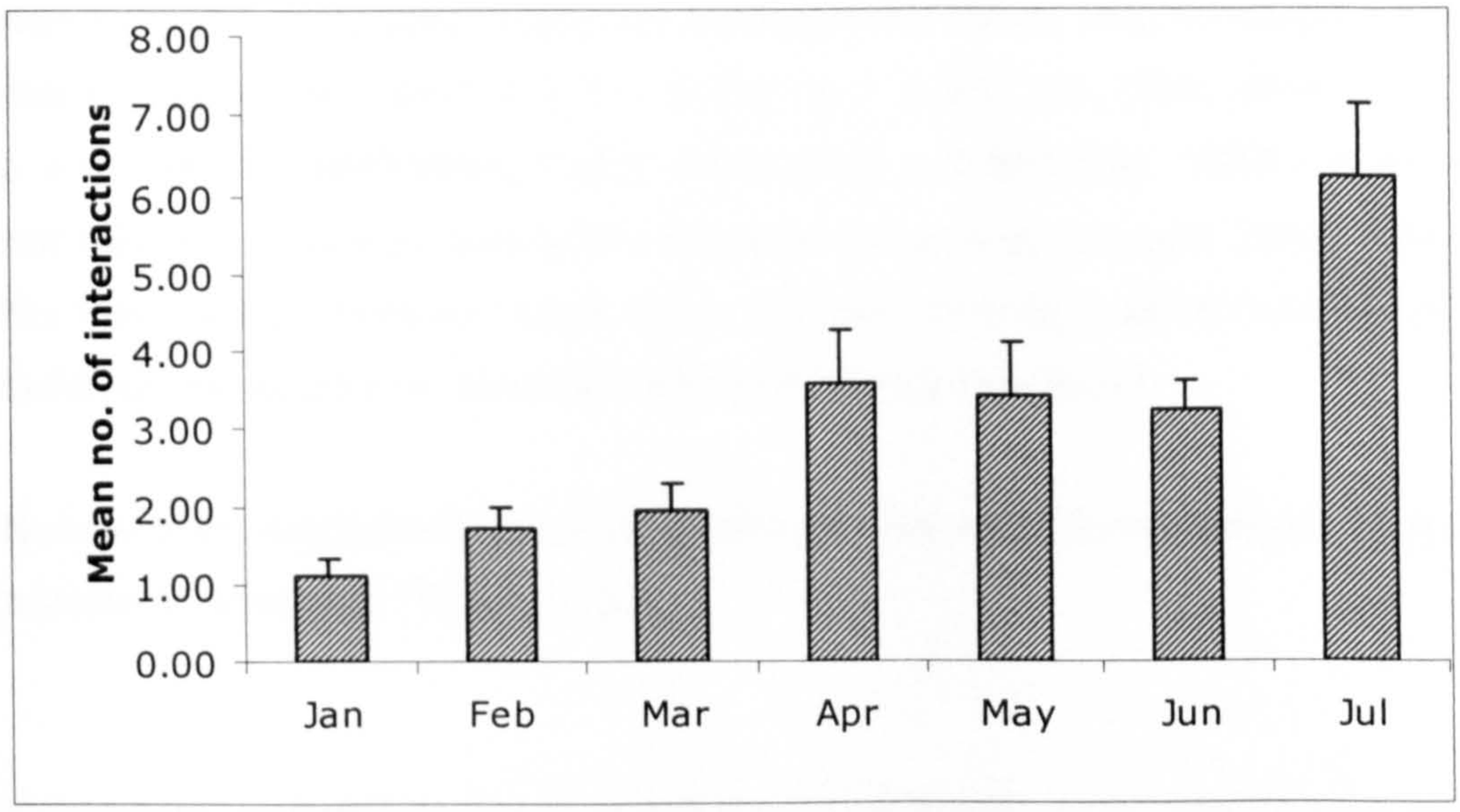


Figure 4.9: Mean number of male:female interactions with respect to month

Error bars represent Standard Error

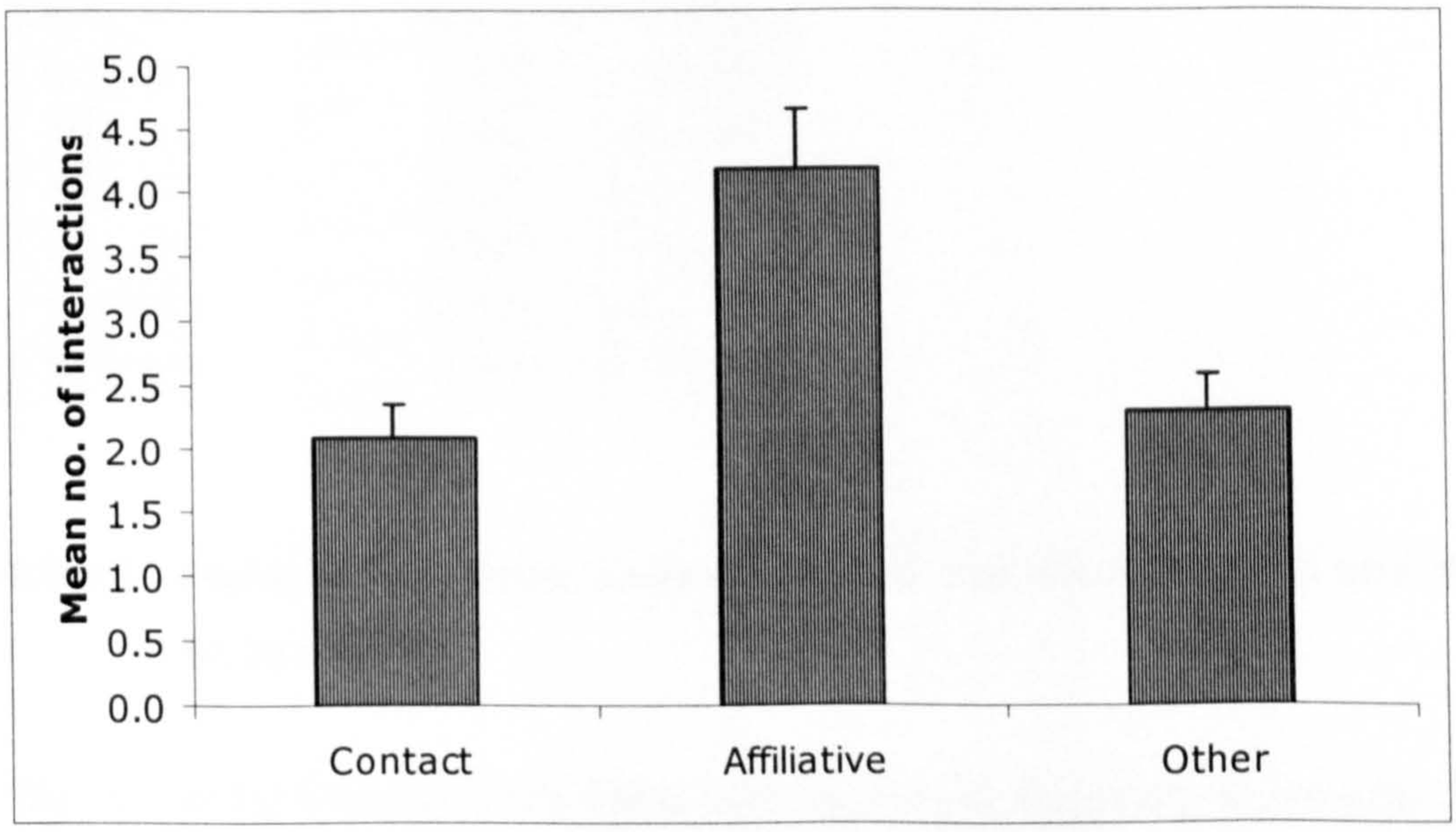


Figure 4.10: Mean number of male:female interactions with respect to behaviour

Error bars represent Standard Error

The overall number of interactions observed occurring between males and females showed a normal distribution with respect to time (months) (Kolmogorov-Smirnov 0.523; $p = 0.947$ NS). BM2 and BF1 were excluded from this analysis due to their respective death and disappearance.

Numbers of interactions occurring between the dyads also followed a normal distribution ([BM1:BM3] K-S Z = 0.766; p = 0.601 NS. [BM1:BM4] K-S Z = 0.708; p = 0.698 NS. [BM3:BM4] K-S Z = 0.414; p = 0.995 NS). BM2's interactions were not tested in this way due to his death at the end of January 2002. The results of the Kolmogorov-Smirnov tests show, overall, that no substantial change in behavioural quality or quantity occurred during the study.

Numbers of interactions occurring between the male:female dyads also followed a normal distribution (Table 4.31).

Table 4.31: Kolmogorov-Smirnov test results for Bryces Farm male:female dyads

Dyad	K-S Z	P
BM1:BF2	0.466	0.981 NS
BM1:BF3	0.600	0.865 NS
BM1:BF4	0.474	0.978 NS
BM3:BF2	0.878	0.423 NS
BM3:BF3	0.852	0.462 NS
BM3:BF4	0.620	0.837 NS
BM4:BF2	0.533	0.939 NS
BM4:BF3	0.636	0.813 NS
BM4:BF4	0.664	0.769 NS

4.3.11 Male:female dyad analysis before the death of BM2 and disappearance of BF1

The G-test for heterogeneity (data can be seen in Appendix 5) detected no significant heterogeneity between the dyads ($\chi^2_{15} = 23.826$; $p > 0.05$ NS), meaning that no particular dyad differed from the others with regard to behaviours performed or received.

Goodness of Fit (Table 4.32):

Table 4.32: Bryces Farm male:female dyad interaction frequency, Sep 2001-Jan 2002

	Observed	Ratio of presence	Expected
BM1:BF1	11	0.15	32.172
BM1:BF2	29	0.24	51.475
BM1:BF3	35	0.33	70.779
BM1:BF4	14	0.19	40.751
BM2:BF1	66	0.13	27.883
BM2:BF2	0	0.24	51.475
BM2:BF3	0	0.31	66.489
BM2:BF4	0	0.18	38.607
BM3:BF1	5	0.19	40.751
BM3:BF2	158	0.33	70.779
BM3:BF3	273	0.41	87.937
BM3:BF4	49	0.24	51.475
BM4:BF1	21	0.11	23.593
BM4:BF2	55	0.21	45.041
BM4:BF3	53	0.22	47.186
BM4:BF4	16	0.18	38.607
TOTAL	**785**	**3.66**	**785**

$\chi^2_{14} = 812.946$; $p < 0.001$

Involvement of each cat in turn (Tables 4.33-4.36 [males]; Tables 4.37-4.40 [females]):

Table 4.33: Bryces Farm BM1:female dyad interaction frequency, Sep 2001-Jan 2002

BM1	Observed	Ratio of presence	Expected
BM1:BF1	11	0.15	14.670
BM1:BF2	29	0.24	23.473
BM1:BF3	35	0.33	32.275
BM1:BF4	14	0.19	18.582
TOTAL	**89**	**0.91**	**89**

$\chi^2_2 = 3.579$; $p > 0.100$ NS

Table 4.34: Bryces Farm BM2:female dyad interaction frequency, Sep 2001-Jan 2002

BM2	Observed	Ratio of presence	Expected
BM2:BF1	66	0.13	9.977
BM2:BF2	0	0.24	18.419
BM2:BF3	0	0.31	23.791
BM2:BF4	0	0.18	13.814
TOTAL	**66**	**0.86**	**66**

$\chi^2_2 = 370.605$; $p < 0.001$

Table 4.35: Bryces Farm BM3:female dyad interaction frequency, Sep 2001-Jan 2002

BM3	Observed	Ratio of presence	Expected
BM3:BF1	5	0.19	78.761
BM3:BF2	158	0.33	136.795
BM3:BF3	273	0.41	169.957
BM3:BF4	49	0.24	99.487
TOTAL	**485**	**1.17**	**485**

$\chi^2_2 = 160.459$; $p < 0.001$

Table 4.36: Bryces Farm BM4:female dyad interaction frequency, Sep 2001-Jan 2002

BM4	Observed	Ratio of presence	Expected
BM4:BF1	21	0.11	22.153
BM4:BF2	55	0.21	42.292
BM4:BF3	53	0.22	44.306
BM4:BF4	16	0.18	36.250
TOTAL	**145**	**0.72**	**145**

$\chi^2_2 = 16.896$; $p < 0.01$

Table 4.37: Bryces Farm BF1:male dyad interaction frequency, Sep 2001-Jan 2002

BF1	Observed	Ratio of presence	Expected
BF1:BM1	11	0.15	26.638
BF1:BM2	66	0.13	23.086
BF1:BM3	5	0.19	33.741
BF1:BM4	21	0.11	19.534
TOTAL	**103**	**0.58**	**103**

$\chi^2_2 = 113.544$; $p < 0.001$

Table 4.38: Bryces Farm BF2:male dyad interaction frequency, Sep 2001-Jan 2002

BF2	Observed	Ratio of presence	Expected
BF2:BM1	29	0.24	56.941
BF2:BM2	0	0.24	56.941
BF2:BM3	158	0.33	78.294
BF2:BM4	55	0.21	49.824
TOTAL	**242**	**1.02**	**242**

$\chi^2_2 = 152.333$; $p < 0.001$

Table 4.39: Bryces Farm BF3:male dyad interaction frequency, Sep 2001-Jan 2002

BF3	Observed	Ratio of presence	Expected
BF3:BM1	35	0.33	93.803
BF3:BM2	0	0.31	88.118
BF3:BM3	273	0.41	116.543
BF3:BM4	53	0.22	62.535
TOTAL	**361**	**1.27**	**361**

$\chi^2_2 = 336.475$; $p < 0.001$

Table 4.40: Bryces Farm BF4:male dyad interaction frequency, Sep 2001-Jan 2002

BF4	Observed	Ratio of presence	Expected
BF4:BM1	14	0.19	19.000
BF4:BM2	0	0.18	18.000
BF4:BM3	49	0.24	24.000
BF4:BM4	16	0.18	18.000
TOTAL	**79**	**0.79**	**79**

$\chi^2_2 = 45.580$; $p < 0.001$

A G-test was then carried out to test the quality of the interactions, by looking for heterogeneity in the type of interactions (data from Appendix 5). BM2:BF2, BM2:BF3 and BM2:BF4 dyads were omitted from this analysis as no interactions occurred. The result ($\chi^2_{30} = 112.346$; $p < 0.001$) showed that one or more dyads differed from the others with regard to behaviours performed or received.

The individual styles of each male (with each female) were then analysed in turn (data from Appendix 5) (Table 4.41).

Table 4.41: Bryces Farm males' interactions with females

Individual	Result
BM1	$\chi^2_6 = 6.454$; $p > 0.250$ NS
BM2*	$\chi^2_2 = 2.340$; $p > 0.250$ NS
BM3	$\chi^2_6 = 13.973$; $p < 0.05$
BM4	$\chi^2_6 = 5.959$; $p > 0.250$ NS

BM2* only interacted with one female (BF1), therefore the analysis was slightly different (one-way classification with Williams' Correction Factor).

4.3.12 Male:female dyad analysis after the death of BM2 and disappearance of BF1

The G-test (data can be seen in Appendix 5) was calculated as $\chi^2_{40} = 113.571$; $p < 0.001$. One or more dyads differed from the others with regard to behaviours performed or received.

Goodness of Fit (Table 4.42):

Table 4.42: Bryces Farm male:female dyad interaction frequency, Feb-Jul 2002

	Observed	Ratio of presence	Expected
BM1:BF2	97	0.24	183.443
BM1:BF3	130	0.48	366.887
BM1:BF4	53	0.19	145.226
BM3:BF2	411	0.28	214.017
BM3:BF3	449	0.45	343.957
BM3:BF4	153	0.21	160.513
BM4:BF2	158	0.12	91.722
BM4:BF3	205	0.26	198.730
BM4:BF4	102	0.07	53.504
TOTAL	**1758**	**2.3**	**1758**

$\chi^2_7 = 558.035$; $p < 0.001$.

Involvement of each cat in turn (Tables 4.43-4.45 [males]; Tables 4.46-4.48 [females]):

Table 4.43: Bryces Farm BM1:female dyad interaction frequency, Feb-Jul 2002

BM1	Observed	Ratio of presence	Expected
BM1:BF2	97	0.24	73.846
BM1:BF3	130	0.48	147.692
BM1:BF4	53	0.19	58.462
TOTAL	**280**	**0.91**	**280**

$\chi^2_1 = 9.889$; $p < 0.01$.

Table 4.44: Bryces Farm BM3:female dyad interaction frequency, Feb-Jul 2002

BM3	Observed	Ratio of presence	Expected
BM3:BF2	411	0.28	301.745
BM3:BF3	449	0.45	484.947
BM3:BF4	153	0.21	226.309
TOTAL	**1013**	**0.94**	**1013**

$\chi^2_1 = 65.971$; $p < 0.001$.

Table 4.45: Bryces Farm BM4:female dyad interaction frequency, Feb-Jul 2002

BM4	Observed	Ratio of presence	Expected
BM4:BF2	158	0.12	124.000
BM4:BF3	205	0.26	268.667
BM4:BF4	102	0.07	72.333
TOTAL	**465**	**0.45**	**465**

$\chi^2_1 = 36.578$; $p < 0.001$.

Table 4.46: Bryces Farm BF2:male dyad interaction frequency, Feb-Jul 2002

BF2	Observed	Ratio of presence	Expected
BF2:BM1	97	0.24	249.750
BF2:BM3	411	0.28	291.375
BF2:BM4	158	0.12	124.875
TOTAL	**666**	**0.64**	**666**

$\chi^2_1 = 151.323$; $p < 0.001$.

Table 4.47: Bryces Farm BF3:male dyad interaction frequency, Feb-Jul 2002

BF3	Observed	Ratio of presence	Expected
BF3:BM1	130	0.48	316.235
BF3:BM3	449	0.45	296.471
BF3:BM4	205	0.26	171.294
TOTAL	**784**	**1.19**	**784**

$\chi^2_1 = 194.781$; $p < 0.001$.

Table 4.48: Bryces Farm BF4:male dyad interaction frequency, Feb-Jul 2002

BF4	Observed	Ratio of presence	Expected
BF4:BM1	53	0.19	124.511
BF4:BM3	153	0.21	137.617
BF4:BM4	102	0.07	45.872
TOTAL	**308**	**0.47**	**308**

$\chi^2_1 = 111.468$; $p < 0.001$.

The G-test (data from Appendix 5) on male:female interaction type for the period following the death of BM2 and disappearance of BF1 gave a significant result ($\chi^2_{10} = 47.491$; $p < 0.001$). This result showed that one or more dyads differed from the others with regard to behaviours performed or received.

At this stage, interactions classed as Other (*Feed With* and *Watch*) appeared to be playing a significant part in the analysis, and it was therefore decided to isolate them from each other (Table 4.49):

Table 4.49: Bryces Farm male:female dyad interaction type (expanded), Feb-Jul 2002

	Contact	Affiliative	Other = FW	Other = WA	TOTAL
BM1:BF2	15	63	15	4	**97**
BM1:BF3	24	77	19	10	**130**
BM1:BF4	5	38	8	2	**53**
BM3:BF2	113	193	68	37	**411**
BM3:BF3	118	210	92	29	**449**
BM3:BF4	41	70	29	13	**153**
BM4:BF2	42	58	39	19	**158**
BM4:BF3	62	87	36	20	**205**
BM4:BF4	23	52	22	5	**102**
TOTAL	**443**	**848**	**328**	**139**	**1758**

$\chi^2_{24} = 55.485$; $p < 0.01$

The individual styles of each male were then analysed in turn (Tables 4.50-4.52):

Table 4.50: Bryces Farm BM1 interaction type, Feb-Jul 2002

	Contact	Affiliative	Other = FW	Other = WA	TOTAL
BM1:BF2	15	63	15	4	**97**
BM1:BF3	24	77	19	10	**130**
BM1:BF4	5	38	8	2	**53**
TOTAL	**44**	**178**	**42**	**16**	**280**

$\chi^2_6 = 4.804$; $p > 0.500$ NS

Table 4.51: Bryces Farm BM3 interaction type, Feb-Jul 2002

	Contact	Affiliative	Other = FW	Other = WA	TOTAL
BM3:BF2	113	193	68	37	**411**
BM3:BF3	118	210	92	29	**449**
BM3:BF4	41	70	29	13	**153**
TOTAL	**272**	**473**	**189**	**79**	**1013**

$\chi^2_6 = 3.885$; $p > 0.500$ NS

Table 4.52: Bryces Farm BM4 interaction type, Feb-Jul 2002

	Contact	Affiliative	Other = FW	Other = WA	TOTAL
BM4:BF2	42	58	39	19	**158**
BM4:BF3	62	87	36	20	**205**
BM4:BF4	23	52	22	5	**102**
TOTAL	**127**	**197**	**97**	**44**	**465**

$\chi^2_6 = 10.438$; $p > 0.100$ NS

4.3.13 Further effects caused by the death of BM2 and disappearance of BF1

Figures 4.11 – 4.17 illustrate interaction rates between male:female dyads before and after the death of BM2 and disappearance of BF1. For graphical clarification, the four males have been represented individually.

The paired *t*-test was used to investigate whether interaction rates between the other male:female dyads changed after the death of BM2 and disappearance of BF1. The significant result ($t = -4.347$; df = 8; $p = 0.002$) shows interaction rates between male:female dyads were greater during the second period, after the death of BM2 and disappearance of BF1.

4.4 Evidence of sociality within the Bryces Farm colony

Following Macdonald *et al.*, 1987 and Brown, 1993, it was decided to investigate whether or not the cats were behaving socially (indicating interactions were socially based), or just interacting randomly as they happened to encounter each other. If the cats interacted at random, then the number of interactions between each dyad would be directly proportional to the amount of time they were available to interact (Macdonald *et al.*, 1987). As mentioned earlier, availability to interact with each other was calculated as the number of occasions both cats from each pair were sighted in the study area during any particular study session. Rates of interaction would be the same for every pair of cats and would therefore be independent of time available to interact. In other words, if the cats were interacting in a random fashion then there would be a significant correlation between the number of

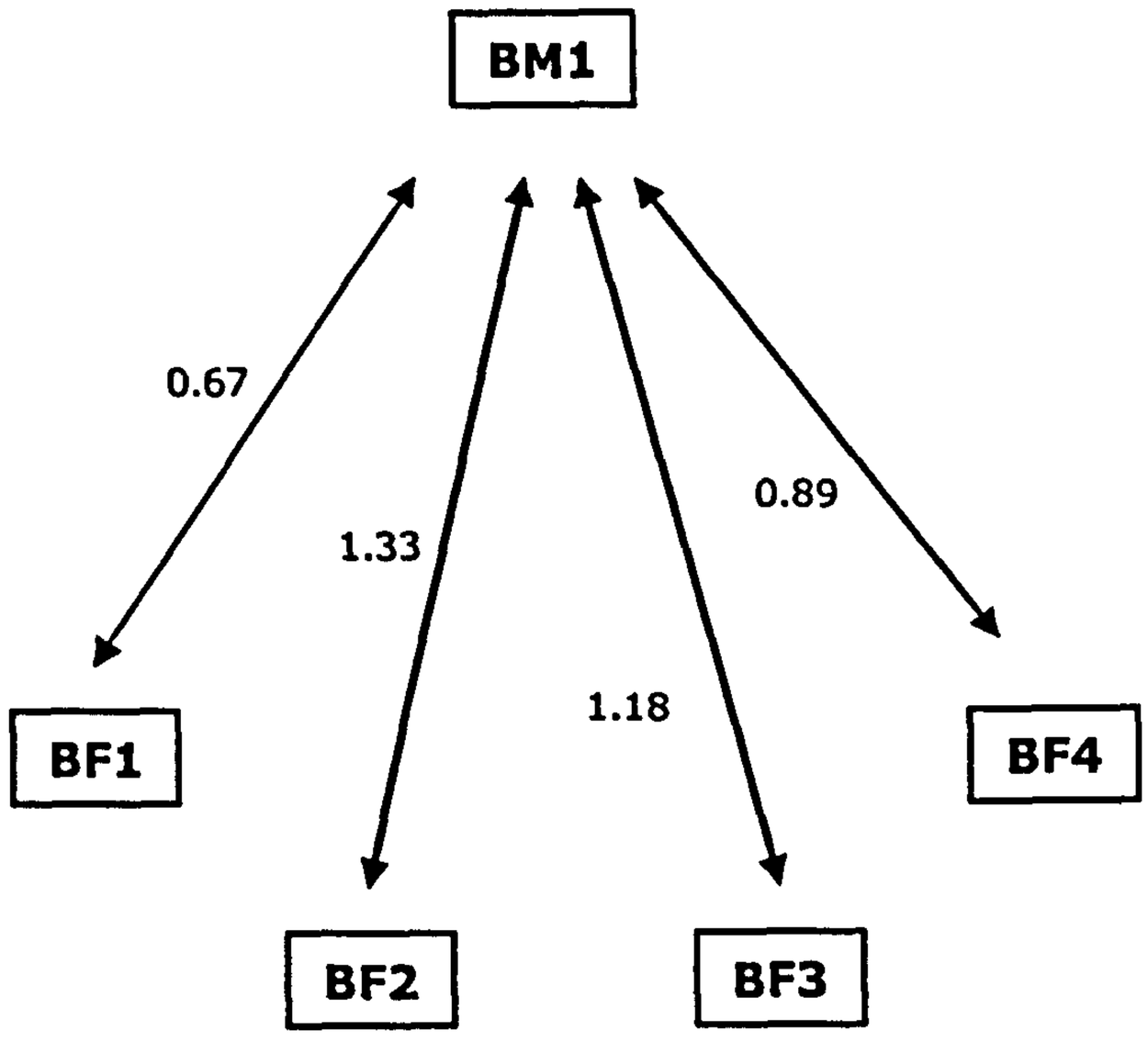


Figure 4.11: Rates of interaction* between male (BM1):female dyads before the death of BM2 and disappearance of BF1

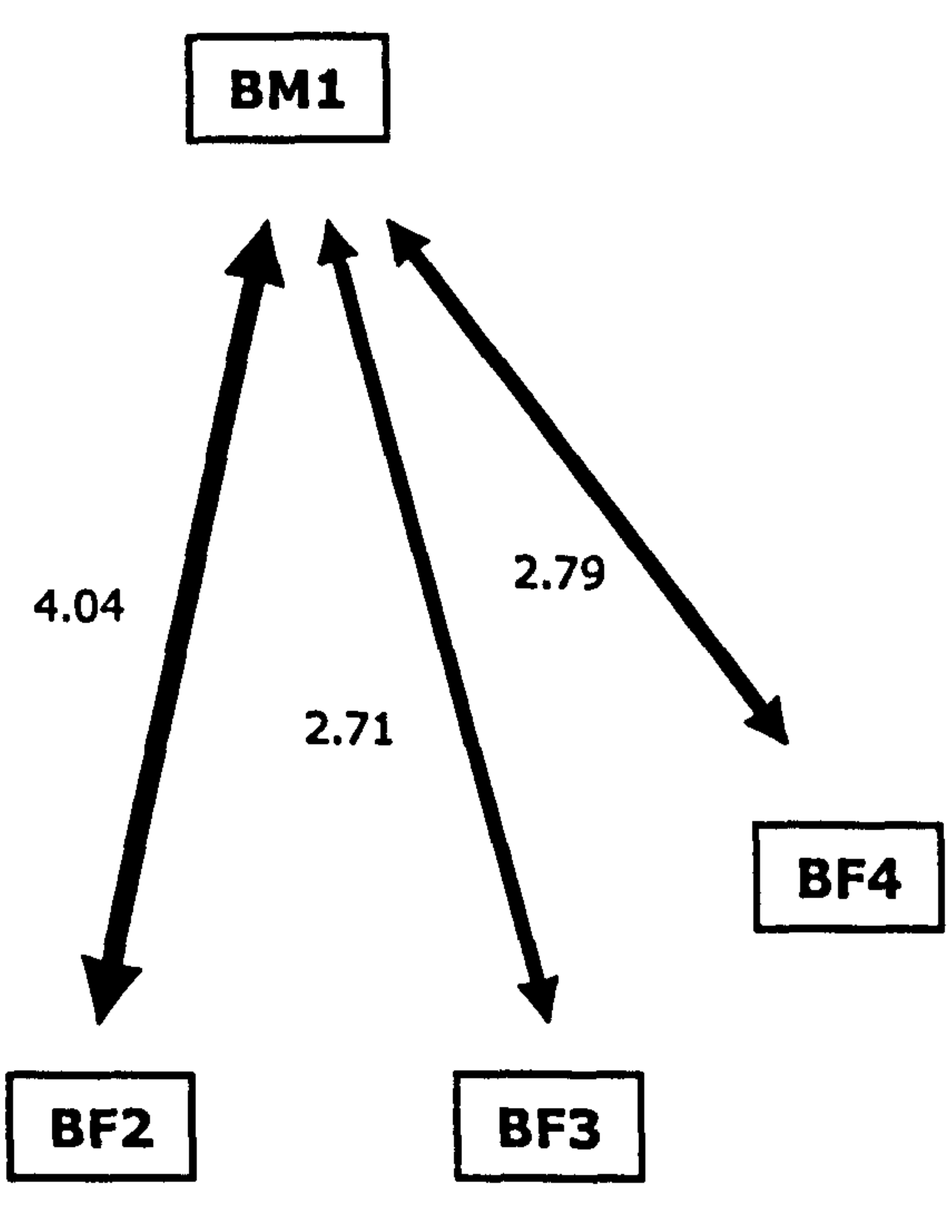


Figure 4.12: Rates of interaction* between male (BM1):female dyads after the death of BM2 and disappearance of BF1

*Rate of interaction = no. of interactions/availability

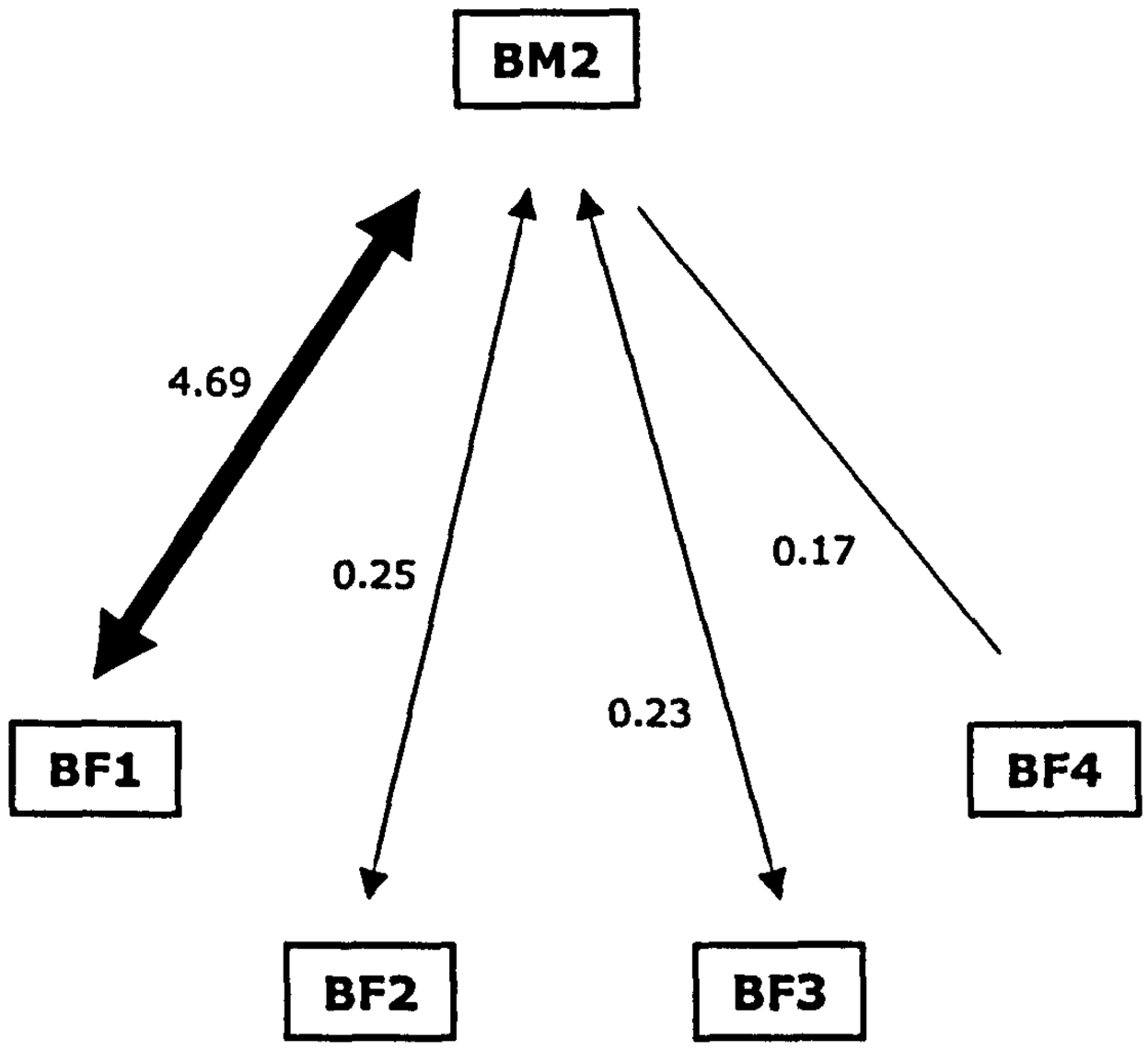


Figure 4.13: Rates of interaction* between male (BM2):female dyads before the death of BM2 and disappearance of BF1

*Rate of interaction = no. of interactions/availability

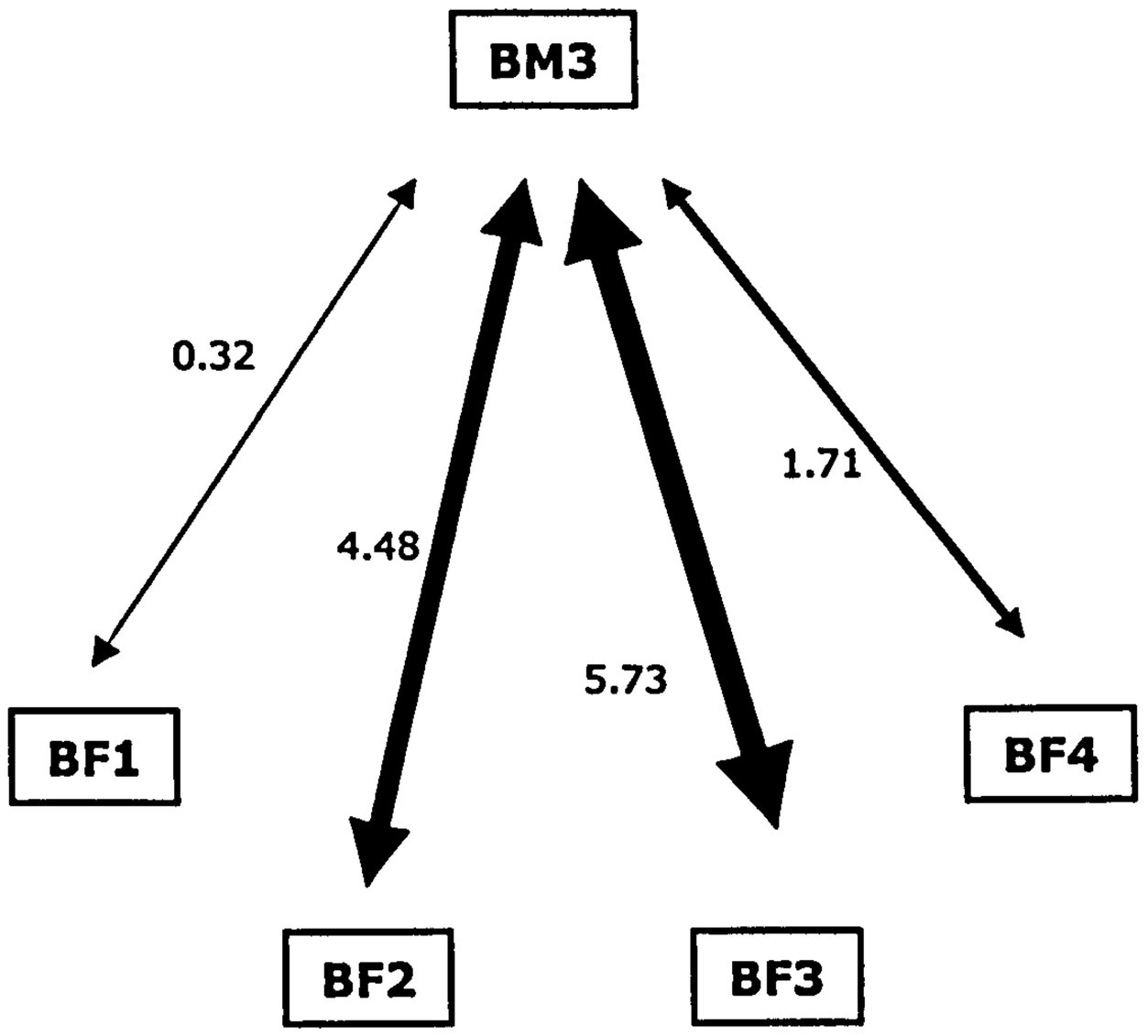


Figure 4.14: Rates of interaction* between male (BM3):female dyads before the death of BM2 and disappearance of BF1

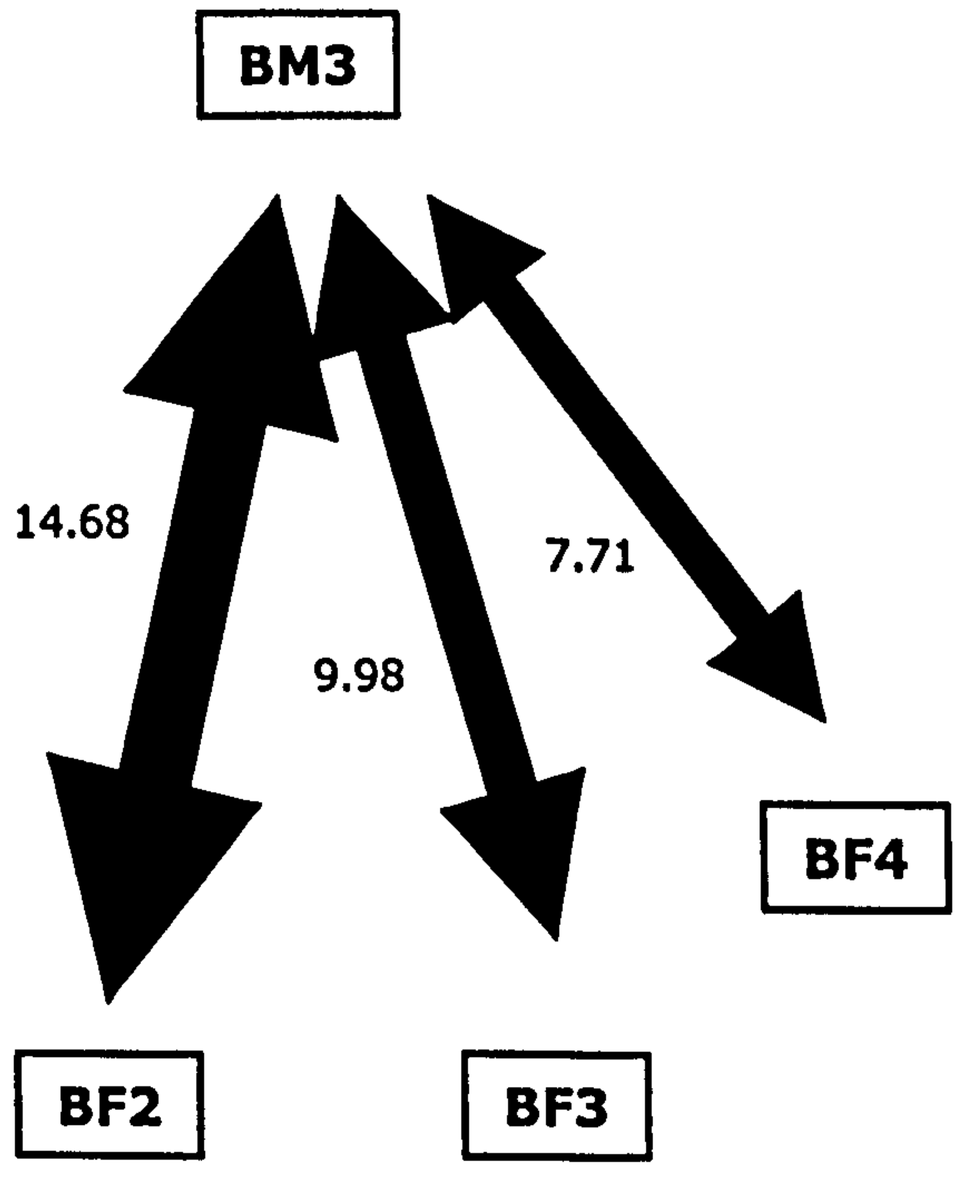


Figure 4.15: Rates of interaction* between male (BM3):female dyads after the death of BM2 and disappearance of BF1

*Rate of interaction = no. of interactions/availability

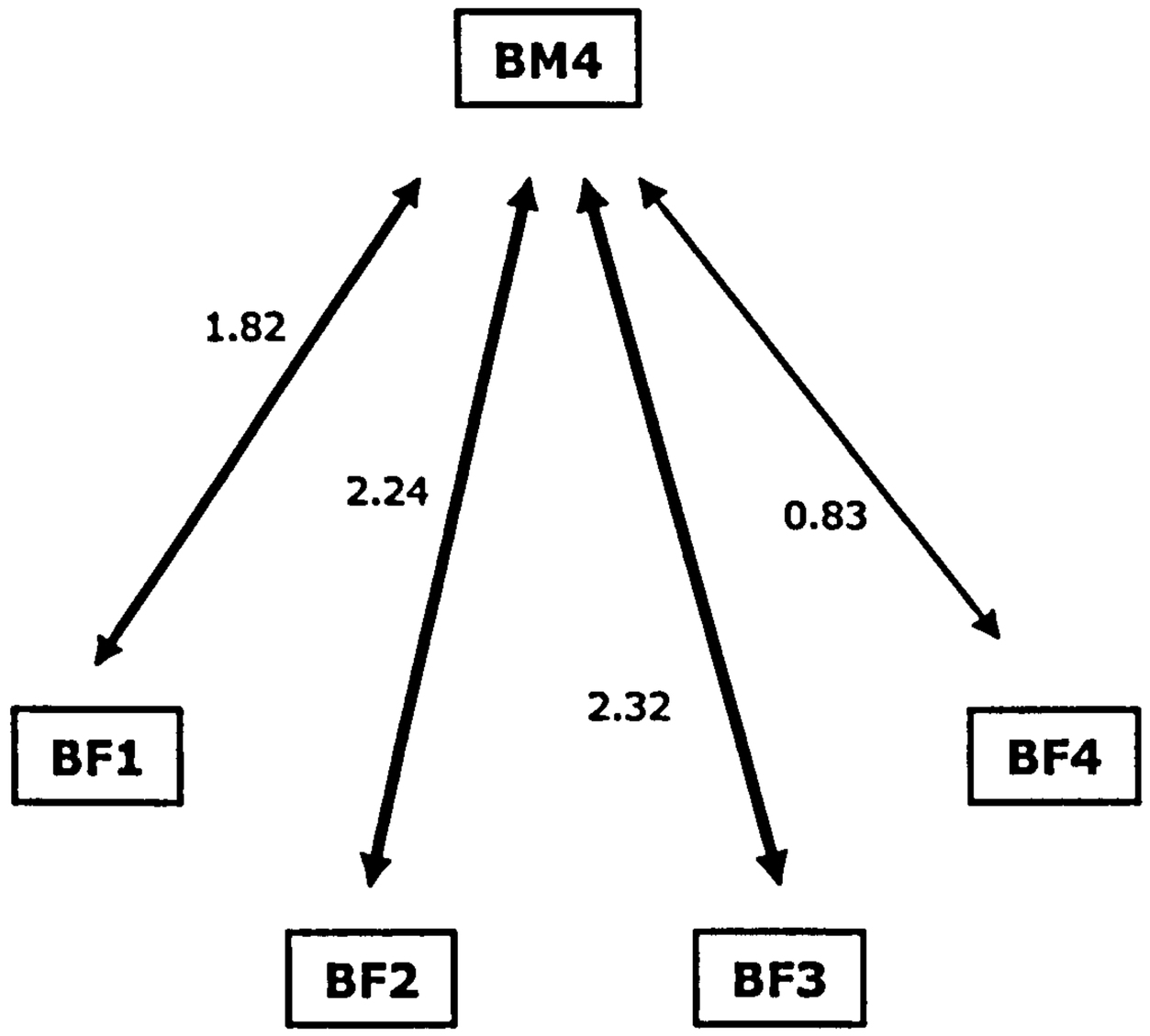


Figure 4.16: Rates of interaction* between male (BM4):female dyads before the death of BM2 and disappearance of BF1

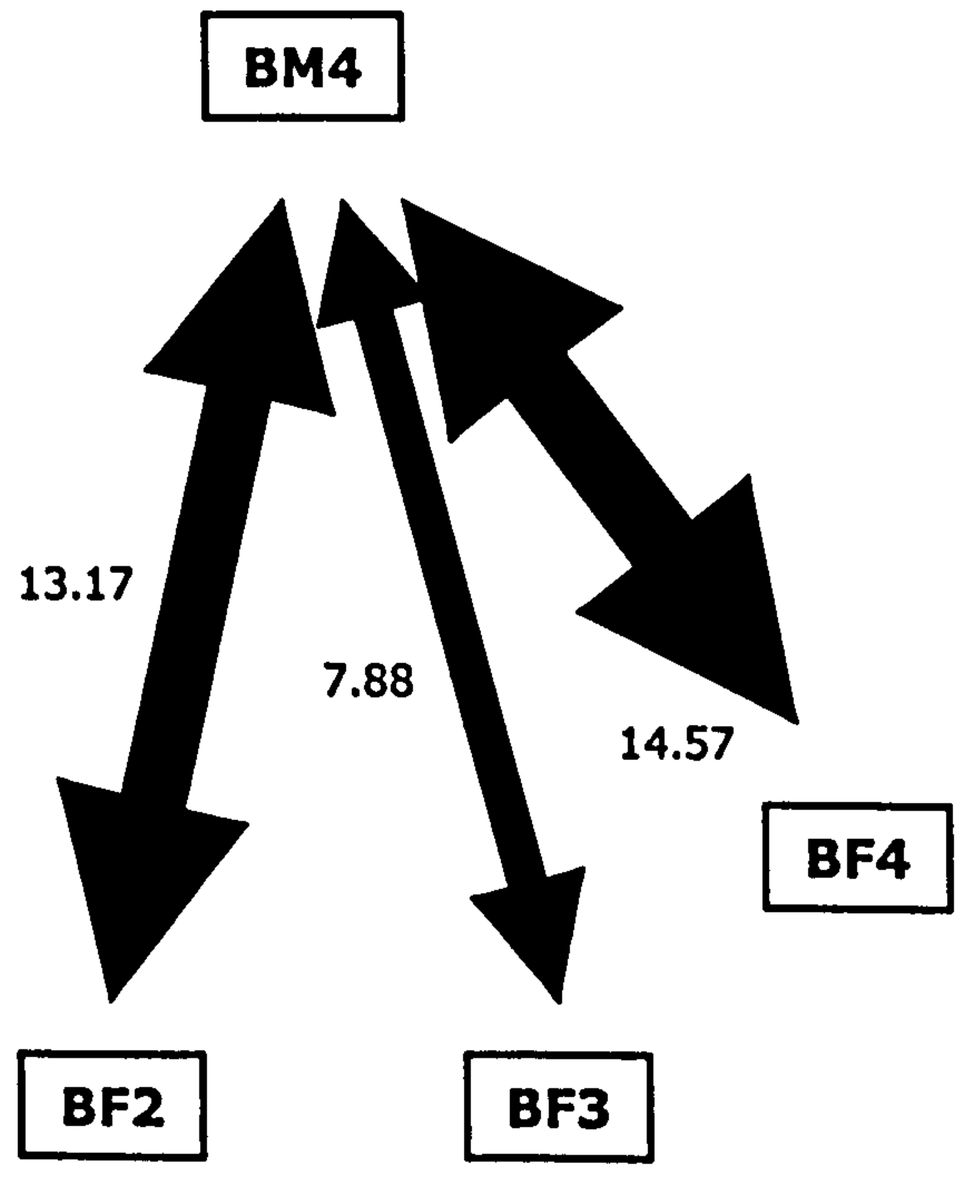


Figure 4.17: Rates of interaction* between male (BM4):female dyads after the death of BM2 and disappearance of BF1

*Rate of interaction = no. of interactions/availability

interactions and availability, and a significant positive correlation between the rate of interaction and availability. Pearson's product-moment correlation was used to test these theories, for the two time periods before (Period 1) and after (Period 2) the death of BM2 and disappearance of BF1. Dyads that did not interact were omitted from this analysis.

4.4.1 Male:male sociality

Table 4.53 shows the analysis of sociality for the male:male dyads.

Table 4.53: Pearson's product-moment correlation for male:male dyads

	No. of interactions *vs.* availability	**Rate of interactions *vs.* availability**
BM2 present (Period 1)	r = -0.045; d.f. = 3; p = 0.933 NS	r = -0.193; d.f. = 3; p = 0.714 NS
BM2 absent (Period 2)	r = -0.480; d.f. = 1; p = 0.682 NS	r = -0.800; d.f.= 1; p = 0.410 NS

Before the death of BM2, interactions between males did not occur at random; the cats did not interact with each other according to how often they encountered one another and may therefore be considered to have been behaving socially. Dyads present at the study site together more frequently interacted at a higher rate than those present together less often.

After the death of BM2, dyads present together more frequently interacted at a lower rate than dyads present together less frequently.

4.4.2 Female:female sociality

Table 4.54 shows the analysis of sociality for the female:female dyads.

Table 4.54: Pearson's product-moment correlation for female:female dyads

	No. of interactions *vs.* availability	**Rate of interactions *vs.* availability**
BF1 present (Period 1)	$r = 0.749$; d.f. = 1; p = 0.461 NS	$r = 0.084$; d.f. = 1; p = 0.946 NS
BF1 absent (Period 2)	$r = 0.714$; d.f. = 1; p = 0.494 NS	$r = -0.310$; d.f. = 1; p = 0.800 NS

For the periods both before and after the disappearance of BF1, interactions between females did not occur at random; the cats did not interact with each other according to how often they encountered one another. This result is, therefore, a positive indicator of sociality between the female cats.

4.4.3 Male:female sociality

Table 4.55 shows the analysis of sociality for the male:female dyads.

Table 4.55: Pearson's product-moment correlation for male:female dyads

	No. of interactions *vs.* availability	**Rate of interactions *vs.* availability**
All cats present (Period 1)	$r = 0.676$; d.f. = 13; p < 0.001**	$r = 0.370$; d.f. = 13; p = 0.159 NS
BM2 and BF1 absent (Period 2)	$r = 0.491$; d.f. = 7; p = 0.180 NS	$r = -0.408$; d.f. = 7; p = 0.275 NS

For the periods both before and after the death of BM2 and the disappearance of BF1, interactions between males and females did not occur at random; the cats did not interact with each other according to how often they encountered one another. The significance of the correlation between number of interactions and availability does not necessarily indicate asociality, but may simply mean that the males and females were interacting in a different way, possibly due to a reorganisation of the social structure following the death of two cats from the colony. The results given

in Table 4.55 are, therefore, positive indicators of sociality between the male and female cats.

Overall, a social hierarchy is evident in the Bryces Farm colony and is discussed below.

4.5 Discussion

In order to define social groups and to describe social dynamics, interactions must be described that may be positive, tolerant, or negative in terms of their consequences for those involved (Macdonald *et al.*, 2000); two animals can respond to each other randomly, with attraction, or with avoidance (Minta, 1992). It was more difficult to draw conclusions from the results of this chapter because, as explained in Section 4.2.1, the initiator and receiver in the interacting dyad could not always be identified, therefore the interactions often lacked direction. Previous studies of farm cat interactions (eg. Kerby, 1987; Kerby and Macdonald, 1988; Macdonald *et al.*, 1987, 2000) have used such directional flows of interactions (asymmetry) as indicators of dominance and social position.

A more dominant individual would be expected to consistently *initiate* particular behaviours whereas a subordinate may only ever be the *recipient*, for example, with displays of aggression. Interpretations of dominance based on this chapter may therefore be subject to limitations, as initiator and recipient were not identified.

4.5.1 Glebe Farm conclusions

The results of the Glebe Farm study indicate a degree of tolerance bordering on avoidance between GM2 and the other males, and positivity between GM1 and GM3. Dards (1979) found that adult males were never amicable but either avoided, tolerated or attacked one another, and actively persecuted younger males; thus defining avoidance and tolerance as agonistic behaviour.

The results from Chapter 3 showed that GM2's home range encompassed that of both GM1 and GM3. GM1 and GM3 had largely, but not completely, overlapping home ranges. The fact that despite this, GM2 may have been avoiding the other males may be explained by the fact that both GM1 and GM3's home ranges mostly

consisted of the Glebe Farm Central Resource Area, which was also regularly utilised by GM2. It would appear therefore, that his overlap in territory with two males he tended to avoid interacting with was due to his need for the resources provided by the CRA in the form of food, shelter and females.

Other studies of farm cat colonies which have involved observations of adult males and kittens (Kerby, 1987; Kerby and Macdonald, 1988; Macdonald *et al.*, 1987, 2000) have shown conflicting results to this current study, with adult males interacting least frequently with kittens than any other class. For the Glebe Farm colony, GM2 showed a high rate of interaction with the kittens, and all interactions were affiliative. The results of the microsatellite study (Chapter 5) may show that GM2 has solely fathered these kittens, which may lead to new hypotheses and perhaps a previously unexplored area of domestic cat behaviour not dissimilar to the behaviour exhibited by male kin helpers in other mammalian societies (Woodroffe and Vincent, 1994). The interactions of GM2 with the kittens have largely involved close physical contact (sleeping together during the winter) and could be interpreted as a protective, paternal behaviour to guard offspring against cold weather and predators, although this theory has not been documented in published literature. Turner, Feaver, Mendl and Bateson (1986) and McCune (1995), found that kittens could be differentiated by their father's temperament; those sired by a "friendly" father were themselves more sociable towards humans. However, these two studies related to domestic pet cats, and the fathers had no contact with their kittens, thus concluding the effect was genetic.

4.5.2 Bryces Farm conclusions

Studies of the interactions occurring between the Bryces Farm cats were more extensive and therefore the analysis was more complex, further complicated by the very variable attendance of different individuals and different dyads at the study site. However, despite this, it must be noted that no agonistic behaviour was recorded at Bryces Farm between any cats.. Macdonald *et al.* (1987) also found aggression to be rare between adult members of the study colony. At Bryces Farm also, no sexual behaviour was evident during the course of this study, confirmed by the absence of new kittens. Oestrus females were not observed. This may account for the lack of agonistic behaviour, particularly between male cats. However, several litters of kittens were born at *Treeside* (see Chapter 2 for site descriptions) but as explained earlier, access to this site was very restricted and it was not possible to record interactive behaviour. In fact, many elements of cat behaviour

observed by Brown (1993), and Kerby and Macdonald (1988) were not observed in the Bryces Farm colony. It is hypothesised that with no breeding females at Bryces Farm to defend or monopolise, agonistic behaviour between the males would not have been necessary. However, at *Treeside*, the presence of six reproductively-active females could well have incited aggression among the males. Although, as stated earlier, access to this property was very limited and interaction data not collected, disputes between male cats involving defence of females would most likely have been heard, if not seen, unless the contesting male backed down with little persuasion from the aggressor.

Males: In summary, the interactive behaviour of the four males may be described as follows.

BM1 interacted with BM2 and BM3 at a lower frequency than expected, and with BM4 at a higher frequency than expected.

BM2 did not interact with BM3. His interactions with BM4 were slightly lower in frequency than predicted.

BM3 interacted with BM4 at a higher frequency than expected.

BM4's interactions may be concluded from the above.

BM1 and BM4 were highly mobile, interactive cats. However, despite having home ranges encompassing the whole of Bryces Farm and continuing down the lane leading from the farm (see Chapter 3 for details of home ranges), interactions with the two less mobile males BM2 and BM3 were less frequent than expected for BM1. On the whole, BM4 was more interactive than BM1. BM1 was noticeably absent from the study site for considerable periods, during which time he was not located. It is impossible to say for certain whether or not BM4 followed the same pattern as he was not radiotracked; sightings were therefore occasional and dependent on habitat visibility. Also, the risk of missing less frequented parts of the home range is higher when range size is based only on sightings (Liberg *et al.*, 2000).

The two, relatively sedentary males BM2 and BM3 did not interact with each other but remained in their respective CRAs. It appears that interactions only occurred between them and BM1 and BM4 because the latter two were frequently mobile, and their territories encompassed both BM2 and BM3's.

To summarise the above, of the four Bryces Farm males, two (BM2 and BM3) were philopatric of their respective CRAs, and avoided each other, although they displayed no obvious active defence mechanisms against each other. However, they were undoubtedly aware of each other's presence. They were not matched in terms of size and age (BM3 being both considerably larger and older), and the results from Chapter 5 will determine whether reproductive success was a factor distinguishing them. BM2 and BM3 did not, however, avoid the other males. In addition, both males were highly interactive with females and had overlapping home ranges with them. Despite this affiliation with females, neither male appeared to leave their respective CRAs in order to seek further females.

BM1 and BM4 ranged throughout the territories of the non-ranging males. BM4 was very interactive, particularly with BM3. Both BM1 and BM4 were matched in terms of age and size, and both ranged around females. The results from Chapter 5 will determine how successful these liaisons were.

In terms of the quality of interactions between males, with the exception of BM2:BM4, interactions were far more Affiliative than actual Contact being made. Based on age and coat colour, it is highly likely that BM4 was the father of BM2, which *may* account for a higher degree of Contact behaviour between these two males. However, a literature search failed to find any evidence to support this: it is not known for male domestic cats to show parental care in any form to their adult offspring.

After the premature death of BM2, no obvious differences were noted in the quantity of interactions occurring between the surviving male dyads. BM1 continued to interact with BM3 at a lower frequency than expected, while BM3 continued to interact with BM4 at a higher frequency than expected.

In terms of quality, Affiliative interactions between BM1 and BM3 were observed twice as often as the other categories. BM1 and BM4, the two more nomadic cats also interacted largely more affiliatively with each other. It should also be noted that these two cats fed less together but spent considerably more time watching each other. BM3 and BM4 were very affiliative towards each other in their interactions, and also were frequently observed sleeping or sitting in close proximity to each other.

Males with females: BM1 interacted with the females at an expected frequency. BM2 only interacted with BF1. This female did not range from the piggery section. BM3 interacted extremely often with BF2 and BF3, although less so with BF4 and rarely with BF1. In order for him to interact with BF1, one or both of the dyad would have had to have left their respective CRAs, as their home ranges overlapped only very slightly. BF4 was, on the whole, very interactive with the females, although less so with BF4. In terms of quality, BM2 and BF1 exhibited more Contact behaviour than Affiliative; from this observation it may be that BM2 was more inclined to seek close contact than the other cats. The dairy barns were noticeably warmer than the piggery barns due to the milking machinery; this fact, although tenuous, may play a role in interpreting this observation.

Following the death of BM2 and the disappearance of BF1, no noticeable changes in interactive behaviour were observed between the remaining males and females.

Females with females: In brief, the social structure of the females was as follows. BF1 remained in the piggery section and did not interact with the other females. The other three females (BF2, BF3 and BF4) were philopatric to the dairy section, and interacted with each other frequently and amicably at all times. BF3's high ratio of presence was due to her disability caused by a traffic accident, mentioned in Chapter 2. Of all the Bryces Farm cats, she was the least afraid of humans and could be considered to be semi-tame. In terms of quality, BF3 exhibited more Affiliative than Contact behaviour with her conspecifics females, whereas BF2 and BF4 engaged in more Contact than Affiliative behaviour with each other.

Figure 3.18 (in Chapter 3) represents a summary graphic of home range in the Bryces Farm cats; it is therefore also an indication of interactions recorded between the cats.

Previous studies of dominance in farm cats (e.g. Liberg *et al.*, 2000) suggest that dominant cats have larger home ranges than cats thought to be subdominant, although this is not necessarily always the case. On Bryces Farm, the males almost certainly held different statuses within the colony, demonstrated by the different relationships held by the females with the different males. Could BM1, for example, be considered dominant due to his large home range which exceeded the boundaries of the study area, and his consequent infrequent attendance in the study area, and his complete inclusion into his home range of the ranges of the two possibly subdominant males BM2 and BM3? However, he showed an apparent

subdominant attitude to the females in terms of the quantity and quality of his interactions with them compared to BM3, who himself had a much smaller home range but a much higher attendance rate. The females sharing BM3's home range showed a preference for interacting with him – this in itself may be a measure of dominance.

Brown (1993) found that dyads present together for less time interacted at a higher rate than those together for longer. This implies that interactions may occur more intensely between cats which have not encountered each other for some time. However, in this study, this conclusion could not be drawn. In addition, the results from Chapter 5 will allow investigations into the possible effects of relatedness on interactions between cats, and will distinguish between the breeding and non-breeding males. Kerby and Macdonald (1988) categorised breeding and non-breeding males according to four main factors: observational copulation with or without intromission, presence at study site, proximity to other cats and rate of interaction when present. Actual measures of reproductive success (Chapter 5) will obviously add a major dimension to these categories.

Overall, it can be concluded that the Glebe Farm, and in particular the Bryces Farm colonies had social structures and were not simply aggregations (as suggested by Laundré, 1977) or *ad hoc* collections of animals exploiting resource-rich habitats; interaction frequencies were not purely a function of simultaneous presence in the study areas and therefore opportunity for interaction.

CHAPTER 5: REPRODUCTIVE SUCCESS

5.1 Introduction

Molecular techniques have enabled behavioural ecologists to reassess mating systems from a genetic perspective. Although parentage assessments for many species are often apparent from field observations (Denny *et al.*, 2002), this method alone is not sufficient to draw conclusions about species such as feral cats which exhibit promiscuity on the part of both sexes, multiple paternity, and communal rearing of kittens. The mating system of the cat has been detailed in Chapter 1: this system is not monogamous and no obvious pair-bonding is seen. Furthermore, males show no parental care towards their offspring. It is therefore impossible to identify father-offspring relationships purely from observational methods, unless breed or coat colour genes give definitive results without the need for DNA testing (see Wright and Walters, 1981). This was not the case for the Glebe and Bryces Farm cats.

Estimations of genetic kinship are a prerequisite for understanding the behavioural and ecological interactions occurring within animal societies (Gompper and Wayne, 1996).

This study focuses on male reproductive success. Although many of the mother-offspring relationships were previously known from observation, the genotyping results for the adult females were analysed in addition to the males. This sought to test the reliability of the genotyping methodology (i.e. where the outcome was already known). Females have the added complication of often engaging in communal reproduction, raising their kittens in a crèche system shared by other kittens and attended by the various adult females. Often, all the adult females exhibit allosuckling and allogrooming of the kittens, even females who have not given birth, thus making it very difficult to identify mother-offspring relationships by observation alone. Furthermore, kittens may be abandoned by their mothers for a variety of reasons such as age and experience (both too old and too young), disease/death of the mother and/or disturbance of the mother; these kittens are sometimes adopted by other females.

To minimise the risk of abandonment of the kittens, heavily pregnant or lactating females were not disturbed or followed during this study, and neonate litters at

known locations were not approached. Therefore, parturition was not observed, and any subsequent cross-fostering of kittens was not always known from its initiation.

The results of this chapter will enable reproductive success, measured in terms of the number of kittens sired by the individual adult males, to be accepted or rejected as an attribute of dominance in cats. Contrary to most of the literature, De Young *et al.* (2002) suggested that dominant males do not necessarily have greater paternal prowess (see also Yamane, 1998).

5.2 Methods

Many of the adult cats at both farms were trapped previously for radiotracking purposes as outlined in Chapter 3, and hair samples taken at that time. For this chapter, efforts were made to obtain hair samples from all remaining cats, including kittens born during the study period. Tables 5.1 and 5.2 show the final identification of the cats trapped for radiotracking and/or microsatellite analysis. The coding system has been explained in Section 3.2.3.

A total of 49 cat hair samples and two cat tissue samples were sent, on dry ice, to Lark Technologies Inc., Houston, Texas, USA, for genotyping. Of the 49 hair samples, 19 were from Glebe Farm cats and the remaining 30 were from Bryces Farm cats. The two tissue samples were also from Bryces Farm cats (taken from carcasses discovered on the farm. One of these dead cats (BF32) had been previously trapped when alive (BF5), and a hair sample taken at that time). The following paragraphs (Sections 5.21-5.23) describe work carried out by Lark Technologies Inc.

Table 5.1: Glebe Farm cats

	ID	Main colours
Adults	GM1	White and black
	GM2	Black
	GM3	Black
	GF1	Grey tabby
	GF2	Blue
	GF3	Orange tortoiseshell
Juveniles/kittens	GM14	Black
	GM15	Orange tabby
	GM17	Black
	GM19	Black
	GF7	Black
	GF8	Black
	GF9	Black
	GF10	Black
	GF11	Tabby
	GF12	Orange tabby
	GF13	Black
	GF16	Black
	GF18	Tabby

Table 5.2: Bryces Farm and *Treeside* cats

(*T*) indicates *Treeside*

	ID	Main colours
Adults	BM1	Cream, orange points
	BM2	Grey and white
	BM3	Orange tabby
	BM4	Grey and white
	BF1	Dark tortoiseshell
	BF2	Orange tortoiseshell
	BF3	Tortoiseshell
	BF4	Orange tortoiseshell
	BF9 (*T*)	Tortoiseshell
	BF10 (*T*)	Tortoiseshell, calico
	BF11 (*T*)	Soft tortoiseshell
	BF12 (*T*)	Soft tortoiseshell
	BF13 (*T*)	Black and white
	BF14 (*T*)	Tortoiseshell
	BF15 (*T*)	Grey
Juveniles/kittens	BM8	Grey and white
	BM16 (*T*)	Orange tabby
	BM18 (*T*)	Black
	BM19 (*T*)	Grey and white
	BM21 (*T*)	Cream and white
	BM26 (*T*)	Grey
	BM27 (*T*)	Cream and white
	BM30 (*T*)	Black
	BF5	Cream, orange points
	BF17 (*T*)	Black and white
	BF20 (*T*)	Grey
	BF22 (*T*)	Blue tortoiseshell
	BF23 (*T*)	Grey
	BF24 (*T*)	Grey
	BF25 (*T*)	Black
	BF28 (*T*)	Grey tabby
	BF29 (*T*)	Grey tabby
	BF31	Grey and white (found dead)
	BF32	Cream, orange points (found dead: = BF5)

5.2.1 DNA extraction

DNA was extracted using a Qiagen kit, following the protocol for the isolation of genomic DNA from nails and hair, and also a tissue protocol (for the two tissue samples). Full methods are given in the Qiagen handbooks and may be found on www.qiagen.com.

5.2.2 Primer characteristics

Table 5.3 shows the summary information on the four primer pairs (Menotti-Raymond and O'Brien, 1995) used in this study. These loci were found to be the most variable in previous studies (Horsfield, 1998).

Table 5.3: Summary of primer characteristics

Locus	No. of repeats	PCR product range (bp)	Forward primer sequence 5' to 3'	Reverse primer sequence 5' to 3'
FCA008	$(CA)_{24}$	122-148	ACTGTAAATTTCTGAGCTGGCC	TGACAGACTGTTCTGGGTATGG
FCA023	$(CA)_{17}$	127-148	CAGTTCCTTTTTCTCAAGATTGC	GCAACTCTTAATCAAGATTCCATT
FCA078	$(CA)_{19}$	188-200	TGAACTGAAGTCAGATGCTTAACC	CGGAATCAGCTATTTTTACGG
FCA090	$(CA)_{17}$	93-120	ATCAAAAGTCTTGAAGAGCATGG	TGTTAGCTCATGTTCATGTGTCC

5.2.3 PCR

PCR was performed using fluorescently labelled forward primers on the 51 DNA samples. PCR products were run on an ABI377 Automatic Sequencer (Applied Biosystems) with GeneScan 500-TAMRA internal size standards. Raw data were processed using GeneScan 3.0, and allele sizes determined using Genotyper 2.1.

5.3 Results

Many mother-offspring relationships, and littermate relationships among kittens, were known prior to the microsatellite analysis. This information can be seen in Tables 5.4a, 5.4b and 5.4c. The different columns (groups) represent known litters, or for cats which had already reached sexual maturity at the start of this study, possible litters. It should be noted that communal reproduction, which is commonly seen in farm cats and includes the communal nursing of the young, means that the kittens observed being raised together as a litter may not necessarily have been siblings, although they are likely to have been closely related. Communal reproduction has been described in more detail in Chapter 1, Section 1.4.3.

Tables 5.5a and 5.5b display the obtained genotypes in allele sizes from the four markers (loci) for the two farms. Gaps in the data indicate where DNA extraction and/or PCR failed (see Section 5.4 below).

Table 5.5a: Alleles scored for the Glebe Farm cats

Cat ID	Locus			
	FCA008	FCA023	FCA078	FCA090
GM1	116/134	136/136	192/196	
GM2	116/116	136/144	192/196	98/106
GM3	116/116			98/106
GM14		144/148	196/196	84/98
GM15	116/116	136/148		106/106
GM17	116/116	136/148		88/106
GM19		144/148		
GF1	116/134	136/148	192/196	84/102
GF2	116/116	148/148	196/200	84/106
GF3	116/134	148/148		84/88
GF7	116/116	136/148	192/196	106/106
GF8	116/116	136/148	196/200	84/106
GF9	116/134	148/148	196/196	84/84
GF10	116/116	136/148	196/200	84/106
GF11	116/116	144/148	196/200	84/98
GF12	116/134	148/148		106/106
GF13	116/116	136/148	192/196	84/98
GF16	116/116	144/144	192/192	106/106
GF18	116/134	136/144	192/196	84/106

Table 5.4a: Glebe Farm cats grouped according to age and littermates

Oldest → Youngest

1	2	3	4 born 07/99	5 born 12/99	6 born 12/99	7 born 06/00	8 born 06/00	9 born 07/00	10 born 03/02	11 born 03/02
GF1	GM2	GF2	GF7	GF12	GF13	GF10	GM15	GF16	GM17	GM19
		GF3	GF8		GM14	GF11			GF18	
		GM1	GF9							
		GM3								

Groups 1-3 (shaded): Cats present as adults at start of study and grouped according to age.

Groups 4-11: Cats born during the course of the study and grouped as littermates. Due to communal reproduction (described in Section 1.4.1), kittens raised together as a litter are not necessarily siblings.

Table 5.4b: Bryces Farm cats grouped according to age and littermates

Oldest → Youngest

1	2	3	4	5	6	7 born approx.10/00	8 born 07/01
BM4[Ψ]	BM1	BM3	BF3	BF1	BF5/B32	BF31	BM8
		BF4[Ψ]	BF2	BM2			

Groups 1-5 (shaded): Cats present as adults at start of study and grouped according to age.

[Ψ] escaped (no hair sample taken)

Group 6 (shaded): Cat present as juvenile at start of study; mother previously unknown. Later found dead: both live hair and dead tissue sample taken.

Group 7: Cat carcass discovered on Bryces Farm during study; mother previously unknown.

Group 8: Cat born during the course of the study; mother BF2.

Table 5.4c: *Treeside* cats grouped according to age and littermates

Oldest → Youngest

1	2	3	4	5	6 born 02/02	7 born 02/02	8 born early 05/02	9 born mid 05/02
BF13	BF9	BF12	BF14	BF15	BF28	BM30	BM16	BF24
	BF11	BF10			BF29		BF17	BF25
							BM18	BM26
							BM19	BM27
							BF20	
							BM21	
							BF22	
							BF23	

Groups 1-5 (shaded): Cats present as adults at start of study and grouped according to age.

Group 6-7: Cats born during the course of the study and grouped as littermates.

Groups 8-9: Cats born during the course of the study and grouped as littermates, raised communally by mothers in Groups 2-5.

Table 5.5b: Alleles scored for the Bryces Farm cats

Cat ID	Locus			
	FCA008	FCA023	FCA078	FCA090
BM1	128/130	136/136	194/198	84/106
BM2	128/134	148/148		84/106
BM3		148/148	192/196	
BM8	128/134	136/148	192/198	106/106
BM16	130/134			
BM18	116/134	136/148	196/198	106/106
BM19	130/134	136/148	194/198	106/106
BM21	116/134			
BM26	134/134	136/148	196/198	106/110
BM27	128/134		194/198	
BM30				
BF1	128/134	148/148		
BF2	134/134	148/148		
BF3	128/128	148/148		
BF5	128/130	136/148	194/194	84/84
BF9	130/130	136/136		
BF10				
BF11	128/130			
BF12	128/130	136/148		106/106
BF13		130/136		
BF14	116/134	136/148	194/198	106/110
BF15	116/134	148/148	196/198	106/110
BF17	130/134	136/148	194/198	84/106
BF20	116/134	148/148	194/198	84/106
BF22	128/134			
BF23	130/134	136/148	196/198	106/110
BF24	116/134	136/148	194/198	106/110
BF25	134/134	148/148	198/198	106/110
BF28				106/106
BF29				
BF31	134/134		196/196	106/106
BF32*	128/130		194/194	

*BF32 = BF5 (BF32 was a tissue sample; BF5 was a hair sample from the same cat).

5.4 Genotyping problems

The gaps in the data (in Tables 5.5a and 5.5b) indicate failure with either the original DNA extraction, or with subsequent PCR. It should also be noted that DNA extraction and genotyping was carried out twice, due to problems with the first analysis; many errors were discovered in the original results sent by Lark Technologies Inc. (these errors were apparent because some of the mother-offspring relationships already known with 100% certainty from observation were not recognised in the original results), and consequently the whole data set had to be rejected. It is questionable as to whether the DNA samples (hair and tissue) were kept at optimal conditions after the first analysis was completed, as at this point a second analysis had not been deemed necessary. Possible genotyping errors associated with genetic sampling have been highlighted by Taberlet *et al.*, 2001.

5.5 Methods of analyses

By visually studying the printed genotypes, manual analysis of the allele sizes was carried out based on the principle that a parent-offspring pair *must* share one allele at each locus. This analysis was further supported with the use of statistics: this helped with the acceptance or rejection of the manual results within recognised degrees of confidence (manual analysis does not take into account the overall frequencies of alleles in the sample, i.e. it does not account for the fact that common alleles are likely to be shared by individuals purely by chance, and not necessarily always by direct descent (M. Knight, pers. comm.). Statistical analysis, however, shows the actual degree of possibility, i.e. level of significance (likelihood) of a relationship).

5.6 Manual analysis

Looking manually at the data given in Tables 5.5a and 5.5b, possible parent-offspring relationships can be identified by comparing allele sizes. A mother-offspring pair must share one allele at each locus (unless mutation has occurred, which is an extremely rare event even at microsatellite loci (estimated rate of 10^{-5} - 10^{-2}; Jarne and Lagoda, 1996)). In the same way, a father-offspring pair must share one allele at each locus. For loci where data are missing, accuracy of the

likelihood of the relationship is reduced.

Among the cats which were already sexually mature adults at the time the study began but were judged as being approximately the same age, the possibility remains that parent-offspring relationships existed between them. Although dentition is a reliable method of estimating animals' ages, it is subject to human errors of judgement. Furthermore, it is biologically possible for a male cat as young as five or six months to reproduce, and females usually have their first oestrus at this age (however, Say *et al.* (1999) found that reproduction in male cats was delayed until they were three years old in a rural population, but occurred at ten months of age in an urban population). Therefore, cats previously thought to be of the same age based on appearance and dentition are nonetheless compared for parent-offspring relationships, as there is very little visible difference between adult cats only six to eight months apart in age.

For the following tables, the legend is given in Table 5.6. Possible father-offspring relationships have been identified for the Glebe Farm cats from the data given in Table 5.5a, and can be seen in Table 5.7. Offspring are shown in the far left hand side of the tables going down the rows; fathers are represented by the columns.

As this chapter is concerned with male reproductive success, mother-offspring relationship results are not included in this section, but can be found in Appendix 6.

Table 5.6: Legend relating to Tables 5.7 and 5.8

Symbol	Meaning
Blank space	No relationship found
✓	Possibility of relationship
✓*	Possibility of relationship, but missing data at one or more loci for one or both cats
*	Relationship undetermined due to missing data at all corresponding loci
a	Impossible relationship due to age of cats (younger individuals cannot be parents of older individuals, or the cats were too young to have produced offspring)
b	Impossible relationship - cat already dead/disappeared before offspring conceived

For simplicity, fathers and offspring are only shown where possibilities of relatedness occur for at least one individual father, i.e. complete rows or columns where father-offspring relatedness is impossible (Table 5.6 gives an explanation of impossible relationships), or has not been found, have been omitted.

Table 5.7: Glebe Farm father-offspring relationship possibilities (manual analysis)

Offspring	Father			
	GM1	GM2	GM3	GM14
GM3	✓*	✓*	—	a
GM14		✓*	✓*	—
GM15	✓*	✓*	✓*	
GM17	✓*	✓*	✓*	
GM19		✓*	*	✓*
GF7	✓*	✓	✓*	a
GF8	✓*	✓	✓*	a
GF10	✓*	✓	✓*	a
GF11		✓	✓*	a
GF12			✓*	a
GF13	✓*	✓	✓*	a
GF16		✓	✓*	
GF18	✓*	✓	✓*	✓*

Possible father-offspring relationships within the Bryces Farm and *Treeside* cats have been identified from the data given in Table 5.5b, and can be seen in Table 5.8.

Due to the proximity of the two study sites to each other and the lack of variability seen in the respective genotypes, possible father-offspring relationships across the two farms were also determined from the data given in Tables 5.3a and 5.3b, to see if the males from one farm ranged sufficiently during the breeding seasons to include the oestrus females of the other farm into their home ranges and successfully reproduce with them. As discussed in Chapter 1, Section 1.4.4, females are philopatric and are not thought to disperse.

Table 5.8: Bryces Farm and *Treeside* father-offspring relationship possibilities (manual analysis)

Offspring	Father		
	BM1	BM2	BM3
BM2		—	✓*
BM8	✓	✓*	✓*
BM16	✓*	b	*
BM18		b	✓*
BM19	✓	b	
BM21		b	*
BM26		b	✓*
BM27	✓*	b	
BM30	*	*	*
BF1		✓*	✓*
BF2		a	✓*
BF3		a	✓*
BF5*	✓	✓*	
BF15		a	✓*
BF17	✓	b	
BF22	✓*	b	*
BF23	✓	b	✓*
BF28	✓*	b	*
BF29		b	*
BF31		✓*	✓*

*BF32 has been omitted and BF5 data used instead (BF32 = BF5), where allele sizes were obtained for all four loci.

Table 5.9 shows the possibilities of Glebe Farm male reproductive success at Bryces Farm (legend given in Table 5.6).

Table 5.9: Glebe Farm father-Bryces Farm offspring relationship possibilities (manual analysis)

	Father (Glebe)		
Offspring (Bryces)	**GM1**	**GM2**	**GM3**
BM8	✓*		
BM16	✓*		
BM18	✓*	✓*	✓*
BM21	✓*	✓*	✓*
BM26	✓*		
BM30	✓*		
BF20			✓*
BF22	✓*		
BF23	✓*		
BF24			✓*
BF28	✓*		
BF29	✓*		
BF31	✓*		

Table 5.10 shows the possibilities of Bryces Farm male reproductive success at Glebe Farm (legend given in Table 5.6).

Table 5.10: Bryces Farm father-Glebe Farm offspring relationship possibilities (manual analysis)

	Father (Bryces)
Offspring (Glebe)	BM3
GM3	✓*
GM14	✓*
GM15	✓*
GM17	✓*
GM19	✓*
GF3	✓*
GF7	✓*
GF8	✓*
GF9	✓*
GF10	✓*
GF11	✓*
GF12	✓*
GF13	✓*

The above analysis also uncovered the following relationship possibilities, seen in Table 5.11, indicating the dispersal of juvenile or adult males from their natal farm (Glebe Farm) to the other (Bryces Farm) (legend given in Table 5.6).

Table 5.11: Glebe Farm mother-Bryces Farm offspring relationship possibilities (manual analysis)

	Mother (Glebe)	
Offspring (Bryces)	GF1	GF3
BM2	✓*	✓*
BM3	✓*	

5.7 Statistical analysis

Kinship 1.2 (Goodnight and Queller, 1999; http://www.gsoftnet.us/GSoft.html) is a programme for testing hypotheses of pedigree relationships between pairs of individuals using data from co-dominant, single-locus genetic markers such as DNA microsatellites.

The user must specify a primary hypothesis about a relationship using two variables, r_p and r_m, which define the probabilities that individuals in the dyad share an allele by direct descent from their father or mother respectively. Table 5.12 gives a list of common pedigree relationships relevant to this study, and their associated *r*-values.

Table 5.12: *r*-values for different pedigree relationships

Relationship	R_m	R_p
Father-offspring	0.0	1.0
Mother-offspring	1.0	0.0
Full sibling	0.5	0.5
Half-sibling (paternal)	0.0	0.5
Half-sibling (maternal)	0.5	0.0

Kinship 1.2 uses the overall allele frequencies, and the genotypes of the two individuals under consideration to calculate the likelihood that this genotype combination could have been produced by the relationship as specified. For this study, the input files were presented as shown in Table 5.5a and 5.5b. These tables were combined, due to the proximity of the two study sites to each other and the lack of variability seen in the respective genotypes.

The primary hypothesis and a corresponding null hypothesis are selected, and *Kinship 1.2* calculates the ratio between them (primary:null). A high ratio favours the primary hypothesis and a low ratio rejects it in favour of the null hypothesis.

Significance levels do not correspond to likelihood ratios in a simple way: as the size of the data set increases, the ratio needed to obtain a significant result decreases (Horsfield, 1998). The user is given the option of choosing how many simulated pairs *Kinship 1.2* will generate in order to find the significance levels.

The significance of levels of likelihood ratios are calculated empirically through simulations using the allele frequencies in the data set (input file). The likelihood ratios required to exclude randomly generated null pairs, under the specified hypotheses, at 0.05, 0.01 and 0.001 levels of significance are calculated. Then, the proportion of randomly generated pairs that match the primary hypothesis, but are excluded at the likelihood ratios for each significance level, are reported as the Type II error rate (rate of false rejection of the primary hypothesis) (Queller and Goodnight, 1989).

The default value for the number of pairs to simulate is 1,000, which represents a compromise between speed of calculation and precision of results (M. Knight, pers. comm.). This value can be increased the improve the precision of the appropriate ratio.

For the analysis used in this study, a significance flag was reported instead of the actual numerical ratio, i.e. NS = not significant; * for $p < 0.05$; ** for $p < 0.01$; *** for $p< 0.001$.

Results were output in a symmetrical matrix and saved to a tab-formatted text file which can be read by a spreadsheet programme such as Microsoft Excel.

It should be noted that for the purposes of this chapter, males and females were not differentiated when inputting data for *Kinship 1.2*. This is due to the relatively small samples sizes and variability, and means that the same matrix results were obtained for both mother-offspring and father-offspring, and may therefore be categorised as parent-offspring.

5.7.1 Paternity results from *Kinship 1.2*

Parent-offspring: for 1,000 and 500,000 simulated pairs

Population contains: 51 individuals and four loci; there are six alleles at the most polyallelic locus. Allele frequencies calculated from individuals. There is one group with 51 individuals in the largest group.

Settings for primary hypothesis:

Rm: 0.0

Rp: 1.0

Settings for null hypothesis:

Rm: 0.0

Rp: 0.0

The results can be seen in Table 5.13, and the actual output for 500,000 simulations is shown in Appendix 7.

Table 5.13: Results of significance simulations: parent-offspring

	p <	1,000 simulations		500,000 simulations	
		Ratio	Type II error	Ratio	Type II error
*	**0.05**	5.77+00	0.519	4.98+00	0.460
**	**0.01**	1.56E+01	0.805	1.26E+01	0.758
***	**0.001**	6.95E+01	0.973	3.79E+01	0.935

5.7.2 Summary of paternity results from *Kinship 1.2*

Again, complete rows or columns where father-offspring relatedness is impossible (Table 5.6 gives an explanation of impossible relationships), or not found, have been omitted.

Table 5.14: Glebe Farm father-offspring relationship possibilities from *Kinship 1.2*

Offspring	Father			
	GM1	GM2	GM3	GM14
GM1	—	*		a
GM3		**	—	a
GM14		**	*	—
GF7	*			a
GF11		***		a
GF13	*	**	**	a
GF16		***		
GF18	*	*		*

Table 5.15: Bryces Farm and *Treeside* father-offspring relationship possibilities from *Kinship 1.2*

Offspring	Father	
	BM1	BM2
BM19	*	
BM27	*	
BF1		*
BF3		a
BF5	***	
BF9	a	a
BF12	a	a
BF17	**	
BF32	**	

5.8 Discussion

For Glebe Farm, manual analysis suggests that all three adult males (GM1, GM2, GM3) were reproductively active, plus one male (GM14) who was born during the study period and matured to adulthood (Table 5.6). For many offspring, there is more than one possible father identified (see below for the reasons for this). However, after three years of observational work, these results can be disputed in favour of one male, GM2. Whilst mating behaviour was not observed in any of the Glebe Farm males during the study period, GM3 in particular gave no indications whatsoever that he was reproductively active, from his general behaviour and that directed towards the females. GM1 similarly gave cause to doubt his reproductive potential, though to a lesser extent than GM3. GM14 did however, behave as a normal, reproductively active male, though was much younger than the aforementioned males. The remaining male, GM2, was consistently the preferred candidate for paternity of most, if not all, of the kittens born at Glebe Farm during the study period, due to his superior age, size, home range and behaviour towards the other cats. Although it is not possible to state paternity categorically on the basis of observation, it is *likely* that this hypothesis is correct.

Therefore, the results from *Kinship 1.2* seen in Table 5.14, which support the hypothesis of GM2 being the most likely father for many of the offspring, may be accepted.

On Bryces Farm and *Treeside*, much the same scenario has resulted from the manual analysis, with more than one possible father identified for many of the offspring (Table 5.8). With regard to the more realistic possibilities of BM1 and BM3 (BM2 was much younger and smaller, never observed outside a small core area, and only seen interacting with one female, BF1), as discussed in Chapter 4, both BM1 and BM3 interacted with the Bryces Farm females, but BM1 alone was observed at *Treeside*. However, the manual analysis indicates that BM3 may have indeed been reproductively active with these females. Although this seems unlikely, this hypothesis cannot be ruled out. Furthermore, the wide-ranging BM4 (see Chapter 3) was not genotyped, but based on coat colour is likely to have fathered some of the kittens during this study.

Interestingly, *Kinship 1.2* does not support the hypothesis that BM3 has fathered any kittens belonging to either the Bryces Farm or *Treeside* females, and supports BM1 as the most reproductively successful male. As stated earlier, BM4 was not genotyped, so is not included in this analysis, but he was frequently observed interacting with Bryces Farm females, and ventured close to *Treeside*. He may well have also interacted with the *Treeside* females and had high mating success (this is supported by coat colour gene observations).

As stated in Chapter 3, BM2 and BM3's ranges were not observed to overlap. The degree of range overlap is thought to be determined by kinship (Langham and Porter, 1991; Barratt, 1997); this is supported by their apparent lack of relatedness, seen in both coat colour and by running *Kinship 1.2* for sibling analysis (results not shown).

Discrepancies between the two methods used for calculating paternity, i.e. manual analysis and *Kinship 1.2*, are highlighted by comparing Table 5.7 with 5.14, and Table 5.8 with 5.15 for Glebe and Bryces Farms respectively. For both data sets, possible father-offspring relationships are not identified by both methods for every individual; in general, more possible fathers are identified manually than by using *Kinship 1.2*. The necessity of statistical analysis is outlined in Section 5.5.

Due to missing genotyping data, where DNA extraction and/or PCR failed, many possible relationships remain uncertain. Also, the cat populations studied show low variability at a reasonably low number of loci, factors which limit the effectiveness of *Kinship 1.2*. Low variability is to be expected in a group-living species where the females are philopatric and thus form closely-related breeding groups. Also, in

such a promiscuous, relatively high-density population, there is a lack of resource defence by males resulting in low male dispersal, again reducing variability. The data strongly indicate inbreeding, although this may not necessarily cause detrimental effects to the offspring; Devillard *et al.* (2003) reported *low* costs of inbreeding in cats.

It is evident that not every individual cat in this study has been assigned a possible father. This is due to the following reasons. Firstly, it was not possible to genotype every cat. Although trapping was carried out intensively at both farms, the possibility remains that some cats were simply not trapped. This is supported by the fact that some cats were occasionally seen (in some cases, only once) on the farms but never trapped. These cats disappeared during the course of the study, but their initial sighting was noted (see Chapter 3; also Chapter 2, Section 2.7 for reasons for disappearance). Two of the trapped cats at Bryces Farm escaped before hair samples could be taken, and were never recaptured. It should also be mentioned that some of the fathers of the study cats may simply have died or disappeared altogether from the study area, particularly the fathers of the older cats.

Secondly, the possibility exists that male cats visited Glebe and Bryces Farms' females when in oestrus and mated successfully with them, but were never seen by the observer. As outlined in Chapter 3, observation was not carried out continuously (i.e. 24 hours a day, every day) during the study period and night vision equipment was not available. Although the farmers and farm workers at both farms were asked throughout the study to note the presence of any unfamiliar cats, the possibility remains that such cats were missed. The fact that these non-resident cats were apparently securing matings is a focus of this study, highlighting the hypothesis that resident males do not necessarily enjoy supreme reproductive success within their territories (Liberg and Sandell, 1988).

As indicated in Chapter 2, Glebe and Bryces Farm are situated only a few kilometres apart. Manual analysis (not supported by *Kinship 1.2*) has shown that the two farm populations share alleles, and may indicate interbreeding between the two farms. However, in a truly interbreeding population, differences in allele frequencies between the two farms would not have been expected; Glebe and Bryces Farm appear to be separate populations. In domestic pet cats, the most obvious mechanism for gene flow is human-mediated dispersal. Horsfield (1998) found that 67% of pet cats in his study area (city of Southampton) were brought in

from another region of the city or further away. Neutering rates are extremely high among pet cats (Southampton: males 96.8%; females 98.7% (Horsfield, 1998)). The local surveys carried out (see Chapter 2) in the environs of Glebe and Bryces Farm support these figures: in fact, of all households responding to the questionnaire, no entire pet cats were found which could be contributing reproductively to the feral population. As with most wild terrestrial animals, feral farm cats are never introduced from distant gene pools in this way, and their reproductive behaviour is not under human control. Gene flow is thus limited and the cats of Glebe and Bryces Farm were expected to have been closely related; this is not supported by the genotyping data.

The results of manual analysis and *Kinship 1.2* also highlight the errors of previous authors in assuming parenthood of kittens based on apparent littermates. This study has shown that kittens raised together as littermates are not always siblings, although they are usually closely related. One elderly Glebe Farm mother (GF1) frequently abandoned her kittens to the care of her daughter with her own litter, yet allosuckled all the kittens and was often found acting as "babysitter" whilst her daughter left the nest to find food (see also Roulin, 2002). With other females this behaviour was not observed, but microsatellite results have shown this to be the case, with apparent littermates having different mothers as well as fathers.

It is difficult to categorically state whether or not multiple paternity occurred within litters of the Glebe and Bryces Farm cats (again due to missing genotyping data), but there are certainly indications of this behaviour from these data, as many littermates were found not to be full siblings.

CHAPTER 6: GENERAL DISCUSSION

Most studies of dominance involve individuals competing vigorously for high-ranking status, which then determines their priority of access to receptive females and other contested resources at a later time, such as food and den sites; in other words, dominance is thought to correlate positively with fitness (Dewsbury, 1982; Kaufmann, 1983; Ellis, 1995). However, in practice it is difficult to prove that dominance provides priority of access to a resource which actually does increase fitness (Kaufmann, 1983), and indicators of dominance itself are often based purely on observation and are not, therefore, measured. This study has attempted to clarify these points in a group-living, free-ranging carnivore, the feral farm cat *Felis silvestris catus*.

In this final chapter, a brief revision of preceding chapters will be given. The results of the experimental chapters 3, 4 and 5 will be summarised before all chapters are linked together, in order to reconsider and discuss the original title of the study: *Behavioural aspects defining male dominance in feral farm cats*. Suggestions for future work are made.

Chapter 1 provided an in-depth and overall introduction to the study species, *Felis silvestris catus*, in terms of its evolution, ecology, history and social behaviour.

Chapter 2 comprised an introduction to the animals studied, and included detailed descriptions of the study sites of Glebe and Bryces Farm.

Chapter 3 was a study of home range. Was the size of an individual male's home range linked to his age, health and body size? For both Glebe and Bryces Farm, it would appear that this was the case. On Glebe Farm, cat GM2 was certainly considerably older and larger than his conspecific males GM1 and GM3, and overall, ranged much further than them. Healthwise, however, GM2 and GM3 were both diagnosed as being positive for FIV. Without an intrusive clinical examination, it was not possible to determine how advanced the infection was in these two cats, although GM3 was in a poorer overall body condition, and displayed signs of neurological malfunction (which may be associated with advancing FIV infection). Despite his FIV status, throughout this study GM2 was considered an extremely healthy and robust individual, displaying no outward indications of any of the symptoms associated with an advancing FIV infection. His comparatively larger

overall home range over the other two males may therefore indeed be an indication of his superior age, size and health; body condition is a major component in the ability to compete for resources and sexual partners (Devillard *et al.*, 2003). However, GM2's home range did not appear to be larger than that of the other males in *every* temporal and/or seasonal category, with diurnal ranges being generally the most unremarkable category for the three males. It should also be noted that soon after this study ended, GM2 left the core of Glebe Farm and moved a few hundred metres across the main road to the grounds of a small garden centre with adjoining house, where he gradually became a little tamer and ventured into the house itself, despite the existing presence of three pet neutered cats (two females and one male) and a dog. GM2 was later castrated at the request of the garden centre owner, and at the time of writing, has adapted well to domestic household life and remains fit and healthy. The main point to be taken from this information is that despite his apparent superiority over the other Glebe Farm males in terms of home range, age, body size and health, he may have been approaching his "peak" during the study and has since been usurped by another male.

During the study, GM2 regularly left the boundaries of Glebe Farm and travelled to neighbouring farms and even to a cattery, whereas GM1 and GM3 remained within a much smaller area on Glebe Farm. There was no indication whatsoever that GM2's tendency to leave the core of his home range was due to his being driven out by the other cats, or as a means of avoiding confrontation altogether, because no aggressive encounters of this nature were observed during the study period. He also spent a considerable amount of time in close, amicable (i.e. non-agonistic) contact with other members of the Glebe Farm colony including the males. It may be concluded that as a heavier, older and healthier male, he enjoyed a larger home range (greater resources) than the other males. Whether or not his greater access to resources than the other males meant that GM2 also enjoyed higher reproductive success than the other males, remains to be discussed.

Cat GM1, although not diagnosed with FIV, did not range far. He was the only male with a preference for resting inside the farmhouse, and would accept a degree of handling and certainly feeding by the farmer. As a result, he benefited from regular titbits. The possibility remains that GM1's most important resources took the form of food and shelter, although for an entire young male cat this seems an unlikely explanation for his comparatively small home range. Instead, he may have

maximised his reproductive success purely with the females in his core range, and not sought such resources elsewhere. This will be explored further below.

On Bryces Farm, the two largest and oldest males were BM1 and BM4. BM4 was not radiocollared although a home range was estimated from visual sightings. He was in slightly better overall condition than BM1, but this may have been due to his popularity with some of the farm workers (he was the only cat they had named), who occasionally left him titbits. BM1 on the other hand, remained aloof and fearful of humans, despite spending considerable time at *Treeside*.

BM1, for whom radiotracking data *are* available, ranged much further overall than his conspecific males, including extended periods when he could not be located, indicating he was out of range and thus considerably far from Bryces Farm and its environs. He tested positive for FIV, but, as with GM2, displayed no obvious symptoms of the disease. He remained a large and apparently healthy male throughout the study period.

Unlike GM2, whose home range was significantly larger than that of the other Glebe Farm males for many of the different temporal and/or seasonal categories analysed, BM1's home range was not usually found to be larger than that of BM2 and/or BM3 when broken down into categories. Similarly, there were far fewer range size differences in BM1's individual (i.e. when not being compared with the other males' ranges) temporal and seasonal comparisons than for GM2. However, due to the periods when BM1 had travelled so far so as to be out of radiotracking range, it is safe to say his home range *was* significantly larger than that of the other radiotracked males.

When within radiotracking range, BM1 spent much time at *Treeside* where an all-female colony of adult feral cats resided. The owner of the smallholding generally sold any kittens born to these females to customers from outside the area, and so the size of this colony was not regulated naturally. The other Bryces Farm males BM2, BM3 and BM4 were not observed at this location, although BM3 in particular was observed more frequently than BM1 in the presence of the resident Bryces Farm females. This may indicate some kind of mutually agreed female resource allocation by the males (whereby BM1 did not enjoy greater reproductive success with *all* the females within his range), as BM1 was the only male with exclusive sections within his range; all other males had ranges which overlapped with that of at least two other males (see Chapter 3, Figures 3.10 and 3.18), but no territorial

aggression or defence of the females was observed among the Bryces Farm males. This is an interesting concept and will be explored more fully in the context of the paternity studies discussed below.

However, the main conclusion from the Bryces Farm home range study almost mirrors that of the Glebe Farm cats: the older and larger males had the greater home ranges. However, these wider-ranging males were not definitively the healthiest: BM1 was FIV-positive and of poorer body condition than the much smaller-ranging FIV-negative BM3, although BM1 was certainly not considered to be in poor condition or showing visible signs of illness.

A greater home range did not necessarily indicate greater activity levels. Seemingly, several of the males were equally active in their smaller ranges as those ranging further. However, as explained in Chapter 3, the activity sensors in the radiocollars were triggered by head movement caused by behaviours in addition to actual movement over distance; for example grooming, which is performed with the cat in a resting state. Other behaviours causing motion such as fighting and mating are generally not quietly performed activities by cats, and for the most part such noise would have been heard whilst radiotracking. Therefore, it may be safely hypothesised that the behaviours most likely to trigger the activity sensors were actual physical movement of the cat over distance, grooming and eating.

Lindstedt *et al.* (1986) found that in carnivore species, home range was linearly proportional to body mass. In this study, although the relationship between home range and body size of the cats was not categorically linear, there was a definite positive correlation between the two. Home range size correlates directly to prey availability for many carnivore species (see Fuller and Sievert, 2001); this was not thought to apply to study cats benefiting from human-mediated food resources, but is an area for further research.

Fisher and Lara (1999) found that home range in male bridled nailtail wallabies influenced the number of associations with oestrous females, and was a significant component of reproductive success. The following chapters explore this possible link and its connection to dominance.

Chapter 4 looked at the social dynamics of the colonies. By analysing dyadic interactions among the cats, it was hoped that a hierarchy of social relationships

would emerge, and dominant individuals would be identified: Kaufmann (1983) suggested that social interaction eventually provides priority of access to resources.

These hierarchies do not involve only male:male interactions, but instead the males' quality and quantity of interactions towards all other colony members serve cumulatively in the construction of such a hierarchy.

In a study of domestic pet cats, Curtis, Knowles and Cromwell-Davis (2003) found that familiarity and relatedness were significantly associated with allogrooming and proximity of another cat. The results of Chapters 4 and 5 may therefore be linked.

For the Glebe Farm males, the oldest, largest and widest-ranging male GM2 appeared to exhibit tolerance bordering on actual avoidance of the other males. Occurrences of aggression between the Glebe Farm males, and in particular between GM2 and the other males were extremely low, despite overlapping home ranges (seen in Chapter 3) and the presence of reproductively active females. In other words, GM2 did not appear to defend, in any way, his apparent wealth of resources (compared to that of the other males), evident by his far greater home range which is assumed to have encompassed other reproductively-available females, and general body size. A strong possibility remains that disputes regarding such resource defence were settled before this study began. This is supported by GM2's scarred ears and face, and FIV-positive status (FIV is most commonly spread in males by saliva, i.e. bites (E. Abraham, pers. comm.)). However, the absence of scars on either GM1 or GM3 implies that GM2's battles were fought against other males, and there may have been subtleties to his body language, not evident to humans, which, together with GM1 and GM3's size and age disadvantages, prevented them from challenging GM2.

GM1 and GM3 on the whole showed positivity towards each other, existing fairly amicably in almost-completely overlapping home ranges.

In conclusion, for the Glebe Farm males, it would appear that the small-ranging, younger and lighter males maintained equal ranking with each other, but there is evidence to suggest a hierarchical difference between them and the wide-ranging, older and heavier GM2. GM2 was not observed actively defending his position against the other males at Glebe Farm, but instead may have done so simply by adopting an avoidance strategy. On many occasions throughout this study and in observations of pet cats, males in particular have been seen to actually move out of

sight rather than risk being seen by another cat, thus avoiding potential conflict. Also, cats will watch each other for long periods without apparent threat or intimidation but rather with a degree of mutual tolerance. Such techniques of passive supplanting and avoidance indicate stable hierarchies; actual fights are more likely to indicate disputed status (Kaufmann, 1983).

The males tended to interact with the females in proportion to the time they were present in the farmyard. GM2 rarely fed with females, but was most likely to sit/sleep in contact with them; GM1 was rarely seen in contact with any female. Similarly, in proportion to the time spent in the Central Resource Area (CRA), GM2 was significantly more likely to interact with kittens than were the other two males. His interactions were predominantly sitting/sleeping in contact, whereas GM1 tended to feed with, rather than sit with, the kittens.

For Bryces Farm, where a more intensive study of interactions was carried out, more detailed conclusions may be drawn. Aggressive interactions were not observed during the study period, and all the males' home ranges overlapped with each other in part, if not completely (Chapter 3). It should be noted that there was a distinct lack of successful breeding on Bryces Farm during the study period, thus reducing the need for male:male competition. Despite this, not all of the Bryces Farm males were observed ranging as far as *Treeside* in search of oestrous females, which in itself implies a hierarchy existed among the males and questions the Resource Dispersion Hypothesis (RDH; Macdonald, 1983); these males are not defining their home ranges on the basis of available resources (i.e. females). However, the absence of observed mating behaviour and birth of kittens does not categorically imply a lack of oestrous females on Bryces Farm; observations of oestrous periods may have been missed and pregnancies may have failed in their early stages. This is supported by the observation (Chapter 3, Section 3.7.2) of an apparently pregnant female which is assumed to have miscarried later.

With the exception of one male (BM2), all Bryces Farm males interacted with all Bryces Farm females within their overlapping home ranges, but some did more than others and there was no indication of competition. Furthermore, the only male (BM1) with exclusive areas within his range (i.e. range included areas of no overlap with other male ranges) had apparently exclusive rights to the females within this section (*Treeside*), although this was investigated fully by paternity studies (Chapter 5). However, this male was never observed exerting mating rights over the other males on account of the Bryces Farm females; these other

males in fact interacted frequently with the females. In conclusion, it is evident that a pre-determined hierarchy existed among the Bryces Farm males (Leyhausen, 1979; Fisher and Lara, 1999). The older, heavier, wider-ranging males (BM1 and BM4) had access to more females than the younger, lighter, smaller-ranging males (BM2 and BM3), but yet did not monopolise all the females in the study area by active defence. In other words, some males were "satisfied" by their apparently unhindered access to the resources available in a smaller home range, whereas other males ranged further and encountered further resources *in addition* to those available (and shared) in their core areas. These latter males are therefore assumed to hold a higher rank than those males remaining in the core areas. A hierarchy must therefore have come into existence before this study began, which would explain the lack of agonistic behaviour observed during the study period.

Chapter 5 investigated the third factor thought to influence dominance: reproductive success. Dominant animals are assumed to have greater overall reproductive success (Smith, 1993; Ellis, 1995). Chapters 3 and 4 sought to identify dominant cats on the basis of age, body size, home range and social interactions; Chapter 5 introduced the additional factor of reproductive success, as the males fathering the most offspring are assumed to have exerted some form of dominance over the other competing males.

Using microsatellite analysis of DNA obtained from hair samples, it has been possible to qualify and quantify reproductive success. Previously, most studies of reproductive behaviour in cat colonies have identified fathers based on observations of courtship and time spent with oestrous females, as well as copulatory behaviour (see Chapter 1, Section 1.5.2). However, these behaviours may not always result in successful reproduction. This study has also highlighted the problems regarding assumed maternity of kittens. The concept of communal nursing in cats has been discussed in Chapter 1, Section 1.4.3, stressing the need for DNA analysis in order to correctly assign maternity, but in addition, this study has shown that even in instances where only one mother is in evidence, the kittens in her litter may not all be hers, and instead may include the abandoned offspring of her relatives. Therefore, littermates may not be full-, or even half-siblings.

The findings of Chapter 5 indicated that at both Glebe and Bryces Farm, one male appeared to monopolise breeding, although it must be stated, not completely (see below). At Glebe Farm this was GM2, who fathered more kittens than the other males. He was also older, larger and heavier than the other males, ranged much

further than them (Chapter 3) and appeared to rank higher than them (Chapter 4). At Bryces Farm, BM1 mirrored this role, although possibly closely shadowed by BM4 (for whom DNA was unfortunately not obtained, but a good estimate of home range and social interactions was calculated from observation). Similarly, BM1 was older, larger, heavier, wider-ranging and apparently higher-ranking than the other males.

This monopolisation of females by GM2 and BM1 was not absolute. Some offspring were apparently fathered by the younger, smaller, lighter, smaller-ranging and lower-ranking males, and for other offspring no father has been identified from the Glebe or Bryces Farm cats. Both these situations need further discussion.

In his study of cat mating systems, Liberg (1983) identified a central male who completely monopolised mating opportunities. He remained with the female whilst she was receptive and then often moved off to another group of females in oestrus, leaving the subordinate males to copulate with any other females coming into oestrus. In contrast, Natoli and Devito (1987, 1988) found no central male but ranked all males equal in terms of access to the females (although the authors claimed that not all males achieved intromission). However, neither of these studies involved the use of DNA analysis.

However, the Glebe and Bryces Farm males' strategies are consistent with those of the males studied by Yamane (1998). He also identified a heavier, more "dominant" male who mated successfully (qualified using microsatellite analysis) within his own colony as well as ranging further and mating successfully with unfamiliar females. However, this male suffered a loss in rank once outside his own colony. The lighter, subordinate males who remained within their smaller home ranges also mated successfully, but only with the females of their own colonies.

For GM2, whilst the results from Chapter 5 show successful matings within his own colony, it is not known if he achieved such reproductive success elsewhere, when he ranged further from Glebe Farm. However, his liaisons with the oestrous females of the cattery (see Chapter 3), although separated from them by a wire mesh fence, were frequent and persistent. This indicates he behaved similarly towards other oestrous females away from Glebe Farm, to whom he presumably had unrestricted access. As fighting between him and the other Glebe Farm males was not observed during the study, GM2's scars may have thus been obtained during his sexually-driven forays. This would also support Yamane's (1998) claim

of a loss in rank for such a male (representing "relative dominance" and not "absolute dominance"; Leyhausen, 1979).

GM1 and GM3 represent Yamane's (1998) lighter, subordinate, staying males, achieving some reproductive success but not increasing their home ranges to find further resources.

On Bryces Farm, BM1 was the "dominant" individual, achieving reproductive success with the Bryces Farm females and also venturing to *Treeside*, where he enjoyed the same success, and much further afield where he is also assumed to have achieved reproductive success: it seems unlikely he would venture so far and so frequently if he were *not* finding resources. He often returned from these excursions with fresh facial wounds, indicating that he had been forced to compete for these resources. Again comparing him to Yamane's (1998) dominant male, BM1 may well have undergone a reduction in rank (hence the wounds) in achieving reproductive success with unfamiliar females.

Based on coat colour genes, it is highly likely that BM4 also fathered some of the Bryces Farm and *Treeside* kittens. No aggression was observed between these two males, but BM1 was the more wider-ranging of the two (based on sightings for BM4 and not radiotracked fixes).

BM2 and BM3 thus represent Yamane's (1998) subordinate males, achieving reproductive success only within their own territories.

GM2's and BM1's journeys away from their home territories to seek reproductive success elsewhere but consequently having to accept a demotion in rank, suggest that similar males from other areas around the study sites may be adopting exactly the same tactics and venturing to Glebe and Bryces Farm. This provides a possible explanation for the offspring to whom no fathers from this study have been assigned.

The overall reproductive success and lack of agonistic behaviour seen among the Glebe and Bryces Farm males suggest that the strategies described above (similar to those recorded by Yamane, 1998) represent the most successful mating tactics for feral farm cats, with the older, larger and heavier males ranging further and procuring more resources including females, thus enjoying greater reproductive success than their younger and smaller conspecifics. However, when leaving the

core of their range they experience a loss in rank, sometimes decided by fights, but nevertheless achieve reproductive success. The subordinates keep to smaller home ranges, achieving a degree of reproductive success with familiar females but not equalling that of the more dominant males.

Returning to the title and aims of this study, as outlined in Chapter 1, the traditional approach to dominance in animals concerns the individual's priority of access to resources. The ways in which an individual establishes, maintains and utilises this priority illustrate its dominance, and certain attributes also associated with dominance (e.g. large body size, strength, aggressive responses to resource restrictions or aggressiveness in general (Drews, 1993; Ellis, 1995)) may be genetic. Whether dominance itself is genetic has also been discussed: Trivers and Willard (1973) proposed that natural selection would sometimes favour genes that alter the sex ratio of offspring. In this study, if it is indeed the dominant males who reproduce at the highest rates, then natural selection would favour high-ranking females giving birth to a disproportionate shares of males (and low ranking females giving birth to a disproportionate share of females). However, this was disputed by Silk (1983), who claimed that philopatric females (such as cats) have a higher probability of socially inheriting their mothers' rank than is the case for males (who may disperse). Natural selection would then surely favour high ranking females to have daughters. Although there was no evidence of a ranking system among females at either Glebe or Bryces Farm, more females were born than males during the study (males = 12; females = 20). It has been suggested that higher female:male ratios may provide more opportunities for breeding success for younger or less dominant males, as suggested for grey seals (*Halichoerus grypus*) (Ambs, Boness, Bowen, Perry and Fleischer, 1999).

In many social species, a dominance hierarchy forms, whereby the animals arrange themselves into a priority order for access to the available resources (Broom, 2002). Kaufmann (1983) defined the dominance hierarchy as "the sum total of adaptive compromises made by individuals in a group", with dominance rank indicating the differences between animals relating to stable asymmetries in agonistic behaviour (Dewsbury, 1982). To complicate matters, it should be noted that relative social positions are usually dynamic and unstable, and dominance is not necessarily a life-long characteristic of an individual. Solitary species have no need for a hierarchical system, as an individual cannot have a dominance relationship with an unfamiliar individual. For these animals, dominance would be

established at each encounter. The same applies to social animals encountering unfamiliar conspecifics.

It has been suggested that the ability to form dominance hierarchies may have evolved partly because they benefit the group as a whole, rather than because they simply benefit the high-ranking individual (e.g. Wynne-Edwards, 1962, 1986; Ellis, 1995). Although dominance gives the reproductive edge to the highest-ranking individuals, dominance hierarchies may have also made it possible for those low-ranking individuals to reproduce better than they would have done living outside the hierarchy. This indicates the presence of a strategy undertaken by subordinate individuals, explored below. Another group advantage of dominance hierarchies was discussed by Apollonio, Festa-Bianchet and Mari (1989), who found that once a dominance hierarchy had formed in a fallow deer lek, internal social conflict subsided dramatically. Broom (2002) proposed that for many species, a stable hierarchy exists throughout time, with new individuals slotting into pre-allocated positions without any conflict. The author went on to suggest that this situation is more likely to occur when a group consists of related individuals (e.g. cats), but the likelihood of control by the dominant individual is greater.

Mammals compete for three main resources: food, shelter and mates. Ultimately, the former two resources of food and shelter count towards the latter resource of mating opportunities, or reproductive success. As stated earlier, methods of obtaining these resources may be attributed to an individual's dominance status within its environment, therefore there must be a positive correlation between dominance and reproductive success (Ellis, 1995).

This study has looked at three major factors serving cumulatively to identify male dominance in cats: home range, social dynamics and reproductive success. The Resource Dispersion Hypothesis (RDH; Macdonald, 1983) states that carnivore society is influenced by the distribution and abundance of resources. Certainly in group-living species such as feral cats, male home ranges are determined by the distribution of females (Macdonald *et al.*, 1987; Kerby and Macdonald, 1988; Liberg and Sandell, 1988; Yamane *et al.*, 1994; Macdonald *et al.*, 2000), but it should be added that in such group-living species, an individual's status within the group also determines his home range, his level of interaction with his conspecifics and the level of reproductive success he will strive to attain. The fact that different individuals may have different strategies from one another (e.g. due to rank) was not accounted for in the original RDH (Macdonald, 1983), and this was one of the

reasons that has prompted recent criticism (Revilla, 2003a, 2003b; see also Buckley and Ruxton, 2003). This has been rebutted to some extent (Johnson, 2003; Johnson, Macdonald, Kays and Blackwell, 2003) although these authors do now acknowledge rank, referring to "primary" and "secondary" animals, accepting that social spacing behaviour is indeed influenced by a mixture of resources (of different types) and other behaviour-ecological factors. In this study, the fact that (a) some males had larger home ranges than others, (b) the different males interacted with others at different rates and applied different social mechanisms, (c) some individuals achieved greater reproductive success than others but (d) no aggressive behaviour was observed, is surely an indication that a pre-determined hierarchy of ranks is in existence, with dominant males distinguishable from subordinate males. If, as is generally agreed, dominance involves agonistic behaviour (Drews, 1993), this pre-determination of the hierarchy is likely to have involved resource defence at some time. However, Kaufmann (1983) postulated that the dominance-subdominance relationship is often determined by a "mutual assessment of each other's likelihood of winning a serious fight", and this assessment may range from simple recognition of size/age differences (i.e. no agonistic encounter necessary, instead based on passive visual, auditory or chemical cues) to physical contests of agonistic behaviour. Herrera and Macdonald (1993) suggested that dominance hierarchies can be viewed as a means of actually limiting aggression within social groups, so that both dominant and subordinate animals benefit by reducing costs associated with it.

A minimum home range will give the animal assurance of finding sufficient resources within its range: it appears that for male cats, subordinate individuals maximise their reproductive success by restricting their home ranges but still successfully utilising the resources (including females) within this range. Being subordinate, their chances of survival if they were to increase their resource availability, i.e. increase their home range, would presumably be low. This is supported by the fact that these subordinate animals were smaller, younger and lighter than the dominant animals. Kaufmann (1983) suggested that the individual subordinate animal would be better waiting until it is able to compete from a position of greater relative strength at another time or another place; obviously this situation may never arise in that animal's lifetime. Home ranges are of a size to meet the requirements of their occupants: it appears then that dominant animals simply have more requirements than subordinate animals. Interestingly, Kaufmann (1983) claimed that the less conspicuous strategies of the subordinate individuals were actually more important in maintaining the relationships within the hierarchy.

A very subordinate individual may not confer priority of access to anything at all, but may merely survive through avoidance and escape. Rowell (1974) hypothesised that differences in rank are better correlated with the behaviour of subordinate individuals than with that of the dominants.

Alternative hypotheses to the RDH give cause for discussion. If no differences in reproductive success between the males had been found, then the differences in home range sizes may have been explained by some individuals simply having more resource needs than others, most likely in relation to the size of the individual (i.e. the larger individual needs the most resources). This idea is more akin to the Ideal Free Distribution (Fretwell, 1972; cited in Krebs and Davies, 1993), whereby competitors adjust their spatial distribution in relation to habitat quality so that each individual has the same rate of acquisition of resources. In lions, there appears to be no significant relationship between dominance and reproductive success as there is little variability in dominance and females are highly promiscuous, mating with all the adult males (Packer and Pusey, 1983). For such species, differences in socially interactive behaviour between the males may also be explained by differences in resource requirements; adopting different behavioural tactics around different conspecifics may simply be a means of acquiring additional resources. However, this study found that certain individuals did achieve greater reproductive success than others, which suggests an Ideal Despotic Distribution (Fretwell, 1972; cited in Krebs and Davies, 1993), resulting from territory holders excluding newcomers from the preferred habitat and forcing them to settle in less preferred habitats where they experience reduced fitness (e.g. reproductive success) (P. Doncaster, pers. comm.). In other words, this latter hypothesis suggests that resource acquisition by individuals is determined by rank (i.e. by their competitive ability), which is not accounted for by the RDH.

Socially subordinate individuals frequently show low reproductive success or fail completely to breed (Dewsbury 1982; Cooney and Bennett, 2000). Although in this study, subordinate animals did have some degree of reproductive success despite their inferior status, it has been suggested that provisioning (by humans) affects the dominance hierarchy, with stronger indications of dominance when food is provisioned than when food must be obtained by the animals without human assistance (Ellis, 1995). In the case of the feral farm cats studied, food provisioning was relatively scarce but did exist. Shelter was another valuable resource afforded by humans in this study. Smith (1993) found that provisioning allowed subordinate male rhesus macaques to attain body weights that were very

rare in unprovisioned settings, and that this accelerated growth put the younger males in a position to attain dominance and attract females to an unusually high degree.

To conclude: certain individuals have emerged as superior in all three categories: these individuals (GM2 and BM1) may therefore be considered dominant. This study has succeeded in qualifying and quantifying the traditional behavioural aspects of dominance and identifying hierarchical ranks among the study animals. Among male feral farm cats, the oldest, largest, heaviest individuals range the furthest, are higher ranking within their respective hierarchies, and achieve the most reproductive success: all attributes of dominance. Although dominance is evidently an effective male strategy, under some circumstances alternative strategies do exist and are effective; subordinate males do achieve a degree of reproductive success.

The fact that just two individuals are capable of achieving relatively high reproductive success and maintaining their respective populations of cats, assisted to a small extent by a hierarchy of subordinate males, may provide an explanation for the fact that animal welfare charities both in the United Kingdom and abroad are currently reporting a population explosion in cats, despite widespread neutering practices. This raises concerns of severe reductions in genetic variability in non-pedigree cat populations, exacerbated by the ample resources (often inadvertently) provided by humans which reduce the need for dispersal in cats and hence restrict gene flow among the feral population.

Future work

A study of a larger colony (sample sizes were relatively small in this study) would be both useful and interesting, and with continuous radiotracking and recording of observations and unlimited restrictions on the radiotrackers' access to the cats' entire home ranges.

It is assumed that reproductive success in male cats is determined only by social dominance but may be influenced by female choice, although there is little evidence to support this latter idea. It would be interesting to look at the possibility of female choice, and the effects of mating order, sperm competition, and possible

male interference during mating. These behaviours were not observed during this study.

A much longer-term study with increased sample sizes would be appropriate, to see how reproductive success changes in a cat's life, as a male surely occupies a range of different ranks in his lifetime. An indication of this is given by the fact that dominant male GM2 relocated to lead an apparently much quieter life after this study had ended.

APPENDIX 1: STUDY SITES

Figures A1.1-A1.3 show maps of the study sites.

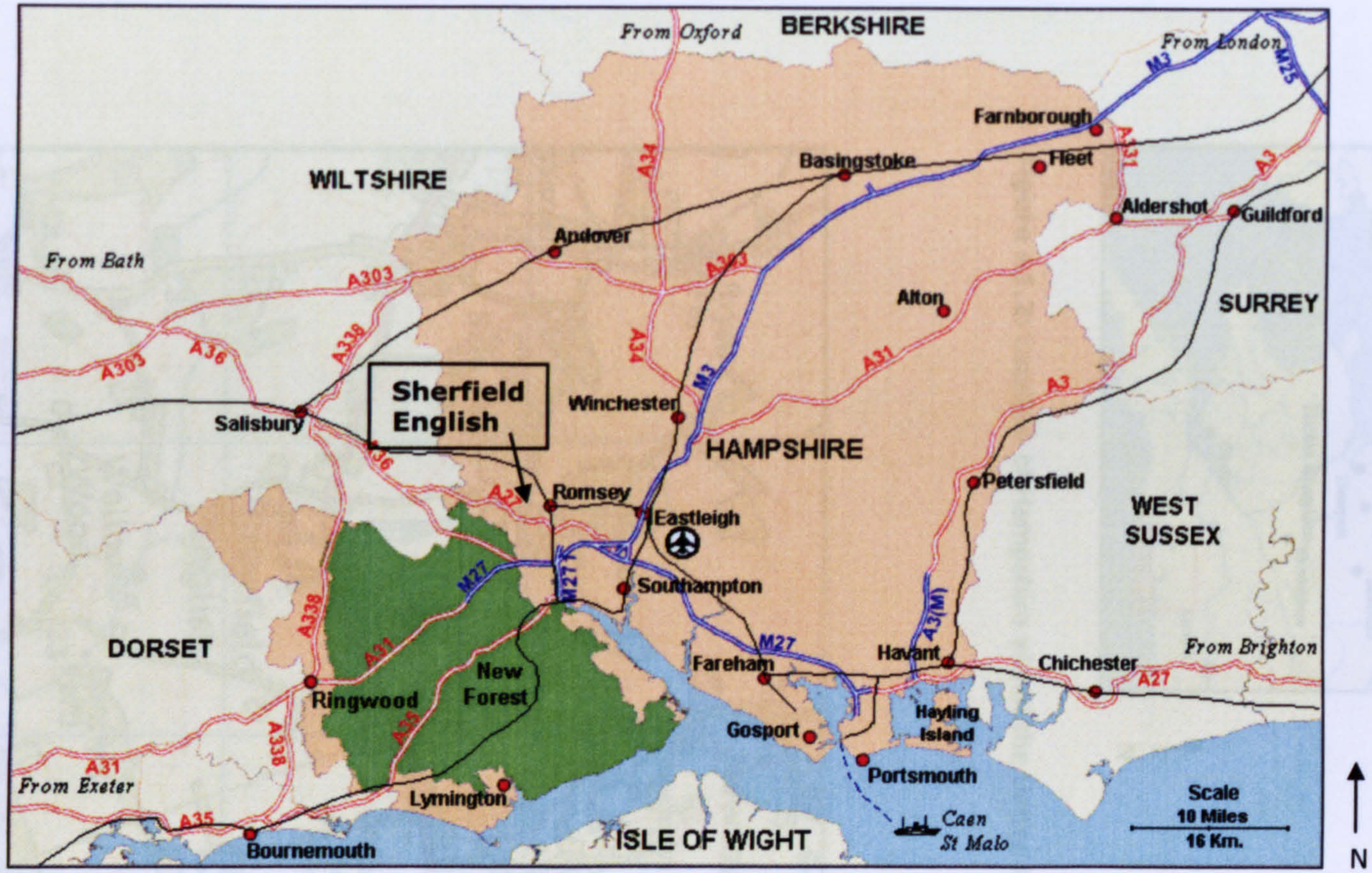


Figure A1.1: Location of study sites within Hampshire
(source: http://www.visit-testvalley.org.uk)



Figure A1.2: Location of Hampshire within the United Kingdom



Figure A1.3: Location of Glebe Farm and Bryces Farm

APPENDIX 2: WEATHER DATA

Table A2.1 (pages 181-193): Weather data for the study sites (taken at The Met Office's nearest station, Middle Wallop 4301E 1390N; altitude = 90m; latitude = 51.2, longitude = -1.6). Data supplied by The Met Office.

tr indicates a trace rainfall total (i.e. less than 0.05mm)

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
25/10/1999	11.3	0.0	
26/10/1999	10.9	0.0	
27/10/1999	9.6	0.0	
28/10/1999	12.0	0.0	
29/10/1999	10.1	0.6	
30/10/1999	12.7	4.2	
31/10/1999	12.0	0.4	
01/11/1999	13.6	3.2	
02/11/1999	10.9	0.0	
03/11/1999	10.3	0.0	
04/11/1999	9.3	0.8	
05/11/1999	11.2	9.8	
06/11/1999	8.2	0.0	tr
07/11/1999	6.4	0.0	tr
08/11/1999	8.5	0.0	
09/11/1999	10.4	0.0	tr
10/11/1999	8.2	0.0	tr
11/11/1999	8.8	0.0	
12/11/1999	7.7	0.0	
13/11/1999	7.3	0.0	
14/11/1999	8.3	0.0	
15/11/1999	7.1	2.0	tr
16/11/1999	6.6	0.0	
17/11/1999	4.1	4.8	
18/11/1999	3.4	0.0	
19/11/1999	4.5	0.2	
20/11/1999	4.1	0.0	
21/11/1999	4.5	3.0	
22/11/1999	5.8	0.2	tr
23/11/1999	7.2	0.0	
24/11/1999	9.2	1.6	tr
25/11/1999	11.8	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
26/11/1999	10.3	11.0	
27/11/1999	8.0	0.2	
28/11/1999	8.7	5.0	
29/11/1999	8.7	3.8	
30/11/1999	6.0	0.4	
01/12/1999	8.2	1.2	tr
02/12/1999	7.6	0.0	
03/12/1999	8.7	0.6	
04/12/1999	4.2	0.0	tr
05/12/1999	5.1	0.0	
06/12/1999	6.2	1.2	
07/12/1999	9.1	1.4	
08/12/1999	6.9	7.2	tr
09/12/1999	6.3	0.0	
10/12/1999	7.3	5.2	
11/12/1999	8.1	3.2	
12/12/1999	6.6	0.0	
13/12/1999	5.0	2.2	tr
14/12/1999	1.8	0.0	
15/12/1999	1.5	0.0	
16/12/1999	4.2	0.4	
17/12/1999	6.9	2.6	
18/12/1999	3.1	9.0	
19/12/1999	-3.1	0.0	
20/12/1999	-3.5	6.2	
21/12/1999		0.4	
22/12/1999	6.7	18.0	
23/12/1999	7.3	25.2	
24/12/1999	8.4	22.0	
25/12/1999	4.9	11.8	
26/12/1999	4.7	5.4	
27/12/1999	2.7	0.4	
28/12/1999	3.1	0.0	
29/12/1999	2.2	2.2	
30/12/1999	4.0	9.2	
31/12/1999	5.8	0.2	
01/01/2000	7.2	0.4	
02/01/2000	8.1	2.6	
03/01/2000	8.4	8.6	
04/01/2000	5.5	0.8	
05/01/2000	5.8	7.0	tr
06/01/2000	7.7	0.0	
07/01/2000	6.4	1.0	
08/01/2000	6.1	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
09/01/2000	2.4	0.2	tr
10/01/2000	1.7	0.0	tr
11/01/2000	2.8	0.0	
12/01/2000	7.8	4.6	
13/01/2000	3.6	0.2	
14/01/2000	1.6	0.8	
15/01/2000	4.3	0.0	
16/01/2000	3.2	0.0	
17/01/2000	2.2	0.0	
18/01/2000	4.3	0.0	
19/01/2000	4.4	0.0	tr
20/01/2000	0.8	0.0	tr
21/01/2000	3.8	0.0	
22/01/2000	4.7	0.2	tr
23/01/2000	2.4	0.0	
24/01/2000	2.5	0.2	
25/01/2000	0.0	0.0	
26/01/2000	-1.0	0.0	
27/01/2000	-1.8	0.0	
28/01/2000	1.9	0.2	
29/01/2000	7.2	0.0	tr
30/01/2000	11.3	0.0	
31/01/2000	11.0	0.4	
01/02/2000	9.3	9.8	
02/02/2000	7.0	0.0	
03/02/2000	5.5	1.0	tr
04/02/2000	7.4	0.0	
05/02/2000	8.4	0.0	
06/02/2000	9.0	4.2	
07/02/2000	7.5	11.4	
08/02/2000	10.1	0.2	
09/02/2000	7.4	3.0	
10/02/2000	8.0	4.4	
11/02/2000	4.8	5.4	
12/02/2000	5.9	1.2	tr
13/02/2000	7.1	0.0	
14/02/2000	4.3	1.0	
15/02/2000	4.7	3.0	
16/02/2000	3.9	0.0	
17/02/2000	5.5	1.6	
18/02/2000	6.7	0.4	
19/02/2000	7.1	0.0	
20/02/2000	3.1	1.6	
21/02/2000	4.0	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
22/02/2000	3.6	0.2	tr
23/02/2000	5.6	0.0	
24/02/2000	7.6	14.2	
25/02/2000	4.9	0.0	
26/02/2000	4.5	0.2	
27/02/2000	6.1	13.6	
28/02/2000	7.9	15.0	
29/02/2000	6.9	3.8	
01/03/2000	5.4	0.8	
02/03/2000	5.5	8.4	
03/03/2000	7.9	0.4	
04/03/2000	3.3	0.0	tr
05/03/2000	4.6	0.0	
06/03/2000	7.1	0.2	tr
07/03/2000	10.6	0.0	tr
08/03/2000	11.2	0.0	tr
09/03/2000	12.0	0.0	
10/03/2000	11.4	0.0	
11/03/2000	9.5	0.0	
12/03/2000	7.8	0.0	
13/03/2000	9.9	0.6	tr
14/03/2000	9.9	0.0	
15/03/2000	6.9	0.0	
16/03/2000	7.3	0.0	
17/03/2000	8.1	0.0	
18/03/2000	8.9	0.0	
19/03/2000	7.3	0.0	
20/03/2000	6.6	0.0	
21/03/2000	7.4	0.0	tr
22/03/2000	8.1	0.0	
23/03/2000	8.9	3.2	
24/03/2000	9.6	0.4	
25/03/2000	6.3	7.2	
26/03/2000	4.5	0.6	
27/03/2000	6.0	0.8	tr
28/03/2000	5.5	0.0	
29/03/2000	4.6	0.2	
30/03/2000	5.8	0.0	
31/03/2000	6.3	0.2	
01/04/2000	4.2	3.4	
02/04/2000	9.9	18.4	
03/04/2000	7.6	16.0	
04/04/2000	2.7	2.0	tr
05/04/2000	5.8	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
06/04/2000	5.8	0.0	
07/04/2000	6.6	0.0	
08/04/2000	7.8	0.6	
09/04/2000	10.0	0.0	
10/04/2000	7.7	1.0	
11/04/2000	4.6	10.9	
12/04/2000	3.5	7.2	
13/04/2000	4.7	0.6	
14/04/2000	4.9	7.8	
15/04/2000	4.6	0.8	
16/04/2000	4.6	9.2	
17/04/2000	8.4	4.4	
18/04/2000	7.9	16.8	
19/04/2000	8.6	13.8	
20/04/2000	11.1	5.6	
21/04/2000	10.9	6.6	
22/04/2000	11.4	1.0	
23/04/2000	10.4	0.4	
24/04/2000	10.4	17.6	
25/04/2000	10.9	1.4	
26/04/2000	11.8	1.0	
27/04/2000	11.0	0.2	
28/04/2000	9.9	11.6	
29/04/2000	11.6	0.0	
30/04/2000	9.6	0.0	
01/05/2000	12.3	0.0	tr
02/05/2000	11.9	0.0	tr
03/05/2000	9.6	0.0	
04/05/2000	10.6	0.0	
05/05/2000	12.8	0.0	
06/05/2000	16.6	6.0	
07/05/2000	18.0	22.0	
08/05/2000	14.9	0.0	
09/05/2000	15.9	0.0	
10/05/2000	16.4	1.4	
11/05/2000	14.4	0.2	tr
12/05/2000	13.4	0.0	
13/05/2000	16.2	0.0	
14/05/2000	16.6	0.0	
15/05/2000	17.3	0.0	
10/09/2001	12.1	0.0	
11/09/2001	14.9	0.0	
12/09/2001	14.3	0.8	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
13/09/2001	12.3	2.6	
14/09/2001	12.8	0.0	
15/09/2001	13.3	0.0	
16/09/2001	12.2	0.0	
17/09/2001	10.9	0.4	
18/09/2001	12.5	2.4	
19/09/2001	13.0	0.6	
20/09/2001	13.8	0.0	tr
21/09/2001	13.2	0.0	
22/09/2001	12.7	0.0	
23/09/2001	11.5	0.6	
24/09/2001	12.7	0.0	
25/09/2001	11.0	1.2	
26/09/2001	11.4	4.5	
27/09/2001	15.2	0.0	tr
28/09/2001	15.8	1.4	
29/09/2001	16.2	0.6	
30/09/2001	15.2	13.0	
01/10/2001	15.5	17.8	
02/10/2001	13.9	0.0	
03/10/2001	13.2	6.4	
04/10/2001	13.5	0.6	
05/10/2001	15.4	1.2	
06/10/2001	14.5	5.6	
07/10/2001	12.6	33.8	
08/10/2001	12.1	4.0	
09/10/2001	11.7	0.0	
10/10/2001	12.1	0.8	
11/10/2001	14.3	0.0	tr
12/10/2001	14.5	0.0	
13/10/2001	16.4	0.0	
14/10/2001	15.4	10.2	
15/10/2001	13.8	5.2	
16/10/2001	12.2	0.0	tr
17/10/2001	15.3	4.8	
18/10/2001	14.1	0.0	
19/10/2001	13.7	8.6	
20/10/2001	14.4	5.4	
21/10/2001	11.3	0.0	
22/10/2001	10.1	25.2	
23/10/2001	13.9	2.2	
24/10/2001	12.9	9.6	
25/10/2001	13.3	3.6	
26/10/2001	13.4	9.8	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
27/10/2001	12.1	1.2	
28/10/2001	11.5	0.0	
29/10/2001	12.2	0.0	
30/10/2001	14.2	1.6	
31/10/2001	9.9	0.0	
01/11/2001	7.4	0.0	
02/11/2001	7.0	0.2	
03/11/2001	6.2	0.0	
04/11/2001	8.8	0.2	
05/11/2001	7.1	0.0	tr
06/11/2001	11.4	1.4	
07/11/2001	11.6	12.6	
08/11/2001	5.9	0.4	
09/11/2001	2.6	0.0	
10/11/2001	3.4	0.2	
11/11/2001	9.2	0.2	
12/11/2001	9.4	3.8	
13/11/2001	5.0	0.0	
14/11/2001	3.2	0.0	
15/11/2001	3.6	0.0	
16/11/2001	8.8	0.0	
17/11/2001	8.6	0.2	
18/11/2001	7.5	0.0	
19/11/2001	6.9	0.0	
20/11/2001	5.5	0.0	tr
21/11/2001	9.5	0.2	
22/11/2001	9.4	0.2	
23/11/2001	3.9	0.0	
24/11/2001	10.2	0.2	
25/11/2001	9.8	6.0	
26/11/2001	3.2	0.2	
27/11/2001	4.1	2.0	
28/11/2001	6.4	4.0	
29/11/2001	12.0	3.8	
30/11/2001	13.2	10.2	
01/12/2001	9.3	0.8	
02/12/2001	2.9	0.6	
03/12/2001	5.6	8.6	
04/12/2001	8.7	9.4	
05/12/2001	9.1	0.2	
06/12/2001	5.9	0.0	
07/12/2001	7.9	0.0	
08/12/2001	2.5	0.2	
09/12/2001	2.9	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
10/12/2001	3.2	0.0	
11/12/2001	2.6	0.0	
12/12/2001	5.3	0.0	tr
13/12/2001	6.1	0.0	tr
14/12/2001	1.3	0.0	
15/12/2001	1.5	0.0	
16/12/2001	3.1	0.0	
17/12/2001	1.7	0.0	tr
18/12/2001	4.2	0.0	
19/12/2001	2.6	0.0	tr
20/12/2001	1.8	0.0	
21/12/2001	3.8	0.6	
22/12/2001	0.0	0.0	
23/12/2001	-1.1	0.4	
24/12/2001	5.9	0.4	
25/12/2001	4.7	0.0	
26/12/2001	0.6	0.8	
27/12/2001	6.0	0.0	
28/12/2001	6.2	0.8	
29/12/2001	0.3		
30/12/2001	1.1	0.0	
31/12/2001	-1.1	0.0	
01/01/2002	-2.8	0.2	
02/01/2002	0.0	0.0	
03/01/2002	0.5	0.0	
04/01/2002	0.6	0.8	
05/01/2002	6.4	0.2	
06/01/2002	6.3	0.0	tr
07/01/2002	5.1	0.2	
08/01/2002	3.0	0.0	tr
09/01/2002	4.4	2.8	
10/01/2002	4.1	1.2	
11/01/2002	-0.1	0.2	
12/01/2002	5.0	0.8	
13/01/2002	9.0	0.4	
14/01/2002	8.9	3.0	
15/01/2002	5.9	0.0	tr
16/01/2002	4.5	0.2	
17/01/2002	7.4	3.4	
18/01/2002	3.9	2.8	
19/01/2002	6.0	1.6	
20/01/2002	10.1	3.4	
21/01/2002	10.3	3.2	
22/01/2002	7.9	5.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
23/01/2002	9.3	6.2	
24/01/2002	8.2	0.8	
25/01/2002	6.5	13.6	
26/01/2002	10.1	22.8	
27/01/2002	10.1	4.4	
28/01/2002	10.4	0.0	
29/01/2002	10.0	0.4	
30/01/2002	10.0	3.2	
31/01/2002	7.4	8.4	
01/02/2002	10.5	3.8	
02/02/2002	10.8	8.4	
03/02/2002	8.2	11.4	
04/02/2002	7.9	24.0	
05/02/2002	8.9	3.6	
06/02/2002	5.5	0.2	
07/02/2002	5.6	1.2	
08/02/2002	10.6		
09/02/2002	9.3	3.0	
10/02/2002	8.8	1.6	
11/02/2002	11.6	2.4	
12/02/2002	9.9	0.0	tr
13/02/2002	7.2	3.0	
14/02/2002	4.8	0.0	
15/02/2002	3.6	0.0	
16/02/2002	3.9	0.2	
17/02/2002	2.7	1.8	
18/02/2002	5.7	0.2	
19/02/2002	8.7	10.4	
20/02/2002	8.4	0.2	
21/02/2002	4.4	1.2	
22/02/2002	9.1	0.6	
23/02/2002	4.9	0.0	
24/02/2002	5.2	5.2	
25/02/2002	10.2	16.2	
26/02/2002	8.7	5.4	
27/02/2002	4.3	0.4	
28/02/2002	4.6	2.0	
01/03/2002	2.4	0.2	
02/03/2002	3.5	0.2	
03/03/2002	6.5	0.6	
04/03/2002	6.8	0.0	
05/03/2002	6.6	0.0	
06/03/2002	8.7	0.0	tr
07/03/2002	10.8	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
08/03/2002	8.8	0.0	
09/03/2002	5.8	0.4	
10/03/2002	6.7	11.2	
11/03/2002	8.1	0.8	
12/03/2002	7.2	4.0	
13/03/2002	5.6	1.2	
14/03/2002	4.2	5.2	
15/03/2002	7.1	4.4	
16/03/2002	9.5	0.4	
17/03/2002	9.3	6.6	
18/03/2002	8.3	6.0	
19/03/2002	8.8	3.6	
20/03/2002	11.0	1.8	
21/03/2002	11.4	0.0	
22/03/2002	10.9	0.0	
23/03/2002	8.3	0.0	
24/03/2002	6.3	0.0	
25/03/2002	7.8	0.0	
26/03/2002	8.5	0.0	
27/03/2002	6.3	0.0	
28/03/2002	7.4	0.0	
29/03/2002	8.2	0.0	
30/03/2002	8.6	0.4	
31/03/2002	9.1	0.2	
01/04/2002	10.3	0.0	
02/04/2002	11.8	1.2	
03/04/2002	12.5	0.0	
04/04/2002	12.3	0.0	
05/04/2002	10.9	0.0	
06/04/2002	8.4	0.0	
07/04/2002	8.2	0.0	
08/04/2002	7.9	0.0	
09/04/2002	6.8	0.0	
10/04/2002	7.9	0.0	
11/04/2002	7.7	0.0	
12/04/2002	7.6	0.0	
13/04/2002	6.4	0.0	
14/04/2002	6.9	0.0	
15/04/2002	8.4	0.0	
16/04/2002	7.7	0.0	tr
17/04/2002	7.8	1.8	
18/04/2002	7.0	0.6	
19/04/2002	9.4	0.0	
20/04/2002	9.8	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
21/04/2002	11.9	0.0	
22/04/2002	11.9	0.0	
23/04/2002	13.1	0.0	tr
24/04/2002	12.1	0.0	
25/04/2002	11.7	3.8	
26/04/2002	9.7	0.4	
27/04/2002	8.8	9.4	
28/04/2002	9.6	8.6	
29/04/2002	9.0	11.6	
30/04/2002	9.0	15.4	
01/05/2002	8.6	1.0	
02/05/2002	8.4	3.4	
03/05/2002	8.7	0.6	
04/05/2002	8.8	0.0	
05/05/2002	8.7	0.0	
06/05/2002	9.8	4.2	
07/05/2002	10.9	0.2	
08/05/2002	11.1	0.0	
09/05/2002	10.3	0.0	
10/05/2002	13.1	0.0	
11/05/2002	13.2	0.0	
12/05/2002	11.4	3.2	
13/05/2002	11.2	19.4	
14/05/2002	11.9	3.0	
15/05/2002	13.2	0.0	
16/05/2002	16.4	0.0	
17/05/2002	18.0	1.2	
18/05/2002	13.4	0.2	
19/05/2002	13.4	0.0	tr
20/05/2002	13.9	3.6	
21/05/2002	13.3	25.2	
22/05/2002	13.2	0.4	
23/05/2002	13.0	8.6	
24/05/2002	12.2	1.6	
25/05/2002	11.1	7.0	
26/05/2002	9.3	5.6	
27/05/2002	9.4	2.4	
28/05/2002	10.9	2.6	
29/05/2002	11.3	2.4	
30/05/2002	11.6	6.4	
31/05/2002	13.1	0.0	
01/06/2002	15.2	0.0	
02/06/2002	16.9	0.0	
03/06/2002	12.6	1.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
04/06/2002	11.5	0.0	
05/06/2002	12.9	14.8	
06/06/2002	13.8	3.0	
07/06/2002	12.6	2.2	
08/06/2002	13.3	0.4	
09/06/2002	12.4	5.6	
10/06/2002	12.5	3.0	
11/06/2002	12.1	4.0	
12/06/2002	13.1	2.2	
13/06/2002	14.2	0.0	tr
14/06/2002	16.0	0.0	tr
15/06/2002	14.9	1.2	
16/06/2002	15.7	0.0	
17/06/2002	16.4	0.4	
18/06/2002	16.6	0.0	
19/06/2002	14.8	0.0	
20/06/2002	14.4	1.0	
21/06/2002	14.3	3.0	
22/06/2002	15.0	0.0	
23/06/2002	14.2	0.0	
24/06/2002	14.0	0.0	
25/06/2002	13.6	0.0	
26/06/2002	14.9	0.0	
27/06/2002	13.9	0.0	
28/06/2002	12.8	0.0	
29/06/2002	12.9	0.0	
30/06/2002	14.1	0.8	
01/07/2002	13.3	3.0	
02/07/2002	12.3	17.8	
03/07/2002	13.3	4.4	
04/07/2002	13.8	3.8	
05/07/2002	14.9	0.4	
06/07/2002	15.6	0.2	
07/07/2002	15.1	1.6	
08/07/2002	14.9	20.0	
09/07/2002	14.2	0.8	
10/07/2002	12.9	1.8	
11/07/2002	13.5	0.2	
12/07/2002	12.7	0.2	
13/07/2002	14.9	0.0	
14/07/2002	17.3	0.0	
15/07/2002	19.8	0.0	tr
16/07/2002	19.4	0.0	
17/07/2002	16.4	0.0	

Date	Mean daily temperature (°C)	Mean daily rainfall (mm)	
18/07/2002	15.9	0.0	
19/07/2002	17.1	0.0	
20/07/2002	15.7	0.0	
21/07/2002	14.8	0.0	
22/07/2002	15.6	0.0	tr
23/07/2002	16.4	0.2	
24/07/2002	15.2	0.0	
25/07/2002	16.1	0.0	tr

APPENDIX 3: ADULT TRAPPING DATA

Tables A3.1a, A3.1b and A3.1c show the adult trapping records from Glebe Farm, Bryces Farm and *Treeside* respectively.

Table A3.1a: Glebe Farm adult trapping data

Cat	Description	Approx. age at capture (yrs)	Weight (kg)	Body condition		Blood result
				Fleas	General	
GM1	DSH White and black	2	3.0	3	1	FIV-/FeLV-
GM2	DSH Black, white spots on abdomen, big jowls	4	4.0	3	1	FIV+/FeLV-
GM3	DSH Black, white spots on abdomen	2	3.0	3	2	FIV+/FeLV-
GF1	DSH Grey tabby	9	2.5	3	2	N/A
GF2	DSH Blue	2	2.6	3	3	N/A
GF3	DSH Tortoiseshell, orange	2	2.6	3	2	N/A

Key: Fleas and body condition scored on a scale of 0-5: 0 = no infestation/good condition, 5 = serious infestation/poor condition

DSH = Domestic shorthair; DLH = Domestic longhair

Table A3.1b: Bryces Farm adult trapping data

Cat	Description	Approx. age at capture (yrs)	Weight (kg)	Body condition		Blood result
				Fleas	General	
BM1	DSH Cream with orange points. Orange tail bands	7	4.5	3	2	FIV+/FeLV-
BM2	DSH Grey and white, white nose	2	3.8	3	2	FIV+/FeLV-
BM3	DSH Orange tabby	5	4.2	3	1	FIV-/FeLV-
BM4*	DSH Grey and white, grey nose	8	4.0	3	1	-
BF1	DSH Dark tortoiseshell, front left paw white	2	2.5	3	2	N/A
BF2	DSH Orange tortoiseshell, dense coat	3	3.0	3	1	N/A
BF3	DSH Dark tortoiseshell, pronounced limp, broken tail	3	2.3	3	4	N/A
BF4*	DLH Orange tortoiseshell, large	5	3.0	3	1	N/A

*escaped

Key: Fleas and body condition scored on a scale of 0-5: 0 = no infestation/good condition, 5 = serious infestation/poor condition
DSH = Domestic shorthair; DLH = Domestic longhair

Other cats sighted at Bryces Farm but not trapped: 1 x adult black and white, sex unknown. No. of times seen = 1
1 x adult black, sex unknown. No. of times seen = 1

Table A3.1c: *Treeside* adult trapping data

Cat	Description	Approx. age at capture (yrs)	Weight (kg)	Body condition		Blood result
				Fleas	General	
BF9	DSH Tortoiseshell	12	3.0	2	1	N/A
BF10	DSH Tortoiseshell, calico	9	3.0	2	1	N/A
BF11	DSH Soft tortoiseshell	12	3.4	2	1	N/A
BF12	DSH Soft tortoiseshell	10	3.4	2	1	N/A
BF13	DSH Black and white *neutered	17	3.0	2	1	N/A
BF14	DLH Tortoiseshell	7	3.2	2	1	N/A
BF15	DLH Grey	5	3.2	2	1	N/A

Key: Fleas and body condition scored on a scale of 0-5: 0 = no infestation/good condition, 5 = serious infestation/poor condition

DSH = Domestic shorthair; DLH = Domestic longhair

APPENDIX 4: EFFECTS OF WEATHER ON ACTIVITY

The following graphs plot the cats' temporal activity levels exhibited during radiotracking sessions together with mean daily temperature (ºC) and daily rainfall (mm) for the study area, against increasing radiotracking time (on a daily basis as season progressed).

Weather data supplied by The Met Office.

GM1

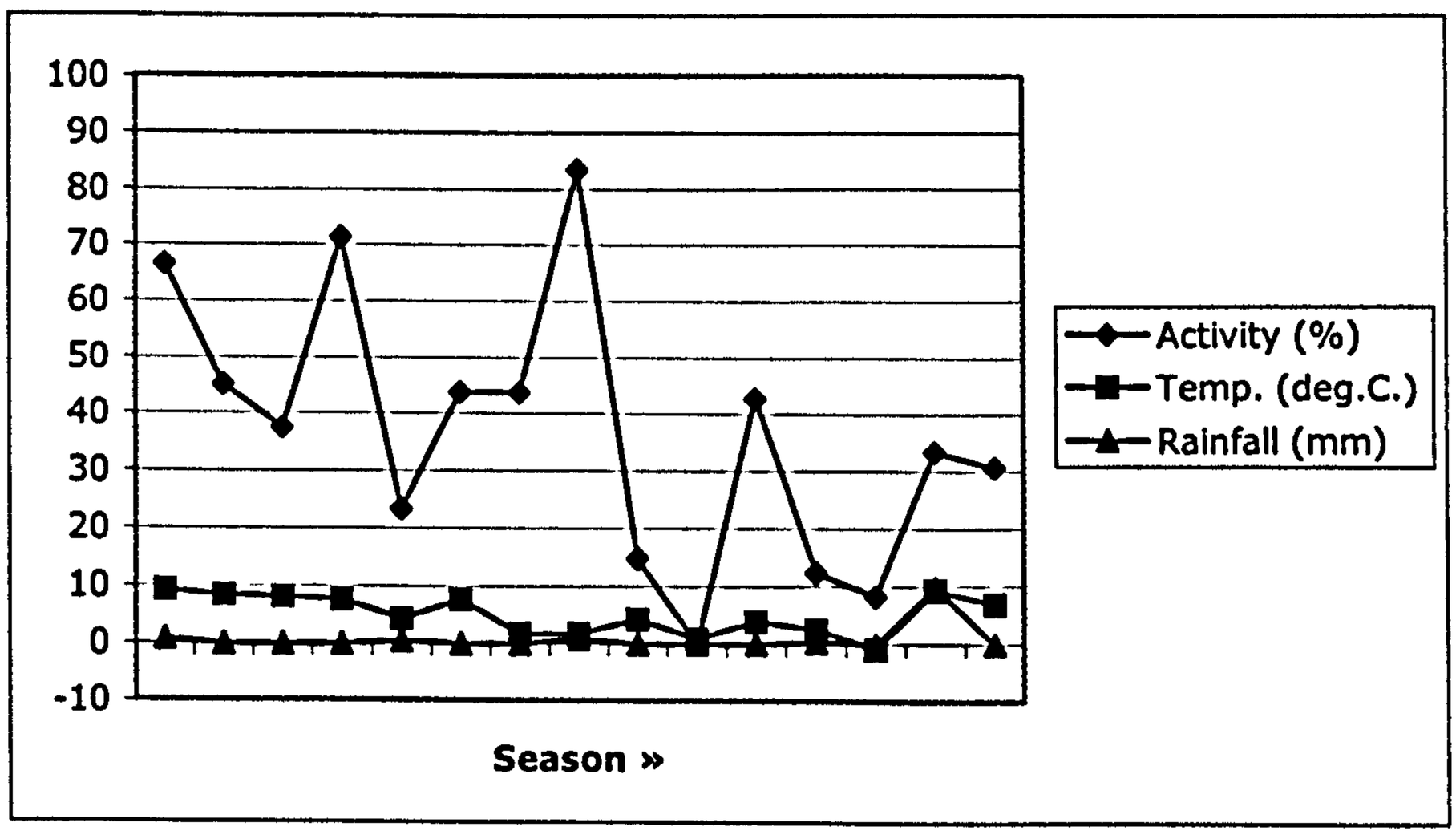


Figure A4.1: GM1 Crepuscular activity

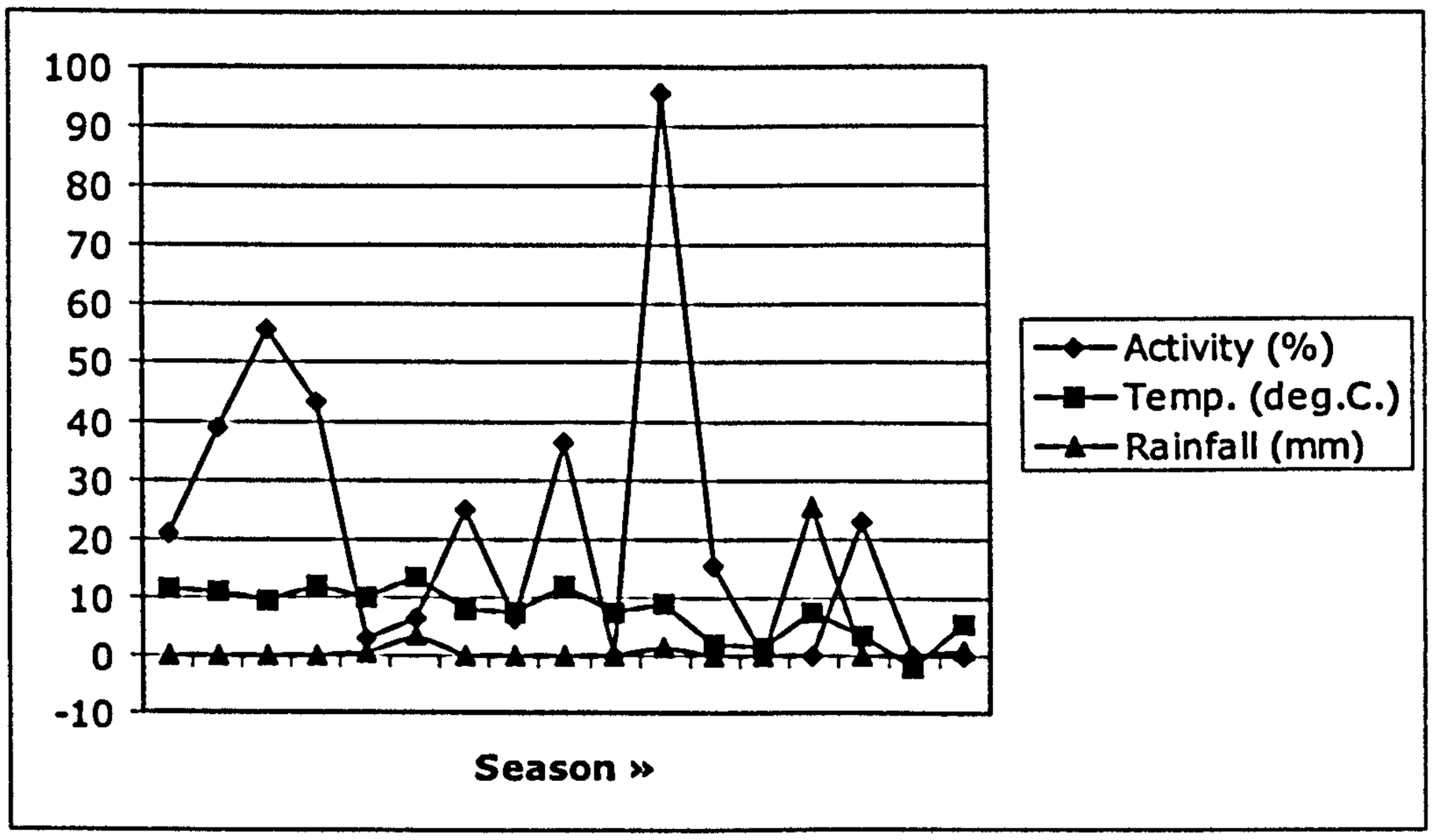


Figure A4.2: GM1 Diurnal activity

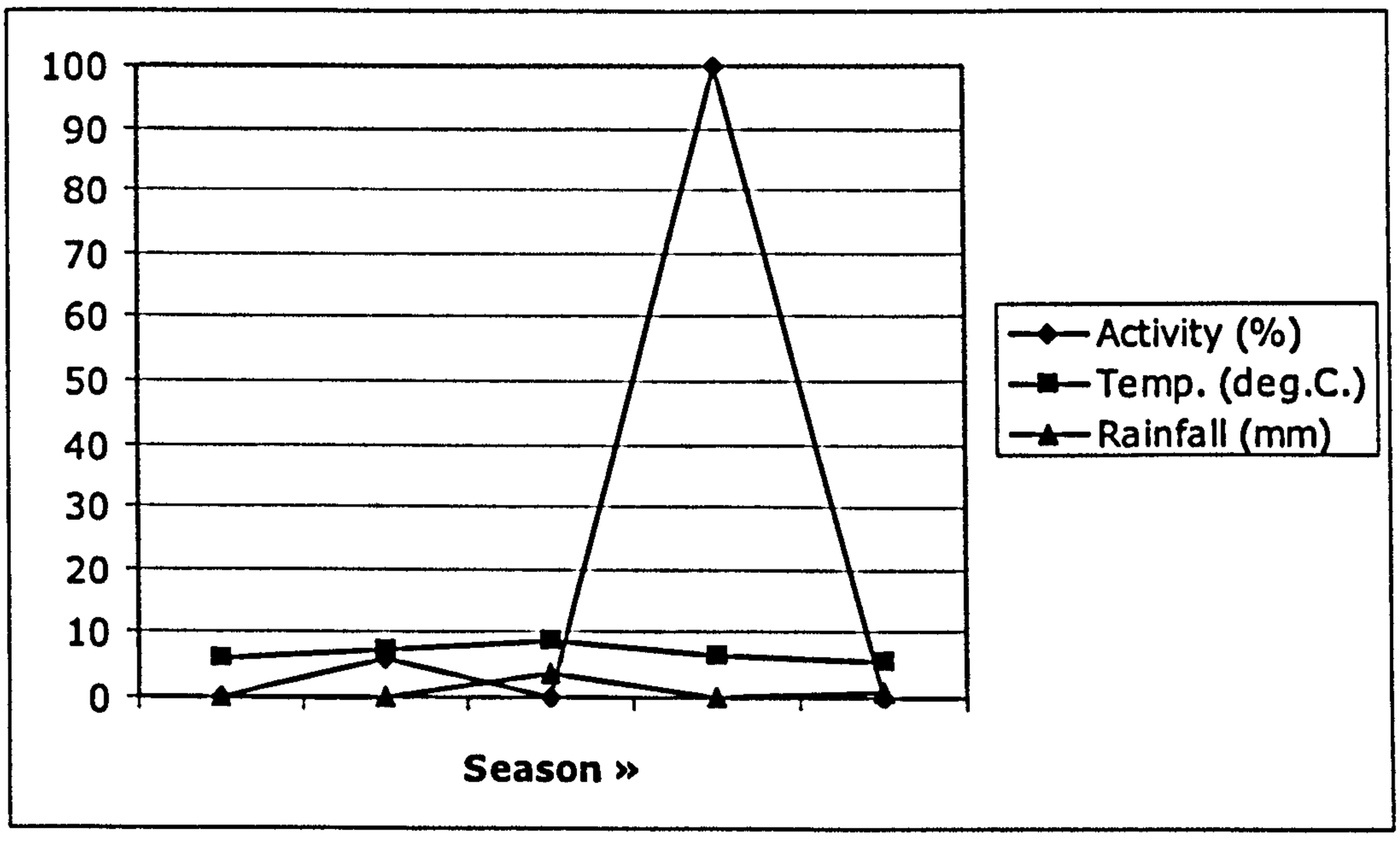


Figure A4.3: GM1 Nocturnal activity

GM2

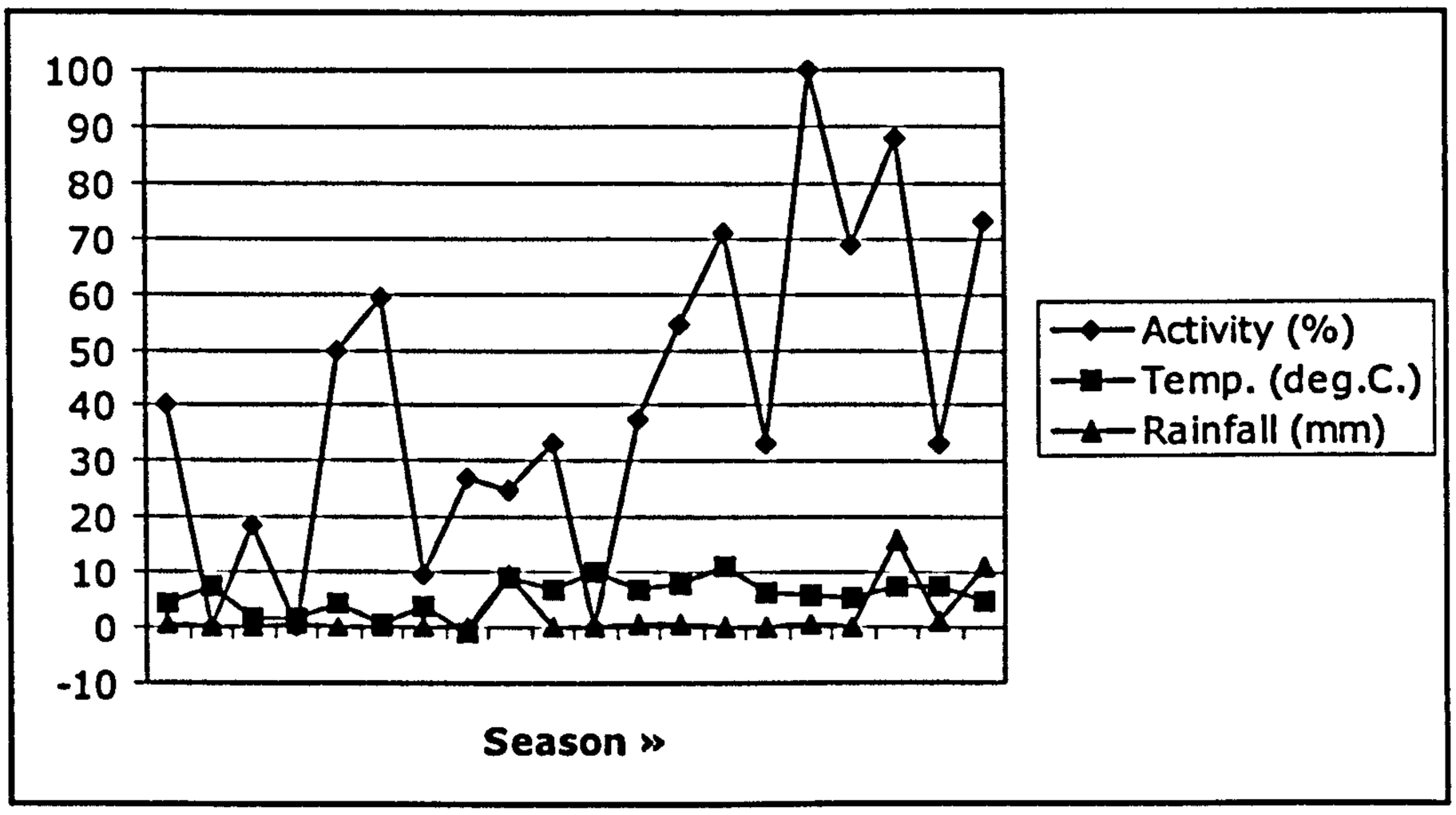


Figure A4.4: GM2 Crepuscular activity

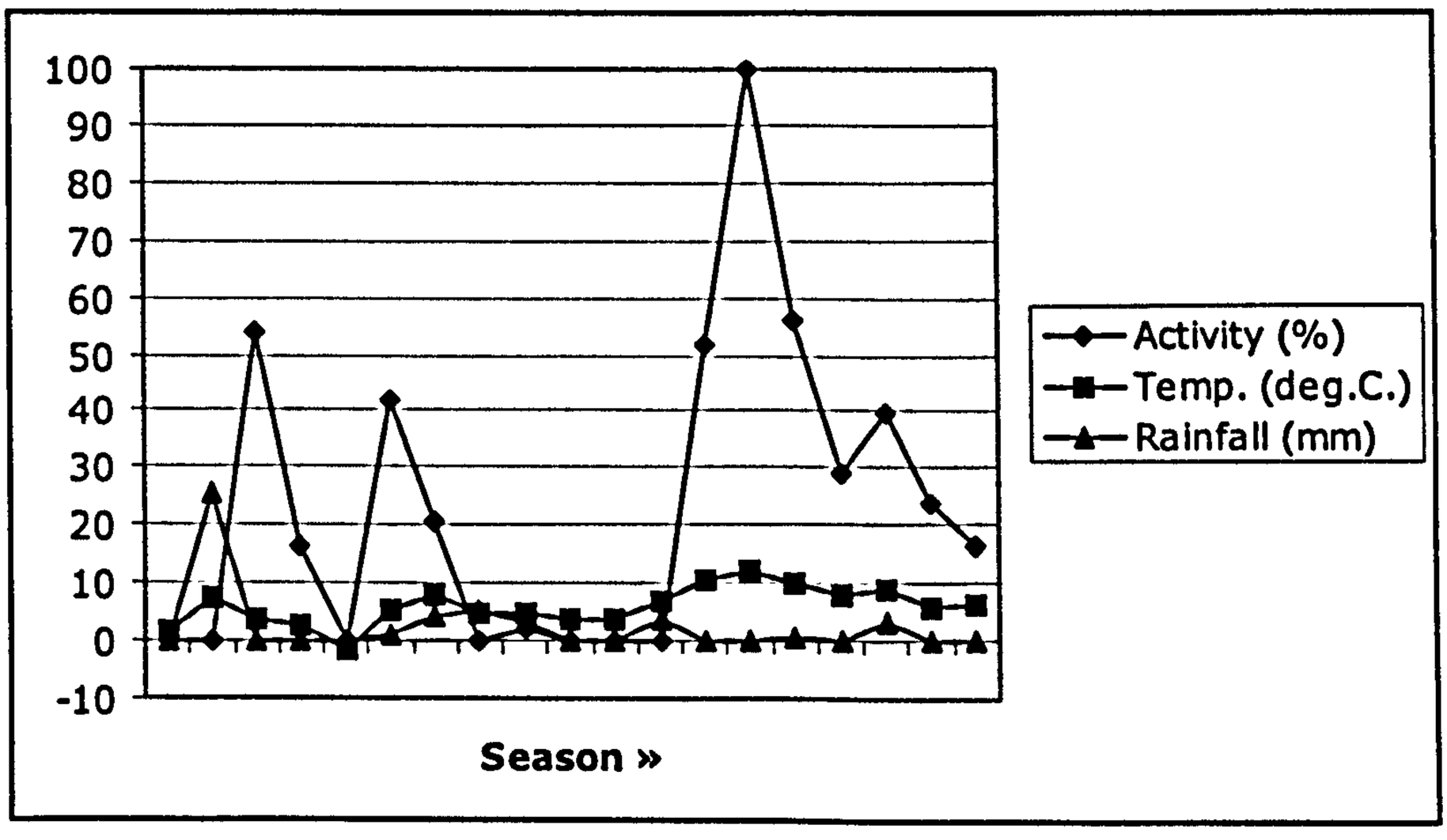


Figure A4.5: GM2 Diurnal activity

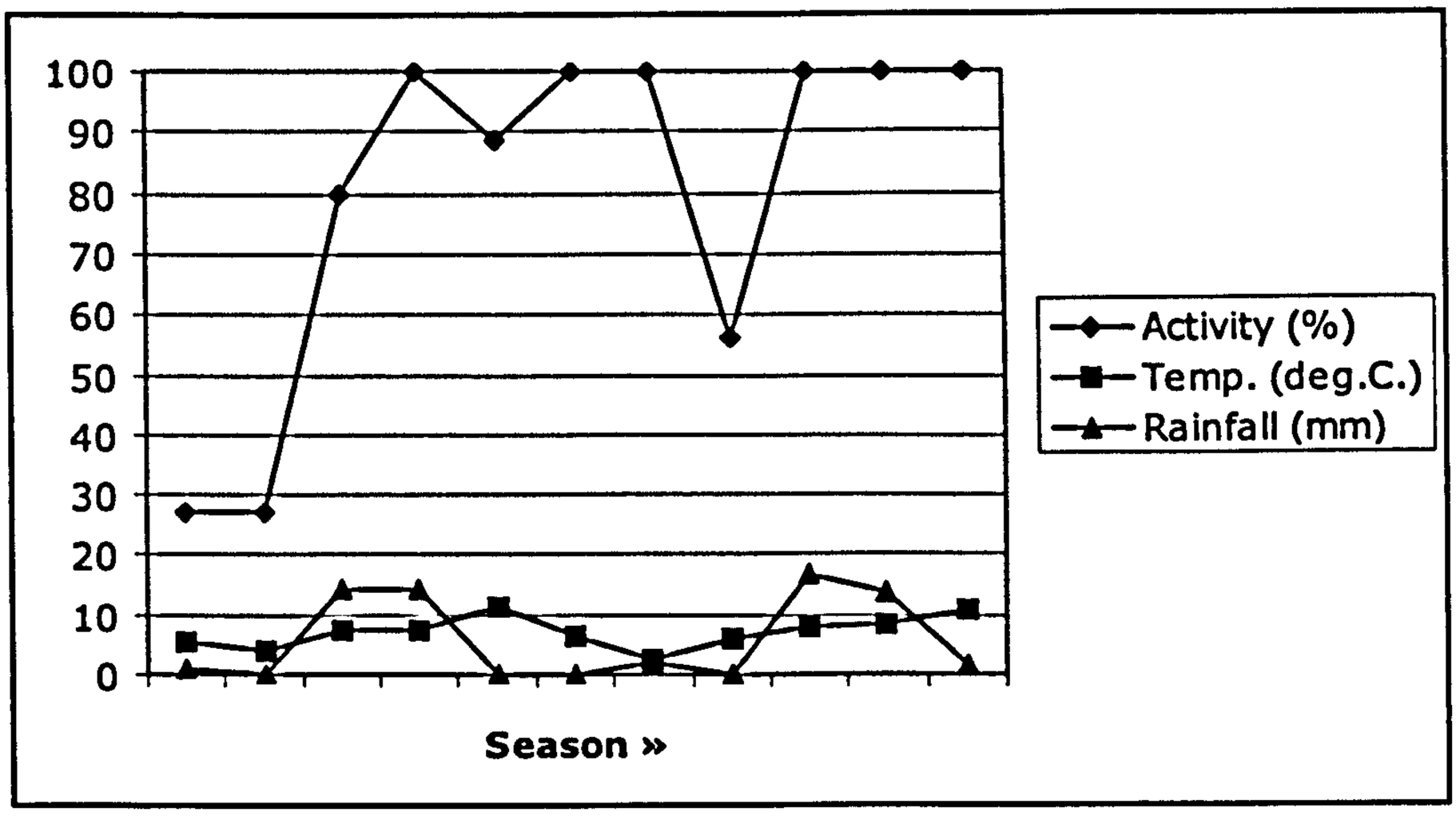


Figure A4.6: GM2 Nocturnal activity

GM3

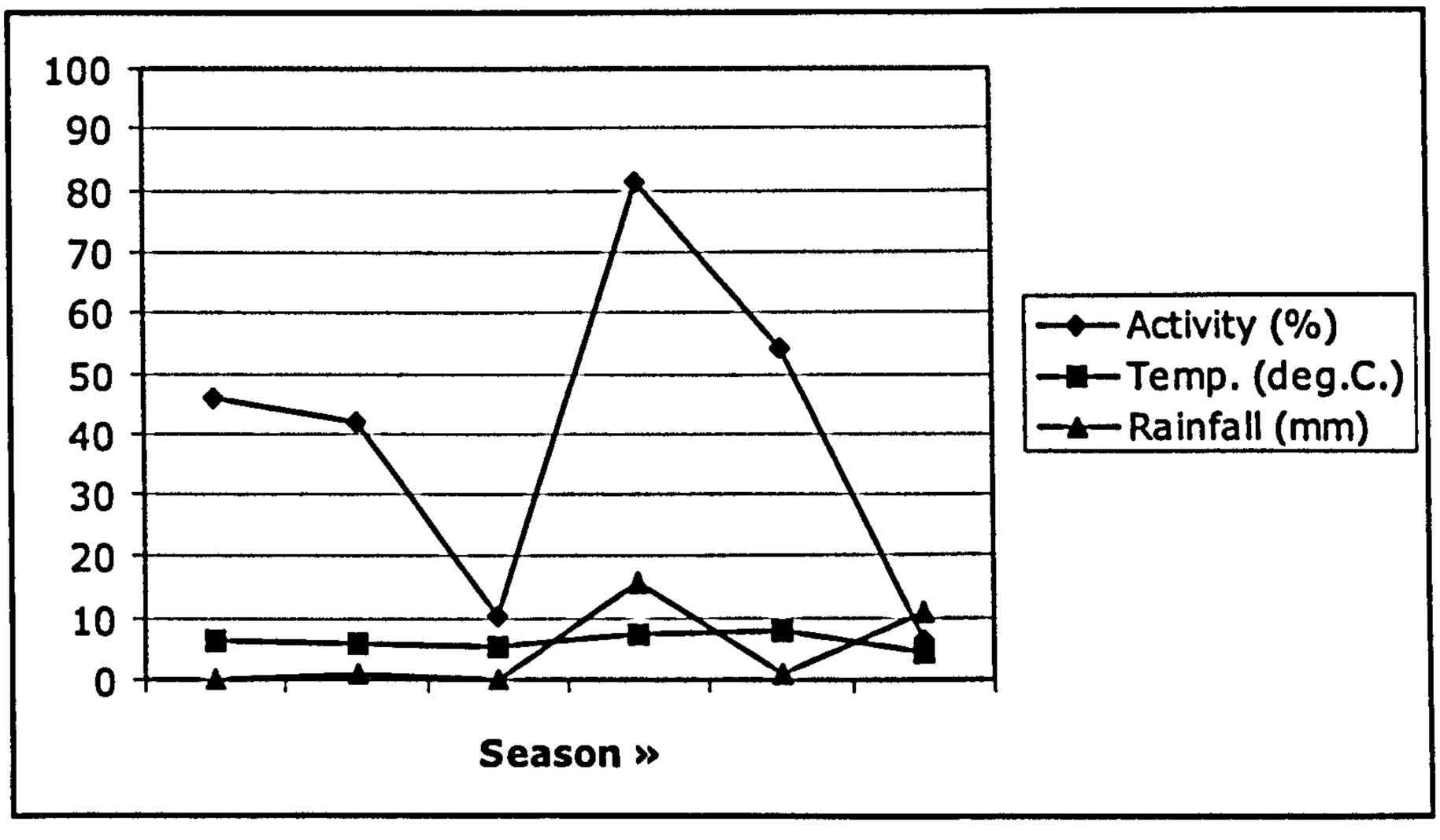


Figure A4.7: GM3 Crepuscular activity

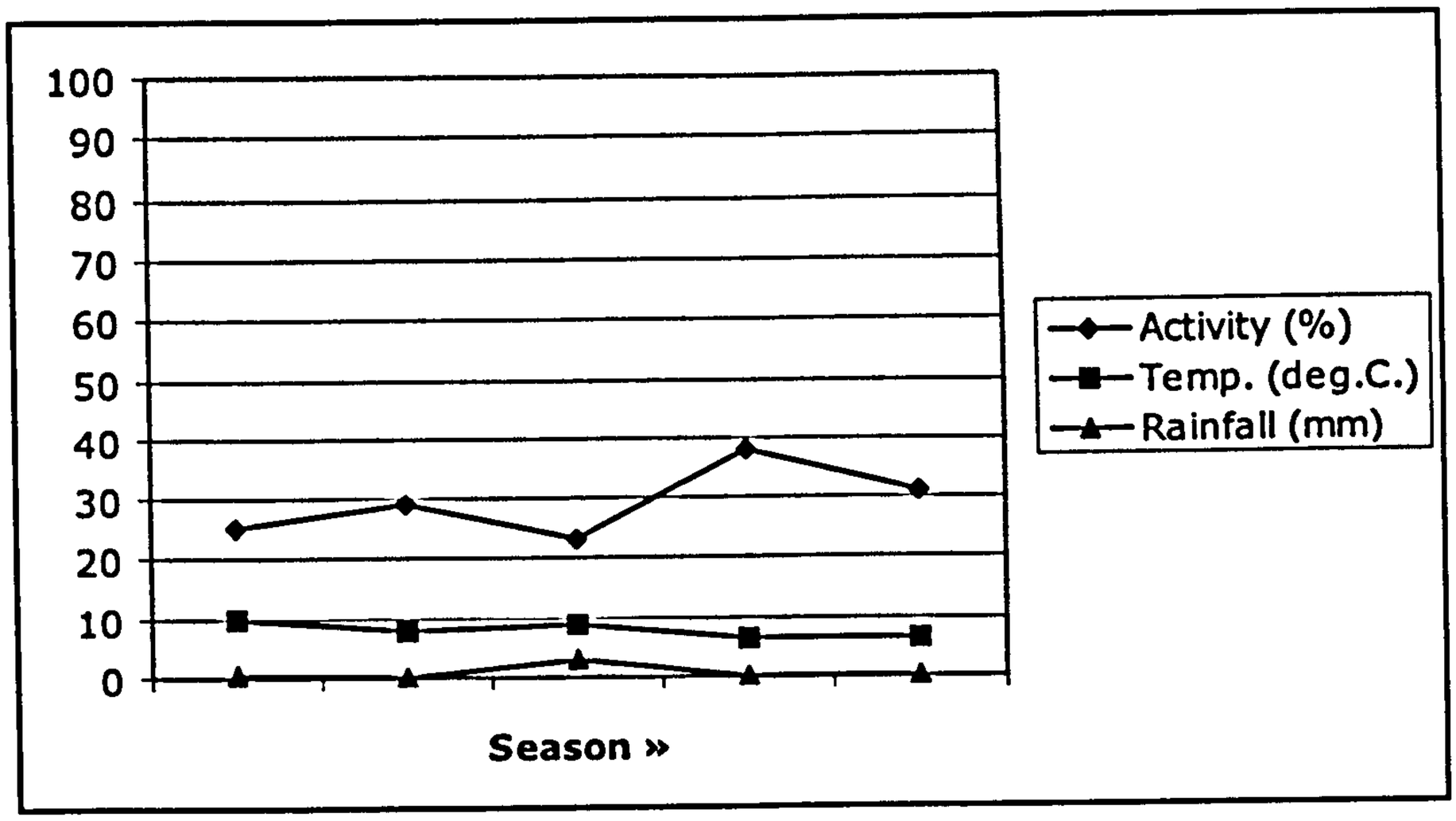


Figure A4.8: GM3 Diurnal activity

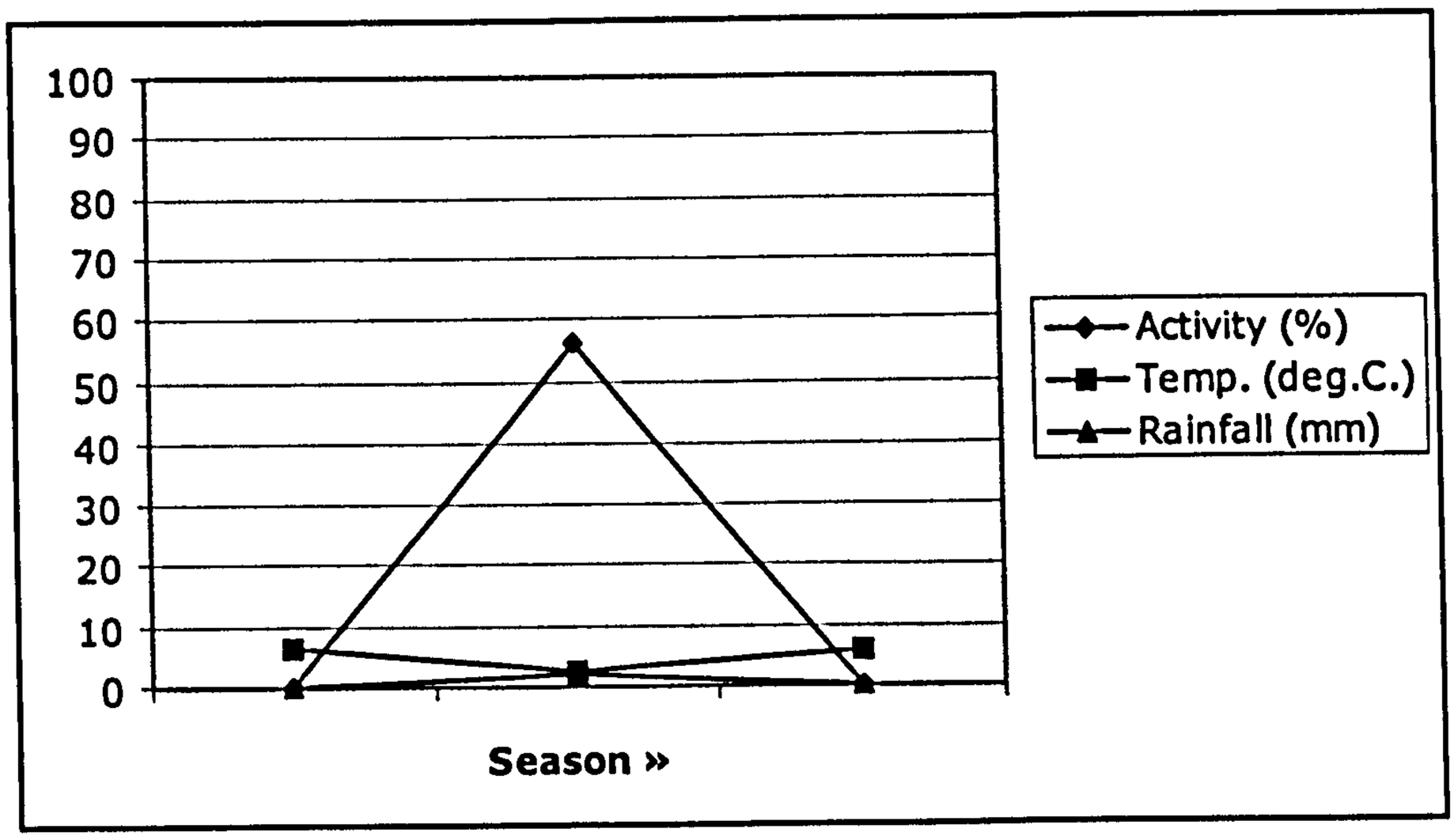


Figure A4.9: GM3 Nocturnal activity

BM1

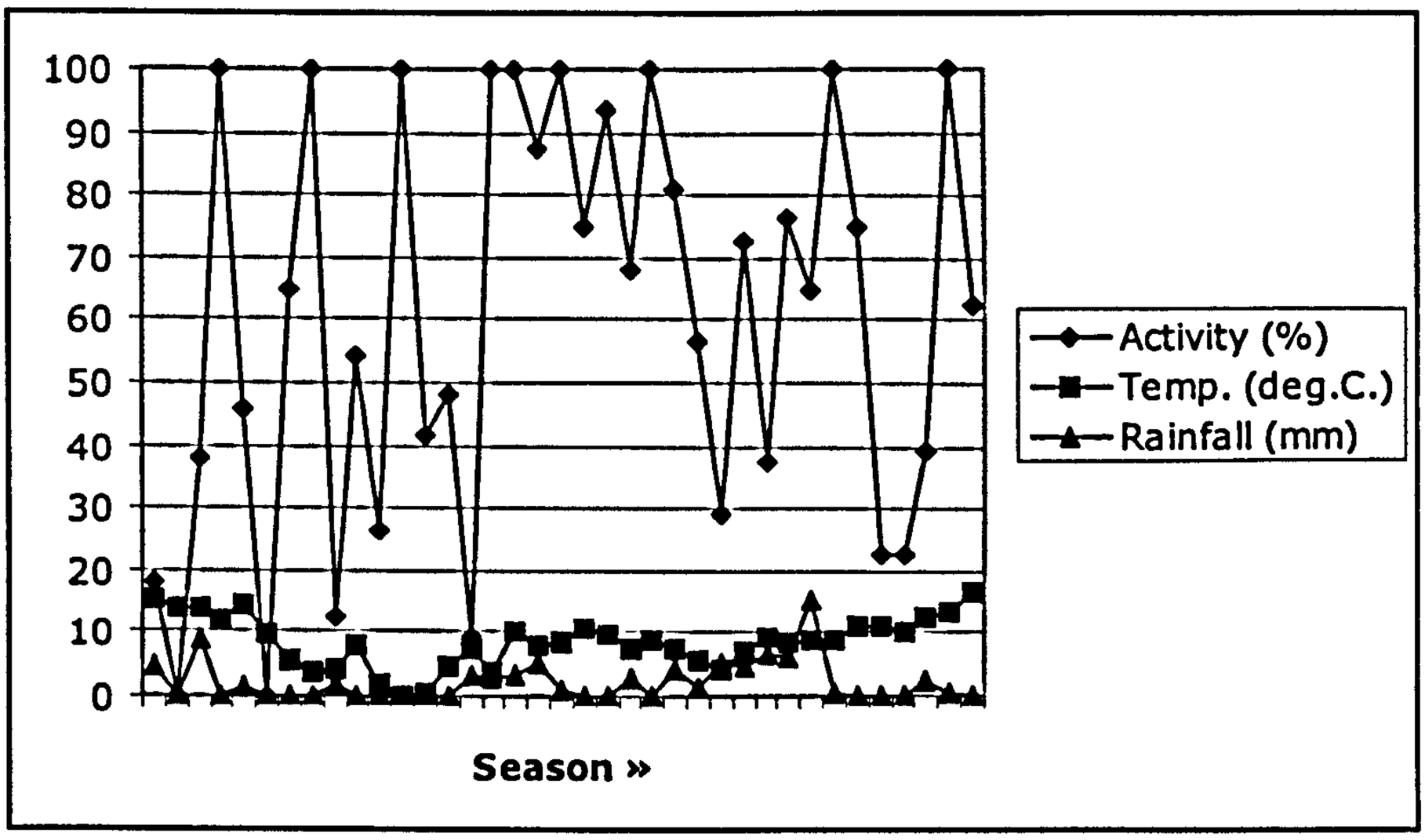


Figure A4.10: BM1 Crepuscular activity

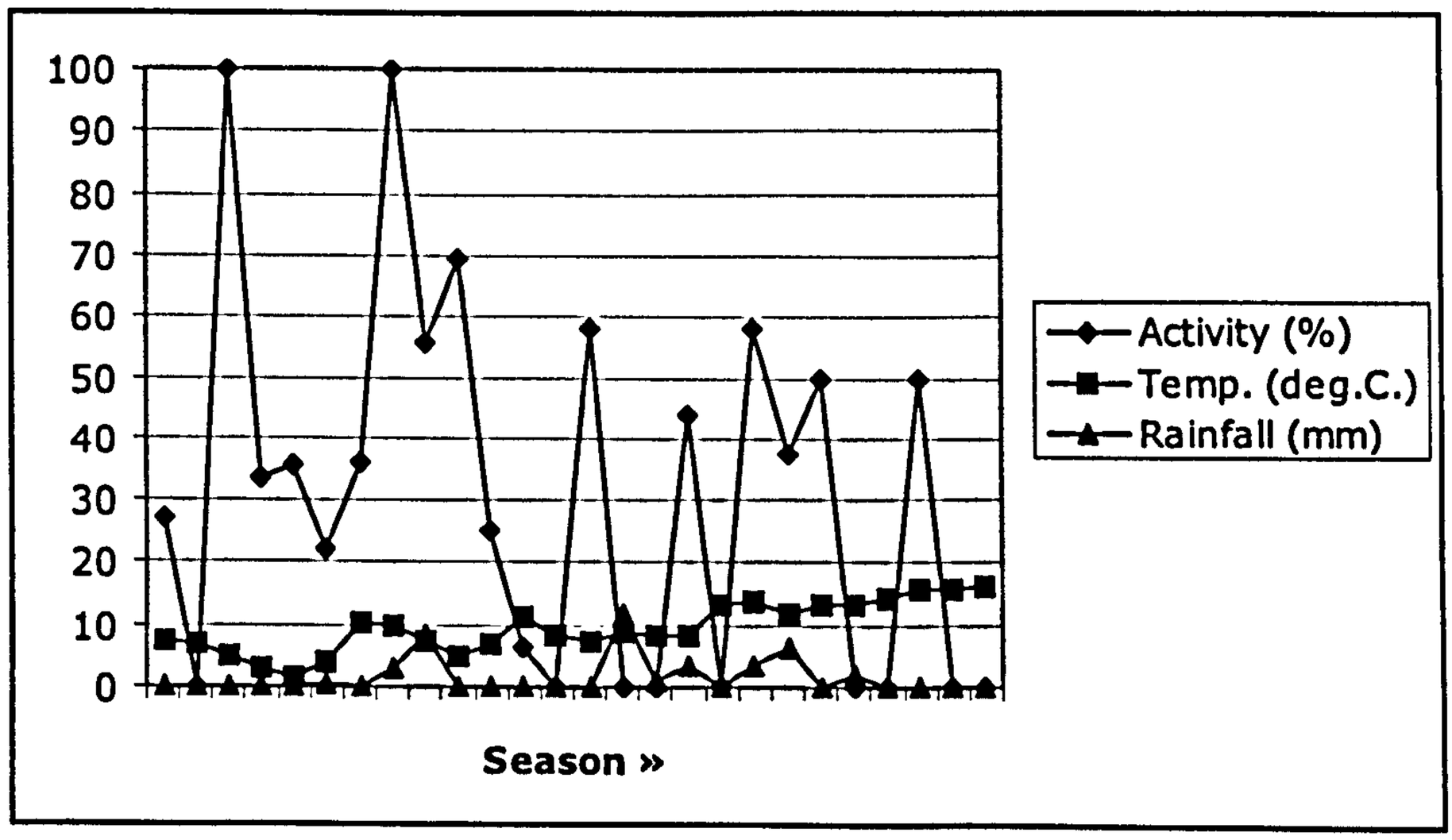


Figure A4.11: BM1 Diurnal activity

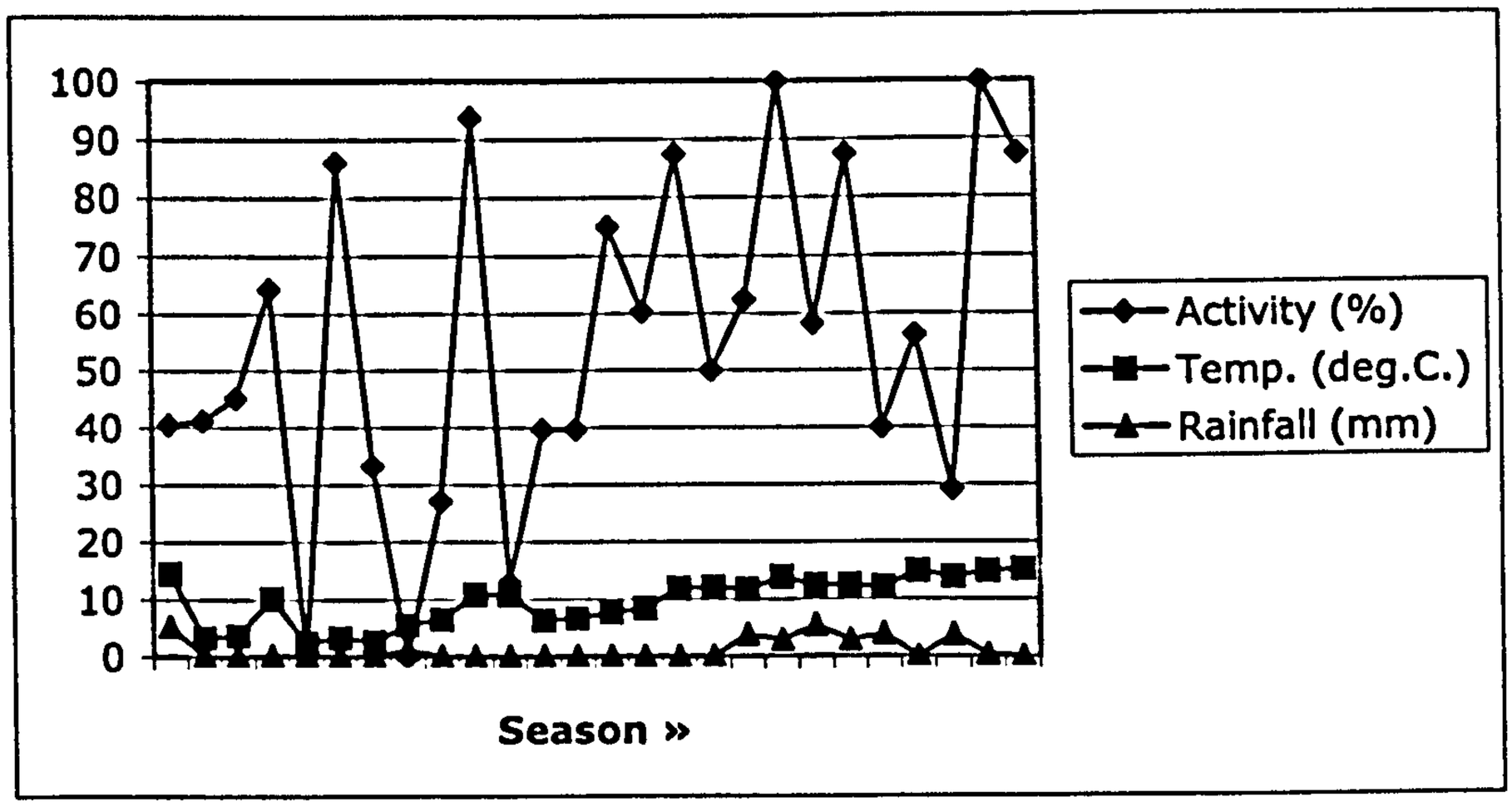


Figure A4.12: BM1 Nocturnal activity

BM2

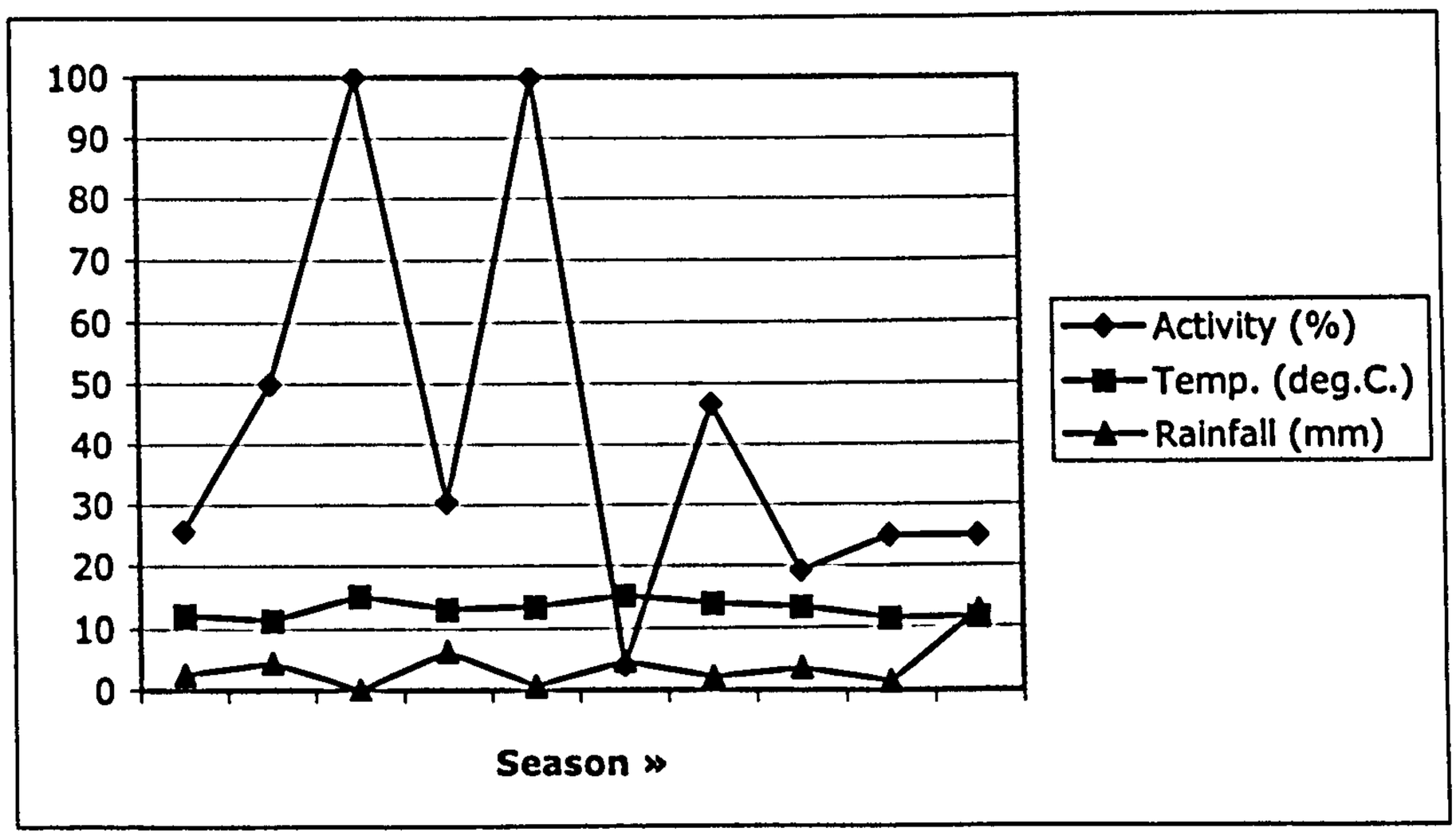


Figure A4.13: BM2 Crepuscular activity

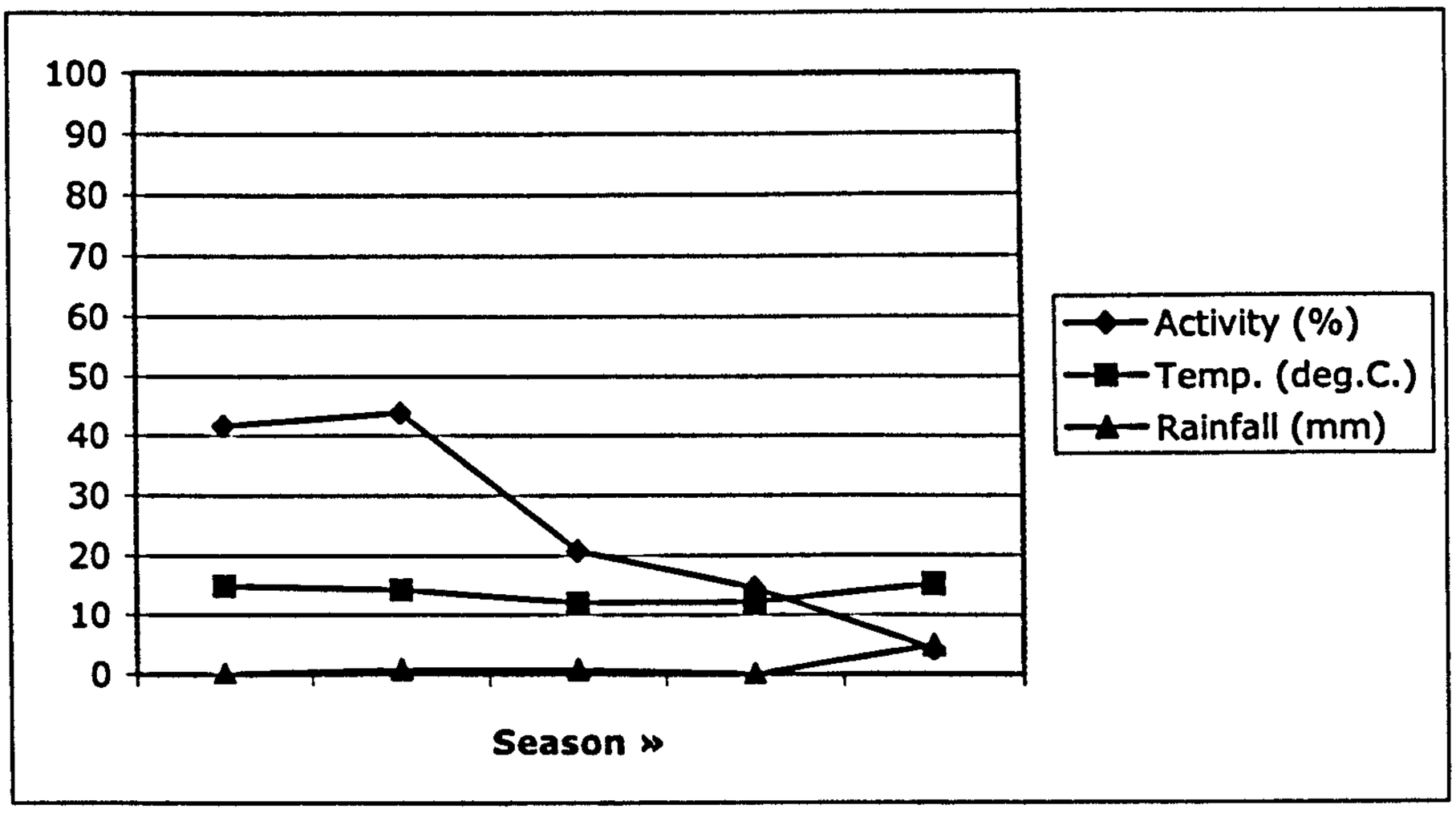


Figure A4.14: BM2 Diurnal activity

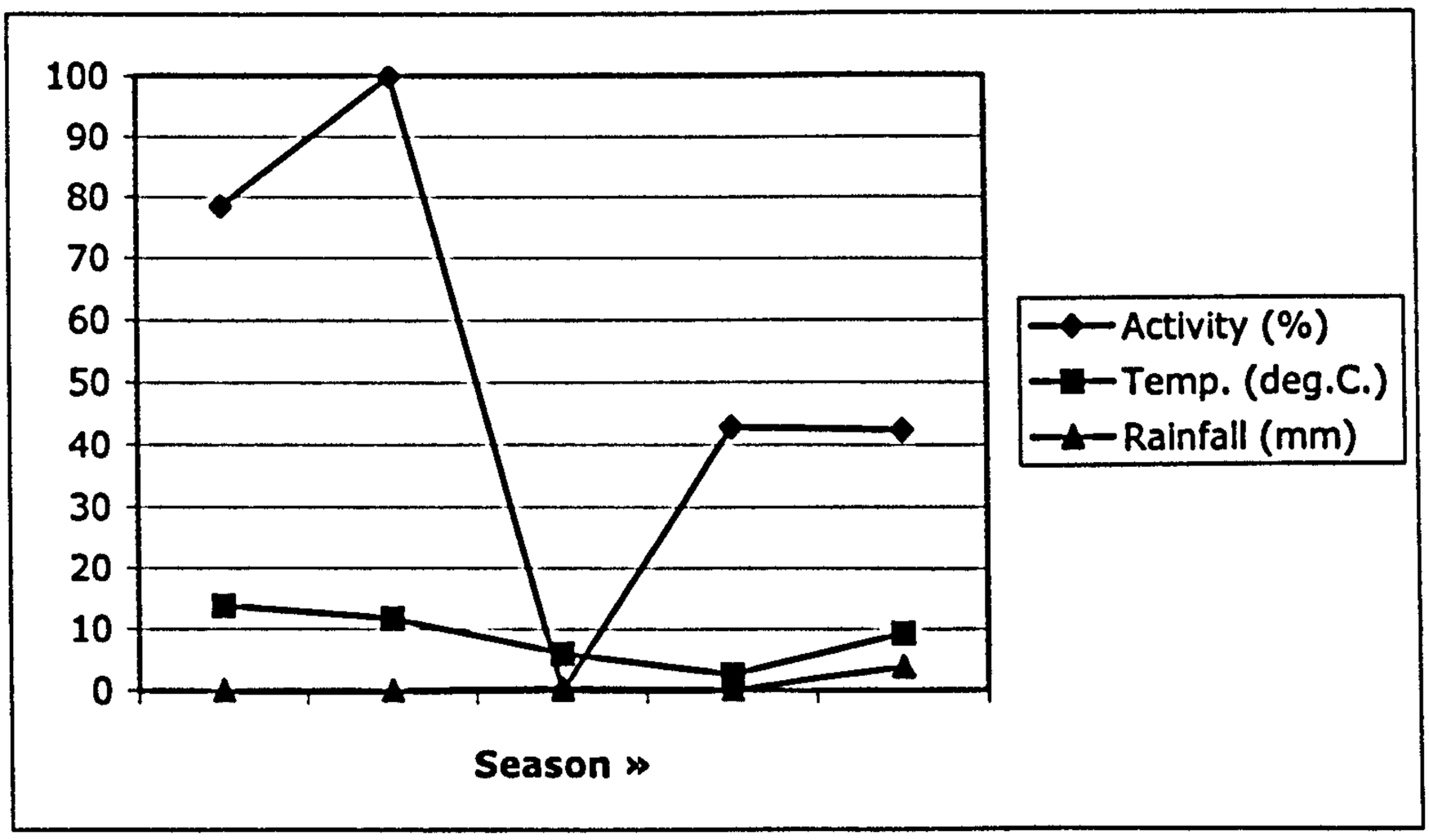


Figure A4.15: BM2 Nocturnal activity

BM3

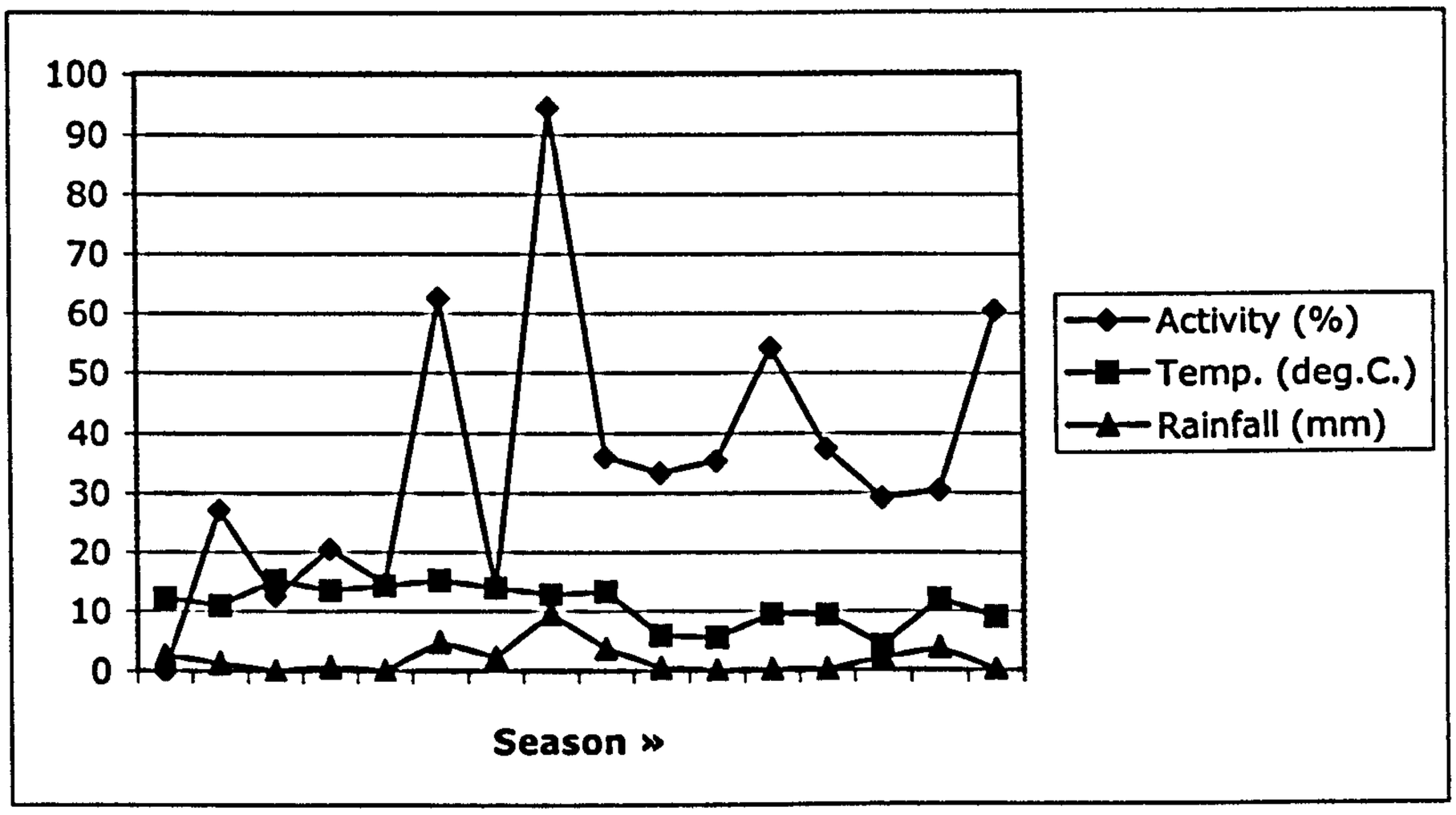


Figure A4.16: BM3 Crepuscular activity

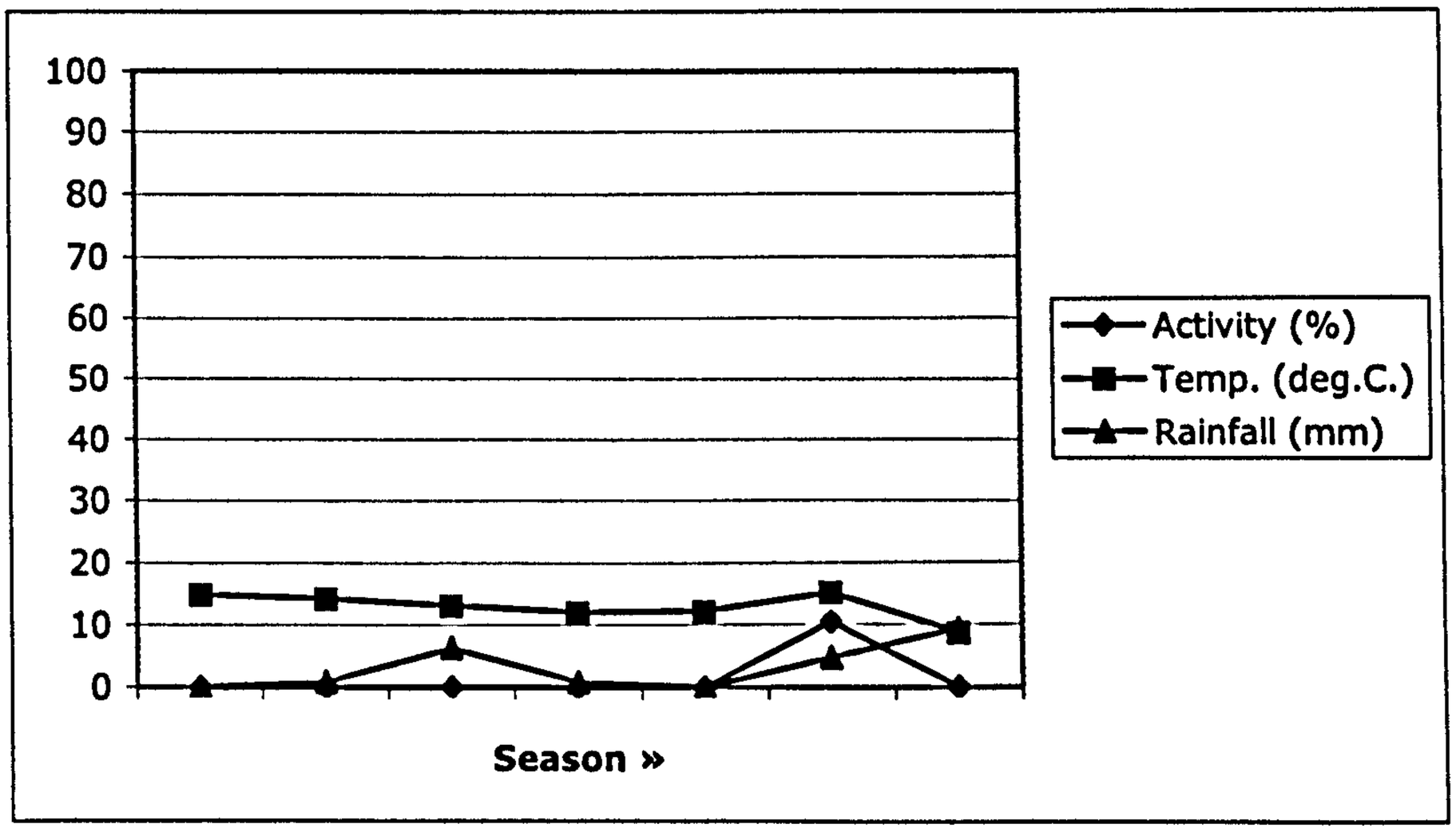


Figure A4.17: BM3 Diurnal activity

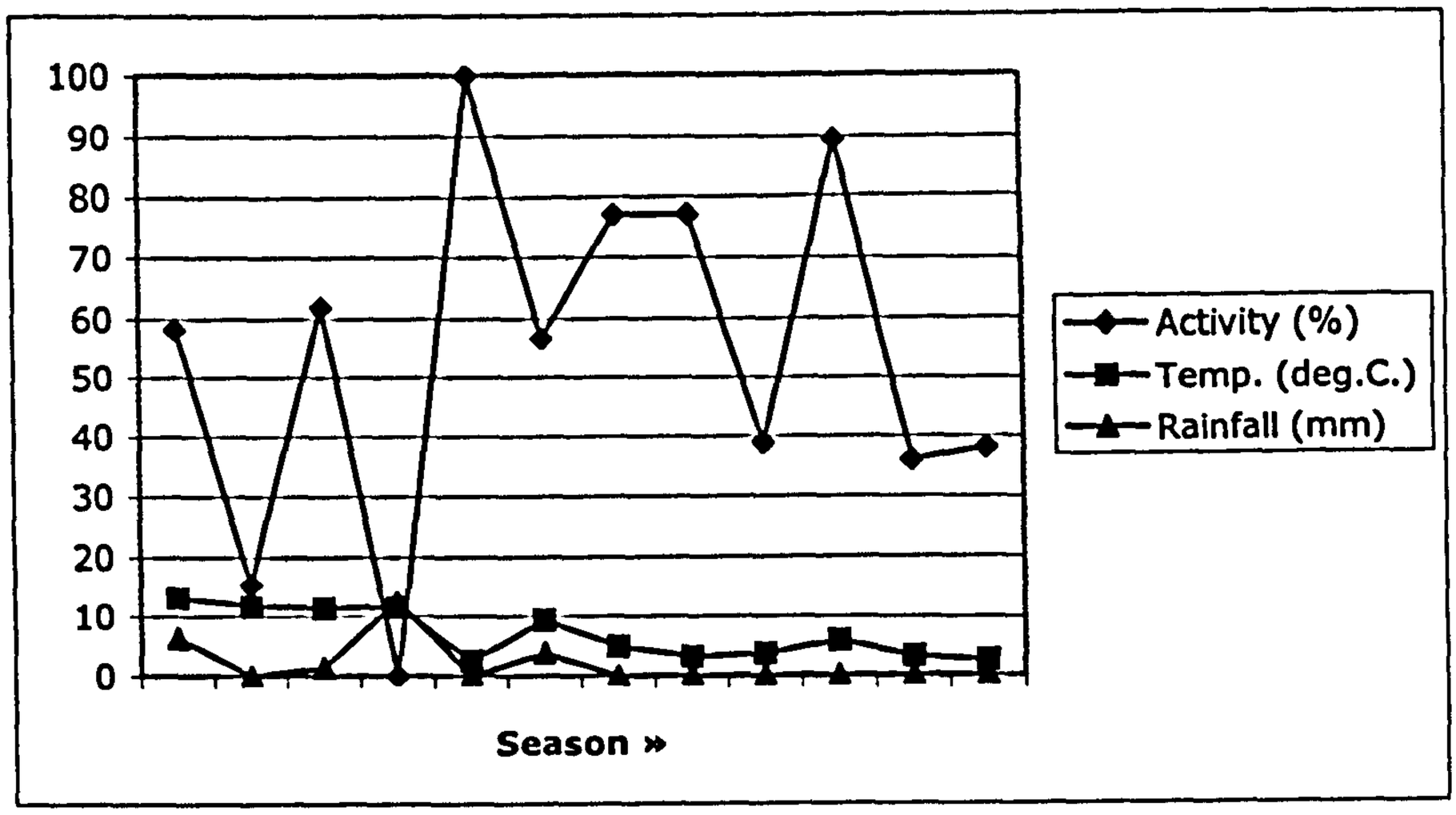


Figure A4.18: BM3 Nocturnal activity

APPENDIX 5: BEHAVIOURAL INTERACTIONS

A5.1 Glebe Farm results

A5.1.1 Male:male dyad results

Table A5.1 shows the matrix of total behavioural interactions between male dyads at Glebe Farm, for the three adult male cats (GM1, GM2 and GM3); Table A5.2 gives the categorised version, as explained in Chapter 4.

Table A5.1: Glebe Farm male:male dyad interactions

	CH	FI	FL	FR	FW	GR	MA	SL	SW	WA	TOTAL
GM1:GM2	0	0	0	0	0	0	1	0	0	2	3
GM1:GM3	4	3	0	0	14	0	0	4	1	1	27
GM2:GM1	0	0	0	0	0	0	0	0	0	3	3
GM2:GM3	3	0	0	0	0	1	0	3	0	2	9
GM3:GM1	0	3	4	0	14	0	0	4	1	1	27
GM3:GM2	0	0	3	1	0	0	0	3	0	2	9
TOTAL	7	6	7	1	28	1	1	14	2	11	78

Table A5.2: Glebe Farm male:male dyad interactions (categorised)

	Aggressive	Contact	Defensive	FW	WA	TOTAL
GM1:GM2	0	0	1	0	5	6
GM1:GM3	7	5	4	14	2	32
GM2:GM3	4	3	1	0	4	12
TOTAL	11	8	6	14	11	50

A5.1.2 Male:female dyad results

Table A5.3 gives the matrix of behavioural interactions between the Glebe Farm adult males and females. For simplification, the categorised version is given.

Table A5.3: Glebe Farm male:female dyad interactions

	Contact	FW	Total
GM1 with females	4	21	25
GM2 with females	18	2	20
GM3 with females	15	15	30
Total	37	38	75

A5.1.3 Male:kitten dyad results

Table A5.4 gives the matrix of behavioural interactions between the Glebe Farm adult males and kittens.

Table A5.4: Glebe Farm male:kitten interactions

	Contact	FW	Total
GM1 with kittens	2	11	13
GM2 with kittens	25	2	27
GM3 with kittens	14	9	23
Total	41	22	63

A5.2 Bryces Farm results

A5.2.1 Male:male dyad results

Tables A5.5-A5.12 show the number and type of interaction of male dyads between September 2001 and July 2002. Categories have been explained in Chapter 4.

Table A5.5: Bryces Farm male:male dyad interactions, Sep-Dec 2001

	Contact	Affiliative	Other	TOTAL
BM1:BM2	0	0	0	**0**
BM1:BM3	1	4	2	**7**
BM1:BM4	3	7	0	**10**
BM2:BM3	0	0	0	**0**
BM2:BM4	6	2	2	**10**
BM3:BM4	6	22	7	**35**
TOTAL	**16**	**35**	**11**	**62**

Table A5.6: Bryces Farm male:male dyad interactions, Jan 2002

	Contact	Affiliative	Other	TOTAL
BM1:BM2	1	0	2	**3**
BM1:BM3	1	6	4	**11**
BM1:BM4	6	11	2	**19**
BM2:BM3	0	0	0	**0**
BM2:BM4	6	4	2	**12**
BM3:BM4	11	26	4	**41**
TOTAL	**25**	**47**	**14**	**86**

As discussed in Chapter 3, Section 3.9.2, BM2 died at the end of January 2002.

Table A5.7: Bryces Farm male:male dyad interactions, Feb 2002

	Contact	Affiliative	Other	TOTAL
BM1:BM3	1	4	3	**8**
BM1:BM4	4	8	3	**15**
BM3:BM4	7	19	5	**31**
TOTAL	**12**	**31**	**11**	**54**

Table A5.8: Bryces Farm male:male dyad interactions, Mar 2002

	Contact	Affiliative	Other	TOTAL
BM1:BM3	6	8	9	**23**
BM1:BM4	2	9	7	**18**
BM3:BM4	10	18	7	**35**
TOTAL	**18**	**35**	**23**	**76**

Table A5.9: Bryces Farm male:male dyad interactions, Apr 2002

	Contact	Affiliative	Other	TOTAL
BM1:BM3	3	11	7	**21**
BM1:BM4	1	6	5	**12**
BM3:BM4	6	12	10	**28**
TOTAL	**10**	**29**	**22**	**61**

Table A5.10: Bryces Farm male:male dyad interactions, May 2002

	Contact	Affiliative	Other	TOTAL
BM1:BM3	2	6	4	**12**
BM1:BM4	2	2	5	**9**
BM3:BM4	3	10	9	**22**
TOTAL	**7**	**18**	**18**	**43**

Table A5.11: Bryces Farm male:male dyad interactions, Jun 2002

	Contact	Affiliative	Other	TOTAL
BM1:BM3	4	6	10	**20**
BM1:BM4	1	7	11	**19**
BM3:BM4	7	12	6	**25**
TOTAL	**12**	**25**	**27**	**64**

Table A5.12: Bryces Farm male:male dyad interactions, Jul 2002

	Contact	Affiliative	Other	TOTAL
BM1:BM3	4	6	10	**20**
BM1:BM4	1	7	11	**19**
BM3:BM4	7	13	6	**26**
TOTAL	**12**	**26**	**27**	**65**

A5.2.2 Female:female dyad results

Tables A5.13-A5.20 show the number and type of interaction of female dyads between September 2001 and July 2002.

Table A5.13: Bryces Farm female:female dyad interactions, Sep-Dec 2001

	Contact	Affiliative	Other	TOTAL
BF1:BF2	0	0	0	**0**
BF1:BF3	0	0	0	**0**
BF1:BF4	0	0	0	**0**
BF2:BF3	51	67	44	**162**
BF2:BF4	28	38	24	**90**
BF3:BF4	19	25	16	**60**
TOTAL	**98**	**130**	**84**	**312**

Table A5.14: Bryces Farm female:female dyad interactions, Jan 2002

	Contact	Affiliative	Other	TOTAL
BF1:BF2	0	0	0	**0**
BF1:BF3	0	0	0	**0**
BF1:BF4	0	0	0	**0**
BF2:BF3	26	43	18	**87**
BF2:BF4	20	17	16	**53**
BF3:BF4	9	11	12	**32**
TOTAL	**55**	**71**	**46**	**172**

Table A5.15: Bryces Farm female:female dyad interactions, Feb 2002

	Contact	Affiliative	Other	TOTAL
BF1:BF2	0	0	0	**0**
BF1:BF3	0	0	0	**0**
BF1:BF4	0	0	0	**0**
BF2:BF3	30	46	15	**91**
BF2:BF4	16	12	16	**44**
BF3:BF4	7	8	11	**26**
TOTAL	**53**	**66**	**42**	**161**

BF1 disappeared at the end of February 2002.

Table A5.16: Bryces Farm female:female dyad interactions, Mar 2002

	Contact	Affiliative	Other	TOTAL
BF2:BF3	36	62	21	**119**
BF2:BF4	14	14	15	**43**
BF3:BF4	10	13	12	**35**
TOTAL	**60**	**89**	**48**	**197**

Table A5.17: Bryces Farm female:female dyad interactions, Apr 2002

	Contact	Affiliative	Other	TOTAL
BF2:BF3	38	66	23	**127**
BF2:BF4	17	14	9	**40**
BF3:BF4	8	18	13	**39**
TOTAL	**63**	**98**	**45**	**206**

Table A5.18: Bryces Farm female:female dyad interactions, May 2002

	Contact	Affiliative	Other	TOTAL
BF2:BF3	39	43	24	**106**
BF2:BF4	13	23	8	**44**
BF3:BF4	7	12	13	**32**
TOTAL	**59**	**78**	**45**	**182**

Table A5.19: Bryces Farm female:female dyad interactions, Jun 2002

	Contact	Affiliative	Other	TOTAL
BF2:BF3	32	34	24	**90**
BF2:BF4	27	16	12	**55**
BF3:BF4	12	19	10	**41**
TOTAL	**71**	**69**	**46**	**186**

Table A5.20: Bryces Farm female:female dyad interactions, Jul 2002

	Contact	Affiliative	Other	TOTAL
BF2:BF3	35	36	31	**102**
BF2:BF4	27	15	15	**57**
BF3:BF4	12	15	9	**36**
TOTAL	**74**	**66**	**55**	**195**

A5.2.3 Male:female dyad results

Tables A5.21-A5.28 show the number and type of interaction of male and female dyads between September 2001 and July 2002.

Table A5.21: Bryces Farm male:female dyad interactions, Sep-Dec 2001

	Contact	Affiliative	Other	TOTAL
BM1:BF1	0	8	0	**8**
BM1:BF2	2	19	0	**21**
BM1:BF3	2	22	0	**24**
BM1:BF4	0	8	1	**9**
BM2:BF1	18	12	12	**42**
BM2:BF2	0	0	0	**0**
BM2:BF3	0	0	0	**0**
BM2:BF4	0	0	0	**0**
BM3:BF1	0	4	0	**4**
BM3:BF2	38	49	23	**110**
BM3:BF3	62	92	22	**176**
BM3:BF4	3	12	2	**17**
BM4:BF1	6	7	2	**15**
BM4:BF2	11	14	9	**34**
BM4:BF3	9	19	7	**35**
BM4:BF4	0	7	1	**8**
TOTAL	**151**	**273**	**79**	**503**

Table A5.22: Bryces Farm male:female dyad interactions, Jan 2002

	Contact	Affiliative	Other	TOTAL
BM1:BF1	0	3	0	**3**
BM1:BF2	1	6	1	**8**
BM1:BF3	3	7	1	**11**
BM1:BF4	1	3	1	**5**
BM2:BF1	10	7	7	**24**
BM2:BF2	0	0	0	**0**
BM2:BF3	0	0	0	**0**
BM2:BF4	0	0	0	**0**
BM3:BF1	0	1	0	**1**
BM3:BF2	18	17	13	**48**
BM3:BF3	31	48	18	**97**
BM3:BF4	16	12	4	**32**
BM4:BF1	1	2	3	**6**
BM4:BF2	3	13	5	**21**
BM4:BF3	3	8	7	**18**
BM4:BF4	1	5	2	**8**
TOTAL	**88**	**132**	**62**	**282**

Table A5.23: Bryces Farm male:female dyad interactions, Feb 2002

	Contact	Affiliative	Other	TOTAL
BM1:BF2	0	3	0	**3**
BM1:BF3	1	8	2	**11**
BM1:BF4	0	1	2	**3**
BM2:BF2	0	0	0	**0**
BM2:BF3	0	0	0	**0**
BM2:BF4	0	0	0	**0**
BM3:BF2	18	29	22	**69**
BM3:BF3	24	43	15	**82**
BM3:BF4	11	10	1	**22**
BM4:BF2	5	3	3	**11**
BM4:BF3	4	5	4	**13**
BM4:BF4	0	3	1	**4**
TOTAL	**63**	**105**	**50**	**218**

Table A5.24: Bryces Farm male:female dyad interactions, Mar 2002

	Contact	Affiliative	Other	TOTAL
BM1:BF2	2	15	2	**19**
BM1:BF3	4	14	4	**22**
BM1:BF4	0	4	1	**5**
BM3:BF2	22	32	20	**74**
BM3:BF3	24	41	25	**90**
BM3:BF4	5	12	5	**22**
BM4:BF2	7	6	8	**21**
BM4:BF3	6	8	10	**24**
BM4:BF4	1	7	1	**9**
TOTAL	**71**	**139**	**76**	**286**

Table A5.25: Bryces Farm male:female dyad interactions, Apr 2002

	Contact	Affiliative	Other	TOTAL
BM1:BF2	4	7	2	**13**
BM1:BF3	6	10	4	**20**
BM1:BF4	1	5	1	**7**
BM3:BF2	19	33	19	**71**
BM3:BF3	21	26	22	**69**
BM3:BF4	6	15	8	**29**
BM4:BF2	10	6	6	**22**
BM4:BF3	12	5	8	**25**
BM4:BF4	3	8	3	**14**
TOTAL	**82**	**115**	**73**	**270**

Table A5.26: Bryces Farm male:female dyad interactions, May 2002

	Contact	Affiliative	Other	TOTAL
BM1:BF2	2	11	1	**14**
BM1:BF3	5	13	4	**22**
BM1:BF4	1	8	1	**10**
BM3:BF2	20	36	13	**69**
BM3:BF3	16	30	22	**68**
BM3:BF4	7	9	6	**22**
BM4:BF2	6	9	10	**25**
BM4:BF3	13	24	10	**47**
BM4:BF4	5	18	6	**29**
TOTAL	**75**	**158**	**73**	**306**

Table A5.27: Bryces Farm male:female dyad interactions, Jun 2002

	Contact	Affiliative	Other	TOTAL
BM1:BF2	4	12	8	**24**
BM1:BF3	6	14	9	**29**
BM1:BF4	2	10	2	**14**
BM3:BF2	16	34	18	**68**
BM3:BF3	17	32	19	**68**
BM3:BF4	6	9	10	**25**
BM4:BF2	7	15	16	**38**
BM4:BF3	13	22	12	**47**
BM4:BF4	9	7	9	**25**
TOTAL	**80**	**155**	**103**	**338**

Table A5.28: Bryces Farm male:female dyad interactions, Jul 2002

	Contact	Affiliative	Other	TOTAL
BM1:BF2	3	15	6	**24**
BM1:BF3	2	18	6	**26**
BM1:BF4	1	10	3	**14**
BM3:BF2	18	29	13	**60**
BM3:BF3	16	38	18	**72**
BM3:BF4	6	15	12	**33**
BM4:BF2	7	19	15	**41**
BM4:BF3	14	23	12	**49**
BM4:BF4	5	9	7	**21**
TOTAL	**72**	**176**	**92**	**340**

APPENDIX 6: MOTHER-OFFSPRING RELATIONSHIPS

A6.1 Mother-offspring results from manual analysis (Tables A6.2-A6.3)

Table A6.1: Legend relating to Tables A6.2, A6.3, A6.4 and A6.5

Symbol	Meaning
Blank space	No relationship found
✓	Possibility of relationship
✓*	Possibility of relationship, but X data at one or more loci for one or both cats
*	Relationship undetermined due to X data at all corresponding loci
a	Impossible relationship due to age of cats (younger individuals cannot be parents of older individuals, or the cats were too young to have produced offspring)
b	Impossible relationship - cat already dead/disappeared before offspring conceived
c	Impossible relationship - mothers already known (from observation: in group-living cats this is generally only possible if no other adult females are pregnant at the time of birth, or the pregnant females are very closely observed)
d	Impossible relationship - cat neutered before first oestrus or at a later known age

For simplicity in Tables A6.2-A6.3, mothers and offspring are only shown where possibilities of relatedness occur for at least one individual mother, i.e. complete rows or columns where mother-offspring relatedness is impossible (refer to Table A6.1 for explanation of impossible relationships), or has not been found, have been omitted.

Table A6.2: Glebe Farm mother-offspring relationship possibilities from manual analysis

Offspring	Mother					
	GF1	GF2	GF3	GF8	GF9	GF13
GM1	✓*			a	a	a
GM3		✓*		a	a	a
GM14	✓*	✓*	✓*	a	a	a
GM15		✓*		✓*	a	a
GM17		✓*	✓*	✓*		
GM19	✓*	✓*	✓*	✓*	✓*	✓*
GF2	✓	—	✓*	a	a	a
GF3	✓*	✓*	—	a	a	a
GF7		✓		a	a	a
GF8	✓	✓	✓*	—	a	a
GF9	✓	✓	✓*	a	—	a
GF10	✓	✓	✓*	a	a	a
GF11	✓	✓	✓*	a	a	a
GF12		✓*		a	a	a
GF13	✓	✓	✓*	a	a	—
GF18	✓			✓		✓

Table A6.3: Bryces Farm and *Treeside* mother-offspring relationship possibilities from manual analysis

	Mother								
Offspring	**BF1**	**BF2**	**BF3**	**BF9**	**BF10**	**BF11**	**BF12**	**BF14**	**BF15**
BM1	a	a	a	✓*	*	✓*	✓*		a
BM2	✓*	✓*	✓*		*	✓*	✓*	✓*	✓*
BM3	a	a	a		*	*	✓*		✓*
BM8	c	✓*	c	c	c	c	c	c	c
BM16	b,c	c	c	✓*	*	✓*	✓*	✓*	✓*
BM18	b,c	c	c		*			✓	✓
BM19	b,c	c	c	✓*	*	✓*	✓*	✓	✓
BM21	b,c	c	c		*			✓*	✓*
BM26	b,c	c	c		*			✓	✓
BM27	b,c	c	c		*	✓*	✓*	✓*	✓*
BM30	b,c	c	c	*	*	*	*	*	*
BF1	—		✓*		*	✓*	✓*	✓*	✓*
BF2	a	—			*			✓*	✓*
BF3	a		—		*	✓*	✓*		
BF5	✓*		✓*	✓*	*	✓*			
BF10	a	a	a	*	—	*	*	a	a
BF11	a	a	a	✓*	*	—	a	a	a
BF12	a	a	a	✓*	a	✓*	—	a	a
BF14	a	a	a		*			—	a
BF15	a	a	a		*			✓	—
BF17	b,c	c	c	✓*	*	✓*	✓*	✓	✓
BF20	b,c	c	c		*			✓	✓
BF22	b,c	c	c		*	✓*	✓*	✓*	✓*
BF23	b,c	c	c	✓*	*	✓*	✓*	✓	✓
BF24	b,c	c	c		*			✓	✓
BF25	b,c	c	c		*			✓	✓
BF28	b,c	c	c	*	*	*	✓*	✓*	✓*
BF29	b,c	c	c	*	*	*	*	*	*
BF31	✓*				*				✓*

A6.2 Mother-offspring results from *Kinship 1.2* (Tables A6.4-A6.6)

Again, complete rows or columns where mother-offspring relatedness is impossible (refer to Table A6.1 for explanation of impossible relationships), or not found, have been omitted.

Table A6.4: Results of significance simulations: mother-offspring

	p <	1,000 simulations		500,000 simulations	
		Ratio	Type II error	Ratio	Type II error
*	**0.05**	4.34+00	0.411	5.03+00	0.453
**	**0.01**	1.16E+01	0.733	1.28E+01	0.760
***	**0.001**	3.23E+01	0.910	3.60E+01	0.930

Table A6.5: Glebe Farm mother-offspring relationship possibilities from *Kinship 2.1*

Offspring	Mother			
	GF1	GF2	GF3	GF8
GM1	*			a
GM17			***	
GF8		**		—
GF9		*		a
GF10		**		***
GF11		**	**	

Table A6.6: Bryces Farm and *Treeside* mother-offspring relationship possibilities from *Kinship 2.1*

Offspring	Mother			
	BF3	BF9	BF14	BF15
BM16	c	*		
BM19	c	*		
BM26	c		*	*
BF1	*			
BF12	a	*	a	a
BF15	a		*	—
BF23	c			*
BF24	c		**	
BF25	c		**	**

APPENDIX 7: PARENT-OFFSPRING RESULTS FROM *KINSHIP 1.2*

For reasons of spatial presentation, the output matrices have been divided into six blocks as explained by Figure A7.1.

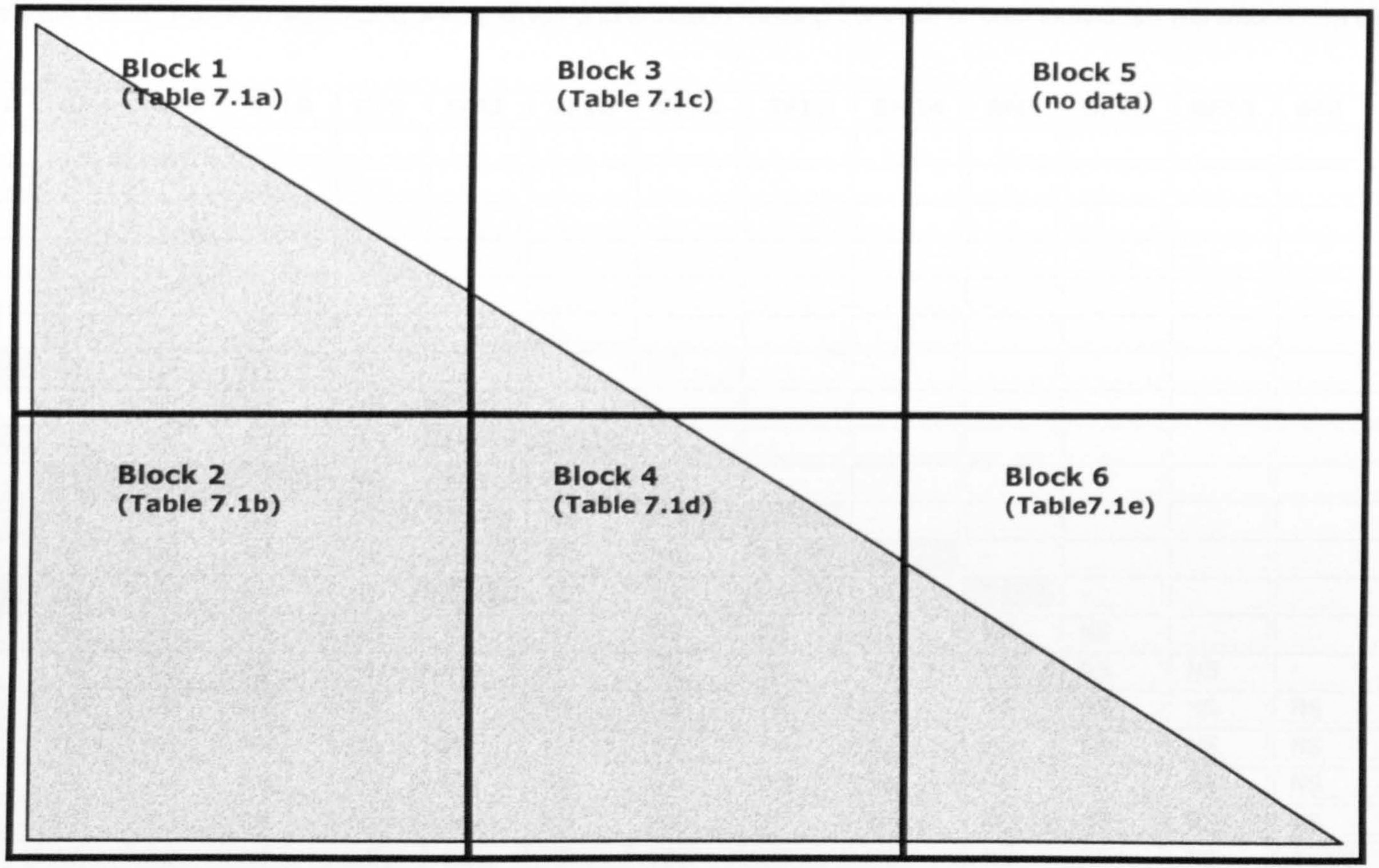


Figure A7.1: Explanation of matrix blocks from Tables A7.1a-e

Table A7.1a: Parent-offspring - Block 1 results of *Kinship 1.2* for 500,000 simulations

Shading indicates significant result; NS=Non-significant; X=Genotyping information missing from one or both individuals (no calculations could be performed)

	GF1	GM1	GF2	GF8	GF10	GF9	GM2	GF16	GF18	GF11	GM14	GM3	GF13	GF12	BF2	BF20	BF14	BF24	BF15	BF25
GF1	-																			
GM1	*	-																		
GF2	NS	NS	-																	
GF8	NS	NS	**	-																
GF10	NS	NS	**	***	-															
GF9	NS	NS	*	NS	NS	-														
GM2	NS	*	NS	NS	NS	NS	-													
GF16	NS	NS	NS	NS	NS	NS	***	-												
GF18	NS	*	NS	NS	NS	NS	*	***	-											
GF11	NS	NS	**	*	*	NS	***	NS	NS	-										
GM14	NS	NS	NS	NS	NS	*	**	NS	*	***	-									
GM3	NS	NS	NS	NS	NS	NS	**	NS	NS	**	*	-								
GF13	NS	*	NS	NS	NS	NS	**	NS	NS	*	NS	**	-							
GF12	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-						
BF2	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-					
BF20	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-				
BF14	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-			
BF24	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	-		
BF15	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	*	-	
BF25	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	**	**	**	-
BM26	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	*	*	**
BF23	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	**
BM21	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	NS	NS
BM1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF32	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF17	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF9	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Table A7.1b: Parent-offspring - Block 2 results of *Kinship 1.2* for 500,000 simulations

Shading indicates significant result; NS=Non-significant; X=Genotyping information missing from one or both individuals (no calculations could be performed)

	GF1	GM1	GF2	GF8	GF10	GF9	GM2	GF16	GF18	GF11	GM14	GM3	GF13	GF12	BF2	BF20	BF14	BF24	BF15	BF25
BM19	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF12	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF11	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	NS	NS
BM16	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	NS	NS
BM2	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF22	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	NS	NS
BM8	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BM27	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
GF7	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
GM15	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF28	NS	X	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X	NS	NS	NS	NS	NS
BM18	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF31	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
GF3	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
GM17	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BM3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	NS
GM19	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	NS
BF13	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	NS
BF10	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
BF29	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
BM30	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Table A7.1c: Parent-offspring - Block 3 results of *Kinship 1.2* for 500,000 simulations

Shading indicates significant result; NS=Non-significant; X=Genotyping information missing from one or both individuals (no calculations could be performed)

	BM26	BF23	BM21	BM1	BF5	BF32	BF17	BF9	BM19	BF12	BF11	BM16	BM2	BF3	BF1	BF22	BM8	BM27	GF7
GF1																			
GM1																			
GF2																			
GF8																			
GF10																			
GF9																			
GM2																			
GF16																			
GF18																			
GF11																			
GM14																			
GM3																			
GF13																			
GF12																			
BF2																			
BF20																			
BF14																			
BF24																			
BF15																			
BF25																			
BM26	-																		
BF23	**	-																	
BM21	NS	NS	-																
BM1	NS	NS	NS	-															
BF5	NS	NS	NS	***	-														
BF32	NS	NS	NS	**	**	-													
BF17	NS	NS	NS	**	**	*	-												
BF9	NS	*	NS	**	*	*	*	-											

Table A7.1d: Parent-offspring - Block 4 results of *Kinship 1.2* for 500,000 simulations

Shading indicates significant result; NS=Non-significant; X=Genotyping information missing from one or both individuals (no calculations could be performed)

	BM26	BF23	BM21	BM1	BF5	BF32	BF17	BF9	BM19	BF12	BF11	BM16	BM2	BF3	BF1	BF22	BM8	BM27	GF7
BM19	NS	NS	NS	*	NS	*	*	*	-										
BF12	NS	NS	NS	*	NS	NS	NS	*	*	-									
BF11	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	-								
BM16	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	-							
BM2	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-						
BF3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	-					
BF1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	*	-				
BF22	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-			
BM8	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-		
BM27	NS	NS	NS	*	*	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-	
GF7	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-
GM15	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*
BF28	NS	NS	X	NS	NS	X	NS	X	NS	NS	X	X	NS	X	X	X	NS	X	NS
BM18	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BF31	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
GF3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
GM17	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
BM3	NS	NS	X	NS	NS	NS	NS	NS	NS	NS	X	X	NS	NS	NS	X	NS	NS	NS
GM19	NS	NS	X	NS	NS	X	NS	NS	NS	NS	X	X	NS	NS	NS	X	NS	X	NS
BF13	NS	NS	X	NS	NS	X	NS	NS	NS	NS	X	X	NS	NS	NS	X	NS	X	NS
BF10	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
BF29	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
BM30	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Table A7.1e: Parent-offspring - Block 6 results of *Kinship 1.2* for 500,000 simulations

Shading indicates significant result; NS=Non-significant; X=Genotyping information missing from one or both individuals (no calculations could be performed)

	GM15	BF28	BM18	BF31	GF3	GM17	BM3	GM19	BF13	BF10	BF29	BM30
BM19												
BF12												
BF11												
BM16												
BM2												
BF3												
BF1												
BF22												
BM8												
BM27												
GF7												
GM15	-											
BF28	NS	-										
BM18	NS	NS	-									
BF31	NS	NS	NS	-								
GF3	NS	NS	NS	NS	-							
GM17	NS	NS	NS	NS	***	-						
BM3	NS	X	NS	NS	NS	NS	-					
GM19	NS	X	NS	X	NS	NS	NS	-				
BF13	NS	X	NS	X	NS	NS	NS	NS	-			
BF10	X	X	X	X	X	X	X	X	X	-		
BF29	X	X	X	X	X	X	X	X	X	X	-	
BM30	X	X	X	X	X	X	X	X	X	X	X	-

REFERENCES

Ambs, S. M., Boness, D. J., Bowen W. D., Perry, E. A. and Fleischer, R.C. 1999. Proximate factors associated with high levels of extraconsort fertilization in polygynous grey seals. *Animal Behaviour* 58:527-535.

Amos, W., Worthington Wilmer, J., Fullard, K., Burg, T. M., Croxall, J. P., Bloch, D and Coulson, T. 2001. The influence of parental relatedness on reproductive success. *Proceedings of the Royal Society of London (B)* 268:2021-2027.

Anon. 1995. Cat and dog ownership and product trends. *Anthrozoos* 8:55.

Anon. 1998. Feral cat contraceptive genetically engineered. *American Journal of Veterinary Research* 59:373.

Anon. 1999. No-kill program to help fix feral feline problem in California. *Journal of the American Veterinary Medical Association* 215:762.

Apollonio, M., Festa-Bianchet, M. and Mari, F. 1989. Correlates of copulatory success in a fallow deer lek. *Behavioral Ecology and Sociobiology* 25:89-97.

Apps, P. J. 1983. Aspects of the ecology of feral cats on Dassen Island, South Africa. *South African Journal of Zoology* 18:393-399.

Apps, P. J. 1986. Home ranges of feral cats on Dassen Island. *Journal of Mammalogy* 67:199-200.

Arnemo, J. M., Linnell, J. D. C., Wedul, S. G., Ranheim, B., Odden, J. and Andersen, R. 1999. Use of intraperitoneal radio-transmitters in lynx *Lynx lynx* kittens: anaesthesia, surgery and behaviour. *Wildlife Biology* 5:245-250.

Asa, C. S. 1999. Male reproductive success in free-ranging feral horses. *Behavioral Ecology & Sociobiology* 47:89-93.

Bales, K., French, J. A. and. Dietz, J. M. 2002. Explaining variation in maternal care in a cooperatively breeding mammal. *Animal Behaviour* 63:453-461.

Barratt, D. G. 1997. Home range size, habitat utilisation and movement patterns of suburban and farm cats *Felis catus*. *Ecography* 20:271-280.

Bartmann, S., and Gerlach, G. 2001. Multiple paternity and similar variance in reproductive success of male and female wood mice (*Apodemus sylvaticus*) housed in an enclosure. *Ethology* 107:889-899.

Bennett, M., Lloyd, G., Jones, N., Brown, A., Trees, A. J., McCracken, C., Smyth, N. R., Gaskell, C. J. and Gaskell, R. M. 1990. Prevalence of antibody to hantavirus in some cat populations in Britain. *Veterinary Record* 127:548-549.

Berteaux, D., Duhamel, R. and Bergeron, J. 1994. Can radio collars affect dominance relationships in *Microtus*? *Canadian Journal of Zoology* 72:785-789.

Bester, M. N., Bloomer, J. P., Bartlett, P. A., Muller, D. D., Van Rooyen, M. and Buchner, H. 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research* 30:53-57.

Bester, M. N., Bloomer, J. P., Van Aarde, R. J., Erasmus, B. H, Van Rensburg, P. J. J., Skinner, J. D., Howell, P. G. and Naude, T. W. 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* 32:65-73.

Bloomer, J. P. and Bester, M. N. 1990. Diet of a declining feral cat *Felis catus* population on Marion Island. *South African Journal of Wildlife Research* 20:1-4.

Bloomer, J. P. and Bester, M. N. 1991. Effects of hunting on population characteristics of feral cats on Marion Island. *South African Journal of Wildlife Research* 21:97-102.

Boitani, L. 2001. Carnivore introductions and invasions: their success and management options. *In* Carnivore Conservation, Conservation Biology Series 5. (Ed. J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne) Cambridge University Press, Cambridge: 123-144.

Braastad, B. O. and Bakken, M. 2002. Behaviour of dogs and cats. *In* The Ethology of Domestic Animals - an Introductory Text. (Ed. P. Jensen) CABI, Wallingford: 173-192.

Bradshaw, J. W. S. 1992. *The Behaviour of the Domestic Cat.* CABI, Wallingford.

Bradshaw, J. W. S. 1993. *The True Nature of the Cat.* Boxtree Ltd., London.

Bradshaw, J. W. S. and Cameron-Beaumont, C. 2000. The signalling repertoire of the domestic cat and its undomesticated relatives. *In* The Domestic Cat - the Biology of its Behaviour. 2nd edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 67-93.

Bradshaw, J. W. S., Healey, L. M., Thorne, C. J., Macdonald, D. W. and Arden-Clark, C. 2000. Differences in food preferences between individuals and populations of domestic cats *Felis silvestris catus. Applied Animal Behaviour Science* 68:257-268.

Bradshaw, J. W. S., Horsfield, G. F., Allen, J. A. and Robinson, I. H. 1999. Feral cats: their role in the population dynamics of *Felis catus*. *Applied Animal Behaviour Science* 65:273-283.

Broom, M. 2002. A unified model of dominance hierarchy formation and maintenance. *Journal of Theoretical Biology* 219:63-72.

Brothers, N. P., Skira, I. J. and Copson, G. R. 1985. Biology of the feral cat, *Felis catus* (L.), on Macquarie Island. *Australian Wildlife Research* 12:425-436.

Brown, S. L. 1993. The Social Behaviour of Neutered Domestic Cats (*Felis catus*). Unpublished PhD thesis, University of Southampton.

Buckley, N. J. and Ruxton, G. D. 2003. The resource dispersion hypothesis and the "future value" of food. *Trends in Ecology and Evolution* 18:379.

Burbidge, A. A. and Manly, B. F. J. 2002. Mammal extinctions on Australian islands: causes and conservation implications. *Journal of Biogeography* 29:465-473.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.

Calhoon, R. E. and Haspel, C. 1989. Urban cat populations composed by season, subhabitat and supplemental feeding. *Journal of Animal Ecology* 58:321-328.

Capuano, S. V., Lerche, N. W. and Valverde, C. R. 1999. Cardiovascular, respiratory, thermoregulatory, sedative, and analgesic effects of intravenous administration of medetomidine in rhesus macaques (*Macaca mulatta*). *Laboratory Animal Science* 49:537-544.

Carpenter, M. A., Brown, E. W., Macdonald, D. W. and O'Brien, S. J. 1998. Phylogeographic patterns of feline immunodeficiency virus genetic diversity in the domestic cat. *Virology* 251:234-243.

Carr, G. M. and Macdonald, D. W. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour* 34:1540-1549.

Caulkett, N. A., Cattet, M. R. L, Caulkett, J. M and Polischuk, S. C. 1999. Comparative physiologic effects of Telazol, Medetomidine-Ketamine, and Medetomidine-Telazol in captive polar bears (*Ursus maritimus*). *Journal of Zoo and Wildlife Medicine* 30:504-509.

Centonze, L. A. and Levy, J. K. 2002. Characteristics of free-roaming cats and their caretakers. *Journal of the American Veterinary Medical Association* 11:1627-1633.

Church, S. C., Allen, J. A. and Bradshaw, J. W. S. 1996. Frequency-dependent food selection by domestic cats: a comparative study. *Ethology* 102:495-509.

Clapperton, B. K., Eason, C. T., Weston, R. J., Woolhouse, A. D. and Morgan, D. R. 1994. Development and testing of attractants for feral cats, *Felis catus* L. *Wildlife Research* 21:389-399.

Clark, J. M. 1975. The effects of selection and human preference on coat colour gene frequencies in urban cats. *Heredity* 35:195-210.

Clarke, A. L. and Pacin, T. 2002. Domestic cat "colonies" in natural areas: a growing exotic species threat. *Natural Areas Journal* 22:154-159.

Clutton-Brock, J. 1995. Origins of the dog: domestication and early history. *In* The Domestic Dog - its Evolution, Behaviour and Interactions with People. (Ed. J. A. Serpell) Cambridge University Press, Cambridge: 7-20.

Clutton-Brock, J. 1996. Competitors, companions, status symbols, or pests: a review of human associations with other carnivores. *In* Carnivore Behavior, Ecology and Evolution, vol. 2. (Ed. J. L. Gittleman) Cornell University Press, New York: 375-392.

Clutton-Brock, T. H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London (B)* 236:339-372.

Clutton-Brock, T. H. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69-72.

Coltman, D. W., Bancroft, D. R., Robertson, A., Smith, J. A., Clutton-Brock, T. H. and Pemberton, J. M. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology* 8:1199-1209.

Cooney, R. and Bennett, N. C. 2000. Inbreeding avoidance and reproductive skew in a cooperative mammal. *Proceedings of the Royal Society of London (B)* 267:801-806.

Corbett, L. K. 1979. The feeding ecology and social organisation of wildcats (*Felis silvestris*) and domestic cats (*Felis catus*) in Scotland. Unpublished PhD thesis, University of Aberdeen.

Courchamp, F., Chapuis, J. L. and Pascal, M. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78: 347-383.

Creel, S. and Macdonald, D. W. 1995. Sociality, group size and reproductive suppression among carnivores. *Advances in the Study of Behavior* 24:203-257.

Cromwell-Davis, S. L., Barry, K. and Wolfe, R. 1997. Social behavior and aggressive problems of cats. *Veterinary Clinics of North America: Small Animal Practice* 27:549-568.

Cullen, L. K. 1996. Medetomidine sedation in dogs and cats: a review of its pharmacology, antagonism and dose. *British Veterinary Journal* 152:519-535.

Cullen, L. K. 1999. Xylazine and medetomidine in small animals: these drugs should be used carefully. *Australian Veterinary Journal* 77:722-723.

Curtis, T. M., Knowles, R. J. and Cromwell-Davis, S. L. 2003. Influence of familiarity and relatedness on proximity and allogrooming in domestic cats (*Felis catus*). *American Journal of Veterinary Research* 64:1151-1154.

Cypher, B. L. 1997. Effects of radiocollars on San Joaquin kit foxes. *Journal of Wildlife Management* 61:1412-1423.

Daniels, M. J., Balharry, D., Hirst, D., Kitchener, A. C. and Aspinall, R. J. 1998. Morphological and pelage characteristics of wild living cats in Scotland: implications for defining the "wildcat". *Journal of Zoology (London)* 244:231-247.

Daniels, T. J. and Bekoff, M. 1989. Feralization - the making of wild domestic animals. *Behavioural Processes* 19:79-94.

Dards, J. L. 1978. Home ranges of feral cats in Portsmouth dockyard. *Carnivore Genetics Newsletter* 3:242-255.

Dards, J. L. 1983. The behaviour of dockyard cats: interactions of adult males. *Applied Animal Ethology* 10:133-153.

Dards, J. L. and Robinson, R. 1983. Gene frequencies in a population of feral cats in Portsmouth Naval Dockyard. *Theoretical and Applied Genetics* 64:197-204.

Deag, J. M., Manning, A. and Lawrence, C. E. 2000. Factors influencing the mother-kitten relationship. *In* The Domestic Cat - the Biology of its Behaviour. 2nd edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 23-45.

Denny, E., Yakovlevich, P., Eldridge, M. D. B. and Dickman, C. 2002. Social and genetic analysis of a population of free-living cats (*Felis catus* L.) exploiting a resource-rich habitat. *Wildlife Research* 29:405-413.

Devillard, S., Say, L. and Pontier, D. 2003. Dispersal patterns of domestic cats (*Felis catus*) in a promiscuous urban population: do females disperse or die? *Journal of Animal Ecology* 72:203-211.

Dewsbury, D. A. 1982. Dominance rank, copulatory behavior, and differential reproduction. *The Quarterly Review of Biology* 57:135-159.

DeYoung, R. W., Demarais, S., Gonzales, R. A., Honeycutt, R. L. and Gee, K. L. 2002. Multiple paternity in white-tailed deer (*Odocoileus virginianus*) revealed by DNA microsatellites. *Journal of Mammalogy* 83:884-892.

Doncaster, C. P. 1990. Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology* 143:431-443.

Doncaster, C. P. and Macdonald, D. W. 1991. Drifting territoriality in the red fox, *Vulpes vulpes*. *Journal of Animal Ecology* 60: 423-439.

Drews, C. 1993. The concept and definition of dominance in animal behavior. *Behaviour* 125:283-313.

Dytham, C. 1999. *Choosing and Using Statistics - a Biologist's Guide.* Blackwell Science, Oxford.

Eason, C. T. and Frampton, C. M. 1991. Acute toxicity of sodium monofluoroacetate (1080) baits to feral cats. *Wildlife Research* 18:445-449.

Eaton, R. L. 1978. Why some felids copulate so much. A model for the evolution of copulation frequency. *Carnivore* 1:42-51.

Edwards, G. P., DePreu, N. D., Shakeshaft, B. J. and Crealy, I. V. 2000. An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildlife Research* 27:143-149.

Edwards, G. P., DePreu, N. D., Shakeshaft, B. J., Crealy, I. V. and Paltridge, R. M. 2001. Home range and movements of male feral cats (*Felis catus*) in a semiarid woodland environment in central Australia. *Austral Ecology* 26:93-101.

Edwards, G. P., Piddington, K. C. and Paltridge, R. M. 1997. Field evaluation of olfactory lures for feral cats (*Felis catus* L.) in central Australia. *Wildlife Research* 24:173-183.

Eidson, M., Tierney, L. A., Rollag, O. J., Becker, T., Brown, T. and Hull, H. F. 1988. Feline plague in New Mexico: risk factors and transmission to humans. *American Journal of Public Health* 78:1333-1335.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethology and Sociobiology* 16:257-333.

Fagen, R. M. 1978. Population structure and social behavior in the domestic cat (*Felis catus*). *Carnivore Genetics Newsletter* 3:276-282.

Fisher, D. O. and Lara, M. C. 1999. Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies. *Animal Behaviour* 58:121-130.

Fitzgerald, B. M. and Karl, B. J. 1986. Home range of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Ecology* 9:71-81.

Fitzgerald, B. M., Karl, B. J. and Veitch, C. R. 1991. The diet of feral cats (*Felis catus*) on Raoul Island, Kermadec Group. *New Zealand Journal of Ecology* 15:123-129.

Fitzgerald, B. M. and Veitch, C. R. 1985. The cats of Herekopare Island, New Zealand - their history, ecology and effects on birdlife. *New Zealand Journal of Zoology* 12:319-330.

Forsyth, S. F., Machon, R. G. and Walsh, V. P. 1999. Anaesthesia of a Sumatran tiger on eight occasions with ketamine, medetomidine and isoflurane. *New Zealand Veterinary Journal* 47:105-108.

Fowler, J., Cohen, L. and Jarvis, P. 1998. *Practical Statistics for Field Biology*. 2nd edition. John Wiley and Sons Ltd., Chichester.

Frenkel, J. K. 1973. Toxoplasma in and around us. *Bioscience* 23:343-352.

Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton University Press, Princeton.

Fuller, T. K. and Sievert, P. R. 2001. Carnivore demography and the consequences of changes in prey availability. *In* Carnivore Conservation, Conservation Biology Series 5. (Ed. J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne) Cambridge University Press, Cambridge: 163-178.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection and importance. *In* Research Techniques in Animal Ecology - Controversies and Consequences. Methods and Cases in Conservation Science. (Ed. L. Boitani and T. K. Fuller) Columbia University Press, New York: 111-164.

Gehrt, S. D. and Fritzell, E. K. 1998. Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. *Animal Behaviour* 55:1211-1227.

Genovesi, P., Besa, M. and Toso, S. 1995. Ecology of a feral cat *Felis catus* population in an agricultural area of northern Italy. *Wildlife Biology* 1:223-237.

Gibson, K., Keizer, K. and Golding, C. 2002. A trap, neuter, and release program for feral cats on Prince Edward Island. *Canadian Veterinary Journal* 43:695-698.

Gittleman, J. L. 1989. Carnivore group living: comparative trends. *In* Carnivore Behavior, Ecology and Evolution, vol. 1. (Ed. J. L. Gittleman) Cornell University Press, New York: 183-207.

Gompper, M. E. and Wayne, R. K. 1996. Genetic relatedness among individuals within carnivore societies. *In* Carnivore Behavior, Ecology and Evolution, vol. 2. (Ed. J. L. Gittleman) Cornell University Press, New York: 429-452.

Goodnight, K. F. and Queller, D. C. 1999. Computer software for performing likelihood tests of pedigree relationships using genetic markers. *Molecular Ecology* 8:1231-1234.

Goodrowe, K. L. 1992. Feline reproduction and artificial breeding technologies. *Animal Reproduction Science* 28:389-397.

Goodrowe, K. L., Walker, S. L., Ryckman, D. P., Mastromonaco, G. F., Hay, M. A., Bateman, H. L. and Waddell, W. T. 2000. Piecing together the puzzle of carnivore reproduction. *Animal Reproduction Science* 60:389-403.

Gorman, M. L. and Trowbridge, B. J. 1989. The role of odor in the social lives of carnivores. *In* Carnivore Behavior, Ecology and Evolution, vol. 1. (Ed. J. L. Gittleman) Cornell University Press, New York: 57-88.

Gorman, S. P., Levy, J. K., Hampton, A. L., Collante, W. R., Harris, A. L. and Brown, R. G. 2002. Evaluation of a porcine zona pellucida vaccine for the immunocontraception of domestic kittens (*Felis catus*). *Theriogenology* 58:135-149.

Gottelli, D., Sillero Zubiri C., Applebaum, G. D., Roy, M. S., Girman, D. J., Garcia-Moreno, J., Ostrander, E. A. and Wayne, R. K. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf, *Canis simensis*. *Molecular Ecology* 3:301-312.

Greene, S. A. 1999. Pros and cons of using α-2 agonists in small animal anesthesia practice. *Clinical Techniques in Small Animal Practice* 14:10-14.

Griffin, B. 2001. Prolific cats: the impact of their fertility on the welfare of the species. *Compendium* 23:1058-1066.

Gross, E. M., Holda G. and Saheh, T. 1996. Opposition to trap-sterilize-release programs for feral cats. *Journal of the American Veterinary Medical Association* 208:1380-1381.

Gunn-Moore, D. A., Jenkins, P. A. and Lucke, V. M. 1996. Feline tuberculosis: a literature review and discussion of 19 cases caused by an unusual mycobacterial variant. *The Veterinary Record* 138:53-58.

Gunther, I. and Terkel, J. 2002. Regulation of free-roaming cat (*Felis silvestris catus*) populations: a survey of the literature and its application to Israel. *Animal Welfare* 11:171-188.

Hall, L. S., Kasparian, M. A, Van Vuren, D. and Kelt, D. A. 2000. Spatial organization and habitat use of feral cats (*Felis catus* L.) in Mediterranean California. *Mammalia* 64:19-28.

Hardy, M. P., Sottas, C. M., Ge, R., McKittrick, C. R., Tamashiro, K. L., McEwan, B. S., Haider, S. G., Markham, C. M., Blanchard, R. J., Blanchard, D. C. and Sakai, R. R. 2002. Trends of reproductive hormones in male rats during psychosocial stress: role of glucocorticoid metabolism in behavioral dominance. *Biology of Reproduction* 67:1750-1755.

Harley, E. H. and Baumgarten, I. 2000. The use of DNA microsatellite markers for determining paternity in a captive cheetah population. *South African Journal of Wildlife Research* 30:22-25.

Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T. and Wray, S. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20:97-123.

Hart, B. L. and Barrett, R. E. 1973. Effects of castration on fighting, roaming, and urine spraying in adult male cats. *Journal of the American Veterinary Medical Association* 163:290-292.

Hart, B. L. and Leedy, M. G. 1987. Stimulus and hormonal determinants of flehmen behavior in cats. *Hormones and Behavior* 21:44-52.

Haspel, C. and Calhoon, R. E. 1989. Home ranges of free-ranging cats (*Felis catus*) in Brooklyn, New York. *Canadian Journal of Zoology* 67:178-181.

Haulena, M., Gulland, F. M. D., Calkins, D. G. and Spraker, T. R. 2000. Immobilization of California sea lions using medetomidine plus ketamine with and without isoflurane and reversal with atipamezole. *Journal of Wildlife Diseases* 36:124-130.

Herrera, E. A. and Macdonald, D. W. 1993. Aggression, dominance, and mating success among capybara males (*Hydrochaeris hydrochaeris*). *Behavioral Ecology* 4:114-119.

Hilsenroth, R. 1999. Feral cat colonies: controlling overpopulation and addressing the issue of parasitology. *Feline Practice* 27:24.

Hirotani, A. 1994. Dominance rank, copulatory behaviour and estimated reproductive success in male reindeer. *Animal Behaviour* 48:929-936.

Horner, M. A. and Powell R. A. 1990. Internal structure of home ranges of black bears and analyses of home-range overlap. *Journal of Mammalogy* 71:402-410.

Horsfield, G. F. 1998. Behavioural Aspects of the Population Genetics of the Domestic Cat. Unpublished PhD thesis, University of Southampton.

Hosken, D. J. and Blanckenhorn, W. U. 1999. Female multiple mating, inbreeding avoidance, and fitness: it is not only the magnitude of costs and benefits that counts. *Behavioral Ecology* 10:462-464.

Hunter, F. M., Petrie, M., Otronen, M., Birkhead, T. and Møller, A. P. 1993. Why do females copulate repeatedly with one male? *Trends in Ecology and Evolution* 8: 21-26.

Inserro, J. C. 1997. Cooperation key to handling feral cat population. *Journal of the American Veterinary Medical Association* 210:1399-1400.

Ishida, Y. and Shimizu, M. 1998. Influence of social rank on defecating behaviors in feral cats. *Journal of Ethology* 16:15-21.

Ishida, Y., Yahara, T., Kasuya, E. and Yamane, A. 2001. Female control of paternity during copulation: inbreeding avoidance in feral cats. *Behaviour* 138:235-250.

Izawa, M., Doi, T. and Ono, Y. 1982. Grouping patterns of feral cats (*Felis catus*) living on a small island in Japan. *Japanese Journal of Ecology* 32:373-382.

Jarne, P. and Lagoda, J. L. 1996. Microsatellites, from molecules to populations and back. *Trends in Ecology and Evolution* 11:424-429.

Jennions, M. D. and Macdonald, D. W. 1994. Cooperative breeding in mammals. *Trends in Ecology and Evolution* 9:89-93.

Jennions, M. D. and Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society* 75:21-64.

Jewell, P. A. 1966. The concept of home range in mammals. *Symposia of the Zoological Society of London* 18:85-109.

Jöchle, W. and Jöchle, M. 1993. Reproduction in a feral cat population and its control with a prolactin inhibitor, cabergoline. *Journal of Reproduction and Fertility* S47:419-424.

Johnson, D. D. P. 2003. Sentenced without trial: reviling and revamping the Resource Dispersion Hypothesis. *Oikos* 101:433-440.

Johnson, D. D. P., Kays, R., Blackwell, P. G. and Macdonald, D. W. 2002. Does the resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution* 17:563-570.

Johnson, D. D. P., Macdonald, D. W., Kays, R. and Blackwell, P. G. 2003. Response to Revilla, and Buckley and Ruxton: the resource dispersion hypothesis. *Trends in Ecology and Evolution* 18:381-382.

Jones, E. and Coman, B. J. 1981. Ecology of the feral cat, *Felis catus* (L.), in south-eastern Australia. I. Diet. *Australian Wildlife Research* 8:537-547.

Jones, E. and Coman, B. J. 1982a. Ecology of the feral cat, *Felis catus* (L.), in southeastern Australia. II. Reproduction. *Australian Wildlife Research* 9:111-119.

Jones, E. and Coman, B. J. 1982b. Ecology of the feral cat, *Felis catus* (L.), in southeastern Australia. III. Home ranges and population ecology in semiarid northwest Victoria. *Australian Wildlife Research* 9:409-420.

Karl, B. J. and Best, H. A. 1982. Feral cats on Stewart Island; their foods, and their effects on kakapo. *New Zealand Journal of Zoology* 9:287-294.

Kaufmann, J. H. 1983. On the definitions and functions of dominance and territoriality. *Biological Review* 58:1-20.

Kaukeinen, D. E. 1982. A review of the secondary poisoning hazard to wildlife from the use of anticoagulant rodenticides. *Pest Management* 1:10, 12-14.

Kenward, R. 1987. *Wildlife Radio Tagging*. Academic Press, London.

Kerby, G. and Macdonald, D. W. 1988. Cat society and the consequences of colony size. *In* The Domestic Cat - the Biology of its Behaviour. 1st edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 67-81.

King, W. B. 1985. Island birds: will the future repeat the past? *In* Conservation of Island Birds: Case Studies for the Management of Threatened Island Species, vol. 3. (Ed. P. J. Moors) ICBP Technical Publications: 3-16.

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals.* Academic Press, London.

Kirkpatrick, R. D. and Rauzon, M. J. 1986. Foods of feral cats *Felis catus* on Jarvis and Howland Islands, central Pacific Ocean. *Biotropica* 18:72-75.

Kitchener, A. 1991. *The Natural History of the Wild Cats.* Cornell University Press, New York.

Konecny, M. J. 1987a. Home range and activity patterns of feral house cats in the Galapagos Islands. *Oikos* 50:17-23.

Konecny, M. J. 1987b. Food habits and energetics of feral house cats in the Galapagos Islands. *Oikos* 50:24-32.

Krebs, J. R. and Davies, N. B. 1993. Parental care and mating systems *In* An Introduction to Behavioural Ecology. 3rd edition. Blackwell Scientific Publications, Oxford: 208-243.

Krebs, J. W., Noll, H. R, Rupprecht, C. E. and Childs, J. E. 2002. Rabies surveillance in the United States during 2001. *Journal of the American Veterinary Medical Association* 221:1690-1701.

Kruuk, H. and Macdonald, D. W. 1985. Group territories of carnivores: empires and enclaves. *In* Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. (Ed. R. M. Sibly and R. H. Smith) Blackwell, Oxford: 521-536.

Langham, N. P. E. 1992. Feral cats (*Felis catus* L.) on New Zealand farmland - 2. Seasonal activity. *Wildlife Research* 19:707-720.

Langham, N. P. E. and Porter, R. E. R. 1991. Feral cats (*Felis catus* L.) on New Zealand farmland - 1. Home range. *Wildlife Research* 18:741-760.

Laundré, J. 1977. The daytime behaviour of domestic cats in a free-roaming population. *Animal Behaviour* 25:990-998.

Lawler, D. F., Johnston, S. D., Hegstad, R. L., Keltner, D. G. and Owens, S. F. 1993. Ovulation without cervical stimulation in domestic cats. *Journal of Reproduction and Fertility* 47:57-61.

Leyhausen, P. 1979. *Cat Behavior. Garland Series in Ethology*. Garland STPM Press, New York.

Liberg, O. 1980. Spacing patterns in a population of rural free roaming domestic cats. *Oikos* 35:336-349.

Liberg, O. 1983. Courtship behaviour and sexual selection in the domestic cat. *Applied Animal Ethology* 10:117-132.

Liberg, O. 1984. Food habits and prey impact by feral and house-based domestic cats in a rural area in southern Sweden. *Journal of Mammalogy* 65:424-432.

Liberg, O. and Sandell, M. 1988. Spatial organisation and reproductive tactics in the domestic cat and other felids. *In* The Domestic Cat - the Biology of its Behaviour. 1st edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 83-98.

Liberg, O., Sandell, M., Pontier, D. and Natoli, E. 2000. Density, spatial organisation and reproductive tactics in the domestic cat and other felids. *In* The Domestic Cat - the Biology of its Behaviour. 2nd edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 119-147.

Lindstedt, S., Miller, B. J. and Buskirk, S. W. 1986. Home range, time, and body size in mammals. *Ecology* 67:413-418.

Littin, K. E. and Cockrem, J. F. 2001. Individual variation in corticosterone secretion in laying hens. *British Poultry Science* 42:536-546.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379-384.

Macdonald, D. W. 1992. *The Velvet Claw*. BBC Books, London.

Macdonald, D. W. and Apps, P. J. 1978. The social behaviour of a group of semi-dependent farm cats, *Felis catus*: a progress report. *Carnivore Genetics Newsletter* 3:256-268.

Macdonald, D. W., Apps, P. J., Carr, G. M. and Kerby, G. 1987. Social dynamics, nursing coalitions and infanticide among farm cats, *Felis catus*. *Advances in Ethology - Supplement* 28:1-66.

Macdonald, D. W., Courtenay, O., Forbes, S. and Mathews, F. 1999. The red fox (*Vulpes vulpes*) in Saudi Arabia: loose-knit groupings in the absence of territoriality. *Journal of the Zoological Society of London* 249:383-391.

Macdonald, D. W., Stewart, P. D., Stopka, P. and Yamaguchi, N. 2000. Measuring the dynamics of mammalian societies: an ecologist's guide to ethological methods. *In* Research Techniques in Animal Ecology - Controversies and Consequences. Methods and Cases in Conservation Science. (Ed. L. Boitani and T. K. Fuller) Columbia University Press, New York: 332-388.

Macdonald, D. W. and Thom, M. D. 2001. Alien carnivores: unwelcome experiments in ecological theory. *In* Carnivore Conservation, Conservation Biology Series 5. (Ed. J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne) Cambridge University Press, Cambridge: 93-122.

Macdonald, D. W., Yamaguchi, N. and Kerby, G. 2000. Group-living in the domestic cat: its sociobiology and epidemiology. *In* The Domestic Cat - the Biology of its Behaviour. 2nd edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 95-119.

Macdonald, D. W., Yamaguchi, N. and Passanisi, W. C. 1998. The health, haematology and blood biochemistry of free-ranging farm cats in relation to social status. *Animal Welfare* 7:243-256.

Magnarelli, L. A., Anderson, J. F., Levine, H. R. and Levy, S. A. 1990. Tick parasitism and antibodies to *Borrelia burgdorferi* in cats. *Journal of the American Veterinary Medical Association* 197:63-66.

Maher, C. R. and Lott, D. F. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* 49:1581-1597.

Mahlow, J. C. and Slater, M. R. 1996. Current issues in the control of stray and feral cats. *Journal of the American Veterinary Medical Association* 209:2016-2020.

Martin, G. R., Twigg, L. E. and Robinson, D. J. 1996. Comparison of the diet of feral cats from rural and pastoral Western Australia. *Wildlife Research* 23:475-484.

Martin, P. and Bateson, P. 1998. *Measuring Behaviour - an Introductory Guide.* 2nd edition. Cambridge University Press, Cambridge.

Masuda, R., Lopez, J. V., Slattery, J. P., Yuhki, N. and O'Brien, S. J. 1996. Molecular phylogeny of mitrochondrial cytochrome b and 12S rRNA sequences in the Felidae: Ocelot and domestic cat lineages. *Molecular Phylogenetics and Evolution* 6:351-365.

McColm, A. A., Hutchinson, W. M. and Slim, J. C. 1981. The prevalence of *Toxoplasma gondii* in meat animals and cats in central Scotland. *Annals of Tropical Medicine and Parasitology* 75:157-164.

McCune, S. 1995. The impact of paternity and early socialisation on the development of cats' behaviour to people and novel objects. *Applied Animal Behaviour Science* 45:109-124.

Mech, L. D. and Barber, S. M. 2002. *A critique of wildlife radio-tracking and its use in national parks: a report to the U.S. National Park Service.* U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota.

Menotti-Raymond, M., David, V. A., Lyons, L. A., Schaffer, A. A., Tomlin, J. F., Hutton, M. K. and O'Brien, S. J. 1999. A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). *Genomics* 57:9-23.

Menotti-Raymond, M. and O'Brien, S. J. 1995. Evolutionary conservation of ten microsatellite loci in four species of Felidae. *Journal of Heredity* 86:319-322.

Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. *Ecological Applications* 2:178-188.

Mirmovitch, V. 1995. Spatial organisation of urban feral cats (*Felis catus*) in Jerusalem. *Wildlife Research* 22:299-310.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *The American Midland Naturalist* 37:223-249.

Moller, H. and Alterio N. 1999. Home range and spatial organisation of stoats (*Mustela erminea*), ferrets (*Mustela furo*) and feral house cats (*Felis catus*) on coastal grasslands, Otago Peninsula, New Zealand: implications for yellow-eyed penguin (*Megadyptes antipodes*) conservation. *New Zealand Journal of Zoology* 26:165-174.

Molsher, R., Newsome, A. and Dickman, C. 1999. Feeding ecology and population dynamics of the feral cat (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. *Wildlife Research* 26:593-607.

Monies, R. J., Cranwell, M. P., Palmer, N., Inwald, J., Hewinson, R. G. and Rule, B. 2000. Bovine tuberculosis in domestic cats. *The Veterinary Record* 146:407-408.

Moppin, M. G. and Kerwin, S. C. 2000. Evaluation of medetomidine hydrochloride, butorphanol tartrate, and glycopyrrolate in six military working dogs for short-term anesthesia. *Canine Practice* 25:12-14.

Mtambo, M. M. A., Nash, A. S., Blewett, D. A., Smith, H. V. and Wright, S. 1991. Cryptosporidium infection in cats - prevalence of infection in domestic and feral cats in the Glasgow area. *Veterinary Record* 129:502-504.

Murray, D. L. and Fuller, M. R. 2000. A critical review of the effects of marking on the biology of vertebrates. *In* Research Techniques in Animal Ecology - Controversies and Consequences. Methods and Cases in Conservation Science. (Ed. L. Boitani and T. K. Fuller) Columbia University Press, New York: 15-64.

Naidenko, S. V. and Hupe K. 2002. Seasonal changes in home range use in feral tomcats in Solling, central Germany. *Zoologichesky Zhurnal* 81:1371-1381.

Natoli, E. 1983. Behavioural evolution of the feral cat (*Felis catus* L.) as a response to urban ecological conditions. *Monitore Zoologico Italiano - Italian Journal of Zoology* 17:200-201.

Natoli, E. 1984. Chemo-communication in a group of stray cats - preliminary data on individual recognition by olfactory cues. *Monitore Zoologico Italiano - Italian Journal of Zoology* 18:173-174.

Natoli, E. 1985a. Behavioral responses of urban feral cats to different types of urine marks. *Behaviour* 94:234-243.

Natoli, E. 1985b. Spacing patterns in a colony of urban stray cats (*Felis catus* L) in the historic center of Rome. *Applied Animal Behaviour Science* 14:289-304.

Natoli, E. 1989. Reactions of female domestic cats (*Felis catus* L) to sprayed urine of a strange male - olfactory behavior. *Ethology Ecology & Evolution* 1:247-254.

Natoli, E. 1990. Mating strategies in cats - a comparison of the role and importance of infanticide in domestic cats, *Felis catus* L and lions, *Panthera leo* L. *Animal Behaviour* 40:183-186.

Natoli, E., Baggio, A. and Pontier, D. 2001. Male and female agonistic and affiliative relationships in a social group of farm cats (*Felis catus* L.). *Behavioural Processes* 53:137-143.

Natoli, E. and DeVito, E. 1987. Promiscuity in urban feral cats living in group. *Monitore Zoologico Italiano - Italian Journal of Zoology* 21:195.

Natoli, E. and DeVito, E. 1988. The mating system of feral cats living in a group. *In* The Domestic Cat - the Biology of its Behaviour. 1st edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 99-108.

Natoli, E. and DeVito, E. 1991. Agonistic behaviour, dominance rank and copulatory success in a large multimale feral cat, *Felis catus* L, colony in central Rome. *Animal Behaviour* 42:227-241.

Natoli, E., DeVito, E. and Pontier, D. 2000. Mate choice in the domestic cat (*Felis silvestris catus* L.). *Aggressive Behavior* 26:455-465.

Natoli, E., Ferrari, M., Bolletti, E. and Pontier, D. 1999. Relationships between cat lovers and feral cats in Rome. *Anthrozoos* 12:16-23.

Neff, B. D. 2003. Decisions about parental care in response to perceived paternity. *Nature* 422:716-719.

Neville, P. F. and Remfry, J. 1984. Effect of neutering on two groups of feral cats. *Veterinary Record* 114:447-450.

Nichol, S., Ball, S. J. and Snow, K. R. 1981. Prevalence of intestinal parasites in feral cats in some urban areas of England. *Veterinary Parasitology* 9:107-110.

Nicholson, G. 1981. Government policy on rabies control. *In* The Ecology and Control of Feral Cats. (Ed. UFAW) UFAW, Potters Bar: 50-59.

Niewold, F. J. J. 1986. Voedselkeuze, terreingebruk en aantalsregulatie van in het veld opererende huiskatten *Felis catus* L., 1758 (Food habits, spacing patterns and population dynamics of free-roaming domestic cats *Felis catus* L., 1758.). *Lutra* 29:145-187.

Nogales, M. and Medina, F. M. 1996. A review of the diet of feral domestic cats (*Felis silvestris catus*) on the Canary Islands, with new data from the laurel forest of La Gomera. *Zeitschrift fur Saugetierkunde - International Journal of Mammalian Biology* 61:1-6.

Nogales, M., Rodriguez, J. L., Delgado, G., Quilis, V. and Trujillo, O. 1992. The diet of feral cats (*Felis catus*) on Alegranza Island (north of Lanzarote, Canary Islands). *Folia Zoologica* 41:209-212.

Norbury, G. L., Norbury, D. D. and Heyward, R. P. 1998. Space use and denning behaviour of wild ferrets (*Mustela furo*) and cats (*Felis catus*). *New Zealand Journal of Ecology* 22:149-159.

O'Brien, S. J. 1996. Molecular genetics and phylogenetics of the Felidae. *In* Wild Cats - Status Survey and Conservation Action Plan. (Ed. K. Nowell and P. Jackson) IUCN/SSC Cat Specialist Group, Gland xxiii-xxiv.

O'Brien, S. J., Menotti-Raymond, M., Murphy, W. J. and Yuhki, N. 2002. The Feline Genome Project. *Annual Review of Genetics* 36:657-686.

Ortolani, A. and Caro, T. M. 1996. The adaptive significance of color patterns in carnivores: phylogenetic tests of classic hypotheses. *In* Carnivore Behavior, Ecology and Evolution, vol. 2. (Ed. J. L. Gittleman) Cornell University Press, New York: 132-188.

Packer, C., Gilbert, D. A., Pusey, A. E. and O'Brien, S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351:562-565.

Packer, C., Lewis, S. and Pusey, A. E. 1992. A comparative analysis of non-offspring nursing. *Animal Behaviour* 43:265-281.

Packer, C. and Pusey, A. E. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 296:740-742.

Packer, C. and Pusey, A. E. 1983. Cooperation and competition in lions. *Nature* 302:356.

Packer, C., Scheel, D. and Pusey, A. E. 1990. Why lions form groups: food is not enough. *The American Naturalist* 136:1-19.

Page, R. J. C., Ross J. and Bennett, D. H. 1992. A study of the home ranges, movements and behaviour of the feral cat population at Avonmouth Docks. *Wildlife Research* 19:263-277.

Paltridge, R. 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* 29:389-403.

Paltridge, R., Gibson, D. and Edwards, G. 1997. Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research* 24:67-76.

Panaman, R. 1981. Behaviour and ecology of free-ranging female farm cats (*Felis catus* L). *Zeitschrift fur Tierpsychologie* 56:59-73.

Patronek, G. J. 1998. Free-roaming and feral cats - their impact on wildlife and human beings. *Journal of the American Veterinary Association* 212:218-226.

Patton, S., Johnson, S. L., Loeffler, D. G., Wright, B. G. and Jensen, J. M. 1986. Epizootic of toxoplasmosis in kangaroos, wallabies and potaroos: possible transmission via domestic cats. *Journal of the American Veterinary Medical Association* 189:1166-1169.

Pearl, M. C. and Schulman, S. R. 1983. Techniques for the analysis of social structure in animal societies. *Advances in the Study of Behavior* 13:107-146.

Pontier, D. and Natoli, E. 1996. Male reproductive success in the domestic cat (*Felis catus* L): a case history. *Behavioural Processes* 37:85-88.

Pontier, D. and Natoli, E. 1999. Infanticide in rural male cats (*Felis catus* L.) as a reproductive mating tactic. *Aggressive Behavior* 25:445-449.

Pontier, D., Say, L., Debias, F., Bried, J., Thioulouse, J., Micol, T. and Natoli, E. 2002. The diet of feral cats (*Felis catus* L.) at five sites on the Grande Terre, Kerguelen archipelago. *Polar Biology* 25:833-837.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. *In* Research Techniques in Animal Ecology - Controversies and Consequences. Methods and Cases in Conservation Science. (Ed. L. Boitani and T. K. Fuller) Columbia University Press, New York: 65-110.

Price, E. O. 1984. Behavioral aspects of animal domestication. *Quarterly Review of Biology* 59:1-32.

Price, E. O. 1999. Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science* 65:245-271.

Pusey, A. and Packer, C. 1994. Non-offspring nursing in social carnivores: minimising the costs. *Behavioral Ecology* 5:362-374.

Queller, D. C. and Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution* 43:258-275.

Ragg, J. R., Moller, H. and Waldrup, K. A. 1995. The prevalence of bovine tuberculosis (*Mycobacterium bovis*) infections in feral populations of cats (*Felis catus*), ferrets (*Mustela furo*) and stoats (*Mustela erminea*) in Otago and Southland, New Zealand. *New Zealand Veterinary Journal* 43:333-337.

Ragni, B. and Possenti, M. 1996. Variability of coat-colour and markings system in *Felis silvestris*. *Italian Journal of Zoology* 63:285-292.

Ragni, B. and Randi, E. 1986. Multivariate analysis of craniometric characters in European wild cat, Domestic cat, and African wild cat (genus *Felis*). *Zeitschrift fur Saugetierkunde* 51:243-51.

Ranheim, B., Arnemo, J. M., Ryeng, K. A., Søli, N. E. and Horsberg, T. E. 1999. A pharmacokinetic study including some relevant clinical effects of medetomidine and atipamezole in lactating dairy cows. *Journal of Veterinary Pharmacology and Therapeutics* 22:368-373.

Read, J. and Bowen, Z. 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research* 28:195-203.

Rees, P. 1981. The ecological distribution of feral cats and the effects of neutering a hospital colony. *In* The Ecology and Control of Feral Cats. (Ed. UFAW) UFAW, Potters Bar: 12-22.

Remfry, J. 1982. Control of feral cat populations. *Applied Animal Ethology* 9:196-197.

Remfry, J. 1996. Feral cats in the United Kingdom. *Journal of the American Veterinary Medical Association* 208:520-523.

Revilla, E. 2003a. What does the Resource Dispersion Hypothesis explain, if anything? *Oikos* 101:428-432.

Revilla, E. 2003b. Moving beyond the resource dispersion hypothesis. *Trends in Ecology and Evolution* 18:330.

Risbey, D. A., Calver, M. C. and Short, J. 1997. Control of feral cats for nature conservation. I. Field tests of four baiting methods. *Wildlife Research* 24:319-326.

Risbey, D. A., Calver, M. C. and Short, J. 1999. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential impact using diet analysis. *Wildlife Research* 26:621-630.

Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S. and Wright, I. W. 2000. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* 27:223-235.

Røed, K. H., Holand, O., Smith, M. E., Gjøstein, H., Kumpula, J. and Nieminen, M. 2002. Reproductive success in reindeer males in a herd with varying sex ratio. *Molecular Ecology* 11:1239-1243.

Roper, T. J., Shepherdson, D. J. and Davies, J. M. 1986. Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour* 97:94-117.

Roulin, A. 2002. Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Animal Behaviour* 63:201-208.

Rowell, T. E. 1974. The concept of social dominance. *Behavioural Biology* 11:131-154.

Ruiz-Garcia, M. 1999. Genetic structure of different cat populations in Europe and South America at a microgeographic level: importance of the choice of an adequate sampling level in the accuracy of population genetics interpretations. *Genetics and Molecular Biology* 22:493-505.

Ruxton, G. D., Thomas, S. and Wright, J. W. 2002. Bells reduce predation of wildlife by domestic cats (*Felis catus*). *Journal of Zoology* 256: 81-83.

Sanchez, A. E. and Silva, M. E. 2002. Biology of pregnancy in the domestic cat (*Felis catus*). *Archivos de Medicina Veterinaria* 34:147-156.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. *In* Carnivore Behavior, Ecology and Evolution, vol. 1. (Ed. J. L. Gittleman) Cornell University Press, New York: 164-182.

Say, L., Bonhomme, F., Desmarais, E. and Pontier, D. 2003. Microspatial genetic heterogeneity and gene flow in stray cats (*Felis catus* L.): a comparison of coat colour and microsatellite loci. *Molecular Ecology* 12:1669-1674.

Say, L., Devillard, S., Natoli, E. and Pontier, D. 2002a. The mating system of feral cats (*Felis catus* L.) in a sub-Antarctic environment. *Polar Biology* 25:838-842.

Say, L., Gaillard, J. M. and Pontier, D. 2002b. Spatio-temporal variation in cat population density in a sub-Antarctic environment. *Polar Biology* 25:90-95.

Say, L., Pontier, D. and Natoli, E. 1999. High variation in multiple paternity of domestic cats (*Felis catus* L.) in relation to environmental conditions. *Proceedings of the Royal Society of London Series B* 266:2071-2074.

Say, L., Pontier, D. and Natoli, E. 2001. Influence of oestrus synchronization on male reproductive success in the domestic cat (*Felis catus* L.). *Proceedings of the Royal Society of London (B)* 268:1049-1053.

Schär, R. and Tschanz, B. 1981. Use of motion sensitive transmitters for studying the behaviour of rural free roaming domestic cats. *Biotelemetry VI, Proc. 6th International Symposium on Biotelemetry.* Leuven: 52-55.

Schär, R. and Tschanz, B. 1982. Social behaviour and space utilisation of farm cats using biotelemetry. *Biotelemetry VII, Proc. 7th International Symposium on Biotelemetry.* Stanford: 120-123.

Schramm, R. D., Briggs, M. B. and Reeves, J. J. 1994. Spontaneous and induced ovulation in the lion (*Panthera leo*). *Zoo Biology* 13:301-307.

Seabrook, W. 1990. The impact of the feral cat (*Felis catus*) on the native fauna of Aldabra Atoll, Seychelles. *Revue D Ecologie-La Terre et la Vie* 45:135-145.

Serpell, J. A. 1988. The domestication and history of the cat. *In* The Domestic Cat - the Biology of its Behaviour. 1st edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 151-158.

Serpell, J. A. 2000. Domestication and history of the cat. *In* The Domestic Cat - the Biology of its Behaviour. 2nd edition. (Ed. D. C. Turner and P. Bateson) Cambridge University Press, Cambridge: 181-192.

Short, J., Turner, B. and Risbey, D. A. 2002. Control of feral cats for nature conservation - III. Trapping. *Wildlife Research* 29:475-487.

Short, J., Turner, B., Risbey, D. A. and Carnamah, R. 1997. Control of feral cats for nature conservation - II. Population reduction by poisoning. *Wildlife Research* 24:703-714.

Silk, J. B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *American Naturalist* 121:56-66.

Sillero Zubiri, C. and Gottelli, D. 1995. Diet and feeding behavior of Ethiopian wolves (*Canis simensis*). *Journal of Mammalogy* 76:531-541.

Sillero Zubiri, C., Gottelli, D. and Macdonald, D. W. 1996. Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behavioural Ecology & Sociobiology* 38:331-340.

Smith, D. G. 1993. A 15-year study of the association between dominance rank and reproductive success of male rhesus macaques. *Primates* 34:471-480.

Smith, D. F. E., Durman, K. J., Roy, D. B. and Bradshaw, J. W. S. 1994. Behavioural aspects of the welfare of rescued cats. *The Journal of the Feline Advisory Bureau* 31:25-28.

Smith, R. E. and Shane, S. M. 1986. The potential for the control of feral cat populations by neutering. *Feline Practice* 16:21-23.

Sokal, R. R. and Rohlf, F. J. (1995) *Biometry*. 3rd edition. W. H. Freeman and Company, New York.

Southam, N. 1981. Health hazards in hospital areas. *In* The Ecology and Control of Feral Cats. (Ed. UFAW) UFAW, Potters Bar: 63-67.

Spong, G., Stone, J., Creel, S. and Björklund, M. 2002. Genetic structure of lions (*Panthera leo* L.) in the Selous Game Reserve: implications for the evolution of sociality. *Journal of Evolutionary Biology* 15:945-953.

Steigerwald, E. S., Sarter, M., March, P. and Podell, M. 1999. Effects of feline immunodeficiency virus on cognition and behavioral function in cats. *Journal of Acquired Immune Deficiency Syndromes and Human Retrovirology* 20:411-419.

Stockley, P. 2003. Female multiple mating behaviour, early reproductive failure and litter size variation in mammals. *Proceedings of the Royal Society of London (B)* 270:271-278.

Taberlet, P., Luikart, G. and Geffen, E. 2001. New methods for obtaining and analyzing genetic data from free-ranging carnivores. *In* Carnivore Conservation, Conservation Biology Series 5. (Ed. J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne) Cambridge University Press, Cambridge: 313-334.

Tabor, R. 1989. The changing life of feral cats (*Felis catus* L.) at home and abroad. *Zoological Journal of the Linnean Society* 95:151-161.

Tidemann, C. R., Yorkston, H. D. and Russack, A. J. 1994. The diet of feral cats, *Felis catus*, on Christmas Island, Indian Ocean. *Wildlife Research* 21:279-286.

Tregenza, T. and Wedell, N. 2002. Polyandrous females avoid costs of inbreeding. *Nature* 415:71-73.

Trivers, R. L. and Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90-92.

Turner, D. C., Feaver, J., Mendl, M. and Bateson, P. P. G. 1986. Variation in domestic cat behaviour towards humans - a paternal effect. *Animal Behaviour* 34:1890-1901.

Turner, D. C. and Mertens, C. 1986. Home range size, overlap and exploitation in domestic farm cats (*Felis catus*). *Behaviour* 99:22-45.

Tuyttens, F. A. M., Macdonald, D. W. and Roddam, A. 2002. Effects of radio-collars on European badgers (*Meles meles*). *Journal of the Zoological Society of London* 257:37-42.

Utami, S. S., Goossens, B., Bruford, M. W., deRuiter, J. R. and Van Hooff, J. A. R. 2002. Male bimaturism and reproductive success in Sumatran orang-utans. *Behavioral Ecology* 13:643-652.

Vähä-Vahe, A. T. 1990. Clinical effectiveness of atipamezole as a medetomidine antagonist in cats. *Journal of Small Animal Practice* 31:193-197.

Valenzuela, D. and Macdonald, D. W. 2002. Home-range use by white-nosed coatis (*Nasua narica*): limited water and a test of the resource dispersion hypothesis. *Journal of Zoology (London)* 258:247-256.

Van Aarde, R. J. 1978. Reproduction and population ecology in the feral house cats, *Felis catus*, at Marion Island. *Carnivore Genetics Newsletter* 3:288-316.

Van Aarde, R. J. 1980. The diet and feeding behaviour of feral cats *Felis catus* at Marion Island. *South African Journal of Wildlife Research* 10:123-128.

Van Aarde, R. J. 1983. Demographic parameters of the feral cat *Felis catus* population at Marion Island. *South African Journal of Wildlife Research* 13:12-16.

Van Aarde, R. J., Erasmus, B. J. and Blumenberg, B. 1981. Frequencies of mutant alleles in the cat populations of Cape Town and Pretoria, South Africa. *South African Journal of Science* 77:168-171.

Van Rensburg, P. J. J. and Bester, M. N. 1988. Experiments in feral cat population reduction by hunting on Marion Island. *South African Journal of Wildlife Research* 18:47-50.

Van Rensburg, P. J. J., Skinner, J. D. and Van Aarde, R. J. 1987. Effects of feline panleucopaenia on the population characteristics of feral cats on Marion Island. *Journal of Applied Ecology* 24:63-73.

Verstegen, J., Fargetton, X., Donnay, I. and Ectors, F. 1990. Comparison of the clinical utility of medetomidine/ketamine and xylazine/ketamine combinations for the ovariectomy of cats. *Veterinary Record* 127:424-426.

Vinogradov, A. E. 1997. Fine structure of gene frequency landscapes in domestic cat: the Old and New Worlds compared. *Hereditas* 126:95-102.

Wall, P. G., Threlfall, E. J., Ward, L. R. and Rowe, B. 1996. Multiresistant *Salmonella typhimurium* DT104 in cats: A public health risk. *Lancet* 348:471.

Warner, R. E. 1985. Demography and movements of free-ranging domestic cats in rural Illinois. *Journal of Wildlife Management* 49:340-346.

Waser, P. M. 1996. Patterns and consequences of dispersal in gregarious carnivores. *In* Carnivore Behavior, Ecology and Evolution, vol. 2. (Ed. J. L. Gittleman) Cornell University Press, New York: 267-295.

Wayne, R. K. and Koepfli, K. P. 1996. Demographic and historical effects on genetic variation of carnivores. *In* Carnivore Behavior, Ecology and Evolution, vol. 2. (Ed. J. L. Gittleman) Cornell University Press, New York: 453-484.

Weber, J. M. and Dailly, L. 1998. Food habits and ranging behaviour of a group of farm cats (*Felis catus*) in a Swiss mountainous area. *Journal of Zoology (London)* 245:234-237.

Wells, E. S., Rosen, L. W. and Waishaw, S. 1997. Use of feral cats in psychotherapy. *Anthrozoos* 10:125-130.

West, P. M. and Packer, C. 2002. Sexual selection, temperature and the lion's mane. *Science* 297:1339-1343.

White, G. C. and Garrott, R. A. 1990. *Analysis of Wildlife Radio-Tracking Data.* Academic Press, London.

White, P. C. L. and Harris, S. 1994. Encounters between red foxes (*Vulpes vulpes*): implications for territory maintenance, social cohesion and dispersal. *Journal of Animal Ecology* 63:315-327.

Wildt, D. E., Bush, M., Goodrowe, K. L., Packer, C., Pusey, A. E., Brown, J. L., Joslin, P. and O'Brien, S. J. 1987. Reproductive and genetic consequences of founding isolated lion populations. *Nature* 329:328-331.

Wiseman, R., O'Ryan, C. O. and Harley, E. H. 2000. Microsatellite analysis reveals that the domestic cat (*Felis catus*) and southern African wild cat (*F. lybica*) are genetically distinct. *Animal Conservation* 3:221-228.

Woodroffe, R. and Vincent, A. 1994. Mother's little helpers - patterns of male care in mammals. *Trends in Ecology and Evolution* 9:294-297.

Woods, M., McDonald, R. A. and Harris, S. 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Review* 33:174-188.

Worton, B. J. 1987. A review of models of home range for animal movement. *Ecological Modelling* 38:277-298.

Wright, M. and Walters, S. 1981. *The Book of the Cat*. Pan Books Ltd., London.

Wynne-Edwards, V. C. 1962. *Animal Dispersion in Relation to Social Behaviour*. Oliver and Boyd, Edinburgh.

Wynne-Edwards, V. C. 1986. *Evolution through Group Selection*. Blackwell Scientific Publications, Oxford.

Wynne Jones, J. and Jenkins, P. A. 1995. Is tuberculosis in domestic cats hazardous to human beings? *The Lancet* 346:442-443.

Yamaguchi, N., Macdonald, D. W., Passanisi, W. C., Harbour, D. A. and Hopper, C. D. 1996. Parasite prevalence in free-ranging farm cats, *Felis silvestris catus*. *Epidemiology and Infection* 116:217-233.

Yamane, A. 1998. Male reproductive tactics and reproductive success of the group-living feral cat (*Felis catus*). *Behavioural Processes* 43:239-249.

Yamane, A. 1999. Male homosexual mounting in the group-living feral cat (*Felis catus*). *Ethology Ecology and Evolution* 11:399-406.

Yamane, A., Doi, T. and Ono, Y. 1996. Mating behaviors, courtship rank and mating success of male feral cat (*Felis catus*). *Journal of Ethology* 14:35-44.

Yamane, A., Emoto, J. and Ota, N. 1997. Factors affecting feeding order and social tolerance to kittens in the group-living feral cat (*Felis catus*). *Applied Animal Behaviour Science* 52:119-127.

Yamane, A., Ono, Y. and Doi, T. 1994. Home range size and spacing pattern of a feral cat population on a small island. *Journal of the Mammalogical Society of Japan* 19:9-20.

Zaunbrecher, K. I. and Smith, R. E. 1993. Neutering of feral cats as an alternative to eradication programs. *Journal of the American Veterinary Medical Association* 203:449-452.

Zeh, J. A. and Zeh, D. W. 2001. Reproductive mode and the genetic benefits of polyandry. *Animal Behaviour* 61:1051-1063.

Zoran, D. L. 2002. The carnivore connection to nutrition in cats. *Journal of the American Veterinary Medical Association* 221:1559-1567.