Pine marten diet and habitat use within a managed coniferous forest

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Abstract

Increased afforestation and protective legislation in the latter half of the 20th Century allowed the British pine marten *Martes martes* population to recover from near extinction. Although still largely confined to northern Scotland, the marten population is expanding its size and range by utlising coniferous plantation forests which have become increasingly available. However, little is known about the marten's ecology in plantation forestry, and less about how they may adapt to changing silvicultural trends. This study investigated aspects of pine marten ecology within Morangie forest, a managed plantation in NE Scotland, with the ultimate aim of formulating management guidelines for modern plantation forests.

During the course of the study 11 pine marten were radiotracked and their home ranges mapped to examine marten-habitat associations at several spatial scales. Compositional analysis of habitat based on dominant vegetation type showed that martens established their home ranges in areas dominated by mature forest, whilst showing relative avoidance for open heath moor and grazed pasture. Within home ranges, foraging martens utilised patches of graminoid vegetation, such as those typically associated with *Microtus* voles, in areas with little or no tree canopy cover. These findings provide unequivocal evidence that fine-scale patches of non-forested habitat provide crucial foraging resources for marten, and therefore ought to be provisioned for in forest management plans. To assist the implementation of these requirements in forest planning, a model was developed to predict the fine scale distribution of *Microtus*-rich foraging habitat for marten using GIS-based habitat variables that are routinely available to forest managers: topographic wetness index, stand tree height and stand basal area. Management recommendations of ways to improve wind-firm plantation forests as habitats for pine marten are provided.

To augment the investigation of marten spatial ecology, the diet of martens was examined seasonally through the analysis of contents from c. 2450 scats, 86 % of which were genetically identified as being pine marten in origin. Marten diets displayed marked seasonality, but small mammals, berries and small birds were the principal foods consumed based on both frequency of occurrence and estimated weight of biomass ingested. Comparison of the relative composition of small mammal species in the diet with those available in the environment revealed that marten displayed an indisputable preference for *Microtus* voles. Such habits demonstrate that the niche of Scottish martens has diverged from those in mainland populations which predominantly prey upon *Clethrionomys* voles. A comparison of the marten's winter diet with those found in studies at similar latitudes (58°N) demonstrated that the Scottish diet was more similar to diets at more southerly latitudes as they contained more fruit and fewer large mammals than typically boreal diets. Investigation of inter-annual variation of the marten's spring diet from five successive years revealed that *Microtus* were consistently the most important prey species in the diet each year. Indirect evidence of the relative abundance of *Microtus* suggested that *Microtus* populations were non-cyclic. Findings are discussed with reference to the unique ecological circumstances confronting marten in the Scotland; typical of insular populations the UK has a depauperate native fauna in comparison with mainland Europe, in addition to this, mild climatic conditions, particularly over winter, and a historically fragmented landscape appear to have allowed the niche of the Scottish marten to diverge from that considered typical elsewhere in its range. The Scottish marten is dependent on both forested and open habitats, and is both a *Microtus* specialist and trophic generalist.

Declaration

I submit this thesis for examination in accordance with the Regulations for Higher Degrees by Research. I declare that the thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others included in the thesis.

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Fiona Mae Caryl

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Chapter 1

Introduction and Review

1.1 The Pine Marten *Martes martes* L. 1758

1.1.1 Taxonomy

The Eurasian pine marten *Martes martes* is one of six members of the Family *Mustelidae* (Order *Carnivora*) native to the British Isles, and the only representative of the genus *Martes* in Great Britain (Birks 2002). World-wide, the genus *Martes* includes seven other species, four of which occur in the subgenera to which the pine marten belongs: the stone marten *Martes foina*, the sable *M. zibellina*, the Japanese marten *M. melampus*, and the American marten *M. Americana* (Anderson 1970). These four holarctic *Martes* species share many morphological and ecological similarities, and can be considered as a circumpolar "super species" (Anderson 1970), the distribution, ecology and status of each of which are reviewed in Proulx *et al.* (2004).

1.1.2 Distribution & Status

The pine marten is indigenous to most of Europe, inhabiting a diverse range of biotopes between southern Mediterranean and northern Fennoscandia, and from Ireland and Great Britain to western Siberia and Iran (Proulx *et al.* 2004). The marten is listed under Appendix III of the Bern Convention (Harris *et al.* 1995, Strachan *et al.* 1996), yet hunting or trapping is permitted in 13 European countries where forested regions cover large areas and marten populations are considered stable e.g. Sweden (Helldin 1998, Proulx *et al.* 2004). Marten pelts are highly prized, and mean annual harvests of marten range from less than 1,000 in Latvia and Austria, to over 5,000 in France, Germany and Sweden (Proulx *et al.* 2004). In some countries where the marten is fully protected its status is unknown (i.e. Italy), whereas in others (i.e. The Netherlands and Spain) populations are believed to be vulnerable or threatened (Proulx *et al.* 2004). In Britain the marten population is thought to be increasing due to habitat improvement and decreased hunting pressure. The marten is currently protected under Schedule 5 of the Wildlife and Countryside Act 1988 (Velander 1991), making it an offence to deliberately kill, injure or take pine marten (unless under licence) and protecting pine marten dens from intentional damage, destruction or obstruction.

1.1.3 Morphology & Reproductive Biology

The pine marten is a small forest carnivore that is typically described as a weasel-shaped mustelid, roughly the size of a domestic cat, with dense brown fur and a long bushy tail (Velander 1991). There is pronounced size dimorphism between the sexes: females weigh between 1200-1500g, whereas males weigh between 1600-2300g (*own unpublished data*). The pine marten is a solitary forager living in an intra-sexual territorial system (Balharry 1993b) in which males disperse themselves with respect to females, whereas females are dispersed with respect to those resources essential for rearing young (Powell 1979, 1994). Marten have a polygynous mating system (Balharry 1993b). Mating occurs during summer, but as females display delayed-implantation, embryonic development does not begin until late winter (Mead 1994). Between one and five young are born in late March to late April, and subadults disperse from their natal territories in their first autumn (*D. Balharry personal communication*) though may be tolerated to remain within the home range of a member of the same sex for longer if resources are plentiful (Balharry 1993b). Some aspects of the pine marten's ecology such as diet are well studied (see review by Zalewski 2004), but our understanding of the factors that restrict marten density and distribution remain limited, particularly in relation to inter-specific competition and predation (Helldin 1998). The marten's small size, elusive nature and largely nocturnal habits in remote habitats means that it has been less intensively studied than other British carnivores e.g. fox *Vulpes vulpes* (MacDonald 1988), badger *Meles meles* (Kruuk 1989) and weasel *Mustela nivalis* (King 1989).

1.1.4 Thesis Terminology

For the purpose of this thesis, the terms “marten” or “pine marten” will be used to refer to *M. martes*. However, “marten” may at times also include reference to *M. Americana*, about which a considerable volume of research literature exists, largely due to the economic value of their pelts (Strickland 1991). Additionally, research on the ecology of American marten is generally published in English whereas research on the European marten has been published in wide variety of languages, which can complicate literature synthesis. The behavioural traits and life requisites of these two sister-species in particular are so similar that many authors often draw comparisons across the literature (i.e. Balharry 1993a, Buskirk & Powell 1994). Reference to any other species of marten will be specified. Please also note that “marten” will be used to refer to marten in the plural as well as the singular.

Small mammal species will be referred to by their genus rather than by species, as is commonly done so in the literature when summerising findings from across large geographic extents (e.g. Martin 1994, Zalewski 2004). Vole species within a particular genus tend to fulfil the same ecological niche as species in the same genus elsewhere in the marten’s geographic range; for example, Europe’s field vole *Microtus agrestis* is a characteristic denizen of herbaceous meadows (Hansson 1978), as is its American counterpart, the meadow vole *Microtus pennsylvaticus*

(Folinsbee *et al.* 1973). Similarly, Europe's bank vole *Clethrionomys glareolus* is an inhabitant of forest interiors (Jedrzejewski *et al.* 1993), as is its North American equivalent, the red-backed vole *Clethrionomys gapperi* (Pearce & Venier 2005).

1.1.5 Marten Dietary Habits

The Eurasian pine marten is often characterised as a food generalist and opportunist, consuming a broad range of food items as they become abundant and accessible (see reviews: Clevenger 1994a, Martin 1994, de Marinis & Masseti 1995, Zalewski 2004). There is significant geographic and seasonal variation in the marten diet (Zalewski 2004), but typical foods commonly consumed include a wide variety of mammals, birds, fruits, invertebrates, amphibians, and reptiles (Nyholm 1970, Pulliainen 1981a, Warner & O'Sullivan 1982, Marchesi & Mermod 1989, Clevenger 1993, Helldin 2000). Despite this catholic diet however, there is universal consensus that rodents, particularly microtines, are the most important food for marten throughout their range (Nyholm 1970, Garzon *et al.* 1980, Reig & Jedrzejewski 1988, Jedrzejewski *et al.* 1993, Clevenger 1993, Pulliainen & Ollinmaki 1996, Helldin 2000, and literature cited in Zalewski 2004). However, in contrast with the findings from continental Europe (e.g. Jedrzejewski *et al.* 1993), it is voles of the genus *Microtus* rather than *Clethrionomys* that are the principal rodent in the diet of British marten (Lockie, 1961, Velander 1983, Balharry 1993a., Gurnell *et al.*

1994, Halliwell 1997, Putman 2000, Coope 2007). British studies that have assessed small mammal abundance alongside marten diet have found a considerable selective preference for *Microtus* over *Clethrionomys* (Lockie, 1961; Balharry, 1993), and similar preferences have also been demonstrated for American marten (Weckwerth & Hawley 1962, Francis & Stephenson 1972, Douglas *et al.* 1983, Buskirk & MacDonald 1984, Martin 1987). The occurrence of *Microtus* in the diet of Eurasian marten is not unique to Britain, as the species has been found in the diet of marten across Europe: e.g. Spain (Garzon *et al.* 1980, Brana & del Campo 1982, Clevenger 1993), Poland (Jedrzejewski *et al.* 1993), Germany (Ansorge 1989), Finland (Pulliainen & Ollinmaki 1996) and Sweden (Helldin 2000).

1.1.6 Marten-Habitat Associations

Studies quantifying the habitat associations of pine marten in western and central Europe are relatively few (Degn & Jensen 1977, Nesvadbova & Zejda 1984, Marchesi 1989, Clevenger 1994b). Indeed, habitat studies are predominantly limited to the northern latitudes of the species' European range (Pulliainen 1981b, Storch *et al.* 1990, Brainerd 1990, Brainerd *et al.* 1994, Brainerd & Rolstad 2002). In boreal Europe, marten are considered to be forest specialists, being particularly associated with late-successional coniferous forest whilst displaying avoidance for areas with no over-story or shrub cover (Brainerd 1990, Pulliainen 1981b, Storch *et* *al.* 1990). The habitat associations of American marten have been studied more extensively (see reviews by Clark *et al.* 1987, Buskirk & Powell 1994, Buskirk & Ruggiero 1994), and reached similar conclusions: that marten are habitat specialists requiring old growth coniferous forest for survival. Marten are presumed to associate with older, more structurally complex forests because they fulfil life requirements, such as providing protection from predators, access to prey, and thermal insulation (Buskirk & Powell 1994). Predator avoidance is frequently suggested to be the most important determinant of marten habitat use, and avoidance of open, non-forested habitats is commonly regarded as evidence for this (Buskirk & Powell 1994, Buskirk & Ruggiero 1994, Proulx *et al.* 2004). Predators of marten include red fox (Pulliainen 1981b), wolf *Canis lupus* (White *et al.* 2002), lynx *Lynx lynx* (Jonsson 1986), eagle owls *Bubo bubo* (Nyholm 1970), and golden eagles *Aquila chrysaetos* (Nyholm 1970, Pulliainen 1981b). A mature over-story provides protection from avian predators (Herman & Fuller 1974, Hargis & McCullough 1984), as well as vertical escape routes from foxes (Pulliainen 1981b, Storch *et al.* 1990). Old growth forests are also more likely to have greater presence of arboreal cavities and increased complexity of structures near the ground than young forests, both of which provide den sites that reduce the energetic costs of thermoregulation during winter (Buskirk *et al.* 1989, Taylor, 1993, Zalewski 1997). As well as providing cover, complex ground structures also provide subnivean access to prey in winter (Steventon & Major 1982, Hargis & McCullough 1984), and are therefore associated with increased marten foraging success in old growth forests (Thompson 1986, Thompson & Harestad 1994).

In both boreal Europe and much of North America, the staple prey species in the marten diet are forest-associates such as *Clethrionomys* voles, which partly explain the species' close association with forested environments (Buskirk & Ruggiero 1994, Zalewski 2004). However, marten are highly catholic in their dietary habits (Clevenger 1994, Martin 1994, Zalewski 2004), and are found in an equally wide variety of habitats including shrub-lands, deciduous woodland and mesic pine stands (Clevenger 1993, Marchesi 1989, Balharry 1993a., Jedrzejewski *et al.* 1993). The marten's varied diet and habitat-use over much of Europe reflects the diversity of biotopes encompassed within the marten's range, but means there is a lack of consistency in marten-habitat relations other than a general association with forest habitats (Proulx *et al.* 2004). Even within the relatively small geographic extent of Scotland, habitat studies have produced incongruent results (Balharry 1993a., Bright & Smithson 1997, Halliwell 1997, Chapter 3). At the home range scale, Scottish marten were found to select for open-canopy coniferous forest (Balharry 1993a., Chapter 3), old growth forest (i.e. 85+ years old: Halliwell 1997) and close-canopied coniferous forest (Bright & Smithson 1997). Discrepancies in habitat preferences may have resulted for a variety of reasons: the difference in management practises between study areas, differences in definitions of habitat types, small sample sizes (i.e. Halliwell 1997), the coarse accuracy of tracking achieved (i.e. Balharry 1993a.), or because the population under investigation was the result of a translocation (i.e. Bright & Smithson 1997). However, it is increasingly suggested that fine-scale vertical and horizontal structure within forest stands are more important influences on marten habitat use than age or species composition of the forest over-story (Buskirk & Powell 1994, Buskirk & Ruggiero 1994, Bisonette *et al.* 1997, Chapin *et al.* 1997, Payer & Harrison 2004). Although habitat structure is sometimes correlated with stand maturity and species composition, structurally complex habitats may still be present in a variety of habitats not typically associated with marten use (e.g. young coniferous forest: Brainerd *et al.* 1994, young deciduous forest: Porter *et al.* 2005, open scrub-land: Clevenger 1994*b*). These habitats may be suitable for marten as long as they provide the structural elements needed to fulfil their life requirements (Brainerd *et al.* 1994).

1.2 Background to the Present Study: The Pine Marten and Modern Forestry in Great Britain.

The British Isles have a prolonged history of extensive deforestation, which began earlier and was done more completely than parts of central, eastern and northern Europe, creating a fragmented and highly depleted forest cover for several centuries (Rackham 1990, Tipping 1994, Williams 2000, Birks 2002). By the beginning of the 20th century, forest cover in Scotland had fallen to just c. 5 % of the total land area (Gill 1994). Loss of forested habitat coupled with persecution from humans resulted in the near extermination of the British pine marten population (Lockie 1964, Langley & Yalden 1977). By the early 1900s, pine marten in Scotland existed only as a small, relict population that was restricted to the northwest Highlands (Ritchie 1920, Langley & Yalden 1977). A relaxation in trapping and reduction in the intensity of game preservation during two World Wars allowed the marten population sufficient respite to make a small increase in numbers (Lockie 1964). Population recovery and range expansion were helped when a post-war need to secure the domestic wood supply lead to the establishment of the Forestry Commission (Lockie 1964, Heitzman 2003). Subsequent afforestation rapidly converted previously non-forested landscapes into commercial coniferous plantations, and by 1992, c.15 % of Scotland had forest cover (Forestry Commission

1992). However, these plantation forests were predominantly formed by uniform monocultures of fast-growing conifers, typically non-native species such as Sitka spruce *Picea sitchensis* rather than native broadleaf species or Scots pine *Pinus sylvestris* (Summers *et al.* 1999, Heitzman 2003). Concern was expressed that the composition and structure of these plantations was so dissimilar to ancient native pine woods that they would be of limited value to wildlife and lacked aesthetic appeal (Tompkins 1986, Avery & Leslie 1990). Increasing societal demand for plantations to be managed in sustainable and ecologically sensitive ways to provide conservation and recreational amenities as well as economic value, has resulted in a change in silvicultural practices (Mason & Quine 1995). There is now increased interest in planting native species such as oak *Quercus* spp., birch *Betula pendula*, ash *Fraxinus excelsior* and Scots pine (Heitzman 2003). Alternatives to large-scale clear felling are also being sought, resulting in the creation of multi-aged and structurally complex semi-natural forests (Malcolm *et al.* 2001, Heitzman 2003, Pommering & Murphy 2004).

The increase in afforestation and changes to forest management in recent years means that parts of the pine marten's former range that were previously unsuitable (i.e. non-forested) are now available for recolonisation. Consequently, the pine marten has begun to recover some of its original distribution, aided by its legal protected status under the Wildlife and Countryside Act, 1988 (Velander 1983a, Balharry *et al.* 1996). Small numbers of marten have been reintroduced to forested areas of southwest Scotland (Bright & Smithson 1997), and further reintroductions to parts of England and Wales are a possibility (Bright *et al.* 1995, Bright & Halliwell 1999, Birks *et al.* 2003). A recent revision of Balharry *et al.*'s (1996) marten population estimate put the number of marten in Scotland in 2004 at c. 3350 individuals, with a further 180 estimated for England and Wales (*J.D.S. Birks personal communication*). This upturn in numbers of Scottish marten is encouraging, yet the current distribution of pine marten in Britain remains restricted; whilst populations in Scotland are largely confined to the north, evidence suggests that relict populations surviving in parts of northern England and Wales remain isolated, vulnerable and difficult to monitor (Messenger & Birks 2000, Proulx *et al.* 2004). Marten are slow breeding habitat-specialists whose distribution is likely to diminish in the face of factors that reduce their population productivity by even a small amount (Bright 2000). The availability of suitable habitat is therefore critical to the species' further recovery (Birks *et al.* 2003). The ecology of the species within plantation forests is not well known (Bright & Smithson 1997, Brainerd *et al.* 1994) yet plantations now form the majority of habitat available for re-colonisation. More conservation effort is therefore needed to characterise the marten's ecological requirements in order to direct the management of plantations, particularly as the nature of plantation forests themselves has changed so dramatically: moving away from a system of monoculture clear-felled rotations, to one of semi-natural forest-continuity.

Management of wildlife populations, whether for conservation or control, inevitably entails the management of habitat (Garshelis 2000), and it is assumed that animals will utilise those habitat resources that maximise their fitness (Buskirk & Powell 1994). To capitalise the effectiveness of managing modern plantation forests for pine marten, information directing forest management must be centred on habitat known to be of high quality, from a study within the same ecological circumstances and under relevant management considerations. Previous studies of pine marten ecology in Scotland have been conducted in varied ecological contexts: a highly fragmented landscape of ancient forest remnants and open mountainside (Balharry 1993a), a population reintroduced to a plantation forest with coarse-grain clear-felling and little stand thinning (Bright & Smithson 1997), and a lowland game-hunting estate where predators are controlled (Halliwell 1997); none of which adequately exemplify the environmental and ecological conditions found in modern plantation forests which have fine-grain clear-felling and within-stand thinning to encourage sub-canopy vegetative layers. The contrasting results found in these studies, particularly with regards to population densities, illustrate the importance of conducting further research explicitly within modern plantation forestry.

Of particular interest to forest and wildlife managers are aspects of marten habitat-use concerning the habitat types that are important for fulfilling the pine marten's life requirements such as foraging and resting. There is concern among conservationists that suitable resting sites, such as arboreal cavities, are lacking in plantation forests, which may limit the marten's population growth and range expansion (Birks *et al.* 2003, Birks *et al.* 2005). The preference for *Microtus* voles and apparent avoidance of forest-dwelling rodents such as *Clethrionomys* and *Apodemus* differentiates the foraging habits of the British pine marten from those of its continental counterparts. This implies that British marten use different habitat in which to forage than marten in continental Europe, therefore generalising the marten's ecological habits from studies conducted elsewhere in their geographic range may not necessarily be justifiable.

It remains unclear how the British marten, a forest-dwelling predator, preferentially preys upon the *Microtus* vole, a species characteristic of open areas. Densities of *Microtus* are high in early successional and non-forested habitats to which marten have displayed avoidance (Balharry 1993a., Halliwell 1997). As

Microtus populations fluctuate seasonally or annually (e.g. Petty 1992), there is specific interest by wildlife managers about how pine marten respond to such changing availabilities of these prey (*R. Raynor personal communication*), particularly concerning which alternate prey species are taken when preferred prey become less available. Expanding marten populations are likely to come into increasing contact with species of conservation concern such as the red squirrel *Sciurus vulgaris* and capercaillie *Tetrao urogallus*, which are sometimes preyed upon by marten (Nyholm 1970, Warner & O'Sulivan 1982, Marcström *et al.* 1988, Storch *et al.* 1990, Halliwell 1997), or with species of economic value such as game birds. Predator control is a large part of game management aimed at increasing game bag returns (Mason 1989, Tapper 1992), and the alleged effect of pine marten on the economic viability of sport shooting estates was one of the driving factors in the persecution that lead to the historic decimation of their population. The ecological impact of predators on vulnerable species such as capercaillie remains under contention. British marten are currently legally protected and therefore not controlled, but there is concern that reports of predation of capercaillie nests by marten (e.g. Summers *et al.* 2004) may lead to a call to control marten numbers in capercaillie areas, despite the effect of marten predation being much less of a threat to capercaillie than that from other predators (Baines *et al.* 2004). It is therefore important to manage marten in a way that is sympathetic with other land-uses, which prevents them from being considered as a pest species in need of control. Relatively little is known about the ecology of marten within modern plantation forestry, and further understanding is needed about how best to manage forest habitats in order to promote further increase and range expansion of the marten population, whilst minimising conflict with other land-use issues.

1.3 Objectives

A thorough understanding of marten ecology within modern plantation forest is needed in order to make informed decisions about how best to manage this habitat for the benefit of marten, whilst reducing any ensuing conflicts that may result in the marten being considered a pest. The overall objectives of this study were therefore to investigate the marten's diet and habitat use within a modern managed plantation forest.

- To identify how pine marten use habitat within and surrounding the forest in comparison to its availability at different spatial scales, and relate the habitat selection found at each scale to the scale-specific factors that influence marten life-requirements.

- To identify and assess both the principal and preferred prey of marten in different seasons, and to examine whether there is any inter-annual variation in diet with changing availabilities of preferred prey.
- To review all aspects of the methodologies utilised in previous studies and employ recent technical and analytical advances where possible in order to improve upon them.
- To discuss the implications of the results with respect to forest management and conservation of marten, and relate findings to those of other studies reviewed from Britain, Europe and North America.

1.4 Thesis Contents

The four data chapters of this thesis are presented as discrete units, two of which concern pine marten habitat use, two of which concern pine marten diet.

Chapter 2 provides a brief outline of the general methods employed in the present study along with discussion about the methodological concerns faced when interpreting data from both habitat-use and dietary studies. A description of the study area is also provided.

Chapter 3 is the first of the four data chapters; in this chapter, aspects of pine marten spatial ecology are investigated. More specifically, pine marten home range size and macrohabitat composition are investigated. Macrohabitats are determined by dominant vegetation and habitat-selection is analysed at two spatial scales: selection of the home range, and selection within home ranges. The importance of the different ecological attributes associated with each vegetation type at both scales of selection is discussed.

Chapter 4 continues with the investigation of marten spatial ecology but focuses specifically on the microhabitats used by female marten for foraging. Areas of core foraging habitat are modelled based upon site-attribute data relating to fine-scale habitat elements. The resulting model can be used to predict core marten foraging habitat using characteristics of forest stand structure rather than dominant over-story species and age, with GIS data that are routinely available to forest managers.

Chapter 5 provides a detailed description of the marten's seasonal diet based on the analysis of c.2500 scats, 84 % of which have been genetically identified as pine marten in origin. Dietary preference of small mammal species is investigated by comparing the relative abundance of small mammal species estimated from live trapping within several distinct habitats within the forest, to the relative proportion of those species in the diet. These results, and those from other Scottish dietary studies, are discussed in relation to the geographic dietary trends observed across Europe, highlighting the similarities and differences between Britain and mainland Europe.

Chapter 6 describes and compares the composition of the marten diet across a time period of five years to investigate whether there is significant inter-annual variation, and if so, whether this is related to the abundance of *Microtus* voles in the study area during the same period. The implications of these results are discussed with reference to concerns about prey-switching behaviour and alternate prey.

Finally, Chapter 7 summarises the main findings presented in the preceding data chapters and provides discussion of the results in relation to conservation management of marten and modern plantation forestry.

Chapter 2

Methodological review and methods

2.1 Review of the Methodological Considerations

The following two sections describe some of the methodological considerations, and subsequent consequences, faced by investigators examining aspects of animal spatial ecology or diet. Specific reference is made to studies of *Martes* sp. where possible, but broader reference is made to studies of other carnivore species where necessary. The ways in which these issues were tackled during this study are given in detail within methods sections of the relevant chapters.

2.1.1 Habitat Studies

To evaluate a species' preference for a resource, such as a habitat type, a comparison is made between the usage and availability of that habitat (Krebs 1989). However, this process is fraught with problems (see Garshelis 2000 for greater discussion), and the methods used for measuring the use, selection and importance of habitats are subject to on-going review, which are too numerous and complex to go into detail here (e.g. Allredge & Ratti 1986, Worton 1987, White & Garrott 1990, Harris *et al.* 1990, Aebsicher *et al.* 1993, Manly *et al.* 1993, Arthur *et al.* 1996). For example, the inconsistencies in findings between marten-habitat studies can be partly explained by the variety of methods used for data collection, such as snow tracking (e.g. Jedrzejewski *et al.* 1993), scat surveys (e.g. Clevenger 1993) or radiotracking (e.g. Marchesi 1989), each of which has its own specific biases meaning results cannot necessarily be directly compared. The results of habitat selection studies can also be confused if data are pooled across the sexes or seasons, as this may reduce both the biological meaning and the statistical significance of analyses (Garshelis 2000). As female marten distribute themselves around the resources that are essential for the rearing of young (Powell 1979, 1994), females may be more selective of habitat than males (Paragi *et al.* 1996). A failure to detect habitat preferences may therefore arise if the selective preferences of one sex are nullified by combining data with the other sex in analysis. A similar situation may also follow from combining data across seasons. Seasonal differences have been frequently observed in marten habitat use, particularly a reduction in the use of non-forested habitats during winter (Koehler & Hornocker 1977, Campbell 1979, Soutiere 1979, Steventon & Major 1982, Spencer *et al.* 1983, Wilbert 1992). The implications are that habitat studies are likely to include selection for different habitat types depending on the season tracking is being conducted, or which sex is being tracked.

The scale at which habitat studies are conducted is critical to results, and may account for the inconsistencies in conclusions drawn from previous habitat studies (Bissonette *et al.* 1997, Payer & Harrison 2004). Studies of marten-habitat associations typically relate patterns of use to dominant vegetation types, such as forest over-story species, which may be too coarse to detect patterns of selection occurring at finer scales (Payer & Harrison 2004). It is increasingly recognised that habitat selection by animals is the product of several hierarchical decisions made at different spatial scales (Johnson 1980, Buskirk & Powell 1994, Bissonette *et al.* 1997). No universal scale for habitat selection studies exists, as different aspects of a marten's life history motivate habitat selection at each scale, therefore the scale used must match the aims of the investigation (Rahel 1990, Bissonette *et al.* 1997). At the smallest scale, the extent of which encompasses just a few metres, marten select site-specific elements needed for certain activities such as foraging, resting or scent marking (Payer & Harrison 2003, Porter *et al.* 2005). At the next scale up, decisions occur within a few tens of metres, involving the selection of habitat types needed to fulfil basic life requirements such as protection from predators (Hargis & McCullough 1984), thermoneutral resting sites (Buskirk *et al.* 1989), or access to prey (Sherbourne & Bissonette 1994). At coarser scales of a few hundred to a few thousand metres, marten maintain territories that include the habitats they need to fulfil year-round life-history requirements, which may vary seasonally (Buskirk & Ruggiero 1994). At even coarser scales involving several kilometres to several hundred kilometres of landscape, the spatial configuration of forest mosaics and other land-uses determines the areas that are suitable for the establishment of marten home ranges (Potvin *et al.* 2000). Habitat selection at larger scales inevitably affects selection at successively smaller scales i.e. habitats selected within the landscape will affect those present within a marten's home range (Johnson 1980). Therefore, if the distribution of selected habitat elements at the finest scale (i.e. woody debris) always occurs within the same coarser-scale habitat (i.e. mature forest stand), then a study conducted at one hierarchical level may well provide a parsimonious, mechanistic explanation for habitat selection at the next level (Bissonette *et al.* 1997). However, if the distribution of preferred fine-scale habitat elements is unrelated to the broader habitat type, particularly to those arbitrarily defined from the perspective of the human observer, then a use-availability study at a coarser level will either fail to detect selection, or else may return spurious results (Garshelis 2000).

To overcome these issues, great attention was paid to ensure the accuracy of the radiotracking methods used to collect data on marten habitat use as well as the mapping of habitat types. Habitat selection was investigated at nested spatial scales; first the use and availability of 'macrohabitats' (defined according to their dominant vegetation type) were investigated at the home range level, and then within home ranges before assessing the selection of specific habitat elements or 'microhabitats' within the core foraging areas of marten home ranges. For the purpose of this study, the terms ‘macro-‘ and ‘microhabitat’ refer to the scale at which habitat features are defined, which affects the scale at which selection can be assessed.

2.1.2 Diet Studies

The question of how many scats are sufficient to detect temporal or geographic differences in diet is often not considered yet has implications for the interpretation of results (Trites & Joy 2005). As sample sizes of scats are reduced the variance of results increases and interpretations become less meaningful (Carss & Parkinson 1996). The sample sizes used in marten diet analyses are often too small to allow general conclusions to be drawn and little attempt is made to estimate the number of marten contributing scats to the analyses (Balharry 1993a.). Home range sizes of marten within Scotland vary from 33 km^2 for males in Galloway (Bright & Smithson 1997), to less than 1 km^2 for females in Morangie (Chapter 3), therefore even a large number of scats could come from just a few individuals if they are collected from too small a study area. Characterising the diet from a few individuals may result in biased diet diversity estimates (Fedriani & Kohn 2001). Indeed, failure to recognise the individual as the sample unit rather than the number of scats is tantamount to pseudoreplication (Hurlbert 1984), as has commonly long been accepted in studies of animal habitat use (Johnson 1980, Harris *et al.* 1990, Aebischer *et al.* 1993). Of the previous diet studies of marten in Scotland, only two have used large sample sizes (i.e. greater than 500 scats), and more importantly provided information about the known minimum population contributing to the sample (Balharry 1993a., Halliwell 1997). Although both located within roughly the same geographic area as the present study (57-58°N, 4 -5°W), the difference in management practices between sites means that diets cannot simply be inferred between sites.

Dietary studies of carnivores have traditionally used scat identification criteria that rely upon morphological characteristics, scent, and location to determine the species from which the scat originated. Scats from sympatric carnivores may be confused when using morphology alone (Hansen & Jacobsen 1999, Farrell *et al.* 2000), and even expert naturalists can fail to consistently distinguish pine marten scats from those of red fox (Davison *et al.* 2002). It is crucial that management decisions based on the outcomes of dietary studies are informed by reliable field data, but the misidentification of scats can lead to the misrepresentation of the diet of the species being investigated (Reed *et al.* 2004). For example, rejecting scats that do not conform to typical morphology or other identifying characteristics may lead to bias in results towards a narrower dietary range. Recent developments using DNA methods on scats, or 'molecular scatology', provide great potential to improve the accuracy of scat identification (Piggott & Taylor 2003, O'Reilly *et al.* 2007). Such techniques are increasingly being used for applications such as species distribution surveys (e.g. Ruiz-Gonzalez *et al.* 2008), and population density estimates (e.g. Kalz *et al.* 2006), and are beginning to be applied to dietary studies (Posluszny *et al.* 2007), but have yet to be applied to a dietary study of British marten.

Scat content analysis has been widely applied to dietary studies of carnivores (e.g. red fox: Lockie 1959, wolves Floyd *et al.* 1978, coyotes *Canis latrans*: Livaitis & Shaw 1980, cougars *Felis concolor*: Ackerman 1984, grizzly bears *Ursus arctos*: Hewitt & Robbins 1996, otters *Lutra lutra*: Carrs & Parkinson 1996). Analysis of post-ingested diet allows large sample sizes to be collected in a non-intrusive manner, making it compatible with the protected status of species such as the pine marten in the UK. However, methods of scat analysis are subject to ongoing review (Corbett 1989, Reynolds & Aebischer 1991, Ciucci *et al.* 1996, Zabala & Zuberogoitia 2003), and numerous analytical procedures have been used to quantify the contribution of individual foods to the marten diet, including frequency of occurrence (e.g. Nyholm 1970), relative volume (e.g. Pulliainen 1981) and relative weight intake (e.g. Lockie 1961). The lack of unambiguous technical and analytical procedures in quantifying diet creates difficulties in the comparison and interpretation of results, as each method is subject to its own particular biases (Reynolds & Aebischer 1991). For example, frequency based methods, which express the occurrence of remains as a percent of the number of faecal samples or of the number of occurrences of prey species, tend to over-estimate the importance of small food items, which may be eaten frequently but contribute little to calorific intake. In contrast, volumetric methods which estimate of the relative volume composition of each scat, tend to over-estimate the importance of prey which leave a greater contribution of indigestible parts per unit mass consumed (e.g. insect exoskeletons; feathers from small birds) than larger prey (Zielinski 1986, Balharry 1993a.). After an extensive comparison and critique of techniques, Zabala & Zuberogoitia (2003) concluded that diet composition was most thoroughly expressed using a combination of a frequency-based method with a volumetric method.

To overcome these issues a large sample size of scats (c. 2500) was collected from an extensive network of transects (c. 85 km) throughout a study area covered by approximately 60 km^2 of forest where the minimum population size of marten potentially contributing scats to the sample was known (20 individuals). Genetic identification was used to confirm the origin of scats, and scat contents were represented using both frequency-based and volume-based methods.

2.2 Summary of Methods Used

What follows is a brief summary of the methods used in this study. A detailed description of the methods used is provided within each individual chapter. However, as many of the methods used in the collection of habitat use data are common to both Chapter 3 (Macrohabitat Selection) and Chapter 4 (Microhabitat Selection), universal methods will only be included in the former, whilst additional methods are included where relevant. Similarly, the two dietary chapter share many metholodical procedures in common, therefore Chapter 5 contains detail about the universal methods used for dietary analysis, though details of additional methods are given where relevant.

Details of all statistical analyses and statistical software used are contained within the relevant chapters. All means are given with standard deviations unless otherwise indicated.

2.2.1 Collection of Habitat-Use Data

During this study, sixteen pine marten (eight males and eight females) were captured and fitted with radio-collars after being weighed, sexed and aged. Marten were caught in Tomahawk live traps at pre-baited trap sites, and were immobilised with an intra-muscular injection using a combination of ketamine and medetomidine, antagonised by atipamezole. In the weeks after release, marten were radiotracked by two observers working as a team taking simultaneous bearings of the tagged marten's position at regular time intervals with which to estimate the marten's location using bi-angulation. Over a period of one year, each marten was tracked for several days during a single season until an asymptote was reached of home range size against time tracked. Sufficient data were collected from seven females and four males on which to conduct analyses. Tracking data were treated in two ways to estimate marten home ranges and analyse habitat selection, each of which is contained within a separate chapter. Minimum convex polygons were generated from tracked marten locations and used to examine macrohabitat selection at the scale of marten home range and then forest stand level (Chapter 3). Habitats within each home range were mapped along with those available within the greater landscape based on cover by dominant vegetation type. Compositional analysis and Bonferrni confidence intervals were used to determine whether habitat types were used more or less than would be expected by their availability and ranked accordingly. A sub-sample of the raw marten tracking locations containing data only from active females was used to examine microhabitat selection by foraging females (Chapter 4). Home ranges were generated using kernel density estimators, and core habitat was defined by the smallest area containing 25% of female activity. Random sites were generated inside the core area as well as in the remaining home range of each female. At each site, various attributes were measured relating to fine-scale habitat elements. Two sets of attribute data were collected for entry into two different multivariate models: field-measured attribute data were entered into a logistic regression model, whereas GIS-derived attribute data were entered into a classification tree model.

2.2.2 Collection of Dietary Data

During the same study period that spatial data were being collected, data on marten diet were also gathered. To examine seasonal diet (Chapter 5), marten scats were collected at monthly intervals from c. 85 km of transects throughout the study area. In total, c. 2500 scats were collected from an area where a minimum population of 20 individual marten were known to be present. Scat locations were recorded with GPS and the scats were bagged and before being frozen until needed for content analysis. A small amount of scat material was analysed genetically for 84 % of scats collected to determine each scat's species of origin. Those that were not genetically tested (14%) were visually identified by the author, whom in trials was able to accurately identify pine marten scats on 98 % of occasions. Scats were defrosted and their contents determined from macro- and microscopic examination and comparison with the authors own reference collection of food remains, and with published identification keys. Food remains were identified to species where possible, though time constraints prevented the microscopic identification of small mammal species found in scats lacking immediately identifiable teeth. Food items were grouped into six broad categories: small mammals, large mammals, birds, invertebrates, plant material and 'other', and data were grouped according to month and season. Small mammals included shrews, voles and mice, whereas squirrels, rabbits and anything larger were considered to be large mammals. Birds included eggshell remains found in scats. The 'other' food category included reptiles, annurans, fungi and miscellaneous or unidentified items. Diet was expressed using two methods: frequency of occurrence, which provides a measure of the frequency with which a food type is consumed; and estimated weight of intake, which uses conversion factors derived from captive feeding trials to relate the number of items consumed to the actual amount of food consumed based on prey remains. In order to determine whether a preference for any small mammal species existed, live trapping was conducted during April 2007 in various habitats. The relative abundance of small mammal species caught in traps was then compared to that found in scat contents.

Scats used to investigate inter-annual variation in marten diet (Chapter 6) were provided by an external investigation (details of which are given in Chapter 6) for four of the five years of the time period investigated, and were collected by the author during the fifth year. Scats were collected from two study sites, one of which was a sub-section of principal study site used in all other chapters; the other was a nearby forest located less than 5 km from the first site. At each site, a 10 km transect was walked at monthly intervals during spring and summer from 2003 to 2007 and all scats found were bagged and frozen. The species of origin was determined genetically for all scats collected, and scat contents were then examined macro- and microscopically as in Chapter 5. Data from the two study sites were combined, and data were grouped by year and expressed as the frequency of occurrence of food types. Tawny owl *Strix aluco* breeding data were acquired from a local raptor group to use as an index of changing *Microtus* abundance between years, as tawny owl clutch sizes have been found to be strongly positively associated with *Microtus* spring abundance. Owl data were available from 18 nests within the immediate vicinity of the study site that were repeatedly visited each year between 2003 and 2007, and data were available for the period 1995 to 2007 from over 30 nests that were spread over a larger geographic extent.

2.3 Study Site Description

Morangie forest (Fig. 2.1) is a Forestry Commission plantation located in the north east Highlands of Scotland with approximately 60 km^2 of forested area. A mosaic of arable farmland, permanent pasture and woodland surrounds the forest to the north, east and south, whereas the west is bordered by open hillsides of rough grazed land and heath moors. The landscape is hilly, with elevations ranging from 0 to 396 m above sea level (a.s.l.), but with the majority of the site lying between 100 and 300 m a.s.l. The area is dominated by podzolic ironpan soils and peaty gleys. The study area has a maritime climate with warm summers (July mean 13.3^{o}C) and mild winters (January mean 3.3^{o}C), with rainfall of c.1750-2050 mm per annum. Snow covered the ground for less than 20 days a year during the study period. The forest has good access, with over 100 km of roads and tracks varying in their degree of usage by forestry vehicles. There is no vehicular access to the forest by the public.

The forested area consists a post-war coniferous plantation subdivided by a ride network into stands (mean area = 8.3 $\pm$ 12.3 km^2), and interspersed with pockets of

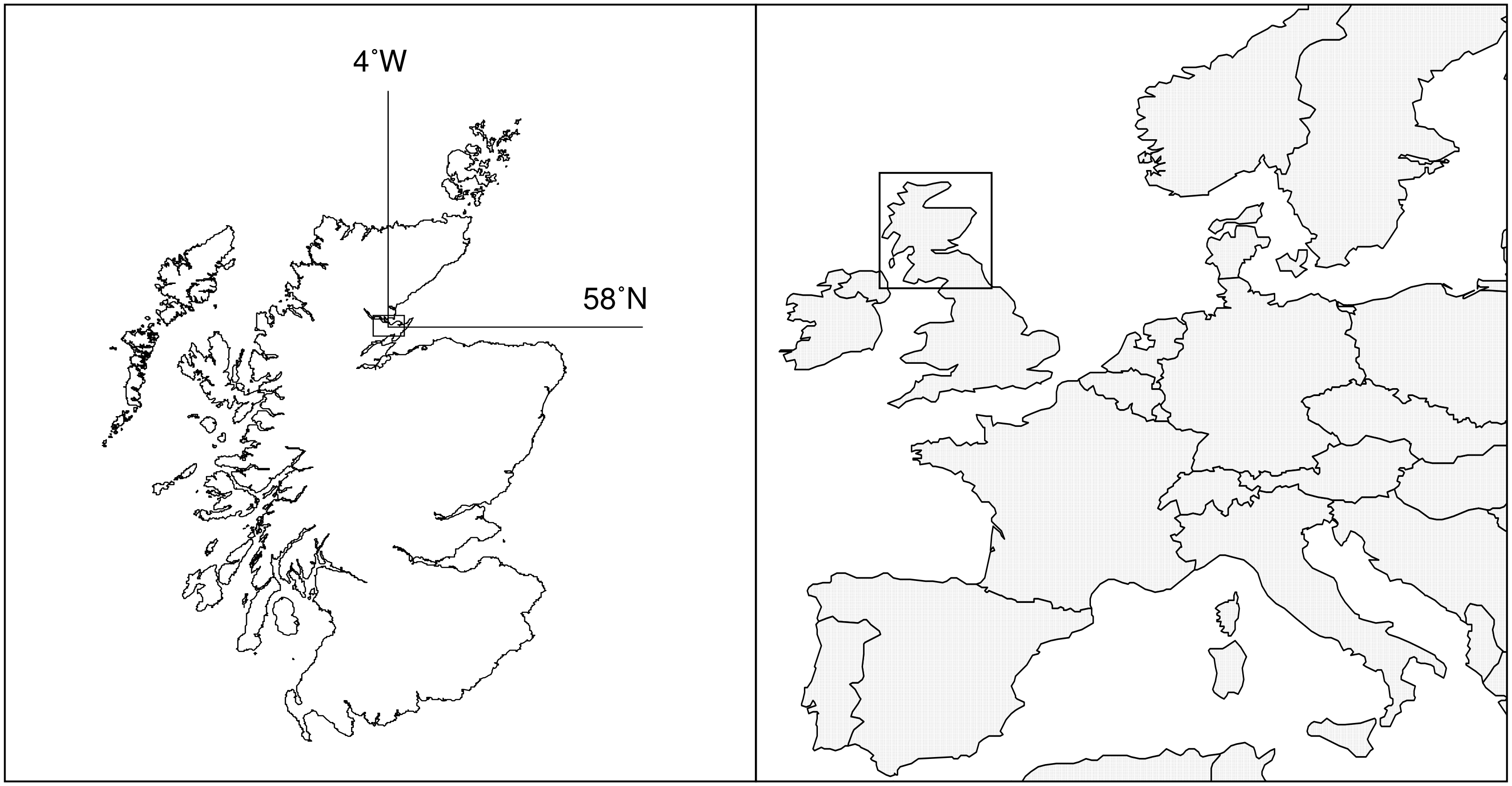


Figure 2.1 Outline of Scotland showing site location within Easter-Ross, Highland, 57.8° N, 4.1° W (left), and location of study site in relation to mainland Europe (right).

old growth forest (> 80 years of age). Scots pine dominates the forest in lowland areas, particularly to the north, east and south-west. For the past two decades areas of Scots pine have been managed to create a more naturally structured pinewood for capercaillie conservation (Leslie 1998). A well-developed field layer of blaeberry (*Vaccinium myrtillus*), heather (*Calluna vulgaris*) and heaths (*Erica* sp.) has been established by selectively thinning forest stands and preserving uncut shelter strips (Leslie, 1998). In some such areas, a low impact silviculture system of continuous cover has been established since 2002. In this system forest coupes are selectively cut to encourage natural regeneration and an uneven stand age (Heitzman, 2003; Pommerening & Murphy, 2004). Upland areas are dominated by monoculture, even-aged stands of lodgepole pine (*Pinus contorta*), Sitka spruce, and Norway spruce (*Picea abies*) of varying developmental stages, particularly to the west of the study area. These are managed by clearfell rotation, and consist of large-scale harvest and replanting units. In these stands, a vegetative field layer is largely absent and the ground is instead covered by mosses, needle litter and fine woody debris. Broad-leaved species such as beech (*Fagus sylvatica*), sallow (*Salix cinerea*), birch, rowan (*Sorbus acuparia*), ash and cherry (*Prunus* spp.) are locally common throughout the study area, particularly to the north-west where a privately owned woodland adjoins and forms part of the study area. Gorse (*Ulex europeaus*), rhododendron (*Rhododendron ponticum*) and bracken (*Pteridium aquilinum*) often encroach upon open areas and in canopy gaps.

Unplanted uplands are predominantly covered by heather – cotton grass *Eriophorum vaginatum* blanket bogs in damp areas, with matt grass *Nardus stricta* or purple moor grass *Molinea caerulae* in drier areas. Saturated valley bottoms are unplanted and consist of bogs of rushes *Juncus* spp., and mosses *Sphagnum* spp.. In unplanted lowland areas, particularly along road verges, rides and areas after clear-felling, the vegetation is frequently dominated by grasses such as bent *Agrostis* spp., wavy-hair grass *Deschampsia flexuosa*, tufted-hair grass *D. cespitosa*, Yorkshire fog *Holcus lanatus*, or fescue *Festuca* spp., with rushes in damper areas. Red fox are present in the area but at unknown densities, their numbers are not routinely controlled within Morangie forest. Other predators present in the area include the badger, wild cat *Felis silvestris*, stoat *Mustela erminae*, weasel, otter, buzzard *Buteo buteo*, tawny owl, goshawk *Accipiter gentiles*, sparrowhawk *A. nisus*, kestrel *Falco tinnunculus*, and golden eagle. Mammalian herbivores include red deer *Cervus elaphus*, sika deer *C. nippon*, roe deer *Capreolus capreolus*, rabbit *Oryctolagus cuniculus*, brown hare *Lepus capensis* and red squirrel. Grey squirrel *Sciurus carolinensis* are not present. The deer population is controlled with regular culling throughout most of the year, although the "gralloch" (the internal organs) is no longer routinely left *in situ* where the animal was shot as it was in during the studies of Balharry (1993) and Halliwell (1997).

Chapter 3

Pine marten macrohabitat selection

3.1 Introduction

Marten are often described as habitat specialists that require old growth coniferous forest for survival (Brainerd 1990, Pulliainen 1981b, Storch *et al.* 1990, Buskirk & Powell 1994, Buskirk & Ruggiero 1994). This habitat provides marten with resources that fulfil their life requirements, particularly protective cover from predators, access to prey, and thermoneutral resting sites (Buskirk & Powell 1994). Throughout much of their range, the staple prey of marten are *Clethrionomys* voles, which partly explains the species' close association with forested environments (Buskirk & Ruggiero 1994, Zalewski 2004). However, marten are highly catholic in their dietary habits (Clevenger 1994, Martin 1994, Zalewski 2004), and are capable of using a wide variety of habitat types that do not fit this pattern (Clevenger 1993, Marchesi 1989, Jedrzejewski *et al.* 1993, Brainerd *et al.* 1994). The most consistent marten-habitat relation therefore appears to be a general association with forest habitats, and avoidance of open, non-forested habitats (Buskirk & Powell 1994, Buskirk & Ruggiero 1994, Proulx *et al.* 2004). However there are exceptions to this rule, for example marten have been found to be indifferent of over-head cover in the absence of predators (Clevenger 1994b). Interpretations of marten-habitat associations therefore require that the ecological context, sampling approach, and landscape of the study be understood. Marten are adaptable and opportunistic animals, and it may well be that the degree to which they can be considered habitat generalists or specialists is entirely dependent on the unique set of ecological circumstances affecting local populations.

In Britain, marten display a preference for forested habitats whilst avoiding use of open, non-forested habitats such as moor, grassland and clear-fells (Balharry 1993a., Halliwell 1997). It is somewhat paradoxical then that *Microtus* voles, which are specialists of open graminoid habitats (Hasson 1978), are consistently found to be the most frequently occurring small mammal species in their diet (Lockie 1961, Velander 1983, Gurnell *et al.* 1994, Putman 2000, Coope 2007, Chapters 5 and 6). The way in which marten utilise habitats according to dietary evidence appears to be in direct contradiction with the findings of simultaneously conducted macrohabitat studies (e.g. Balharry 1993a., Halliwell 1997). The failure to detect such important aspects of marten habitat requirements in these studies is likely due to a variety of reasons, for instance data pooled across sexes and seasons may mask any existing relationships. Marten also select their habitats different habitat for different activities (Porter *et al.* 2005), yet data from active or resting marten are not always explicitly separated for analysis, therefore may be biased towards the habitats in which den sites are found. Another contributory factor is the resolution of habitat classification and radiotracking data used. Indeed, Balharry (1993a.) suggested that the marten use of closed-canopy coniferous forest found in his study may have been over-estimated because habitat mapping was too crude to distinguish canopy breaks caused by riparian strips. Such areas would provide suitable *Microtus* habitat that marten may have been using to hunt; yet the low resolution at which data were collected and analysed was insufficient to differentiate this use (Balharry 1993a.). The findings of Halliwell (1997) were no doubt affected by the small sample sizes of animals tracked, but also because the coarse nature of habitat classification used in which all non-forested habitats (including grassland, moor, clearfell and open water) were grouped together for analysis. It is unsurprising that marten were seen to avoid open habitats given that the functional uses and availability of each of these sub-habitats varies so greatly. Bright & Smithson (1997) revealed more subtle patterns of habitat selection by conducting analysis at a series of nested spatial scales. Marten displayed a clear preference for woodland at the landscape scale, but within home ranges, marten displayed preference for certain microhabitats that were based on the presence of tussock-forming grasses and streams, in what appeared to be homogenous closed-canopy plantation. The use of low-canopy cover areas within forest blocks was attributed to the greater presence of *Microtus*. The lack of agreement between the findings of previous habitat-association studies warrants further investigation as to how the preferred prey of a forest-dwelling predator is found in open habitats. This work will have implications both for the management of existing forests within the marten's range, as well as potential reintroductions of the species to England and Wales (Bright & Smithson 1997).

The objectives of this chapter were to describe the spatial aspects of pine marten foraging ecology within a coniferous plantation forest. Only data from active pine marten were used in order to infer associations with habitats used for foraging rather than resting. Estimates of home range size were provided for comparison with marten population densities found in other studies to assess the effect of various management and ecological scenarios on population densities. A comparison of the general differences in habitat composition of home ranges between sexes and seasons was made, although sample sizes precluded a comparison of habitat selection between sexes or seasons. Habitat-selection was investigated using a series of nested spatial scales based upon data that was collected and analysed at high resolution. Comparisons of habitat use and availability were made at the scale of home ranges within the greater landscape, and then habitats within home ranges, answering the following questions at each level: 1. Is use of habitats by adult marten selective or random? 2. If use is selective, which habitat types are used more or less than would be expected if use were random? Results will be discussed with reference to the unique ecological contexts affecting pine marten in the UK, and their implications for management.

3.2 Methods

3.2.1 Trapping

Marten trapping was conducted periodically between January 2006 and March 2007 following the methods of Balharry (1993a.). All forest roads and paths within the study area were surveyed to identify sites bearing signs of recent marten activity, indicated by the presence of fresh scats. Prior to trap installation, each site was pre-baited using hen eggs or deer hearts, and scent “flagged” by placing honey, deer blood, or commercial lure (*“Magnum Call”, Blackie’s Blend, Glenmount, OH, USA*) on prominent trees branches above and around the site. Baited sites were checked regularly, and bait was replaced where it had been removed. Once bait had been removed from a site three to four times in succession, a trap (*Collapsible live traps # 205 and # 206, Tomahawk Live Trap Co., P.O. Box 323, Tomahawk, WI, USA*) was deployed there. Traps were positioned on level, dry ground and completely covered with woody debris and mosses, which acted both to insulate and camouflage traps. Large rocks were used to steady the traps and prevent any attempts by marten to dig beneath them. All traps were fitted with a “bite bar” to prevent trap injuries. Where possible, traps were left in position, and those that weren’t set were “locked open” with a cable tie or a large stick, but continued to be baited. Trapping efforts were concentrated within a localised section of the study area for around a week, where up to 20 traps would be set and checked twice a day (morning and evening), after which attention would move on to another section of forest. No trapping was attempted from the onset of the breeding season (late March) to late summer (August), to avoid disturbance to pregnant females or those with kittens. Trap site baiting however, was continued throughout the study period to maintain marten interest. All trapping was carried out under licence from Scottish Natural Heritage (*Scientific Licence No. 6146*).

3.2.2 Capture & Marking

Captured marten were immobilised and sedated under Home Office licence (*Animals Scientific Procedures Act 1986, PIL 60/10174*). An intramuscular injection of ketamine combined with medetomidine, and antagonised by atipamezole (respectively*: Ketalar®, Domitor®, Antisedan® Pfizer Animal Health, Pfizer Inc. NY, USA*) was administered at dosage rates used for European mink (*Mustela lutreola*) and polecats (*Mustela putorius*) (Fournier-Chambrillon *et al.* 2003). This combination provides a rapid, safe anaesthesia protocol that substantially reduces or eliminates the adverse effects associated with ketamine anaesthesia alone, and can be reversed when needed to reduce recovery times (Fernandez-Moran *et al.* 2001; de Leeuw *et al.* 2004). Marten were generally placid within traps, and the most effective method of reducing trauma during immobilisation was to inject the anaesthetic whilst distracting the attention of the marten elsewhere. Where this was not possible, a makeshift "squeeze-panel" was improvised using a thick blanket pushed into one end of the trap. Induction was smooth and rapid (within 5 min.), and marten remained sedated for at least 20 min., during which time they were weighed, sexed, and radio-collared. All captured animals were uniquely identified with a passive transponder (*Trovan ®, Identify UK Ltd., Hessle, East Yorks, UK*) implanted subcutaneously to the scruff of the neck. The age of each animal was determined by body size and tooth condition into two classes: juvenile or adult (>1 year). Only adult marten were fitted with radio-collars because of the welfare implications of collaring an animal that has not yet reached full body size. Adult marten were fitted with VHF-transmitters (*TW-3, Biotrack Ltd., Wareham, Dorset, UK*) mounted on nylon collars with an external aerial transmitting on 173 Mhz, fastened by a brass locking plate. The complete package weighed approximately 26gms, representing on average 1.4 % and 1.9 % of male and female body weights respectively. Transmitters had an operational life expectancy of 12 months, and a ground to ground line of sight range of up to 3 km. Each transmitter was fitted with an activity sensor that pulsed faster when the marten was moving, and slower when the marten was stationary, thus allowing locations to be differentiated into those of active or inactive marten. Marten that had been anaesthetised were placed into wooden recovery boxes (110cm x 30cm x 30cm) and allowed to recover fully for up to 2-3 hours before being released.

3.2.3 Radiotracking

Radio-collared marten were tracked using Sika receivers and three-element flexible Yagi antennas (*Biotrack Ltd., Wareham, Dorset, UK*). The fast-moving, wide-ranging nature of active marten combined with the difficult tracking terrain meant that taking multiple sequential bearings with which to triangulate the animal's position would be inherrently inaccurate (Saltz 1994). Accuracy could be greatly improved by taking bearings concurrently, and so two observers worked in synchrony to take two simultaneous bearings for each active location estimate, co-ordinated with communication over 2-way radios (*Kenwood TK3201 Protalk T2, Wildtalk, York, UK*). Multiple bearings were taken for stationary animals.

As was also found by Balharry (1993a.), locating several radio-tagged individuals at discrete time intervals was frequently thwarted by the inability to relocate those individuals without incurring substantial periods of unproductivity whilst searching for them. Maintaining contact continually with one focal animal per tracking session proved to be the only reliable method for collecting consistent and unbiased data on habitat use. If the focal animal was lost during a tracking session, another individual was found and tracked where possible. Tracking was split into 8-hour sessions, the majority of which occurred between 1600 and 0800 to coincide with the marten's period of greatest activity

(Balharry, 1993), but with at least one session per animal outside these times. Location estimates were taken every 10 minutes where possible. Observer positions were recorded using a high-sensitivity GPS receiver with improved satellite reception (*GPSmap 60Cx, Garmin Ltd. Europe, Southhampton, UK*), which gave an average positional accuracy of 5.38 m (± 0.99m SD, range 4m - 11m), even under heavy canopy cover. Compass bearings taken towards the marten estimated location were recorded along with the marten's activity status (either active or inactive). Marten that remained inactive for two or more location estimates were considered to be resting, in which case only one location was recorded for the rest site but no new locations were taken until the marten moved elsewhere. It was generally possible for the observers to position themselves with a GPS accuracy of ± 5 m by making use of canopy gaps and rides, before taking a bearing on the animal's location. To minimise the error polygons generated when triangulating with two bearings, observers positioned themselves relative to each other so that bearings would intercept at 90°, with one observer closer to the marten's estimated location than the other (White & Garrott, 1990). Marten were tracked over several days until their home ranges reached a stable size that did not increase with the addition of further locations (Fig 3.1), or until they were lost. All marten that could be recaptured at the end of the study period had their radio collars removed.

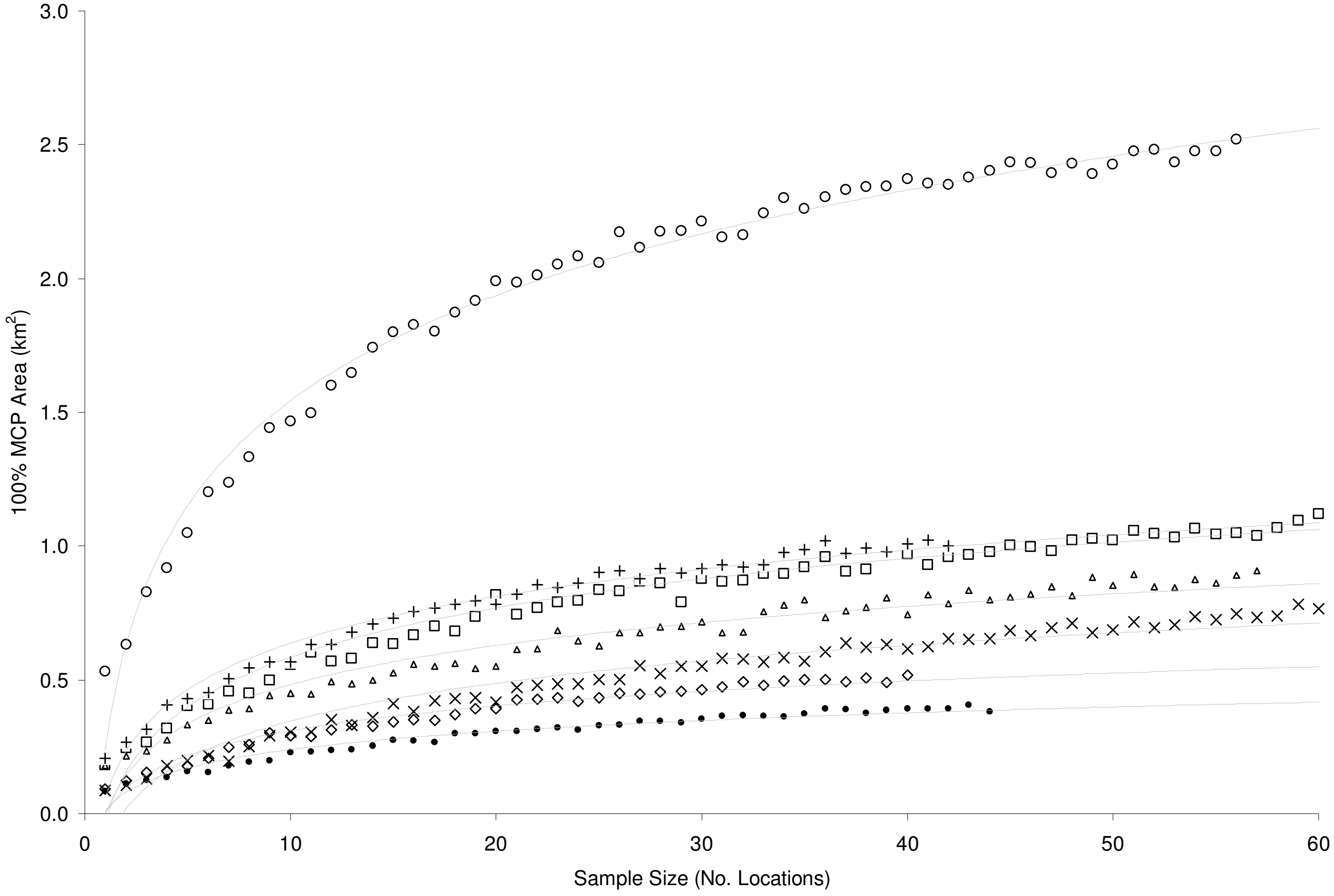


Figure 3.1a Cumulative home range (100% MCP) area increment with successive number of fixes calculated using a bootstrap method with 100 samples for 7 female pine marten. All females reach asymptote after c. 35 fixes.

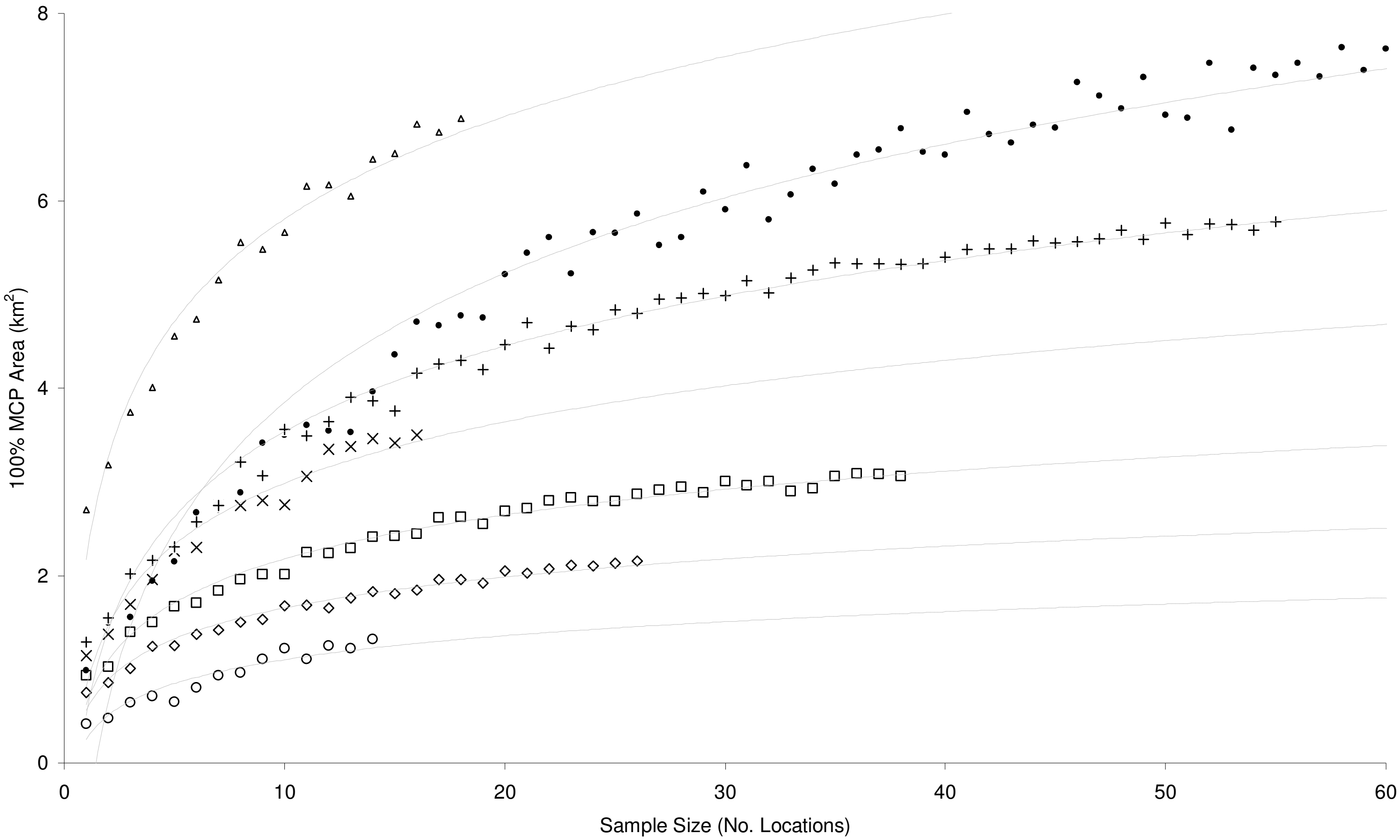


Figure 3.1b Cumulative home range (100% MCP) area increment with successive number of fixes for 7 male pine marten. Only Male 1 (open diamonds), Male 2 (*open squares*), Male 7 (*closed circles*) and Male 8 (*plus sign*) reach an asymptote after c. 25, c. 35, c. 55 and c. 45 fixes respectively.

3.2.4 Tracking Error & Location Estimation

Far from being exact points, the locations provided by telemetry are at best estimations of an animal's position located within a surrounding error area, the size of which is unique to each location and a function of many interacting factors (Heezen & Tester, 1967; Springer 1979; White & Garrott, 1990). By evaluating the size of each location's error, an observer can create an ellipse or polygon in which they can be confident that the animal's true position is contained. Location error in this study was calculated using two methods: the Location Error Method (LEM: Zimmerman & Powell 1995), and Lenth's (1981) Maximum Likelihood Estimator (MLE). In order to achieve this, a series of test triangulations was run where transmitters ($n = 42$) were placed at various locations within the study area and their locations recorded using GPS. Transmitter locations were selected to be representative of where a pine marten might be located. These included two levels of vertical positioning: i.) at ground level, ii.) elevated above ground level, in each of three broad habitats: forest interior, forest edge, and open ground, with 7 replicates of each. Care was taken to ensure ground level positions included placing some transmitters behind obstacles such as rocks and tree stumps, or in ditches so as best approximate real life scenarios. Transmitter locations were then estimated by inputting bearings and observer positions to the radiotracking software package Locate III (Nams 2006), and compared with actual locations in ArcView®GIS

(Environmental Systems Research Institute Inc., 1999). The mean Euclidean distance between estimated and actual locations (LEM) was 55 m (± 68 m SD), and the absolute difference in azimuth (bearing error) was 12° (± 10° SD). The standard deviation of bearing error was used in all subsequent location estimations, and MLE was used within Locate III to calculate an error ellipse for each location to serve as a 95 % confidence area ellipse of the animal's true location (Nams 2006).

Although biologists often estimate telemetry error, it is not always taken into account when testing for habitat selection (Nams, 1989). Due to the inherent inaccuracy of telemetry, each animal location used in a habitat study should be thought of as an area containing a mosaic of habitat patches, rather than a single point within a discrete habitat patch, so it is crucial that location error areas do not exceed habitat patch size (Nams 1989, Rettie & McLoughlin 1999). As 99 % of macrohabitat patches defined within the study site had an area greater than 100 ha, only locations whose error ellipse was an order of magnitude smaller (< 10 ha) were used in home range estimation and analysis, of which 58 % had an error ellipse < 1 ha. However, as the mean LEM determined from radiotracking trials was 55 m, a minimum location area of 0.95 ha was used (the area of a circle with radius = 55 m) for locations with an error ellipse < 1 ha.

3.3 Analytical Techniques

Between February 2006 and March 2007 eighteen pine marten were trapped, including eight adult females, eight adult males, and two juvenile females. Radiotracking was conducted from April 2006 and June 2007. Of the sixteen radio collared adults, one male and one female were never relocated again after initial capture, and one male was found road killed. Of those remaining, sufficient data were collected for seven females and four males to map stable home ranges.

3.3.1 Home range size and habitat Composition

Location data from the eleven marten were entered into GIS (ArcView 3.2, Environmental Systems Research Insitute, Inc. 1999) for home range analysis using the Home Range Extension for ArcView® (Rodgers & Carr 1998). Home range sizes were calculated using the minimum convex polygon (MCP: Harris *et al.*1990) based on 100 % of all fixes (active and stationary) for comparison with other studies (Balharry 1993a, Halliwell 1997, Bright & Smithson 1997). For compositional analysis of habitats within the home range however, MCPs were recalculated using 95 % of fixes, using the 'Area Added' method to remove outlying locations (White & Garrott 1990).

Defining habitat types as discrete entities can prove problematic as the number of habitats defined can directly affect the results of habitat selection studies (Knight & Morris 1996). In addition, habitat distinctions are not clear-cut, and the criteria used to partition habitats in to functional types may not correspond with the animal's biological perspective. As more types are defined, the observations per type are reduced, thereby diminishing the power of statistical tests to distinguish selection (Garshelis 2000); therefore land cover was limited by characterisation in to one of seven broad homogenous classes based on dominant vegetation type og the ground layer, field layer and canopy (Table 3.1). To increase precision of habitat classification, spatial habitat data of the study site were gathered from a variety of sources including the Forest Enterprise subcompartment database (SCDB: Forest Enterprise, Forestry Commission, UK), orthorectified aerial photographs (OAP), OS MasterMap™ (OSMM: Ordnance Survey®, Southampton, UK), Land Cover Map 2000 (LCM2000: CEH, Monks Wood, UK), and ground-truthing surveys (GTS).

3.3.2 Compositional Analysis

Selection of habitats was examined with Aebischer *et al.'s* (1993) method of compositional analysis. In this method, the proportional use $_u$ and availability $_A$ of habitats are transformed into log-ratios y_u and y_A using one habitat type as the denominator $y_i = ln\ (x_i / x_j)$. The differences between log-ratios are then

Table 3.1: Habitat classification criteria based on dominant vegetation of field, shrub and canopy layers. Source details are given in text (Section 3.2.5).

Habitat	Source	Description	Classification criteria		
			Ground / field layer	Shrub layer	Over-story
HEATH	LCM2000 OAP GTS	Open heath moorland.	Dominated by *Ericaceous* spp.	Absent	Absent
ROUGH	LCM2000 OAP GTS	Open unimproved tussock grassland.	Dominated by ***Poaceae**, Juncaceae* & *Cyperaceae.*	Absent	Absent
AGRI	SCDB LCM2000 OAP GTS	Open agricultural land.	Bare soil Cultivated crops or pasture	Absent	Absent
SCRUB	SCDB LCM2000 OAP GTS	Shrubs / scattered trees / wind-thrown trees / clear-fell or regenerating conifer forest < 16yrs old.	As ROUGH / HEATH Coarse woody debris *Pteridium* spp.	*Ulex europaeus / Rhododendron ponticum / Cytisus scoparius / Salix* spp. conifer saplings aged < 16yrs	< 30% cover from coniferous and/or non-coniferous trees
NONCON	SCDB LCM2000 OAP GTS	Non-coniferous woodland.	As ROUGH. Bare soil. Leaf litter.	As SCRUB	> 30% cover from non-coniferous trees
CLOSED	SCDB	Closed-canopy commercial conifer plantation (pre-thinning).	Needle litter. Coarse woody debris. Bryophytes.	Absent	> 70% cover from coniferous trees aged 17-44yrs
MATURE	SCDB	Open-canopy commercial conifer plantation (2+ thinnings).	As HEATH. Occasionally as ROUGH.	Largely absent or as SCRUB Occasionally *Betula spp.*, *Sorbus spp.*, or *Ilex* spp.	30-70% cover from coniferous trees aged > 45yrs

calculated, $d = y_u - y_A$. The null hypothesis is that there is no difference between paired log-ratios ($d \neq 0$) i.e. habitats are used randomly. This can be tested by calculation of Wilks' Lambda (λ). Where: $\lambda = | R_1 | / | R_2 |$ and R_2 is a residual matrix of raw sums of squares and cross products calculated from d assuming a null model, and R_1; a residual matrix of mean-corrected sums of squares and cross products calculated from d assuming a test model. The quantity $-N \ln \lambda$, where N is the number of rows within the log-ratio data matrix, is distributed approximately as χ^2 ($df = n - 1$). If habitat use is shown to deviate from the null model, habitat types can be ranked in order of relative use. A ranking matrix is produced for each animal of the pair-wise differences in utilised and available log-ratios, for all possible combinations of habitat types. Each matrix element is averaged over the sample of animals to produce a matrix of means and standard errors. For each element, the ratio of mean / standard error gives a t values measuring departure from random use. The number of positive elements in each row of the matrix is an integer between 0 and $D - 1$, where D is the number of habitat types, that ranks habitats in order of increasing relative use, where 0 is least preferred, and $D - 1$ is most preferred.

This approach was favoured as it avoids many of the shortfalls affecting other techniques such as inappropriate sampling units, non-independence of proportional data, and arbitrary definitions of availability (e.g. Friedman 1937, Neu *et al.* 1974, Quade 1979). In this method it is the individual animal rather than the radio location that is regarded as the sample unit, so reducing the non-independence of data (Garshelis 2000) and circumventing the problems associated with autocorrelation (Swihart & Slade 1985). By transforming habitat proportions into log-ratios, this method overcomes the problem of the 'unit-sum constraint' (Aitchison 1986), whereby the proportions of habitats used are not independent of each other as an animal's avoidance of one habitat will invariably lead to an apparent preference for another.

By considering habitat selection at different levels, this method can also be used to account for the hierarchical nature of resource selection by animals. In resource selection studies 'available' habitat is frequently arbitrarily defined from the total study area, however an animal's use of a habitat is the product of choices at several levels, or orders (Johnson 1980). Selection of habitats within the home range will be of higher order than selection of the home range, because the availability of each habitat within the home range is determined by the selection of the home range itself (Johnson 1980). As different forms of habitat selection may occur at each level, analyses should be carried out in stages to identify their effects (Aebischer *et al.* 1993). This first stage determines selection of an individual animal's home range from the landscape by comparing the habitats used within the home range with those available in the total study area. This provides an indication of the broad environmental or social determinants of home range selection, and is the equivalent of Johnson's second-order selection. Next, selective use of habitats within the home range can be determined by comparing the habitats used at each radio location with those available within the home range. This is the equivalent of Johnson's third-order selection, and pertains to the use of various habitat components within the home range.

As marten display intra-sexual territoriality (e.g. Balharry 1993a.), social exclusion may preclude the use of certain habitats and it is therefore reasonable to assume that only habitats contained within that individual's home range are available to it at that level. However, different methods of home range delineation will yield different availabilities of habitats, and so results will largely depend on the home range estimator used. Similarly, without fully understanding the decisions influencing home range placement at the landscape scale, lower order selection will be strongly dependent on how availability with the total study area is defined. Although definitions of availability are still somewhat arbitrary in Aebischer *et al.*'s (1993) method, separating habitat utilisation in to two stages avoids the greater loss of biological meaning that would result from relying solely on comparisons of use with availability within an arbitrarily defined study area.

For this study, comparison of use and availability were made at two levels: home range composition vs. total study area, and proportional use at radio locations vs. home range composition. The total study area was defined as the smallest polygon that fully contained the MCPs of all eleven tracked animals buffered by a distance equal to the length of the average female home range (1.8 km). Home ranges were defined using the 95 % MCP for each animal whose home range reached an asymptote. As all location estimates were accurate to within 55 m, each MCP was buffered by a 55 m strip to ensure that all true locations fell within the MCP home range used for compositional analysis. Both active and inactive locations were used to generate MCPs, which meant that at the home range level, data from inactive marten were included. However, due to the extended time periods spent in or near dens, particularly during cold weather (e.g. Thompson & Colgan 1994) only one location was recorded each time a marten was judged to be at a resting site, therefore the majority of locations (73 % ± SD 9 %) used to generate MCPs were from active marten. In contrast, at the location level of analysis only active locations were used, allowing conclusions to be drawn about which habitats within the home range are important for foraging and movement. Active locations in close proximity to resting sites were omitted as these may bias selectivity indices towards habitats containing den sites. Although marten locations were recorded every 10 minutes, a minimum interval of 20 minutes between successive locations was chosen to maximise the number of locations that could be used whilst maintaining independence between points. Examination of the distance travelled over time for a subset of locations taken every 10 minutes during the early stages of the study showed that marten were equally as likely to travel ≥ 500 m in 20 mins as they were in 120 mins. Where locations were required to be made redundant to increase the time interval, those with the smallest error ellipses were retained.

Aebischer *et al.'s* (1993) method of compositional analysis regards a location as a single point, but as this does not account for the inherent imprecision of estimating locations from radiotracking data, it was adapted slightly for this study by instead considering each location as an area defined by its error ellipse; the habitat with greatest proportional cover within the error ellipse was used for that location. Scrub was the habitat used as the denominator for log-ratio transformation as it was common to the home ranges of all animals. As log-ratio transformations of zero are invalid, all cases where a proportion of 0% was recorded were replaced with a value of 0.001 %, two orders of magnitude less than the smallest recorded nonzero percentage (0.1 %).

As it uses individuals rather than locations as sample units means, this method is more sensitive to inter- rather than intra-individual variability, therefore the number of individuals sampled is more important than the number of locations per individual (Girard *et al.* 2006). A sample size of six constitutes the absolute minimum for adequate statistical analysis comparing utilised with available habitats (Aebischer *et al.* 1993) and it was therefore not appropriate to use on our four male marten. Instead, habitat selection in males was examined using Bonferroni confidence limits on data pooled across four males (Cherry 1998). An equal number (n = 22) of randomly selected locations from each male to avoid unequal weighting of animals with different numbers of relocations (Thomas & Taylor 2004). This method was also used to compare differences in habitat selection between the sexes at each level of habitat selection. In addition, the distance travelled by marten outside forested habitats was investigated by measuring the distance to the nearest forested habitat (nonconiferous, closed or mature) whenever marten were located in 'open' habitat (i.e. rough, pasture or heath). Inter-sexual differences in the mean maximum distance travelled from forest cover were tested for with t-tests for independent samples after testing for normality and equality of variance (Zar 1999). A Chi-square with Yates' correction was used to test for a difference in the proportion of fixes outside forested habitat between sexes.

All statistical analysis of habitat compositions was conducted within Resource Selection for Windows (RSW v. 1.0, Leban 1998), and all other statistics were performed in SPSS® 13.0 for Windows (SPSS® Inc. 2004) or Microsoft® Office Excel 2003 (© Microsoft Corporation, 1985-2003). All averages are given as means with standard errors unless specified otherwise.

3.4 Results

3.4.1 Home Range Size

A total of 568 locations separated by 20 minutes or more were obtained for the eleven marten whose home ranges reached asymptote (Fig 3.2). Sample sizes of locations per individual ranged from 34 to 75 (Table 3.2). Based on the 100 % MCP, the mean home range size for females and males was 0.70 km^2 (± 0.12 km^2), and 5.63 km^2 (± 1.65 km^2) respectively. Home range areas decreased to 0.50 km^2 (± 0.09 km^2) and 3.53 km^2 (± 0.75 km^2) for females and males respectively if just 95 % of fixes were used to generate the MCP. The home range sizes from previous studies are given in Table 3.3 for comparison. It is clear from examination of range sizes that those observed in Morangie were among the smallest in the UK. As found in previous studies, female home ranges were significantly smaller than those of males (Mann-Whitney-Wilcoxon $W_{(12)} = 28.00$, $P < 0.01$).

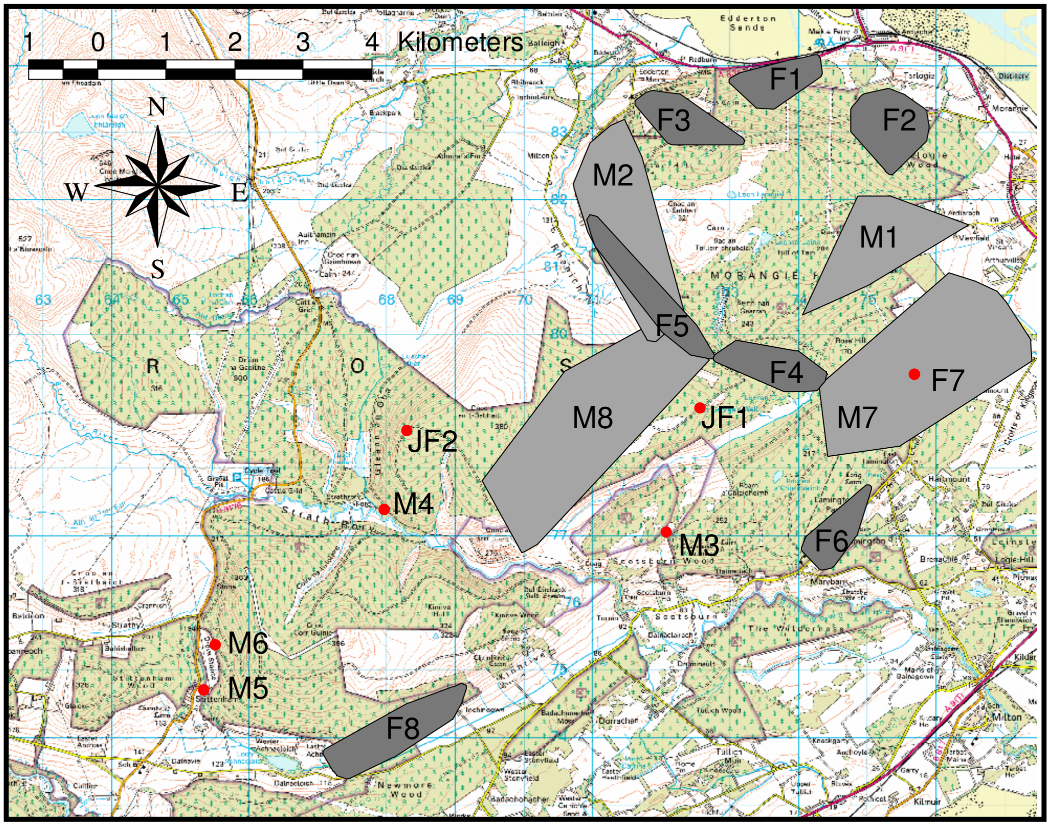


Figure 3.2 Home range polygons (95% MCP) of seven female (dark grey), and four male (light grey) pine marten radiotracked between April 2006 and June 2007. Red dots indicate locations of other known pine marten within the study area that were not tracked sufficiently to be included in analysis due to: disappearance before radiotracking of them commenced (F7, M5); road-killed (M6); juvenile so not collared (JF1, JF2); only partially tracked within the study period (M4, M3).

Table 3.2 Home range areas (km^2) of pine marten radio tracked to an asymptote of area over time based on minimum convex polygons. Number of locations used to generate MCP in parenthesis.

	Female Marten			**Male Marten**		
	100% MCP	**95% MCP**	**Tracking duration**	**100% MCP**	**95% MCP**	**Tracking duration**
	0.46 (34)	0.34 (32)	09 / 03 / 2007 – 27 / 05 / 2007	3.43 (42)	2.77 (40)	15 / 05 / 2006 – 28 / 07 / 2006
	0.79 (70)	0.64 (67)	08 / 04 / 2006 – 11 / 07 / 2006	9.86 (75)	4.80 (70)	11 / 01 / 2007 – 07 / 03 / 2007
	0.54 (45)	0.51 (43)	10 / 01 / 2007 – 07 / 02 / 2007	6.61 (59)	4.75 (56)	09 / 04 / 2007 – 07 / 06 / 2007
	0.53 (60)	0.21 (57)	11 / 05 / 2006 – 17 / 07 / 2006	2.63 (39)	1.81 (37)	10 / 05 / 2006 – 03 / 08 / 2006
	1.29 (57)	0.83 (54)	05 / 11 / 2006 – 06 / 03 / 2007			
	0.40 (46)	0.25 (44)	19 / 04 / 2007 – 07 / 06 / 2007			
	0.87 (41)	0.73 (39)	12 / 05 / 2006 – 31 / 07 / 2006			
Mean	0.70	0.50		5.63	3.53	
SE	0.12	0.09		1.65	0.75	

Table 3.3 Home range sizes (km^2) from this study* and other studies in Scotland, Ireland, and Poland. Sources: Balharry (1993a.); Bright & Smithson (1997); Halliwell (1997); O'Sullivan (*unpublished data*, cited in Birks 2002) and Zalewski *et al.* (1995). Sample size of radiotracked marten shown in italic parenthesis.

Location		**Habitat type**	**Males**	**Females**
Scotland	Galloway	Upland *Picea* monoculture	32.86 *(3)*	9.78 *(3)*
	Kinlochewe	Fragmented upland conifer	23.63 (*7*)	8.83 (*5*)
	Galloway	Lowland mixed conifer	8.36 *(3)*	4.52 *(2)*
	Strathglass	Lowland mixed conifer	6.28 (6)	3.57 (6)
	Novar	Lowland mixed conifer	3.04 *(2)*	2.01 *(2)*
	Morangie*	Lowland mixed conifer	5.63 *(4)*	0.63 *(7)*
Ireland	County Clare	Lowland broadleaf	0.42	0.20
Poland	Bialowieza	Lowland broadleaf	2.23 *(5)*	1.49 *(8)*

3.4.2. Sexual Differences in Habitat Use

Bonferroni confidence limits revealed sexual differences in the way marten used available habitat (Table 3.4). At the home range level, males and females used rough grassland and scrub in similar proportions, yet males used more closed coniferous forest, heath and pasture than females, whereas female used more mature forest and deciduous woodland than males. Within home ranges however there was no difference in the use of habitats between the sexes except that males made more frequent use of heath moorland than females.

In general males seemed to make more use of open habitats than females; in addition to using heath more than females at both levels of selection they also used pasture more than females at the home range level, though there was no difference between sexes in their use of rough grassland at either selection scale. The females' reluctance to use open habitats was reflected when the comparison was made between the distance travelled into non-forested habitat between males and females; males would travel twice as far as females outside the forested boundary (males $\bar{x}$ = 199.6 m + 46.3; females $\bar{x}$ = 93.7 m + 19.9; $t_{(9)} = -2.405$, $P < 0.05$). Males also spent proportionally more time outside forested habitats than females based on the number of locations within and outwith forest stands ($\chi^2 = 8.79$, *df 1*, $P < 0.01$).

Table 3.4 Bonferroni confidence limits to compare habitat use between male and female pine marten at two scales of selection: i. selection of the home range is given by the proportion of hectares of habitat used within home ranges, and ii. selection within the home range is given by the proportion of active locations used within each habitat type. Bonferroni confidence limits were calculated with k = 7, α = 0.05. An indication of the comparative use of each habitat type between males and females is given.

Habitat	Home Ranges			Locations		
	Female CI	Male CI		Female CI	Male CI	
CLOSED	9.5 - 17.7	23.8 - 30.1	M > F	4.3 - 17.2	5.4 - 28.7	M = F
DECIDUOUS	2.9 - 8.5	0.8 - 2.7	F > M	3.5 - 15.9	0* - 6.9	M = F
HEATH	0.4 - 3.9	9 - 13.5	M > F	0 - 2	4.5 - 27.3	M > F
MATURE	39.1 – 51.0	20.5 - 26.6	F > M	33 - 53.7	17.3 - 46.3	M = F
PASTURE	1.3 - 5.7	6.6 - 10.5	M > F	0 - 2	0* - 14.7	M = F
ROUGH	13.3 - 22.5	11.7 - 16.6	M = F	13.8 - 31.1	0.8 - 19.6	M = F
SCRUB	8.0 - 15.8	11.3 - 16.3	M = F	5.8 - 19.7	4.5 - 27.3	M = F

* Indicates where negative lower confidence limit replaced by a value of 0.0

3.4.3 Habitat selection

The selection of foraging habitats by female marten was significantly non-random at both scales of selection: at the home range level ($\Lambda = 0.0197$, df = 6, $P < 0.001$) and within home ranges ($\Lambda = 0.1436$, df = 6, $P < 0.05$). The selection ranks of habitat types varied between scales, yet at both scales of selection mature forest and rough grassland were the most preferred habitat types relative to others (Tables 3.5 and 3.6). The ranking matrix for selection of habitats at the home range level can be summarised as follows: mature coniferous forest > rough grassland > scrub > deciduous woodland > mid-successional coniferous forest > heath moorland > agricultural land. Mature forest, rough grassland and scrub were all significantly preferred relative to agricultural land and heath moorland, indeed agricultural land was significantly avoided relative to all other habitats except heath moorland. The combined coverages of mature forest and rough grassland accounted for over 60 % of the area used by female marten within the study area, despite them forming less than 30 % of habitats available. Conversely, whilst mid-successional forests cover nearly a third of the study area, they make up less than 15 % of female home ranges. Deciduous woodland was the least available habitats with the study area (forming 4 % of the study area), yet marten appear to include this habitat within their home ranges more than would be expected from their availability.

Table 3.5: Log-ratio differences (mean ± SE) derived from compositional analysis on habitat use at the home range (MCP) level for seven female marten.

Habitat category	**Habitat category (denominator)**							
Habitat	Mature forest	Rough grass	Scrub	Deciduous forest	Closed forest	Heath	Agricultural	Rank
Mature forest	n/a	0.103 ± 0.380 +	0.945 ± 0.818 +	1.915 ± 1.525 +	3.041 ± 1.551 +	4.750 ± 1.601 +++	7.950 ± 1.744 +++	6
Rough grass		n/a	0.843 ± 0.737 +	1.813 ± 1.257 +	2.938 ± 1.317 +	4.647 ± 1.490 +++	7.848 ± 1.757 +++	5
Scrub			n/a	0.97 ± 1.386 +	2.096 ± 1.593 +	3.805 ± 1.204 +++	7.005 ± 1.653 +++	4
Deciduous forest				n/a	1.126 ± 0.556 +	2.835 ± 1.702 +	6.035 ± 1.770 +++	3
Closed forest					n/a	1.709 ± 1.985 +	4.909 ± 1.95 +++	2
Heath						n/a	3.200 ± 2.543 +	1
Agricultural							n/a	0

Positive values indicate that the numerator habitat type is preferred to the corresponding denominator habitat type, (*) denotes a non-significant trend, (***) denotes significance at P < 0.05. Negative values indicate avoidance (-) denotes a non-significant trend, (---) denotes significance at P < 0.05. Habitat types are ranked in order of preference (rank 0, least preferred relative to other habitat categories, rank 6, most preferred).

Table 3.6: Log-ratio differences (mean ± SE) derived from compositional analysis on habitat use at the location (within home range) level for seven female marten.

Habitat	**Habitat (denominator)**							
Habitat	Mature forest	Rough grass	Scrub	Deciduous forest	Closed forest	Heath	Agricultural	Rank
Mature forest	n/a	0.074 ± 0.237 +	1.234 ± 1.127 +	1.537 ± 1.211 +	1.577 ± 1.233 +	1.918 ± 1.424 +	4.184 ± 1.410 +++	6
Rough grass		n/a	1.161 ± 1.126 +	1.464 ± 1.226 +	1.504 ± 1.348 +	1.845 ± 1.287 +	4.110 ± 1.393 +++	5
Scrub			n/a	0.303 ± 1.216 +	0.343 ± 2.012 +	0.684 ± 1.258 +	2.950 ± 2.275 +	4
Deciduous forest				n/a	0.040 ± 2.062 +	0.381 ± 1.773 +	2.647 ± 1.792 +	3
Closed forest					n/a	0.341 ± 2.136 +	2.607 ± 1.542 +	2
Heath						n/a	2.266 ± 1.983 +	1
Agricultural							n/a	0

Positive values indicate that the numerator habitat type is preferred to the corresponding denominator habitat type, (*) denotes a non-significant trend, (***) denotes significance at P < 0.05. Habitat types are ranked in order of preference (rank 0, least preferred relative to other habitat categories, rank 6, most preferred).

The ranking matrix for selection of habitats within home ranges (i.e. use at the location level) can be summarised as follows: rough grassland > mature coniferous forest > mid-successional coniferous forest > deciduous woodland > agricultural land > scrub > heath moorland. Heath moorland is still avoided relative to all other habitats, but only significantly so by mature coniferous forest and rough grassland. Rough grassland is the most selected-for habitat relative to others at this scale, and both mature coniferous forest and deciduous woodland are used more than would be expected from their availability. Despite being the third most used habitat at the home range level, scrub habitat is ranked as the second most avoided at the location level suggesting that this habitat serves a function at the home range level, but is not utilised at active locations. When represented graphically (Fig. 3.3) selection by females shows significant avoidance of heath moorland and agricultural fields relative to their availability within home ranges. Conversely, female use of deciduous woodland at the location level shows a distinct preference for this habitat where it was available.

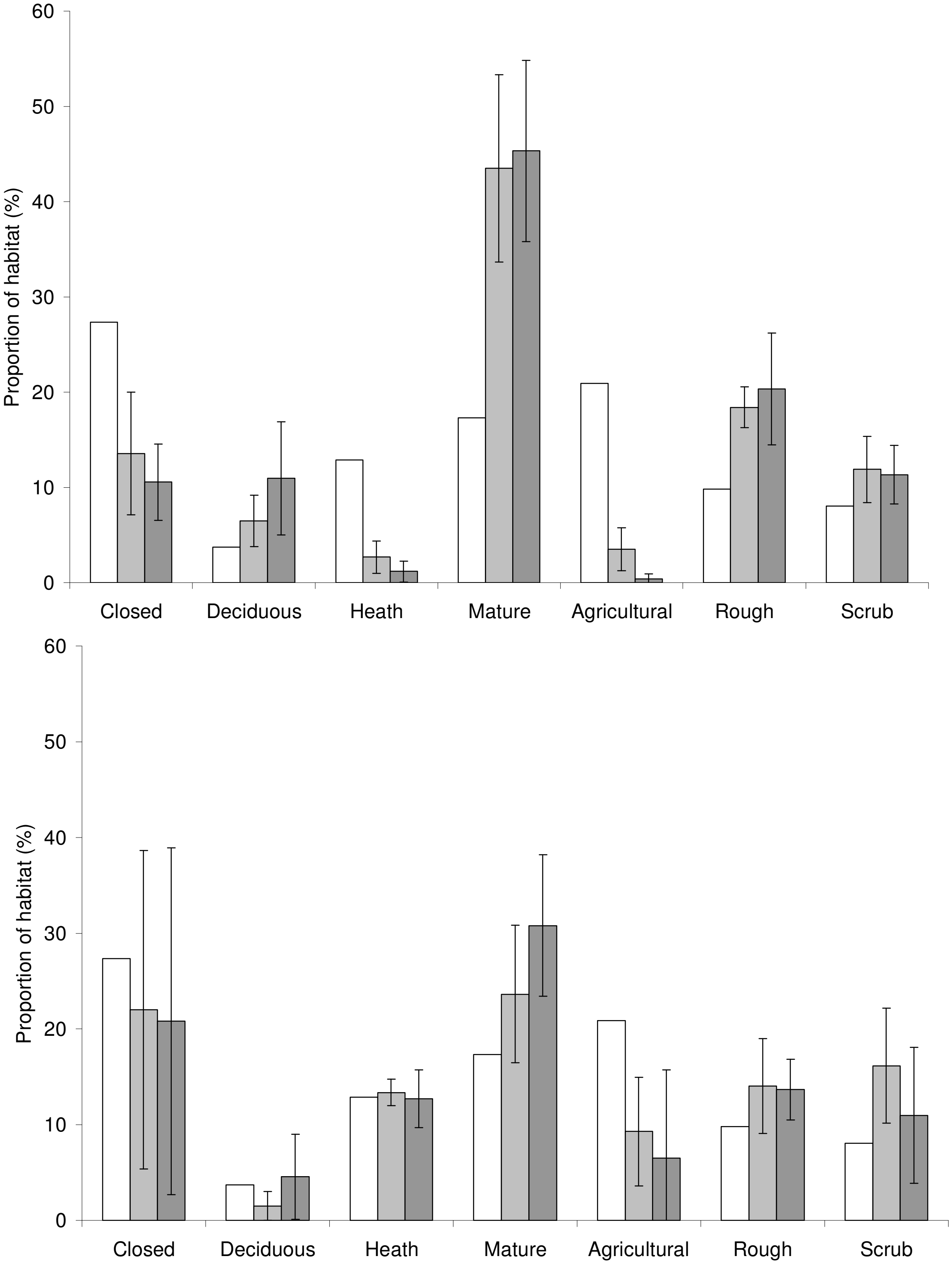


Figure 3.3 The proportional use of habitats by a. female (n = 7) and b. male (n = 4) marten showing availability of habitats within the study area (open bars), and average use (± SE) at the home range (light grey) and at location (dark grey) levels.

The sample size of male martens (n = 4) precluded analysis of their habitat selection through compositional analysis; however examination of the Bonferroni confidence limits of habitat use and availability at both levels of selection do allow some general trends and patterns to be highlighted (Table 3.7). At the home range level male marten appear to have selected to establish home ranges in areas of mature forest, rough grassland and scrub habitat, avoiding areas of open pasture and deciduous woodland. Both closed canopy coniferous forest and heath moorland appear to have been used in proportion with their availability. At the location level however, male marten showed no preference for any one habitat over any other based on confidence intervals. When represeneted graphically however (Fig 3.3b), the large error bars associated with most habitat types suggests that there was considerable variability in the preferences of males to each habitat at both levels of selection.

Table 3.7 The availability and Bonferroni confidence limits of observed use of habitats habitats by male marten (n = 4) at two levels of selection: i. selection of the home range is given by the proportion of hectares of habitat used within home ranges compared to the proportion of hectares of habitat available within the study area; ii. selection within the home range is given by the proportion of active locations used within each habitat type compared with the proportion available hectares of habitat available within home ranges. Equal sampling of locations from each male marten (n = 22) was used to ensure unbiased weighting of results. Bonferroni confidence limits were calculated with k = 7, α = 0.05. An indication of the selective preference for habitat is given where relevant; otherwise habitats are used in proportion with their availability.

Habitat	Home ranges			Locations		
	Available	Used CI		Available	Used CI	
CLOSED	27.3	23.8 - 30.1	-	26.9	5.4 - 28.7	-
DECIDUOUS	3.7	0.8 - 2.7	Avoided	1.8	0* - 6.9	-
HEATH	12.9	9 - 13.5	-	11.3	4.5 - 27.3	-
MATURE	17.3	20.5 - 26.6	Preferred	23.6	17.3 - 46.3	-
PASTURE	20.9	6.6 - 10.5	Avoided	8.6	0* - 14.7	-
ROUGH	9.8	11.7 - 16.6	Preferred	14.1	0.8 - 19.6	-
SCRUB	8.1	11.3 - 16.3	Preferred	13.8	4.5 - 27.3	-

* Indicates where negative lower confidence limit replaced by a value of 0.0

3.5 Discussion

At the home range level of selection, the results of this study are consistent with the hypothesis that marten select forested areas, whilst avoiding open habitats (Brainerd 1990, Pulliainen 1981b, Storch *et al.* 1990, Balharry 1993a., Buskirk & Powell 1994, Halliwell 1997). However, the pattern does not apply to habitat use within home ranges, and even at the home range level, not all types of forest were selected for, and not all open habitats were avoided. For example, closed-canopy forest was generally used less than it was available at the home range level whereas grassland and scrub were used more; however heath moorland and pasture appeared to be avoided in relation to all other habitats, particularly by female marten. The lack of any consistent patterns of habitat selection by male marten is likely due to the very small sample size that was analysed. It remains unclear whether male marten would have shown similar habitat preferences to females had the sample size been large enough; though this result is also likely in part to the male marten different life requirements to females. Male martens do not require dens secure enough for rearing young and males seem to show less aversion to open habitats, suggesting that they may not face the same threats as females, or that in their efforts to maintain a defended territory they are more willing to cross less hospitable habitats. Martens display considerable size dimporphism between sexes and the larger body size of males may offer them more protection from predators. Size dimorphism is often believed to be related to resource partitioning to reduce intra-specific completiton (McDonald 2002); however contrary to expectation, despite their larger size male marten do not consistently take larger prey than sympatric females (Zalewski 2006). It is possible that the female's smaller, and thus more energetically efficient, size allows her to co-exist with competitively dominant males. Behavioural niche separations such as displaying different habitat preferences and foraging strategies may provide females with sufficiently advantageous access to certain resources to reduce food competition with males, whereas by occupying larger home ranges male marten increase their probability of obtaining patchily distributed trophic resources as well as access to one of more mates (Zalewski 2006).

3.5.1 Marten Use of Open Habitats

The avoidance of heath by marten has been previously documented in Scotland (Balharry 1993a., Halliwell 1997, Bright & Smithson 1997). Heath supports a low biomass of small mammal prey, and lacks physical structures near the ground that offer protection cover from predators such as golden eagles or fox (Balharry 1993a., Chapter 5). It is likely that grazed pastures are avoided by marten for similar reasons (Balharry 1993a.). In contrast, the increased importance of rough grass at finer levels of selection suggests that it is herbaceous vegetation occurring within and in close proximity to the forest that provides marten with foraging habitat; this idea is supported by the tendancy of marten to remain close to the forest edge when venturing in to open habitats, though males appear to be more willing to venture further. Marten selected habitats within home ranges in which their preferred prey, *Microtus* voles, occurred in the highest densities (Chapters 5 and 6). Studies have shown that *Microtus* voles are taken in excess of their availability in the UK (Lockie 1961, Balharry 1993, Chapter 5). A similar preference has been observed in North American (Martin 1994), where marten display a strong selection for patches of herbaceous or low shrub meadows in which local prey numbers are high, particularly in riparian forest stands (Buskirk & MacDonald 1984, Zielinski *et al.* 1983). American marten also display a preference for forest-meadow edges and the interfaces between forest and regenerating clear fells (Hawley 1955 cited in Buskirk & Powell 1994, Simon 1980, Spencer *et al.* 1983), where small mammal densities are high (e.g. Hargis *et al.* 1999). Overall predation success of marten increases if rich habitat patches such as riparian meadows can be quickly identified and located (Buskirk & MacDonald 1984, Martin 1994). The distribution of herbaceous foraging habitats within mature stands is therefore critical to the suitability of forests as marten habitat.

Marten have been documented to make use of dense shrub habitat and scrub (Martin 1987, Magoun & Vernam 1986, Paragi *et al.* 1996, Slauson *et al.* 2007), particularly if over-story cover is not available (i.e. Clevenger 1994). In this study, regenerating clear-fells, wind-thrown trees, dense shrubs, and scattered trees were grouped together as scrub habitat. A greater selection for scrub habitat at the home range rather than at the stand level suggests that this habitat fulfils important life requirements that are not necessarily associated with marten foraging. The inclusion of scrub habitat in marten home ranges is likely to be related to its role in the connectivity of forest habitats, as well as the provision of resting sites. Marten appeared to make heavy use of scrub cover as conduits for travel between forest patches; one male was observed resting over 700m from the forest edge in dense gorse shrubs that were surrounded by fields of permanent pasture. Once active again, tracking revealed that rather than directly crossing the open fields, he made use of hedgerows and shrub patches as corridors, which eventually reconnected with the forest. A similar use of scrubby connective habitat such as hedgerows has been recently observed in a highly fragmented landscape in France (Pereboom et al. 2008). The heavy use of dense shrubs by marten in California has been linked to the apparent avoidance of this habitat type by the larger bodied predators, fisher (*Martes pennanti*) and grey fox (*Urocyon cinereoargenteus*: Klug 1996, Weir & Harestad 2003, Slauson & Zielinski 2004, Slauson *et al.* 2007). Use of shrubby ground cover for resting sites has been observed in a young deciduous forest in British Columbia, Canada (Porter *et al.* 2005). Many shrub species, particularly willow (*Salix* sp.) and alder (*Alnus* sp.), grow along the edges of clearings or riparian habitats (Johnson *et al.* 1995), where they provide resting sites and cover close to prey-rich edge habitats (Menzel *et al.* 1999). In the absence of suitable arboreal cavities for denning in managed forests (Birks *et al.* 2003, Birks *et al.* 2005), the highly complex ground structures formed by scrub habitat appears to provide suitable protective resting sites for marten that are secure enough from red fox to be used as natal dens (*personal observation*): seven of the eleven radiotracked marten were observed to rest within patches of gorse, rhododendron, and willow, or under the brash debris remaining from wind-throw or clear felling. The importance of scrub and shrub habitats, particularly those forming a transitional boundary between open and forested areas should not be overlooked in forest management for pine marten.

3.5.2 Marten Use of Forest Habitats

Marten establish their home ranges in areas dominated by mature forest rather than younger forest stands. Vertical and horizontal structure of the forest rather than its age that is more important to marten, though these features are often correlated with forest age (Katnik 1992, Brainerd *et al.* 1994, Buskirk & Powell 1994, Buskirk & Ruggiero 1994, Chapin *et al.* 1997). Repeated thinning of mature stands creates a patchy distribution of low canopy cover that increases the small-scale horizontal and vertical heterogeneity of sub-canopy vegetation layers. In contrast, unthinned, early-to-mid successional stands have a high degree of canopy closure, and therefore lack complexity and diversity within ground, field and shrub layers. Under low canopy cover, increased light transmission to the ground allows the development of a dense field layer of vegetation, predominantly blaeberry and heather which provide marten with important structural and trophic resources. Where light transmission is higher still, such as under canopy gaps or at forest edges, patches of herbaceous vegetation form, providing suitable habitat for *Microtus* voles (Hansson 1978). *Microtus* spp. occur in forest openings but are most abundant in meadows associated with riparian systems within a forest landscape (Chapter 5). Naturally occurring canopy gaps are more common in damp and riparian areas, where saturated soils mean that conifers cannot be planted and soil nutrient content is higher as a result of flushing, thus providing suitable conditions for the establishment of graminoid communities such as those preferred by *Microtus* voles.

Several studies have reported high densities of marten in low altitude deciduous woodland (Marchesi 1989, Zalewski *et al.* 1995, O'Sulivan cited in Birks 2002). Both

Balharry (1993a) and Halliwell (1997) found that deciduous woodland was used in greater proportion than its availability, accrediting this to a well developed field layer providing cover for both marten (Koehler & Hornoker 1977) and small mammals (Mallorie & Flowerdew 1996). Deciduous areas are also frequently associated with riparian habitats in the form of alder-carr woodland, which would provide marten with both structural and trophic resources. However it was the dominance of fruit bearing trees, particularly cherry and rowan in non-coniferous areas, which provided seasonally important components of the diet that was the likely cause of the high selection of this habitat where it was available; the use of local high-density patches of vegetative foods such as berries may provide lower energetic cost/benefit ratios than would hunting mammalian prey (Martin 1994).

3.5.3 Conclusions

It is clear that martens showed selection for habitats at both the home range level and the forest stand level. At each of these scales, mature forest was being used more than would be expected by its availability, even though it was one of the most abundant habitats in the greater landscape. Though the small sample size of male martens reduced the conclusiveness of their results, it is clear that within home ranges female martens selected to use the habitat typical of their preferred prey, *Microtus* voles: rough, ungrazed graminoid vegetation. The use of this habitat will be investigated further in Chapter 4. The marten's avoidance of heath, also one of the most abundant habitats within the landscape, was in accordance with the findings of other studies (Balharry 1993a, Halliwell 1997), and could have severe implications for marten conservation. The marten's unwillingness to cross this habitat type may restrict the species' ability to disperse and colonise new forested areas, as large areas of the Scottish landscape are formed by heath moors and open hillside. The connectivity of forest patches will therefore affect the marten's ability to extend its distribution naturally; but the issues surrounding forest fragmentation and management at large scales will be discussed in detail in Chapter 7.

Chapter 4

Pine marten microhabitat selection

4.1 Introduction

In most species, habitat preference patterns during foraging are influenced by the animal's need to obtain food whilst avoiding predation (Lima & Dill 1990). Habitat-use by foraging marten has been linked to the availability of prey (Spencer *et al.* 1983, Buskirk & MacDonald 1984), and the need for complex physical structure near the ground which provides cover from predators (Buskirk & Powell 1994, Buskirk & Ruggiero 1994). The association between foraging marten and mature coniferous forest stands in parts of their range is linked to the habitat preferences of forest dwelling rodents such as *Clethrionomys* voles, which are widely recognised as a major component of the marten's diet (Sherburne & Bissonette 1994, Martin 1994, Thompson & Curran 1995, Zalewski 2004). However, several studies have shown that *Microtus* voles can also be an important component of the diet (Weckwerth & Hawley 1962, Francis & Stephenson 1972, Douglas *et al.* 1983, Buskirk & MacDonald 1984, Martin 1987). A dietary preference for *Microtus* voles is particularly apparent in the UK (Velander 1983, Gurnell *et al.* 1994, Halliwell 1997, Putman 2000, Coope 2007), even in areas where *Clethrionomys* predominate numerically (Lockie 1961, Balharry 1993a., Chapter 5). *Microtus* are habitat specialists of graminoid vegetation (Hansson 1978, Chapter 5), and are therefore generally absent from forest interiors except where suitable environmental conditions allow patches of herbaceous vegetation to occur (Hansson 1978, Charles 1981, Petty 1992).

Scottish marten appear to avoid open habitats (Balharry 1993a., Halliwell 1997), so it is unclear how they access suitable habitat for hunting *Microtus*.

The coarse scale at which previous habitat studies in Scotland were conducted affected their ability to detect use of small-scale microhabitats used for hunting by marten, although it has been suggested that marten make use of areas of low canopy cover within seemingly homogenous forest stands (Balharry 1993a., Bright & Smithson 1997). Different aspects of an animal's life history motivate habitat selection at different scales, therefore the scale used in habitat-selection studies must match the aims of the investigation (Bissonette *et al.* 1997). However, studies of habitat selection by marten typically relate patterns of use to forest over-story characteristics such as stand age and relative species composition (Bissonette *et al.* 1997, Payer & Harrison 2004). Even within the relatively small geographic extent of Scotland, habitat selection analyses based on such characteristics have produced incongruent results (Balharry 1993a., Bright & Smithson 1997, Halliwell 1997, Chapter 3). For example, at the home range scale Scottish marten were found to select for open-canopy coniferous forest (Balharry 1993a., Chapter 3), old growth forest (i.e. 85+ years old: Halliwell 1997) and closed-canopy coniferous forest (Bright & Smithson 1997). It is increasingly suggested that fine-scale vertical and horizontal structure within forest stands is a more important influence on marten habitat use than age or species composition of the forest over-story (Buskirk & Powell 1994, Buskirk &

Ruggiero 1994, Bisonette *et al.* 1997, Chapin *et al.* 1997, Payer & Harrison 2004). A variety of habitats not typically associated with marten use (e.g. young coniferous forest: Brainerd *et al.* 1994, young deciduous forest: Porter *et al.* 2005, open scrub-land: Clevenger 1994*b*) may therefore be suitable for marten so long as they provide the structural elements needed to fulfil their life requirements (Brainerd *et al.* 1994). Quantification of the structural components related to habitat-use by marten is therefore necessary in order to develop silvicultural guidelines for managing plantation forests.

In order to identify the microhabitat elements associated with foraging activity by marten in Scottish plantation forestry, analysis of habitat-selection by active marten must be made at a fine-scale. Fine-scale habitat selection is often explored using a site-attribute study design; multiple habitat-related variables are measured at specific sites, then multivariate statistics are used to identify the variables that characterise sites that are used versus those that are not used (Garshelis 2000). Logistic regression is a commonly used means of modelling the complex ecological data in site-attribute studies (Garshelis 2000). This technique has been applied to investigations of the microhabitat-associations of American marten (Sherburne & Bissonette 1994, Fecske *et al.* 2002, Payer & Harrison 2004, Porter *et al.* 2005, Mowat 2006, Baldwin 2008), and stone marten (Virgos & Casanovas 1998, Virgos & Garcia 2002) but has rarely been applied to Eurasian pine marten. Classification and regression trees (CART: Breiman *et al.*

1984, Clark & Pregibon 1992, Ripley 1996), are an alternative statistical technique for exploring and modelling complex data, that has only recently been applied in ecology (De'ath & Fabricus 2000, Palomino & Carrascal 2007, Bearer *et al.* 2008, Murray *et al.* 2008). Both techniques allow one to predict a discrete outcome such as group membership (i.e. used or unused sites) from a set of explanatory variables that may be continuous, discrete, dichotomous, or a mix, and both identify the best predictor variables of group membership (De'ath & Fabricus 2000, Tebachnik & Fidell 2007). However, the results of logistic regression models are often difficult to interpret in a way that is accessible to wildlife managers as they are enumerated by abstract coefficient values which are difficult to translate into a meaningful management recommendations. CART offers a greater ease of interpretation as they graphically represent the best predictor variables and provide more specific information on variable thresholds and their relationship to use (De'ath & Fabricus 2000).

The objectives of this chapter were to examine and quantify fine scale patterns in the structural elements of microhabitats associated with intensive use by foraging marten in order to answer the following questions: Is it possible to model the microhabitats used by foraging marten based on fine-scale habitat characteristics with no consideration of stand characteristics such as tree species or age? If so, is it possible to re-create the first model using only data derived from GIS databases, but again with no consideration of stand-level characteristics? The first question will be answered using logistic regression to model fine-scale site-attributes measured in the field. The second question will be answered using classification tree analysis to model fine-scale site-attributes derived using spatial databases that are available to forest managers. The purpose of developing the GIS-based classification model is to determine whether the marten′ core foraging habitat can be predicted at a fine scale without necessitating measurement of variables in the field, whilst providing a series of management decision steps that will be easily interpreted by wildlife managers. The results of both models were then used to relate marten foraging behaviour with the habitat associations of small mammal prey species. Only data from the seven female marten tracked in Chapter 3 were used because habitat utilisation may serve different functions between the sexes; as solitary carnivores, female marten distribute themselves around the resources that are essential for the rearing of young, whilst males distribute themselves around females (Powell 1979, Sandell 1989). A small sample size of males ($n = 4$) precluded a similar separate analysis of male marten data. Only active locations of females were used under the assumption that foraging would be the main activity of female marten when not at a resting site.

4.2 Methods

To achieve the aims of this chapter, a comparison was made between the patterns of habitat characteristics in areas associated with intensive use by active marten, with those areas that were used less frequently within the home range. Identification of a non-random pattern in habitat characteristics associated with use requires a comparison of the site-attributes of a "*used*" test group with the site-attributes of an "*unused*" control group (Garshelis, 2000). For the purpose of this chapter, data taken from core habitat areas were considered as the test group and those from non-core habitat were considered as the control group. However, it is worth noting that both core and non-core habitats were still *used* by marten, as both were drawn from within the marten's home range. Animal locations estimated from radiotracking had an average linear error of 55m (Chapter 3), therefore it was inappropriate to use them as the sites at which to measure microhabitats at a scale of < 1ha. Instead, core and non-core habitats were characterised from the fine-scale measurements taken at numerous random locations within each area, thus providing more generalised information about the patterns of microhabitats occurring in areas of intensive use.

4.2.1 Home Range Estimation

The estimated radio locations of seven female marten for whom a sufficient number of locations had been obtained to suggest home-range size stability (Chapter 3), were entered into ArcView®GIS (Environmental Systems Research Institute, Inc., 1999). A fixed-kernel technique was used to estimate the size and utilisation distribution of each individual's home range (Worton 1989) using the Animal Movement Extension to ArcView® (Hooge & Eichenlaub 1997). The utilisation distribution is a probalistic model that describes the relative amount of time that an animal spends in any place within their home range (Seaman & Powell 1996). Whilst this method tends to over-estimate the over-all size of home ranges, it provides information about the intensity of use of habitats contained within that is not available from minimum convex polygons (Powell 2000). Isopleths can be defined around the smallest region that contains a specified proportion of the total utilisation, thus enabling the distinction of core areas within the home range (Powell 2000). In this study, the home range was defined for each female as the smallest area containing 95% of active radio locations. Core habitats were defined as those containing 25% of active radio locations, thus non-core habitat comprised the area within the total home range which lay outside the core area containing the remaining 75% of active locations. Using 25% of locations for delimiting core areas is an arbitrary, yet commonly used, definition (Powell 2000). It was assumed that defining core habitat in this way would retain sufficient locations to optimise the accuracy of with which core habitats were identified, without losing the precision and spatial cohesion of those areas. A smoothing factor, *H*, was estimated from the data and optimised by least square cross validation (LSCV). This method is better at identifying tightly clumped areas of peak use, such as core areas, than other smoothing parameters (Seaman & Powell 1996, Gitzen *et al.* 2006).

Random plot points were generated within the core and non-core areas of each home range. The number of core plots was roughly relative to the size of that individual's core area, and an overall ratio of two non-core plots to every one core plot was generated to allow for the greater variance in the physical characteristics of non-core areas (Pereira & Itami 1991).

4.2.2 Site Attributes

Site-attribute data were collected in two ways for entry into two methods of modelling analyses. Field-based patch-level habitat variables were collected for entry into a logistic regression model by visiting each plot site in the field and measuring various physical habitat properties (from now on referred to as the *field model*). GIS-based patch-level habitat elements were derived from spatial databases within a GIS for entry into a classification tree model (from now on referred to as the *GIS model*).

4.2.2.1 Field Model Variables

Field-based variables (Table 4.1) were sampled within plots of radius 5.64m (giving each plot a circular area of 0.1ha) in both core and non-core areas of female home-ranges during June 2006. The first four variables concerned the nature of ground cover form and structural complexity. The dominant ground cover type within each 0.1ha plot was visually determined and defined into one of nine types. Vegetation height was taken from the mean average height of ten measurements taken at 1m intervals across the diameter of each plot using a sward stick. The presence or absence of coarse woody debris (CWD) was recorded on an ordinal scale to represent an increasing level of complexity, where 0 = no debris was present, 1 = fine debris such as twigs and small branches were present, 2 = coarse woody debris (i.e. logs greater than 7cm in diameter) was present, 3 = both fine and coarse woody debris were present. The number of fallen tree stems (or root plates from fallen trees) was counted within each plot. The remaining four variables concerned the physical structure of forested environments, and therefore could only be taken if the plot site fell within a forested area. The number of trees with a diameter at breast height (DBH) of over 7cm was counted within each plot. Any trees that were considered to be borderline, because they only partially fell within the 5.64m radius, were included within the count. Basal area was estimated using a relascope (a glass wedge prism lens) from the centre of each plot. Using the

Table 4.1 Habitat variables used in the *Field Model*. Variables were sampled within 5.64 m radius plots (area = 0.1 ha) within core-use and control areas of seven female home-ranges.

Variable		Measure	Description
COVER†	GRASS	Nominal	Presence / absence of graminoid species with a mean sward height of < 40 cm as the dominant ground cover.
	TUSSOCK	Nominal	Presence / absence of graminoid species with a mean sward height of ≥ 40 cm as the dominant ground cover.
	BLAEBERRY	Nominal	Presence / absence of *Vaccinium myrtillus* as the dominant ground cover.
	BRACKEN	Nominal	Presence / absence of *Pteridium* sp. as the dominant ground cover.
	CLEARFELL	Nominal	Presence / absence of clear fell debris as the dominant ground cover.
	SHRUBS	Nominal	Presence / absence of dense shrubs (e.g. gorse, rhododendron, *Salix* sp.) as the dominant ground cover.
	HEATHER	Nominal	Presence / absence of *Erica* sp., *Calluna* sp. as the dominant ground cover.
	MOSS	Nominal	Presence / absence of *Bryophyta* as the dominant ground cover.
	LITTER	Nominal	Presence / absence of needle or leaf litter as the dominant ground cover.
VEGHEIGHT		Continuous	Mean height (cm) of ground cover based on ten height measurements taken 1m apart across plot diameter.
CWD		Ordinal	Index representing the increasing complexity of woody debris on the ground from 0 = none to 3 = abundant coarse
NUM_FALLEN		Continuous	The number of fallen trees or root plates within the plot site.
NUM_TREE		Continuous	A count of all trees of > 7cm DBH at 1.3 m within the plot site.
BASAL		Continuous	Basal area (m^2 ha^{-1}) of trees surrounding plots measured using a relascope prism lens.
TREESIZE		Continuous	An index of tree size and spacing produce by the ratio of the BASAL over NUM_TREE variables.
CANOPY		Continuous	Percentage cover based on 10 measurements across the diameter of the plot of presence or absence of canopy obtained using a sighting tube with an internal crosshair taken 1 m apart

† Dominant ground cover (judged visually over the whole 0.1 ha plot) was dummy coded so that only one ground cover was recorded for each plot site.

relascope, all trees 360° sweep are viewed and counted, or not, dependent on the degree of lateral displacement (Fig 4.1). Any trees that were considered borderline were included in the count. Trees that were outside the 0.1ha plot but within still adhered to the count-criteria were included in the count. The counted number of trees was then multiplied by the Basal Area Factor (2) to convert to square-metres per hectare. An index of tree size and spacing was calculated by from the basal area (BASAL) divided by the number of trees (NUMBTREE) variables. This is not the equivalent as calculating individual tree basal area as the BASAL measure also includes trees counted outside of the 0.1ha plot, as long as they are large enough not to display too much image displacement. Low values from this ratio suggest young, small trees that are densely packed together: i.e. if 20 stems were counted within a plot, but 18 trees were counted through the relascope giving a basal area reading (after conversion) of $36m^2/ha$, tree size = 36 / 20 = 1.8. Larger values suggest large, well-spaced trees: i.e. if only 3 stems were counted in a plot, but 16 trees were counted through the relascope giving a basal area of $32m^2/ha$, tree size = 32 / 3 = 10.7. The percentage canopy-cover was obtained using a sighting tube with an internal crosshair. The presence or absence of tree canopy was determined by viewing the canopy through the sighting tube, and if the crosshair touched canopy, canopy was recorded as present ("hits"). This was repeated at 10 points across the diameter of each plot at 1m intervals, and the number of "hits" was multiplied by ten to give percentage canopy cover.

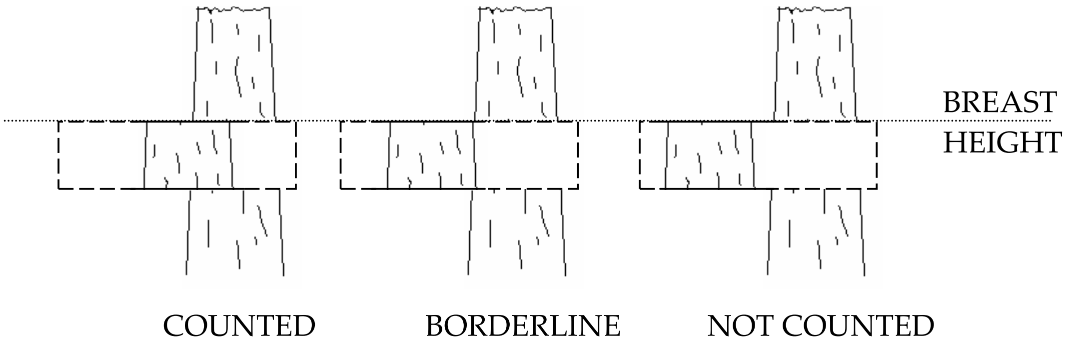


Figure 4.1 The image of trees when viewed through a relascope. The degree of lateral displacement of the tree determines whether or not a tree is included in the count.

4.2.2.2 GIS Model Variables

GIS-based variables (Table 4.2) were derived using ArcView®GIS (Environmental Systems Research Institute, Inc., 1999) from data within the Forest Enterprise subcompartment database (*SCDB: Forest Enterprise, Forestry Commission, UK*), a 10m resolution digital elevation model (DEM), OS MasterMap™ (*OSMM*: *Ordnance Survey®, Southampton, UK*), and the habitat blocks created for macrohabitat analysis in Chapter 3. The first three variables were all related to topographical elements of each site's location. Aspect was calculated from the DEM and recorded as a categorical variable into one of the eight cardinal and intercardinal directions. The Topographic Wetness Index (TWI) is commonly used to quantify topographic control on hydrological processes, and provides an index of spatial soil moisture patterns based upon

Table 4.2 GIS-based habitat variables for entry into the GIS Model. Variables were derived from data within the Forest Enterprise subcompartment database (SCDB: Forest Enterprise, Forestry Commission, UK), a 10m resolution digital elevation model (DEM), OS MasterMap™ (OSMM: Ordnance Survey®, Southampton, UK), and the habitat blocks created for analysis in Chapter 3.

Variable	Measure	Description
ASPECT	Nominal	8 cardinal / inter-cardinal directions: N, NE, E, SE, S, SW, W, NW.
TWI	Continuous	Topographic Wetness Index (TWI): a topographic index of spatial soil moisture patterns derived from DEM.
ELEVATION	Continuous	Elevation above sea level (m) derived from 10m DEM.
TOPHT	Continuous	If site is forested, the expected stand top-height (m) derived using ForestGALES (Gardiner *et al.* 2004) applied to tree planting and yield data taken from the SCDB.
STEMS	Continuous	If site is forested, the expected number of tree stems per hectare derived using ForestGALES (Gardiner *et al.* 2004) applied to tree planting and yield data taken from the SCDB.
BAREA	Continuous	If site is forested, the expected basal area (m^2 / ha) derived using ForestGALES (Gardiner *et al.* 2004) applied to tree planting and yield data taken from the SCDB.
DIST_HUMAN	Continuous	Distance to nearest building (m) derived from Ordnance Survey MasterMap™.
DIST_FOREST	Continuous	Distance to nearest forest edge (m) derived from SCDB.
DIST_LINEAR	Continuous	Distance to nearest road or rides (m) derived using the SCDB.
DIST_FLUSH	Continuous	Distance to nearest hydrological flush (m) where a flush is defined as TWI $\geq$14.
DIST_GRASS	Continuous	Distance to nearest patch of open grass habitat (m) derived using habitats classified in Chapter 3.

local topography (Moore 1994). The TWI was a calculated from the DEM using the algorithm:

$$ln (\alpha / tan \beta)$$

where α is the local upslope area draining through a certain point per unit contour length, and $tan \beta$ is the local slope (Beven & Kirkby 1979). Elevation above sea level was calculated from the DEM. Three variables relating to the structure of forested sites (stand top-height, number of trees per hectare and basal area per hectare), were only taken if the plot fell within a forested area. These variables were calculated using the ForestGALES programme (a programme for predicting stand wind damage: Gardiner *et al.* 2004) using stand planting data characteristics (tree species, age and yield class). Despite being generated using stand data, these variables were not considered to be stand-level because the values obtained for each of these variables could be generated by multiple combinations of planting data characteristics. For example, a given top height could be generated by a high yield class of younger age stand from a quick-growing species, or a much older but unproductive yield class of the same or a different slow growing species, and therefore were considered to reflect within-stand structural differences rather than being typically related to stand age and species. Five variables were related to the proximity of each plot to potentially ecologically meaningful features. The first, proximity to the nearest human use (i.e. building), was measured to account for the potential affect of human disturbance on marten choice of habitat, whilst the remaining four related to the proximity of habitat that may provide suitable *Microtus* habitat as evidenced from small mammal trapping (Chapter 6). Distance to linear features that created openings in the forest canopy (i.e. roads and rides) were measured. Hydrological flushes were defined as locations where TWI > 14, which is associated with damp communities of vascular plants, such as riparian habitats. Distance to the nearest open area of grassland was also measured, although no distinction was made between grassland type, such as heath-grasses (*Nardus–Carex* communities: Rodwell 1998) or tussock grasses (*Holcus – Deschampsia* communities: Rodwell 1998). Finally, distance to the nearest forest edge, defined as the interface between forested and non-forested habitat, was measured.

4.2.3 Statistical Analyses

Data from 428 plots (from 133 core sites and 295 non-core sites) were used in both the field model and GIS model analyses. Data for all females were pooled as the number of variables was too large relative to the number of cases (plot sites) to analyse each individual home range separately. A split-sample approach was used to assess the accuracy and predictive power of each model; the models were built using a training data set comprising just c. 40 % of core points and c. 40 % of non-core control points, they were then validated using a further c. 30 % of the data, and the resultant models were tested using the remaining c. 30 %. By testing each model using data that was completely independent from those used in training and validation, the robustness of each model could be verified. To overcome some of the biases that may result from pooling across females, the data used for each stage of model development were randomly partitioned and stratified to ensuring that each female's home range contributed an equal proportion of plot sites, however this did mean that females with larger home ranges would contribute a larger number of plots. This whole process was repeated 12 times for each modelling technique, each time randomly selecting different subsets of data with which to build, validate and test the model, until consistently significant predictors that distinguished between core and non-core areas were identified. The quality of the final model was assessed by the rate of successful classifications i.e. the percentage of plots correctly assigned. All statistical analyses were performed using SAS Enterprise Miner 4.3 (SAS Institute Inc., 2007).

4.2.3.1 Field Model

A logistic regression analysis was performed using the 16 field predictor variables (which included all nine dummy coded ground cover variables) to build a model that would predict the presence or absence of core habitat at plots sites. A forward stepwise procedure was used to optimise the model that used Akaike's Information Criterion (AIC) for inclusion and removal of predictor variables from the model. The AIC criterion penalizes for adding parameters to the model and is a standard criterion for assessing the fit of a number of candidate models. Predictors that lead to the model with the smallest AIC value are retained in the model.

4.2.3.2 GIS Model

A classification tree analysis was performed using the 11 GIS-based predictor variables to build a model that would predict the presence or absence of core habitat at plots sites. At each "branch" of the decision tree, all 11 predictor variables were assessed for their ability to maximize the homogeneity of the resulting branches if a single predictor variable is split at a single value using the Chi-square criterion with the default probability of $P = 0.2$. As a split-sample validation method was used, the 40% test data was used to "grow" the tree (i.e. splitting of the data into branches was continued until the Chi-square criterion didn't improve the classification at $P = 0.2$). Trees were then "pruned" using the validation data set (i.e. branches that relate only to the training dataset and not to the data as a whole are removed). As pruning takes place the percentage of misclassifications in the validation dataset will fall to a minimum before increasing again as one prunes important nodes that are important is separating the classes. Pruning therefore stops when the percentage of misclassifications of the validation dataset is at a minimum.

4.3 Results

4.3.1 Field Model

The final model retained three predictor variables that significantly contributed to the model equation: tussock forming grass cover, ground cover height, and tree size (Table 4.3). Classification success was reasonable; in total, 77 % of all plot sites were correctly classified, 91 % in non-core areas, and 63 % in non-core areas. Each of the predictors retained in the final model positively influenced the probability of a site being part of core marten habitat. Core plots had a greater cover by tussock forming grasses than non-core plots ($\chi^2 = 71.857$, *df 1*, $P < 0.001$). Ground cover height was greater in core plots than in non-core plots (Mann-Whitney $U = 10978.5$, $P < 0.001$, $r = 0.35$:). Core plots were associated with higher tree size indices than non-core plots (Mann-Whitney $U = 16465$, $P < 0.01$, $r = 0.13$), indicating an association with large, well spaced trees. In addition to the variables included in the final habitat model, only one other predictor variable found to differ between core and non-core areas: cover by needle litter. Needle litter appeared in significantly fewer core plots than non-core plots ($\chi^2 = 16.616$, *df 1*, $P < 0.001$).

Table 4.3 Results matrix of the logistic regression model showing variables that predict whether a plot site was likely to be from a core area or a non-core area. A test of the full model with all three predictors against a constant only model was statistically significant (χ^2 *= 48.813, df 3, P < 0.001*), indicating that predictors, as a set, reliably distinguish between core and non-core areas, and showing the model had a good fit to the data. According to Wald criterion, all three habitat variables reliably predict core and non-core areas.

Variable	DF	B	SE	Wald Chi^2	Odds Ratio	P
Tussock cover present	1	1.75	0.45	15.17	1.173	< 0.001
Tree size	1	0.19	0.06	10.52	1.204	< 0.001
Cover height	1	0.02	0.01	14.88	1.022	< 0.001
Constant	1	-0.88	0.49	3.22		

4.3.2 GIS Model

The final regression tree obtained from classification modelling included three variables as significant criteria for predicting whether a site was likely to be in a core or non-core area of the home range: Topographic Wetness Index (TWI), tree top height, and basal area (Fig 4.2). The presence of core marten foraging habitat was positively influenced by the site's topographic wetness index; plots with higher values of TWI were more likely to be in core habitat than those with lower values. The model indicated a threshold TWI value of 17.86 which successfully predicted group membership for 90 % of the validation dataset, and 78 % of the test dataset; thus if a site had a TWI value of greater than 17.86, there was over a c.75 % probability that that it would be in core marten foraging habitat. It was still possible for plot sites with lower values of TWI to be in core

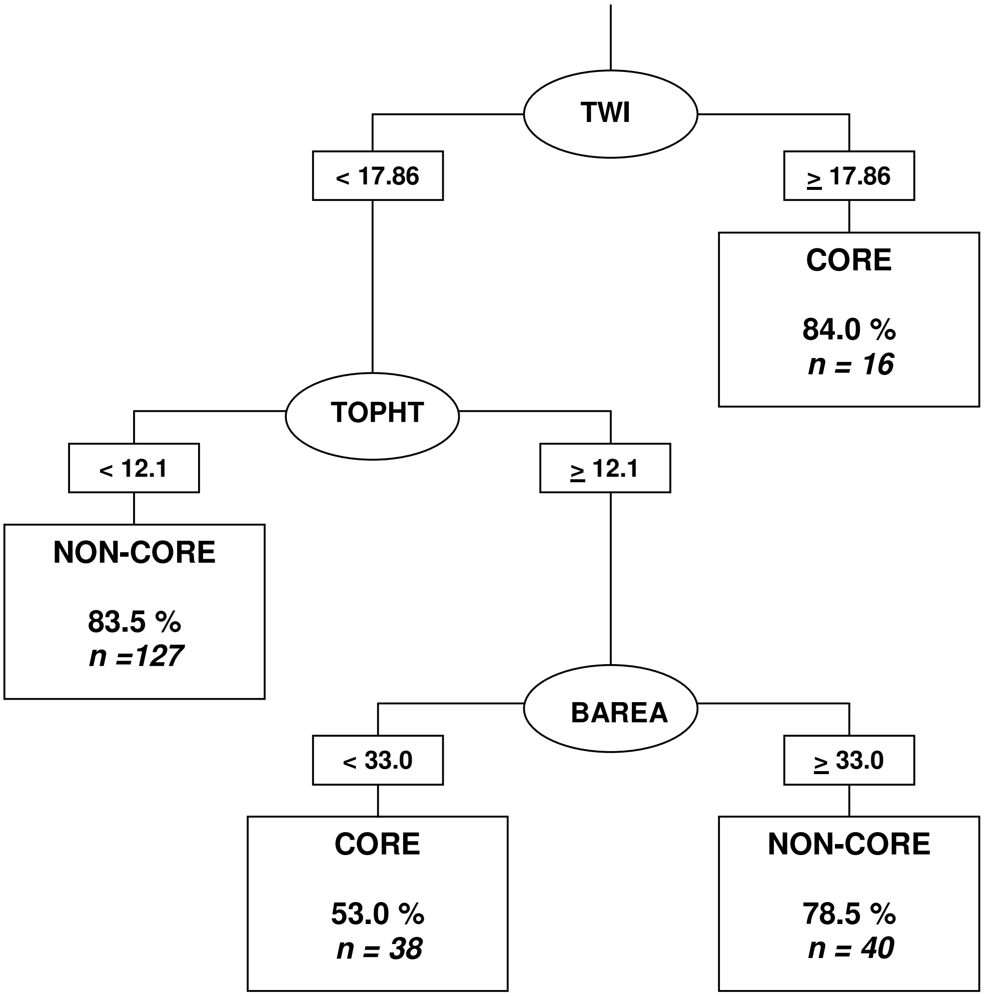


Figure 4.2 Schematic of the classification tree for the presence/absence of core activity habitat. Each leaf (box) is labelled (classified) according to whether core or non-core habitat is present. Each leaf shows the success rate of the model as the precentage of correct observations in that class. Success rates are given as the mean average of the success rate of the *validation* data set (30% of data) and the *test* data set (30% of data). The total number of sites (from the *validation* and *test* data) observed that correctly met the criteria for each class are given (italic).

habitat if they met the next two selection criteria. Tree top height was the next determinant of whether sites were in core or non-core habitat, as plots with lower tree heights were less likely to be core habitat. The model indicated a threshold height of 12.1 m, below which 84 % of the validation data were correctly identified as non-core habitat, and 83 % of the test data. Where plots had trees greater than 12.1 m in height, a final criterion determined whether they were likely to be in core habitat or not; below a threshold basal area value of 33 m^2 per hectare, plot sites were more likely to be core habitat. However, these final two criteria appeared to be more successful at predicting none-core habitat than core habitat; of the plots where basal area was greater than 33 m^2 per ha, almost 80 % were non-core habitat, compared with only just over 50 % of plots with less than the threshold basal area being correctly identified as core habitat.

To further understand the relationship between TWI and marten habitat-use, TWI was measured at sites where live trapping was conducted to determine the small mammal species composition in different forest habitats (see Chapter 5 for details on trapping methodology). TWI showed a strong positive association with the number of *Microtus* captures per 100 trap nights (*Spearman's rho* $= 0.73$, $P < 0.01$, $n = 21$: Fig 4.3).

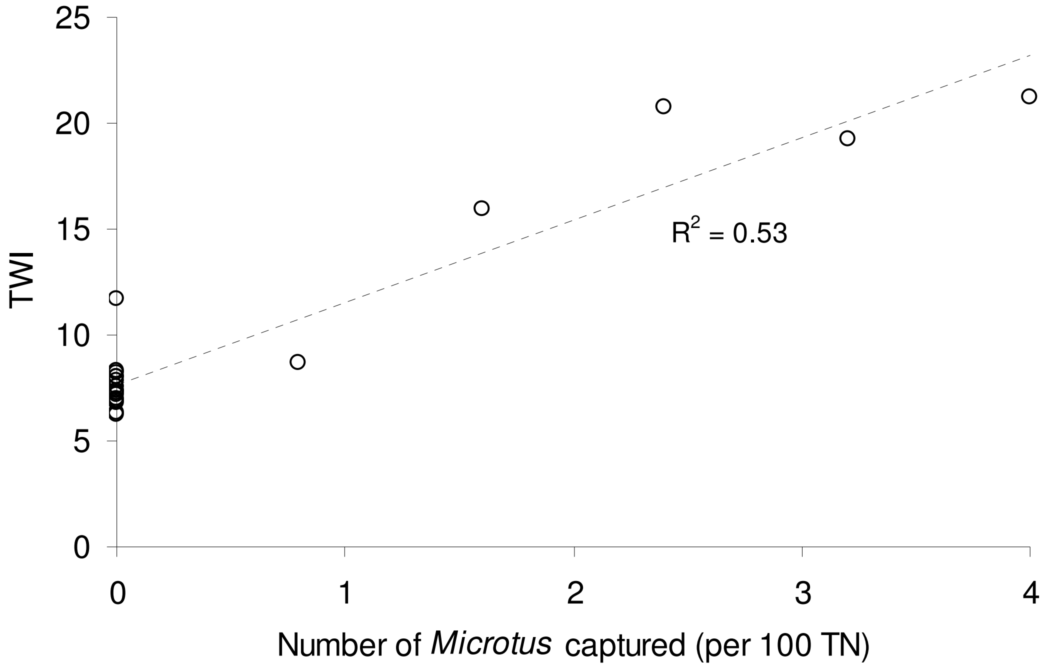


Figure 4.3 The relationship between topographic wetness index (TWI) and the number of Microtus captured per 100 trap nights (see Chapter 5 for details about small mammal trapping).

4.4 Discussion

4.4.1 Ground Vegetation

The results of both the field- and GIS-models indicate that ground vegetation and forest-stand structural characteristics are important determinants of core foraging habitat for Scottish marten. Ground vegetation showed the strongest predictive power in both models; marten clearly selected to forage in sites where tussock grass was present, and tussock grass was present in areas with higher values of TWI. The distribution and abundance of small mammal species are strongly linked to vascular plant species composition (Hansson 1978), the spatial organisation of which is determined by the non-random distribution of various factors i.e. soil moisture and nutrient gradients (Day & Monk 1974, Whittaker & Niering 1975, Host & Pregitzer 1992), and canopy-coverage (Uemura 1994, MacDonald & Fenniak 2007). Soil characteristics such as moisture, pH and groundwater level are determined by ground water flow, which is itself determined by local topography; therefore local topography has a direct affect on vascular plant species richness and community structure (Moore *et al.* 1994, Giesler *et al.* 1998, Zinko et al 2005). The link between topography and plant species richness means that the TWI has been found to be a useful tool for predicting the spatial distribution of vascular plant communities (Sorensen *et al.* 2005), and it is not surprising therefore that it is also a useful predictor of *Microtus* habitat. The association of high TWI values with core marten habitat and vole density clearly demonstrates that marten are selecting *Microtus*-rich microhabitats within the forest in which to forage.

4.4.2 Ground Structure

The positive associations between core areas and increasing ground cover height reinforce the importance of well-developed ground and field-layer vegetation (Chapter 3). The highest values of cover height (of 1m+) were associated with dense shrubby trees, gorse, rhododendron, and coarse woody debris from felling or windthrow, whilst intermediate heights (30cm+) were associated with dense layers of heather, blaeberry, and grasses and rushes. At the lowest end of the cover height scale was cover by needle litter and mosses, and explains why needle litter was found in significantly fewer core sites than non-core sites. This ground cover is associated with closed-canopy forest, which was shown to be used less than would be expected from its availability at coarser scales (Chapter 3), despite it ranking as the most productive habitat in terms of the abundance of woodland rodents (Chapter 5). A well developed field layer provides cover for both marten (Koehler & Hornoker, 1977) and small mammals (Mallorie & Flowerdew 1996), and complex structures near the ground have therefore often been found to be important features in habitat studies of American marten (Buskirk *et al.*, 1989; Hargis &

McCullough, 1984; Spencer & Zielinski, 19083). As well as providing trophic resources, coarse woody debris and small-scale horizontal heterogeneity within the field and shrub layers of vegetation provide structural features that are important to marten, such den sites, and overhead cover, thus allowing marten to fulfil their life requirements in small areas (Buskirk & Ruggiero 1994).

4.4.3 Forest Stand Structure

The prediction of the GIS model that core habitats were more likely to contain forested stands with lower basal area per hectare suggests that the light regime beneath the forest canopy is an important determinant of suitable marten habitat. There is a loose relationship between stand basal area and average light transmittance through the canopy, with transmitted light decreasing as basal area increases (Hale 2004, Hale *et al. in prep*). The understorey light environment is one of the primary factors influencing the growth of vegetation beneath a forest canopy (Lieffers *et al.*, 1999), and the development of a dense vegetative field and shrub layers becomes increasingly possible as sub-canopy light levels increase. Grasses (e.g. *Deschampsia flexuosa* and *Molinia caerulea*) and rushes (e.g. *Juncus spp.*) need the greatest amounts of light, and will out-compete heather and heaths (e.g. *Calluna vulgaris* and *Erica* sp.), which in turn need more light than blaeberry (*Vaccinium myrtillus*: Parlane *et al.*, 2006). However, light transmission to the ground is not a function of basal area alone; a high basal area stand with many small trees (e.g. unthinned 45-year-old Sitka spruce) will have a very dense canopy, and will transmit less light than a stand with the same basal area but fewer, larger trees (e.g. a stand that has been well thinned in the past: Hale 2004, Hale *et al. in prep*). The association between core habitats and field-measured factors relating to tree size and spacing suggested that core habitats were associated with large, well-spaced mature trees, which in Morangie were predominantly planted Scots pine. The tree crowns of Scots pine are smaller than those of species such as Sitka spruce, and therefore let a greater amount of light through for a given basal area (Hale *et al. in prep*). The importance of large, mature trees indicated by the field model is supported by the inclusion of tree height within the GIS model, as trees under 12m in height were generally less than 29 years old, or those with exceptionally low yield classes indicating low habitat productivity (Edwards & Christie 1981).

4.4.4 Core Marten Habitats

The implication of a link between open-structured, mature forest stands with their accompanying dense ground flora, and core marten habitats is that marten are using herbaceous vegetation occurring within canopy gaps, areas of low canopy within the forest, or at forest edges rather than the large tracts of open habitat. The association with TWI also implies the use of riparian habitats by marten, as the highest TWI values occur in areas where ground water accumulates such as in valley bottoms and along riparian strips. Damp soils are generally left unplanted within plantation forests, and the resulting canopy gaps allow graminoid ground vegetation to develop, providing suitable habitat for *Microtus* within the forested landscape. Such associations have been found previously in American marten, which display strong selection for patches of herbaceous or low shrub meadows in which local prey numbers are high (Buskirk & MacDonald 1984, Zielinski *et al.* 1983), or at forest-meadow edges (Simon 1980, Spencer *et al.* 1983). A preference for riparian habitats is common among Mustelids e.g. American marten (Zielinski *et al.* 1983, Hargis *et al.* 1999), polecat *Mustela putorius* (Rondinini *et al.* 2006) and stone marten (Virgos 2001, Rondinini & Boitani 2002), and become particularly important in landscapes that are highly fragmented or disturbed (Forsey & Baggs 2001). Riparian zones are characterized by sharp gradients in plant communities, ecological processes and environmental factors, and by high species-richness (Nilsson *et al.*, 1989; Gregory *et al.*, 1991, Jones *et al.*, 1994; Nilsson *et al.*, 1994). The patchiness and heterogeneity of habitats offered by riparian zones provide marten with a greater variety of microhabitats than may be available from a landscape composed of mature forest, agricultural land and open heath such as that surrounding Morangie. The increased density of hydrological flushes in low-lying forested areas may also explain why marten habitat use at coarser scales was predominantly associated with lowland rather than upland forests (Chapter 3).

4.4.5 Conclusions

To enable the findings of the field model to be widely applied would require extensive and labour intensive data collection (e.g. assessing ground cover type, measuring cover height, and measuring tree size index) meaning that it is of more use as informative research than providing management tools for practical forestry. For practical purposes, models that relate marten habitat use to forest stand parameters that are routinely measured by foresters are required, which is why the development of the GIS-based model is particularly relevant. A DEM of adequate spatial resolution (in this case 10 m) is all that is required to generate topographic wetness indices, and basal area and tree height are parameters that can easily be derived from data that are routinely-available to forest managers. The parameters highlighted by the GIS-model can therefore be applied at a large scale in the planning and management of new and existing forests. Whilst no association is drawn between these parameters and the population densities of marten observed using the forest, they can illustrate where forest managers could expect to see heavy utilisation by marten; at a landscape scale, forests managed to create mature, well spaced stands with well developed sub-canopy layers in areas where high TWI values are patchily distributed could be expected to support high numbers of pine marten. Implications for forest management are discussed further in Chapter 7.

Chapter 5

Seasonal diet of pine marten

5.1 Introduction

Like their North American counterpart, the American marten (*Martes americana*), the Eurasian pine marten (*Martes martes*) is often characterised as a food generalist and opportunist, consuming a broad range of food items with significant geographical and seasonal variation (see reviews: Clevenger 1994a, Martin 1994, de Marinis & Masseti 1995, Zalewski 2004). The food taken commonly represents what is locally and temporally abundant or accessible, and typically includes a wide variety of mammals, birds, fruits, invertebrates, amphibians, and reptiles (e.g. Nyholm 1970, Pulliainen 1981a, Warner & O'Sullivan 1982, Marchesi & Mermod 1989, Helldin 2000, and literature cited in reviews). The winter diet of the pine marten displays particularly strong geographic trends (Zalewski 2004); plant material and insects are consumed more frequently at southern latitudes (e.g. Clevenger 1993), whereas birds and medium-sized mammals are consumed more often at high latitudes (e.g. Grakov 1981, cited in Zalewski 2004). A longitudinal association is also found where plant material is consumed more often in the west (e.g. Clevenger 1995), and small mammals in the east (e.g. Aspisov 1973, cited in Zalewski 2004).

Zalewski's (2004) review is invaluable in that it has synthesised and made accessible the findings of studies that have yet to be translated from their original Russian. His subsequent meta-analysis has also provided a model by which to determine how the dietary habits of British marten compare to those in continental Europe and Russia. Given the geographic variation in marten diets, caution should be used when making generalisations about the dietary habits of British marten based on the results of studies from elsewhere in their range. For example, a popular public perception in the UK appears to be that squirrels form an important component of the marten's diet (i.e. BBC 2008), and yet red squirrels have only occasionally been found to occur within UK dietary studies (Velander 1983, Halliwell 1997). This generalisation is no doubt because of the importance of squirrels to marten elsewhere within their range (e.g. Storch *et al.* 1990), and demonstrates the need for a thorough understanding of the foraging ecology of British marten within their own ecological context. The overwhelming dominance of *Microtus* in the diet of British marten does however suggest that there may be aspects of their foraging ecology that differ from those in mainland Europe.

In this chapter I present year-round data on pine marten diet in a commercial coniferous forest in Scotland, along with estimates of the relative abundance of small mammal species found in different habitats within the forest and surrounds. Molecular identification techniques were employed to ensure that only pine marten scats were included in the analysis. Two dietary indices are used to allow comparison with other studies, and to represent the diet according to the frequency and volume with which foods are consumed. The contents of c. 2500 scats that were collected at monthly intervals from an area where 20 individual marten were known to be present were analysed. The results are used to answer the following questions:

i. What are the principal food sources of pine marten in Scottish commercial forestry?

ii. How do principal prey change seasonally?

iii. How does the diet in a commercial forest differ from the findings of Balharry (1993a.) and Halliwell (1997)?

iv. How does the diet compare with those from studies at similar latitudes or longitudes in continental Europe?

v. Are *Microtus* voles taken in preference over *Clethrionomys* voles, and what can this tell us about habitat use by foraging British pine marten as determined from Chapters 3 and 4?

5.2 Methods

5.2.1 Scat Collection

Pine marten scats were collected between June 2006 and May 2007 by walking a standard route of transects along forest roads totalling over 85km in length, each month. Transects were initially walked and all existing scats were removed, once in April 2006 and again in May 2006, meaning that all subsequently collected scats could be assigned to a collection month. Where possible, morphological characteristics (Fig. 5.1), scent, and location of scats were used to distinguish the scats of marten from those of other carnivores (i.e. fox). However, even expert naturalists can fail to consistently distinguish pine marten scats from those of red fox (Davison *et al.* 2002), so molecular identification was used to determine species of origin. Scats were individually bagged and labelled with a unique number and date of collection. Bagged scats were stored in a freezer at -20°C until needed for analysis. The position of the scat location was recorded using a high-sensitivity GPS receiver.

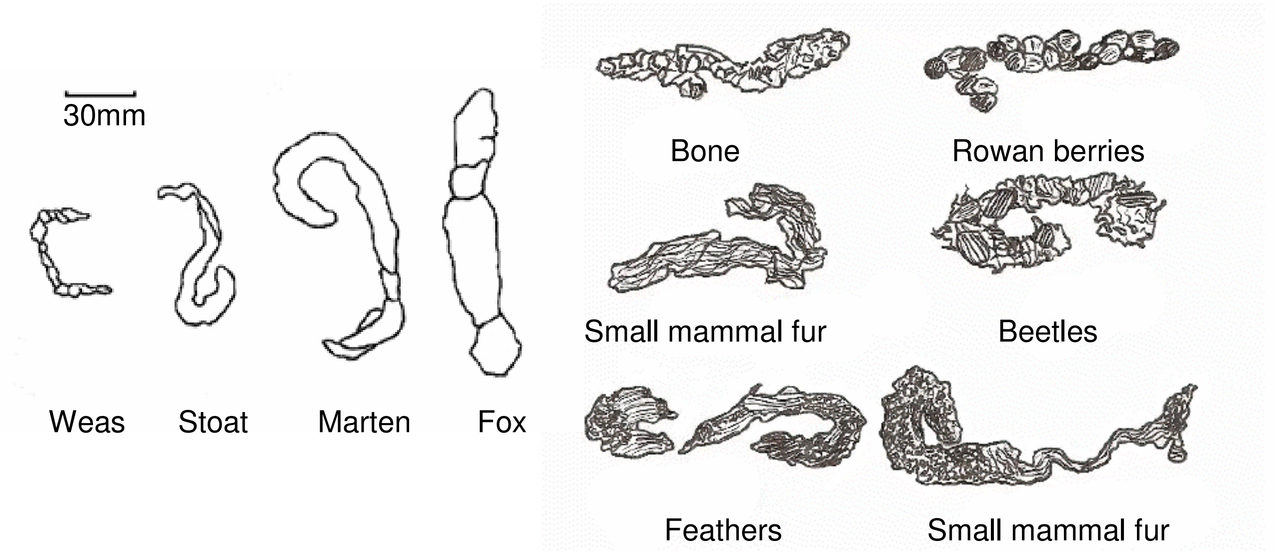


Figure 5.1 *Left* Typical scats of three mustelids and fox (adapted from Lockie 1961). *Right* Scats of pine marten demonstrating the diversity of morphologies resulting from differences in prey type consumed (adapted from Strachan *et al.* 1996).

5.2.2 Molecular Identification of Scats

Molecular identification of scat origin was determined by the genetics laboratory at Forest Research (*Northern Research Station, Roslin, Midlothian, Scotland*). DNA was isolated and extracted from scat samples using a PCR Template Preparation Kit according to the manufacturer's instructions (*Roche Inc.*). The protocols from O'Reilly *et al.* (2007) for real-time PCR were then closely followed. This method looks for species-specific sequences in the DNA extracted from scats with four possible outcomes: i. Pine marten DNA present. ii. Fox DNA present. iii. Both fox and pine marten DNA present. iv. Neither fox nor pine marten DNA present. If either iii or iv occurred, the sample was repeatedly run again up to three times to verify the outcome.

5.2.3 Scat Content Analysis

Frozen scats were defrosted before being examined and dissected macroscopically. Food remains were compared to the author's own reference collection and published identification guides (i.e. mammalian teeth: Corbet & Harris 1991, invertebrates: Chinery 1993, seeds and berries: Ross-Craig 1956) or with assistance from experts (*R. Coope, R. Coope, O. Nevin, C. Stevenson*). Each prey remain was identified to order level, and to species level (or lowest taxnomic level) where possible. Although microscopic identification of mammalian hairs can aid identification to species level (e.g. Teernik 1991), time constraints associated with large sample sizes precluded the use of this technique on small mammals, though large mammal hair was identified microscopically where possible. Small mammal remains found without identifiable teeth were therefore categorised as “unidentified small mammal”. Based on the analysis of red fox diet, Lockie (1959) found that the relative proportions of small mammal teeth recovered in faeces are a good measure of the proportions in which these rodents were eaten, as determined from identification of hair. It was therefore deemed appropriate to classify unidentified small mammals in the same ratios as they appeared in the diet for some analyses (Balharry 1993a.). Time constraints also precluded the identification of bird species from feathers (e.g. Day 1966). Instead, avian prey were grouped into ‘large birds’ and ‘small birds’ based on the diameter of the largest quill (large > 2mm, small < 2mm). This would place birds up to the size of a blackbird (*Turdus merula*) into the small bird category. Whilst marten are known to consume earthworms (e.g. Lynch & McCann 2007), scats were not specifically searched for earthworm chaetae.

Prey items were categorised into six broad food classes to allow comparison with other studies: small mammals, large mammals, birds, invertebrates, vegetation (fruit, berries, seeds), and ‘others’ (which was predominantly reptiles and annurans, but also included fungi and miscellaneous or unidentified items). Small mammals included shrews, voles and mice, whereas squirrels, rabbits and anything larger were considered to be large mammals. Scats containing few hard remains were classed as containing carrion, and this was often confirmed by the presence of a few deer hairs in the scat (Balharry 1993a., Halliwell 1997). Carrion was included in the large mammal category, although it is noted that some authors (i.e. Zalewski 2004) include it under 'others'. Scats containing pollen were included in the invertebrate's food class as were those containing beeswax as both pollen and beeswax would occur in the diet where marten had raided bees' nests.

In this study both volumetric and frequency-based methods of quantifying scat contents were used (Zabala & Zuberogoitia 2003). The frequency-based method used was the percent of relative frequency of occurrence i.e. the total number of occurrences of each food item divided by the total number of occurrences identified across all samples. An occurrence of a food item was defined as the presence of a prey species (or lowest identified taxon) within a scat therefore a food item could be constituted by several similar small prey, or part of a large prey. A volumetric measure was given using the estimated weight of prey intake (EWI), which was calculated by converting the frequency with which individual items of prey remains occur, by correction factors calculated by Balharry (1993a.) from captive feeding trials (Table 5.1). Development of digestibility coefficients or conversion factors for relating prey remains with prey consumed have the greatest potential for estimating actual biomass

Table 5.1 Summary of correction factors used to convert the occurrence of prey items into comparable quantities of food consumed, or the Estimated Weight Intake (EWI), from Balharry (1993).

Correction Factor	**0.5**	**5**	**16**	**25**	**51**	**77**
Prey	Insects Fruit *	Reptile Shrew Fungi	Mouse Vole Small bird Frog Egg shell	Large bird Squirrel Pollen	Rabbit	Deer Carrion

* As an additional conversion, the number of seeds of blaeberry found in each scat were divided by 35. This was the average number of seeds per fruit and could be used to convert the number if seeds found to a number of berries consumed (Coope 2007).

consumed (Litvaitis 2000). Correction-factors are generated through consumer-specific feeding trials where known amounts to food are fed to the animal, and the resulting faecal material is collected, allowing the number of scats containing a particular prey remain to be related to the amount of that prey consumed. Using a combination of frequency based and volume based dietary measures provides quantification on both the frequency with which an item is consumed (FO), as well as the relative importance of the item to the marten's diet in terms of the volume consumed (EWI). Data were pooled for each month, and months were then defined into four three-month seasons: spring (April to June), summer (July to September), autumn (October to December) and winter (January to March). The total composition of the diet was given by pooling data across all months, thus providing the over-all year-round diet.

Seasonal differences in the consumption of each food group were tested using G-test contingency tables of frequency of occurrence data. The diet niche breadth index (B) for each month based on frequency of occurrences of the six food categories, was calculated with Levin's formula:

$$B = 1 / \Sigma p^2_i$$

where B is the diet breadth, and p is the proportion of the diet formed by species i. This index was then standardised (Ba) using the formula:

$Ba = B / (n - 1)$

where n is the number of food types. Standardised values range between 0 and 1, with higher values indicating a wider niche breadth i.e. dietary generalists, and lower values indicating narrow niche breadth i.e. dietary specialists (Krebs 1989). Monthly values were averaged to give seasonal diet breadths, and compared between seasons using a Kruskal-Wallis test (Zar 1999).

The results were compared with the diet compositions found in other pine marten dietary studies using G-test contingency tables on frequency data based on a standardised 100 occurrences divided into food groups at the ratio they were found in that diet. The food groups used included small mammal, bird, invertebrate, large mammal and fruit. Fruit was distinguished specifically by several authors rather than using all plant material. The 'other' group was not included due to the fact that inclusion of items into this group was more variable and less defined between studies than in other food groups, and because it wasn't considered an important food group because of such low occurrences. Despite low frequency of occurrences of large mammals, this group was included because it was found by many European studies to be important, particularly when volumetric diet measures were considered.

5.2.3 Prey Availability

An index of the relative abundance of small mammal species was obtained by live trapping at several locations within the study area. Trapping was conducted in April 2007 to coincide with the low phase of the small mammal seasonal population cycle in spring (Hansson 1978). It was assumed that trapping during the low phase would mean that species' distributions would be more restricted to their core habitats.

Trapping was conducted concurrently in three replicates of each of seven broad habitat types that were defined based on canopy closure and ground cover into three open habitats, three forest habitats and one linear habitat (Table 5.2). In each habitat, a trapping grid was laid with 5 rows of 5 multiple-capture live traps (*Ugglan, Grahnab, Sweden*) spaced at 10 m intervals, except in the linear habitat, where the 25 traps were spaced in a single line 10 m apart. Each trap was protected from the elements with a storm cover, provided with straw bedding, and baited with rolled oats, peanut butter, and frozen fly casters. All seven habitats were trapped simultaneously for five consecutive nights, after which the trapping grid would be replicated in the same habitat type but at a new location. Trapping within three replicates of each habitat was carried out in immediate succession. Traps were checked daily and captured animals were

Table 5.2 Categorisation of habitats in which small mammal species relative abundances were assessed through live trapping. Three replicates were conducted in each habitat. Habitat definitions were guided by those of habitats used in Chapter 3.

Habitat		Description
Forest	Closed [†]	Dense coniferous plantation 16 - 44 yrs old, > 90 % canopy closure, cover: needle litter > moss*
	Mature	Thinned Scots pine plantation 45+ yrs old, 40-50 % canopy closure, cover: blaeberry / heather > grass > gorse
	Regenerating	Young trees < 16 yrs old, no canopy closure, cover: heather / blaeberry / grass / coarse woody debris / moss
Open	Moor	No tree canopy, cover: heather > moss
	Grass	No tree canopy, cover: ungrazed graminoid vegetation > 30 cm tall
	Arable	No tree canopy, cover: grazed improved pasture < 30 cm tall
Linear	Road verge / ride	Tree line within 10m, < 20 % canopy closure, cover: as grass > heather

[†] One of the three replicates was each conducted in larch (*Larix* spp.), spruce (*Picea* spp.) or pine (*Pinus* spp.) dominated plantations.

* Cover types are given in order of dominance as indicated, a dash indicates that there was no dominance in cover types observed between replicates of that type.

marked by fur clipping. All trapping was carried out under licence from Scottish Natural Heritage (*Scientific Licence No. 6146*).

The habitat niche breadth of each small mammal species was calculated using Levin's formula above, but with the alteration that this time B is the habitat niche breadth, and p is the proportion of total captures of a species in habitat i. Again, this was standardised but with n as the number of habitat types. Higher values of Ba indicate habitat generalists, lower values indicate habitat specialisation. Species diversity and species evenness indices were calculated and ranked for each habitat. The species diversity (H') of each habitat were calculated from Shannon-Weiner index:

$$H' = - \Sigma P_i \log P_i$$

where P is the proportion of total captures per habitat belonging to species i. Higher values indicate greater species diversity in terms of species richness and abundance of individuals within those species. Species evenness (J') is given by:

$$J' = H' / \log n$$

where n is the total number of possible species occurring (Krebs 1989). Values range from zero to one, where a value of one indicates a habitat with equal numbers of individuals within species.

Evaluating the relative abundance of small mammal species found in habitats does not provide sufficient information to discuss their absolute availability to pine marten, as the relative numbers caught in traps is wholey dependent upon which habitat the traps are set in. To convert trapping figures into a more meaningful measure, the species-specific densities per hectare of habitat were multiplied by the amount of habitat available. The relative abundances from trapping gave the number of each species caught per 100 TN in 0.16 ha (5 x 5 traps at 10 m intervals = 40 m x 40 m) of habitat. However, multiplying this value up to give a density per hectare must take into account that different species have different ranging distances, meaning that the effective trapping area is specific to each species (Korpimaki & Norrdahl 1991). The outer traps of each trapping grid can potentially catch more small mammals than the inner ones as they may overlap the home ranges of individuals outside the grid area. To correct for this "edge effect", an edge belt of mean home range radius was added to the sampling area using values of mean home range radius taken from the literature: *Microtus* and *Sorex* sp. = 20.5 m (Korpimaki & Norrdahl 1991); *Clethrionomys* = 25 m and *Apodemus* = 26 m (Crawley 1969). For example, for the actual area covered by the trapping grid of 0.16 ha, the effective trap area for *Microtus* is 0.37 ha, but is 0.44 ha for *Apodemus*. For a trapline of 25 traps at 10 m intervals, the effective trapping area is 0.23 ha for *Microtus*, and 0.30 ha for *Apodemus*. These values can be used to calculate species-specific densities per hectare, i.e. if one *Microtus* was trapped in 0.37 ha, there would be 2.7 *Microtus* per hectare (or 270 per km^2). The average number of small mammals of each species caught per 100 TN per hectare of each habitat type (totalled over three replicate grids) was used to extrapolate the densities (individuals per km^2) of small mammals available to marten. The amount of each habitat available was determined from the average composition of the seven female marten home ranges from Chapter 3.

Differences in the occurrences of small mammal species in the environment and the diet were tested using G-tests. Selection indices were then calculated for small mammal species to demonstrate whether marten show a dietary preference based on small mammal consumption and availability in the environment using the following equation:

$$W_i = O_i / P_i$$

Where W_i is the selection index for species i, O_i is the proportion of species i in the diet, and P_i is the proportion of species i available in the environment. Selection indices above 1.0 indicate preference, values less than 1.0 indicates avoidance (Krebs 1989).

5.3 Results

5.3.1 Scat Identification

Between June 2006 and May 2007, 2862 scats were collected and their locations recorded, of which 2417 scats were tested using molecular identification. Of these, 159 (7 %) were unsuccessful meaning there was either no fox or marten DNA to be extracted from the scat, or any DNA present had deteriorated too much to be amplified with PCR. Of those scats successfully identified, 147 (6 %) were fox, and 2111 (87 %) were pine marten. The sample size of scats collected meant that it was not possible to test all scats genetically, therefore the remaining scats collected were visually identified by the author as being definitely pine marten in origin ($n = 338$), or definitely not pine marten in origin ($n = 107$). Scats that had been visually identified as not pine marten in origin were not included in subsequent scat analysis. To validate the use of visual identification of scat origin, and to verify the identification abilities of the author, genetic tests were run on a sub-sample of scats from the "definitely marten" ($n = 58$), and "definitely not marten" ($n = 22$) groups. These tests returned correct identification success rates of 98 % and 36 % respectively. Positive identification of marten scats was significantly more successful than positive identification of non-marten scats ($\chi^2 = 36.17$, $df\ 1$, $P < 0.001$). This meant that whilst a small number of pine marten scats were likely to be discarded in error, the inclusion of non-marten scats in content analysis was unlikely.

5.3.2 Year-Round Diet Composition

A total of 2449 scats, identified as pine marten either genetically (86 %), or visually (14 %), were dissected and their contents analysed. The relative contribution of each of the six food groups to the total year-round composition of the diet differed depending on the diet measure used (Fig. 5.2). Based upon relative frequency of occurrence, the greatest contribution to the diet came from plant material (32 %) and small mammals (30 %) followed by birds (18 %) and invertebrates (16 %). Larger mammals and 'others' formed only 3 % and 2 % of occurrences respectively. Although the rank order of importance changed when EWI was considered, the three largest contributors remained the same: small mammals (38 %), birds (23 %) and plant material (18 %). The greatest changes came from a greatly increased contribution from large mammals which accounted for 17 % of the diet based on EWI, and from invertebrates whose contribution fell to just 4 % of total EWI. The 'others' food category remained the least consumed food (< 1 %).

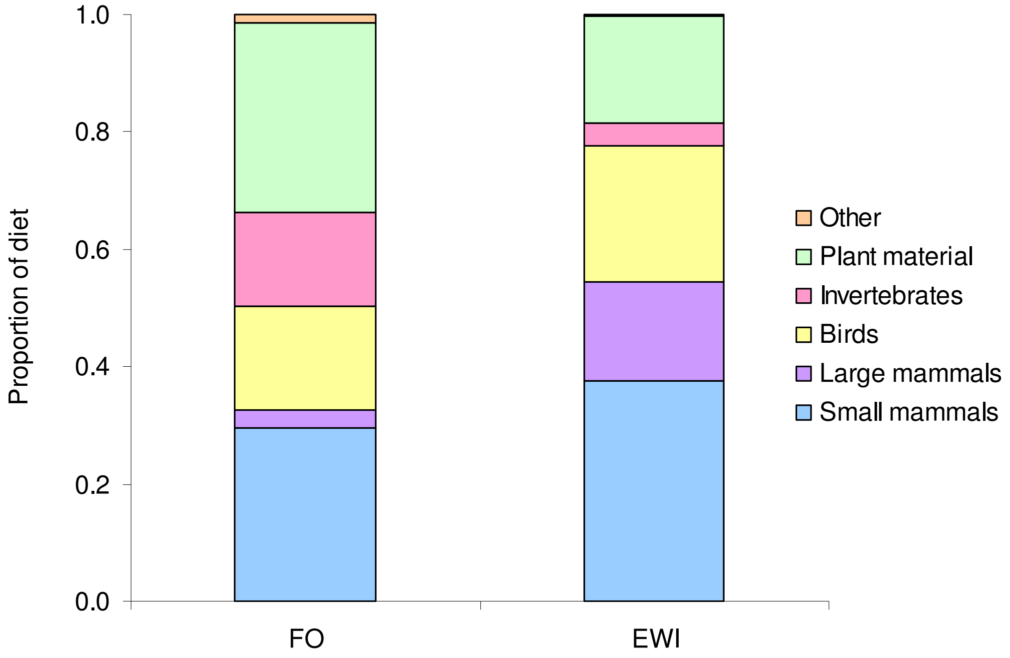


Figure 5.2 The diet of pine marten based upon the total contents of 2449 scats collected throughout one year (June 2006 to May 2007) in Easter-Ross, Highland, Scotland. The diet is shown represented by the percent relative frequency of occurrence (FO), and the percent of estimated weight of intake (EWI).

5.3.3 Seasonal Diet Composition & Diet Breadth

5.3.3.1 Comparison between dietary indices

The rank order of relative seasonal consumption did not differ between the two dietary measures used for any food group except for the invertebrate and 'others' food categories (Fig. 5.3). Based upon FO, the greatest consumption of invertebrates occurred during summer, whereas based upon EWI it occurred during winter. This difference could be attributed to a greater incidence of pollen in winter scats, and the high correction factor given to pollen by Balharry (1993a). The correction factor for pollen is far greater than the correction factors assigned to other invertebrates because of its high calorific value, but as this correction factor was somewhat arbitrarily assigned (Balharry 1993a, Appendix 2), the result should be viewed with some caution. The differences between measures observed in the 'others' food category are a result of the wide variety of correction factors used in this group reflecting the diversity of prey types included in this group. Due to the limitations and discrepancies of some of the correction factors used to calculate EWIs mentioned above, the dietary results will subsequently be described primarily in terms of FO, although corresponding EWIs will be given in the text where relevant. Using FO also allows for ease of comparison of the results with published reviews of marten diet (Clevenger 1994, Zalewski 2004).

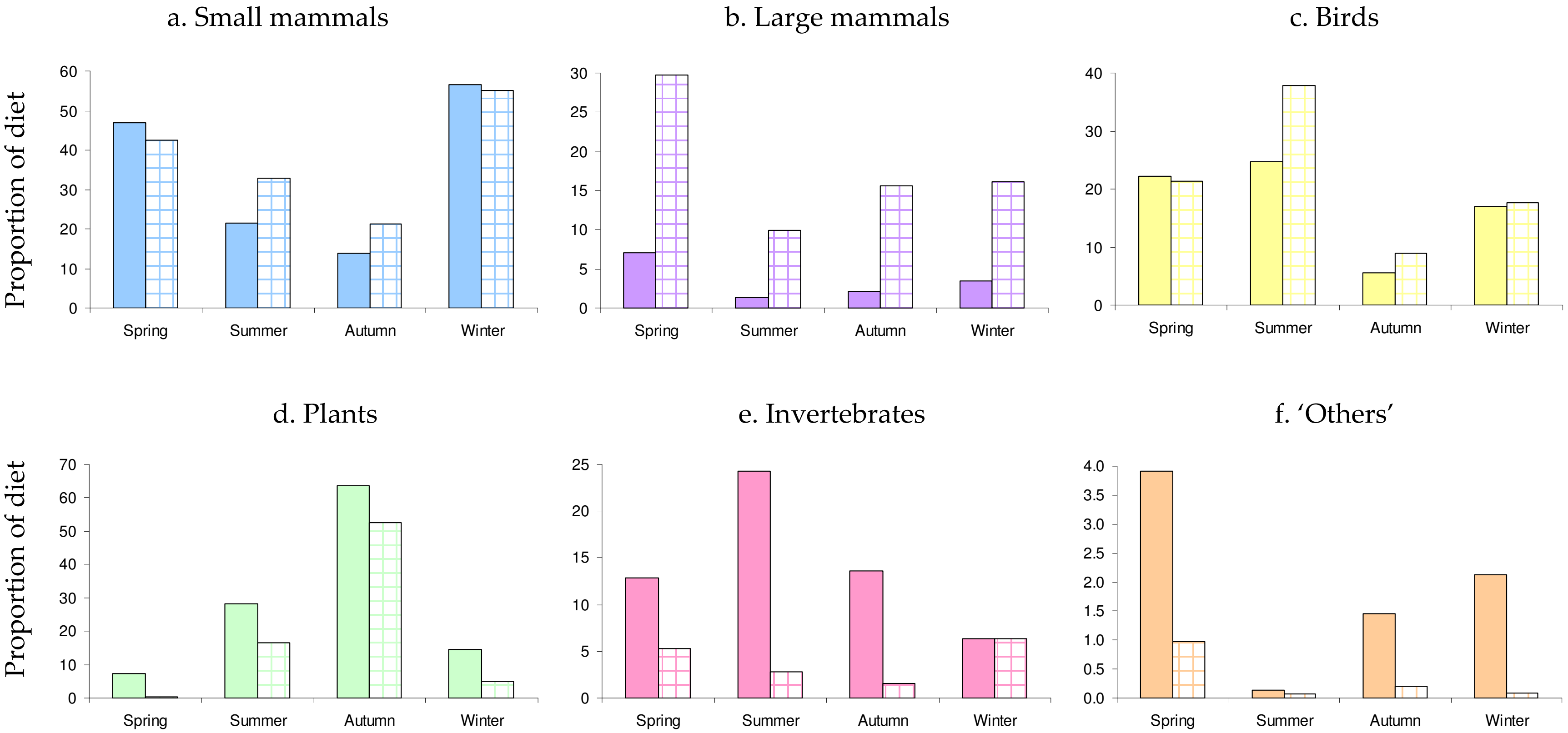


Figure 5.3 Comparison of the seasonal importance of food groups dependent on diet index used. Solid bars represent frequency of occurrence data and hatched bars represent EWI. Seasonality of prey consumption appears to be independent of diet index for small mammals, larger mammals, birds, and plant material, but not for invertebrates and others.

Percentage frequency of occurrence of individual species (or otherwise lowest taxonomic group identified) within food groups (i.e. the proportion of large mammal occurrences that are deer) will be used to provide a more detailed description of individual species' contribution to each food category.

5.3.3.2 General description of the seasonal diet

The diet of marten included a wide variety of prey items, with over 30 different food types classified, and diet composition demonstrated marked seasonality (Fig. 5.4). Plant material dominated the diet in autumn, whilst small mammals were most numerous in winter and spring, and the summer diet was reasonably well balanced between food groups. This was reflected through comparison of the average standardised food niche breadths, which differed between seasons (Kruskal-Wallis $\chi^2 = 7.89,\ df\ 3,\ P < 0.05$); autumn had the narrowest diet width ($\tilde{x}\ Ba = 0.26$), indicating the most specialised diet, whereas summer had the broadest diet width ($\tilde{x}\ Ba = 0.53$), indicating the most generalised diet. The restricted autumn diet was characterised by a heavy consumption of plant material, notably berries, which alone accounted for 64% of autumn food occurrences. In contrast the summer diet was balanced, with small mammals, birds, invertebrates and plants being equally important in terms of the frequency with which they appeared; accounting for 21 %, 25 %, 24% and 28 % of summer occurrences respectively. The spring diet was largely

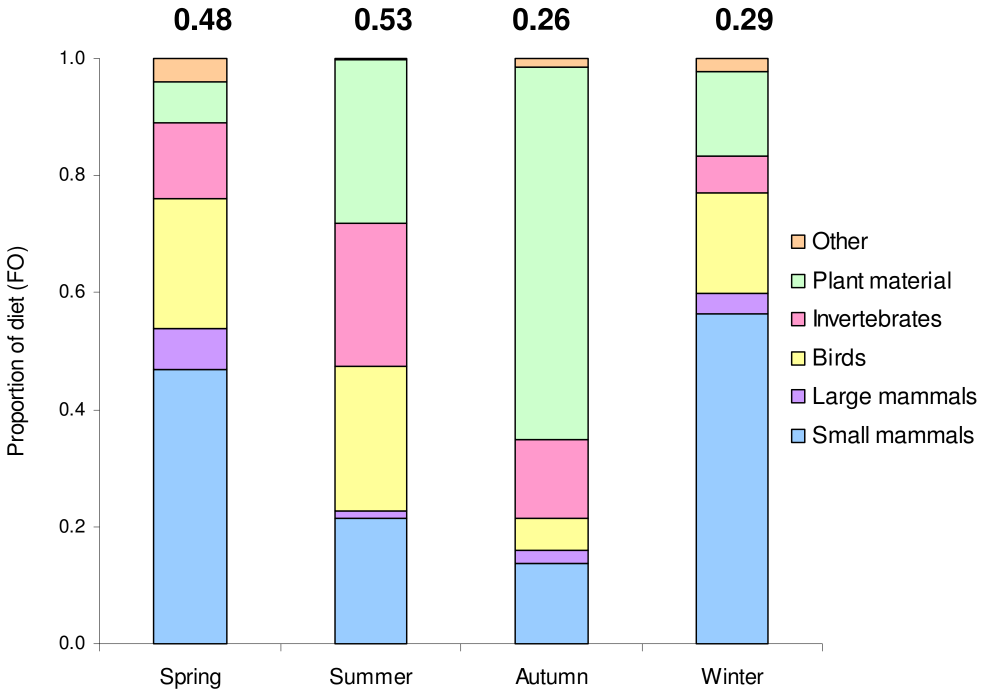


Figure 5.4 Seasonal differences in pine marten diet based on percent relative frequency of occurrence (FO). Average standardised diet breadth (*Ba*) is given for each season, calculated from the median diet breadth value of three months in each season.

dominated by small mammals, which formed 48 % of occurrences, although this was not reflected by the relatively high diet breadth. The winter diet breadth indicated that marten were specialising more on small mammals at this time, which formed 56% of winter food occurrences. A detailed description of the prey items occurring in each of the major food groups is given in the following sections, and is summarised for comparison with other studies in Table 5.3.

5.3.4 Principal prey species

Closer inspection of the food groups reveal that 77 % of occurrences in the diet are accounted for by just six prey species or otherwise lowest taxonomic group identified (Table 5.4). The large disparity between diet indices for beetles and berries suggest that their importance is indeed exaggerated by the use of frequency of occurrence. The rank order of importance for vertebrate prey items however remains the same regardless of diet index.

Unidentified small mammals accounted for the greatest proportion of both FO and EWI. Small mammal remains could be separated to species level by identification of teeth for 45 % of small mammal occurrences (*n = 503*), however time constraints prevented further identification of those samples without tooth remains (*n = 610*) by microscopic examination of fur. The proportion of small

Table 5.3 Food items in the diet of pine marten. Data are expressed as the percentage relative frequency of occurrence of six food categories in each season (bold), and percentage of seasonal EWI (bold parenthesis). The percentage relative frequency of total occurrences *(n = 3762*) is also given for each of the lowest taxonomic level identified within each category (plain text). The number of scats analysed each season is also given.

Food Items	SPRING	SUMMER	AUTUMN	WINTER	TOTAL
Small Mammals	**46.8 (42.4)**	**21.3 (32.8)**	**13.7 (21.3)**	**56.2 (55.0)**	**29.6**
Microtus agrestis	16.4	8.2	4.3	18.1	10.2
Apodemus sylvaticus	3.0	0.4	0.2	1.8	1.0
Clethrionomys	1.2	0.5	0.3	3.3	1.0
Sorex sp.	0.8	1.9	0.1	1.4	1.1
Unknown spp.	26.6	10.2	8.9	31.6	16.2
Large mammals	**7.2 (29.8)**	**1.4 (9.9)**	**2.1 (15.6)**	**3.5 (16.1)**	**2.9 (17.1)**
Deer sp.	2.3	0.0	0.0	1.5	0.6
Ovis aries	0.3	0.1	0.1	0.2	0.2
Oryctolagus cuniculus	0.5	0.0	0.0	0.0	0.1
Carrion	3.2	1.0	1.4	1.4	1.5
Birds	**22.7 (21.3)**	**24.5 (37.8)**	**5.5 (8.9)**	**16.9 (17.6)**	**17.7**
Small bird	15.7	21.9	4.6	12.7	14.6
Large bird	2.5	0.9	0.6	2.4	1.3
Egg shell	4.5	1.6	0.3	1.8	1.8
Invertebrates	**13.2 (5.3)**	**24.1 (2.8)**	**13.5 (1.5)**	**6.3 (6.3)**	**16.3 (3.9)**
Coleoptra	7.9	16.1	8.8	0.9	10.1
Vespa sp.	0.0	3.3	1.6	0.2	1.8
Bombus sp.	0.7	3.7	1.1	0.3	1.9
Pollen / wax	3.5	0.5	0.1	3.9	1.5
Scarabaeiform larvae	1.2	0.5	1.9	1.1	1.1
Plant material	**7.4 (0.3)**	**27.7 (16.6)**	**63.6 (52.5)**	**15.1 (4.9)**	**32.1**
Vaccinium myrtillus	0.2	20.0	17.6	1.4	12.9
Rubus sp.	0.0	0.1	1.5	0.2	0.5
Prunus sp.	0.0	4.9	6.4	0.0	3.7
Sorbus sp.	0.5	2.4	37.2	8.3	12.7
Misc. berries	0.7	0.0	0.1	0.8	0.3
Unknown large fruit	1.5	0.2	0.6	3.8	1.1
Misc. vegetation	4.5	0.1	0.3	0.8	1.0
Other	**1.5 (1.0)**	**1.1 (0.1)**	**1.5 (0.2)**	**2.0 (0.1)**	**1.4 (0.3)**
Lacerta vivipara	0.2	1.0	0.0	0.0	0.4
Anguis fragilis	0.0	0.1	0.0	0.0	0.0
Bufo bufo & Rana	1.0	0.1	0.3	0.0	0.3
Fungi	0.0	0.0	0.6	0.9	0.3
Misc.	0.3	0.0	0.6	1.1	0.4
Total no. scats	**420**	**487**	**668**	**874**	**2449**

Table 5.4 The six principal prey items in the diet of pine marten, each of which account for > 10 % of the yearly total of 3762 food occurrences. The percent EWI is given for comparison.

Species	No. Occurrences	FO (%)	EWI (%)
Unidentified small mammal	610	16.2	20.3
Small bird	548	14.6	18.2
Blaeberry	486	12.9	7.4
Rowan berry	487	12.9	9.2
Microtus	383	10.2	13.1
Beetle	380	10.1	0.5
Adjusted *Microtus* †	853	22.7	28.8
Total‡	2894	76.9	68.7

† Calculated by dividing the unidentified small mammal category using the monthly ratios of known identified small mammal species: referred to in greater detail in the text.

‡ Does not include adjusted *Microtus* value.

mammal occurrence identified to species per season ranged from 35 % to 52 % ($\bar{x}$ = *44* $\pm$ *7* %), and were shown to differ seasonally (χ^2 *= 11.8, df 3, P < 0.05*), with the highest proportion of small mammal species identified in summer (52%), and the lowest in autumn (35 %). Seasonal differences may have been due to climatic factors; rainfall during autumn 2006 was exceptionally high, with parts of north-east Scotland receiving over double the average amount of rainfall (*Met Office data, accessed 2008*). Heavy rain may have caused scats to disintegrate and small remains such as teeth may have been partially washed away.

A sub-sample of 100 unidentified small mammal scats were selected randomly from throughout the year and re-analysed to double-check if teeth may have been over-looked in the initial analysis. The re-analysis resulted in a single occurrence of *Apodemus* teeth that had been previously missed. The implications of this are that a very small proportion (c. 1 %) of scats may have been incorrectly classified as "unidentified small mammal species", but this would not have made a significant impact on the ratios of species identified.

The proportion of identified small mammal species was comparable with those found in Chapter 6 (50 % identified), and by Lockie (1959). If the unidentified small mammals were classified in the same ratios that identified species appeared in the diet, then *Microtus* would become the single most important prey item, accounting for 23 % of total relative frequency of occurrence and 29% of EWI. Small birds were the second-most important “species” within the diet, followed by rowan and blaeberries.

5.3.5 Principal food groups

Figure 5.5 demonstrates the pronounced fluctuations in the diet throughout the course of a year. Three food groups dominate the diet: small mammals, plant material and birds, each of which appears to prevail in the diet for a particular seasonal period before being supplanted by another. From late summer to early winter, plant material is the most important component of the diet, accounting for 40 to 80 % of occurrences. Throughout winter and spring small mammals dominate, forming between 40 and 60 % of occurrences. The diet at this time is augmented by birds, which form 15 to 35 % of occurrences from spring into early summer. Other food groups add to the diet seasonally: invertebrates in summer, large mammals in spring, and “others” in winter, but none of these groups dominate the diet in the way the principal food groups do.

5.3.5.1 Plant Material

Plant material was the most important food group in terms of total year-round FO, accounting for 32 % of all occurrences (Fig 5.5 a). Its ranking fell to third most important food group when EWI was considered however, forming 18 %

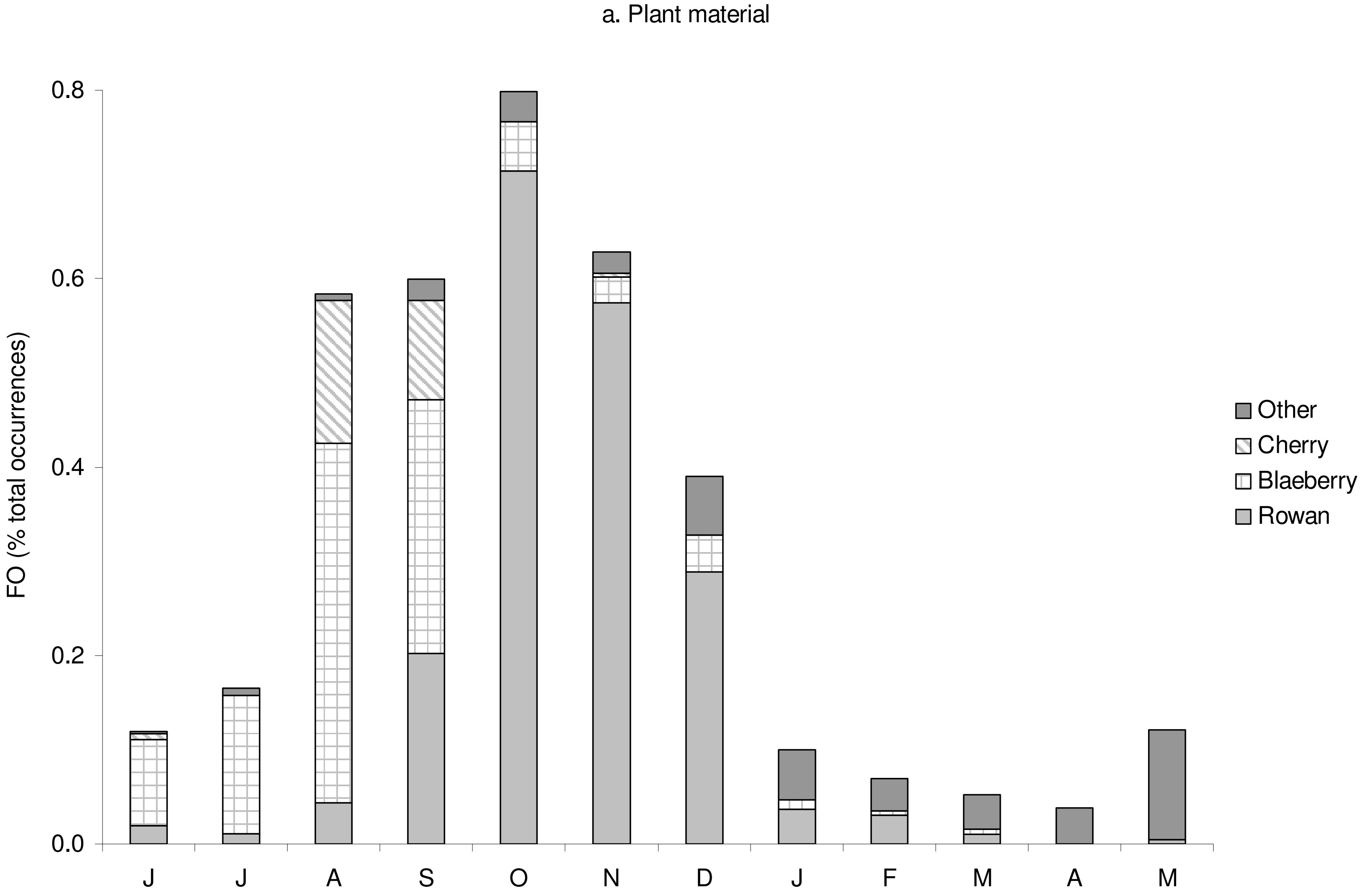
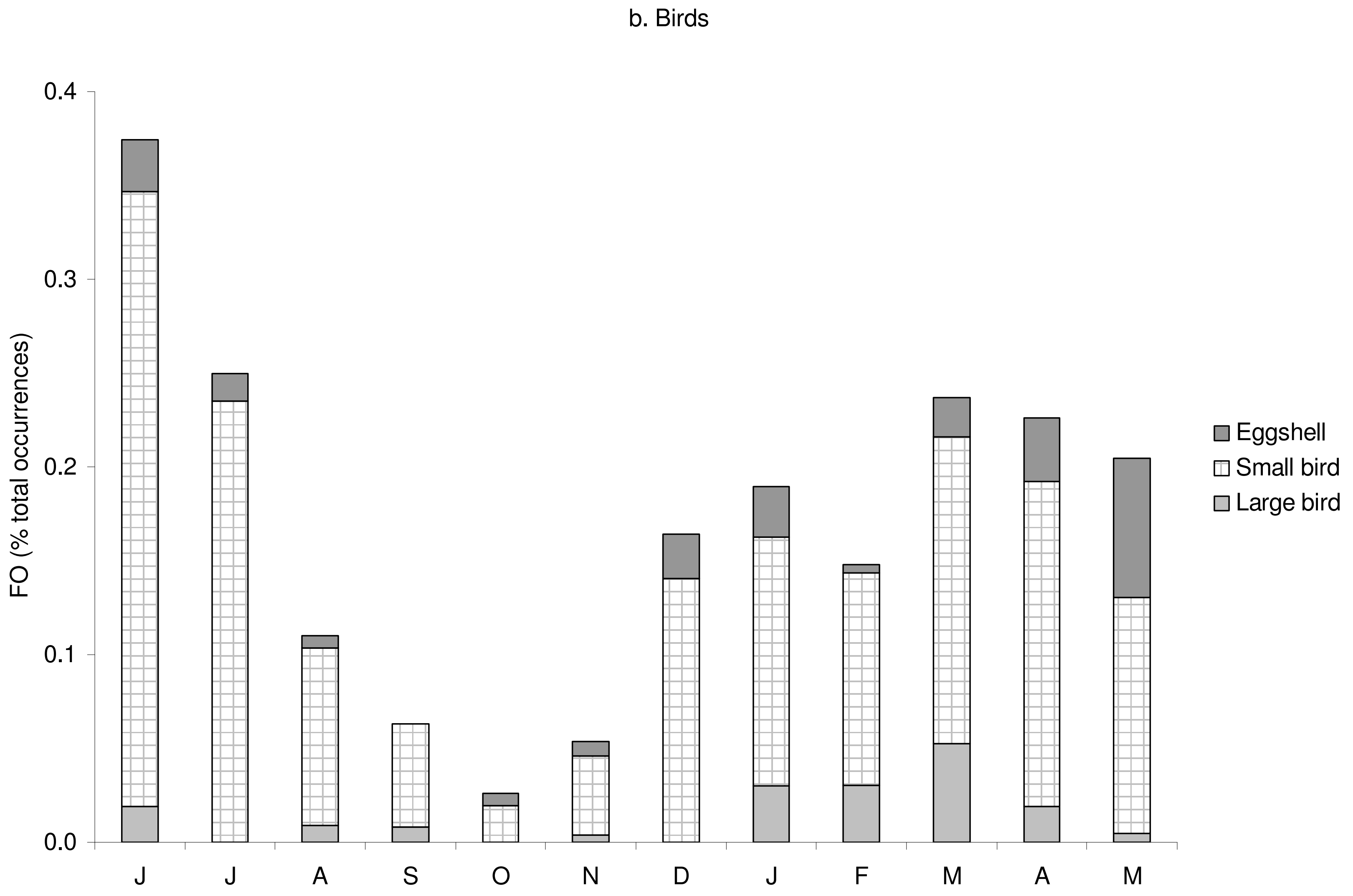
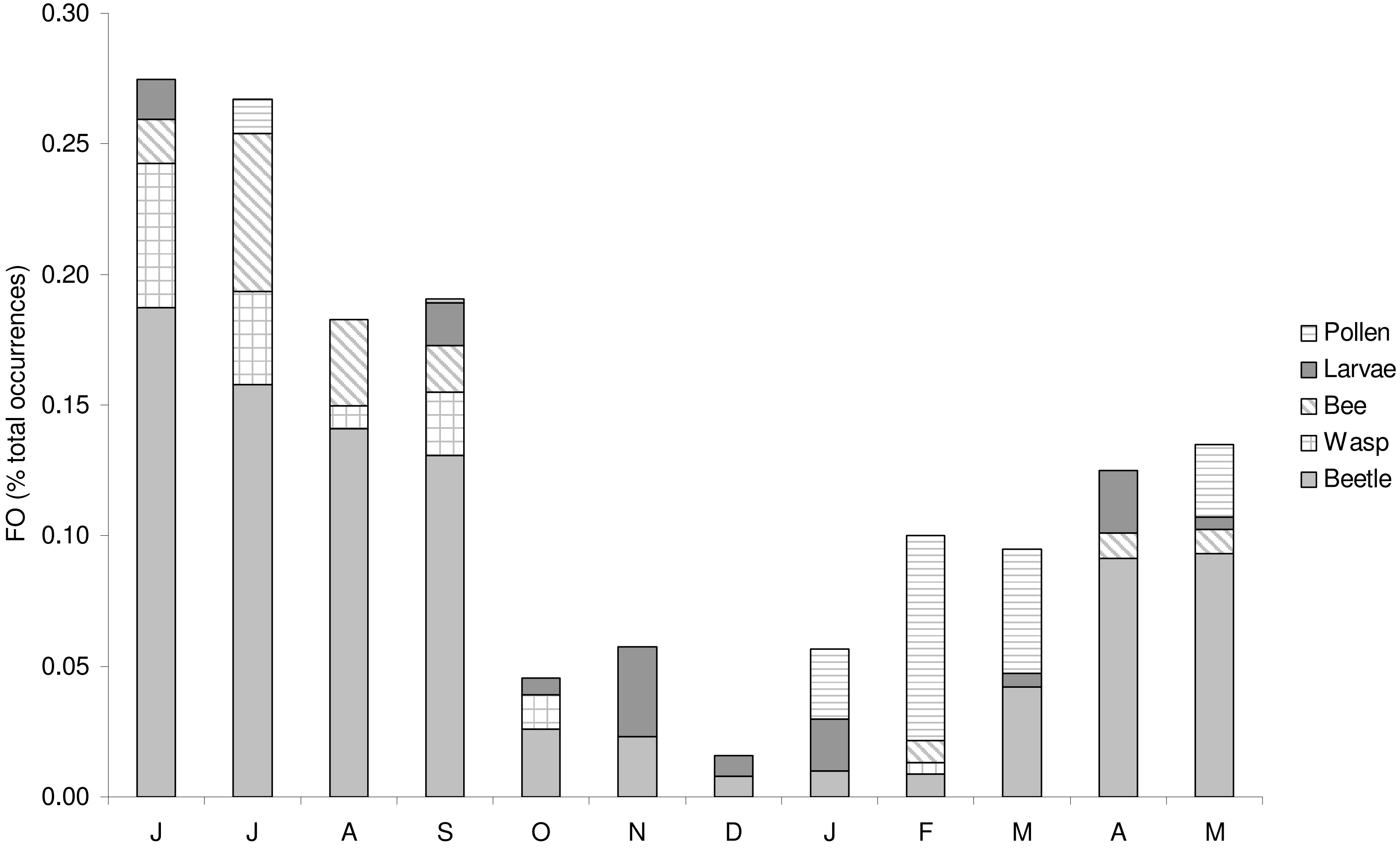
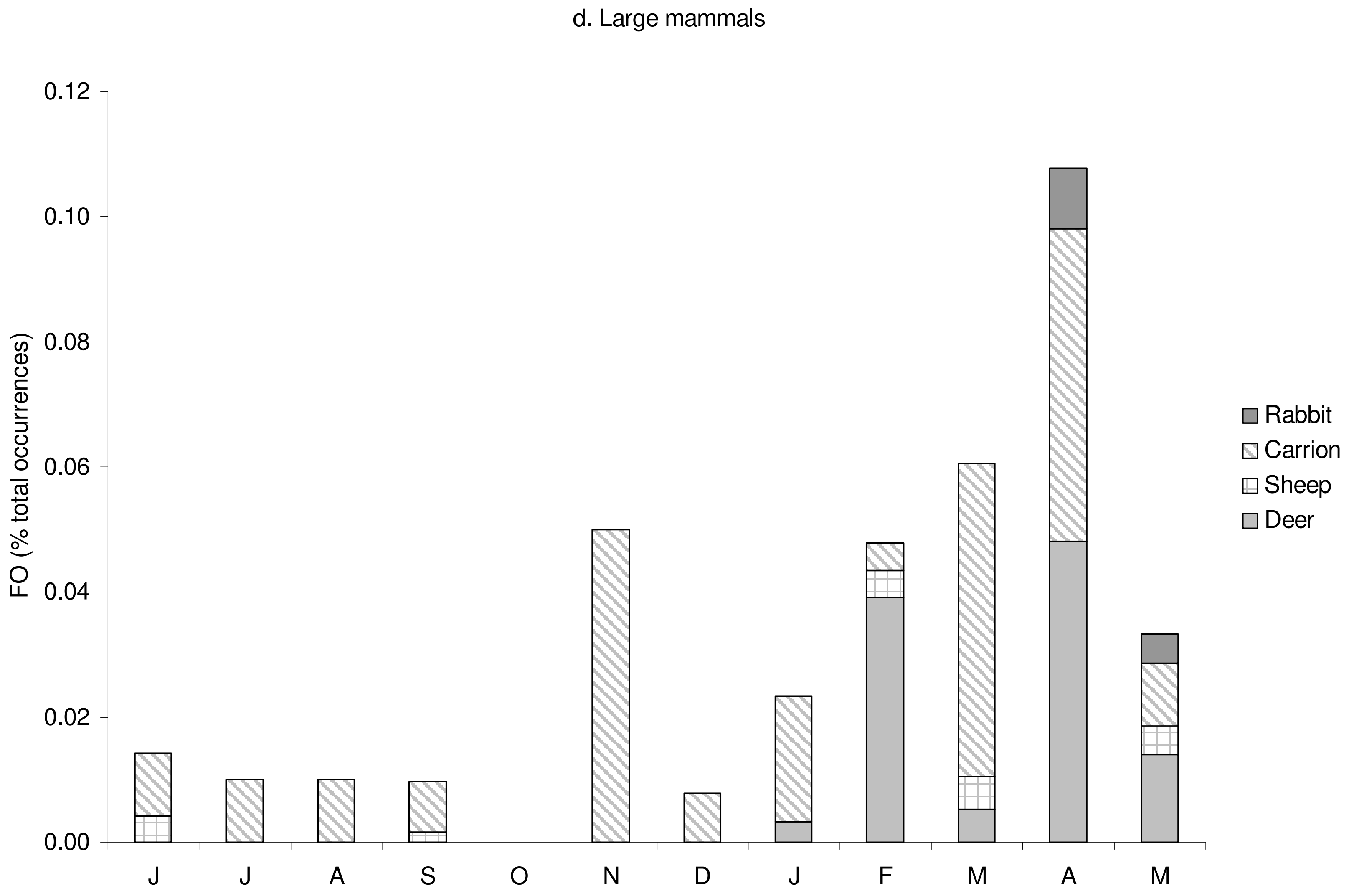


Figure 5.5 Monthly composition of each food group (based on FO %). Note the difference in scale between figures.

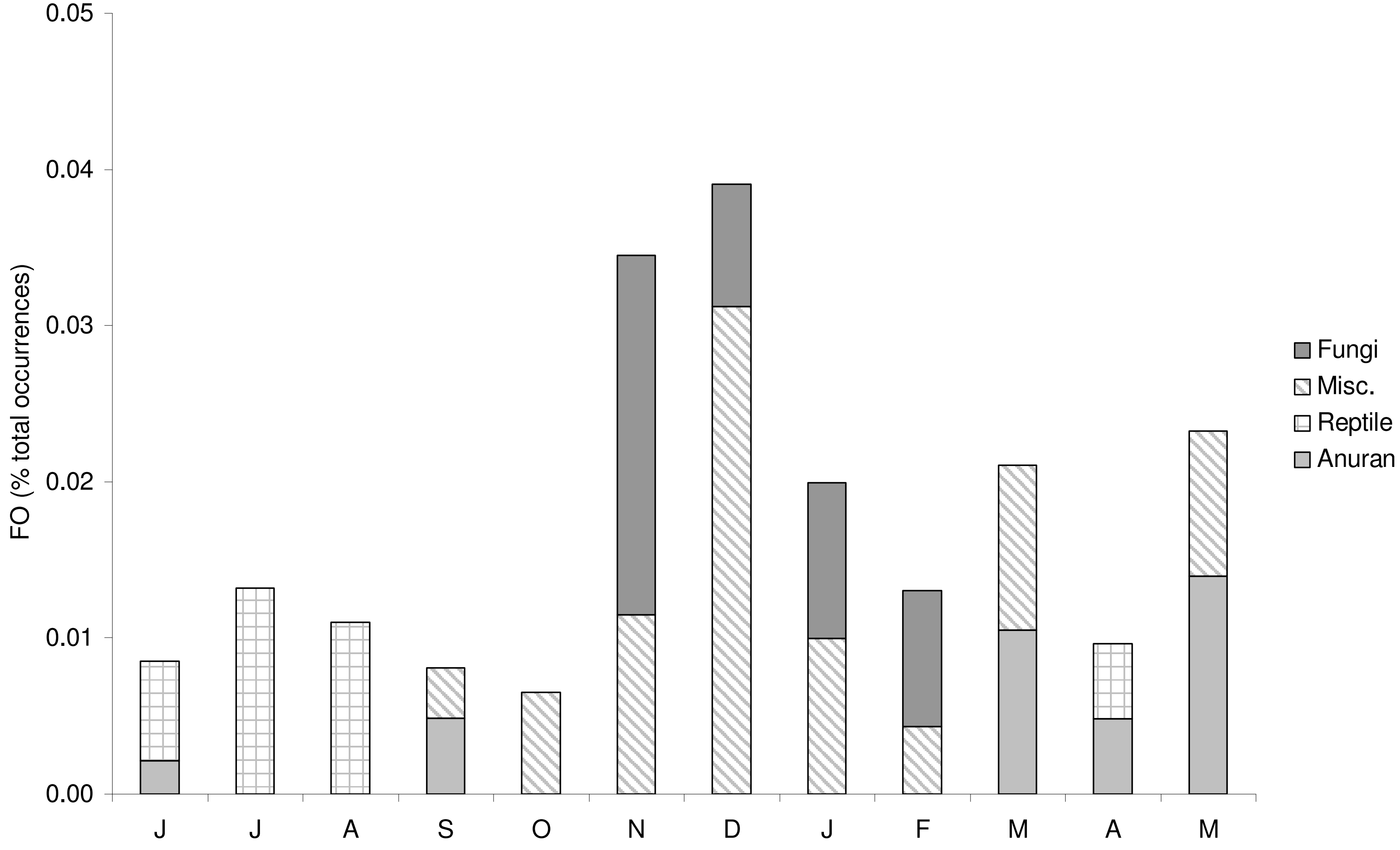

b. Birds
FO (% total occurrences)
0.4
0.3
0.2
0.1
0.0
J
J
A
S
O
N
D
J
F
M
A
M
Eggshell
Small bird
Large bird

c. Invertebrates



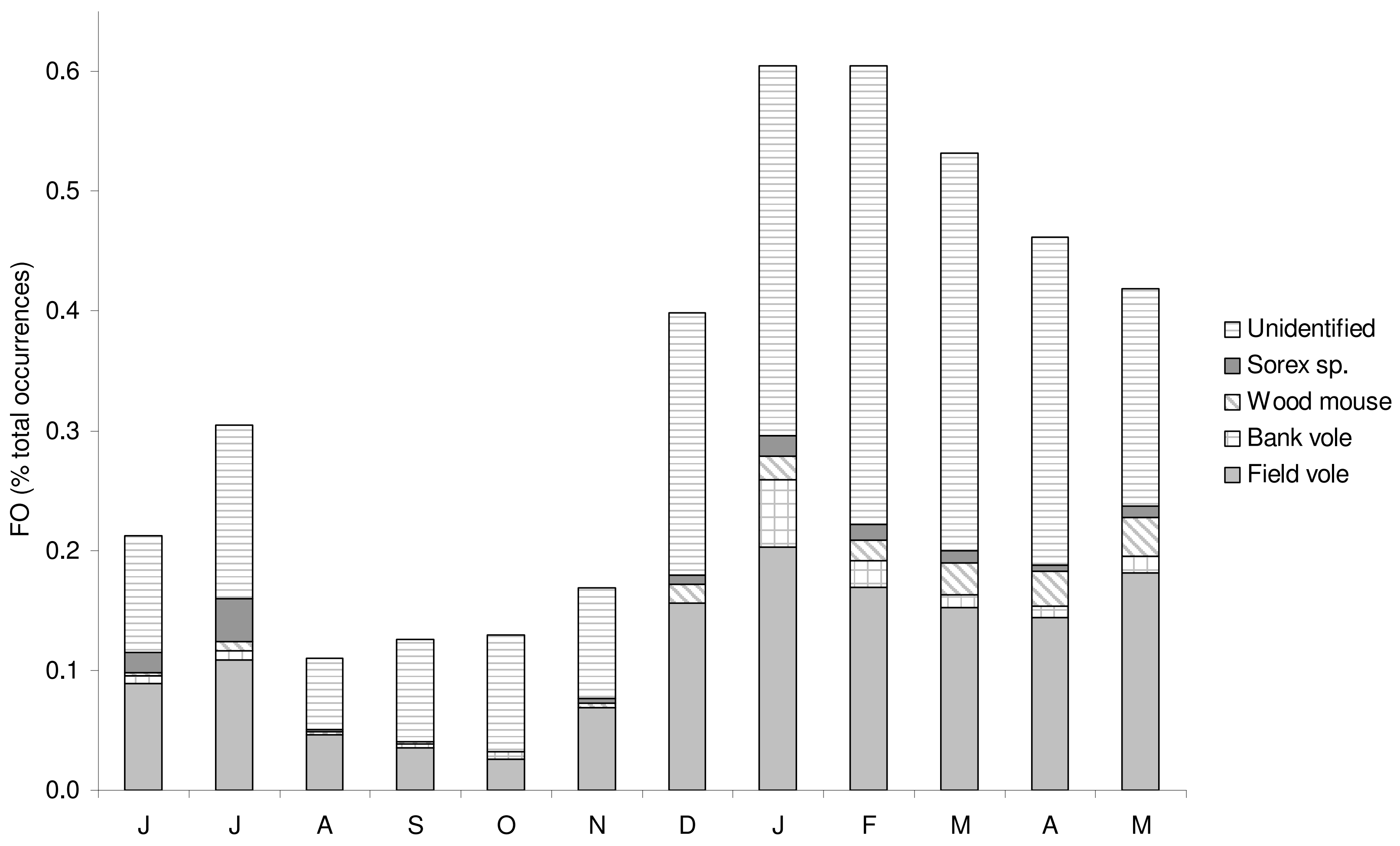

d. Large mammals
FO (% total occurrences)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
J
J
A
S
O
N
D
J
F
M
A
M
Rabbit
Carrion
Sheep
Deer

e. Other



FO (% total occurrences)
0.05
0.04
0.03
0.02
0.01
0.00
J
J
A
S
O
N
D
J
F
M
A
M
Fungi
Misc.
Reptile
Anuran

f. Small mammals



of ingested food weight. Plant material also showed the greatest variability in monthly consumption, forming 4-80 % of occurrences ($\bar{x} = 31 + 28$ %). Plant material was identified to species level where possible, but will be reported here based on the following groups: rowan, blaeberry, cherry, and 'other' plant material. 'Other' plant material consisted of miscellaneous berries (raspberries *Rubus* sp., rose hips *Rosa canina*, ivy *Hedera sp*., hawthorn *Crataegus monogyna*, and unidentified berries); large fruit (plum *Prunus* sp., apple *Malas sp*., and unidentified large fruit), grass seeds (barley *Hordeum* sp.) and unidentified vegetative matter that had been ingested rather than picked up incidentally with the scat. Rowan and blaeberry were the most important species, each accounting for 40 % of plant occurrences, cherries for 11 % of plant occurrences, and the remainder made up by other plant material. Consumption of fruit reflected the species' seasonal appearance; blaeberries and cherries were taken most during summer, whilst rowanberries dominated the diet in autumn and into winter. By spring very little plant material was found in scats and berries were largely absent, instead the vegetation found at this time comprised mostly of mosses. Closer inspection of these moss filled scats revealed that 25 % ($n = 9$), all of which occurred during April and May, were found to contain no other prey items. As they had tested positively for pine marten DNA they were certainly marten scats rather than incidentally picked up vegetation.

5.3.5.2 Birds

Consumption of birds showed quite marked seasonality; during spring and early summer, birds accounted for 20-37 % of occurrences ($\bar{x} = 26 \pm 7$ %), but fell to just 3-6 % of occurrences ($\bar{x} = 5 \pm 5$ %) during autumn (Fig 5.5 b.).

Separating birds based on size revealed that 83% of bird occurrences came from small birds, 8 % came from large birds, and 10% came from eggs. Small birds could include smaller species, or young birds of larger species. Further inspection of the seasonal occurrences of small birds showed that the highest proportion occurred during summer ($\chi^2 = 26.75$, *df 1*, $P < 0.001$), and the lowest during spring ($\chi^2 = 20.19$, *df 1*, $P < 0.001$). Large birds were eaten in the highest proportions during winter ($\chi^2 = 7.70$, *df 1*, $P < 0.05$), and the lowest during summer ($\chi^2 = 15.95$, *df 1*, $P < 0.001$). However, even during winter, small birds accounted for the vast majority (75 %) of bird occurrences.

The remains of bird eggshell were found in the highest proportion during spring ($\chi^2 = 17.41$, *df 1*, $P < 0.001$), which coincides with the beginning of the bird breeding season. There were several constraints associated with data on egg consumption however, because hen eggs were the principal bait used throughout the habitat-utilisation study conducted simultaneously with scat collection

(Chapter 3). The effects that baiting had on apparent egg consumption is demonstrable as 18 % of eggshell remains were found during winter. Whilst it is possible that marten cached eggs during spring for later consumption, the effect of baiting cannot be separated out. Eggs were placed throughout the entire study area continuously throughout the year, with some periods of very intensive baiting on the run up to trapping particularly during July and August 2006, and from December 2006 to April 2007. The lull in trapping during autumn, and consequent absence of bait eggs, happens to coincide with the lowest level of egg consumption during the year.

5.3.5.3 Invertebrates

The importance of invertebrates varied between diet indices, forming 16 % of total occurrences, but accounting for just 4 % of total EWI. Coleopteran beetles were the most frequently consumed invertebrates, accounting for 62 % of invertebrate occurrences, half of which belonged to the *Carabidae* (ground beetles), 21 % to *Curculionidae* (weevils), and 18 % to *Scarabidae* (dor beetles). *Silphidae* (carrion beetles), *Chrysomelidae* (leaf beetles), *Staphylinidae* (rove beetles) and *Elateridae* (click beetles) occurred in smaller numbers. Seasonal consumption patterns followed the beetles availability in the environment (Fig. 5.5 c.), with lowest proportion of beetles occurring in the diet during winter ($\chi^2 = 40.95$, *df 1*, $P < 0.001$), and the highest occurred during summer ($\chi^2 = 7.93$, *df 1*, $P < 0.01$). Hymenoptera formed 23 % of invertebrate occurrences, split evenly between *Bombus* sp. (12 %) and *Vespa* sp. (11 %), 75 % of which occurred during summer as would be expected. An unidentified *Scarabaeiform* larvae formed 7 % of invertebrate occurrences, half of which occurred during autumn. Larvae were frequently found in scats also containing fragments of wood and vegetation suggesting the larvae were from a species that utilises deadwood, and had been deliberately excavated by foraging marten. Pollen accounted for 9 % of invertebrate occurrences, the highest proportions of which occurred in winter ($\chi^2 = 148.37$, *df 1*, $P < 0.001$) and spring ($\chi^2 = 32.18$, *df 1*, $P < 0.001$), suggesting that marten raided bees nests opportunistically at a time when other prey was scarce, and when high calorie food sources most crucial.

5.3.5.4 Large Mammals

Large mammals accounted for just 3 % of occurrences throughout the year. Their contribution increased substantially based upon EWI however, forming 10-30 % of ingested food ($\bar{x} = 18 + 8$ %). The proportion of large mammal occurrences in the diet was highest during spring ($\chi^2 = 43.34$, *df 1*, $P < 0.001$), with peak consumption in April (Fig. 5.5 d.). It was generally possible to identify large mammal hair where present to species level based on microscopic hair characteristics. The bulk of the large mammal group (69 % of large mammal occurrences) was however formed by unidentified carrion, which generally had no hair present but was characterised by its "tar like" consistency (Balharry 1993a). The highest proportion of carrion occurred in spring ($\chi^2 = 5.23, df\ 1, P < 0.05$). The remaining large mammal occurrences came from deer (22 %), all of which were found in winter and spring; sheep (6 %), half of which were found in winter-spring, half in summer-autumn; and rabbits (3 %), all of which came from young rabbits in spring. Although red squirrels were present at the study site, albeit in low densities, no red squirrel remains were recorded in any of the 2449 scats analysed.

5.3.5.5 Other

The 'other' food item group consisted of annurans, reptiles, fungi and miscellaneous items, which combined accounted for 0-4% of occurrences in each season ($\bar{x} = 2 \pm 2\%$). Reptiles accounted for 29 % of the occurrences in this group, of which 94% occurred during summer (Fig. 5.5 e.). Most reptiles found were common lizard *Lacerta vivipara,* except for one occurrence of slow worm *Anguis fragilis*. No attempt was made to identify anuran remains, however common toad *Bufo bufo* and common frog *Rana temporaria* were abundant in the study area

(*Personal observation*). It was not possible to identify fungi species, though the species typical of northern pine forests were seasonally abundant, and correspondingly, all fungi occurrences came from autumn and winter.

5.3.5.6 Small Mammals

Small mammals ranked as the second most common food group overall, forming 29 % of FO. When based upon EWI however, they became the most important food group, accounting for 38 % of the diet. Between December and May small mammals consistently accounted for over 40 % of FO, with peak consumption occurring in January and February, when small mammals accounted for 60% of food occurrences (Fig. 5.5 f.). The lowest consumption occurred during autumn, although they still accounted for 11-17 % of FO.

Of the species of small mammal identified in the diet, *Microtus* were by far the most abundant, accounting for 69-91 % of identified species each month ($\bar{x} = 80 \pm 8\%$). Once adjusted to include the correct ratio of unidentified small mammals, then *Microtus* alone account for 42 % of the winter diet and 36 % of the spring diet. Other small mammal species appeared in greatly reduced numbers compared to *Microtus*, even after being similarly adjusted to include unidentified small mammals. The combined occurrences of *Clethrionomys, Apodemus* and *Sorex* sp. only accounted for 1-10 % of FO in each season ($\bar{x} = 5 \pm 4$ %).

Seasonal trends were evident in the species composition of small mammals in the diet, *Microtus* formed a greater proportion of consumed small mammals in autumn than during the rest of the year ($\chi^2 = 9.71$, *df* 1, $P < 0.01$). *Clethrionomys* were found more during winter ($\chi^2 = 15.63$, *df* 1, $P < 0.001$), *Apodemus* occurred more during spring ($\chi^2 = 11.50$, *df* 1, $P < 0.001$), and *Sorex* spp. were found in the highest proportions in summer ($\chi^2 = 29.35$, *df* 1, $P < 0.01$). Dietary preferences for different small mammal species can only be assessed alongside information on their availability, so in the following section the results of the relative abundance of small mammals in the diet are compared with their availability in the environment.

5.3.6 Small Mammal Availability

Although seasonal trends were evident in the diet, it was not possible to assess changes in seasonal relative abundance in the environment, and small mammal trapping was only conducted during spring. Total trapping effort involved 2625 trap nights (TN), but the number of individuals captured per 100 TN totalled across the three replicates is used for comparison of relative densities (Table 5.5). In terms of rodent abundance, closed canopy forest ranked as the most productive habitat, however only two species were trapped in this type of habitat (*Clethrionomys*s and *Apodemus*), which resulted in lower ranking for species diversity and evenness for this habitat. The most diverse habitat was mature forest ($H' = 0.91$), which supported all species, except *Microtus*s, in relatively high numbers.

Regenerating forest was the second most diverse habitat, which shared a similar small mammal species composition as mature forest. The highest ranking habitat for species diversity evenness were linear features, such as rides, road verges and riparian strips. Linear features were the only habitat in which all species were trapped, albeit in relatively low numbers compared with the trapping rates of those species in other habitats. There were no small mammal captures in rough grassland, however this was likely due to the heavy grazing in these areas at the time of trapping. These grasslands had little cover and an average sward height of 20 cm (± 4 cm), which may not have provided sufficient suitable cover for the *Microtus* that would normally be expected to associate with this habitat.

Table 5.5 Productivity of 7 habitat types as indicated by diversity indices and the relative abundance of small mammal species (total number of captures per 100 trap nights pooled from three successive replicates). *M* = *Microtus*, C = *Clethrionomys*, *A* = *Apodemus*, *S* = *Sorex* spp. Total trapping effort = 2625 trap nights. The Shannon-Weaver Diversity Index (H') and Evenness Index (J') of each habitat type are also given ranked (Krebs 1989).

Habitat	M	C	A	S	Captures / 100 TN	H'	Diversity Rank	J'	Evenness Rank
Forest									
Closed	-	0.91	0.46	-	1.37	0.63	4	0.46	5
Mature	-	0.46	0.38	0.08	0.91	0.91	1	0.69	2
Regen	-	0.50	0.38	0.08	0.95	0.91	2	0.66	3
Open									
Moor	-	0.11	-	0.04	0.15	0.56	5	0.41	6
Grass	0.46	-	-	0.30	0.76	0.67	3	0.49	4
Arable	-	-	-	-	-	-	7	-	7
Linear									
Verge / ride	0.11	0.04	0.04	0.23	0.42	0.12	6	0.81	1
Total	**0.57**	**2.02**	**1.26**	**0.72**	**4.57**				

Clethrionomys and *Apodemus* were the most numerous species caught in trapping, with the highest densities of both species occurring in closed canopy forest. Their occurrence in five of the seven habitats assessed is reflected by their broad habitat niche values, which indicated that they were habitat generalists (Table 5.6). Though less commonly captured, *Sorex* spp. had the highest niche breadth (*Ba = 0.55*) and were found in six of the seven habitat types demonstrating the generalist nature of this species. Shrews were most frequently caught in open grassland and on linear features, but were still present in forest habitats and moorland. In contrast, *Microtus*s had the lowest niche breadths indicating the highest level of habitat specialisation (*Ba = 0.25*). *Microtus*s did not occur in any forest habitats and were restricted to just two habitats: open grassland and linear features. Within the grass habitat however, *Microtus*s were equally as abundant as *Clethrionomys*s were in mature forest, and wood mice were in closed forest, with each species achieving capture rates of 0.46 / 100TN in these respective habitats. Across all habitats however, *Microtus*s were caught least frequently.

Table 5.6 Proportion of captures of small mammal species in each habitat. Standardised habitat niche breadth (*Ba*) of small mammal species calculated using Levin's formula (Krebs 1989). Higher values of *Ba* indicate wider niche breadth (habitat generalists); lower values indicate narrow niche breadth (habitat specialists).

	Forest			*Open*			*Linear*	
Species	**Mature**	**Closed**	**Regen.**	**Moor**	**Grass**	**Rough**	**Verge**	**Ba**
M	-	-	-	-	0.80	-	0.20	0.25
C	0.23	0.46	0.25	0.06	-	-	0.02	0.50
A	0.30	0.36	0.30	-	-	-	0.03	0.53
S	0.11	-	0.11	0.05	0.42	-	0.32	0.55

The relative availability of each small mammal species in the average female home range was calculated (Table 5.7). *Clethrionomys*s were the most numerous species, accounting for 39 % of small mammals in the environment, yet they constituted a small fraction of the marten's diet, forming just 7 % of small mammal occurrences (even after adjusting for inclusion of unidentified small mammals). *Apodemus* were also relatively abundant in the environment (28 % of small mammals), yet accounted for just 5 % of small mammals in the diet. Conversely, whilst *Microtus*s accounted for just 16 % of small mammals in the environment, they comprised 83 % of small mammal occurrences in the diet. Shrews occurred in similar numbers to *Microtus*s in the environment (17 %), yet only accounted for 5% of occurrences in the diet. A comparison of the occurrence of each species in the environment and in the diet was highly significant ($\chi^2 = 98.79$, *df 3*, $P < 0.001$). A selection index (Manly *et al.* 1993) was calculated to provide a measure of relative preference for each small mammal species (Table 5.8), and demonstrated a clear selective preference for *Microtus* relative to other species, whereas all other species appear to be avoided

Table 5.7 The availability of small mammal species within female home ranges (HR). See Chapter 3 for details of HR estimation. The top of the table shows the estimated densities (individuals / 100 TN / ha) of *Microtus* (*M*), *Clethrionomys* (C), *Apodemus* (A), and *Sorex* spp. (*S*) in forested, open and linear habitats. These values were then used to calculate the average number of individuals occurring within the area of each habitat found per HR. Habitats relate to those used in Chapter 3: *closed* = pole and thicket stage forest, *mature* = mature stage forest, *regenerating* = scrub habitat (inc. establishing forest, clear-fell, and scattered shrubs and trees), *moor* = heath, *grass* = grass and scrub (scrub included as ground cover in this habitat was often grass), *linear* = linear feature.

Habitat		M	C	A	S
Forest	**Closed**	-	18.64	9.08	-
	Mature	-	9.32	7.57	1.8
	Regenerating	-	10.1	7.57	1.8
Open	**Moor**	-	2.33	-	0.9
	Grass	10.8	-	-	7.2
Linear	**Linear**	4.35	-	1.11	8.7
No. per HR ($\bar{X} \pm$ SD)		388 ± 273	936 ± 710	667 ± 559	422 ± 340
Ratio of spp. in HRs		1.0	2.4	1.7	1.1
Ratio of spp. in diet		12.2	1.0	0.7	0.7

Table 5.8 Selection indices for small mammal species, values greater than 1.0 indicate preference, values less than 1.0 indicate avoidance (Krebs 1989).

Species	Selection Index (W)
Microtus agrestis	5.2
Sorex spp.	0.3
Apodemus sylvaticus	0.2
Clethrionomys glareolus	0.2

5.3.7 Comparison of diet with other studies

The results presented here represent the largest sample size of scats in a dietary study of British pine marten, the majority of which (86 %) have been confirmed as being pine marten in origin using genetic tests. The 2449 scats were collected from an area where 18 individual marten were trapped (Chapter 3), and a further two individuals were found road-killed, giving a known minimum population size of 20 contributing individuals. In addition, the relative abundance of small mammals was assessed in different habitats throughout the study area, and related to the availability of those habitats within marten home ranges to allow investigation of underlying prey preferences by foraging marten. It is therefore appropriate to compare the results from this chapter to answer the questions posed in the introduction.

5.3.7.1 Comparison with Scottish studies

Table 5.9 shows the 95% Bonferroni confidence intervals of the relative composition of the diet found in the present study and three other Scottish studies with large sample sizes of scats (i.e > 500 scats sampled). Comparison of confidence limits revealed that there were several distinct similarities between diets, including little variation in the consumption of birds, large mammals or herptiles between the four study sites. Birds consistently formed approximately 10-20% of the diet, the bulk of which were formed by passerine bird species (89%: Balharry 1993, 40%: Halliwell 1997) with lesser amounts of columbiforms (8% Balharry 1993, 17% Halliwell 1997), galliformes (1.5% Balharry 1993, 8% Halliwell) and eggs (7.5% Balharry 1993, 12% Halliwell 1997). Whilst bird species were not identified in the present study (but grouped according to size of birds based on feather quills), a similar pattern was observed with small birds (i.e. passerines) forming the builk of birds consumed (83%), and large birds (i.e. columbiforms and galliformes) and eggs forming a lesser part (8% and 10% respectively). Large mammals generally formed less than 10% of the diet (Table 5.9), the majority of which was formed by carrion from deer and sheep (91% Balharry 1993, 62% Halliwell, 1997, 97% present study). Lagomorphs were consumed in small amounts in Balharry's study (9%) and the present study (3%), though were consumed more frequently in Novar (33%, Halliwell 1997). Squirrels were not present in the diet found either in present study or that of Balharry (1993), though they formed a small proportion of the large mammal group consumed in Novar (5%, Halliwell 1997). Herptiles generally formed less than 10% of the diet (Table 5.9). Small mammals were generally the main component of the diet. In three of the four sites small mammals were consumed in similar proportions of around 30%, only in Kinlochewe did they contribute significantly more to the diet ($\chi^2 = 16.73$, *df 1*, $P < 0.001$). The consumption of invertebrates and berries seemed to display the greatest amounts of variability between sites; whilst invertebrates were consumed in similar proportions in Kinlochewe as Morangie, they formed a significantly greater part of the diet in Strathglass and Novar (χ^2 *= 11.71, df 1, P < 0.001*). The consumption of berries was similar in Kinlochewe, Strathglass and Novar but were consumed in significantly greater proportion in Morangie (χ^2 *= 36.91, df 1, P < 0.001*).

Table 5.9 Comparison of year-round pine marten diet composition using 95% Bonferroni confidence intervals (with α = 0.05, k = 6) based on the percent frequency of occurrence in scats* from four studies in Scotland. Sample size of number of scats analysed (n) is shown. Sources: [1.] Balharry (1993a.), [2.] Halliwell (1997), [3.] Present study. Strathglass is located at 57˚N, 5˚W, Morangie and Novar are at 58˚N, 4˚W and Kinlochewe is located at 58˚N, 5˚W.

Food group	Kinlochewe[1] n = 723	Strathglass[1] n = 581	Novar[2] n = 1938	Morangie[3] n = 2449	$\bar{X}$	SD
Small mammal	50.5 - 58.1	25.2 - 32.7	29.3 - 33.2	28.7 - 32.4	35.2	12.8
Larger mammal	4.9 - 8.7	7.1 - 11.9	8 - 10.4	2.3 - 3.7	6.8	2.8
Bird	10.6 - 15.8	10.7 - 16.3	18.3 - 21.6	16.6 - 19.8	15.5	2.6
Invertebrate	10.5 - 15.7	32.6 - 40.5	25.6 - 29.3	15.3 - 18.4	22.6	10.3
Berry†	3.4 - 6.7	4.4 - 8.3	10 - 12.6	28.9 - 32.6	13.0	12.0
Herptile	5.6 - 9.6	3.4 - 7.1	0.5 - 1.3	0.4 - 1	3.6	3.4

† Note that berries have been separated from the plant material group for comparison between studies.

* Data on percentage frequency of occurrence of items (n = 4006) was used for Novar as no information was provided regarding the total number of occurrences in scats in Halliwell (1997).

5.3.7.2 Comparison with European studies

The overall diet found in Morangie shared the same patterns as Zalewski (2004) described when reviewing pine marten diet across Europe. Based on frequency of occurrence, small mammals were the most important food, followed by plant material and birds, with larger mammals becoming more important during winter, and insects during summer. Zalewski (2004) graphically modelled the geographic variation in pine marten winter diets across Europe based on latitudinal trends in the proportions of major food groups (Fig. 5.6). Using the regression equations generated by this model, the winter diet composition for Morangie, at a latitude of 57°N, was predicted and compared to the winter diet found in the present study. The the ratio of major food groups in the diet predicted from Zalewski's model was found to closely match those found ($\chi^2 = 5.74$, *df 4*, $P > 0.05$).

Despite fitting Zalewski's model, the winter diet observed in Morangie differed from the majority of studies (7 / 8) at similar latitudes to Morangie: 56 °N to 58°N ($\chi^2 = 12.62\text{-}34.62$, *df 4*, $P < 0.05$: Sidorovich 1997, Yurgenson 1951, Aspisov 1973, Morozov 1976, Pleshank 1976, Chashchin 1956, Bakeev 1966: all cited in Zalewski 2004). The only winter diet from a similar latitude that did not differ was that in Grakov (1981: cited in Zalewski 2004), from the Perm region of Russia ($\chi^2 = 1.19$, *df 5*). The Morangie winter diet differed from these studies by having a lower proportion of large mammal prey, and a greater proportion of fruit. The Morangie winter diet showed greater similarity with study sites at more southerly latitudes, particularly 54 °N to 55 °N, where diets contained fewer large mammals, but more birds and fruit. When the Morangie winter diet was compared with the diets from this region, there was no significant difference in composition for four of the six study sites reviewed ($\chi^2 = 4.63\text{-}6.00$, *df 4*: Serzhanin 1973, Aspisov 1973 two study sites, Maldzhiunaite 1959: all cited in Zalewski 2004).

Zalewski (2004) did not find a strong latitudinal association for the summer diets he reviewed, and there did not appear to be any latitudinal relationship between the summer diet in the present study and those across Europe. The Morangie summer diet was similar to that found as far south as the Balearic island of Menorca (40°N Clevenger 1993: $\chi^2 = 2.67$, *df 4*), and as far north as northern Russia (62°N Yurgenson 1951: $\chi^2 = 8.07$, *df 4:* and 64°N Parovschikov 1961, cited in Zalewski 2004: $\chi^2 = 6.86$, *df 4*). Each of these diets were characterised by a high diet breadth ($Ba = 0.76 - 0.91$) indicating a broad generalised diet where all five food groups were taken in similar proportions, as was found in Morangie ($Ba = 0.70$).

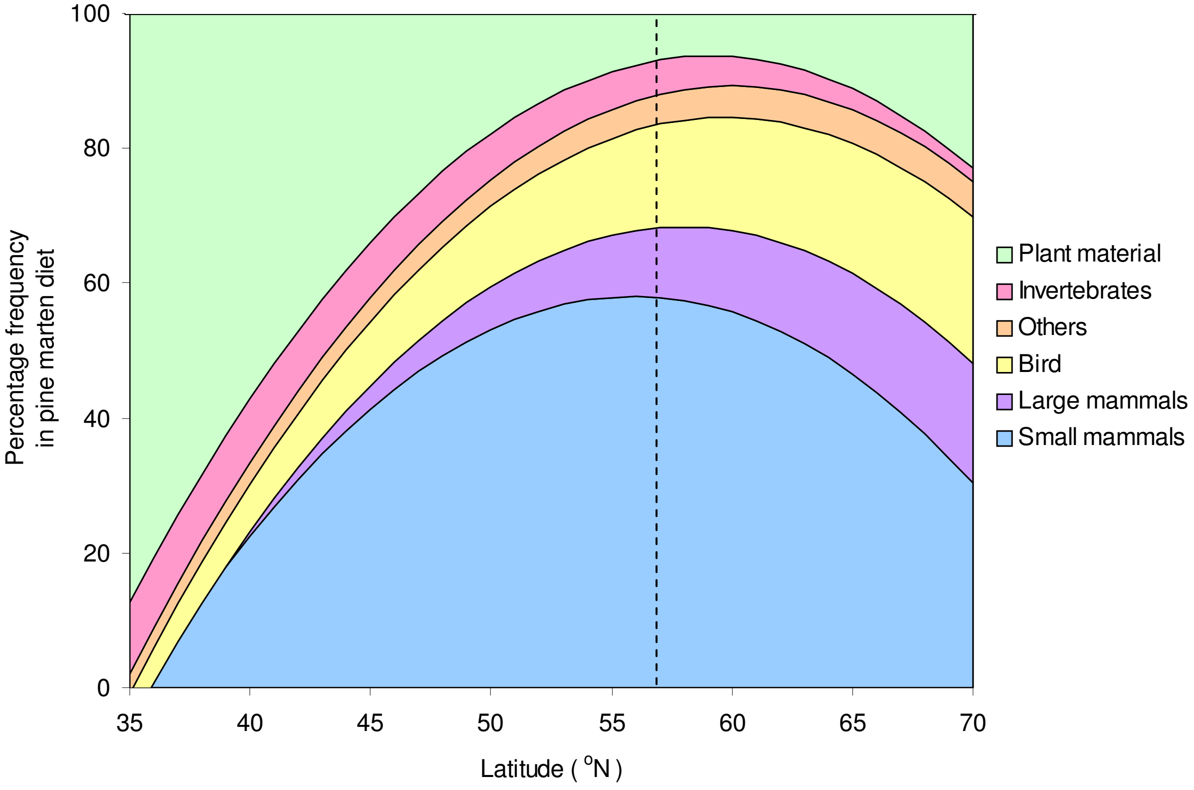


Fig. 5.6 Generalised model of latitudinal variation in percent relative frequency of occurrence of food groups in the winter diets of pine marten in Europe, based on regressions calculated from empirical data from 45 localities (after Zalewski, 2004). The predicted diet for Morangie at 57°N is indicated with a dashed line, and comprises: 58 % small mammals, 10 % larger mammals, 15 % birds, 5 % invertebrates, 9 % plant materials, 4 % other. The actual winter diet observed at this latitude was: 56 % small mammals, 3 % larger mammals, 17 % birds, 6 % invertebrates, 15 % plant materials, 2 % other.

5.4 Discussion

5.4.1 Principal Prey

Small mammals were the most important food group in the year-round marten diet; not just in terms of the frequency with which they were consumed (29 % of food occurrences), but in the amount of ingested biomass they formed annually (38% of diet). Of the small mammals, *Microtus* as a single species accounted for 29% of the biomass ingested by martens within a year, making it clearly the most important species in the pine marten diet. Plant material was the most frequently consumed food group (32 % of occurrences), predominantly from rowan, blueberry and cherry. Whilst the importance of plant material was no doubt over-estimated when represented by a frequency-based dietary measure, which tend to inflate the importance of small items (Reynolds & Aebischer 1991), plant material remained of importance when measured using ingested biomass (18 % of diet). Birds were the second largest contributor to annual ingested biomass (23 % of diet), the majority of which came from small birds. However, the high proportion of indigestible remains left by bird feathers may have caused this to be a slight over-estimate (Zielinski 1986).

5.4.2 Seasonal Variation in Diet

In accordance with the conclusions of marten dietary reviews (Clevenger 1994, de Marini & Marsseti 1995, Zalewski 2004), the diet in the present study showed marked seasonal variance, the patterns of which are explainable by food availability. Berries form the bulk of the diet from late summer through to winter (40-80 % of food occurrences); small mammals become the dominant food group in the diet from winter and into spring (40-60 % of occurrences) when they are augmented by birds, the consumption of which increases through into early summer (15-35 % of occurrences). Other items such as invertebrates, herptiles and large mammals are taken seasonally, but form a lesser component at the diet.

5.4.3 Comparison of Diet with Scottish Studies

In terms of the overall diet, the proportions of two principal food groups differed little between this study and the two other Scottish studies; small mammals (predominately *Microtus*) generally formed a third of the diet, and birds (predominately small birds) generally formed a fifth. The main differences between Scottish sites were between the consumption of fruit and invertebrates. The importance of fruits *Prunus* spp., *Vaccinium myrtillus*, and *Rubus* spp. has been repeatedly noted in the summer marten diet in Europe (Goszczynski 1976, Marchesi & Mermod 1989, Russell & Storch 2004), however the Morangie diet particularly stands out in Britain as fruit was equally as important as small mammals in the year-round diet, and was consumed three times as much as it was elsewhere in Scotland.

Temporal variation in fruit crops is unlikely to explain the high consumption of berries in the year of this study (2006) given that the results of a concurrent multi-annual diet study (Chapter 6) indicate that the highest proportion of fruit in the diet occurred in 2007. The high prevalence of fruit in the Morangie diet may instead be the result of the author knowing that scats would be genetically identified, which meant that scats of dubious origin were less likely to be discarded. This notion is supported as the scats collected in 2007 of the multi-annual study were also collected by the author. Of the scats collected from Morangie in the present chapter, 25 % contained berries but no other food group. Based on visual identification alone, it is very difficult to classify whether pine marten or other carnivores, particularly fox, produced such scats as all that often remains is a pile of berry skins or pits, with little distinguishing matrix holding them together, particularly after heavy rain. The uncertainty in identifying these scats visually meant that every scat found containing nothing but berries in the present study was automatically genetically tested for species of origin, and only those identified as being from pine marten were included in the results of this study. The certainty that genetic testing provided here may have meant that scats were included in this study which may have ordinarily been over-looked in other studies. Rather than inferring that marten in Morangie are consuming more fruit than found elsewhere, this therefore highlights that molecular scatology allows previously under-estimated foraging behaviours to be better detected.

5.4.4 Comparison with Continental European Diet

Put into context with studies from mainland Europe, the results presented here suggest that the winter diet of Scottish pine marten is more similar to those found at slightly more southerly than equal or northerly latitudes. The marten here display less reliance on large mammalian and large avian prey through the winter, and greater reliance on fruits, small mammals and small birds. This is likely the result of the UK's maritime climate with its short, mild winters. Continental winters are characterised by extended periods of snow-cover during which fruits and small mammals are less available to marten, forcing them to switch to alternative prey such as squirrels (i.e. Storch *et al.* 1990, Hoglund 1960, de Jounge 1981). Although the density of red squirrels in Morangie appeared to be relatively low (*Personal observation*), red squirrels and pine marten have co-existed in the forest since at least the 1950s (Lockie 1964, Halliwell 1997). However, in c. 2500 scats sampled, no squirrel remains were encountered even after microscopic examination of large mammal guard hairs. Predation of squirrels by marten has previously been observed in the UK (Halliwell 1997, Velander 1983), yet on each occasion, squirrels have accounted for just a small proportion of the diet (< 1 %). Balharry (1993a) demonstrated that the remains of a single squirrel fed to a captive pine marten was found to occur in a total of 12 scats produced by that marten, and it is unclear whether multiple scats containing squirrel remains in these two studies were the result of one squirrel carcass being consumed or several. Without information regarding the spatiotemporal distribution of scats containing squirrel remains, it remains unclear whether the occurrences of squirrel remains found by Halliwell (1997) in each season (*winter n = 5, spring n = 4, summer n = 3, autumn n = 3*) did not each come from one animal, meaning that a minimum of four squirrels were consumed. Incidentally, during the same study, the remains of four squirrels were found in a goshawk nest. Poplar public opinion, particularly among the hunting community, appears to regard the British pine marten as an ardent squirrel predator (e.g. The Observer 2008). Such apparent misnomers are damaging to the pine marten's reputation as a predator in need of conservation management, and dangerous given the historical persecution of the species. Such beliefs are likely the result of inferences being drawn from the results of Swedish studies (e.g. Storch *et al.* 1990, Hoglund 1960, de Jounge 1981). These studies were conducted at more northerly and climatically extreme latitudes than are present in the UK. The environmental and ecological differences between these two geographic regions mean that their resident marten are subject to quite different life requirements. It is worth noting that each of the Swedish studies cited above was based on very small sample sizes of scats (< 100). This last point is important as it is crucial to ensure that samples sizes used in dietary studies are large enough to be representative of many individuals before making generalisations about diet. Whilst working in the same area of Sweden as de Jounge (1981), Helldin (1998) analysed the stomach contents of almost 500 marten carcasses and found greater consumption of microtines and berries, and fewer incidences of squirrels than were recorded by de Jounge (1981). Caution should therefore be used if making generalisations about marten diet between geographic regions, and particular attention should be paid to the samples sizes which studies base their results on.

The increased consumption of small birds observed in Morangie during spring and early summer was likely to be related to the increased seasonal availability of migrant passerines and fledging chicks. During winter, consumption of large birds increased which coincided with the departure, and therefore reduced availability, of smaller summer migrants. However, whilst marten may take more large resident birds, such as *Collumbiformes* and *Galliformes* in winter than during the rest of the year, small passerines still form the majority of winter bird occurrences (75 %, compared to just 16% of occurrences from large birds). Zalewski (2004) found a positive association between latitude and the occurrence of large birds in the diet, which can be largely attributed to the reduced availability of migrant passerines as they leave for more southerly latitudes for the winter. The high proportion of small birds in the diet during winter may therefore be due to the milder UK climate allowing greater numbers of passerines to reside here permanently. Halliwell (1997) found that resident passerines such as wren *Trodlodytes troglodytes*, thrushes *Turdus* spp. and finches *Fringillidae* spp. were the most commonly consumed bird species in winter. Passerines accounted for half of birds identified in winter, with a further third formed by wood pigeon *Columba palumbus*. These findings were in accordance with Jedrzejewski *et al.* (1993) who noted that there appeared to be a trend of selective predation by marten on tits, thrushes, wrens and woodpeckers in the deciduous woodlands of Poland. Of the large forest birds that are increasingly consumed in northern Europe (Jedrzejewski *et al.* 1993, Helldin 1998, Zalewski, 2004), hazel hen *Tetrastes bonasia* and willow grouse *Lagopus lagopus* are absent from Scottish forests. Whilst capercaillie and black grouse *Tetrao tetrix* are present, albeit in small numbers, introduced game birds such as red-legged partridge *Alectoris rufa* and common pheasant *Phasianus colchicus* are often abundant due to the high level of game-keeping. Halliwell (1997) found that of the game birds occurring in diet, the majority was from common pheasant, duck *Anas platyrhynchos*, and woodcock *Scolopax rusticola*, with only one record of an unidentified game species.

5.4.5 Small Mammal Species Preferences

The dominance of *Microtus* in the diet of British marten is unmistakable, and comparisons with relative species abundance measures clearly demonstrates that marten display a strong selective preference for this species. Some studies in North America have also shown that *Microtus* voles are taken in excess of their availability, where they are caught in some herbaceous meadow openings (Buskirk & Powell 1994; Martin 1994), and riparian areas (Zielinski *et al.* 1983). Likewise some studies in Europe have found greater consumption of *Microtus* than *Clethrionomys* (Parovscikov 1961, cited in Jedrzejewski *et al.* 1993, Morozov 1976). *Microtus* voles are generally considered more profitable than *Clethrionomys* due to their larger size and clumped distribution (Buskirk & MacDonald 1984, Hansson 1987). The relative abundance of small mammal species in this study demonstrated that although *Microtus*s are absent from forest habitats, they are locally abundant and "available" in high densities within their preferred habitat, demonstrating that marten are choosing to forage within such habitats (Chapters 3 and 4). It is interesting that the lowest contribution of small mammals to the diet occurred in late summer and autumn, when small mammal populations reach their seasonal peak (e.g. Hansson 1978). This coincided with a period of restricted dietary breadth, and it appears that despite the higher densities of small mammals in the environment, marten instead specialised on berries at this time. The increased consumption of *Clethrionomys*s and wood mice in winter and spring may have been the result of marten shifting their habitat selection towards more thermoneutral closed-canopy forest areas during the colder months (Chapter 3), where these species were found to be most abundant.

5.4.6 Conclusions

The Morangie diet was dominated by *Microtus*, and to a lesser extent, fruit and small birds: a diet more characteristic of those at more southerly latitudes (around 54°N) than from locations of similar latitude to the present study site (57°N). The most likely explanation for this is the mild and stable British climate, which creates less extreme conditions for foraging marten; small mammals, small birds and fruit are still available during winter, meaning the marten is not forced to prey switch on to larger mammals or birds. Caution should therefore be used when inferring that British marten will behave in similar ways to their counterparts in northern Fennoscandia, particularly from studies based on small sample sizes. British marten clearly have marked differences to most continental marten in terms of the rodent preference. Other differences should be expected given the unique ecological conditions faced by British marten, both in terms of differences in abiotic factors such as climate, and differences in biotic factors such as intra-guild competition or predation, and the historical extent of deforestation and habitat fragmentation. In Chapter 7, the possible influences that these factors have had on the ecology of martens in Britain will be discussed further.

Chapter 6

Annual diet of pine marten

6.1 Introduction

Microtine population cycles are a well-documented phenomenon in northern Europe (Hansson & Henttonen 1985, Lambin *et al.* 2000; Hanski *et al.* 2001, Tkadlec & Stenseth 2001). These populations exhibit pronounced 3 to 4 year cycles in density to which many predators have been shown to display both functional and numerical responses (Lindstrom 1989, Korpimaki & Norrdahl 1991, Jedrzejewski & Jedrzejewski 1992, Petty 1992; 1999, Leckie *et al.* 1998, O'Mahony *et al.* 1999). Long-term studies of marten diet have demonstrated a distinct functional response to fluctuations in microtine numbers, with a positive relationship between microtine abundance in the environment and their occurrence in the diet (Pulliainen 1981, Helldin & Lindstrom 1993; Jedrzejewski *et al.* 1993; Pulliainen & Ollinmaki 1996, Helldin 1998). As generalists, marten switch to alternative prey when densities of their principal prey decline (Pulliainen & Ollinmaki 1996; Helldin 1998; 2000), although alternative species vary geographically (Zalewski 2004), and are not always taken consistently (Helldin 1998).

The marten's dietary response to fluctuating microtine numbers has been shown to be more pronounced for *Clethrionomys* voles than for *Microtus* voles (Jedrzejewski *et al.* 1993, Pulliainen & Ollinmaki 1996, Helldin 1998). Indeed, throughout temperate and boreal forests, *Clethrionomys* voles are the most prevalent small mammal species in the diet, with marten displaying an apparent preference for them over *Microtus* voles (Zalewski 2004). This however, is in stark contrast to the findings from British studies, in which *Microtus* voles are the predominant small mammals in the marten diet (Lockie 1961, Velander 1983, Balharry 1993a., Gurnell *et al.* 1994, Halliwell 1997, Putman 2000, Coope 2007). Although the diet of British pine marten are quite well known, there is scant information about their response to changes in small mammal abundance, although evidence suggests that *Microtus* consumption is lower in areas with lower densities (Balharry 1993a., Bright & Smithson 1997). Alternative foods taken in areas of low *Microtus* density are predominantly invertebrates (Balharry 1993a., Bright & Smithson 1997), but also passerine birds (Bright & Smithson 1997). Long-term studies of sufficient duration to assess both extremes of the vole population cycle are lacking. Of particular concern in Great Britain is the alternative prey species marten will switch to if they are affected by low vole densities. Alternative species found elsewhere in northern Europe include squirrels, hares, large birds and eggs (Pulliainen & Ollinmaki 1996; Helldin 1998; 2000), prompting growing anxiety that British marten may predate red squirrel, capercaillie or other species of conservation concern.

In this chapter I present multiannual data on the spring and summer diet of pine marten in north-east Scotland, to explore in more detail the relationship between British marten, *Microtu*s and alternative prey. Specifically, I will focus on the relationship between *Microtus* abundance in the environment and their occurrence in the marten diet as evidenced from remains found in scats collected over five successive years. In the absence of long-term small mammal trapping data for the study area, records of tawny owl (*Strix aluco*) productivity (clutch size) will instead be used as an index of vole density in spring (Southern 1970, Petty 1992; 1999, Solonen 2002; 2005). I will evaluate the hypothesis that Scottish marten demonstrate a dietary response to *Microtus* numbers by testing predictions that: i. Field vole populations under-go periodic cyclicity of high and low densities, ii. There is a positive association between the *Microtus* abundance and consumption, iii. Pine marten diet niche breadth is negatively associated with *Microtus* density, and therefore *Microtus* consumption, iv. Food resources that display a negative association with *Microtus* consumption, and therefore a positive association with diet niche breadth, can be considered as alternative prey.

6.2 Methods

The methods used in this chapter followed all aspects of those set out in Chapter 5 except for scat collection. The scats used for analysis of inter-annual diet were collected as part of a continuing body of research and monitoring within the EU LIFE Project 'Urgent Conservation Management for the Scottish Capercaillie' (*R. Trout, unpublished data*). The objectives of this project are to investigate the effectiveness of predator control by monitoring indices of predator abundance (red fox, pine marten and crow) in sites with and without predator control. Seven forests were selected for monitoring, one of which (Wallace Hill) was a sub-section of Morangie forest (the study site used in Chapters 3 to 5) in which there is no predator control, and neighbouring Novar in which fox and crow populations are controlled; the protected status offered to pine marten means that they can not legally be controlled.

Scats were collected from each forest on a monthly basis between February and September each year. Within each forest, a 10 km transect was searched for fox and pine marten scats. Vehicle tracks were used rather than footpaths, and each route formed a circuit which passed through representative forested habitat that were also searched for capercaillie hens and chicks. The initial visit was made in February 2003 in which all scats were removed to allow subsequently deposited scats to be dated to month. Monthly scat collections were conducted for four years as part of the LIFE project, from 2003 to 2006, monthly scat collections were then continued after cessation of the LIFE project during 2007 by the author. Every scat found was bagged and then frozen until being defrosted for genetic and content analysis. The laboratory that conducted genetic identification of the scats used in Chapter 5 (*Forest Research, Roslin, Midlothian, Scotland, UK*) was also responsible for genetically determining the species of origin of all scats collected under this project using the same methods. Financial constraints meant that only scats collected from months April to August were genetically identified. This period was chosen as it is the most critical time for capercaillie, i.e. during and shortly after breeding. Only those scats identified as being pine marten in origin were included in scat content analysis. Scat contents were analysed as in Chapter 5, but results were represented in terms of one dietary measure: percent relative frequency of occurrence i.e. the total number of occurrences of each food item, divided by the total number of occurrences identified across all samples. An occurrence of a food item was defined as the presence of a prey species (or lowest identified taxon) within a scat, therefore a food item could be constituted by several similar small prey, or part of a large prey. Data from each month were pooled for each year.

Differences in the diet composition between sites were tested with a G-test contingency table for each year: the frequency of occurrence of the six food categories from one site was compared with the occurrences of food groups at the other site. Between-year comparisons of diet composition using a separate G-test contingency table for each year: the relative frequency of occurrence in each food category in one year was compared with the occurrences in all other years combined. Inter-annual variation in consumption of each food group was examined using G-test contingency tables: each group was tested separately against the frequency of occurrences of all other food items in each year. The diet niche breadth index (B) for each month using frequency of occurrences of the six food categories, was calculated with Levin's formula:

$$B = 1 / \Sigma p^2_i$$

where B is the diet breadth, and p is the proportion of the diet formed by species i. This index was then standardised (Ba) using the formula:

$$Ba = B / (n - 1)$$

where n is the number of food types. Standardised values range between 0 and 1, with higher values indicating a wider niche breadth i.e. dietary generalists, and lower values indicating a narrow niche breadth i.e. dietary specialists (Krebs 1989). Relationships between annual diet breadth and percent frequency of occurrence each year were tested for using Spearman's rho correlations.

Direct data on prey abundance from small mammal trapping were not available for the study period, so tawny owl productivity data from the local area were used as an indirect index of *Microtus* density (*B. Swann, unpublished data*). Two data sets were available: a short-term data set covering the study period from 2003 to 2007, and collected within c. 10km of the study sites in which the raw count data from breeding surveys were known to the author, and a longer-term data set spanning 13 years (1995 to 2007), which were collected from a wider geographic that included parts of Sutherland and a greater extent of Easter-

Ross. Detailed information regarding the locations and exact numbers of nests surveyed for the long-term data set were not available to the author, nor were data pertaining to the variance of the means generated by these data. Synchrony of avian predator and vole activity has been recorded previously in kestrels, hen harriers *Circus cyaneus*, buzzards and short-eared owls *Asio flammeus* (Rijnsdorp *et al*. 1981, Raptor Group 1982, Reynolds & Gorman 1999), and tawny owl clutch size shows a strong positive association with spring *Microtus* density (Southern 1970, Petty 1992; 1999, Solonen 2002; 2005), therefore clutch size was assumed to be a good index of *Microtus* abundance.

6.2.1 Study areas

Wallace Hill (57.7°N, 4.2°W: Fig. 6.1) is a sub-section of the greater area referred to throughout the rest of this thesis as 'Morangie forest', therefore the site description from the General Introduction still applies, particularly at the landscape level. The forested extent of Wallace Hill covers an area of 12km^2. The forest comprises large areas of early-to-mid successional coniferous plantations interspersed with areas of mature to old-growth Scots pine, which has been managed sympathetically of capercaillie conservation.

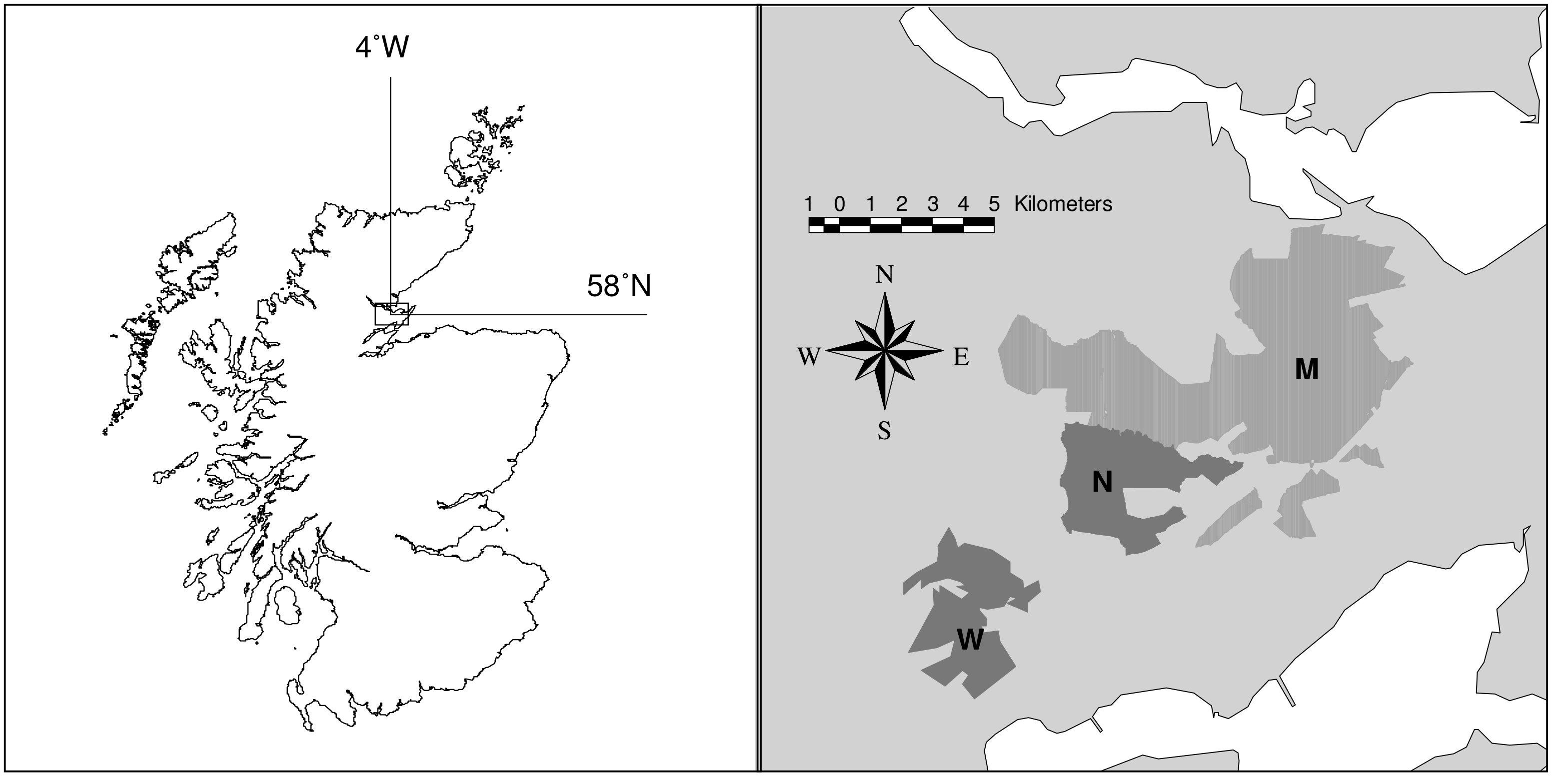


Figure 6.1 Outline of Scotland showing study site locations within Easter-Ross, Highland. Inlay shows the locations of the forested extents of Wallace Hill (*dark grey*: W) and Novar (*dark grey*: N) in relation to Morangie forest (*pale grey*: M). The distance from nearest edge to nearest edge between the two study sites is 4.1km.

The second study site, Novar (57.7°N, 4.3°W), is an estate located just a few kilometres south-west of Morangie: the distance from nearest edge to nearest edge is 4.1 km, and the centre to centre distance is 6.5km. The forested extent of Novar covers an area of 11 km^2, at an altitude of 30-350 m a.s.l. In terms of age and species composition, Novar has a similar forest composition to Morangie. The estate is primarily managed for timber extraction and hunting, with both productive conifer forest and the occasional stands of ancient Caledonian pine wood. The forest area is dominated by Scots pine, lodgepole pine, larch, sitka spruce and silver birch. In areas with older stands of pine, there is a thick under-story of blaeberry, heather and heaths. The surrounding areas are low level agricultural land and deer forest, deer hunting takes place throughout most of the year (Halliwell 1997),

6.3 Results

6.3.1 Inter-Annual Diet

During the spring and summer months of five consecutive years, 2003 to 2007, 426 scats were collected from two neighbouring study sites (*annual* $\bar{x} = 85 \pm 14$), and were confirmed as being pine marten in origin using genetic tests (*R. Trout, unpublished data*). The sample sizes of scats collected from each site in each year was too small to allow separate analyses of inter-annual diet variation in each site (Table 6.1), therefore dietary data from the Wallace Hill and Novar sites were combined for each year for analysis. To justify pooling data, the composition of the diet was compared between study sites in each year, though was not found to differ for years 2003 to 2005 ($\chi^2 = 1.32 - 12.06$, *df* 5, $P > 0.05$). The only difference in diet composition between sites occurred in 2006 ($\chi^2 = 26.24$, *df* 5, $P < 0.05$), when a greater proportion of the Novar diet was formed by plant material (40 % compared with only 4 % in Wallace Hill). However when the samples size of scats from sites were compared for that year, it became apparent that this result was likely the result of only 17 scats being contributed from Novar. It was therefore considered justified to pool data from the two sites for analysis. In 2007 scats were collected from Wallace Hill, but were not available from Novar, however it was assumed that the diet observed in Wallace Hill in 2007 would adequately represent the diet for that year.

The relative contribution of food groups to the diet over five years is shown in Figure 6.2. Between-year comparisons of diet composition revealed the relative frequencies of each food group remained consistent throughout years 2004 to 2006 ($\chi^2 = 2.11$ *to* 9.27, *df* 5, $P > 0.05$), but differed in 2003 ($\chi^2 = 13.29$, *df* 5, $P <$

Table 6.1 The total number of scats collected in each year from Wallace Hill (W) and Novar (N) during spring and summer months (April to August). The range of scat numbers collected per month are given for each year along with the mean number of scats collected each month.

Year	Range	Mean	No. Scats Wallace	No. Scats Novar	Total No. Scats
2003	9 - 30	19.0 ± 8.2	44	51	95
2004	4 - 37	14.6 ± 13.1	21	52	73
2005	12 - 24	15.0 ± 5.1	48	27	75
2006	8 - 29	15.8 ± 9.2	62	17	79
2007	13 - 29	20.8 ± 5.8	104	0	104

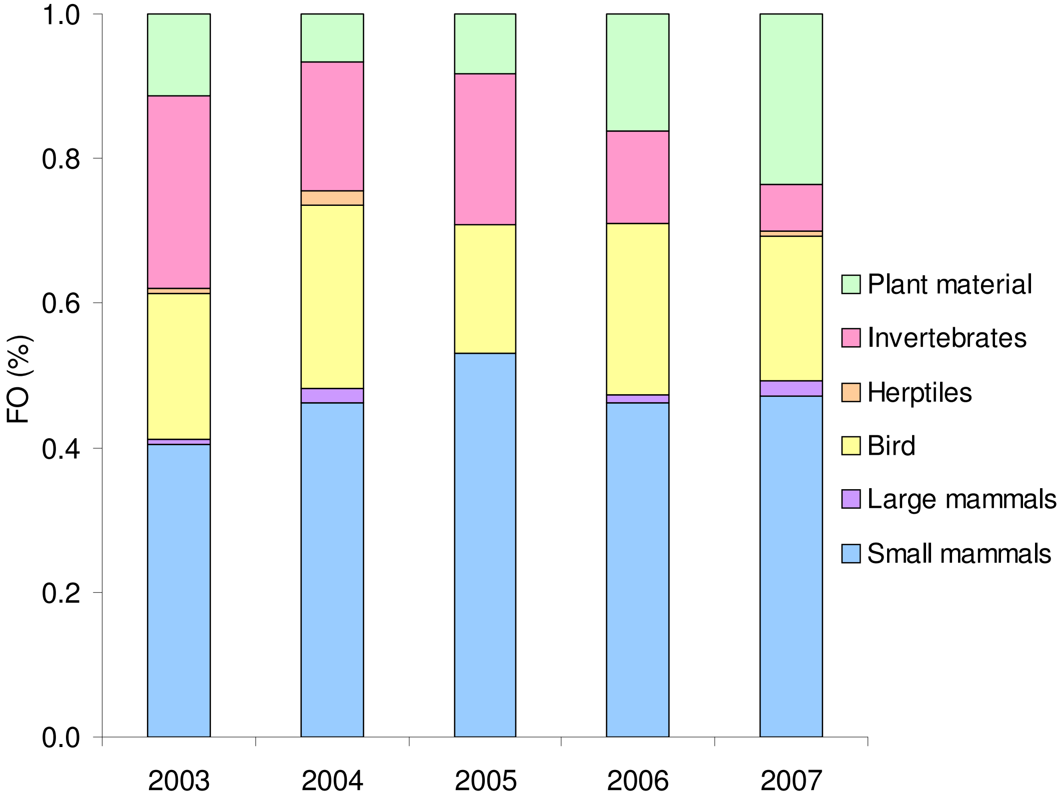


Figure 6.2 The summer diet of pine marten in Novar and Wallace Hill, Easter Ross, Scotland, based on the analysis of prey remains found in scats collected from April to August, annually between 2003 and 2007. Diet is expressed as a percent of relative frequency of occurrence i.e. the total number of occurrences of each food item, divided by the total number of items identified across all samples. An occurrence of a food item is defined as the presence of a prey species (or lowest identified taxon) within a scat, therefore a food item could be constituted by several similar small prey, or part of a large prey.

0.05) and 2007 ($\chi^2 = 28.39$, $df\ 5$, $P < 0.001$) however. A greater proportion of invertebrates was taken in 2003 than in other years ($\chi^2 = 12.61$, $df\ 1$, $P < 0.001$), and in 2007 dietary analysis indicated reduced intake of invertebrates ($\chi^2 = 14.35$, $df\ 1$, $P < 0.001$), and increased intake of plant material ($\chi^2 = 13.64$, $df\ 1$, $P < 0.001$).

The inter-annual variation in the consumption of each individual food category was then examined. The two most frequently consumed food groups, small mammals and birds, showed no between-year variation in they frequency in which they were consumed ($\chi^2 = 3.05$, $df\ 4$, $P > 0.05$), and ($\chi^2 = 2.58$, $df\ 4$, $P > 0.05$) respectively. Small mammals consistently formed 41-52% of the diet in each year ($\bar{x} = 46 \pm 4$ %), whereas birds accounted for 20-28 % of the occurrences each year ($\bar{x} = 23 \pm 3$ %). Large mammals and herptiles both showed no between-year variation ($\chi^2 = 0.20\text{-}1.57$, $df\ 4$, $P > 0.05$), though each only accounted for less than 2 % of occurrences each year. Only two food groups showed between-year variation: invertebrates ($\chi^2 = 17.71$, $df\ 4$, $P < 0.05$), and plant material ($\chi^2 = 18.15$, $df\ 4$, $P < 0.05$). In some years these food groups could each form almost a quarter of the diet, but also accounted for less than 10% of the diet in other years (invertebrates: $\bar{x} = 15 \pm 6$ %; plant material: $\bar{x} = 13 \pm 7$ %).

A detailed breakdown of the composition of each food category to its lowest identified taxonomic groups is given in Table 6.2. The majority of plant material was accounted for by berries (85 %), 46 % of which were blaeberry (*Vaccinium myrtillus*), 29 % rowan (*Sorbus aucuparia*), and 10% raspberry (*Rubus* sp.). Invertebrate materials comprised of 52 % *Coleoptera,* 34 % *Hymenoptera*, and 6 % an unidentified *Scarabaeiform* larvae that was usually found in large numbers within single scats. The majority of small mammal remains that were reliably identified to species level, by the presence of lower jaws and teeth, were *Microtu*s, which formed 86 % of identified species. A small number of *Sorex* sp. (13 %) was also identified, but no bank voles were found in the diet, and only one occurrence of wood mouse. Within the bird food category: 76 % were comprised of small birds, 16 % large birds and 8 % egg shell. The large mammal group was divided equally between deer and sheep (*Ovis aries*). Finally, two instances of reptile prey (*Lacerta vivipara*), and one of amphibian (*Bufo bufo*) formed the herptiles group.

6.3.2 Annual Variation in Prey Abundance

A comparison of average annual clutch size from the short-term data-set using a Kruskal-Wallace test failed to show any difference between years (χ^2 *= 5.97, df 4, P = 0.20*). Clutch size appears to decrease through the study period, before

Table 6.2 Food items in the summer diet of pine marten expressed as the percentage relative frequency of occurrence of six food categories (bold). The percent composition of the lowest taxonomic level identified within each food group is also given for each (plain text).

Food Items	2003	2004	2005	2006	2007
Small Mammals	**40.1**	**45.6**	**52.1**	**45.7**	**47.1**
Microtus	57.8	36.7	41.2	44.2	26.5
Apodemus	-	2.0	-	-	1.5
Sorex spp.	4.7	8.2	3.9	11.6	10.3
Unidentified spp.	37.5	53.1	54.9	44.2	61.8
Large mammals	**0.7**	**1.9**	**0.0**	**1.1**	**2.1**
Deer sp.	100.0	50.0	-	-	66.7
Ovis aries	-	50.0	-	100.0	-
Birds	**22.8**	**28.2**	**20.8**	**24.5**	**20.0**
Small bird	68.8	85.2	64.7	81.8	75.0
Large bird	25.0	7.4	17.6	13.6	17.9
Egg shell	6.2	7.4	17.7	4.5	7.1
Invertebrates	**22.8**	**16.5**	**18.8**	**12.8**	**6.4**
Coleoptra	54.8	68.4	45.0	25.0	100.0
Hymenoptera	33.3	26.3	40.0	41.7	-
Scarabaeiform larvae	4.8	-	5.0	25.0	-
Unidentified spp.	7.1	5.3	10.0	8.3	-
Plant material	**12.1**	**6.8**	**8.3**	**16.0**	**23.6**
Vaccinium myrtillus	44.4	42.9	12.5	66.7	52.9
Rubus sp.	-	-	25.0	20.0	2.9
Sorbus aucuparia	38.9	28.6	37.5	13.3	41.2
Unidentified spp.	16.7	-	25.0	-	-
Hordeum spp.	-	28.6	-	-	2.9
Herptiles	**0.7**	**1.0**	**0.0**	**0.0**	**0.7**
Lacerta vivipara	100.0	-	-	-	100.0
Bufo bufo	-	100.0	-	-	-
Total no. occurrences	**158**	**105**	**96**	**93**	**143**
Total no. scats	**95**	**73**	**75**	**79**	**104**

picking up again in 2007 (Fig. 6.3). The highest clutch size was in 2007, and the lowest in 2006, but pair-wise comparisons using Mann-Whitney U tests revealed that there was no difference in clutch size between these two years ($U = 145.5$, $z = -0.543$, $P = 0.54$). No relationship between clutch size and diet breadth could be determined with such a small sample size ($n = 5$). It was unclear whether the apparent peak (2007) and trough (2006) were part of a multi-annual population cycle without referring to the longer-term data set to determine if these vole populations cycled regularly (Fig. 6.4). The trends in the data suggest that *Microtus* populations (as inferred from tawny owl clutch size) do not demonstrate the pronounced periodic fluctuations with the dramatic perturbations one would expect from a cyclic population (e.g. Klemola *et al.* 2002). Whilst it is possible that there are annual fluctuations of low amplitude occurring, it remains unclear whether the apparent peaks in 1997, 2003 and 2007 are part of a 4 to 6 year cycle, or naturally occurring random fluctuations. The data are more representative of a stable, non-cyclic population similar to that found by Petty (1992) in Glenbranter, Argyll (56^{o}N 5^{o}W), which was markedly different to the cyclic population he observed in Kielder Forest (55^{o}N 2^{o}W), Northumberland, during the same study.

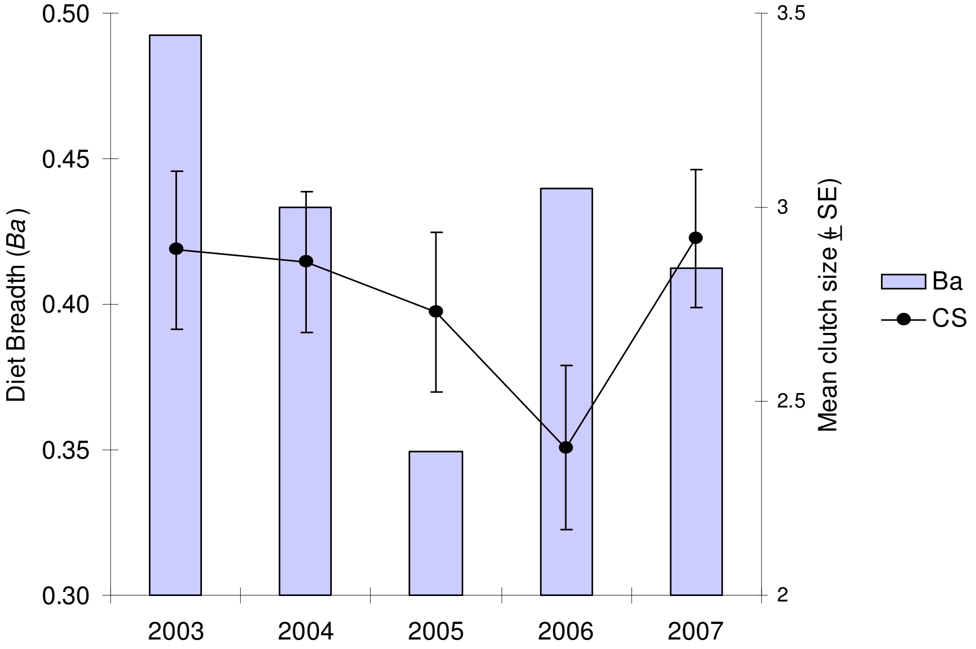


Figure 6.3 The relationship between standardised niche breadth of pine marten (*Ba*), and mean clutch size (± standard error) of tawny owl broods (CS) in the Tain region of Easter Ross-shire from years 2003 to 2007. Owl data come from nests (*n = 18*) that were all located in the vicinity of the study areas that were first visited in 2003 and subsequently visited each year.

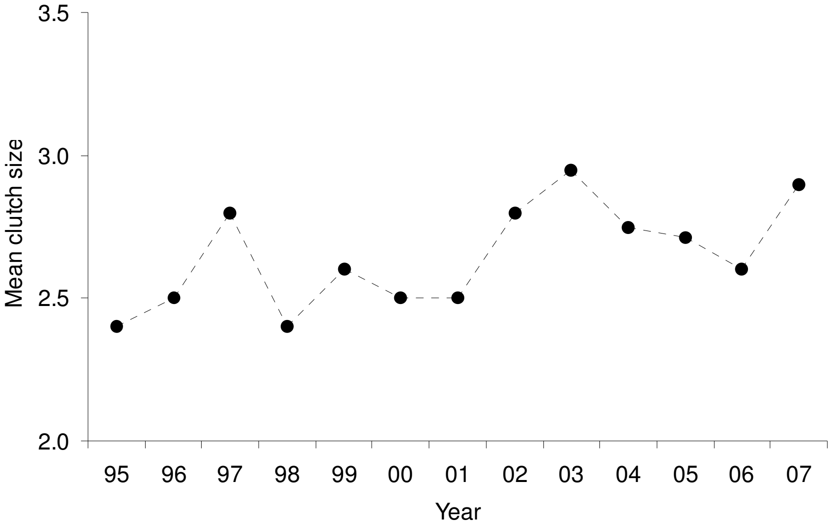


Figure 6.4 Mean clutch size of tawny owl nests located in Easter-Ross, Sutherland and the Black Isle (*B. Swann* $^{c}/_{o}$ *the Highland Raptor Study Group, unpublished data*). Note that raw data were not available to calculate measures of deviance about the mean, so error bars cannot be shown. Data from 2000 to 2007 come from > 30 nests surveyed each year, sample sizes were not available for earlier years.

6.3.3 Annual Variation in *Microtus* Consumption

On average, only 50 % of the marten scats containing small mammal remains also contained teeth which enabled them to be identified to species level. Although this figure is in keeping with the 57 % reported by Lockie (1961) for pine marten scats, and 50% for fox scats (Lockie, 1959), it meant that unidentified small mammals accounted for 15-30 % of occurrences each year ($\bar{x} = 24 \pm 6$ %). Such a high proportion of unidentified small mammals may mask any association between dietary patterns and the consumption *Microtu*s. Lockie, (1959) determined that the relative proportions of small mammal species identified from teeth recovered from scats was a good measure of the proportions in which those species were consumed. The proportion of *Microtu*s was therefore adjusted to include unidentified small mammals in the same ratios as they were observed in identified species in each study site, in each year. For example, in Novar in 2003, 93 % of identified small mammals were *Microtu*s, hence 93 % of the 18 unidentified small mammals in that year were added to the *Microtus* group. Prior to adjusting species numbers, the frequency of the unidentified small mammals within the small mammals group was compared between years to ensure that there was no temporal bias in identification success. No difference was found ($\chi^2 = 3.02$, *df 4*), and the proportion of unidentified small mammals remained consistent each year ($\bar{x} = 50 \pm 10$%).

Microtus were the most abundant small mammal species identified, accounting for 69-93% of identified small mammals each year ($\bar{X} = 82 \pm 10\%$). Before adjustment, *Microtus* as a single species accounted for 13-23% of all food occurrences each year ($\bar{X} = 19 \pm 4\%$), and occurred in 17-39% of scats ($\bar{X} = 27 \pm 8\%$). When unidentified small mammals were included, these figures increased to 33-50% of occurrences ($\bar{X} = 40 \pm 6\%$), and 44--64% of scats ($\bar{X} = 55 \pm 10\%$). Only the adjusted *Microtus* numbers will subsequently be referred to. The results of G-test contingency tables of frequency of *Microtus* occurrences suggested that they make a stable contribution to annual food occurrences, as there was no between-year difference in their contribution ($\chi^2 = 7.05, df\ 4, P > 0.05$). A pair-wise Chi-square comparison of *Microtus* occurrences between the year with the highest tawny owl clutch size (2007) and the lowest (2006) failed to show any difference in *Microtus* consumption ($\chi^2 = 0.33, df\ 1, P > 0.05$).

6.3.2 Annual Variation in Diet Breadth

The standardised diet breadth was calculated separately for each of the two study sites in each year to allow a finer scale of assessment using correlation comparisons. Trends between diet breadth and the occurrence of food groups in the diet indicate that marten take a greater proportion of *Microtus* when the diet breadth is narrowest (Fig. 6.5a.). The principal food taken when *Microtus* were less abundant in the diet was plant material (Fig. 6.5 b.), though this relationship was not significant (*r = -55, n = 9*). However, Spearman's rho correlations performed to compare the standardised diet breadth with the proportion of each food group from the corresponding site and year demonstrated that no food group showed a significant relationship with diet breadth (Table 6.3).

6.4 Discussion

6.4.1 General Findings

Direct comparisons with the spring-summer diets found in other Scottish studies are somewhat limited as many present the results of the diet across a whole year (Balharry 1993a., Gurnell et al. 1994, Coope 2007), and few of the studies that report seasonal diet enumerate specific results in detail (Lockie 1961, Halliwell 1997, Putman 2000). However, the patterns that do emerge from the literature are in agreement with the findings presented here; small mammals form the bulk of the spring-summer diet, and of these, *Microtus* account for almost all small mammal occurrences (Lockie 1961, Halliwell 1997, Putman 2000). It is therefore justified to assume that a relationship between *Microtus* density and their consumption by pine marten exists as it does for Clethrionomys voles elsewhere in Europe (Pulliainen 1981, Helldin & Lindstrom 1993; Jedrzejewski et al. 1993; Pulliainen & Ollinmaki 1996, Helldin 1998). However, both the abundance and consumption of *Microtus* was found to

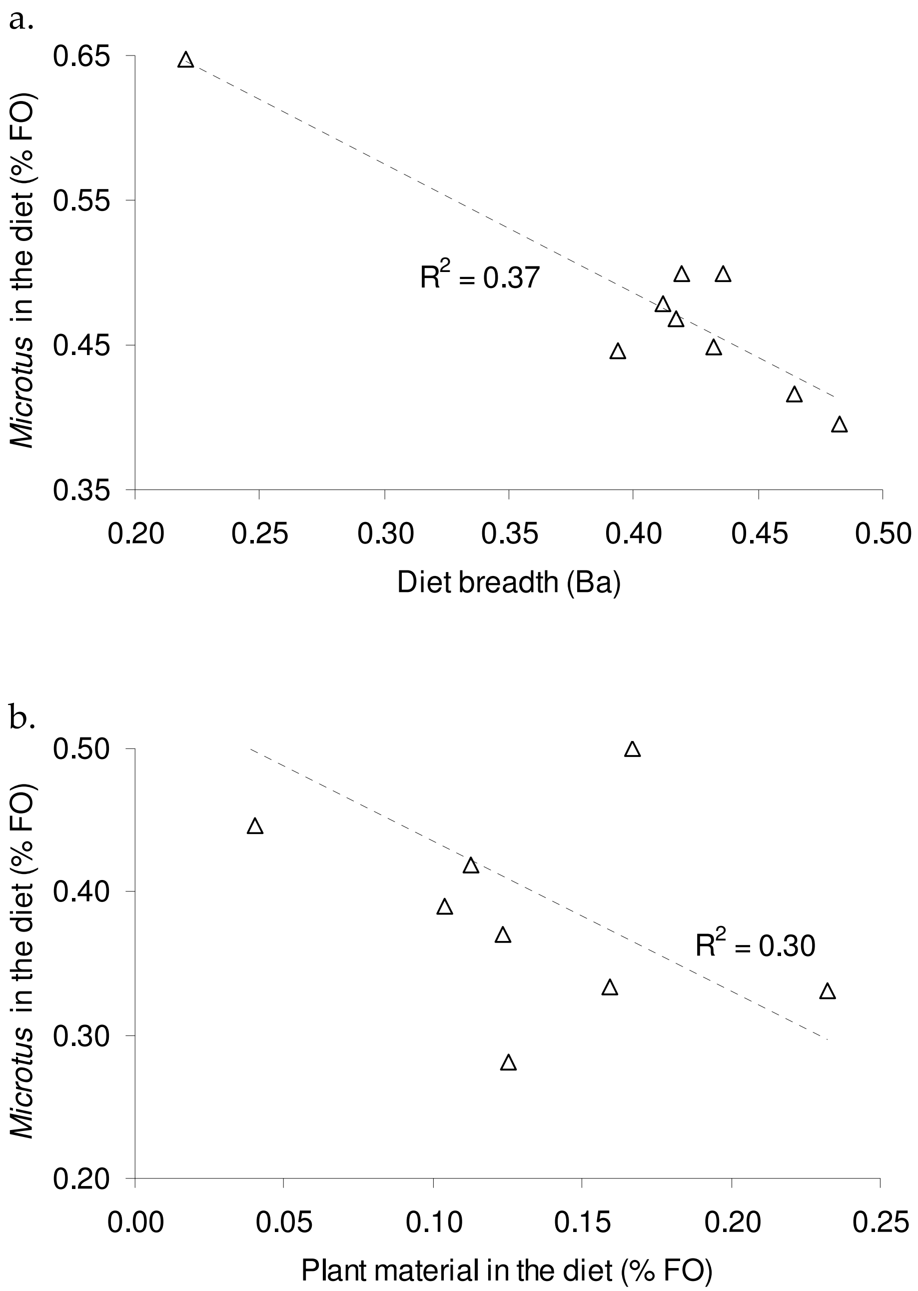


Figure 6.5 The relationship between the proportion of *Microtus* in the diet (based upon percent frequency of occurrence) and a. Standardised diet breadth, b. The proportion of plant material in the diet.

Table 6.3 Spearman rank correlation coefficients (*r*) of annual percent frequency of occurrence of principal food groups (i.e. those forming on average > 10 % of annual diet) in relation to standardised diet breadth (*Ba*) and the occurrence of *Microtus* in the diet (*n = 9*).

Food	**Diet breadth (*Ba*)**		***Microtus* (% FO)**	
	r	**P**	***r***	**P**
Microtus	-0.56	*0.11*		
Bird	-0.35	*0.35*	0.21	*0.59*
Invertebrate	0.60	*0.09*	0.03	*0.95*
Plant material	0.23	*0.54*	-0.55	*0.12*

remain stable throughout the five year study period, thus it remains unclear whether or not marten changed their foraging behaviour depending on *Microtus* availability. It is worth noting however, that other long-term diet studies have also found only a weak association between *Microtus* consumption and abundance (Jedrzejewski et al. 1993, Pulliainen & Ollinmaki 1996, Helldin 1998), although in each of these studies fluctuations in *Microtus* abundance were more evident.

6.4.2 *Microtus* Abundance Index

Tawny owl clutch size has repeatedly shown a strong association with spring *Microtus* density (Southern 1970, Petty 1992; 1999, Solonen 2002; 2005), but the results of the long-term data set presented here provide little evidence of multi-annual periodicity, or pronounced between-year differences in the densities of the *Microtus* population in NE Scotland. Failure to observe a distinct cyclic pattern within *Microtus* population cycles may have occurred if the scale at which tawny owl breeding data were collected was larger than the scale at which spatiotemporal variability affects local *Microtus* populations. Patterns resembling periodic travelling waves in densities create spatial asynchrony among *Microtus* populations (Lambin *et al.* 1998, MacKinnon *et al.* 2001, Sherratt *et al.* 2002, Bierman *et al.* 2006). *Microtus* population patterns averaged over a large spatial area may well hide large amplitude occurring more locally (*X. Lambin, personal* *communication*). The scale at which tawny owl breeding data were collected and averaged is therefore pertinent to the detection of vole population fluctuations, however this information is not available for the long term data set. Nest locations used to generate the short-term data set were collected from within 0.4 km and 10.3km of the forest edge ($\bar{x} = 3.1 \pm 3.3\ km$), and covered an area of c. 47 km^2; whether or not this may have masked the existence of *Microtus* population cycling is unclear, and therefore uncertainty remains about whether the apparent peaks in vole densities are the result of low amplitude 4- to 5-year cycles, or random fluctuations between years. A biogeographical gradient in microtine cycles is well documented in Fennoscandia, where both the length and amplitude of cycle increase with increasing latitude (Hanson & Henttonen 1985, Hansen *et al.* 1990, Henttonen & Hanski 2000), with non-cyclic populations occurring at more southerly latitudes (e.g. Erlinge *et al.* 1983). Much debate exists about the causal factors of these cycles (reviewed in Stenseth & Ims 1993), but the predation hypothesis is increasingly implemented as an explanation for the phenomenon (Hansson 1984, Henttonen 1985, Korpimaki 1986, Hanksi *et al.* 1991, Norrdahl & Korpimaki 2000). Density-dependent predation by generalist predators is thought to stabilise small mammal population cycles driven by specialist predators, and latitudinal changes in the influence of predators cause a gradient in the length and amplitude of rodent cycles (Hansson & Henttonen 1988, Hanski *et al.* 1991, Norrdahl 1995, Norrdahl & Korpimaki 2002). However, a high-amplitude density cycle is by no means a universal phenomenon (e.g. Saitoh *et al.* 1998), and the latitudinal gradient does not appear to apply to parts of mainland Europe (Tkadlec & Stenseth 2001, Lambin *et al.* 2006). It is interesting to note that *Clethrionomys* are not known to experience cycling in Kielder (Petty 1999), or elsewhere in Britain, unlike their counterparts in mainland Europe (e.g. Jedrzejewski & Jedrzejewski 1996).

6.4.3 Vole Population Dynamics

Cyclic populations of *Microtu*s have been observed in Great Britain, although with much lower amplitudes than that manifest in Fennoscandia (Lambin *et al.* 2000). The bulk of British studies demonstrating cyclicity have however been conducted within a relatively small geographic area in the Borders between Scotland and England (Leckie *et al.* 1998, O'Mahony *et al.* 1999, Lambin *et al.* 2000, Petty *et al.* 2000, Redpath, Thirgood & Clarke 2002). Lambin *et al.* (2000) state there is further evidence of *Microtus* population cycling in western and northern Scotland (Petty 1992, Swann & Etheridge 1995, Chitty 1996), although evidence is not as forthcoming as one might expect. Whilst Petty (1992) found obvious *Microtus* cycles in Kielder, northern England, his concurrent study in Argyll, western Scotland, was inconclusive about whether apparent low amplitude cycles were not just random fluctuations. Petty attributed the increased stability of the Argyll population to a greater diversity and abundance of generalist predators compared with Kielder, a diversity that the present study in Easter Ross-shire shares. Further complicating conclusions about the existence of population cycling among *Microtus* populations is the recent observation that over the last two decades the amplitude, periodicity and synchrony of *Microtus* cycles in Kielder have changed (Bierman *et al.* 2006). The dynamics of this population, which at first appeared strongly cyclic, now display a clear intra- rather than inter-annual pattern in population growth rates, a trend which is most apparent in more recent years. Similar changes have been recorded to *Microtus* populations in Fennoscandia (Hornfeldt 2004), and Bierman *et al.* (2006) conclude that these changes to vole dynamics are the likely results of climatic changes which have resulted in a less seasonal environment with shorter winters such as a marked decrease in the number of days with snow cover each year. Winter-dependent demographic traits, which contribute to drive *Microtus* population cycling, such as winter survival and propensity of winter breeding, are higher in the increase phase of the population cycle (Ergon *et al.* 2001a, b), thus winter is a ley factor in generating vole cycles (Bierman *et al.* 2006). Whilst climatic data were not available for this specific study area during this time period, the similarities in changes to Fennoscandian vole populations indicate that climatic changes over large spatial scales are affecting rodent dynamics in Europe (Bierman *et al.* 2006). It is therefore clear that an explicit study of *Microtus* populations at sites in Scotland, other than the Borders, in relation to climatic factors would be timely given the concern about the foraging habits of marten during vole population crashes.

6.4.4 Marten Predation of *Microtus*

Regardless of whether *Microtu*s in the present study site exhibited low amplitude cyclicity or not, they appear to have been abundant enough not to cause any effect on the breeding productivity of tawny owls, or on the foraging behaviour of marten. Field voles were the single most important species in the marten diet, as has repeatedly been found in Scotland (Lockie 1961, Balharry 1993a., Gurnell *et al.* 1994, Halliwell 1997, Putman 2000, Coope 2007). The results from five consecutive years clearly indicate that the marten diet in this locality did not differ annually, and that *Microtu*s consistently contributed approximately half of occurrences in scats each year. This alone does not rule out that *Microtus* populations were cycling however, as Jedrzejewski *et al.* (1993) found that even during years of microtine population crashes, rodents still comprised 40% of marten scats. Although evidence suggests that the proportion of microtines in the marten diet varies wildly where vole populations have pronounced amplitudes (Pulliainen 1980), and becomes much more stable where vole populations are only weakly cyclic

(Goszczynski 1986). The stability of *Microtus* consumption in the present study therefore implies that the *Microtus* population is either stable, or that fluctuating with such low amplitude that even during low phases, marten are still able to access a sufficient supply.

6.4.5 Alternate Prey

Annual dietary breadth displayed a strong negative association with Microtus occurrence in the diet. Sorex sp. and herptiles were taken significantly more often when Microtus were less abundant in the diet, as has been found elsewhere (Jedrzejewski et al. 1993, Helldin 1998). However these items only accounted for 4 + 2 % and 1 + 1 % of food occurrences each year, and therefore were not considered to form a substantial alternative food. Consumption of plant material, particularly from berries, increased when Microtus consumption decreased. Fruit formed between 7 and 24 % of annual occurrences, and the between-year variation observed suggests that the importance of fruit in the diet changed annually, although it is unclear if this is due to changes to the availability of Microtus, or berries. Helldin (1998) found that the proportion of berries in the diet was strongly negatively correlated with microtine density in the environment, but it was also positively correlated with the crop of the species. Invertebrates were strongly positively associated with diet breadth but failed to show a strong negative relationship with Microtus occurrence as would be expected. Invertebrates have been found to form an important source of alternative prey in localities where vole densities are low in Scotland (Balharry 1993a, Bright & Smithson 1997). Birds are commonly taken as alternative prey when Microtus are scarce (Grakov 1962 cited in Zalewski 2004, Yazan 1962 cited in Zalewski 2004, Jedrzejewski et al. 1993, Pulliainen & Ollinmaki 1996, Helldin 1998), however in the present study bird consumption was positively correlated with Microtus, albeit weakly so. A fifth of the marten' annual diet in all years came from birds, particularly small birds, and showed no between-year variation. This was to be expected given that scats in this study represented the spring and summer diet, when the greatest consumption of birds frequently occurs (Lockie 1961, Balharry 1993a, Jedrzejewski et al. 1993, Halliwell 1997, Helldin 1998: Chapter 5). As there was no between-year variation in either Microtus density index, Microtus consumption, or bird consumption, we can only infer that the contribution of birds to the diet observed in the present study demonstrates that they form a stable component of the seasonal diet (see Chapter 5). There is nothing to suggest that birds are predated upon more heavily when Microtus are scarce.

6.4.6 Limitations of the Data

The season in which the diet study was conducted may have affected the ability to detect changes in consumption of voles between years. The importance of small mammals in the diet generally reaches a peak in winter, coinciding with a decline in the availability of seasonal foods such as berries, invertebrates and passerine birds (Lockie 1961, Balharry 1993a, Halliwell 1997, Coope 2007, and literature cited in Zalewski 2004). If scats had been available from winter-spring, rather than spring-summer, annual trends in *Microtus* consumption may have been clearer due to the more restricted availability of alternative prey. Separately analysing the spring scats from the present study was prevented by the small sample sizes of scats this would have resulted in (*n = 154 over 5 years*). However, given the lack of evidence that *Microtus* populations experienced pronounced multiannual fluctuations, and the absence of any between-year variation in *Microtus* consumption, the results presented here are likely to be irrespective of season. Similar data collected from winter months would have only served to confirm the dietary habits of marten in response to seasonal fluctuations in the availability of *Microtu*s rather than multiannual fluctuations brought about by population booms and crashes.

Interpretations of the diet may be limited by the small sample sizes of scats used to represent the diet each year ($\bar{x} = 85 \pm 14$). The sample sizes used in diet studies are often too small to allow general conclusions about the species' diet to be drawn (Balharry 1993a). Despite this, several frequently cited dietary studies have been based upon small sample sizes of scats (de Jounge 1981, Reig & Jedrzejewski 1988, Storch *et al.* 1990, Bright & Smithson 1997, Putman 2000). As sample sizes of scats are reduced, the variance of results increases, often becoming too large for estimates to be meaningful (Carss & Parkinson 1996). In addition, there is often little attempt made to estimate the number of marten contributing scats to the analyses, and even fewer that estimated a minimum population size by trapping, so findings can often represent the diet of only a few individuals (Balharry 1993a). Considering the number of scats rather than the number of individuals in a diet study could be regarded as pseudoreplication (Hurlbert 1984). Unless a faecal sampling scheme is used that maximises the number of different individuals included in a survey, individual foraging variation may result in biased diet diversity estimates (Fedriani & Kohn 2001). It would not be beyond reason to suppose that a single individual marten could have produced the majority of scats found in Wallace Hill. If that individual had sufficient contact with good *Microtus* habitat, it may still have access to adequate numbers to have been unaffected by a vole population crash had there been one.

6.4.7 Conclusions

In accordance with the findings of other British studies, *Microtu*s are the most important prey species in the diet of pine marten in Scotland (Lockie 1961, Velander 1983, Balharry 1993a., Gurnell *et al.* 1994, Halliwell 1997, Putman 2000, Coope 2007). As a generalist predator, the pine marten is capable of taking alternative prey in habitats where *Microtus* densities are low (Balharry 1993a, Bright & Smithson 1997), or during periodic crashes where microtine populations cycle (Grakov 1962 cited in Zalewski 2004, Yazan 1962 cited in Zalewski 2004, Jedrzejewski *et al.* 1993, Pulliainen & Ollinmaki 1996, Helldin 1998). However, the lack of any between-year variation in the contribution of *Microtu*s to the diet suggests that *Microtu*s were consistently available during the present study. It remains unclear whether *Microtus* populations were non-cyclic, or cycling with low and lengthy amplitude. An explicit study of microtine population dynamics outside of the Scottish Borders would be timely to determine whether vole population crashes occur, and if so, whether they have any impact on the feeding habits of marten. There is little in the present study to suggest that marten were limited by *Microtus* availability, neither was any distinct switch to an alternative food source observed. Of the prey items taken more frequently when *Microtu*s occurred less, berries appear to have been most important in terms of numbers, but there was also an unmistakable increase in the occurrences of both herptiles and shrews. Invertebrates are likely to be seasonally important when available. There appeared to be no relationship between *Microtu*s and birds in the diet, other than a weakly negative one.

Chapter 7

General discussion

Today, plantation forests form the majority of habitat into which British pine marten can extend their distribution, yet relatively little is known about the ecology of marten in these forests. Previous studies of marten ecology in Scotland have produced inconsistent results (Balharry 1993a., Halliwell 1997, Bright & Smithson 1997), and the diversity of ecological and management conditions in each precludes any generalisation of findings. The aims of this study therefore, were to provide a thorough description of the ecology of marten in plantation forests, and to suggest management recommendations based on this knowledge. More specifically, the study aimed to identify which habitats and habitat elements fulfil the marten's life-requirements, whilst determining what the principal prey of marten are in different seasons, and whether the importance of these prey shows inter-annual variation.

7.1 Overview of Main Findings

Chapter 3 showed that the modern plantation forest in this study supported the highest density of pine marten yet observed in Scotland. Results of the habitat selection study demonstrated that marten use of habitat was selective at two scales: at the home range level as well as within home ranges. Marten selected to establish their home ranges from the greater landscape in areas dominated by late (45+ years old) rather than early-to-mid (17-44 years old) successional forest. In doing so, they also avoided areas of open heath moor and grazed pasture. From this it is clear that marten are choosing to utilise habitats with more structural complexity than those which lack horizontal and vertical diversity. Scrub habitats, which included areas of dense shrub (e.g. gorse, willow, rhododendron) or coarse woody debris (e.g. clear-fells, wind throw), were included within home ranges but were less associated with marten activity. Shrubs and other such complex ground structures provide marten in plantation forest with secure den sites, as was frequently observed (*personal observation*). Additionally, the vegetative and structural layers provided by these habitats provide marten with sufficient cover for them to forego an over-story canopy. Within home ranges, marten utilised ungrazed grass habitats, such as the herbaceous meadows found along riparian corridors, more than would be expected from their availability. The implication of which is that marten selected to hunt in *Microtus*-rich habitat, but that these areas were associated with the forest rather than at distance to it. Deciduous woodland was not abundant in the study area, but it was selected by marten at both scales where it was available.

In Chapter 4 it was demonstrated that areas of core foraging habitat share various characteristics concerning ground vegetation cover and aspects of the forest-stand's physical structure that relate to light transmission. Marten selected to hunt in areas where species-rich graminoid vegetation occurred, in areas that were associated with large, but well-spaced trees, and a well-developed field layer. Areas of graminoid vegetation were patchily distributed throughout the forest, but could be predicted using data that are routinely available to forest managers; using just data pertaining to local topography, soil moisture can be mapped and the distribution of the species-rich vegetative communities that are commonly associated with *Microtus* can be predicted.

The contents of c.2500 scats analysed in Chapter 5, most of which had been genetically identified as being from pine marten, conclusively confirmed that the most important prey species in the diet of British pine marten is the *Microtus* vole, to which marten exhibited considerable preferential selection. Other small mammal species, which were more abundant in forest environments, were only taken in negligible amounts. In additional to *Microtus*, a substantial part of the annual diet was also formed by berries (*Sorbus* spp., *Vaccinium myrtillus*, and *Prunus* spp.) and small passerine birds, each of which increased in the diet depending on season, the former in summer, autumn and early winter, the latter in spring and summer. Other prey groups (invertebrates, large mammals and herptiles) were also consumed seasonally, but did not contribute a large part of the diet even then. The principal foods found in this study (*Microtus*, passerine birds and berries) were consumed in similar quantities as in two previous studies in Scotland (Balharry 1993a., Halliwell 1997), though berries formed a greater proportion of the diet in the present study. The increased appearance of fruit in the present study may have been a consequence of the increased certainty in including scats for analysis afforded by using molecular tests to identify scat origin. Comparison of the present results with studies from Europe indicated that the diet of British martens was more typical of marten diets at more southerly latitudes than from those at equal or more northerly latitudes. The implication of this is that caution should be used when making inferences about the behaviour of British martens based on studies from, for example, Fennoscandia. The British climate has milder winters with less snow cover than those in continental Europe, allowing British marten to continue to feed upon their principal foods throughout winter, and negating the need for them to switch to alternate species.

Chapter 6 was in agreement with the findings of Chapter 5 in that *Microtus* were again found to be the staple prey of pine marten. Consumption of *Microtus* showed no between-year variation over a period of five years, with the species consistently occurring in, on average, 55 % of scats each year, and accounting for an average 40 % of food occurrences. There was little evidence to suggest that *Microtus* populations were under-going periodic cycling of the sort witnessed in

Fennoscandia, which was unexpected given that such cycles have been observed in other areas of Britain (e.g. Lambin *et al.* 2000). It remains unclear whether spatiotemporal factors in vole population dynamics were masked by the spatial extent over which these data were collected (c.47 km^2). However, data relating to *Microtus* cycles in Scotland is surprisingly lacking outside of some parts of southern Scotland and northern England, and therefore warrants further investigation, as there is evidence from western Scotland (Petty 1992) indicating a similar non-cyclic pattern to that presented here. Although there was nothing to suggest that *Microtus* abundance in the diet or in the environment varied between years, examination of the relationship between annual diet breadth and consumption of principal food groups indicated that marten specialised on *Microtus*. Plant material was the only principal food to show an association with *Microtus* consumption; a negative trend indicated that more fruit was consumed in years of reduced *Microtus* consumption. Birds formed a staple annual food source, consistently forming an average 23 % of the diet, the majority of which were from small birds.

7.2 Ecology of Marten in a British Context

Whilst the dominance of *Microtus* in the diet of British pine marten has been demonstrated in previous studies (Velander 1983, Gurnell *et al.* 1994, Putman 2000, Coope 2007), few studies were based on sample sizes of more than five-hundred scats (Balharry 1993, Halliwell 1997), and few simultaneously collected data on relative prey abundance in order to draw conclusions about dietary preferences (Lockie 1961, Balharry 1993). The findings presented in Chapters 5 and 6 demonstrate unequivocally that British pine marten preferentially preys upon *Microtus* voles, and the results of Chapters 3 and 4 clearly indicate that marten select to utilise habitats associated with this prey. The highly localised nature of *Microtus* distributions along with their apparent palatability, relatively large body size and relative lack of anti-predator behaviours compared to other small mammal species (MacDonald 1977, Hansson 1978, Buskirk & MacDonald 1984, King 1985, Pearson 1985) are all valid reasons why *Microtus* are preyed upon by marten where available. However, the ultimate reasons why British marten in particular show such a marked and habitual preference for *Microtus* when their counterparts elsewhere in Europe and north America commonly prefer *Clethrionomys* remains unclear. The answer will almost certainly involve the influence of the prolonged and extensive historic deforestation of the British Isles however (Rackham 1990, Birks 2002). The extent, structure, distribution and composition of British woodlands have evolved as a result of both anthropogenic and environmental influences (Tipping 1994, Smout 2006, Holl & Smith 2007). The tree line in the upland fringes of England during pre-historic (Mesolithic) times for example, is consistently below the altitude at which climatically it is possible for trees to grow (Williams 2000). An element of climatic stress is implicated in the failure of pinewoods to regenerate in Scotland (Smout 2006). Indeed it has even been suggested that Scots pine, a continental tree in Scotland at the oceanic edge of its global range, has not naturally been very widely or continuously distributed here under the climatic conditions of the last 500 years, and that it was easily further discouraged by episodes of adverse climate change within that period (Tippping 2003, Smout 2006). A pastoral-woodland system of agriculture prevailed in the Highlands of Scotland from at least the 11th century until the 1800s (Holl & Smith 2007). Grazing by livestock in natural clearings prevented the regeneration of woodland, causing deforestation by woodland senescence (Brown 1997), whilst continuous fertilisation from livestock has influenced the development of ground vegetation (Haldane 1995). Centuries of grazing created open-structured woodlands with low tree density and open canopies, which has shaped the characteristic appearance of today's ancient pinewoods (Summers *et al.* 1999, Smout 2003). Under changing forest conditions, marten probably faced strong pressure to exploit alternative habitats and food resources, making them less forest-dependent. The marten's ability to adapt its behaviour to changing habitats and environments has allowed it to inhabit diverse habitats from the Mediterranean islands to Fennoscandia (Proulx *et al.* 2004). Adaptations to

Scotland's historically open and fragmented forests may have left a legacy on marten diet and habitat use that persists to present day (Birks *et al.* 2004).

Along with abiotic factors, ecological niches are shaped by competition and predation, but anthropological changes to natural community structures can cause the roles of these inter-specific interactions to change rapidly (Kurki *et al.* 1998). It therefore seems unlikely that the results of ecosystem change, such as habitat fragmentation, can be predicted without accounting for inter-specific interactions (Davis *et al.* 1998). Given that most of the explanations afforded to marten habitat relationships involve fulfilment of life requirements, the biological context in which investigations are conducted should not be neglected. This is particularly important with regard to interspecific competition and predation, which may be limiting to marten populations (Helldin 1998), as the marten's life requirements will differ under differing ecological pressures. For example, in the absence of species that may prey upon marten, an insular population of marten on the Mediterranean island of Minorca are indifferent to overhead cover, and open non-forested habitats are equally as important as closed ones (Clevenger 1994b). This finding indicates that marten may be more habitat generalists than specialists, depending on ecological circumstances (Clevenger 1994b). The level of intra-guild competition faced by marten in Britain is an unknown quantity, but will differ from that experienced by marten elsewhere in Europe or North America as the species diversity of competing small carnivores is lower in Britain than elsewhere in the marten's range. In particular, Britain lacks many of the species with which the marten competes for food resources on mainland Europe, such as the stone marten, spotted genet *Genetta genetta*, and racoon dog *Nyctereutes procynoides* (Clevenger 1994, Baltrunaite 2002, Barrientos & Virgos 2006, Posluszny *et al.* 2007). The absence of such competitors in Britain means that marten here are subject to different ecological pressures, therefore how they use habitats and the resources they contain cannot simply be assumed. For instance, marten occur sympatrically with fox across the extent of their geographic range, but whilst there is a high degree of dietary overlap between the two species (e.g. Storch *et al.* 1990, Baltrunaite 2002, Russell & Storch 2004), the fox is generally regarded to have a preference for *Microtus* voles (e.g. MacDonald 1977, Storch *et al.* 1990), whilst the pine marten is generally regarded to show preference for *Clethrionomys* voles (e.g. Pulliainen 1981, Storch *et al.* 1990). However, this is clearly not the case in Britain (Lockie 1964, Balharry 1993a., Halliwell 1997, Chapters 5 and 6), suggesting that British martens may be fulfilling a different role to that filled by the species elsewhere. Stone marten are morphologically similar to pine martens, and occur sympatrically with them throughout much of their European range (Clevenger 1994a). It has been suggested that habitat selection is the main feature differentiating these two species (Powell & Zielinski 1983); pine martens are more common in extensive forests, whereas stone martens are regarded as synanthropic, being associated with rural, agricultural and urban areas (Proulx *et al*. 2004, Herr 2008). Given the similarities between these two species, presumably they must face the same levels of intra-guild competition and predation, and be affected by similar climatic constraints; yet stone marten are considered to be habitat generalists, and are frequently associated with open areas (Jensen & Jensen 1970 cited in Herrmann 1994, Degn & Jensen 1977 cited in Herrman 1994, Herrmann 1994, Genovesi & Boitani 1997, Goszczynski *et al.* 2007), whereas pine marten are considered to be habitat specialists of old-growth forests (e.g. Brainerd *et al.* 1990), though it is often neglected that stone marten frequently occur in forest environments also (Virgos & Garcia 2002). Both species are food generalists, and where they occur allopatrically, small rodents, fruits and birds are important foods for both species (reviewed by Clevenger 1994a.). Where they occur sympatrically however, pine marten take more *Clethrionomys* voles, whereas stone marten take more *Microtus* voles (Posluszny *et al.* 2007). The absence of stone marten and other small generalist predators in Great Britain allow the British pine marten to make use of food resources that it would otherwise compete for on the continent, specifically *Microtus* voles and fruit.

7.3 Suitability of Modern Plantations as Habitats for Marten

The results of this study indicate that lowland conifer plantation forests provide good habitat for pine marten that is capable of supporting high population densities. The mean home range size of female marten observed in this study was the smallest yet recorded in the UK, and that for males was the lowest in any UK study with a comparable sample size (the only smaller being from a sample size of two males: Halliwell 1997). Habitat productivity or food availability are generally identified as the primary determinants of home-range size within a species (McLoughlin & Ferguson 2000); home ranges with high proportions of sub-optimal habitat that offer fewer resources tend to be larger (Soutiere 1979, Thompson & Colgan 1987, Balharry 1993a., Smith & Schaefer 2002). Comparison of home range sizes between this and other British studies suggests that lowland areas are capable of supporting higher densities of marten than upland areas (Balharry 1993a., Halliwell 1997, Bright & Smithson 1997). Lowland plantations are more productive and therefore provide a higher biomass of trophic resources for marten than upland plantations (Bright & Smithson 1997). In Scotland, lowland areas are often characterised by mature stands of forest, which provide greater structural complexity, habitat heterogeneity and species diversity than early-to-mid successional forests typical of upland areas (Balharry 1993a., Bright & Smithson 1997), addressing several important marten life requirements (Buskirk & Powell

1994, Buskirk & Ruggiero 1994). Ten of the eleven radiotracked marten were located in lowland rather than upland areas of Morangie, yet it remains undetermined whether these marten were selecting lowland habitats because they were inherently more productive, or because this is where their preferred habitats (i.e. mature forest and grass) occurred. Similarly, it remains unclear whether the quality of habitats offered by upland plantations could not be improved by management to produce a more natural forest structure and diversity.

Habitat quality cannot always be inferred from population density however, and the population density-habitat quality assumption can break down for several reasons (Van Horne 1983). High population densities can occur in marginal habitat if juveniles and sub-ordinates are prevented from entering high quality habitats and forced into habitat "sinks" where survival and reproduction rates are low. Whether the habitats in Morangie create a population source or sink cannot be tested unless demographic parameters such as reproductive or mortality rates are available from this and other studies for comparison. However, given that 89% of all animals captured within the study area were adults, many of which were displaying signs of breeding (i.e. 71% of tracked females), there is little to suggest that the habitats found were of poor quality. Small-scale variability in resources such as staple prey may cause temporal variability in local population densities which do not necessarily reflect habitat quality (Van Horne 1983). Populations of American marten have been reported to display six-fold fluctuations in size between years of high and low prey density (Thompson & Colgan 1987), and the existence of a similar pattern has been suggested in the UK (Lockie 1964). Particular caution should therefore be used when viewing the densities from studies that span a period of just one year, unless information about the inter-annual variability in prey populations at study sites is known. A long-term population density index of the marten's preferred prey, *Microtus* voles, was available in the present study (Chapter 6). This suggested that prey density during the study was neither unusually high nor low, and therefore the high densities observed were not likely to be the result of a *Microtus* population boom. However, as other UK studies have not reported prey densities, it remains unclear whether differences in marten densities between sites are due to variability in habitat quality or other factors such as prey availability. Temporal variability in local population densities can also occur where animals display a seasonal dependency for certain critical habitats (Van Horne 1983). There is some indication that habitat selection by Morangie marten differed seasonally; winter home ranges contained less grass than summer home ranges, and a greater proportion of locations occurred in closed-canopy forest in winter than in summer. Similar patterns have been observed in American marten; winter is associated with reduced use of non-forested habitats (Koehler & Hornocker 1977, Soutiere 1979), and an increase in the use of coniferous stands (Campbell 1979, Steventon & Major 1982, Spencer *et al.* 1983, Wilbert 1992). Marten are energetically constrained in winter, and therefore select habitats that reduce their energetic costs, particularly while resting (Buskirk & Powell 1994). Whilst seasonal habitat use has been reported, there is little evidence to suggest that marten seasonally shift their home range boundaries to encompass different habitat types, rather they seasonally adjust their selection of habitats within stable home ranges (Buskirk & Ruggiero 1994). Indeed, whilst each marten in this study was tracked in only one season, they were frequently trapped throughout their home range regardless of the season, so it is unlikely that seasonal use of habitats would affect population density estimates. However, it will almost certainly have implications for the results of habitat selection studies; generalisations about which habitat is best may depend upon season, and seasonal variation may even be mistaken for habitat flexibility or lack of selectivity (Buskirk & Powell 1994).

7.4 Habitat Fragmentation

In addition to forestry, the Scottish landscape is dominated by agriculture (predominantly livestock grazing pasture), and game-hunting (predominantly kept grouse moors). In these landscapes, forest fragmentation increases as the landscape matrix changes from forest to open (Forman & Godron 1986), with remnant forest fragments being increasingly separated by habitats that are avoided by marten (i.e. heath and pasture: Balharry 1993a., Bright & Smithson 1997, Halliwell 1997). For Mustelids such as marten, which are confined to a few habitat types, habitat fragmentation poses an especially great threat (Bright 1993, 2000). Compounding this there is growing evidence that Mustelids are subject to intra-guild predation by larger carnivores, which may be particularly prevalent in fragmented habitats (Brainerd *et al.* 1994, Kurki *et al.* 1998). Therefore Mustelids may face two threats as a result of habitat loss: from fragmentation effects and predation (Bright 2000). Habitat fragmentation has a disproportionately negative impact on habitat-specialist species, and favours those that can exploit the anthropogenic matrix between semi-natural habitats (Bright 1993, 2000). The implication of the marten's reluctance to cross areas without cover (e.g. Hargis *et al.* 1999; Bright & Smithson 1997, Smith and Schaefer 2002) is that at the landscape scale, the size and distribution of forest patches affects the intensity with which they are used (Snyder & Bissonette 1987, Chapin *et al.* 1997, Hargis *et al.* 1999). Even large-sized forest remnants may not be used if they are isolated from other suitable habitat patches (Chapin *et al.* 1997, Buskirk & Powell 1994). Forests should therefore be managed at the landscape scale to ensure that connectivity between forest patches is maintained, but further understanding of marten habitat requirements is needed in order to achieve this, which involves aspects of habitat other than composition; further investigation is needed in to the spatial configuration of forest mosaic attributes, such as forest patch size, shape, isolation, connectivity and edge characteristics.

The findings presented here and elsewhere (e.g. Brainerd *et al.* 1994, Clevenger 1994b) tend to suggest that the marten is more adaptable than previously believed. Whilst the existence of some structural elements of old-growth forests are important for pine marten, a high proportion of old-growth forest in the landscape is probably not (Brainerd *et al.* 1994, Kurki et al 1998). The marten's tolerance of forest fragmentation increases under certain circumstances, and marten will utilise open areas that provide sufficient structure as protective cover e.g. regenerating clear fells and brash (Steventon & Major 1982, Buskirk & MacDonald 1984, Bissonette *et al.* 1997, Potvin & Breton 1997, Potvin *et al.* 2000), rock fields (Streeter & Braun 1968, Balharry 1993a. Slauson 2003), and dense shrubs (Martin 1987, Clevenger 1994b., Paragi *et al.* 1996, Slauson *et al.* 2007). Indeed, the structural complexity provided by rock habitats appears to have enabled British marten to inhabit areas with high levels of forest fragmentation, although population densities were lower as a result (Balharry 1993a., Webster 2001). The importance of non-forested scrub or transitional habitats, which provide marten with essential physical structure and trophic resources, should not be underestimated. These habitats are particularly important for connecting larger forest fragments and are potentially the principal source of rest sites in plantation forests, though it should be noted that these habitats cannot necessarily replace continuous extents of forest. Although sufficient horizontal and vertical structure are essential for retaining marten in fragmented areas, interspersion of stands in various seral stages may benefit marten by providing multiple foraging opportunities (Brainerd 1990, Thompson & Harestad 1994, Payer & Harrisson 2003). Fragmentation of old-growth forests with early-successional stages may favour forest dwelling generalist predators by increasing the amount of areas with grass-dominated vegetation that are suitable habitat for their preferred prey, *Microtus* voles (Henttonen 1989, Angelstam 1992, Hansson 1994). For example, the abundance of fox (Kurki *et al.* 1998) and crows *Corvus* spp. (Andrén 1992) increase with increasing fragmentation in Fennoscandia, though the relationship appears to be less clear for pine marten however (Kurki *et al.* 1998). Although a positive response to low fragmentation may be expected by marten as long as habitat connectivity is maintained, and population densities may even increase if non-forest areas were small enough to permit marten movements across them whilst being large enough to support increased densities of *Microtus* (Hargis *et al.* 1999). Increased abundance of generalist predators due to fragmented forest landscapes may however be in direct conflict with habitat management for species of conservation concern, such as capercaillie (Kurki & Linden 1995; Kurki *et al.* 1997). Although whilst increased abundances of fox and crows are potentially able to cause elevated predation pressure on ground-nesting birds when forests become fragmented (Henttonen 1989, Rolstad & Wegge 1989, Angelstam 1986, Summers *et al.* 2004), the evidence against pine marten is weaker (Kurki et al 1998, Smedshaug *et al.* 1999, Baines *et al.* 2004). In fact it has been suggested that controlling fox numbers through legal means would be beneficial to both small game and marten (Baines *et al.* 2004), as marten numbers appear to increase in the absence of competition and predation from fox (Smedshaug *et al.* 1999).

7.5 Martens & the Future of Forest Management in Britain

For years, the forest management paradigm in Britain has been to plant, clear-cut and replant even-age monocultures of fast-growing non-native conifers (Heitzman 2003). Today, there are approximately 1.5 million hectares of conifer forests in Britain composed entirely of plantations of this sort established since 1900 (Malcolm *et al.* 2001). High-yield species such as Sitka spruce are commonly grown in upland areas in Britain where the risk of wind damage to the stand is an important consideration (Quine & Bell 1998, Heitzman 2003, Hale *et al. in prep.*). To reduce the risks of wind damage, current management of Sitka spruce tends to retain a stand basal area greater than 30 m^2 per hectare throughout most of a 35- to 45-year rotation (Edwards and Christie 1981). The threat of wind throw, along with the low economic value of small diameter stems, means that despite high planting densities some spruce stands may never be thinned (Heitzan 2003). The closed-canopied stands this creates are unsuitable habitat for marten, which they are either reluctant to use (Chapters 3 and 4), or do so at very low densities (Bright & Smithson 1997). However, recent changes in forest management trends have moved the emphasis of forestry towards establishing continuity of woodland conditions whilst increasing the diversity of horizontal and vertical structure within stands; achieved by encouraging mixed age classes and tree species and using selective individual tree silviculture rather than clear-cutting (Pommering & Murphy 2004). An estimated 500-700 thousand hectares of conifer forest in Britain occurs in sites that are sufficiently wind-firm to justify attempting their transformation to greater species and structural diversity through low impact silvicultural systems (Malcolm *et al*. 2001). A vast amount of forest habitat therefore has the potential to be improved for pine marten habitation.

Transformation of regular plantation structures to irregularly-structured stands is still in trials, and there are two contrasting approaches that can be adopted for transformation (Malcolm *et al.* 2001). Stands can be progressively thinned to foster structural diversity and allow the establishment of vegetative layers beneath the canopy; alternatively, canopy gaps of appropriate sizes can be deliberately created in which to foster regeneration within the stand, though this approach requires more explicit guidance of desirable gap sizes for it to be successful (Malcolm *et al.* 2001). Regardless of the method used, it is clear that light management is one of the key considerations when managing forests for increased structural diversity and natural regeneration (Hale *et al. in press*). Light penetration is influenced by the continuity of forest canopy, the presence and size of canopy gaps and by topographical parameters such as slope and aspect (Malcolm *et al.* 2001). Simply structured forest habitats can be rapidly improved for marten by creating spatially extensive cover of mesic shrub and herbaceous species by lowering tree densities and thinning tree stands (Slauson *et al.* 2007). By increasing sub-canopy light conditions forest managers can encourage shrub cover to develop within stands, providing marten with greater vertical and horizontal diversity, and with structures that can be used as dens, waylaying concerns about the lack of arboreal cavities provided by plantation forests (Birks *et al.* 2003, Birks *et al.* 2005). Thinning of stands allows vegetation such as grasses (e.g. *Deschampsia flexuosa* and *Molinia caerulea*) and rushes (e.g. *Juncus inflexus*) to establish, particularly in dampers areas (e.g. those with higher values of TWI). By creating suitable habitat for *Microtus*, forest managers are indirectly creating foraging habitat for pine marten.

Colonisation by dense ground vegetation, particularly grass species, heather, shrubs (e.g. rhododendron), bramble or bracken prevents successful conifer germination (Jones 1945, McNeill 1955, Robertson 1976, Bergman 1981). Increasing light transmission regimes within forest stands has therefore conflicted with forestry interests in the past. However, as forests are increasingly managed for biodiversity conservation rather than economic productivity, encroachment in stands by vegetative field and shrub layers may now be less controversial. The light regime beneath uniform conifer stands is generally inadequate to sustain the development of germinating tree seedlings (Malcolm *et al.* 1999), yet increasingly, forest managers are looking to ways of encouraging the natural regeneration of forest stands, including stands thinning and the creation of canopy gaps (Pommering & Murphy 2004). The increasing willingness of forest managers to plant native Scots pine, a light-demanding species, rather than Sitka spruce, a shade-tolerant species (Mason *et al.* 1999, Hale *et al. in press*), should therefore be congruent with the encouragement of ground vegetation and shrubs. Scottish forests are often managed for capercaillie, for which blaeberry is the ideal ground vegetation (Moss & Picozzi 1994, Kortland 2006). Shade-tolerant blaeberry is out-competed by heaths, which prefer lighter sub-canopy conditions (Parlane *et al.* 2006). Management for capercaillie therefore often involves increasing the basal area of stands to reduce competition with heather. Whilst this practice will limit the amount of grass vegetation within forests stands, blaeberry was a heavily utilised seasonal food source for marten, which also provided them with dense ground cover. Therefore the management of plantation forests for these two species should still be compatible as long as marten have sufficient access to suitable herbaceous habitat in which to hunt.

The concerns that have been raised about forest fragmentation and the threat of marten populations becoming isolated mean that the establishment of forest margins at transitions zones between open and forested landscapes is crucial to maintain the habitat connectivity of forest remnants for marten. Encouragement of shrub habitat within these transition zones is critical to maintaining connectivity between large forested extents and smaller remnants. Riparian corridors, which are naturally structurally and species diverse (Nilsson *et al.* 1989, Jones *et al.* 1994, Nilsson *et al.* 1994) and as they are associated with *Microtus*-rich habitats (Chapter 4) may be particularly effective in connecting larger forest fragments. Riparian habitats have repeatedly been found to be of significance to Mustelid species (Zielinski *et al.* 1983, Hargis *et al.* 1999, Virgos 2001, Rondinini & Boitani 2002, Rondinini *et al.* 2006) but become particularly important in landscapes that are highly fragmented or disturbed (Forsey & Baggs 2001). The ecological gradient between forested and open environment could be lessened further through sympathetic livestock grazing regimes on grasslands at forest boundaries. Grazing pressure has a direct affect of *Microtus* abundance (Hope *et al.* 1996, Evans *et al.* 2006), but also affects shrub generation. Marten will move a short distance (< 50 m) from the forest edge to hunt in tall herbaceous vegetation, but will venture further still (< 150 m) from the edge if shrub cover is present, even if only scattered. Relaxing grazing to create a buffer of tall, dense grass swards dispersed with patches of shrubby vegetation around the forests perimeter can also be used as a means of connecting forested habitats.

7.6 Management Recommendations

The present findings demonstrate that pine marten utilisation of habitats within plantation forests is determined by the need for cover and by prey availability, predominantly that of *Microtus* voles. Management recommendations with which to improve plantation forests for marten habitation are provided below. It is likely that these improvements will be more effectively implemented in productive lowland forests that are already inclined to favour martens due to their increased habitat heterogeneity compared to upland habitats. However, upland plantations may be greatly improved in areas that are widn-firm enough to do so.

- Create more areas of low-canopy cover in which species-rich herbaceous vegetation can develop. This may be particularly effective if canopy gaps are deliberately created in areas with high TWI values on south-facing aspects; damp soils are routinely left unplanted by forest managers and so would be compatible with existing practice, whereas south-facing aspects would receive more sunlight for a given gap size and are more likely therefore to be encroached by grasses with little further encouragement.

- Increase horizontal and vertical structural diversity within stands through the creation of multi-aged, mixed species stands. This is in keeping with the existing aims of forest managers to transform simply structure stands through sympathetic silvicultural techniques into structurally heterogeneous stands.

- Retain and encourage shrubby vegetation, particularly gorse, rhododendron and *Salix* spp. This is particularly important in the transition zone between forested and open land-uses. Shrubby vegetation naturally occurs at forest edges, especially along riparian corridors, making the establishment of this habitat logistically feasible whilst creating the least conflict with forest other interests. Shrub vegetation should also be encouraged within forests;

although this may conflict with seedling regeneration within forest stands themselves, linear features such as rides and power-line gaps are often predisposed to cover of this type thus necessitating only its retention and sympathetic management.

- Encourage heterogeneity in the ground vegetation layer by managing light regimes to promote shade-tolerant blaeberry as well as light-demanding grasses. A diversity of food resources can be provided by creating a variety of vegetation types, providing marten with seasonally important foods.

- Increase forest stand species diversity to include mixtures of deciduous trees, particularly small-leaved or fruit-bearing species. Small leaved species area associated with greater vegetative ground cover, whilst berries are a seasonally important food source for marten.

- Retain all brash and debris resulting from clear-felling or wind-throw *in situ*, particularly if the juxtaposition of the area relative to suitable forested or shrubby habitats would allow it to be utilised by marten without having to cross avoided habitat such as open moor.

- Relax grazing pressure on rough grasslands at forest edges to increase grass sward height and encourage *Microtus* populations.

- Manage forest patches at a landscape scale to maintain habitat connectivity between remnants, though further study is needed to provide guidance recommendations regarding ideal spatial configurations of landscape mosaics.

7.7 Suggested Future Research

Some questions remain unanswered by the topics covered in this thesis, whilst others have been prompted by the results found. What follows is a brief list of topics that warrant further investigation:

- Forests should be managed at the landscape scale to ensure that connectivity between forest patches is maintained, but a true understanding of marten habitat requirements is needed in order to achieve this. Further investigation is needed into the spatial configuration of forest mosaic attributes, such as forest patch size, shape, isolation, connectivity and edge characteristics, which predispose a forest patch within the landscape to be used or not by marten. A study comparing the spatial attributes of several forests of varying degrees of fragmentation with and without pine marten present would therefore be timely.

- The unexpected lack of evidence that *Microtus* populations in the study area were cycling merits an explicit study of vole population dynamics in areas of Scotland outside of the Borders, from where almost all of our information on the subject originates. A long-term population monitoring project to measure seasonal and annual fluctuations in vole abundances using either (preferably) live-trapping or a direct index of vole abundance (e.g. field signs) rather than an indirect index (e.g. raptor breeding productivity).

- The British pine marten is clearly in direct competition with the red fox as the preferred prey species of both predators is the Microtus vole. Estimates of fox abundance were not available from the study area during the period of investigation, therefore it remains unclear what the level of competition the local fox population exerted on pine marten in Morangie. A comparative study of diet and use of foraging habitats, or one comparing diets of marten in areas with differing fox density may allude to how these two generalists allocate resources.

7.8 Concluding remarks

During the course of this study it became apparent that public knowledge about pine marten in Scotland was generally lacking, or was misrepresented because of negative public perception (*personal observation*). Marten were commonly described as “pests” and “vermin”, no doubt because of an historical persecution relating to conflicts with game-keeping. Such emotive labels are unjustifiable, and yet they highlight the public’s ignorance surrounding marten ecology, particularly regarding their dietary habits. Although in a minority, misconceptions about marten ecology also existed among some foresters, particularly relating to the population densities that marten can achieve (*personal observation*). Current attitudes towards the marten could be made more favourable: a shift in public perception could result in a change of attitude, and a clear understanding of the ecology of the animal and reasons for its vulnerability to persecution is essential for future education and conservation (Balharry 1993a.). Public perception is fickle, and can be directed through positive publicity and education. News stories about the potential for pine marten to act as implements of biological control, preferentially preying upon the larger, more terrestrial-dwelling grey squirrel in the fight to save the red squirrel from extinction (i.e. The Scotsman 2008, The Telegraph 2008) are at least positive, if not necessarily supported by anything other than anecdotal evidence and wishful thinking. A more practical message to communicate is that the newly structured plantation forests that are increasingly used by the public for recreation and appreciated for their biodiversity are also proving beneficial for pine marten. Within these forests, the pine marten's staple foods are *Microtus* voles, berries and small birds. Whilst they may occasionally take species of conservation concern, this appears to be the exception rather than the norm. The pine marten is a conservation success story in Scotland, which is sadly something of a rarity. Brought back from the brink of extinction at the beginning of the 20th century, the marten has increased its numbers as well as its distribution, aided by sympathetic land management and protective legislation. Yet the species' long-term viability is dependent on policy, management and public perception. The success of the conservation and forest management efforts responsible for the upturn in the pine marten's status should therefore be widely accredited and publicised to increase public and political recognition.

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