FORAGING, ROOSTING AND SURVIVAL OF NATTERER'S BATS, MYOTIS NATTERERI, IN A COMMERCIAL CONIFEROUS PLANTATION

GARRY MORTIMER

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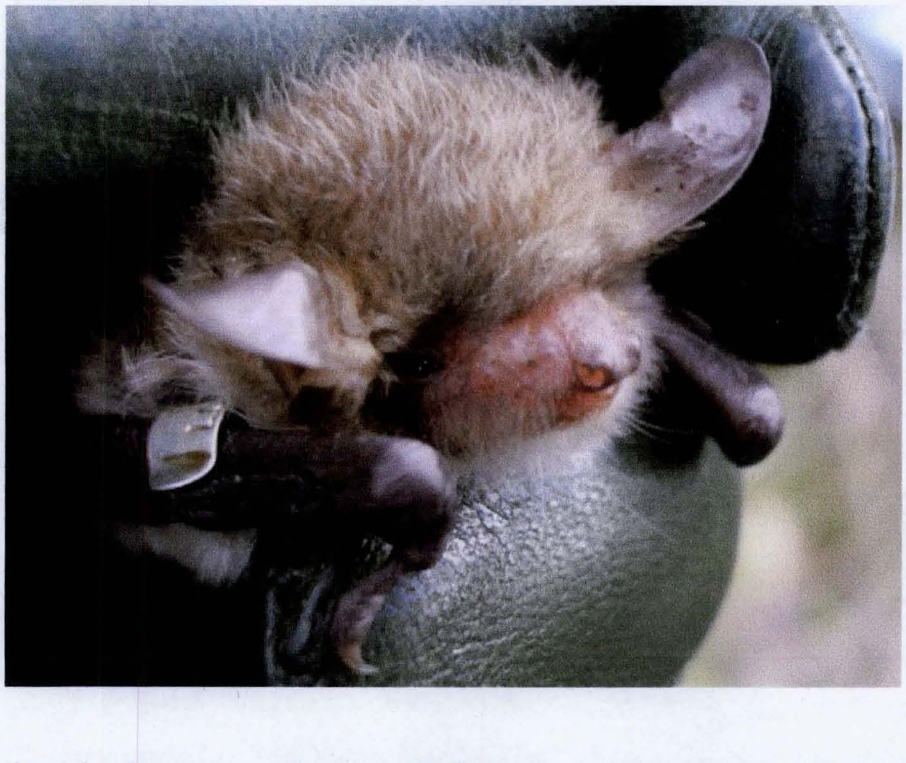

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Thesis supervisor
Dr J Graves
School of Biology
University of St Andrews

Contents

Page

Page

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Abstract

I studied Natterer's bats in Tentsmuir Forest, a 9143-hectare commercial coniferous plantation on the NE coast of Fife, Scotland that has been planted predominantly with Scots and Corsican pine. Two maternity colonies of approximately 111 & 68 adult females regularly use bat boxes within the forest as summer and maternity roosts. The foraging ecology, roost dynamics, population structure and survival rates of the Natterer's bats present were determined in this study by radio tracking and banding.

The two colonies occupied home ranges of 4.43 & 6.46 km^2 with densities of approximately 25 & 10 adult females per km^2. Individual bats had a mean foraging home range of 0.47 km^2 that contained 1-3 core foraging areas, which did not overlap with the core areas of other individual bats.

Adult female Natterer's bats preferentially foraged in stands of mature Corsican pines and around water bodies; grazing meadows and arable land adjacent to the forest were avoided. They also foraged extensively in mature Scots pine, the predominant habitat. However, it was underused relative to its availability.

Out of a set of five different bat box types, the bats preferentially chose old square wooden and round woodcrete boxes to use as summer and maternity roosts. I found that the bats also roosted in a specific type of natural cavity in double-leadered Corsican pines that has not been recorded before. Bats changed roost sites every 2.5 days on average.

Natural tree roosts were used significantly more than bat boxes; however, there were no significant difference in the number of day's bats occupied the different roosts.

Once a female was older than 1 year old the annual survival rate was between 0.79-0.87. Juveniles had a first year survival rate of 0.38-0.58. It was not possible to calculate male survival rates.

These findings shed new light on how commercial plantations are a valuable foraging and roosting habitat for Natterer's bats and given the large amount of commercial coniferous forest now planted in the U.K. this has important implications for planning and implementing conservation management of these species. Chapter 7 contains an action plan with recommendations on how to improve existing and new coniferous forests to make them more "bat friendly" and to promote bat conservation.

CHAPTER 1

General introduction

1.1 General introduction

Worldwide, bat populations are threatened, to a large degree, by degradation or destruction of roosting and foraging habitats. It is estimated that worldwide over 50% of bat species are listed as vulnerable, endangered, critically endangered or recently extinct (Hutson et al. 2001, Jones 2002). In the USA about 50 percent of North American species are currently considered endangered or threatened at the national or State level (O'Shea & Bogan 2000). In the U.K. bats are also under pressure with several species now seriously threatened. There has been serious concern that bats in the U.K. have been suffering a long-term decline (Mayle 1990, Harris et al.1995, Stebbings 1995). Of the 16/17 species considered resident, 8 are thought to be under threat, vulnerable or rare. One species, greater mouse-eared bat, *Myotis myotis,* is on the verge of extinction and the numbers of pipistrelles, *Pipistrelle sp.* the most common bats have declined by about 70% between 1978 and 1993 (Entwistle et al. 2001).

Sound conservation management decisions on a species or community basis require at least knowledge of the basic ecology of the species involved. Worldwide, many species of bats are declining for various reasons, and there is an urgent need to collect ecological data for conservation concerns. Effective management relies on several important factors including identifying the location and size of populations and establishing baseline measurements e.g. survival rates, foraging and roost dynamics, movement and home range size against which to measure future changes. There is a paucity of information regarding survival rates and population dynamics on many species of bats, traits that are particularly important in a conservation management context.

All British bats are protected by a range of legal acts, including the Wildlife and Countryside Act 1981 (Schedule 5), The Wild Mammals (Protection) Act 1996 and the Countryside and Rights of Way Act (CROW) 2000. Internationally bats are also protected by the Bonn Convention, the Bern Convention (Appendix II) and listed on Annex IVa of the EC Habitats and Species Directive. Bats may also be protected by means of site safeguard measures, for example by virtue of their roost site or feeding grounds being notified as a Special Area of Conservation (SAC) or a Site of Special Scientific Interest (SSSI).

In the U.K. legislation on preserving foraging and roosting habitat covers all species of bats present, yet for some species there is an alarming lack of species-specific information on habitat requirements. Conservation legislation not only covers the bat but also its foraging and roosting habitats. With the status of over 50% of U.K. bats classed as threatened, vulnerable or rare (Entwistle et al. 2001), there is an urgent need to obtain data so that conservation management issues can be addressed adequately. With many bat species in decline, due in some measure to habitat loss, knowledge of habitat requirements of individual species becomes paramount to conservation management (Entwistle et al. 1996).

In the past 80-90 years there have been major changes to the U.K. woodland landscape. In 1920 woodland accounted for only 5% of the U.K. land surface, this has now doubled to 10% (Kunz & Racey 1998). This increase is mainly due to the Forestry Commission which has planted large areas with commercial coniferous plantations. In the U.K. the proportion of coniferous trees to broadleaf is approximately 65% to 35% while in Scotland (Figure 1.1) the ratio is 80% to 20% (Forestry Commission 2000).

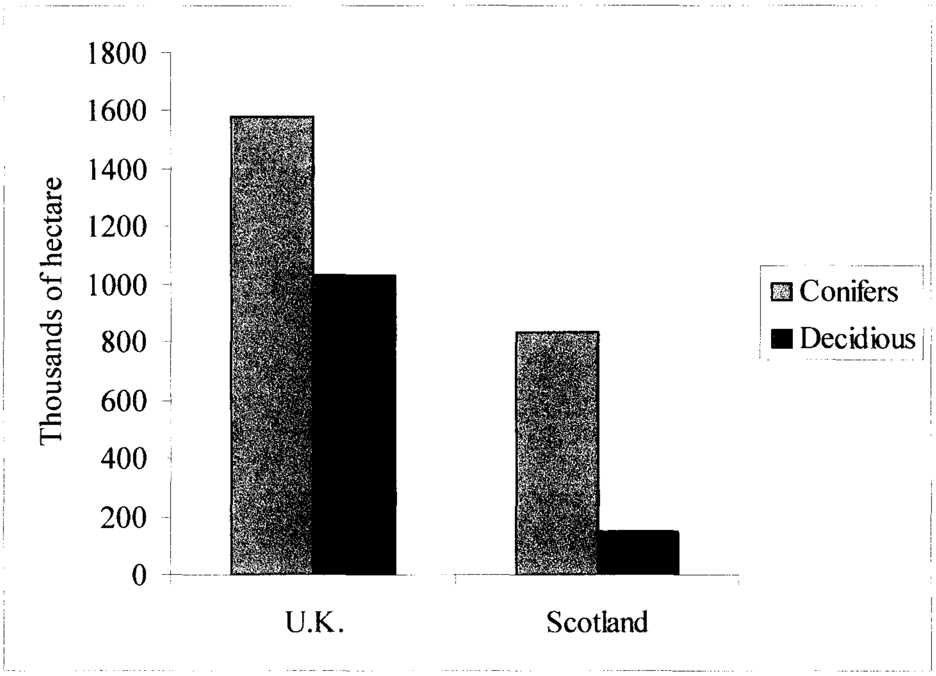


Figure 1.1: Areas of coniferous and deciduous forest in the U.K and Scotland (Forestry Commission 2000).

This has important conservation implications for some species of bats. The results of almost every bat habitat survey on a U.K. national or local scale has stated that commercial coniferous plantations are avoided or used only marginally by bats and that the main foraging areas of vespertilionid bats are associated with broad-leaved woodland and water (Harris et al. 1995, Walsh & Harris 1996a, 1996b, Kunz & Racey 1998). Russ & Montgomery (2002) in a study in Northern Ireland stated that commercial coniferous woodland is potentially less valuable to foraging bats than deciduous woodland and that more emphasis should be placed on increasing areas of semi-natural deciduous woodland.

Commercial coniferous plantations have been considered poor areas for bats for two main reasons: 1). Since the trees are harvested at an early age (60-80 years), there is an almost complete lack of natural roosting cavities (Altringham 1998). Many bat groups have erected bat boxes in commercial coniferous plantations e.g. Thetford Forest (Boyd & Stebbings 1989) and discovered that they are often rapidly used by bats for both roosting and breeding. 2). Commercial coniferous forests, particularly those planted with non-native species, typically do not offer a high level of biodiversity (Garrod & Willis 1997), and are thought to support smaller number of insect species than in equivalent areas of broad leaf forest, which could constitute reduced prey availability (Winter 1983, Entwistle et al. 2000).

With the advent of radio transmitters small enough to attach to the smallest bats there has been an upsurge in habitat studies on several species of bats (Vonhof & Barclay 1996, Boonman 2000, Russo et al. 2004). Some studies have looked at bats living in managed woodland particularly in North America (Grindal & Brigham 1999, Elmore et al. 2004). The scale, the species present, stand structure and age of the North American forests are inherently different from the managed woodland in the U.K, and until this study there has been a paucity of radio tracking studies on any U.K. bat species present in commercial coniferous plantations.

The dynamics of bat populations are more typical of large than small mammals and for their body size, bats live longer than any other order of mammal (Austad & Fischer 1991). Brandt's bat *Myotis brandtii*, (which is a similar size to Natterer's bat) have been recorded up to 38 years old (Wilkinson & South 2002). Bats require high survival rates for populations to persist due to their low reproductive rates (1-2 young per year) and long life spans. A low reproductive rate makes it difficult to reverse downward trends in population which are then consequently very susceptible to elevated mortality or depressed recruitment (O'Shea & Bogan 2000). Even small reductions in fecundity and survival, especially of females, can cause a population to decline (Boyd & Stebbings 1989).

Mark- recapture studies are a powerful tool for providing important information on factors essential for conservation management e.g. estimating population size and trends, survival rates, migration patterns, behavior, evaluating the impacts of threats on survival and highlighting areas where further research is needed (Baker et al. 2001, Lettink & Armstrong 2003). Knowledge of survival rates is of special interest in the study of bat population dynamics. Reliable estimates of annual survival are essential for effective conservation because the probability of survival, particularly of adult survival has the greatest influence on population growth rates of long-lived vertebrates. First-year survival of juveniles, together with emigration and immigration, determines recruitment to reproductive age (Prevot-Julliard et al. 1998, Lebreton et al. 1992, 1993, Lebreton & Pradel 2002, Sandercock 2003, Sendor & Simon 2003). For the last 75 years survival studies have made use of individual-specific alloy rings attached to the forearm of the bat (Baker et al. 2001).

Natterer's bat *Myotis nattereri* (Kuhl 1817) is one of the least studied European bats with relatively little known regarding basic ecological parameters. The aim of this study is to determine Natterer's bats foraging ecology, roost dynamics and survival in a commercial coniferous plantation: Tentsmuir Forest, situated in NE Fife, Scotland.

There have been Natterer's bats present in Tentsmuir Forest at least since 1985 when they were discovered breeding in outbuildings and the Fife Bat Group erected approximately 90 bat boxes in several locations within the forest (the number is uncertain). These were soon holding numbers of both Natterer's bats and pipistrelle species (Mortimer 1993). Since 1998 the bats present in the bat boxes has been ringed. Boxes have been checked twice yearly and any unmarked bats have been fitted with a numbered alloy bat ring on the forearm (Hatton & Cohen 2000).

Many European bat species have been the subject of intensive ecological studies e.g. serotine bat *Eptesicus serotinus* (Catto et al. 1995, 1996), Daubenton's bat *Myotis daubentonii,* (Swift & Racey 1983), Leisler's bat *Nyctalus leisleri,* (Shiel & Fairley 1998, 1999), common pipistrelle *Pipistrellus pipistrellus*, (Arlettaz et al. 2000), lesser horseshoe bat *Rhinolophus hipposideros* (Bontadina et al. 2002), yet there have been relatively few studies on Natterer's bats. Smith (2000) studied the foraging and roosting dynamics of Natterer's bats in open pastureland on the English/Welsh borders and he found that dense conifer plantations were avoided. Other studies in Europe on Natterer's bats found that some foraging occurs in coniferous woodland, but these were natural or ancient coniferous woodland (Siemers et al. 1999). However, no research to date has looked at Natterer's bats present in commercial coniferous plantations. This study has started to address this by using radio tracking methods to investigate the roosting and foraging dynamics of adult female Natterer's bats located in bat boxes and to determine the survival rates from mark-recapture data from the bat-ringing programme for 1998-2004.

1.2 Bat conservation

The main areas of concern for the conservation of bats are a) summer roosting areas, b) foraging areas and c) winter roosts or hibernacula. In the UK the main threats to bat conservation in 2003 were identified as building demolition and alterations, bridge maintenance works, tree works, barn conversions and disturbance at household roosts (BCT 2001). As some species have a very narrow band of roost choice, the above have an obvious impact on roost dynamics, often at a time when maternity colonies are present. This can decrease an already low reproductive rate. Other threats include the use of wood treatment chemicals in roof spaces and persecution by householders.

It is much more difficult to assess the impact to foraging areas. This is particularly relevant for many species when the foraging requirements are either poorly known or completely unknown. Loss of habitat, including isolation through fragmentation, is considered the main threat to foraging bats e.g. in the U.K. 23% of hedgerows and 75% of ponds were lost during 1984-1990. Many species of bats habitually use linear features such as hedgerows, tree lines, woodland edges and rivers for commuting to and from roosts and feeding areas. This is considered particularly important in open agricultural landscapes (Grindal 1996, Walsh & Harris 1996a, 1996b, Verboom & Huitema 1997).

Disturbance or exclusion of hibernating bats e.g. through building works can also have disastrous effects particularly during spells of cold weather. Torpid, hibernating bats are slow to become active and escape from disturbance and also available food supplies will be very limited (Entwistle et al. 2001).

1.3 Bat abundance in U.K.

The first comprehensive reviews of the current status of UK bat populations (Table1.1) were produced by Harris et al. (1995). Before this sizes of bat populations were estimated from counting bats at roosts and hibernacula and by small scale localised mark and recapture studies. The major drawbacks were that it was an ad hoc approach with no standardised techniques applied and therefore it was difficult to make comparisons between areas.

Common name	Latin	Status in United Kingdom
Bandit Pipistrelle	*Pipistrellus pipistrellus*	Not Threatened
Soprano Pipistrelle	*Pipistrellus pygmaeus*	Not Threatened
Nathusius' pipistrelle	*Pipistrellus nathusii*	Unknown
Brandt's bat	*Myotis brandtii*	Vulnerable
Whiskered bat	*Myotis mystacinus*	Vulnerable
Daubenton's bat	*Myotis daubentonii*	Not Threatened
Natterer's bat	*Myotis nattereri*	Vulnerable
Bechstein's bat	*Myotis bechsteinii*	Rare
Greater mouse-eared bat	*Myotis myotis*	Extinct?
Brown long eared bat	*Plecotus auritus*	Not Threatened
Grey long eared bat	*Plecotus austriacus*	Vulnerable (Endangered?)
Noctule	*Nyctalus noctula*	Vulnerable
Leisler's	*Nyctalus leisleri*	Indeterminate
Serotine	*Eptesicus serotinus*	Vulnerable
Barbastelle	*Barbastella barbastellus*	Indeterminate
Greater Horseshoe bat	*Rhinolophus ferrumequinum*	Endangered
Lesser Horseshoe bat	*Rhinolophus hipposideros*	Endangered

Table1.1: Status of bats in United Kingdom (from Harris et al. 1995)

Until recently the Harris et al. (1995) review was the best estimate of population sizes and trends available, but the authors acknowledged that these estimates were not very reliable and should be treated with caution. This was due to the lack of published quantitative data available either historically or currently. In 1996 a pilot scheme, the National Bat Monitoring Programme (NBMP) was launched by the Bat Conservation Trust (BCT) and the Joint Nature Conservation Committee (JNCC) aimed at developing a volunteer network-based strategy to monitor bat population trends at a U.K. level (BCT 2001). The NBMP was fully operational in 2000 and the target was to provide population trend information for all U.K. resident bat species using 3 different methods. These methods, field transect, hibernation and colony surveys are, however, open to improvement with new options being considered when suitable. At present the NBMP is collecting data on 11 of the 16 U.K. resident species and has reasonably good population trend data for 9 species at the U.K. level, *i.e.* the ability to detect declines of 25% over 25 years on a national scale. For Natterer's bats the NBMP can only illustrate trends for hibernation surveys due to a lack of historical data and the difficulty in developing field survey methods for this species (BCT 2001).

As with many species, bat numbers and species diversity decrease with increasing latitude, only nine of the 16/17 British bat species occur in Scotland, and the number of species decreases still further towards the north of the country (Racey et al. 2003). In the U.K. habitat survey, regression analysis identified a south-north negative gradient in bat abundance. The general concept is that as temperature decreases with latitude so does diversity (Walsh & Harris 1996a).

In Scotland, five species are considered to be common and/or widespread, and a further four (or possibly five) are rare and/or with restricted distribution Table 1.2). Recent evidence now suggests that Nathusius' pipistrelle *Pipistrellus nathusii*, might have a small resident population. A further four species have been recorded as occasional vagrants.

Common name	Latin	Status in Scotland
Bandit Pipistrelle	*Pipistrellus pipistrellus*	Not Threatened
Soprano Pipistrelle	*Pipistrellus pygmaeus*	Not Threatened
Brown long-eared bat	*Plecotus auritus*	Not Threatened
Daubenton's bat	*Myotis daubentonii*	Not Threatened
Natterer's bat	*Myotis nattereri*	Vulnerable
Whiskered bat	*Myotis mystacinus*	Rare
Noctule	*Nyctalus noctula*	Rare
Leisler's bat	*Nyctalus leisleri*	Rare
Nathusius' pipistrelle	*Pipistrellus nathusii*	Rare
Brandt's bat	*Myotis brandtii*	Rare

Table 1.2: Status of bats in Scotland (Racey et al. 2003)

1.4 Habitat preferences

The pivotal national surveys on bat abundance and habitat availability by Harris et al. (1995) and Walsh & Harris (1996a, 1996b) provided the first comprehensive studies on a national scale for the U.K. They stated that in general, bat abundances were positively related to the availability of woodland, vegetation corridors, lacustrine and riverine habitats and negatively related to the availability of arable land. They also stated that conifer plantations represent a less optimal woodland type and that a lack of gaps in large contiguous conifer blocks in the uplands confirmed their low value to foraging bats. This and previous studies stated that, in general, broad-leafed woodland and riparian habitat are pivotal to bats in the U.K.

In 2001, the JNCC issued a report on "Habitat management for bats" that was a review of all the available and up to date information on the habitat requirements (Table 1.3) for all U.K. bats (Entwistle et al. 2001). Coniferous forests were found to be used only marginally for most species of bats including Natterer's. The report stated that key habitats for bats are freshwater, deciduous woodland, grassland and linear features. Other habitats that are less favoured include coastal areas, moorland and arable farmland (Entwistle et al. 2001).

Entwistle et al. (2001) found that Natterer's bats are normally associated with broadleaved, wet woodland, tree lines and along woodland edges. Smith & Racey (2002) found that semi-natural broad-leaved woodland and open water sheltered by tree cover were the prime foraging habitats and that dense conifer plantations are avoided.

It is obvious from all the literature that coniferous plantations as a foraging habitat for U.K. bats are considered less optimal than broad-leafed woodland. Yet, several of the major plantations hold large numbers of bats, normally where extensive bat box schemes are present. This present study is one of the first to specifically look at foraging and roosting habitat preferences for any U.K species of bat present in commercial coniferous plantations.

Key ■ = used regularly. ◩ = used occasionally □ = not used	Woodland Edge	Riparian Veg.	B.L.Woodland	Treeline	Parkline	Mixed Woodland	Hedgerows	River/Canal	Woodland ride	Lake/Reservoir	Pond	Wet Woodland	Wood. Clearings	Pasture	Suburban	Single Trees	White Lighting	Meadows	Coniferous Plant.	Ditches	Urban	Coastal areas	Arable
Pipistrelle sps.	■	■	◩	■	■	◩	■	■	◩	■	■	◩	■	◩	■	■	■	◩	◩	◩	◩	□	◩
Serotine	■	◩	◩	■	■	◩	■	◩	◩	◩	◩	◩	◩	■	■	■	■	■	◩	◩	■	□	□
Greater Horseshoe	■	◩	■	■	◩	◩	■	◩	■	◩	◩	◩	◩	■	◩	◩	□	◩	◩	◩	□	□	□
Daubenton's	◩	■	◩	◩	□	◩	■	■	◩	■	◩	◩	◩	□	◩	◩	□	□	◩	■	□	◩	□
Natterer's	■	■	■	■	■	■	■	◩	■	□	◩	■	□	■	□	◩	□	■	□	□	□	□	◩
Bechstein's	■	■	■	■	◩	■	■	◩	■	◩	◩	□	■	□	◩	□	□	□	◩	□	□	□	□
Leisler's	□	□	◩	□	◩	◩	□	■	□	■	■	□	◩	■	□	□	■	◩	■	□	◩	■	□
Noctule	■	■	□	□	■	□	□	■	□	■	■	□	◩	◩	◩	□	■	◩	□	□	◩	□	□
Brown long eared	■	◩	■	■	◩	■	■	□	■	□	□	□	◩	□	□	◩	□	□	◩	□	□	□	□
Whiskered	■	■	■	□	■	◩	□	■	□	■	■	□	◩	□	□	□	□	□	◩	□	□	□	□
Grey long eared	■	□	◩	◩	■	◩	□	□	□	□	□	□	□	◩	■	■	◩	□	◩	□	□	□	□
Barbastelle	■	■	■	□	□	■	□	◩	■	◩	◩	□	■	□	□	□	□	□	□	□	□	□	□
Nathusius'pipistrelle	■	■	■	■	◩	□	□	■	◩	□	□	□	□	□	◩	□	□	□	□	□	□	□	□
Brandt's	◩	■	■	□	□	■	◩	□	□	□	□	□	◩	□	□	□	□	□	■	□	□	□	□
Lesser horseshoe	□	■	■	■	◩	◩	■	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□	□

Table 1.3: Habitats of importance for British bats (from Entwistle et al. 2001).

1.5 Commercial coniferous plantations.

In 2000 the estimated woodland area in Great Britain, was 2,716 thousand hectares, 1,324 thousand hectares in Scotland, 1,104 thousand hectares in England and 288 thousand hectares in Wales. In land cover this equates to approximately 8% of England, 17% of Scotland and 14% of Wales. The British Forestry Commission maintains data on creation of new forest areas and restocking of existing forest areas. Records for the last 10 years suggest that new forests were created at a rate of about 17,000 ha y^{-1} for the period 1990 to 2000 (Forestry Commission 2000).

Approximately 58% of the woodlands in the UK are planted conifer plantations and in Scotland (Figure 1.1) the difference is much more marked, with over 80% of woodlands being commercial coniferous plantations. What is more striking is that these commercial plantations are a new feature of the U.K. landscape. The first plantations were commissioned only 80-90 years ago.

From a conservation aspect these plantations have been successful for some species (goshawk *Accipiter gentiles,* common crossbill *Loxia curvirostra*, siskin *Carduelis spinus*, and pine martins *Martes martes*), yet for many species found at least occasionally in the plantations even baseline data are not available. For bats, very little is known regarding the suitability of commercial plantations for foraging and roosting requirements. Boyd & Stebbings (1989) stated that bat populations in coniferous plantations could be limited more by roost availability than by food. Since these are working forests i.e. the mature trees are harvested, if bats have specific tree-roost requirements, then forest harvesting would be likely to have a negative impact on their roosting ecology (Vonhof 1996).

If appropriately managed, these forests could provide important additional habitat for woodland species. However, the impact of forest harvesting on the foraging ecology of bats may also be beneficial. Forest harvesting creates openings in the forest, and studies have suggested that gaps and the resulting edge habitat are important foraging areas for some bat species (Fenton1997).

It has to be clearly stated that not all coniferous plantations are similar in species, shape and structure. Scotland in particular has large block monocultures of spruce *Picea sps.,* plantations and these are inherently different from plantations like Tentsmuir. They are often planted in upland areas, are not thinned out before maturity, often have no paths or roads through them and are very dense and impenetrable. They also do not appear to have any types of natural cavities present, which could offer potential roosts. Humprey (2005) considers that upland spruce plantations need areas of old-growth stands to enhance and benefit biodiversity. A high proportion of large, old trees, multiple age classes and high volumes of fallen and standing deadwood characterize these old-growth stands. Studies of old spruce stands in the British uplands suggest that old-growth features can begin to develop after 80–100 years, conferring substantial benefits to species-groups such as hole-nesting birds, mammals (e.g. red squirrel), bryophytes, lichens and fungi (Humprey 2005). Tentsmuir is relatively mature with some areas over 70 years old and has many characteristics described above as old-growth. Tentsmuir is very similar to many of the plantations in England and lowland Scotland, which are planted mainly with Scots and

Corsican pines. Chapter 7 contains an action plan, which suggests ways that both types of plantations might be improved to make them more attractive to bats.

1.5.1 Silvicultural systems

The main silvicultural system employed in British commercial forestry is patch clear felling followed by planting or occasionally natural regeneration. It is estimated that this system is employed in at least 90% of managed forests with an average size of clear felled coupe of between five and ten hectares, although there is regional variation (Forestry Commission 1998). There is, however, a change occurring in the UK where increasingly commercial plantations are no longer being clear felled. *The UK Forestry Standard* (Forestry Commission 1998) requires managers to 'identify areas which are, or will be, managed under a continuous cover forestry system and to build them into the forest design'. Continuous cover is defined as the use of 'silvicultural systems whereby the forest canopy is maintained at one or more levels without clear felling'. Clear felling is defined in the text as the cutting-down of all trees on an area of more than 0.25 ha. The distinctive element of 'continuous cover forestry' is therefore the avoidance of clear felling of areas much more than two tree heights wide without the retention of some mature trees. (Forestry Commission 1998) Since 2000 Tentsmuir Forest has changed to continuous cover management and no longer clear fells.

1.6 Bat box schemes

In the U.K. the first bat boxes were erected in 1968 and bats were occupying them within 5 months. This led to more schemes on a national scale with 3000 boxes installed in 6 forests from northern Scotland to southern England (Stebbings & Walsh 1991). At present many local bat groups are also engaged in small-scale projects. Boyd & Stebbings (1989) proposed that roost and food availability might affect bat populations, particularly in commercial coniferous plantations. Also, if appropriately managed, plantation forests could provide important additional habitat for woodland species. Another factor, particularly in southern Britain, that led to increased numbers of bat boxes being erected was the felling of dead, old and hollow trees along with the advent of "Dutch Elm Disease" and the hurricane of 1987 both which considerably reduced the availability of natural roost sites for bats.

At least six species of bats are known to have bred in bat boxes, including Natterer's bat. Boxes that have been erected in commercial coniferous plantations including Wareham Forest Dorset, Thetford Forest East Anglia, Kielder Forest Northumberland and Tentsmuir Forest, Fife have all been used as both day and maternity roosts by a variety of species. Despite the history of bat boxes in commercial coniferous plantations there has been a dearth of habitat/foraging studies on the bats using them.

In Tentsmuir, originally two types of bat box were erected and both were soon used as summer roosts by Natterer's bats and there are now five types of bat box erected in seven locations. There have been very few published papers on bat box selection by bats, especially in commercial plantations. This study will investigate bat box preference and overall roost selection by adult female Natterer's bats in Tentsmuir Forest.

1.7 Natterer's bat *Myotis nattereri*

Kuhl first described Natterer's bat *Myotis nattereri* in Germany in 1817 in his survey of German bats. It was named after an Austrian naturalist, Johann Natterer (Smith 2000, Smith & Racey 2002). Natterer's bat is one of five species of *Myotis* bat in the U.K. and is one of the least studied European bats (Smith & Racey 2005). Some of the main studies carried out so far have been on diet (Shiel et al. 1991), foraging strategy (Arlettaz 1996a, Swift 1997, Siemers & Schnitzler 2000, Smith 2000, Siemers 2001, Swift & Racey 2002, Siemers & Schnitzler 2004), roosting behaviour (Swift 1997, Siemers et al. 1999, Smith 2000, Smith & Racey 2005) and growth rate of infants (Swift 2001). None of these studies has been in commercial coniferous plantations.

1.7.1 General Description

Natterer's bats are medium sized vespertilionid bats with a body mass from 4-13g and wingspan of 245-300mm. A characteristic feature is its conspicuous fringe of stiff hairs, about 1mm long, along the outer edge of the tail membrane. It differs from other Scottish *Myotis* species by its relatively long ears, which reach beyond the end of the muzzle if folded forward, and by the S-shaped bend in the calcar. It is also known as "red-armed bat" due to pinkish limbs (Stebbings 1986, Greenaway & Hutson 1990, Racey et al. 2003).

The echolocation calls of Natterer's bats are very quiet, and the most irregular call of all British *Myotis* bats. They have a frequency range of 16 to 135 kHz which peaks with maximum energy at about 50 kHz (Siemers & Schnitzler 2000, 2004). This makes it very difficult to accurately assess numbers and even species identity using bat detectors.

Recent studies have shown that Natterer's bats forage using an echolocation call of very broadband width and by gleaning. They have been observed gleaning through grass using the interfemoral membrane and also landing and pursuing prey quadrupedally (Swift 1997, Siemers & Schnitzler 2000, Swift & Racey 2002). Their diet varies geographically and it would appear to have the most diverse diet of any U.K. *Myotis*. Analysis by faecal examination has shown that cyclorraphan Diptera, nematoceran Diptera, Coleoptera and Arachnida form the major components of the diet (Shiel et al. 1991, Swift & Racey 2002).

Natterer's bat occurs throughout Europe except for much of Scandinavia and southeast Europe (Figure 1.2). Its southern range includes Morocco and eastwards it occurs as far as Japan (Stebbings 1988, Hutson 1993). In the UK it is widely spread (Figure 1.3), and its range in Scotland extends north to Inverness (Canham 1993) and west to some islands (Haddow & Herman 2000) The latest population estimates from the NBMP are: UK 148,000; England 70,000; Scotland 17,500; Wales 12,500. It would appear to be thinly distributed and uncommon across most of its range and the U.K. population may be of international importance (Hutson 1993).

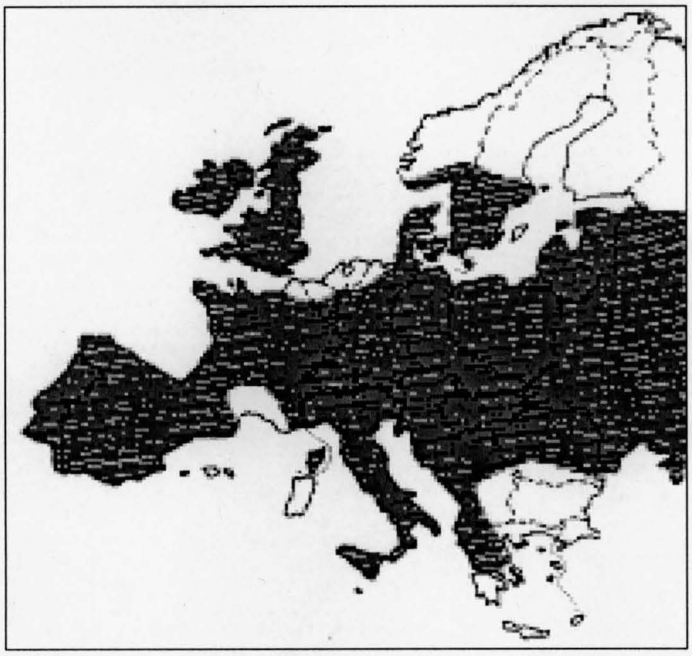
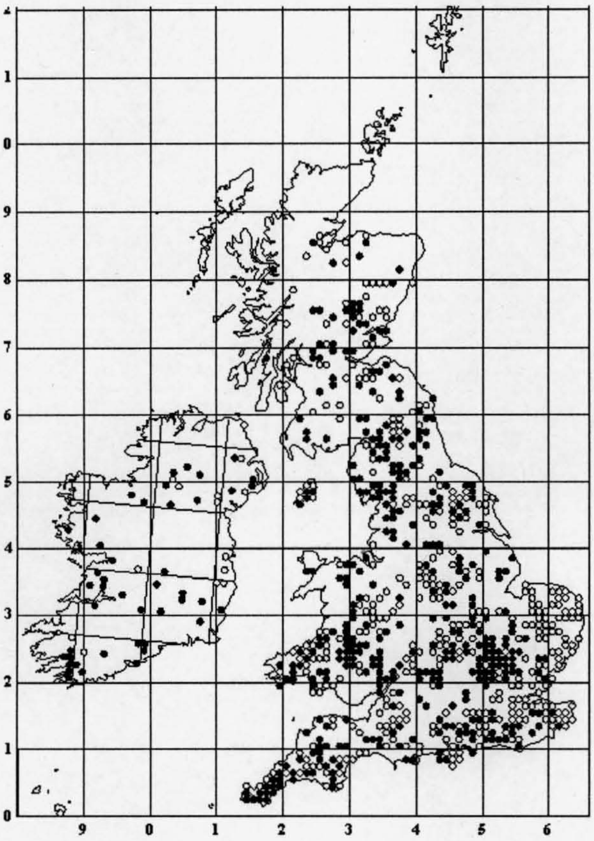


Figure 1.2: European distribution of Natterer's bat (Corbet & Harris 1991).



Full circles = summer roosts.
Hollow circles = bats away from roosts

Figure 1.3: British distribution of Natterer's bat 1980 – 2000 (BCT 2001).

There are three observations of the presence of Natterer's bats in Scotland from the 19th century but none has sufficient detail to warrant definite inclusion in the records. The first definite records were in 1953 and then a spate of records followed from 1972 onwards. This pattern of observation is an indication of increase in the interest in bats at that time and the formation of several Scottish bat groups. The majority of the records up to 1986 were from well-wooded areas of river valleys or loch sides. However, three of the early records are from large commercial coniferous plantations including the present study site, Tentsmuir Forest (Bullock et al. 1986)

1.7.2 Population trends

The NBMP uses the following protocol in assessing population trends: hibernation surveys, colony surveys and field transects.

Hibernation survey.

Natterer's bats regularly hibernate in a diverse range of underground sites but appear less reliant on key sites. This could be related to periods of adverse cold weather, yet assuming that the bats recorded in underground sites are representative of the population and that the weather factor is evened out over time, hibernation site surveys have a high capability to indicate population change. A mean of 124 sites have been counted annually from 1997–2003. Trend analysis indicated a significant overall increase of 42%, representing a mean annual increase of 6% (Battersby 2005).

Colony survey.

Counts of Natterer's bat colonies only commenced in 2000, so there are very limited data available. A total of 58 colonies have been counted, with an annual mean of 39 roosts counted across the UK. The mean numbers of bats per colony is 35, with slightly larger colonies in Scotland (mean 38 bats) than in England and Wales. Sample sizes are too small at this stage to carry out trend analyses (Battersby 2005).

Field transects.

There are no historic or current trends available due to the difficulty in distinguishing between different *Myotis* species both visually and using bat detectors, since Natterer's bats tend to forage in woodland and have relatively quiet echolocation calls. This is probably the most difficult species to monitor by summer roost counts. There are few known roosts; the colonies switch roost often. There are also difficulties in counting bats since Natterer's emerge late and often forage in cluttered environments. This has made it difficult to develop effective field survey methods (Battersby 2005).

1.7.3 Summer roost requirements.

Natterer's bats form nursery colonies from late April onwards. Relatively few summer roost sites are known, but most of these are sited in old stone buildings, castles, manor houses and churches, or large old timbered barns. Crevices in beams or gaps in beam joints are common roost sites. Less common sites include under bridges, entrances to mines, houses, bat boxes and trees. The NBMP records state that approximately 150 summer roosts are known in the U.K. In Scotland Haddow & Herman (2000) have recorded 46 roosts with approximately half the known roosts in houses (Racey et al. 2003). Colony sizes have been recorded numbering from 25-200 with the average in parts of Scotland recorded as 40 (Racey et al. 2003). Howe (1997) has recorded the only known instance of tree roosting in Scotland, however Smith (2000) found it occurred regularly in pastureland in Wales.

1.7.4 Conservation

The conservation requirements of Natterer's bats are largely unknown, but it is probably subject to the same threats as other bat species, *i.e.* the loss of roost sites, foraging habitats and insect prey. A Bat Conservation Trust action plan (Hutson 1993) considered that the U.K. population might be of international importance and highlighted several areas of research that need to be implemented for conservation reasons. These included:

- Identifying habitat requirements.
- Investigating summer roost requirements.
- Diet analysis.

1.8 Study site

Tentsmuir Forest is a 9143 ha commercial coniferous plantation on the NE coast of Fife, Scotland (Figure 1.4). The land was acquired by the Forestry Commission in the 1920s and planted predominantly with Scots pine *Pinus sylvestris* and Corsican pine *Pinus nigra maritima.* In addition to commercial forestry there are small areas of broad-leaf forest, ponds, streams, open spaces and sand dunes. The forest is at sea level and planted on sand dunes. It is flanked on the north by the estuarine River Tay and the North Sea on the east. Inland it is surrounded by agricultural land.

Figure 1.4: Tentsmuir Forest, NE Fife, Scotland, U.K.

1.9 Study aims

Previous work on Natterer's bats has concentrated on semi-natural broad-leafed woodland and pastureland and in general this is considered prime roosting and foraging habitat for this species. There have been no previous published studies on Natterer's bats in commercial coniferous plantations.

The aims of this study are to investigate four main ecological aspects of Natterer's bats that use bat boxes as summer roosts in a commercial coniferous plantation. These are:
1) Foraging dynamics. 2) Habitat preferences. 3) Roosting ecology. 4) Survival rates.

1) To determine the following foraging dynamics by radio tracking individual adult female Natterer's bats (Chapter 3):

- The size, shape and structure of individual and colony home ranges.
- The size, shape and structure of core foraging areas.
- The number and intensity of use of core foraging areas of individual bats.
- The dynamics of night roost usage and distance commuted to foraging areas.
- The nightly time budget of individual bats.

2) To determine habitat preference, diet and invertebrate prey availability (Chapter 4).

- By radio tracking, determine whether adult female Natterer's bats that use summer roosts in Tentsmuir Forest, a commercial coniferous plantation, preferentially choose foraging habitats within or outside the forest boundaries.

- To examine the diet by faecal analysis using scats collected monthly from bat boxes.
- To make a comparison of invertebrate biodiversity between water bodies and young Scots pine within Tentsmuir Forest by four methods of invertebrate trapping.
- To make a comparison of canopy invertebrate biodiversity between mature Scots and Corsican pine in Tentsmuir Forest by pan trapping.
- To examine any correlations between the diet and invertebrates trapped using various trapping methods in young Scots pine and water habitats within the forest boundaries.

3) Roost dynamics (Chapter 5):

- To determine if Natterer's bats preferentially use a particular bat box type.
- To determine the optimum site characteristics for placement of bat boxes.
- To determine the pattern of roost usage between the bat boxes and Kinshaldy stables.

- To locate unknown roost sites.

4) To use live-recapture techniques on two colonies of Natterer's bats present in bat boxes in a commercial coniferous plantation in east Scotland (Chapter 6):

- To estimate survival rates of adult females, juvenile females, adult males and juvenile males
- To determine population abundance and density of Natterer's bats within the forest.
- To determine the population structure of Natterer's bats within the forest.

The above aims will provide an insight into one of Europe's least studied bats in one of the least studied habitats. The results will benefit and greatly enhance conservation management decisions particularly in commercial forests.

CHAPTER 2

Materials and Methods

2.1 History of Natterer's bats in Tentsmuir Forest

Natterer's bats were first recorded breeding in Kinshaldy Stables in Tentsmuir in spring 1985. This coincided with a bat box scheme when approximately 90-100 boxes were erected in ten separate localities (Figure 2.1). The boxes were soon holding numbers of both Natterer's bats and pipistrelle species (Altringham & Bullock 1988). At the start of this project it was known that Natterer's bats were still roosting in Kinshaldy Stables and in bat boxes at two separate locations, Ice House and Beeches (Bullock et al. 1986, Altringham & Bullock 1988, Mortimer 1993, Hatton & Cohen 2000).

It was originally thought that the Natterer's bats present were probably one colony that switched roosts between the stables and the bat boxes. It was decided that an experimental design would be set up with different types of bat box to determine if they preferentially selected a particular type(s). After the field season in 2003 it was becoming clear that instead of one colony of bats there was a minimum of three colonies present in the forest. From radio tracking (Chapter 3) and banding (Chapter 5) it was found that only a very limited interchange occurred between the two distinct colonies (Figure 2.1) occupying bat boxes and no radio tracked bats visited Kinshaldy Stables. The two colonies in the boxes were centered on two different areas:

- The Beeches colony used boxes at four separate locations, Beeches, Morton Lochs, Yard and Fetterdale.
- The Ice House colony used boxes at three separate locations, Ice House, Ice North, and Ice South.

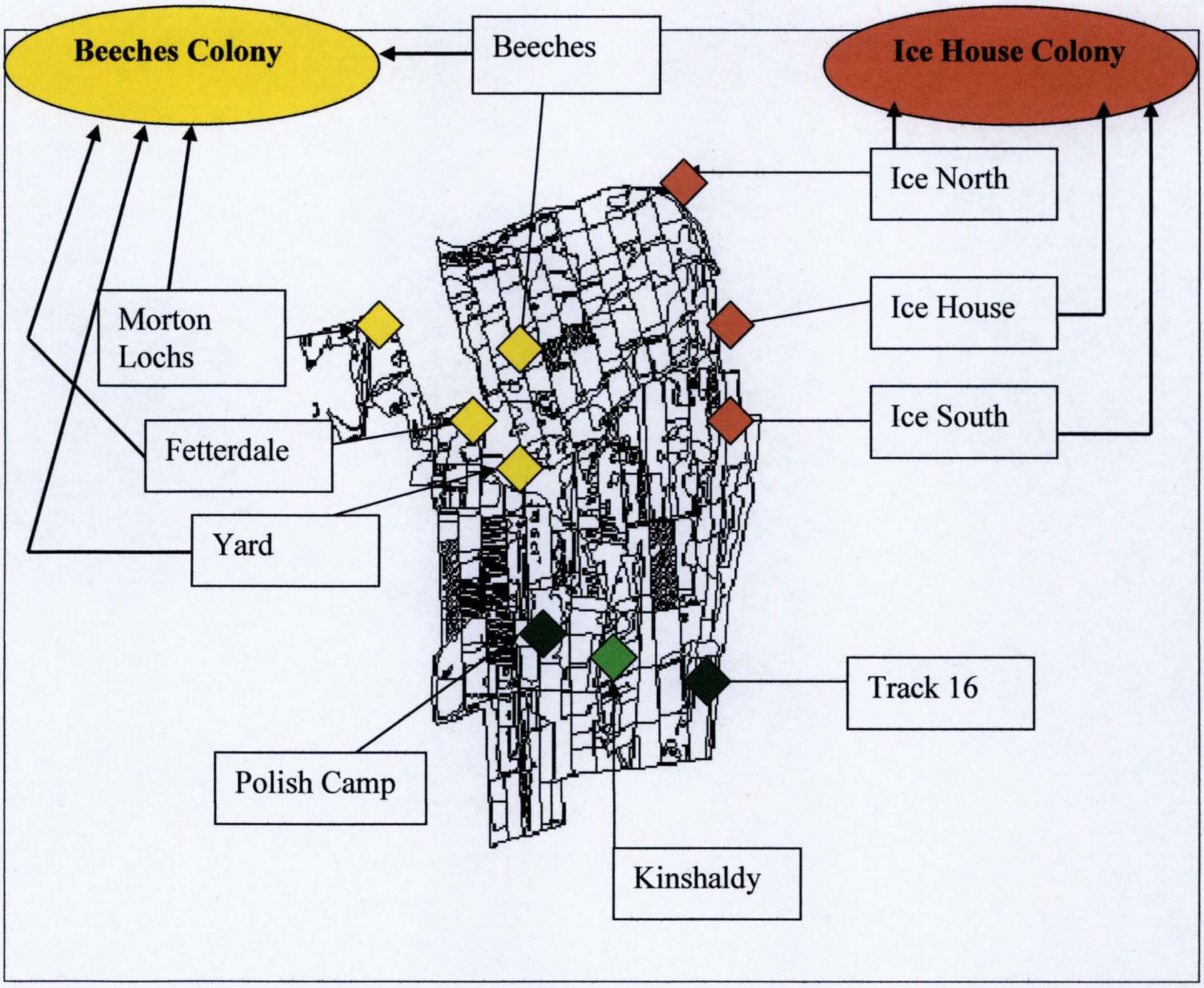


Figure 2.1: Locations of groups of bat boxes in Tentsmuir. The bats have two distinct colonies centered on the Ice House and the Beeches areas. The Kinshaldy bats are located in a stables complex with several roosts known. The bat boxes at Track 16 and around the stables at Kinshaldy have never held Natterer's. The boxes at Polish Camp have occasionally held the odd Natterer's bat, which have not been relocated elsewhere. However, these boxes no longer exist due to tree felling.

2.2 Bat banding

All handling of bats, disturbance at roosts, marking and attachment of radio transmitters was done under licence from Scottish Natural Heritage.

From 1998, 2 separate colonies of Natterer's bats found roosting in the bat boxes at the Beeches and Ice House vicinities has been the object of a bat-banding programme (Tables 2.1a & 2.1b). Boxes have been checked twice yearly in May and August (before and after breeding) and any unmarked bats have been fitted with a numbered alloy bat ring (Mammal Society, London) on the forearm (Hatton & Cohen 2000). Bats were sexed and aged as either juvenile (born that year), or adult (> 1 year). Aging was done by whether epiphyses were fused (adults) or unfused (juveniles) (Racey 1974, 1988). Any adult females were checked for pregnancy, state of lactation and whether parous or non-parous where appropriate.

Year	Ad. Fem	Juv. Fem.	Ad. Male	Juv. Male	Control Female	Control Male	Total
1998	53	2	1	0	55	1	112
1999	5	4	1	8	34	9	61
2000	6	4	1	5	59	6	81
2001	4	14	0	9	37	10	74
2002	7	6	0	5	53	7	78
2003	8	0	2	0	50	4	64
2004	6	6	2	2	65	7	88
2005	0	7	1	7	73	12	100
Total	89	43	8	36	426	56	658

Table 2.1a: Numbers of bats banded at Ice House colony.

Year	Ad. Fem	Juv. Fem.	Ad. Male	Juv. Male	Control Female	Control Male	Total
1998	42	6	2	12	10	1	73
1999	9	5	1	10	36	9	70
2000	0	0	0	0	0	0	0
2001	2	0	1	0	1	1	5
2002	0	0	0	0	0	0	0
2003	59	15	5	14	82	4	179
2004	3	3	2	2	64	2	76
2005	1	10	0	10	88	1	110
Total	116	39	11	48	281	18	513

Table 2.1b: Numbers of bats banded at Beeches colony.

2.3 Radio tracking.

2.3.1 General details

When a bat was required for radio tracking, bat boxes were searched until a roost of Natterer's bats were located. In the afternoon an adult female was selected randomly from those present in the box, weighed, and a transmitter tag attached (Tables 2.2a + 2.2b). Alana Ecology supplied single stage LTM transmitter tags, manufactured by Titley Electronics, in the frequency range 173.200 to 173.350 MHz. The tags weighed approximately 400 milligrams and had a battery life of 10-12 days. The fur between the bats scapulae was trimmed (Aldridge & Brigham 1988) and tags were attached using Skin-Bond rubber latex adhesive (Smith & Nephew, Largo, Florida, U.S.A.). After the tag was attached the bat was returned to the bat box, which had the entrance hole closed with a cloth bag. After a short period of 10-15 minutes when the bat would have settled back to roost, the bag was removed. The box was then checked approximately 1 hour later to ensure that the bat was still present. The mass of transmitter never exceeded 5.88% (mean 5.13 +/- 0.059 s.e., n = 26) of the body weight of the bat. This was assuming that tags weighed 0.4mg and the adhesive a maximum of 0.10mg. The mass of the transmitter compared to body weight was well within the limit of 10% recommended by Wilkinson & Bradbury (1988) and near parity with the 5% rule as recommended by Aldridge & Brigham (1988).

Bat Id	Date Tagged	Nights Tracked	Status	Weight	Tag As % Body Weight (0.5g)	Stop	Date Last Seen
T6865	19/05/03	9/9	F.Preg?	8.5	5.88	Battery	2004
T6965	12/06/03	7/7	F.Preg	9.9	5.05	Battery	2005
T6968	02/07/03	0/1	F.Preg	11.7	4.27	Tag Fail	2003*
T8902	03/07/03	8/8	F.Lac	11.5	5.22	Battery	2004
T6859	28/07/03	0/1	F.Np	9.5	5.26	Tag.Fail	2005
T6876	29/07/03	0/2	F.Lact	9.5	5.26	Tag.Fail	2005
T6977	31/07/03	6/6	F.Np	9.8	5.10	Tag.Fail	2005
T6978	13/07/03	5/5	F Np?	9.6	5.21	Battery	2005
T6934	26/05/04	5/6	F.Preg?	10.1	4.95	Battery	2005
T8920	02/06/04	6/8	F.Preg	9.3	5.38	Battery	2004**
T6838	17/06/04	0/1	F.Preg	10.1	4.95	Tag Fail	2005
T8914	12/08/04	4/4	F.Lact	9.4	5.32	Tag Fail	2005
T8913	21/08/04	2/2	F.Lact	9.0	5.56	Tag Fail	2005

Table 2.2a: Bats with radio tags attached from the Ice House colony.

Bat Id	Date Tagged	Nights Tracked	Status	Weight	Tag As % Body Weight (0.5g)	Stop	Date Last Seen
T6814	31/05/03	3/3	F. Preg	10.3	4.85	Tag.Fail	2004
T9552	03/06/03	6/6	F. Preg	10.7	4.67	Tag.Fail	2003**
T9503	22/06/03	8/8	F. Np	9.9	5.05	Battery	2005
T8931	15/07/03	3/3	F.Lac	9.6	5.21	Tag.Fail	2005
T9573	18/07/03	7/7	F.Lac	9.9	5.05	Battery	2005
T9564	21/08/03	3/3	F. Lac	10.2	4.90	Tag.Fail	2005
T6920	14/05/04	5/5	F.Preg	9.1	5.49	Battery	2005
T9599	19/05/04	2/2	F.Preg	9.8	5.10	Tag.Fail	2005
T8943	19/06/04	5/6	F.Preg	10.1	4.95	Tag.Fail	2005
T8929	27/06/04	6/7	F.Preg	9.8	5.10	Battery	2005
T6917	06/07/04	1/2	F.Preg	9.5	5.26	Tag Fail	2005
T8941	13/06/04	5/6	F.Np ?	9.5	5.26	Tag Fail	2005
T6956	02/08/04	0/1	F.Lact.	9.9	5.05	Tag Fail	2005

Table 2.2b: Bats with radio tags attached from the Beeches Colony.
* = Not found subsequently after tracking. ** = Found later same year after tracking.

2.3.2 Radio-transmitter effect

There have been several studies looking at the effects of radio transmitter loads on bats (e.g. Aldridge & Brigham 1988, Hughes & Raynor 1991). The studies found that 10% of body mass should be considered as the upper limit, although some studies have gone over this limit with no apparent effects on the bats' behaviour or survival (Stebbings 1982). Looking at longer term effects, Kurta & Murray (2002) found in a radio tracking study of Indiana bats *Myotis sodalis*, that eleven out of twelve females that had radio transmitters attached were subsequently recaught in later years. They were all reproductively active and had normal body masses, suggesting negligible long-term effects of the radio tracking process. Neubaum et al. (2005) studied the condition of big brown bats *Eptesicus fuscus*, fitted with either radio transmitters or passive integrated transponders. All bats examined one year after radio tagging were reproductively active and had body masses similar to bats not radio tagged. The authors concluded that the bats do not appear to suffer from major long-term effects of carrying transmitters. It would appear difficult to calculate the effects of radio transmitters on behaviour. One approach by Vekasy et al. (1996) was to compare the behaviour of a tagged individual prairie falcon *Falco mexicanus* to its untagged mate. They found no effects on behaviour for nest attendance, prey delivery, or prey catching.

In this study only one bat (Tables 2.2a +2.2b) was not relocated later in the same year or in subsequent years after having a radio transmitter attached. This suggests that tagging did not have a large effect on survival.

2.3.3 Radio tracking methods

All bats were tracked on foot and by car using the "close approach" method as recommended by White & Garrott (1990). Only one bat was tracked at a time for the entire night. All bats were tracked from time of leaving roost to return to roost unless there were problems with transmitters or heavy rain. Locations of the bats from radio tracking fixes were recorded at 10-minute intervals and behaviour recorded as either roosting, commuting or foraging. This was determined by listening to the radio signal and deducing whether the signal was stationary, moving rapidly and increasing/decreasing in strength in one direction or whether the signal was fluctuating and changing direction constantly, but staying within an area. A Mariner 57 radio receiver was used in conjunction with a three-element Yagi antenna. The structure of the forest and the abundance of roads meant that once a bat left a roost its flight direction was estimated from the signal then it was followed by car. Numerous stops were then performed where I had to get out of the car and try to ascertain what direction the bat was heading. Eventually a forging area(s) was found where the bat stayed for a period of time. Once these areas were located all tracking was done by staying by the roadside at the point nearest to the bat. The structure of the forest with stands of homogonous habitat trees surrounded by roads meant that it was normally quite easy to determine what particular habitat a bat was using. It was possible to drive round the entire perimeter of the habitat and locate the bat at all times.

The location, activity and estimated accuracy of the radio fix were entered into a diary every 10 minutes or frequently more often as changes occurred. The MapInfo (MapInfo Corp. 1999) Geographical Information System (GIS), incorporating both ArcMap and ArcView 3.2 was used to produce a digitised computer-based map of land use and habitat availability within the study area. All fixes were entered onto the correct location on the GIS and the associated data of date, time and activity also recorded in the attribute table associated with each individual fix.

2.4 Invertebrate trapping

Five types of invertebrate trapping methods were used in this project; Malaise tents, window traps, sticky traps, moth traps and pan traps. For a general overview of invertebrate trapping methods see Southwood (1979). All insects caught in the traps (except for the moth traps) were stored in 96% ethanol for later identification in the laboratory. These were then identified to Family and subsequently to Order level and abundance recorded. All moths caught in the moth traps were recorded to their size categories; small (1-7mm), medium (8-14mm) and large (15-22mm).

2.4.1 Malaise tents

Malaise traps are a tent like structure (Figure 2.2) that are very successful in trapping a wide variety of flying insects, particularly Diptera and Hymenoptera (Hoskin 1979). They are composed of a large tent built of netting, approximately 1.2 meters high and 1 meter wide. There are no sidewalls, however a central wall runs through the middle of the tent. The insects fly into the central wall and then fly upwards to escape the obstruction. Once here they then encounter the sloped ridge of the roof. One end of the tent forms a high point where a small entrance to a killing bottle is located. The insects then enter the entrance of the killing bottle to try and escape. This contained 96% ethanol and was emptied every four days.

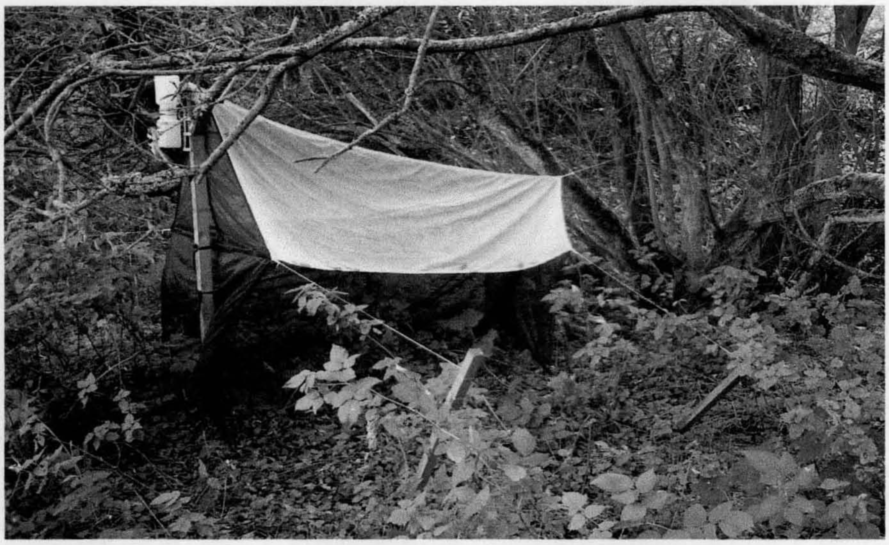


Figure 2.2: Malaise tent as used in Tentsmuir.

2.4.2 Sticky traps

Sticky traps are small (7.8cm x 11.4cm) yellow, sticky two sided plastic strips (Buriff 1973). Jukes et al. (2001) considered them particularly useful for estimations of single insect families that can be easily identified from other trapped invertebrates. The strips were attached to tree trunks at approximately 1.5 metres above ground height (Figure 2.3). Each strip was left attached to the tree for four days before it was replaced by a new strip.

Figure 2.3: Sticky trap as used in Tentsmuir.

2.4.3 Window traps

Window or flight intercept traps are commonly used for invertebrate trapping with many types available. They work on the principle of insects flying into the plastic vanes and then falling into a collection container containing a preservative (Masner & Goulet 1981). In Tentsmuir the traps were suspended from a wooden stake (Figure 2.4) at a height approximately 1 metre above ground level. Insects were collected in a collecting jar containing 96% ethanol. This was emptied at four-day intervals and replaced with new ethanol.

Figure 2.4: Window trap as used in Tentsmuir.

2.4.4 Moth trap

The moth trap used was a Skinner Trap (Figure 2.5) supplied by Anglian Lepidopterist Supplies. It is an easily assembled plywood box measuring 45cm square and 35cm high. The light source was a 15w actinic bulb powered by a car battery. Egg cartons were placed in the box to provide resting places for the moths attracted by the light. A small LED sensor automatically switched the bulb on and off at dusk and dawn. The trap was emptied every morning after use.

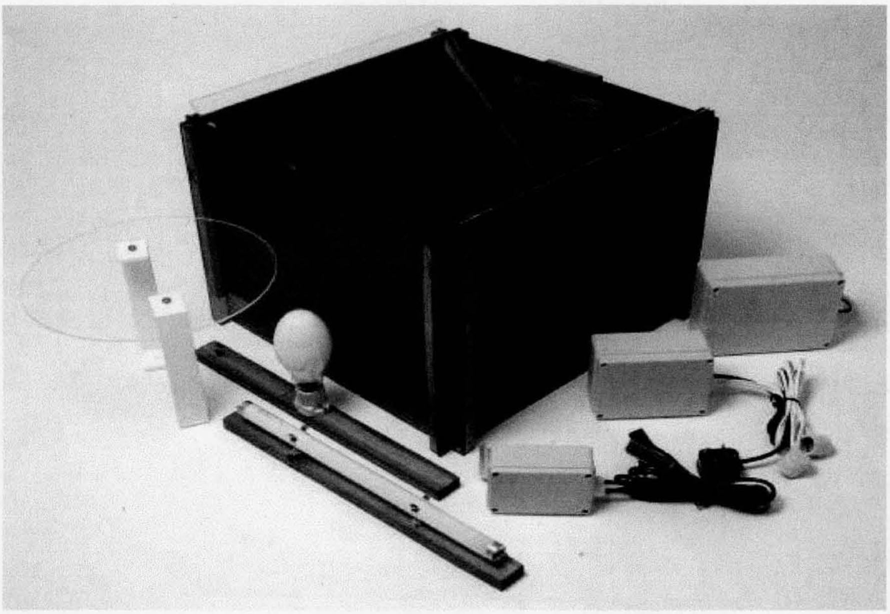


Figure 2.5: Skinner moth trap.

2.4.5 Pan traps

Pan traps are normally plastic containers that are filled with water and placed on the ground. A few drops of detergent are added to lower the surface tension of the water. Insects attracted to the water, fall in and perish and are then collected later. In Tentsmuir the pan traps were not placed on the ground but hauled up the tree canopy by string. Various colours of pan trap attract different taxa of invertebrates (Marshall 1994). The pans in this study were clear plastic. They were emptied every four days.

2.5 Diet analysis

2.5.1 Collection of faecal samples

In 2003/2004 when checking bat boxes I collected faecal droppings monthly from May to September from both the Beeches and Icehouse colonies whenever Natterer's bats were found in a box. Droppings collected were placed in collecting vials, labelled and stored in a cool dry cupboard for later analysis.

2.5.2 Analysis of samples

Forty-two Natterer's bat faecal droppings were randomly selected for analysis from the monthly samples, twenty-one each from the Ice House and Beeches colonies. Droppings were soaked overnight between two layers of cotton wool in a petri dish. After soaking overnight a few drops of glycerol was added to the petri dish and the dropping teased apart with a fine dissecting needle. The separated contents were viewed with a 40x binocular dissecting microscope. Droppings were analysed by extracting and identifying chitinous arthropod fragments using McAney et al. (1997) as the primary means of fragment identification (Clark 2005). Only fragments with clear diagnostic features were counted. If the pellet contained Lepidoptera scales they were considered collectively as one fragment. Results were expressed as percentage frequency of attenuated fragments, i.e. the number of insect fragments attributed to one insect order as a percentage of the total number of insect fragments attributed to all insect orders (Swift et al. 2002).

2.6 Roost visits

On a weekly basis from May to September bat boxes in seven discrete locations were checked for roosting Natterer's bats. Boxes were carefully opened and presence or absence of Natterer's bats recorded. In an effort to avoid undue disturbance no bats were handled. If a roost visit coincided with a banding visit, then bats were sexed, aged and fitted with a band where appropriate.

CHAPTER 3

Home range size, shape and structure and nightly time budget.

3.1 Abstract

Natterer's bats from two different maternity colonies (Beeches and Icehouse) had spatially separate foraging home ranges (4.4 & 6.6 km^2) that displayed no overlap in area. 100% Minimum Convex Polygons (MCP) were used to determine colony home range areas. For the individual bat, a combination of 85% and 50% MCP and Kernel estimators were used to determine the areas, structure and numbers of home ranges and core feeding areas. Bats displayed site fidelity by returning nightly to forage in between one to five core areas, comprising 50% of foraging records. These core areas were used regardless of where the bats roosted. There was no overlap between individual core foraging areas, which ranged in area from 0.001 – 0.19km^2 (mean 0.04, +/- 0.01 s.e.). Natterer's bats left the roost at a mean time of 57 (+/- 1.29 s.e.) minutes after sunset and returned a mean time of 70 (+/- 1.97 s.e.) minutes before sunrise. There was no seasonal variation in time of emergence and return to roosts. Approximately 95% of time away from roosts was spent foraging. Roost visits during foraging time were either due to heavy rain or by females that were lactating.

3.2 Introduction

Burt (1943) originally defined an animal's home range as "the area traversed by the individual in its normal activities of food gathering, mating and caring for young" and that where territoriality was displayed via aggression, as the "protected part of the home range." Also, that "excursions to the area outside its normal area should not be considered part of the home range." This definition has been expanded upon since by several authors to include behaviour and social structure (Brown & Orians 1970, Mares et al. 1982).

However, in this study Burt's definition is followed. In general, animals use space disproportionately within the home range and areas receiving concentrated use can be termed core areas (Wray et al. 1992). These core areas normally contain the home site, refuges and most dependable food sources (Samuel et al.1985).

Kenward (2000) considered that the home range information required to answer biological questions typically involves three measures: size, shape and structure of the area. Two main groups of methods are normally used to calculate these home range measures, and different methods can produce large differences in area and shape of home ranges (Lawson & Rodgers 1997). In reality which method(s) are used depends on the biological questions that are being asked, time and scope of the experiment and the method of data collection (see reviews by White & Garrott 1990, Harris et al 1990, Kenward 2000).

These groups of methods are:

- *Non-probabilistic estimators* – These techniques do not assess probability of occurrence, instead they minimize the sum of link-distances between locations. These include Minimum Convex Polygons, concave and peeled polygons, grid cells and cluster polygons (White & Garrott 1990, Kenward 2000).

- *Probabilistic estimators* – Assess an animal's probability of occurrence at each point in space (probability density function of locations used to assess an animal's probability of occurrence at each point in space). These techniques evaluate home range and size as well as intensity of use within the home range and includes bivariate normal techniques e.g. ellipses, (Jennrich & Turner 1969), harmonic mean techniques (Dixon & Chapman 1980) and kernel-based analysis (Worton 1989).

For this study both a non-probabilistic (MCP) and a probabilistic (Kernel) estimator were used to calculate home range and core area size, shape and structure. The MCP was chosen because it is the most commonly used estimator and comparisons are easily made with other studies. The Kernel estimator is a more sophisticated method, and in simulation tests with harmonic mean estimators produces the most accurate (least biased) estimates of simulated home ranges (Seaman & Powell 1996). Worton (1989, 1995) advocated the use of Kernel methods over other estimators because there was less bias due to scale or grid density. Kernel estimators can also accommodate non-parametric location data while ellipses (Jennrich & Turner 1969, Samuel et al. 1985) require data to be parametric. This creates problems because parametric home ranges assume that a bivariate normal distribution of use occurs, and in general most animal use of a home range is not well approximated by a normal distribution. Kernel analysis also allows for multiple core areas to be identified that are not bound to the central region of the home range. In a study of breeding territories of cerulean warblers *Dendroica cerulean*, Barg et al. (2005) compared the performance of kernel estimators and MCPs and found that the Kernel estimators were far more accurate and informative than the MCPs

3.2.1. Minimum Convex Polygons

The most frequently used method of minimum-linkage estimator is the Minimum Convex Polygon, (Mohr 1947). MCPs are non-probabilistic and do not assess the probability of occurrence; the home range is characterized by a straight line around the outermost fixes or locations that minimizes the sum of link distances between edge locations. It is also non-parametric with no underlying distribution assumptions. MCP can inflate home range sizes due to outlier effects and also include areas that are used predominantly for commuting rather than foraging areas. Animals often make sallies or excursions outside their normal routines for various reasons (Kenward 2000) and if the 100% MCP is used which includes all fixes, then the home range area will be inflated. Since no measure of intensity of use is estimated, there is no indication of where the animal spends most of its time. MCPs also allow relatively easy comparisons between studies and are often used in conjunction with other methods (Harris et al. 1990).

Methods that have been used to provide a more accurate and ecologically relevant description of an animal's home range include concave and peeled polygons. Concave polygons work on the principle of measuring the range span, which is the greatest link distance in the range, and then drawing a peripheral line to an internal location wherever the distance between edge locations is more than a quarter or half of the span (Kenwood 2000). Peeled polygons operate by excluding locations ranked in order of linkage distance from a range centre (Kenward 1987).

3.2.2 Kernel Analysis

Kernel analysis is a contouring method for estimating complex probability distributions. The method has several advantages over MCPs since it can accommodate multiple centres of activity, does not rely on outlying points to anchor their corners and is less influenced by distant points, thereby excluding unused areas and leading to more accurate depictions of space use (Hemson et al. 2005).

The method works on the principle of utilization distribution which Van Winkle (1975) defined as the two dimensional relative frequency distribution for the points of location of an animal over a period of time. Therefore the utilization distribution is a probabilistic home range estimator that describes the relative amount of time that an animal spends in any particular place (Seaman & Powell 1996). The actual mechanism of how Kernel estimators derive the home range is complicated, and the following is a basic explanation. A grid is superimposed on the data and an estimate of the density is obtained at each grid intersection. The model creates home range boundary contours or isopleths of intensity of utilization by calculating the mean influence of data points. To compute the home range area, the estimated density at each intersection of the grid is the average of the densities of all the kernels that overlap that point. A critical component is the smoothing factor or bandwidth, which is the distance over which a data point influences the grid intersections. The larger this value is, the less detailed the final home range estimate (Silverman 1986). The choice of technique used for estimating the smoothing parameter is contentious. One technique frequently is the least squares cross validation (LSCV) technique. This technique utilizes various bandwidths and selects the one that minimizes error (see reviews by Silverman 1986, Seaman & Powell 1996, Hemson et al. 2005). The home range boundary is the contour that encompasses a selected percentage of the total space used (Anderson et al. 1985). In this study 85% & 50% isopleths were selected because they clearly define the fact that between the two isopleths it is possible to identify that Natterer's bats have core feeding areas that do not overlap with other radio tracked individual bats core areas.

3.2.3 Core areas

Core areas are areas inside the home range that display concentrated activity that can be considered the non-random use of space within the home range. These areas are often concentrated around resting areas and key feeding areas, and the number, size and the location of core areas will vary with the method of home range analysis used (Wray et al. 1992). The ranges of problems that are associated with home range boundary analysis are also relevant for core area analysis with the addition of intensity of use as an added factor. It is only recently, since the 1960's, that methods for determining core areas have received as much effort as home range analysis, in particular the development of techniques employing a utilization distribution (Samuel et al. 1985).

3.2.4 Radio-tracking

Radio-telemetry (see Chapter 2) was used to obtain the data for estimating the home range and core areas in this study. Radio-telemetry involves selecting:

- An individual bat "randomly" (Chapter 2) and fitting it with a radio-transmitter.
- Recording the position of the bat at regular time intervals. This allowed some degree of temporal and spatial independence among subsequent telemetry locations (see *3.2.5* for full explanation).

The spatial data obtained are three-dimensional with latitude, longitude and time.

3.2.5 Autocorrelation

Autocorrelation of positional data is the phenomenon whereby the position of an animal at time $t + \Delta t$ is not independent of its position at time t (Rooney et al. 1998). The problem of autocorrelation has been discussed widely and the general consensus is that radio-tracking locations must be statistically independent to achieve valid estimates of home range parameters (Swihart & Slade 1985a, Rooney et al. 1998, Otis & White 1999). Samuel et al. (1985) stated that an important goal is to obtain unbiased and serially uncorrelated samples of animal utilization distributions. Swihart & Slade (1985b) considered that independence between successive observations is an implicit assumption in most statistical analysis of animal movements. Other studies have shown that temporal autocorrelation typically leads to a reduction in range size; however by increasing the time between fixes to achieve independence you reduce your sample size, particularly in small sample sets. This can reduce biological relevance and studies have shown that this can result in an underestimation of range size much more significant than would be seen as a result of temporal autocorrelation (De Solla et al. 1999).

The MCP and Kernel home range estimator techniques make no assumptions about the underlying distribution of positional fixes and therefore should overcome autocorrelation; however Swihart & Slade (1997) in a comparison of six home range estimators found that positive autocorrelation resulted in underestimation of home range size.

Many previous bat radio-tracking studies have not stated what time interval was used between positional fixes (Fuhrmann & Seitz 1992, Waters et al. 1999). Other studies have recorded time intervals of between 5 minutes and 15 minutes (Siemers et al 1999, O'Donnell 2001, Bontadina et al. 2002). O'Donnell (2001) states that 15 minutes was chosen for his study since the bats could easily cross their range in < 15 minutes. White & Garrott (1990) suggest that a rule of thumb time to independence is the time taken for an animal to cross its home range and back again. To overcome any issues with autocorrelation and also maintain a sense of ecological reality, rather than a rigid statistical framework, in this study positional fixes were recorded every 10 minutes. Smith (2000) recorded a mean straight-line flight speed of 5.0 m/s for Natterer's bats when commuting. This would allow a Natterer's bat time to travel anywhere within the forest or leave the forest within a 10 minute time span.

3.2.6 Sample sizes

Home range estimators are also sensitive to the number of locational fixes used to construct estimates and, in general, it is important to determine at what point home range size reaches an asymptote by plotting range size vs. number of locations. Jager & Pechacek (2002) stated that in a study on three toed woodpeckers *Picoides tridactylus,* a minimum sample size of 30 independent observations was needed to determine an accurate Kernel estimation. In reality, problems with bats chewing and destroying tags, variation in tag performance and weather, meant that differing amounts of data were collected for different individuals (Table 2.2a & 2.2b). It was decided that for any individual bat, if data were collected for a minimum of two nights tracking, this would be included in the analysis whether or not an asymptote was reached. In radio tracking studies, where data collection can be limited due to various difficulties, then a compromise needs to be obtained that maintains statistical robustness but also limits loss of ecological data.

3.3 Aims

All of the aims below are for the period April-September, when Natterer's bats are present in the forest for breeding.

- To determine the size, shape and structure of individual and colony home ranges.
- To determine the size, shape and structure of core foraging areas.
- To determine number of core foraging areas and intensity of use.
- To determine dynamics of roost occupancy and distance commuted to foraging areas.
- To determine the nightly time budget of individual bats.

3.4 Methods and materials

3.4.1 Radio tracking

Using radio-tracking methods (Chapter 2) the foraging and nightly roost movements of Natterer's bats from the Icehouse and Beeches maternity colonies were recorded. A total of 20 bats were tracked successfully (Tables 2.2 a, 2.2b), eleven from the Beeches colony and nine from the Icehouse colony. Another six bats had transmitters attached, but due to signal failure or the inability to find the bat, insufficient data were recorded. Any bat with less than two nights' data was omitted from the analysis (range of 2-9 nights; mean 5.25 nights +/- 0.446 SE). All bats were tracked from time of leaving roost to return to roost unless there were problems with transmitters or heavy rain. Locations of the bats from radio tracking fixes were recorded at 10-minute intervals and behaviour recorded as either roosting, commuting or foraging. This was determined by listening to the radio signal and deducing whether the signal was stationary, moving rapidly and increasing/decreasing in strength in one direction or whether the signal was fluctuating and changing direction constantly, but staying within an area. Weather data were obtained from the Met Office at RAF Leuchars, Fife, Scotland.

3.4.2 Nightly time budgets

The nightly time budget of individual bats was determined by calculating how much time was allocated to the following activities:

- Actual time away from roosts as a percentage of the time available from sunset to sunrise.
- Commuting to roosts or foraging areas.
- Foraging
- Visiting roosts during the night period.

3.5 Results

3.5.1 Home ranges

From the 20 radio-tracked bats approximately 3500 radiolocation fixes (Figures 3.1 & 3.2) were recorded to an accuracy of +/- 50 metres and plotted onto a GIS model. There was no correlation between size of individual bats foraging areas and number of foraging fixes ($r^2 = -0.0008$, $p = 0.96$), (Table 3.1).

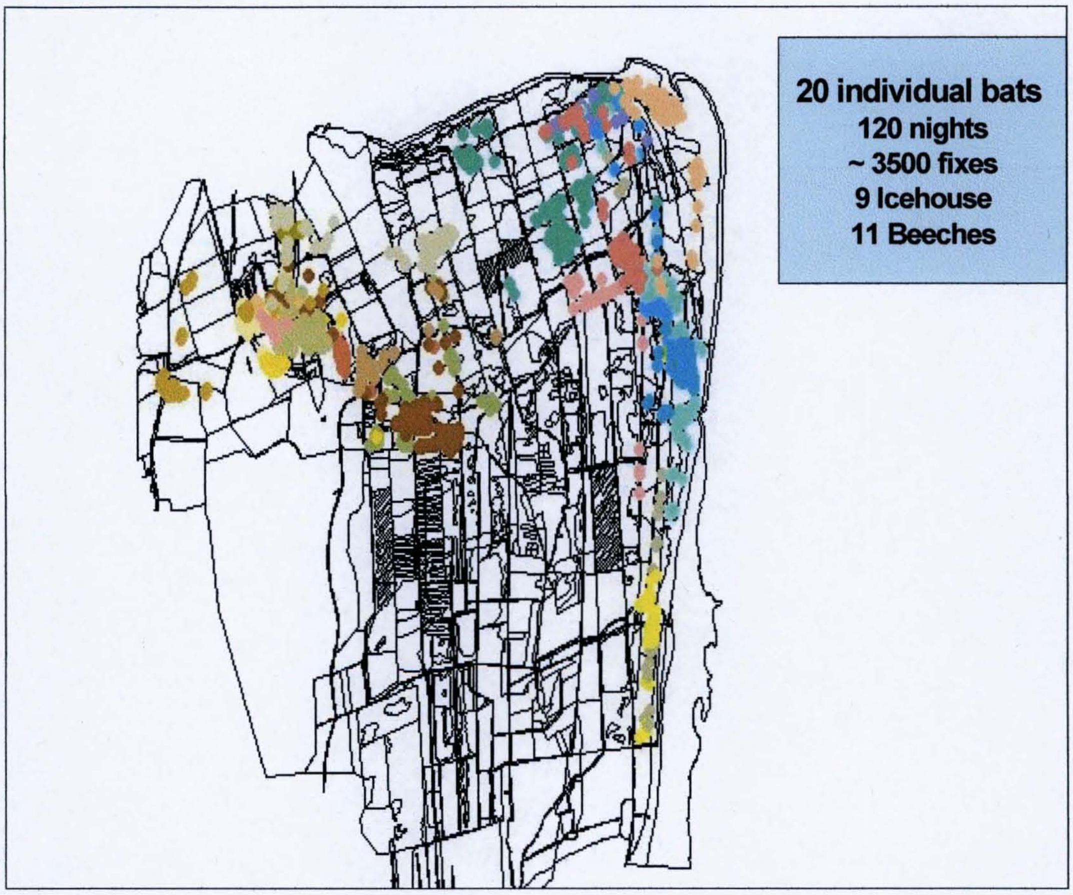


Figure 3.1: Radiolocation fixes for 20 bats tracked from April-September 2003 and 2004. Each bat is represented by a different colour.

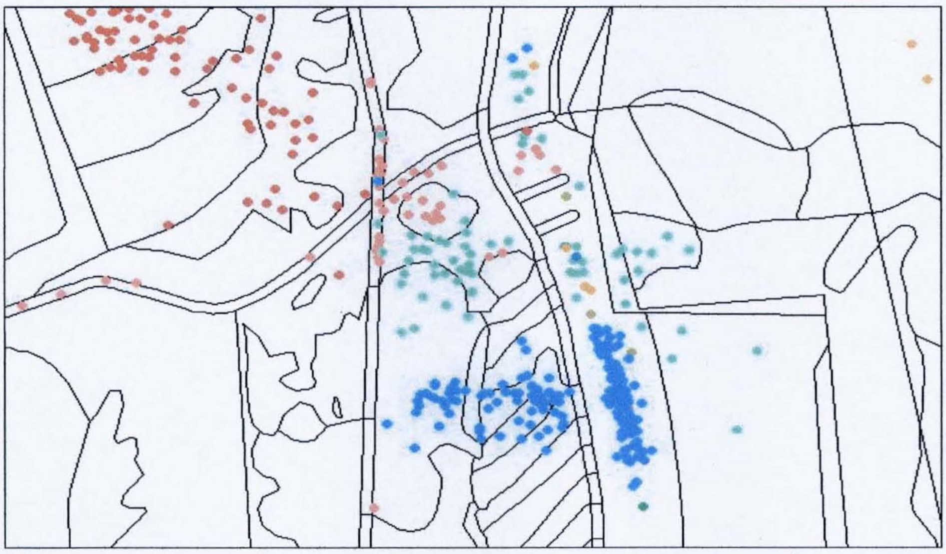


Figure 3.2: Radiolocation fixes for three bats represented by different coloured dots.

Bat	No. foraging fixes	Area o f 100% MCP (km^2)
T6814	53	0.014547
T6865	206	1.109048
T6965	130	0.24543
T6920	115	0.010602
T6934	114	1.35772
T6977	96	1.316306
T6978	183	0.181145
T8902	176	0.099766
T8913	59	1.299117
T8914	150	0.318014
T8920	135	0.584816
T8929	122	0.107583
T8931	71	0.169345
T8941	108	0.678588
T8943	79	0.759123
T9503	152	0.196874
T9552	115	0.49554
T9564	116	0.029022
T9573	167	0.474778
T9599	59	0.005023

Table 3.1: Number of radiolocation foraging fixes for individual bats and recorded size of 100% MCPs. There was no correlation between number of fixes recorded for individual bats and size of foraging area.

From the positional fixes an MCP comprising 100% of accurate (+/- 50 metres) foraging records were constructed at the colony level (Figure 3.3). Colony foraging home range sizes were 4.43 km^2 for the Beeches bats and 6.46 km^2 for the Icehouse bats. It can be seen that the two colony home ranges are separated. It is also apparent that there are no foraging incursions near the roost at Kinshaldy Stables where Natterer's bats were first recorded in Tentsmuir. No bats were recorded in roosts from another colony when tracking radio tagged bats. Lack of interchange was also found in the banding data; from 1998-2004, no significant interchange (16 out of 350 bats banded, 4.6%) was recorded between the different colony roosts (Chapter 6). From this it would seem that the forest has a minimum of three separate colonies of Natterer's bats at present, and that bats from these separate colonies do not associate for foraging or roosting during the spring and summer.

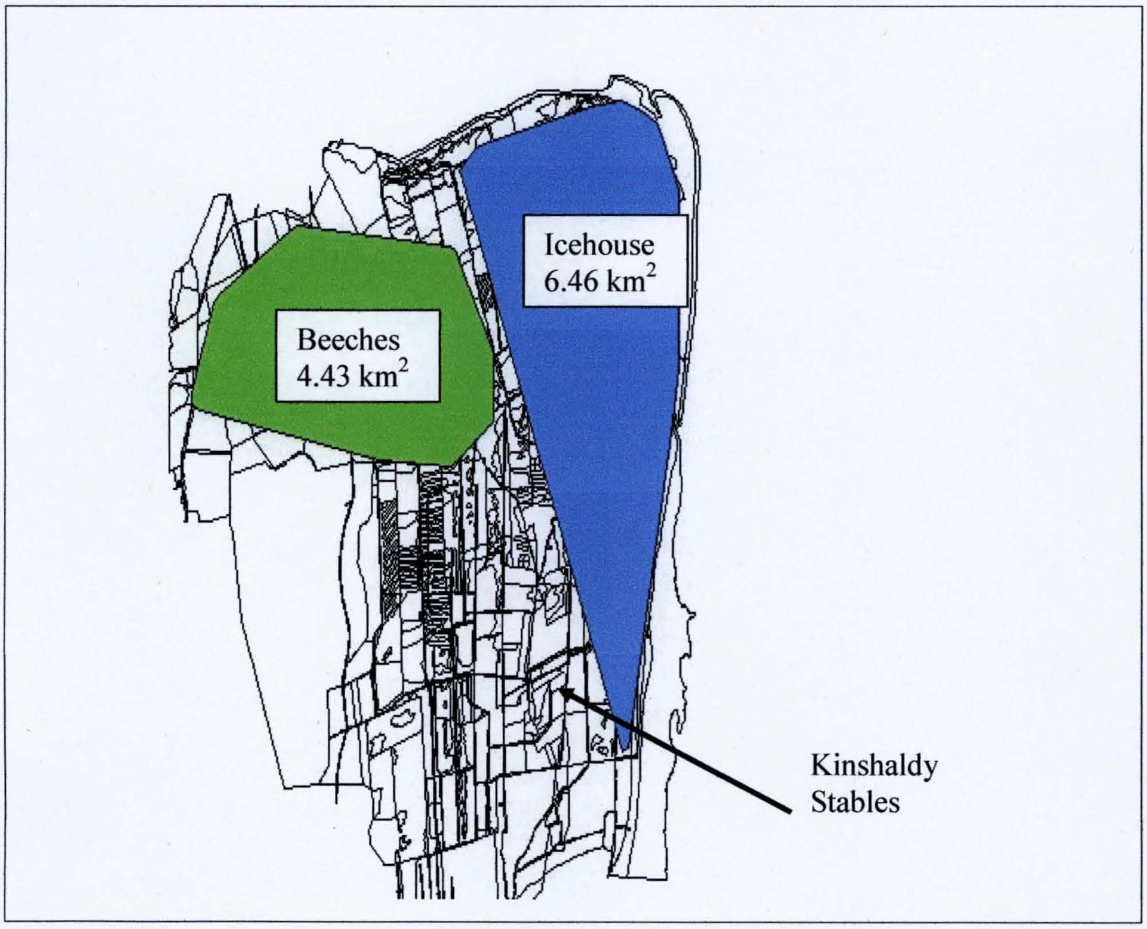


Figure 3.3: 100 % foraging MCPs for Beeches (green) and Icehouse (blue) colonies. Kinshaldy Stables are where Natterer's bats were first located in Tentsmuir.

MCPs for all individual bats were then calculated at the 100%, 85% and 50% levels (Figure 3.4).

Figure 3.4: Example of 100% (red), 85% (grey) and 50% (black) MCP's for two individual bats.

The mean area (km^2) of individual bat MCPs was calculated at the 100%, 85% and 50% levels (Figure 3.5). For the 100% MCPs mean areas of individual bats foraging areas were 0.472 km^2 (s.e. 0.105). For the 85% MCPs it was 0.185 km^2 (s.e.0.056) and they are on average 42% (s.e.6.4%) of the 100% MCPs. The 50% MCPs had a mean area of 0.021 km^2 (s.e.0.007) and were on average 8.7% (s.e. 2.2%) of the 100% MCP. Full descriptive statistics are in Tables 3.2 & 3.3.

	100% MCP (km^2)	85% MCP (km^2)	50% MCP (km^2)	85% Kernels (km$^{2)}$	50% Kernels (km$^{2)}$
Number	20	20	20	20	20
Mean	0.471949	0.185069	0.021041	0.156358	0.047405
S.E. of Mean	0.10471	0.056212	0.007279	0.039614	0.012767
Median	0.281722	0.073815	0.010492	0.096276	0.020499
Std. Deviation	0.468275	0.251389	0.032551	0.177161	0.057098
Range	1.351697	0.994636	0.147197	0.582495	0.191953
Minimum	0.005023	0.001128	0.000278	0.004813	0.001188
Maximum	1.351697	0.995764	0.147475	0.587308	0.193141

Table 3.1: Descriptive statistics for home range areas for all radio tracked bats combined.

Bat	100%MCP	85%MCP	50%MCP	85%Kernel	50%Kernel
T6865	1.109048	0.207296	0.000551	0.557166	0.193141
T6965	0.24543	0.034973	0.006239	0.190141	0.076141
T6977	1.316306	0.450964	0.147475	0.587308	0.188374
T6978	0.181145	0.015532	0.004231	0.025085	0.006277
T8902	0.099766	0.026594	0.008619	0.032388	0.014255
T6934	1.35672	0.334549	0.044074	0.389973	0.089349
T8913	1.299117	0.995764	0.036086	0.252362	0.072032
T8914	0.318014	0.037488	0.0174	0.060099	0.021739
T8920	0.584816	0.052262	0.012364	0.103298	0.036078
T6814	0.014547	0.012054	0.00544	0.022325	0.007456
T6920	0.010602	0.006388	0.002665	0.009228	0.003363
T8929	0.107583	0.068372	0.022054	0.057974	0.012555
T8931	0.156934	0.079257	0.004279	0.026772	0.009676
T8941	0.678588	0.460135	0.016478	0.300556	0.085957
T8943	0.759123	0.498321	0.006905	0.174194	0.061911
T9503	0.196874	0.160434	0.037926	0.124736	0.029207
T9552	0.49554	0.131891	0.025136	0.114608	0.019258
T9564	0.029022	0.001128	0.000278	0.004813	0.001538
T9573	0.474778	0.123641	0.021756	0.089253	0.018613
T9599	0.005023	0.004346	0.000857	0.004889	0.001188

Table 3.2: Area (km^2) of individual bats foraging home ranges for MCPs (100, 85 & 50%) and Kernel (85 & 50%).

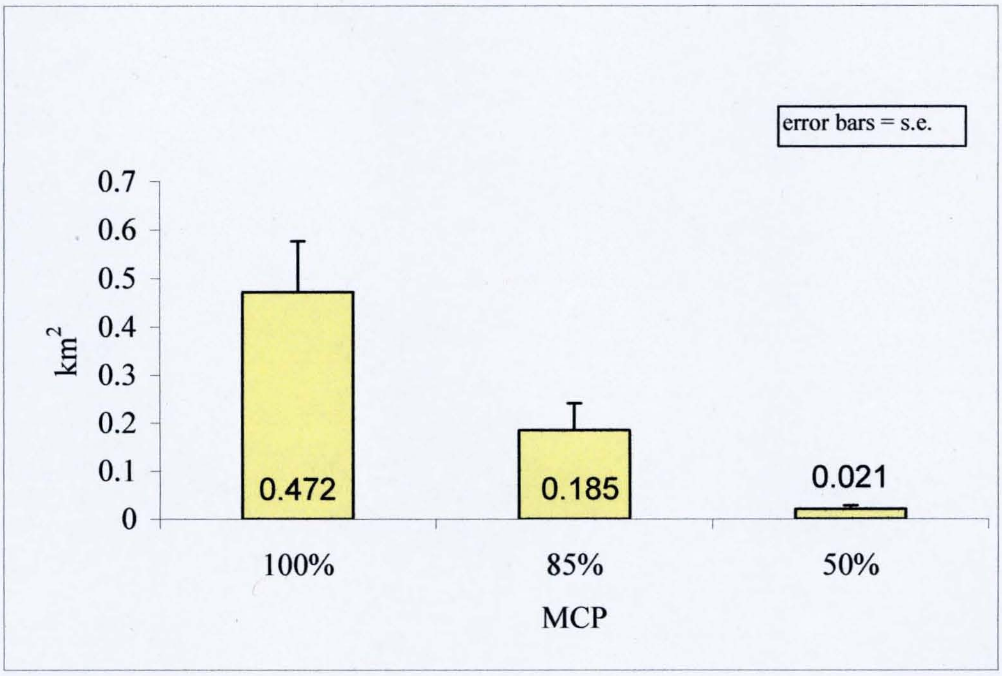


Figure 3.5: Mean areas of foraging home range MCP for combined colonies. 100% is 0.472km^2, 85% is 0.185km^2 and 50% is 0.021km^2.

Kernel estimators were calculated for individual bats at the 85% and 50% level to identify core foraging areas (Figure 3.6). The mean areas for all 85% home ranges were 0.15636 km^2 (s.e.0.04) and for 50% 0.04741 km^2 (s.e.0.013). Full descriptive statistics are in Tables 3.1 & 3.2. For Kernel estimators, cores for individual bats are not necessarily a single core as with MCPs (Figure 3.4). However, the calculated area includes the area for all the cores (Table 3.2). The mean number of 85% cores for individual bats was 2.0 +/- 0.25 s.e., and for 50% mean cores it was 1.35 +\- 0.15 s.e. When compared to the areas of 85% and 50% MCP there was a significant size difference ($t = 2.514$, df = 19, $p=0.021$) between 50% MCP and 50% Kernels (Figure 3.7), but not a significant difference between 85% MCP and Kernel areas ($t = -0.609$, df = 19, $p = 0.549$).

Figure 3.6: 85% (green) and 50% (pink) Kernel estimators for the same two individual bats as in Figure 3.4).

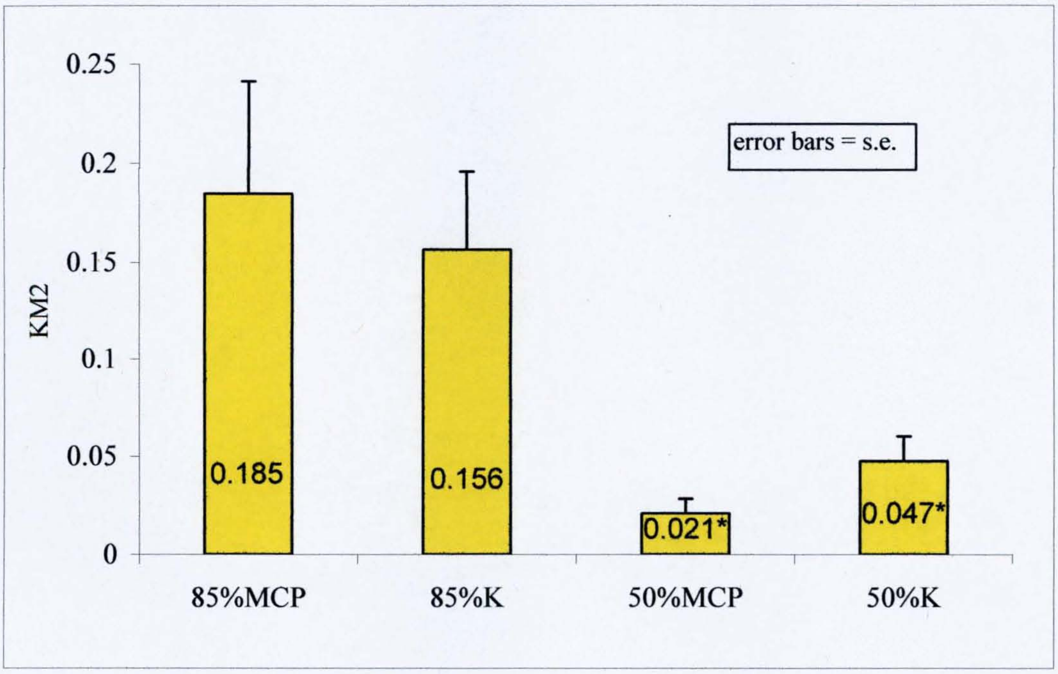


Figure 3.7: Mean area differences between MCP and Kernel estimators.

There were varying amounts of overlap between the 100% MCP areas of individual bats. As bats use a common set of roosts then home ranges containing all foraging records will display a considerable amount of overlap. This is due to bats foraging in the vicinity of roosts before departing to core feeing areas (Chapter 4). When the home range sizes were decreased to 85% MCP and then 50% the overlaps diminished with only 15 recorded at the 85% level and none at the 50% MCP level (Figure 3.6) The results for the 85% and 50% Kernel estimators were similar with only one overlap occurring at the 50% level. As the home range sizes are reduced to 85% then 50% it demonstrates that core-feeding areas do not overlap and, presumably are not shared with other bats.

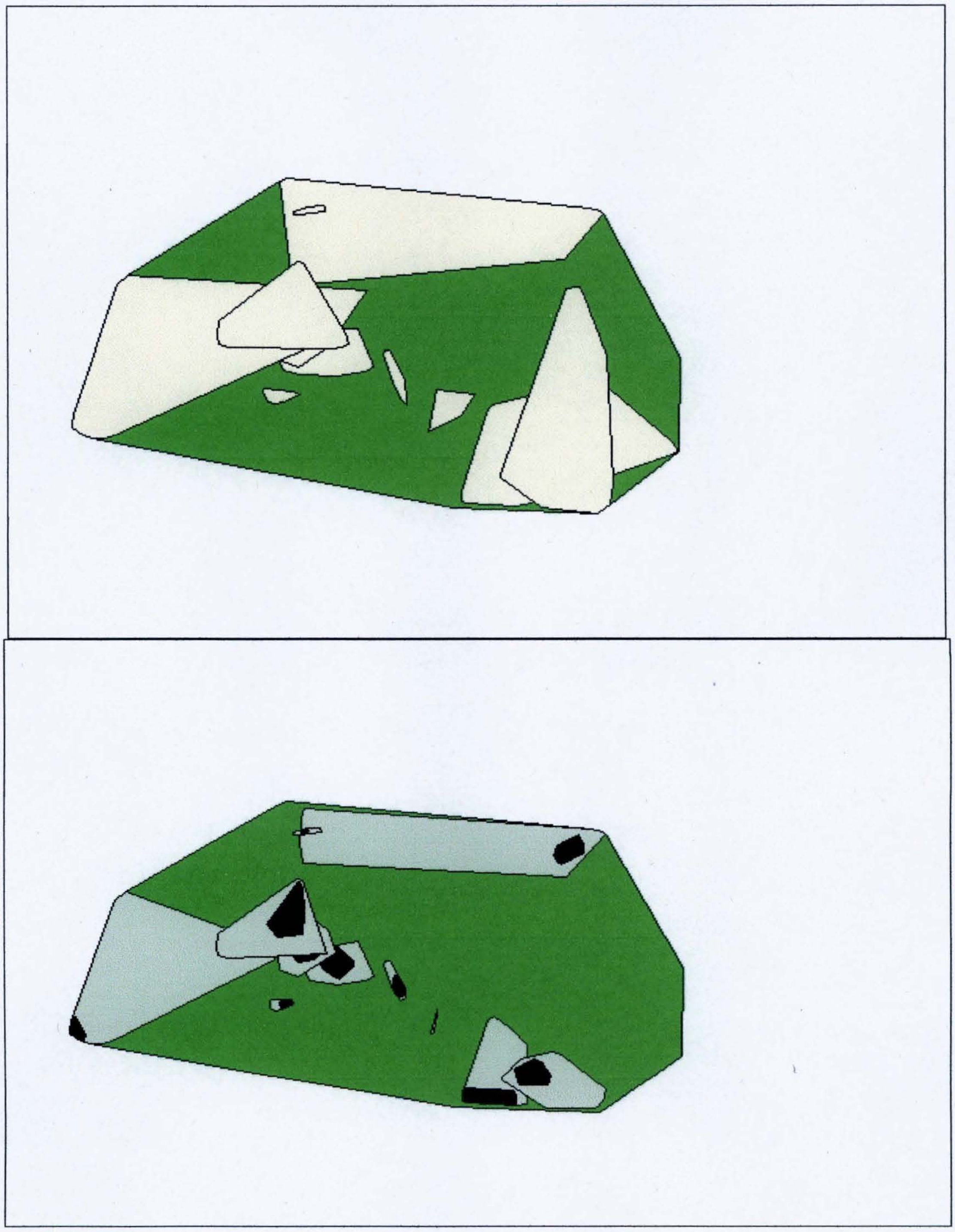


Figure 3.6: Illustration of overlaps at 100% MCP (top Fig.) and at 85% (grey) and 50% (black) MCP (bottom Fig.) for the Beeches colony.

3.5.2 Nightly time budgets

The mean emergence time from May to August was 57.4 minutes (+/- 1.29 SE) after sunset. The mean time for returning to roosts was 70.6 minutes (+/- 1.97 SE) before sunrise.

There was no change in the pattern of emergence/return times throughout the period (Figure 3.7), as the nights get shorter so the bats spend less time foraging. The distance travelled to core areas varied from 100 metres to 4.2 km but was dependent on which roost the bat was using.

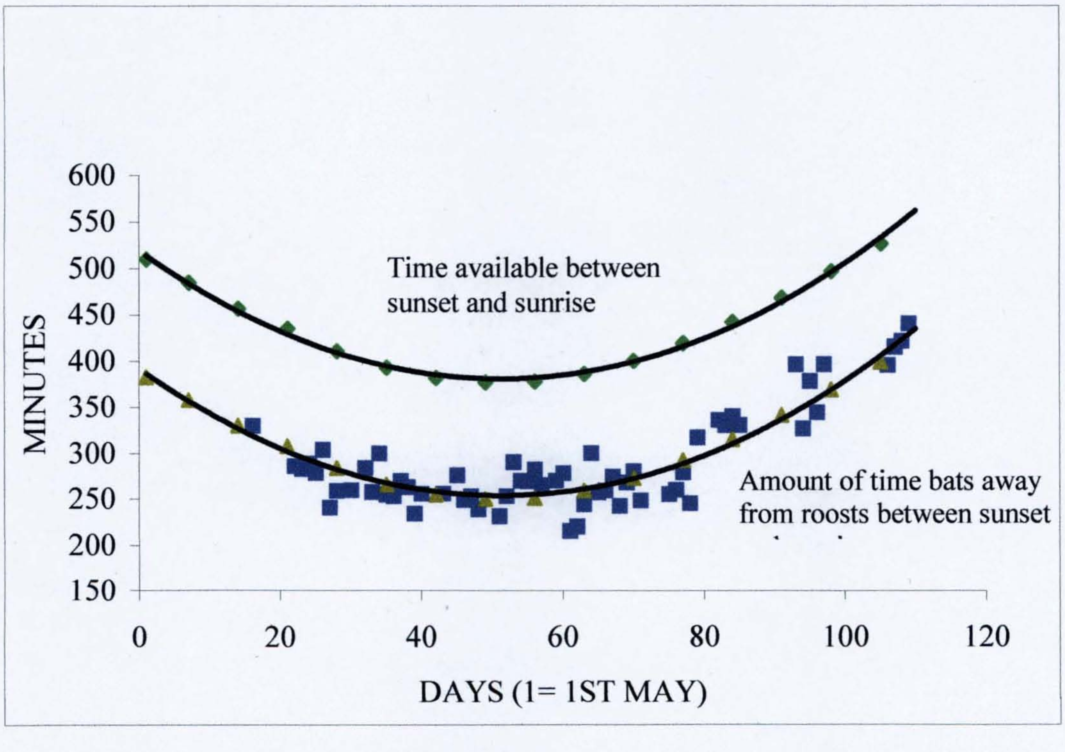


Figure 3.7: Nightly time budgets for period of time away from roosts and time available calculated from weekly sunset to sunrise times from May- August.

Three types of activity were recorded from radio telemetry after the bats left the roost, foraging, commuting and roosting. Bats spent the vast majority of their time foraging (96%) with visits to roosts only occurring in heavy rain (0.7%) or when lactating (0.3%) and commuting (4.4%). Roost visits in wet weather varied in time from approximately 2 minutes in heavy showers to the whole night in a storm. On one occasion the bat left its day roost for approximately 2 minutes in a storm then went back and stayed there until the next night. There were only a few roost visits recorded for lactating bats. Two bats were recorded returning to the box they had roosted in and where young bats where present. They were only present in the box for a maximum of 20-30 minutes.

3.5.3 Weather data

Weather patterns were looked at for the periods May-August 2003 and 2004 to ascertain whether certain weather patterns had an influence on bats foraging activities. All weather data were collected from the Met Office at RAF Leuchars, 1 km from the south end of Tentsmuir Forest. Where possible all data were for the nighttime period since this was when the bats foraged. Wind speed was calculated as a mean speed for the hours 22.00-04.00 with the range the minimum and maximum strengths recorded during that period. Minimum air temperature, grass temperature and rainfall were recorded between 21.00 and 09.00 hours nightly. These were calculated as a mean for each month with minimum and maximum also recorded. The monthly total of rainfall was for the hours 21.00-09.00 only (Figure 3.8). Table 3.3 displays the full range of weather data recorded. It was soon apparent that the only weather condition that had any bearing on foraging activities was heavy rain. Strong winds up to 20 knots appeared to have little effect, since foraging areas in wooded areas are often very sheltered and calm.

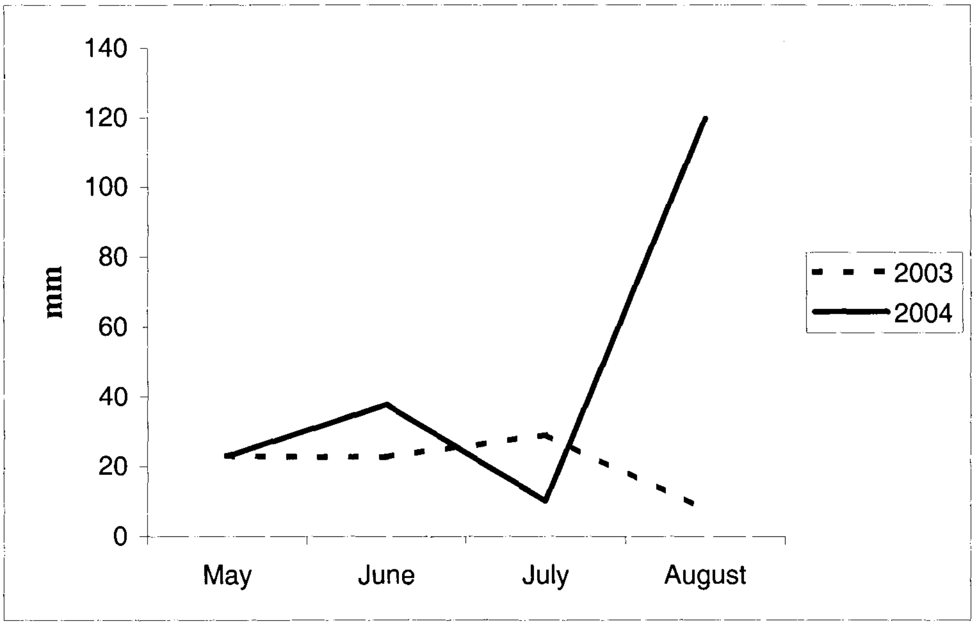


Figure 3.8: Total rainfall (mm) between 21.00 – 09.00 hours May – August 2003/2004.

		Wind speed 22.00-04.00 (Knots)	Min. air temp. 21.00-09.00 (C).	Grass temp. 21.00-09.00 (C).	Rain. 21.00-09.00 (mm)
May 2003	Mean	Na	7.3	4.4	0.7
	Min	Na	2.2	-2.3	0
	Max	Na	12.0	10.3	8.4
	Total	-	-	-	23.0
June 2003	Mean	6.3	10.0	5.9	0.7
	Min	0	6.7	1.7	0
	Max	20	13.1	12.8	10.0
	Total	-	-	-	22.8
July 2003	Mean	6.1	12.4	9.5	0.9
	Min	0	7.5	2.0	0
	Max	15	15.7	15.7	7.2
	Total	-	-	-	29.2
August 2003	Mean	5.7	11.2	7.7	0.2
	Min	1	6.1	0.1	0
	Max	23	16.2	16.4	3.0
	Total	-	-	-	7.6
May 2004	Mean	5.6	6.6	3.1	0.3
	Min	1	0	-5.4	0
	Max	18	11.4	10.5	5.0
	Total	-	-	-	23.0
June 2004	Mean	7.0	10.2	7.7	1.2
	Min	1	6.2	0.7	0
	Max	19	14.1	12.1	16.6
	Total	-	-	-	37.8
July 2004	Mean	5.1	9.6	6.3	0.3
	Min	0	4.9	-2.0	0
	Max	13	14.6	13.9	3.2
	Total	-	-	-	10.2
August 2004	Mean	6.9	12.2	10.3	3.9
	Min	0	4.5	-0.3	0
	Max	17	16.2	16.0	32.8
	Total	-	-	-	119.8

Table 3.3: Weather statistics May-August 2003/2004. All weather data were collected from the Met Office at RAF Leuchars, which is situated next to Tentsmuir Forest.

3.6 Discussion

3.6.1 Home ranges

The difficulties that are central to many home range studies are repeatability, lack of attention given to data collection, inadequate sample sizes and comparability of results Unless explicit details on data collection and analysis are given then the interpretation of the results are flawed since they cannot be repeated or compared (for a review of pitfalls see Harris et al. 1990). It is difficult to compare results from other studies, unless the full methodology is available, and perhaps this is where MCPs are essential. Numerous studies have used the 100% MCP as the basis for home range estimation and it is the baseline estimator that is a necessity in all studies in order that some sort of comparison can be made.

In this study the area of 100% foraging MCP is partially an artefact of where the individual bats roosted and how long the bat was tracked for. If an individual only used one roost or two or more roosts in close proximity throughout the period of tracking, then this affected the size of the MCP. This will occur simply because the bats foraged in the same core areas regardless of where they roost. So if a bat roosted at Morton Lochs and its core foraging areas are also in that area then home range size will be small. However, if that same bat roosted at the Beeches its home range area will increase. Despite this, the areas recorded for the home ranges for the colonies (4.46 & 6.62 km^2) are distinctly smaller than those found for Natterer's bats using open pastureland on the English/Welsh borders (Smith 2000). Smith found that colonies of approximately 35 bats had home range areas between 11.3 – 13.1 km^2. There were also very large differences in the density of bats present in the home ranges studied in this study and those in his (see

Chapter 5). The numbers of bats per km^2 was significantly higher (10 & 25 bats per km^2) in this study than that recorded by Smith (2.88 bats per km^2). This could be attributed to various factors, which include the structure, shape and size of commercial plantations and that foraging sources may be richer than previously suspected. The main foraging areas for Natterer's in Tentsmuir are within the forest in mature pine stands (Chapter 4) which means that there is much more available foraging habitat in a small area. This is compared to the fragmented deciduous foraging habitat found in Smith's study in open pastureland where the bats have to travel across extensive areas of unsuitable foraging habitat to reach suitable foraging areas.

The considerable overlap between the 100% MCPs is, again, an artefact of roost selection, individual bat behaviour and limitations in radio tracking technique. Natterer's bats often forage for a short period of time near the roost before generally foraging slowly on the way to a core feeding area. On the way back to a roost the flight is normally very direct with no foraging happening. They sometimes forage after returning to the immediate vicinity near a roost, so many bats often use the immediate area around roosts as a secondary feeding area. There is also the issue of sociality where bats gather in groups, possibly for information transfer over roost selection (Swift 1997). It was not possible in this study to differentiate between bats foraging or flying socially, so any flight recordings would have been recorded as foraging. This, however, is only considered to be likely to occur immediately before roost selection at the end of the nights foraging. There were odd occasions when small groups of Natterer's bats were observed flying up to several different roosts in close vicinity before either selecting one or leaving the area altogether and roosting at another location in the forest. Any erroneous foraging recordings due to a short period in the vicinity of the roost would be included in the 100% individual MCP, but discarded in the 85% estimators as outliers to the core foraging areas.

The areas covered by the 85% MCPs were 42% of the 100% MCPs. Since the bats spent 85% of their time in an area less than half of the 100% MCP, this probably represents a more accurate portrayal of individual foraging locations within the commercial plantations. These 85% MCPs have very little overlap with those of other individuals. In the case of the 50% MCPs, the areas are all separate from those of other individuals. These 50% MCPs vary in size from 0.00028 - 0.1475 km^2 and this appears to be a feature of the foraging habitat utilised and its shape and structure. Some individual bats were found to forage on linear features, e.g. streams, and had noticeably smaller core areas than bats foraging over young pines. However there were insufficient data to statistically test this.

The area of 85% home ranges calculated by the Kernel estimator were not significantly different in size to the area calculated for the 85% MCP. However, the mean number of Kernel cores was two per individual compared to one for MCPs. The area for the 50% Kernel was significantly bigger than the 50% MCP and had a mean 1.35 cores per individual bat. Again, there was virtually no overlap between the 50% Kernel cores for the bats. Kernel estimators would appear to compliment and enhance home range estimation when used in conjunction with MCP. The biggest asset of Kernel estimators is that, unlike MCP, multiple core areas can be identified, which enables very fine differences to be picked out in foraging habitat (Figure 3.9). This is particularly useful in commercial plantations, where many of types of habitat have clear-cut boundaries e.g. tracks, roads, waterways and of species of tree.

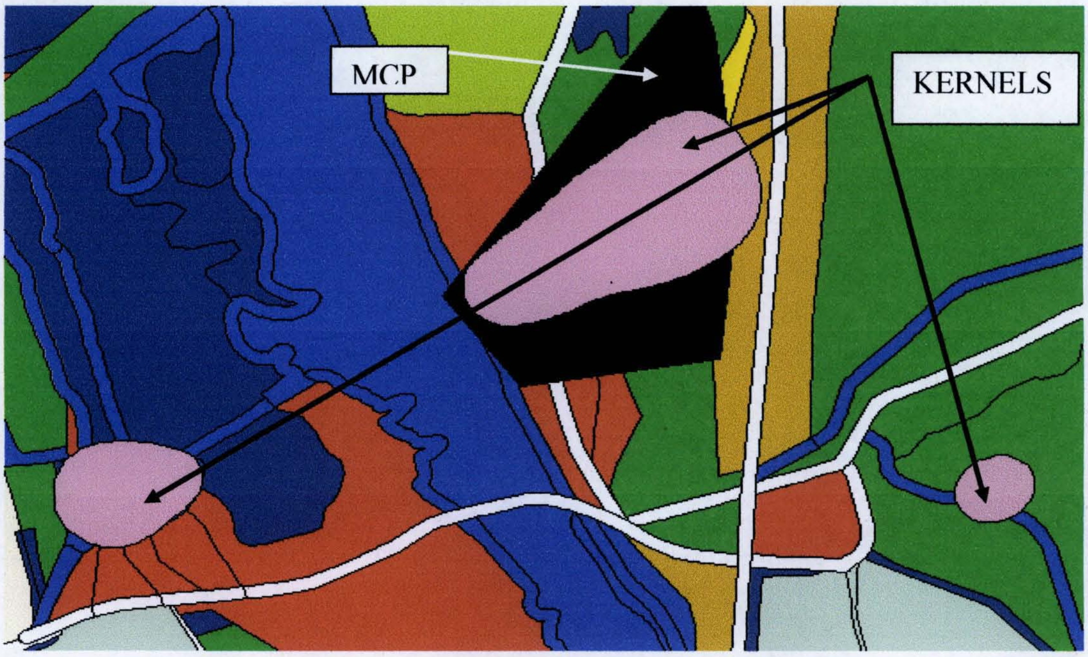


Figure 3.9: Comparisons between 50% MCP (in black) and 50% kernel (in pink) core foraging areas.

Bats are known to respond to localised and unpredictable food patches (Bell 1980), and this was evident occasionally in the bats present at the Beeches colony. This colony is situated close to Morton Lochs where hatches of flying insects periodically occurred over the open water, particularly on warm balmy nights. Natterer's bats would often congregate and forage for 5-20 minutes in small groups of up to twenty individuals before departing to their normal foraging areas (pers. obs.).

Little is known about whether bats partition their foraging ranges, or how they space themselves to minimize potential competition (O'Donnell 2001). In this study Natterer's bats displayed site fidelity in that they always kept to the same 50% core foraging areas throughout the time they were radio tracked. At least two other similar species, greater mouse-eared bat and Geoffroy's bat *Myotis emarginatus* have also demonstrated site fidelity to core areas (Audet 1990, Krull et al. 1991). Since no interactions with other bats were recorded in core areas, it is unknown whether Natterer's bats have exclusive foraging areas maintained by territoriality.

The distance travelled to forage in core areas by individual Natterer's bats was dependent on where the bat roosted. They foraged in the same core areas each night they were followed regardless of where they roosted during the day. The distance to the foraging areas ranged from < 200m to 4.2 km, and is similar to Natterer's studied in England and Germany in open pastureland and orchards (Siemers et al 1999, Smith 2000). Other *Myotis* species travel up to 9 km (Audet 1990, Krull et al. 1991). Female serotine bats usually feed within 4km of the day roost (Catto et al. 1995) and female brown long-eared bats *Plecotus auritus* spent most time foraging within 0.5km of the roost (Entwistle et al. 1996), while Leisler's bats have been recorded travelling up to 13.4 km (Shiel & Fairley 1998).

3.6.2 Nightly time budgets.

The mean nightly emergence time of 57.4 min (s.e. 1.4 min) after sunset compares very closely with the median emergence time of 55.9 minutes (s.e. 1.8 min) recorded for Natterer's bats in Northern Scotland (Swift 1997). However, Siemers et al (1999) in a study in Southern Germany recorded a mean emergence of 31.6 min after sunset. This difference is probably due to the relatively shorter twilight period in Germany than in Scotland, because it gets dark more quickly after sunset at lower latitudes. Several authors have found that the main factor governing time of emergence is light intensity (Shiel & Fairley 1999, Duverge et al. 2000). Other reasons stated for variations in time of emergence can be due to differences in roosts, colony size and reproductive condition (Rydell 1989, Shiel & Fairley 1999). Natterer's bats are known to have at least two foraging strategies, foliage gleaning and aerial hawking. Swift (1997) speculated that a gleaning bat may have to rely less on the dusk peak of flying insects and can therefore emerge later than non-gleaners. As bats that glean are generally slower flyers than aerial hawkers, it is also considered that a later emergence time is due to a predation strategy against diurnal predatory birds (Jones & Rydell 1994, Rydell et al 1996, Speakman et al. 2000).

The time of emergence recorded was that of the bat with the radio transmitter. The bats normally emerged singly with up to five minutes between individuals and sometimes over thirty minutes between the time when the first bat emerged and the tagged bat left. Bullock et al. (1987) considered that time of emergence of the first bat was a less reliable indication of time of emergence than mean or median times. It was not possible in this study to determine the patterns of emergence among all the bats because as soon as the tagged bat left the roost it was followed.

Roost visits by the bats during the night were recorded for only two specific reasons: periods of heavy rain and by lactating females, presumably to feed their young. No roosts were used solely for night use, whenever heavy rain occurred bats used nearby bat boxes or known natural roosts, all of which were used as day roosts. There are only limited data for lactating bats visiting roosts, but no more than two visits in any one night were recorded. This compares well with the findings of Swift (1997) but differs markedly from other European bats, which have been found to make repeated visits to roosts during the night e.g. serotine bat (Catto et al. 1996) and Leisler's bat (Shiel & Fairley 1999).

It is interesting to note that the period of minimum time away from roosts around mid-summer's night is when many of the bats are heavily pregnant. The bats do not adjust to shortening night length by leaving earlier after sunset or returning later before sunrise to roosts. This is markedly different from some other European bats, which show seasonal variation by altering their time of emergence relating to sunset and sunrise, probably to cater for increased energy demands when lactating e.g serotine bat (Catto et al 1996), noctule bat *Nyctalus noctula* (Jones 1995) and Leisler's bat (Shiel & Fairley 1999).

In this study Natterer's bats spent most of the night foraging. Since they exhibit late emergence/early return times, they may have less time available to forage. Other species, e.g. serotine bats spend considerable periods of time resting during the night. They also appeared to more influenced by climatic variables e.g. wind and temperature, that had a significant effect on the total time spent away from the roost (Catto et al. 1996). The only time weather stopped the Natterer's bats foraging was during heavy rain. High winds, up to 23 knots had no effect. Due to the structure of coniferous plantations they can provide some relatively sheltered areas to forage during high winds. Also air temperature and grass temperature never had an effect on foraging. Grass temperature dipped below freezing in every month of this study except June in both years. As Natterer's bats have been found to sometimes glean food off vegetation (Sheil et al. 1991, Arlettaz 1996a, Siemers & Schnitzler 2000, Swift & Racey 2002), then ground frosts could be expected to have a positive impact on foraging success and strategy. Low temperatures inhibit insect flight and movement and this could make them more susceptible to bats that forage by gleaning.

Radio tracking and the subsequent home range and core analyse are not the end result; it is essential must be looked at in the context of biological interpretation and explanation. An empirical measure of home range size will have no relevance unless it is explicitly interlinked with the animal's behaviour and the geographical landscape it inhabits. Comparisons with other bat populations and species are fraught with difficulty since bats adapt to their local environment, climatic conditions and available habitat. It is clear that Tentsmuir Forest, a commercial coniferous plantation, has the capacity to sustain a much higher breeding density of Natterer's bats than recorded in fragmented broad-leafed woodland. Natterer's bats are present in many of the bat box schemes that are present in commercial plantations throughout the U.K. If the densities recorded in Tentsmuir are found to be similar in these forests then commercial plantations may well be the richest habitat for Natterer's in the U.K.

CHAPTER 4

Habitat preference and diet

4.1 Abstract

The habitat preferences for foraging adult female Natterer's bats occupying summer and maternity roosts in a commercial coniferous plantation were investigated by radio tracking. Compositional habitat analysis shows that the bats forage preferentially in mature Corsican pines and around water bodies much more than the availability of these habitats. Diet analysis showed that there is a considerable range of prey taken and that Natterer's bats forage both aerially and by gleaning. There was no significant difference in invertebrate species abundance and richness, as determined by four different trapping methods. There was no relationship between invertebrate abundance and richness caught by trapping and as represented in the diet by faecal analysis. There was no significant difference in invertebrate abundance and richness using various trapping methods, between water bodies and young Scots pine plantations and mature Scots and Corsican plantations.

4.2 Introduction

4.2.1 Foraging habitats used by bats

In the U.K. and Europe, research has demonstrated that bats forage in a variety of habitats. Foraging habitats vary between bat species, but generally include broad-leaved woodlands, water habitats and linear edge habitats (hedgerows and treelines). Walsh & Harris (1996a, 1996b) in a national survey of the U.K. concluded that in general, broad-leaved woodland and riparian habitats are of pivotal importance for the majority of the U.K. bat species and that arable land, moorland and improved grassland were strongly avoided for foraging. Also, they found that within woodland habitats, edges are selected more strongly than openings and semi-natural woodland was more strongly selected than mixed or coniferous woodland. They also stated that coniferous plantations represent a less optimal type of woodland for foraging due to reduced numbers of insects available and that a shortage of gaps/openings in large contiguous coniferous plantations confirms their low value to foraging bats.

The foraging activity of bats in relation to habitat structure can be seen as a combination of factors that include morphology, resource partitioning and echolocation characteristics (Aldridge & Rautenbach 1987, Norberg & Rayner 1987). Aldridge (1986) found that there is a relationship between wing morphology and feeding ecology, while Fenton & Rautenbach (1986) showed differential habitat use for three species of African bats with differing wing morphology. Resource partitoning was demonstrated in two sibling bat species, greater mouse-eared bats and lesser mouse-eared bats *M. blythii,* which are morphologically similar, and often congregate in mixed clusters in their colonies (Arlettaz et al. 1997, Arlettaz 1999). Natterer's bats are sympatric with Bechstein's bats *Myotis bechsteinii* over part of their range and Siemers & Swift (2006) found that differences in sensory ecology contribute to resource partitioning between the two species. They showed that Bechstein's bats hunt more frequently using prey-generated sound, while Natterer's bats predominantly use echolocation. Niche differentiation in five congeneric *Myotis* species demonstrated a strong correlation between the prey-detection ability of the species and the respective search-call bandwidth (Siemers & Schnitzler 2004).

Selective and opportunistic foraging can be seen as the two extremes of a continuum of foraging behaviour. Several studies have identified both in the same bat species, with some species showing considerable plasticity in their foraging behaviour (Anthony & Kunz 1977, Swift et al. 1985, Jones 1990). For Natterer's bats, field observations (Arlettez 1996, Swift 1997), experimental studies (Siemers & Schnitzler 2000), echolocation studies (Siemers & Schnitzler 2000, 2004) and faecal analyses

(Shiel et al. 1991) have shown that they are extremely versatile in their foraging behaviour. They are adapted for prey perception in cluttered habitats close to or within vegetation using low broadband width echolocation (Siemers et al. 2000), trawling for insects with their inter femoral tail membrane and gleaning off vegetation (Siemers & Schnitzler 2000, Swift & Racey 2002) and aerial hawking. This plasticity allows them to utilise both a wide range of prey items and diverse habitats.

Since nothing is known about the foraging of Natterer's bats in commercial coniferous plantations, it is important that foraging areas are identified. This is essential from a conservation and planning aspect (Stebbings 1988, Vaughan 1997). Commercial plantations are working forests where trees are harvested, so knowledge of where bats forage within the forest is indispensable from a management perspective. The effects of forest management practices on the spatial activity patterns of most species of bats are poorly understood with a paucity of information available (Menzel et al. 2002).

When resources are used disproportionately to their availability, use is said to be selective. Two of the most common types of selection studies deal with food and/or habitat selection. For habitat selection variables may be discrete (e.g. forest, arable field) or continuous (distance to water, canopy height) or a combination of the two. For food selection studies, normally a combination of trapping potential prey items and comparing this with faecal analysis or stomach contents is performed.

Habitat use by bats has been assessed by various methods including field observations, ultrasound detectors and radio tracking. It is only recently that radio transmitters are now available that fit the smallest bats. Field observations on foraging behaviour and habitat use were the basis for many of the early papers (e.g. Kunz 1974, Tuttle 1976). Ultrasound detectors have been extensively used on a local scale; e.g. Rydell et al. (1994) showed that common pipistrelle bats and Daubenton's bats foraged mainly over rivers and ponds, occasionally near trees and that agricultural habitat was infrequently used. Lesinski et al. (2000) also used ultrasound detectors and a series of transects, to determine how foraging activity differed between urban and riparian habitats for several species of bat in Poland. The results showed that relative bat densities in the urban areas were only slightly lower than in comparable habitats outside the city. For serotine bats, records decreased with distance from the city centre, while for noctule bats it was the opposite. In a benchmark paper, Walsh & Harris (1996b) reported on a transect survey using ultrasound detectors on a national scale in the U.K. They produced a model relating bat abundance to habitat availability and to predict the impact of past and future large scale land-use changes on vespertilionid bat abundance.

The advent of radio transmitters small enough to attach to most species of bats has transformed foraging and habitat studies. Radio tracking bats has several advantages over using bat detectors. This includes keeping track of individual bats, much greater detail of their behaviour, finding roost sites, the ability to accurately identify where exactly a bat is located at a specific time and to collect much greater amounts of data. Also, particularly for larger species, radio tracking can be automated. This can allow for considerable amounts of data to be collected without the need for personnel in the field. Bat detectors give you the ability to listen to bats and therefore record whether that species is present in a habitat at a specific time. However, they do not differentiate between individuals, you only pick up whether they are present or not.

This can be very useful in determining whether or not a particular species is present in a specific habitat. However, if you require detailed data on e.g. foraging preferences, home ranges, roost selection etc then radio tracking is essential.

There has been a steady increase in radio tracking studies on the feeding behaviour, habitat use and foraging strategies of various species of bats e.g. Geoffroy's bat (Krull et al. 1991), greater mouse-eared bat and lesser mouse-eared bat (Arlettaz 1999), Ozark big-eared bats (Wethington et al. 1996), Natterer's bat (Siemers et al. 1999, Smith 2000) and lesser horseshoe bat (Bontadina et al. 2002, Holzhaider et al. 2002). All of these studies have identified for individual bat species, several aspects of previously unknown bat ecology including foraging habitats, roost sites, home range areas and the use of flight paths. This has greatly improved conservation management for some species of bats because simply, you have to know the facts to make management decisions that will benefit the species involved.

4.2.2 Analysis of habitat use

There has been much discussion on the analysis of habitat use (Neu et al. 1974, Aitchison 1986, Alldredge & Ratti 1986, 1992, Thomas & Taylor 1990, Aebischer et al. 1993, Cherry 1996, Alldredge et al. 1998) and the "best" way to proceed is still being debated. Some areas of particular concern are sampling level, data pooling across individuals, non-independence of habitat proportions and arbitrary definitions of habitat availability (Aebischer et al. 1993). Different methods used include preference indices, chi-square, Friedman and Quade's methods, compositional habitat analysis, discrete models and log-linear models. In a review of the application of four methods, Alldredge & Ratti (1992) concluded that the choice of method should depend upon which statistical hypothesis most closely matches the biological question. In a comparison of six methods, McClean et al. (1998) stated, that since the methods use various assessments of availability and treat individuals differently, the results were also different even when using the same data set. Smith (2000) provided a detailed breakdown of several bat studies identifying habitat selection and the various methods used. This highlighted the difficulties involved in comparisons of habitat usage and complemented the review by Harris et al. (1990) on radio tracking in general.

Studies on foraging by Natterer's bats have revealed a mix of habitat use. Using ultrasound detectors near known roosts, Swift (1997) identified roadside vegetation, woodland edges, parkland and sheltered areas of water as foraging areas. Siemers et al. (1999) radio tracked three adult non-lactating females in a study area in southern Germany characterised by fruit tree orchards, beech dominated deciduous forests and monocultures of spruce *Picea abies*. The results showed that *P. abies* was present in all three of the individuals' core foraging areas although the area is dominated by deciduous forest. The core areas were determined as the MCP comprising 50% of the radio fixes for each individual. Smith (2000) radio tracked a total of 33 bats in pastureland on the borders of England and Wales. Compositional analysis showed that semi-natural broad-leaved woodland and open water habitat were preferred, while arable land and coniferous plantations were avoided. He suggested that a limiting factor for Natterer's bats in his study area may be the amount of tree lined river corridor and semi natural and other broad-leaved woodland available.

4.2.3 Habitat selection

A central concern of analysis on habitat usage is how habitat is defined. Where habitats appear in aggregated patterns, the delineation of boundaries can significantly influence the analysis and poor choice of boundaries may produce misleading results (Porter & Church 1987). Many of the habitats within a commercial plantation are much more easily defined than would be possible in the countryside in general. There are often very defined borders e.g. roads, fences or stands of a particular tree species, which make it easy to record what habitat type a bat is foraging in, when radio tracking. Porter & Church (1987) stated that where habitat boundaries are regular then the impact of study area delineation boundaries on inferential habitat analysis is less important. Schooley (1994) argued that habitat composition is normally in a state of flux and that changes in habitat characteristics may have dramatic effects on habitat selection by animals. However, Arthur et al. (1996) considered that in some studies habitat changes over time might be considered negligible. As Tentsmuir is a working forest, in this study habitats could change due to felling regimes or other working practices. Clear felling of larger blocks or stands of trees is no longer carried out, since the present management practice is a policy of continuous cover. The concept of continuous cover is that felling and regeneration are carried out continually or irregularly throughout the whole of the woodland area, and there is no clear felling of trees when they reach some predetermined age (Helliwell 2002). This means habitat changes would be localised and small scale compared to the previous regime with whole blocks of trees removed at the same time.

4.2.4 Compositional habitat analysis

For this study foraging habitat choice was analysed using the method of compositional habitat analysis as described by Aebischer et al. (1993). Compositional habitat analysis defines resource use as the proportion of resources within the estimated home range of the animal. The home ranges were as defined by MCPs derived from radio tracking of bats (Chapter 3). It is a two stage analysis looking at the proportion of habitat available within a colony home range and assesses proportional use of foraging habitat within that home range by individuals by implementing a type of MANOVA linear model. It allows the analysis of proportional data that overcomes the unit-sum constraint, whereby proportions sum to one. The constraint means that an animal's use of one habitat is not independent of the others. The unit-sum constraint causes problems with interpretation of results with chi-square tests and violates the assumptions required for using the Friedman and Quade tests (Neu at el. 1974, White & Garrott 1990, Aebischer et al. 1993). Aebischer (1993) states that a minimum sample size of six individuals can be used for the analysis, but recommends ten individuals and preferably above 30 individual bats. Compositional analysis has been used in previous studies to analyse habitat use for a wide variety of animals including large mammals (Gabor & Hellgren 2000), doves (Browne & Aebischer 2004) and Natterer's bats (Smith 2000).

4.2.5 Diet

Diet analysis of bats has been done using faecal scats. However, hard bodied and heavier sclerotised insects are over represented in the scats compared to soft-bodied insects. Rabinowitz & Tuttle (1982) found that mayflies fed to bats were underrepresented in the faecal analyses. Whitaker et al. (2004) suspected that bats might be able to produce chitinase, which would further reduce the chances of identifying softer insect body parts. With captive serotine bats prey remains appeared within 33 minutes of feeding and continued to appear for up to 32 hours after consumption (Robinson & Stebbings 1993). However, despite the difficulties in reconstructing diet from scats, faecal analysis is now an accepted and frequently used method (Kunz & Whitaker 1983, Shiel et al. 1991).

4.2.6 Sampling invertebrate and floral communities in coniferous trees.

Invertebrate biodiversity and richness has been stated to be lower in commercial plantations than in broad-leafed woodland (Winter 1983, Garrod & Willis 1997). However, recent work has now questioned this and the results are considerably more complex than previously thought. Comparisons between the canopy fauna of four deciduous broad-leaved and four coniferous tree species show some intriguing results (Ozanne 1999). Quantitative analysis found that both broad-leafed and coniferous trees support defined, but very different, communities and that mean densities of arthropods were significantly higher for conifers. When individuals were allocated to feeding guilds, conifers supported proportionally more scavenger/epiphyte feeders whereas deciduous trees were dominated by phytophages (Ozanne 1999). Fahy & Gormally (1998) concluded that for carabid beetle communities, semi-natural oak woodlands supported a greater range of species than a stand of 34-year-old Sitka spruce. However, clearfelled areas of spruce, that are not replanted, support a wide range of species and can enhance species richness within commercial conifer plantations. This result concurred with the work by Butterfield (1997) who found in Sitka spruce plantations that carabid communities were more diverse and abundant in recently felled (1-4 years) plantations compared to young (5-27 yr after planting) and that both density and diversity were lowest in old plantations (42-63 yr after planting).

Pyrethroid knockdown sampling of canopy arthropods in Scots pine revealed that larger forest patches supported greater populations of arthropod specialists than small patches and that isolated individual trees supported a qualitatively different fauna (Ozanne et al. 2000). Research by Jukes et al. (2001, 2002) on the composition of canopy Coleoptera in a wide range of coniferous plantations found that results varied due to a variety of reasons including climatic factors, soil topography and latitude. They suggested that many studies of the ecology of coniferous plantations in Britain have been site specific and that comparative studies of plantations of different crop species in contrasting bioclimatic zones or on a range of varied site types are needed to reach sound conclusions regarding invertebrate composition (Jukes et al. 2002).

Invertebrate biodiversity is closely linked to vegetation type (Walsh & Harris 1996b) and several studies have now investigated the floral community of coniferous woodlands. Ferris et al. (2000) studied relationships between vegetation, site type and stand structure in coniferous plantations. The results showed that the composition and diversity of the understory plant communities are determined particularly by site type, soil fertility and the variability of canopy structure. They reported that the retention of a greater proportion of stands beyond financial maturity would improve the biodiversity of upland conifer plantations. In a comparison between plantations (Scots pine and Sitka spruce) and semi-natural woodlands (pine and oak) in northern Britain there was no difference in fungal species richness. There were however, large differences in species composition with an unexpected high incidence of rare and threatened fungi in plantation stands of pine and spruce (Humphrey et al. 1999, 2002).

The above studies demonstrate that there is still much to learn about the biodiversity of commercial plantations and that many factors influence species richness and abundance. It is also clear that for some communities of invertebrates, coniferous plantations are the preferred habitat and that they are present in high densities.

4.3 Aims

The aims of this study are to determine:

- By radio tracking, whether adult female Natterer's bats that use summer roosts in Tentsmuir Forest, a commercial coniferous plantation, preferentially choose foraging habitats within or outside the forest boundaries and which habitats they preferentially use.
- To examine the diet by faecal analysis using scats collected monthly from bat boxes.
- To make a comparison of invertebrate biodiversity between water bodies and young Scots pine within Tentsmuir Forest using four different methods of invertebrate trapping.
- To make a comparison of canopy invertebrate biodiversity between mature Scots and Corsican pine in Tentsmuir Forest by pan trapping.
- To examine any correlations between the diet and invertebrates trapped using various trapping methods in young Scots pine and water habitats within the forest.

4.4 Materials and methods

4.4.1 Study site

Tentsmuir Forest is a 9143-hectare commercial coniferous forest on the NE coast of Fife, Scotland. It was acquired by the Forestry Commission in the 1920's and is planted predominantly with Scots pine and Corsican pine. Other species/habitats present include areas of Norway spruce, *Picea abies,* Sitka spruce, broad-leaf woodland, sand dunes, grazing fields, arable land and water bodies. It is flanked on the north side by the estuarine River Tay, farmland on the west and on the east by the North Sea.

4.4.2 Geographical Information Systems

The MapInfo (Mapinfo Corp. 1999) Geographical Information System (GIS), incorporating both ArcMap and ArcView 3.2 was used to produce a digitised computer-based map of land use and habitat availability within the study area (Fig 4.1). Onto this all radiolocation fixes of tracked bats were plotted and roost sites recorded. The home range estimators (MCPs and Kernel) were calculated using the Animal Movement attachment in ArcView 3.2.

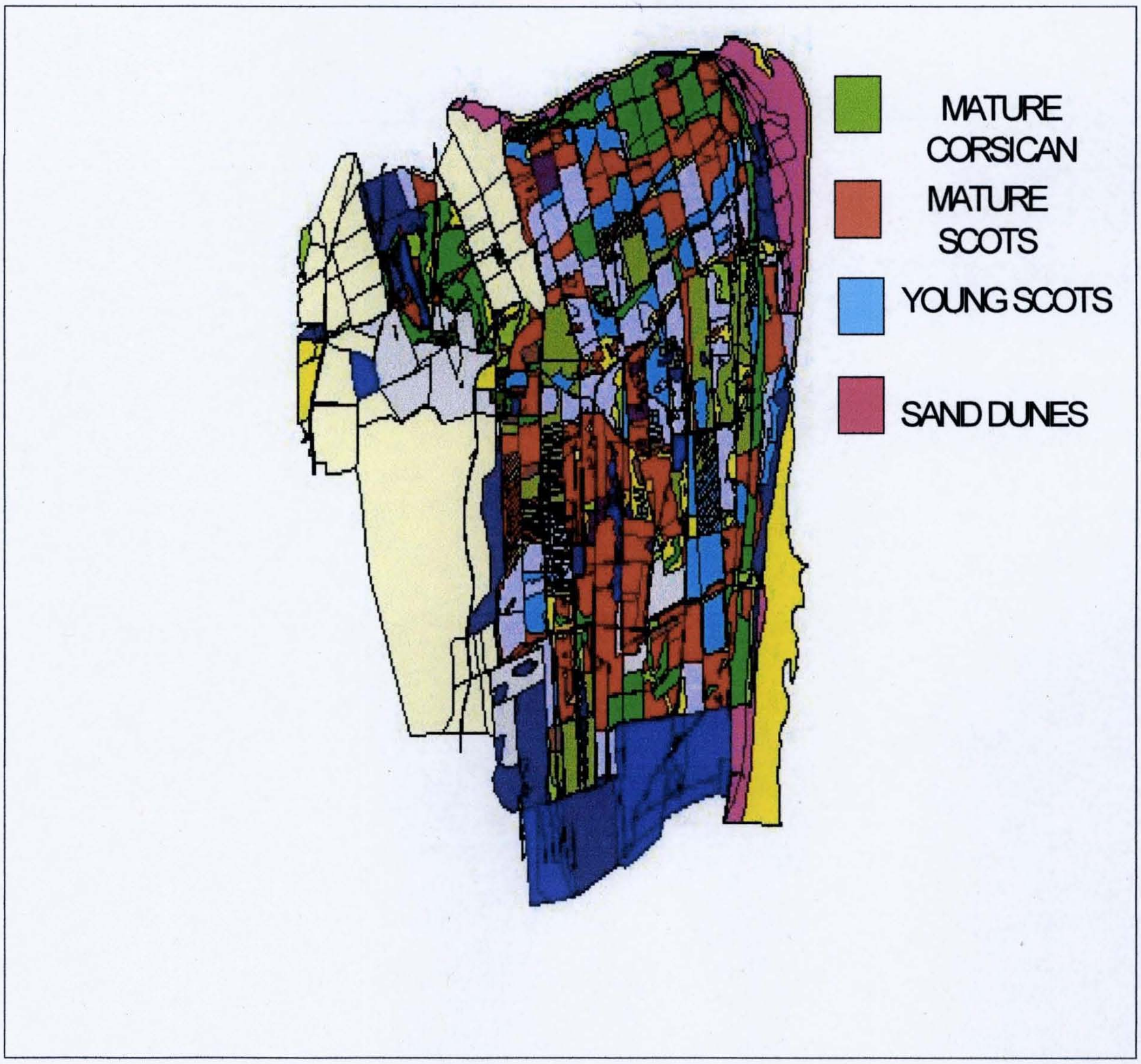


Figure 4.1: Digitised map of Tentsmuir Forest displaying various habitats available for foraging bats. The model extends past the boundaries of the forest to the limits of where radio tracked bats foraged. Full habitat categories are listed in Table 4.1.

4.4.3 Habitat availability

Chapter 3 describes the radio tracking and estimates of home range for the study area. The 100% foraging MCP for individual bats and the colony to which the bat belonged were deemed as the area available for habitat analysis.

Habitats were defined on a mixture of the following criteria:

- Forestry Commission planting regime tables and maps. All stands planted by forestry have species, age of planting, size of stand and other data recorded.
- Ground truthing in the study area where habitat categories were unsure.

Habitats were broken down into two categories, a coarse and fine scale. In the coarse scale some tree species were combined in a single category whilst in fine scale they were split.

Coarse	Fine
Mature pines. All species of pines over 30 years old that have undergone first thinning and removal of surplus trees	Mature Corsican pines Mature Scots pines Mature Lodgepole pines
Young pines. As above before thinning	Young Corsican pines Young Scots pines
Deciduous. All species of broad-leaved trees.	Alder Birch Deciduous (all other)
Spruce	Spruce
Young spruce	Young spruce
Fir	Fir
Young fir	Young fir
Water	Water
Scrub	Scrub
Roads	Roads
Arable	Arable
Sand dunes	Sand dunes
Beach	Beach
Urban dwellings	Urban dwellings
Grazing fields	Grazing fields

Table 4.1: Available habitats as defined in digitised map of Tentsmuir Forest and used in compositional analysis.

4.4.4 Compositional Analysis

A software programme Compos Analysis (Smith 2004), an add-in tool for use with Microsoft Excel, implements fully Aebischer's method for Compositional Analysis. The significance of Wilk's lambda and of t-values was determined by randomisation tests as recommended by Aebischer et al. (1993) to overcome problems arising when the distribution of log-ratio differences is non-normal. When zero values were found in the matrix of used habitats, they were replaced by a small value (by default, 0.01). Also, when zero values are found in the matrix of available habitats, a "weighted mean lambda" was implemented instead of the usual lambda according to the recommendations of Aebischer et al. (1993).

4.4.5 Diet analysis

In 2003/2004 when checking bat boxes I collected faecal droppings monthly from May to September from both the Beeches and Icehouse colonies whenever Natterer's bats were found in a box. These were analysed by Emily Clark as part of an unpublished honours thesis. I designed and set up her project to compliment my own thesis. We used four methods of invertebrate trapping in two different habitats and the results were examined for correlations between invertebrate catches and diet by faecal analysis. Droppings collected were placed in collecting vials, labelled and stored in a cool dry cupboard for later analysis. From each monthly sample three faecal pellets were randomly selected for analysis. Droppings were analysed by extracting and identifying chitinous arthropod fragments using McAney et al. (1997) as the primary means of fragment identification (Clark 2005). Results were expressed as percentage frequency, i.e. the number of insect fragments attributed to one insect order as a percentage of the total number of insect fragments attributed to all insect orders (Swift et al. 2002). When it became plain that there important differences in foraging in Corsican and Scots pine I set up another, different invertebrate trapping method, canopy pan traps (Aguiar & Sharkov 1997) within the forest. For full details of methods see Chapter 2.

4.4.6 Invertebrate trapping methods

Five different invertebrate trapping methods were used (see Chapter 2 for full description). For the project by E. Clark these were:

- Malaise traps.
- Window traps erected 0.5 metres above ground level
- Sticky traps attached 1.5 metres above ground level.
- Moth traps with an actinic bulb.

For the canopy trapping:

- Pan trap's containing water and detergents were hoisted into the canopy approximately 15-20 metres above ground level.

All insects caught in the traps (except from the moth traps) were stored in 96% ethanol for identification in the laboratory. These were then identified to family and subsequently to order level and abundance recorded. All moths caught in the moth traps were recorded as small (1-7mm), medium (8-14mm) and large (15-22mm).

4.4.7 Trapping sites

We selected two different habitat sites, young Scots pine plantations and water sites were chosen to place four types of invertebrate traps (Malaise, moth trap, sticky traps, window traps) All OS map references are to a scale of 1:25000.

- Four young stands of Scots pine, planted after 1980. These stands are between 3-6 metres in height and have not been thinned out. They effectively form a barrier, which is very dense and virtually impenetrable. The bats are unable to fly between the trees generally but foraged amongst the tops or higher (OS 476266, 475267, 476268, 475271).

Four water sites were used:

- Around the margins of Morton Lochs in damp woodland (OS 463263).
- In an area of unimproved grass and scrubland that was used to graze cattle close to the loch edge and a 3 metre wide stream (OS 459264).
- Along the sides of the Powie Burn (OS 494266, 494267), a free flowing stream approximately 2-3 metres wide.
- The Lundin drain, a free flowing stream 2 metres wide (OS 472259).

At the time of planning for E. Clark's project it was unknown that mature Corsican pine was a preferred foraging habitat, so water bodies and young Scots pine were chosen. When I found later that bats were foraging preferentially in mature Corsicans rather than mature Scots pines, I decided that these two habitats would need a base line study to see if there was any difference in prey availability in the canopy using pan traps.

- Mature Scots pine planted in 1934 (OS 493275).
- Mature Corsican pine planted in 1935 (OS 490278).

These mature plantations were quite open, having been thinned out three times to leave approximately 3-4 metres between trees.

4.4.8 Measuring ecological diversity

Whittaker (1972) distinguished three main types of diversity relevant to ecology:

- Alpha diversity – diversity within a particular area or ecosystem
- Beta diversity - the change in alpha diversity between areas or ecosystems..

- Gamma diversity - the overall diversity in a landscape comprised of several ecosystems.

In order to successfully describe the biodiversity of any given habitat, the number of families and their relative abundance must be ascertained, then a measure or index that combines the two is utilised (see Magurran 2004). The following tests were used for non-parametric data:

- Spearman rank correlations compared the relative abundance of insect groups found in each habitat type.
- The Kruskal-Wallis test compared the relative abundance of insect groups between the three trapping methods used.
- The Shannon diversity index (*H*) is an index that is commonly used to characterize species diversity in a community. The index accounts for both abundance and evenness of the species present. The proportion of species *i* relative to the total number of species (p_i) is calculated, and then multiplied by the natural logarithm of this proportion ($\ln p_i$). The resulting product is summed across species, and multiplied by -1:

$$H = -\sum p_i \ln p_i$$

  H-values are calculated for each sample site and compared using a parametric T-test.

- Jaccard's index (J) was used to provide an estimate of the similarity of the insect communities between two habitats. Jaccard's index is calculated by dividing the number of species found in both of two sites (A and B) by the number found only in site A or site B, and multiplying by 100 (Southward 1978, Magurran 2004). The index is thus given by :

$$J = \frac{100xj}{(a+b-j)}$$

where j is the number of species found in both sites, a is the number of species found in site A, and b is the number of species found in site B.

4.5 Results

4.5.1 Compositional analysis

Fig 4.2 shows the available habitat within the 100% foraging MCPs home ranges for the Beeches and Icehouse colonies. Another MCP was also produced combining all the records for the two colonies (Fig 4.3). The areas of the colonies were Beeches (4.43 km^2), Icehouse (6.46 km^2) and combined (15.63 km^2).

Figure 4.2: Habitat available in 100% MCP home ranges for Beeches and Icehouse colonies.

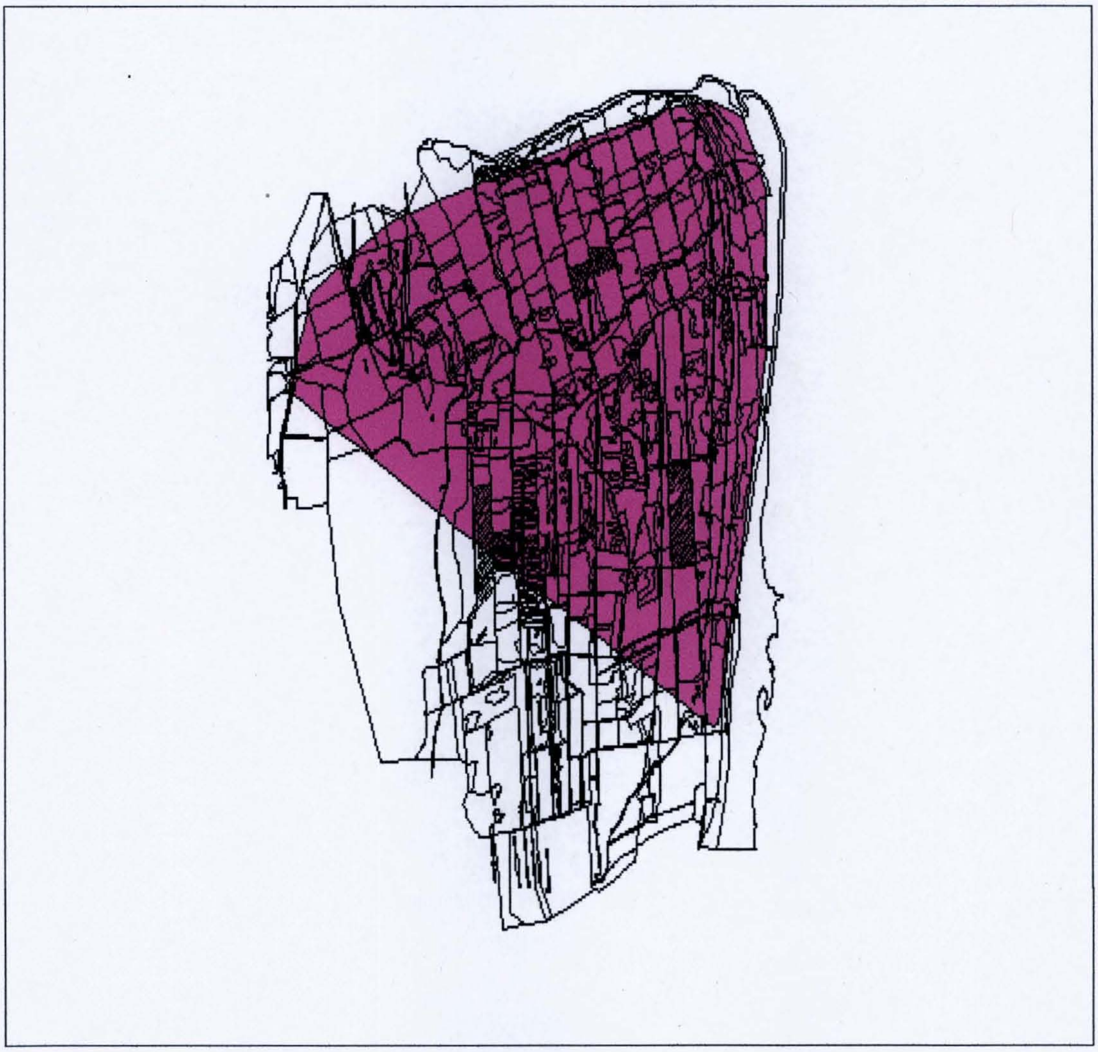


Figure 4.3: Habitat available in 100% MCP home range for both colonies combined.

All available habitat within the 100% foraging MCP (Fig 4.3) for all bats in both colonies was displayed graphically as a percentage of available versus used habitat, at both a coarse scale (Figure 4.4a) and a fine scale (Figure 4.4b). Not all categories of habitat (Table 4.1) are displayed since habitats that had very little usage (< 5%) were dropped from the analysis. At the coarse scale, some habitats were lumped together, e.g. all mature pines, however, at the fine scale habitats were divided into more simpler types, e.g. deciduous was broken down into three separate groups - alder, beech or deciduous. (See Table 4.1 for details).

Mature pine and water were used much more than their availability in the home range (Figure 4.4a). When mature pine was split into mature Scots and Corsican pine then Corsican pine was a preferential foraging habitat (Figure 4.4b) Scots pine was not used significantly more than its availability.

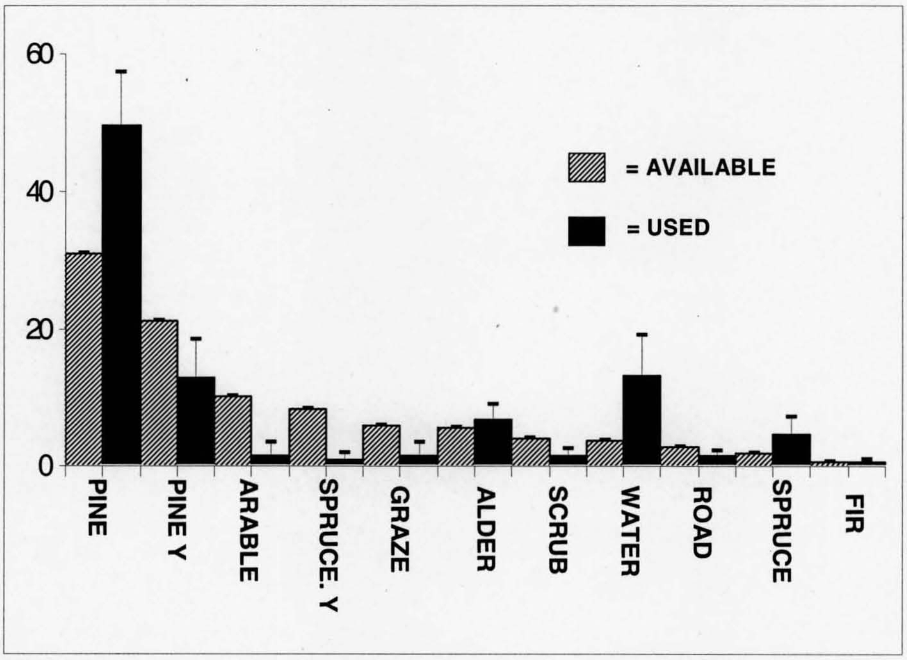


Figure 4.4a: Percentage habitat available and used at coarse scale for the combined colonies. Error bars are S.E.

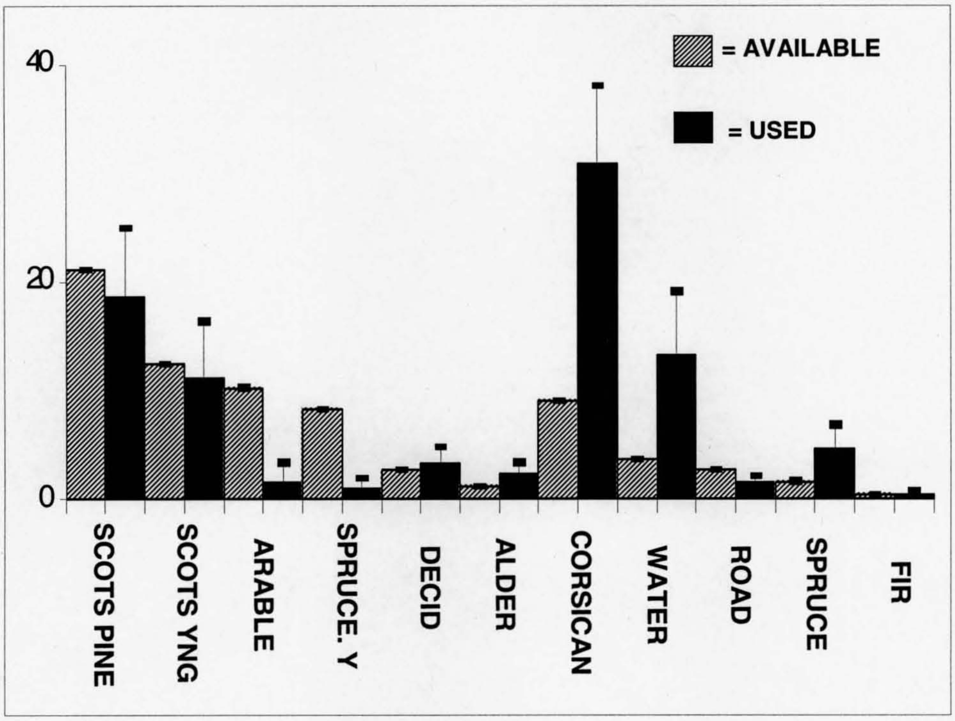


Figure 4.4b: Percentage habitat available and used at fine scale for all bats 2003/4 for the combined colonies. Error bars are S.E.

The Compositional Analysis results for the separate and the combined colonies (Tables 4.2 & 4.3) were originally examined on the coarse scale with all mature pines clumped as one category. The results show slight differences between the colonies but this is probably due to differences in the habitat available within the home ranges e.g. there was no mature spruce available in the Icehouse area and no sand dunes around the Beeches.

Habitat	Ranking order	Statistics
Beeches	PINE SPRUCE, DECID, WATER, FIR, ROAD, SCRUB, PINE YNG, GRAZE, ARABLE.	Chi Sq=56.605. d.f. = 9. P <0 .0001
Icehouse	PINE, WATER, DECID, PINE YNG, ROAD, DUNE, SPR.YNG, SCRUB.	Chi Sq=42.784. d.f. = 7. P < 0.0001
Combined	PINE, DECID, WATER, SPRUCE, FIR, ROAD, SCRUB, DUNES, SPR.YNG, GRAZE, ARABLE.	Chi Sq=72.166. d.f. = 11. P < .0001

Table 4.2: Compositional analysis ranking orders for habitat preference at the coarse scale.

Habitat	Ranking order	Statistics
Beeches	CORSICAN, SPRUCE, ALDER, WATER, FIR, ROAD, SCOTS, DECID, SCOTS.YNG.	Chi Sq=28.4975. d.f. = 8. P < .0001
Icehouse	CORSICAN, WATER, SCOTS PINE, DECID, ALDER, ROAD, CORS.YNG, SCOTS.YNG, BIRCH.	Chi Sq=42.8176. d.f. = 8. P < .0001
Combined	CORSICAN, WATER, ALDER, DECID, SPRUCE, FIR, SCOTS PINE, ROAD, FIR.YNG, SCOTS.YNG, BIRCH, SCRUB, CORS.YNG.	Chi Sq=47.4192. d.f. = 12. P < .0001

Table 4.3: Compositional analysis ranking orders for habitat preference at the fine scale.

It is apparent that Corsican pine is the most preferred foraging habitat compared to its availability either as separate colonies or when the colonies are combined. The MCP for the combined colonies is substantially bigger in area (15.63km^2) than the sum of the MCPs for the separate colonies (4.43 & 6.46, 10.89 km^2). Tables 4.4, 4.5 & 4.6. show whether the foraging preferences between different habitat types are significant. Some of the differences in habitat preference between the two colonies e.g. the use of spruce as a foraging habitat, can be explained by the fact that some habitats were only available in the home range of one colony.

COMBINED COLONIES

	SCOTS PINE	SCOTS.YNG	CORSICAN	CORS.YNG	SCRUB	WATER	DECID	ALDER	ROAD	SPRUCE	FIR. YNG	FIR	BIRCH	Rank
SCOTS PINE		+	---	+++	+	-	-	-	+	-	+	-	+	6
SCOTS.YNG	-		---	+	+	-	-	-	-	-	-	-	+	3
CORSICAN	+++	+++		+++	+++	+	+	+++	+++	+++	+++	+++	+++	12
CORS.YNG	---	-	---		-	---	---	---	-	--- (-)	-	---	-	0
SCRUB	-	-	---	+		---	-	---	-	---	-	---	-	1
WATER	+	+	-	+++	+++		+	+	+	+	+ (+++)	+	+++	11
DECID	+	+	-	+++	+	-		-	+	+	+	+	+++	9
ALDER	+	+	---	+++	+++	-	+		+	+	+++	+	+++	10
ROAD	-	+	---	+	+	-	-	-		-	+	-	+	5
SPRUCE	+	+	---	+++ (+)	+++	-	-	-	+		+	+	+	8
FIR. YNG	-	+	---	+	+	- (---)	-	---	-	-		-	+	4
FIR	+	+	---	+++	+++	-	-	-	+	-	+		+	7
BIRCH	-	-	---	+	+	---	---	---	-	-	-	-		2

Significance levels and ranks are shown according to randomization results, but where significance levels from standard t-tests of observed data differ these are shown in parentheses.

Table 4.4: Simplified ranking matrix showing if foraging preferences between different habitat types are significant or not by compositional habitat analysis. Results for combined Beeches and Icehouse colonies

+++ = positive significant difference, --- = negative significant difference.

ICEHOUSE COLONY

	SCOTS PINE	SCOTS.YNG	CORSICAN	CORS.YNG	WATER	DECID	ALDER	ROAD	BIRCH	Rank
SCOTS PINE		+	-	+	-	+	+	+	+++	6
SCOTS.YNG	-		-	-	-	---	-	-	+	1
CORSICAN	+	+		+	+	+	+	+	+++ (+)	8
CORS.YNG	-	+	-		-	-	-	-	+	2
WATER	+	+	-	+		+	+	+++	+	7
DECID	-	+++	-	+	-		+	+	+ (+++)	5
ALDER	-	+	-	+	-	-		+	+	4
ROAD	-	+	-	+	---	-	-		+	3
BIRCH	---	-	--- (-)	-	-	- (---)	-	-		0

Significance levels and ranks are shown according to randomization results, but where significance levels from standard t-tests of observed data differ these are shown in parentheses.

BEECHES COLONY

	SCOTS	SCOTS.YNG	CORSICAN	WATER	ROAD	DECID	SPRUCE	ALDER	FIR	Rank
SCOTS		+	-	-	-	+	-	-	-	2
SCOTS.YNG	-		---	-	-	-	---	-	-	0
CORSICAN	+	+++		+	+	+	+	+	+++	8
WATER	+	+	-		+	+	-	-	+	5
ROAD	+	+	-	-		+	-	-	-	3
DECID	-	+	-	-	-		-	-	-	1
SPRUCE	+	+++	-	+	+	+		+	+	7
ALDER	+	+	-	+	+	+	-		+	6
FIR	+	+	---	-	+	+	-	-		4

Significance levels and ranks are shown according to randomization results, but where significance levels from standard t-tests of observed data differ these are shown in parentheses.

Table 4.5 + 4.6: Simplified ranking matrix showing if foraging preferences between different habitat types are significant or not by compositional habitat analysis. +++ = positive significant difference, --- = negative significant difference.

4.5.2 Diet analysis

For both the Icehouse and the Beeches colony the relative proportions of the prey items (as found in the faecal pellets) were estimated by calculating the percentage frequency of each insect group according to the number of identified fragments found in the pellets sampled. The results showed no significant difference in the relative abundance of any insect order in the diet of the two colonies (Mann-Witney U-tests with Bonferoni correction). Jaccard's index also found that the two colonies were highly similar in terms of the composition of the diet (J = 0.72, when J=1 would be identical composition). Since there was no difference in either the relative abundance or the composition of insect orders in the two colonies, the results were combined to give one set of relative proportions (Figure 4.6) and also rank abundance (Figure 4.7). As there was no significant difference in foraging habitat preference between the two colonies, the fact that there is no difference in diet composition is not surprising.

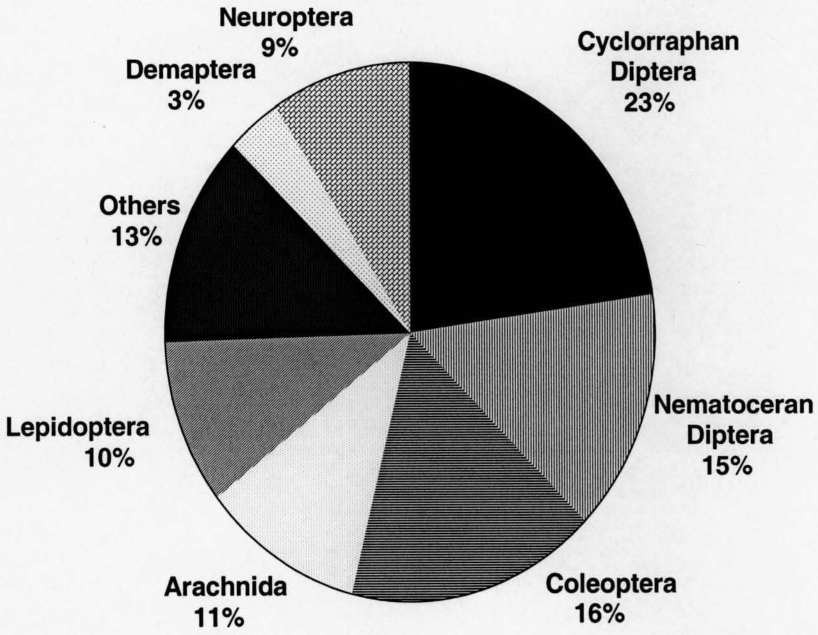


Figure 4.6: Relative proportion of the different insect orders found in the diet of Natterer's bats foraging in Tentsmuir forest according to the percentage frequency of identifiable fragments in 42 faecal pellets (Clark 2005).

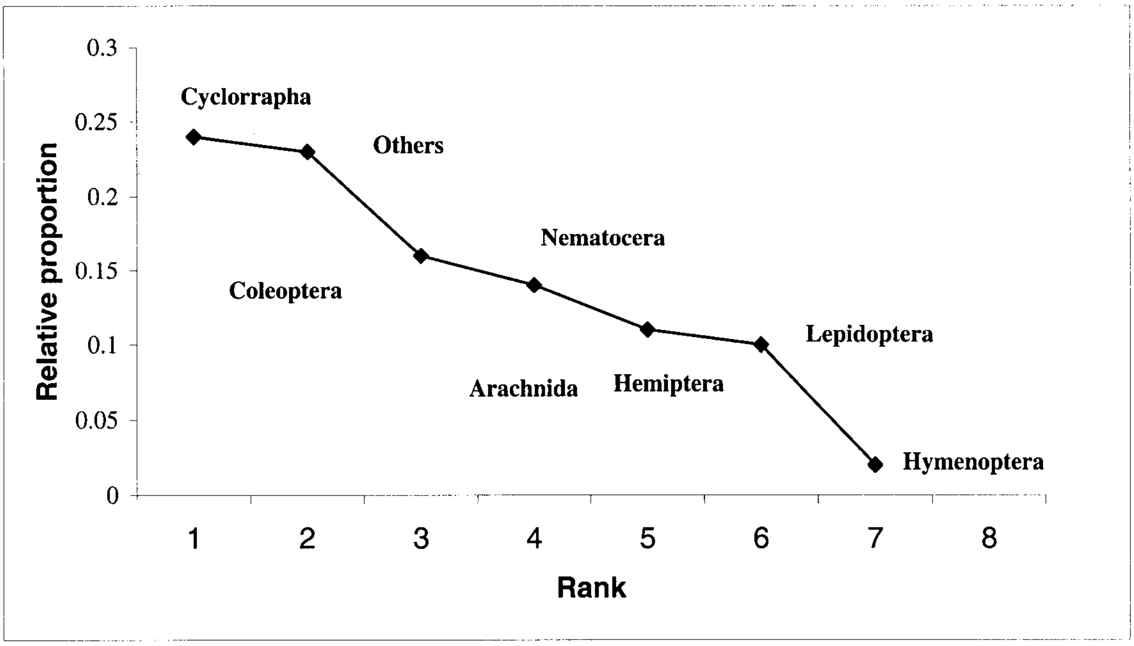


Figure 4.7: Rank abundance plot of insect groups found in the diet of Natterer's bats in Tentsmuir forest from 42 faecal pellets. (Clark 2005).

The results are very similar to those found in other diet studies on Natterer's bats with a wide spectrum of insect orders recorded. This indicated that they forage in a variety of habitats with several different methods of foraging used.

4.5.3 Invertebrate trapping

The different methods used were broken down into three separate categories for the comparisons of invertebrate biodiversity:

1. Between young Scots pine and water habitats using sticky traps, Malaise traps and window traps.
2. Between young Scots pine and water habitats using the moth trap.
3. Between mature Scots and Corsican pine using pan traps.

There was no significant difference between sticky, Malaise and window trapping methods in the rank of each invertebrate taxon in either young Scots pine (Kruskal-Wallis, H= 0.94, d.f. = 2, p= 0.623) or in water habitats (H= 1.19, d.f. = 2, p= 0.548). All three methods caught similar numbers of each invertebrate taxon and did not differ in terms of capture success (Figures 4.8 & 4.9). H values for each sampling site were calculated using the Shannon Index to compare invertebrate diversity between the two sites. There was no significant difference in the H-values for the two habitats (t = 1.861, d.f. =8, p= 0.099). Cyclorrapha and Nematocera diptera were respectively first and second rank in both habitats.

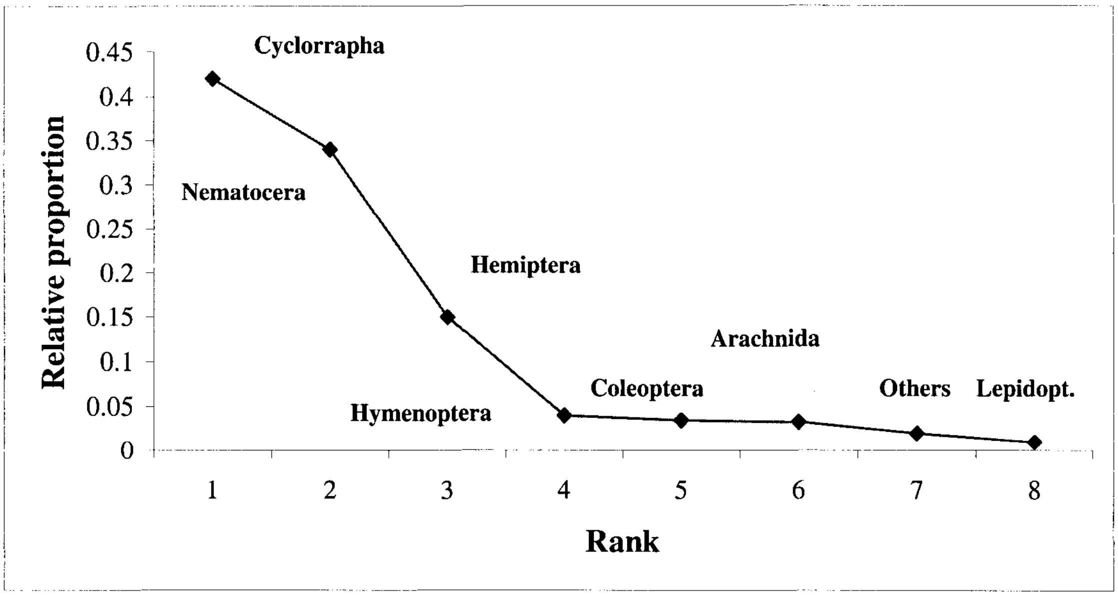


Figure 4.8: Rank abundance plot of insect groups found in water habitat as caught by malaise, sticky and window traps (Clark 2004).

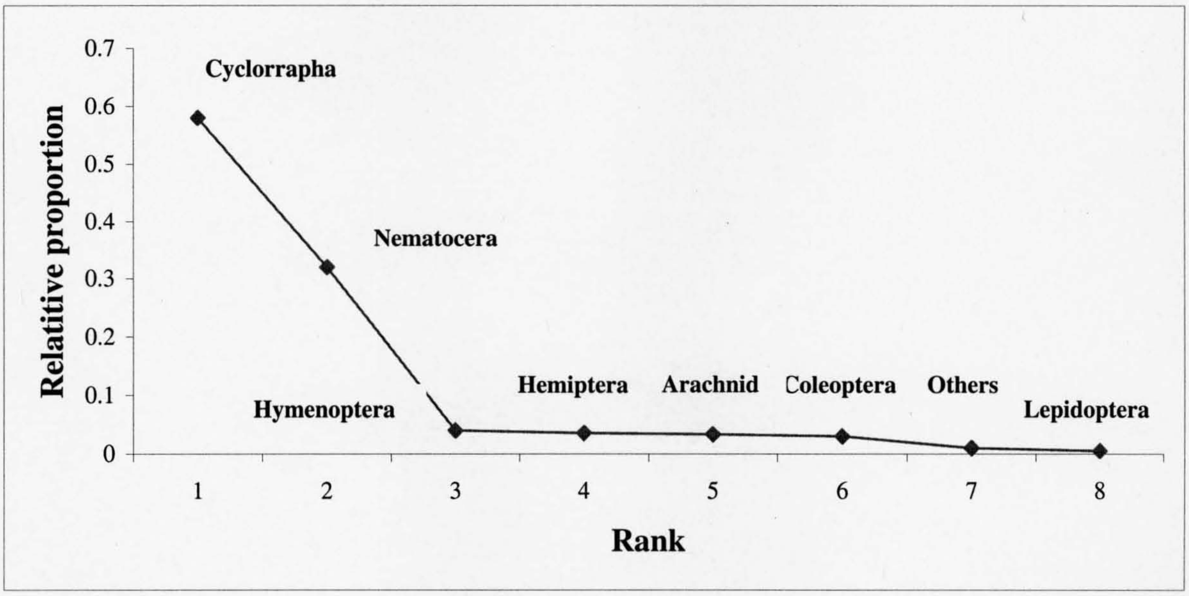


Figure 4.9: Rank abundance plot of insect groups found in young Scots pine habitat as caught by Malaise, sticky and window traps (Clarke 2004).

Moths caught by the moth traps were categorised into three size classes. There was no significant difference between water habitats and young Scots pine in the numbers of moths caught for each size categories. The medium size 8-14mm was much the largest category of moth in both habitats.

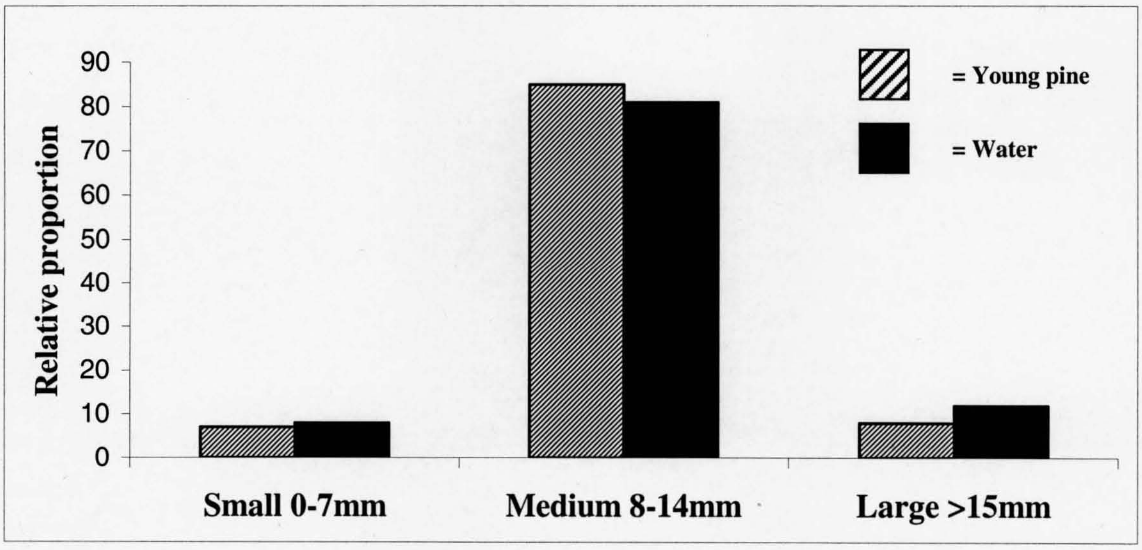


Figure 4.10: Relative abundance of three different moth size classes found in moth trap samples from within young Scot's pine plantations and near water (Clark 2005).

There were no significant differences between mature Scots and Corsican pine in invertebrate diversity caught in canopy pan traps as indicated by Shannon indexes (1.078 & 1.252). Jaccard's index confirmed that the two habitats were highly similar in terms of the composition of the invertebrate community (J = 0.82, when J=1 would be identical composition). Figure 4.11 shows the rank of insect groups in each habitat and it can be seen that all invertebrate orders appear in the same sequence for both habitats.

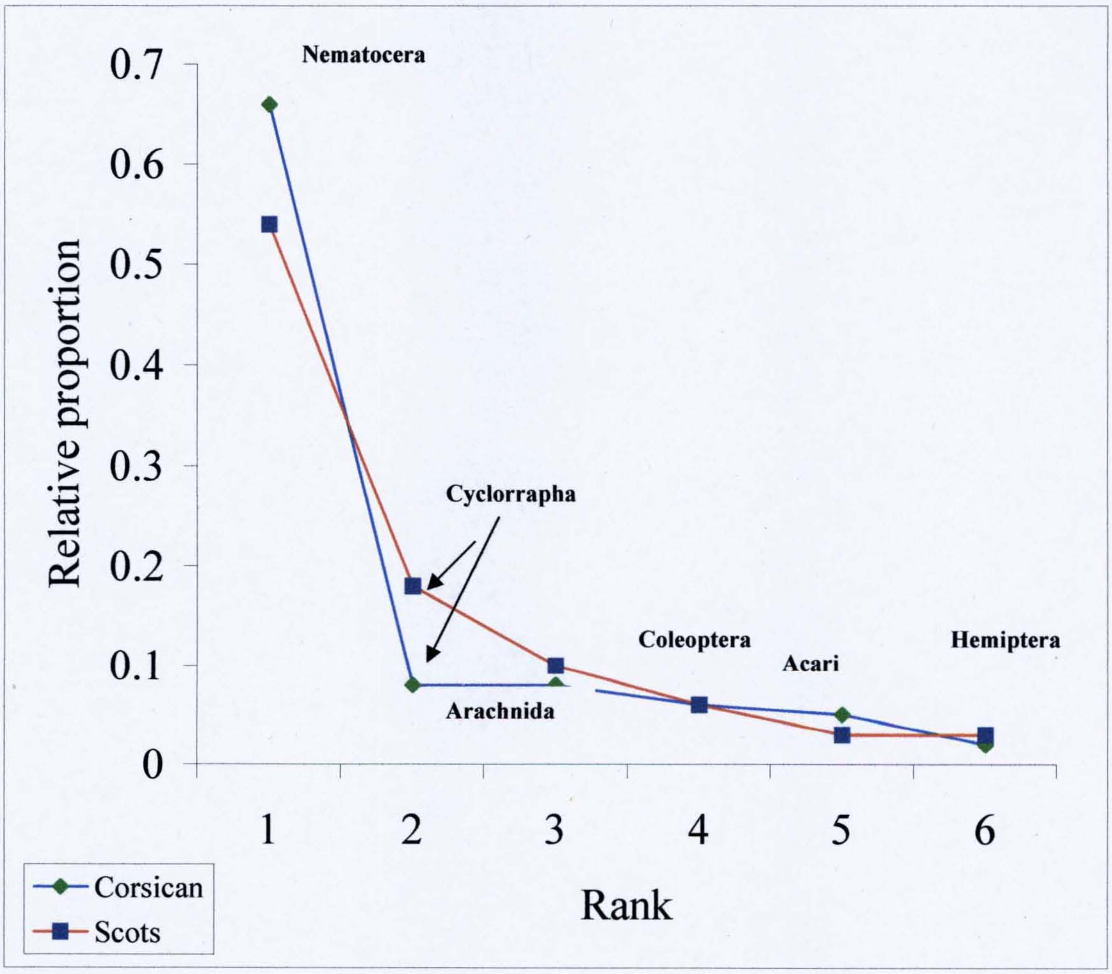


Figure 4.11: Rank abundance plot of insect groups found in mature Corsican and Scots pines as caught by canopy pan traps in May-June 2005.

4.6 Discussion.

4.6.1 Habitat availability

It was unexpected that Natterer's bats would preferentially use mature Corsican pines for foraging. Smith (2000) had found that coniferous plantations were avoided in his study and generally they have been thought of as inferior foraging habitat for virtually all species of bats. In Tentsmuir the bats were expected to forage in different habitats, since there are ample areas of horse grazing fields, dunes grazed by Highland cattle and pig farms. Within a short distance there are also several deciduous woodlands, but only one bat foraged outside the forest boundary, and that was in a spruce plantation.

Even more surprising was the preferential use of mature Corsican over mature Scots pine. Corsican pine is not a native species and might have been expected to have a poorer invertebrate biodiversity than Scots pine, which could impact on foraging rates. Scots pines were still a very important foraging habitat within the forest since approximately twice the area has been planted in Scots compared to Corsican pine.

Water habitats were extensively used both as a core foraging area and also as occasional communal feeding grounds. Tentsmuir is planted on sand dunes and the water supply is very variable depending on weather. Some summers all the standing water in the dykes dries up, although Morton Lochs and the running streams always have some water present.

The limited use of any deciduous woodland, either in or outside the forest was again unexpected. A large percentage of the deciduous habitat available was around water bodies and is generally birch/alder. There were also areas of mature beech/oak woodland but these were not utilised. Mature Scots pines were used for foraging to a greater extent than water (Figure 4.4b) in a straight comparison; however there was considerably more Scots pine available for the bats than water.

4.6.2 Diet

The results of the diet analysis generally confirmed previous work on Natterer's bats with cyclorraphan Diptera, nematoceran Diptera, Coleoptera and Arachnida ranked the most common categories found in the faeces. Swift & Racey (2002) had similar results in Perthshire, Scotland. However, in a study in an area of deciduous woodland, riverine habitat and farmland in east Yorkshire the most numerous prey groups were Diptera (37%), Araneida (12%), Dermaptera and Opiliones (Birkinshaw 1999). There were, however, seasonal variations in this study with Opiliones and Araneida being found more abundantly in the faecal samples, which were collected in August and September. Some differences in diets probably reflect temporal, seasonal and geographical variation in insect abundance (Agosta 2002). Several studies have shown diet variation exists geographically and both between and within colonies of the same species e.g. big brown bat (Whitaker 1995), Mexican free-tailed bats *Tadarida brasiliensis antillularum,* (Whitaker et al. 1996), Leisler's bat (Shiel et al. 1999) and seasonally, Indian pigmy bat *Pipistrellus mimus,* (Whitaker et al. 1999).

In all other studies with Natterer's bats the diet has been found to contain a mixture of both flying and non-flying prey items, which indicates that a variety of catching techniques are used. For Natterer's, this includes using low broadband width echolocation (Siemers et al. 2000), trawling for insects with its interfemoral tail membrane and gleaning off vegetation (Siemers et al. 2000, Swift & Racey 2002) and aerial hawking.

4.6.3 Invertebrate trapping

There is considerable bias associated with any type of invertebrate trapping (Canaday 1987, Duelli & Obrist 1998) and results will be heavily influenced by a wide range of variables e.g. weather, season, type of traps, heights of traps, site characteristics etc. In a Swedish study in Sitka spruce plantations, window-trapped saproxylic Coleoptera and total Coleoptera showed significant positive correlation with wood-inhabiting fungi, and in contrast saproxylic Coleoptera were negatively correlated with indicator bryophytes (Jonsson & Jonsell 1999).

The aims of this project were made even more difficult by the foraging behaviour of Natterer's bats. There is ample evidence from various studies on diet and behaviour that Natterer's bats forage by aerial hawking, by gleaning off vegetation and even by crawling on the ground (Arlettez 1996, Swift & Racey 2002, Siemers & Schnitzler 2000). This means that there is a potential prey catching area ranging from ground level to above the canopy. It also considerably widens the range of available prey items from crawling and non-flying to totally aerial. Insects differ in their spatial distribution (Southward 1978), and height placement of various traps is important and has effects on the species composition captured. There is also the question of whether the bats sensory system and the cues provided by the prey can both constrain its foraging behaviour and limit its access to food. There might be an abundance of a particular type(s) of prey item captured in the invertebrate traps, however if the bat cannot detect this prey then it becomes unavailable. Siemers & Guttinger (2006) in a study of greater mouse eared bats found that prey selection can be explained in part by the specific conspicuousness of the prey to the foragers sensory systems. The bats did not take arthropod taxa in proportions of their abundance as found in pitfall traps. There was an obvious overrepresentation of large individuals or species in the diet. The data showed a close match between the acoustic conspicuousness of epigaeic arthropods and the apparent prey selectivity with respect to taxon and size by the bats. In spite of these problems the results have raised some intriguing questions. No significant relationship was expected or found between trapping results and diet analysis, with the trapping methods used. There is great potential for further research in invertebrate sampling, foraging behaviour and diet of Natterer's bats within Tentsmuir Forest.

It was thought that Malaise traps would catch both a higher abundance and richness of invertebrates. Hoskin (1979) compared various traps, and found that Malaise traps caught significantly more families and species than other methods. I also expected to find a difference in catches between water bodies and young Scots pine plantations. Areas of water, whether still or running are generally considered to be insect rich. Young pine plantations are normally thought to be homogonous with considerably less niches available (Garrod & Willis 1997). However, there was no significant difference recorded.

The results of the pan traps in the canopy of mature Scots and Corsican pines were interesting in that no difference was recorded in either invertebrate diversity or composition between stands of the two species. Scots pines is a native species while Corsican pine is introduced, and I expected that a native tree species would hold a greater biodiversity of insects since insect communities would have less time to adapt to non-native species.

4.6.4 Conclusion

The results of the diet analysis concur with previous work on Natterer's bats and show that they are a versatile species able to forage in a wide range of habitats and with a variety of different techniques. That there was no correlation between the composition of the invertebrates trapped and the relative abundance in the diet measured by faecal analysis is not surprising given the wide range of foraging techniques used by Natterer's bats and the limitations of the trapping methods. The results of the invertebrate trapping also showed no difference in invertebrate biodiversity between water habitats and young Scots pine plantations or mature Scots and Corsican pines; this was also surprising. Although limited by time constraints, the trapping results show the potential for further research in this area and also highlight the difficulties in trapping the actual invertebrate prey of Natterer's bats.

The compositional habitat results are different from any previous work and call into question previous generalizations about the foraging habitats used by bats in the U.K. The preferential foraging use of mature Corsican pines was unexpected, particularly as it is an introduced species and also given the amount of mature Scots pines available in Tentsmuir. The foraging in Corsican pines might possibly be connected to roost choice. Chapter 5 gives details of extensive use of Natterer's bats using previously unrecorded natural roosts found predominately in Corsican pines. The most parsimonious explanation is that bats prefer to forage relatively close to roosts, given that no significant difference was found in invertebrate prey availability between Scots and Corsican pines. Both these findings are important given the extent of the land coverage of Corsican pines in the U.K. This has implications for both conservation management and further detailed research in both foraging ecology of bats and invertebrate communities of commercial plantations.

CHAPTER 5

Roost dynamics

5.1 Abstract

A minimum of three colonies of Natterer's bats are present in Tentsmuir Forest. Two of the colonies (Beeches and Ice House) Tentsmuir Forest use both bat boxes and natural live tree cavities for day roosts with no interchange between the two colonies. The use of bat boxes as day and maternity roosts was common. Two particular types, square wooden and round woodcrete, were the most preferred. No variable in the placement of bat boxes, except site, explained the use of boxes as roosts. A specific type of natural cavity found predominantly in Corsican pine was also commonly used as a roost. This roost type has not been recorded before and has conservation implications for current forestry management practices. While tree roosts were used significantly more often than bat boxes, there was no difference in the length of time bats stayed in either type of roost. Roost switching occurred approximately every 2.5 days. Commuting distance from roosts to core foraging areas was not a factor in roost switching.

5.2 Introduction

5.2.1 Bat roosts

Day roosts are places where bats rest and conserve energy during the day, rear young and generally provide a secure place from predators. The type of roost often depends on the time of year with many species of bat forming summer maternity roosts, which are in a different area from winter roosts; e.g. little brown bat *Myotis lucifugus* has been found to migrate up to 275 km between the summer and winter roosts (Davis & Hitchcock 1965). Some species of bats are roost specialists; e.g. gray bats *Myotis grisescens* roost only in caves throughout the year (Martin et al. 2003) and hoary bats *Lasiurus cinereus* roost in the foliage of trees (Willis & Brigham 2005). Many other species are generalists, using a variety of roost types at any one time of the year; for example, big brown bats *E.fuscus*, use trees, bridges, and buildings in summer and caves, mines, and buildings in winter (Agosta 2002).

Betts (1998) found that much of the detailed work on the roosting ecology of bats has centered on bats roosting in caves or man-made structures, since these locations are often relatively accessible to humans and easy to find. So far few studies have examined the ecology of bats roosting in trees (Vonhof 1996).

Numerous studies have suggested that bats select roosts on the basis of microclimate, yet few have tested this empirically (Willis & Brigham 2005). Kerth et al. (2001) showed that female Bechstein's bats selected their roosts according to roost temperature and season, however they did not know if selection was also influenced by other factors such as ectoparasite infestation. They concluded that access to many roosts providing different microclimatic conditions are important for successful reproduction in female Bechstein's bats.

5.2.2 Bat roosts in commercial forests

There have long been concerns, particularly in the U.S.A., about bat roosts in commercial forests and much research has concentrated on roost site selection. In the U.K. the situation is very different with very little research carried out in commercial coniferous plantations on the use of the forests by bats. From the work done on bats in North America there are two major differences in their results and the findings of this study.

1). It is apparent that, with some exceptions, roost trees selected are often tall, large diameter trees that rise above the surrounding forest or are on the edge of forest clearings. Vonhof (1996) states that in general both big brown bats and silver-haired bats *Lasionycteris noctivagans*, preferred either large-diameter or tall trees that were relatively far away from surrounding trees. In all analyses comparing roost trees with available trees, it was found that either tree height or diameter at breast height (DBH), or both, significantly discriminated between the two groups of trees and that tree size may be the more appropriate factor selected by bats, rather than any particular measure of tree size. It is postulated that such trees are probably most likely to have spaces to hold many individuals--spaces that receive warmth from the sun and are safe from terrestrial predators, yet are easily located and accessible for clumsy juveniles when they start to fly (Barclay & Brigham 1996, Willis & Brigham 2005). Vonhof (1996) suggested that bats might also gain significant energetic benefits by choosing trees that are exposed to sunlight, since low roost temperatures slow fetal and juvenile development in bats. Therefore, reproductive female bats may benefit energetically by selecting roosts that are heated by the sun for at least part of the day. By selecting these taller trees they are exposed to sunlight for a greater length of time than are trees under canopy cover. Vonhof & Wilkinson (1999) studied roost tree selection by northern long-eared bats *Myotis septentrionalis,* in a commercial hardwood forest. These bats have similar foraging techniques to Natterer's bats, being highly maneuverable gleaners with low wing loading and aspect ratio. The roost sites located were not significantly larger and did not extend above the surrounding forest canopy more than randomly located cavity trees.

2). The other major finding was that roosts found in pine trees were invariably in dead or decaying trees. Any roosts in live trees were found in deciduous species; e.g. Indiana bats were found roosting in 13 species of trees, of which the majority were pines followed by oaks. However, while they roosted in living oaks, all the roosts in pines of any species were in dead trees. In a study on roost site selection on big brown bats and silver haired bats, Vonhoff (1996) found that the majority of roosts were in woodpecker cavities, under bark or in trees with defects, e.g. broken tops or internal decay. He also found that the bats preferred tall (mean height 22m), dying or newly dead trees. Thomas (1988) investigated the distribution of bats in different ages of Douglas fir *Pseudotsuga menziesii* forests. He emphasized the importance of old growth habitat for roost selection and suggested that this was because of the characteristics of the dead branches or snags of older decaying trees. The characteristics of these snags for increased roost use included larger size, moderate levels of decay and considerable longevity.

The major difference between the commercial forests in the U.S.A and the U.K. is their age. As stated in Chapter 3, commercial plantations in the U.K are relatively new features on the landscape with planting starting in the 1920s. Thus the oldest stands of tree are only 80 years old. In the U.S.A. the older forest stands with all the available roost sites and dead and decaying trees are often twice that age. It is conceivable, given sympathetic management plans that as the British forests grow older, bat populations will increase as more roost sites become available. Before this study, the great majority of known roost sites in commercial plantations in the U.K. have been in bat boxes or in buildings located within the forests.

5.2.3 Bat boxes

Bat boxes provide bats with alternative roost sites to replace natural ones in tree holes and also to encourage bats into areas where there are few such natural sites. Of the sixteen British bat species, all but three have been reported to use bat boxes (Swift 2004a). According to Stebbings & Walsh (1991) the first description for bat boxes was published in France in 1918 and within 20 years they were becoming well established, especially in central and eastern Europe. In a pilot project in 1968 the first boxes were put up in the U.K. and were soon attracting bats. Soon after this a larger scheme erected over 3,000 boxes in six coniferous forests from northern Scotland to southern England. Now many local bat groups have erected small-scale schemes all over the U.K. The traditional and most commonly used design for a wooden bat box is described in Stebbings & Walsh (1991) and was the type first erected in Tentsmuir (see Chapter 2). Since then other wooden designs have been tried and now many bat boxes are constructed of a mixture of wood and concrete (woodcrete). These have the benefit of longevity and very low maintenance and in Tentsmuir one particular design is proving very popular with Natterer's bats.

One of the original bat box schemes in the U.K. was in a 10,000 ha block of Thetford Forest, a commercial plantation area consisting mainly of Corsican and Scots pine. Brown long-eared bats soon used the boxes. The population showed a rapid increase with a high recapture frequency of individual bats (Boyd & Stebbings 1989). This suggests that the bats used the boxes readily and that there were few alternative roost sites. The authors concluded that the use of bat boxes in commercial plantations could increase bat populations and that bat populations in such areas may be limited more by roost availability than by food (Boyd & Stebbings 1989).

In a study in Poland the use of wooden bat boxes was compared between three different forests (80-year old beech forest, 150-year old oak-beech with a mixture of pine and 50-70 year old pine forest). It was discovered that the occupation of boxes in the pine forest was several times higher than in either deciduous forest. The reasons suggested for this were the almost complete lack of natural roosts in pine forest and the more unfavorable microclimate in broad-leaf forests (Ciechanowski 2005).

There have been few studies on the types of box available and their comparative suitability for occupation by bats in the field. One exception was by Swift (2004a), who collated data from a literature search and a questionnaire sent out to all bat groups in the U.K. The results showed that most bat box schemes used one, two or three different types of bat box design, and that no correlation was found between the number of different types and either occupancy rate or the number of species recorded. In laboratory tests the study also found that bat boxes of all shapes, sizes and materials have different advantages. It was recommended that bat box schemes employ a mixture of both wood and woodcrete boxes of several different shapes to achieve optimum occupancy (Swift 2004a).

Bat boxes not only have a high conservation value for the commoner bat species but also for endangered species; e.g. Ritzi et al. (2005) reported on the first usage of bat boxes for maternity roosts by Indiana bats in the U.S.A. There is also the problem of exclusion of bat colonies, especially nursery colonies, from buildings. Work by Brittingham & Williams (2000) on displaced colonies of big brown bats and little brown bats suggested that bat boxes of the proper design and placement could provide alternative roost sites. In the U.K there has also been work carried out on heated bat boxes for excluded colonies of pipistrelle species, and the results have been encouraging with bats now breeding in some boxes (Swift 2004b). It would seem that unheated bat boxes are of little use for pipistrelles, as they need very warm nursery roosts. It was found that heated bat boxes that provided a steady temperature of 26-27 ^{0}C were successful in attracting breeding bats (Swift 2004b).

5.2.4 Roost switching

Many colonial bat species and specific individuals within a colony are known to switch from one roost to another, particularly species that live in trees. Individuals and colonies move between roosts on a regular basis, sometimes to a site only meters away, but in other cases to roosts at considerable distance. This occurs even when females are nursing their dependent young, presumably carrying the pup from one roost to the next during the night (O'Shea & Bogan 2000). In a review of roost fidelity of bats, Lewis (1995) identified five benefits of roost lability, which included predator avoidance, escape from disturbance, parasite load reduction, avoidance of unfavorable microclimate, and reduction of commuting distance between roost and changing foraging locations. Female Indiana bats for example, change roosts about every three days, and a group of these bats may use more than 17 different trees in a single maternity season (Kurta et al. 1996). In a study of long-eared myotis *Myotis evotis,* Rancourt et al (2005) found that reproductive females switched roosts on average every 2 days and that switching involved the whole colony.

5.2.5 Natterer's bats and day roosts

Natterer's bats are known to use a variety of roost sites. These include tree cavities, castles, bridges, stone walls, and a variety of both inhabited and uninhabited buildings (Swift 1997, Smith 2004). They also readily take to using bat boxes for summer and maternity roosts (Siemers et al. 1999, Park et al. 1998, Hatton & Cohen 2000). Up to 200 adult females have been recorded in summer maternity roosts in buildings (Stebbings 1991). Park et al. (1998) recorded up to 37 adult Natterer's bats in bat boxes and 65 adults have been recorded in Tentsmuir (pers. obs.). Natterer's bats are known to switch roosts frequently, often only spending one day in a roost (Swift 1997, Smith 2000, 2004), and they also demonstrate roost fidelity with particular roosts being used repeatedly over a period of years (Hatton & Cohen 2000, Smith 2004).

5.3 Aims

To determine the dynamics of Natterer's bats summer maternity roosts in a commercial coniferous forest:

- To determine if Natterer's bats preferentially use a particular bat box type.
- To determine the optimum site characteristics for placement of bat boxes.
- To determine the pattern of roost usage between the bat boxes and the Kinshaldy stables.
- To locate unknown roost sites.

5.4 Materials and Methods

5.4.1 Bat boxes

When the project started in 2003 there were groups of bat boxes that had been in the forest since the mid 1980's. These were constructed of wood and of two different styles. There were approximately 100 boxes in ten distinct locations (Figure 2.1). In 2001/2002 the local bat group added two further types of woodcrete bat boxes to three locations. At this time only boxes in four locations were checked annually, the other six had not been checked, so far as it is known, since they were put in place. Two locations were totally unknown to either the Forestry Commission or the local bat group. A substantial number of boxes were in a state of disrepair or useless. A programme of replacement with a mixture of wooden and woodcrete boxes was undertaken in winter 2003 in all locations (Table 5.1). All boxes at Polish Camp were removed in winter 2004 when the trees were felled. Types of box present are shown in Figures 5.1 & 5.2. The "old" type refers to the original wooden boxes erected in the 1980's. The "new" type is the replacement wooden box. Woodcrete boxes are a relatively new innovation and are a mixture of wood chips and concrete. They are very durable and have a long lifespan with minimal maintenance.

Location	Boxes 2003		Boxes 2004	
	No.	Type	No.	Type
Morton Lochs	15	1	15	1
	2	3	14	5
Fetterdale	7	1	5	1
			10	5
Yard	1	1	1	1
			8	5
Beeches	9	1	8	1
	1	2	8	3
	7	3	8	4
	7	4		
Ice North	16	2	9	2
			9	5
Ice House	7	1	6	1
	4	2	6	3
	7	3	6	4
	1	4	6	5
Ice South	11	2	7	2
	3	4	7	4
			7	5
Track 16	13	2	10	2
			8	5
Stables	4	3	6	3
	7	4	6	5
Polish Camp	8	2	6	2
	2	3	6	4
	3	4	6	5

Box Types

1 = Old sq. wood
2 = Old wedge wood
3 = Woodcrete flat
4 = Woodcrete round
5 = New sq. wood

Table 5.1: Numbers, types and locations of bat boxes in Tentsmuir Forest 2003/2004

Figure 5.1: Types of wooden bat boxes erected in Tentsmuir. Left to right:

Old wedge shaped, Old square construction, New square wooden construction.

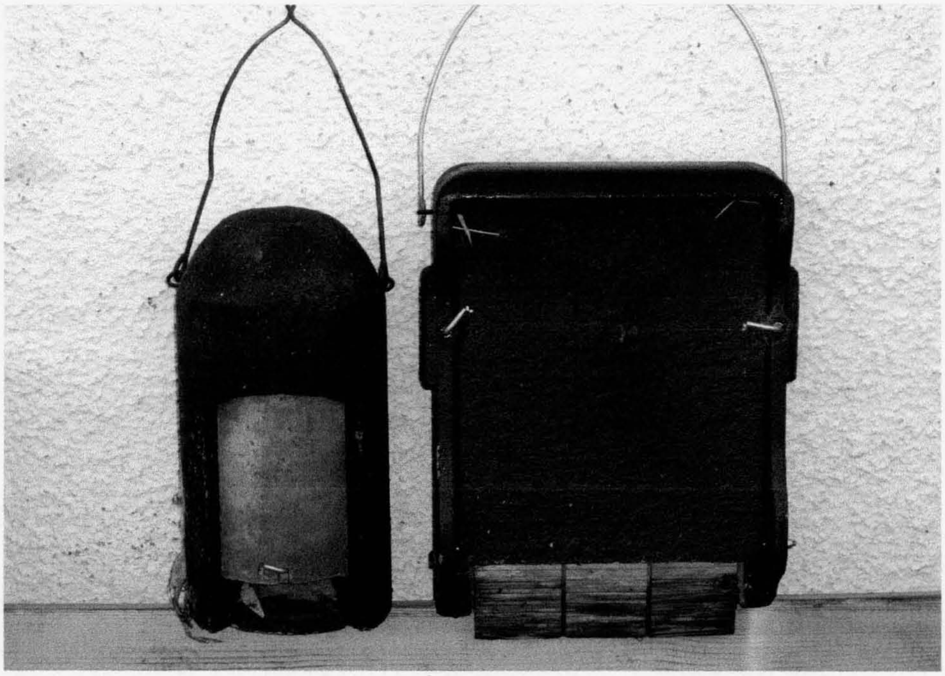


Figure 5.2: Round and flat types of woodcrete bat boxes erected in Tentsmuir.

5.4.2 Statistical analysis

All bat boxes were checked weekly from May-September 2003/2004. In order to minimize disturbance bats were not counted or sexed, just presence recorded. To investigate box dynamics a number of parameters for every box present in the forest were measured (Table 5.2).

Parameter	Notes
Presence	Whether any Natterer's bats were recorded in boxes.
Site	Location where boxes erected.
Bat box type	Five types used, see Table 1.
Aspect	One of eight categories according to compass direction, circle divided into 8 segments e.g. SE, SW.
Height of box above ground (m)	Min 1.64, Max 3.99, Mean 2.87.
Diameter of tree at 1.5m above ground.	Min 0.72. Max 2.67, Mean 1.59.
Tree species bat box attached to	Corsican Pine, Scots Pine, Hemlock, Sycamore, Alder, Beech, Bird Hide
Tree spacing	Related to thinning regime, normally from 3-6 meters.
Distance from road or forest edge (m)	Often the road /edge are the same.
Distance from track (m)	

Table 5.2: Parameters measured for each individual bat box.

5.4.3 Natural roosts

The day roosts of radio-tracked bats were recorded throughout the time they were tracked. It was discovered that the bats were using a particular type of natural cavity in predominantly Corsican pines. For these natural roosts the following details were recorded:

1).Tree species. 2) Live or dead tree. 3) Whether the cavity was a natural hole or a woodpecker hole.

5.5 Results

5.5.1 Roost selection

Over 65% of all day roosts for both colonies were in natural tree cavities. Bat boxes of three types were used 25% of the time (Figure 5.3). Box types used were old square wood, old wedge wood and round woodcrete. Woodpecker holes were only used 9% of the time by bats of both colonies. There was less than a 4.4% interchange of banded bats recorded roosting in one colony switching to roosts in the other colony (319 individual bats banded from 1998-2005, 17 individuals switched colony).

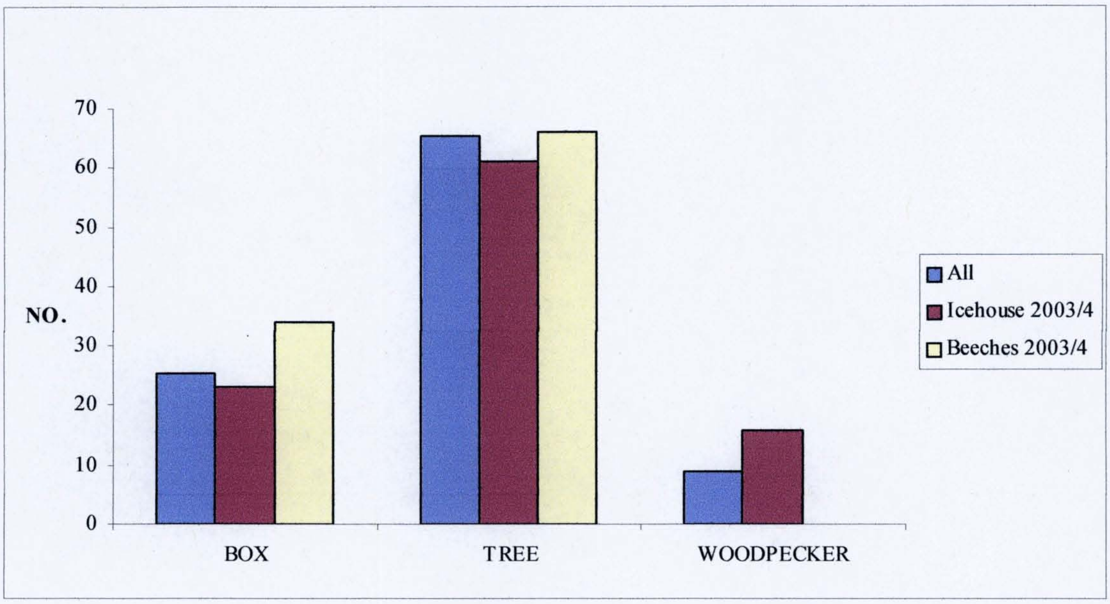


Figure 5.3: The percentage frequency of day roost sites of bats radio tracked May-September 2003/2004.

5.5.2 Natural roosts

The position of all natural roosts was plotted (Figure 5.4). No bats from a particular colony were found to roost in any natural roost site of the other colony. Table 5.4

displays types of natural roosts selected for each colony. Figures 5.5 & 5.6 illustrate the most common type of natural roost selected. These are double leadered Corsican pines, which form a natural cavity where the two leaders split. These cavities can be up to three meters in length (Figure 5.7). The height of the cavitity above ground level varies from 2 meters to approximately 20 meters.

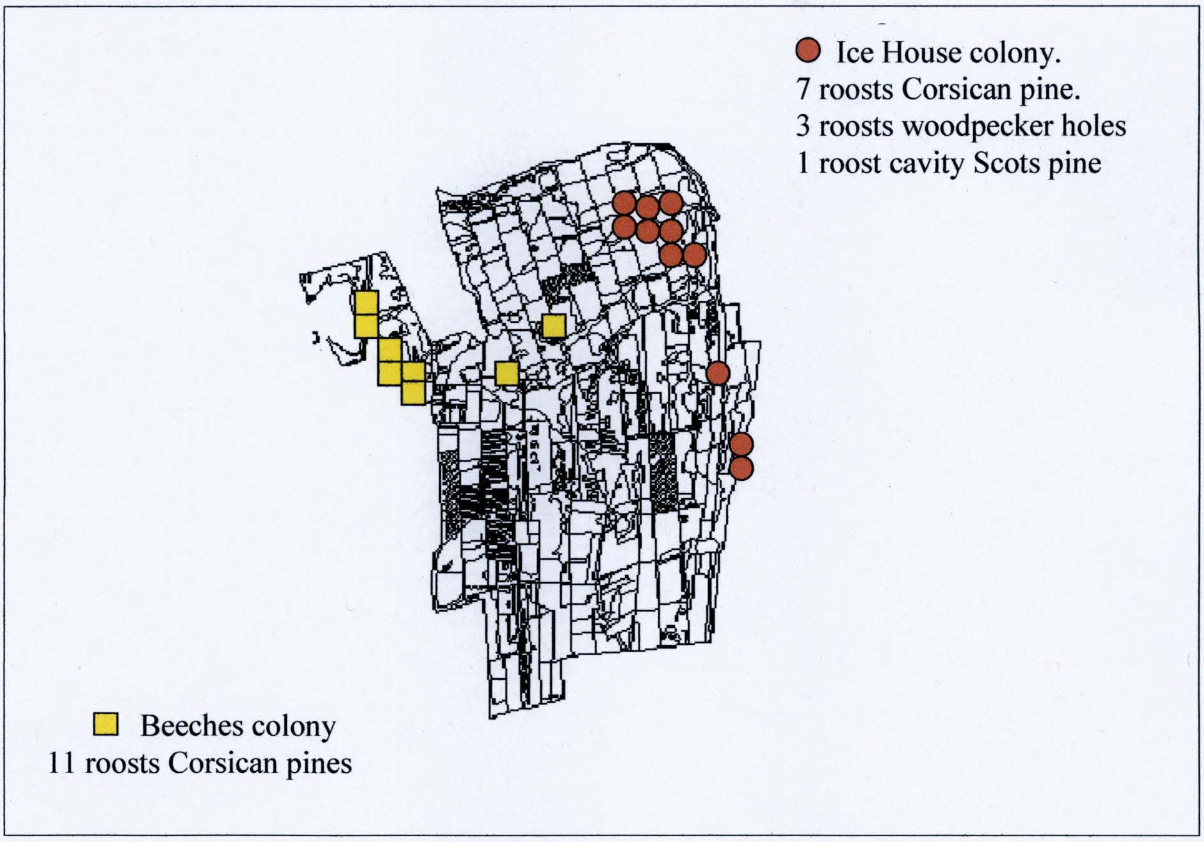


Figure 5.4: Position of natural tree roosts located in Tentsmuir Forest separated by colony

	Beeches colony	Ice House colony
Natural cavity in double – leadered Corsican pine	11	7
Woodpecker hole in snapped off pine.		3
Small cavity in Scots pine.		1

Table 5.4: Numbers and types of natural roosts recorded.

Figures 5.5 & 5.6: Two natural roosts in double leadered Corsican pines.

Figure 5.7: Inside of a natural roost in Corsican pine. The cavity is nearly three meters in depth and is living wood, not a rot hole or with decay present.

5.5.3 Time spent in roosts

From radio tracked bats the number of days spent in each type of roost was recorded (Table 5.5). Data were pooled for different types of bat boxes. Apart from one particular tree, which was used for 4 consecutive days, bats only spent one day in woodpecker holes. There was no significant difference ($t = 0.376$, $df = 35$, $p = 0.709$) in the number of days bats occupied either natural roosts or bat boxes although they significantly selected trees (t = -2.923, df = 6, p = 0.027) more than boxes.

	n	Min-max	Mean no. days	SE of mean	P value	
Natural roosts	26	1-6	2.5	0.339	0.709	
Bat boxes	11	1-6	2.27	0.469		

Table 5.5: Time spent by Natterer's bats in natural tree roosts and bat boxes.

5.5.4 Bat box selection

To determine bat box selection a mixed generalized loglinear model with Poisson Distribution (SAS version 8e, SAS Institute 1998) was used with site as the random factor. Bat box type, aspect, height of box, distance from edge, tree species, distance from track and tree spacing were entered as fixed factors. From this model the variable with the largest p-value was eliminated singly, provided p>0.05 while also looking at all possible pairwise interactions. If these were not significant they were removed from the model. Subsets of results from the generalized loglinear model looking at various parameters regarding bat box choice are in Table 5.6. All variables were removed from the model except box type and site. The final results show that box type is the most important parameter, with two types, old square wooden and round woodcrete being preferentially used.

Effect	Num df	F value	Pr > F
Site	6	1.80	0.1052
Box type	4	5.72	0.0003
Dist. Edge	1	1.25	0.2666
Box height	1	1.20	0.2755
Tree diameter	1	0.28	0.6007
Dist track	1	0.02	0.8923
Tree type	2	0.00	1.000
Tree spacing	1	2.07	0.1528

Effect	Num df	F value	Pr > F
Site	6	2.06	0.0628
Box type	4	5.36	0.0005
Dist. Edge	1	2.58	0.1106
Box height	1	0.93	0.3375
Aspect	1	0.72	0.3991

Effect	Num df	F value	Pr > F
Site	6	2.28	0.0399
Box type	4	1.19	0.3167
Dist. Edge	1	1.30	0.2566
Box height	1	0.56	0.4570
Aspect	1	2.59	0.1103
Aspect*box	4	1.33	0.2616

Effect	Num df	F value	Pr > F
Site	6	Inf.	<. 0.0001
Box type	4	Inf.	<. 0.0001
Dist. Edge	1	2.08	0.1515
Site*Box	3	0.15	0.9192

Effect	Num df	F value	Pr > F
Site	6	1.88	0.0894
Box type	4	4.97	0.0009
Dist. Edge	1	2.04	0.1553

Effect	Num df	F value	Pr > F
Box type	4	4.80	0.0012
Site	1	2.35	0.0349

Table 5.6: Subset of significant results from generalized loglinear model on bat box selection.

5.6 Discussion

5.6.1 Roost selection

At the start of the project it was generally thought that the Natterer's bats in Tentsmuir were moving roosts between the bat boxes and the stables at Kinshaldy. This was assumed because the distances between the locations were short (< 2 km). However, I found that there is a minimum of three separate colonies within the forest that do not use day roosts outside their home ranges and that there was very limited interchange between the colonies in the use of roosts in the forest. There was less than 4.6% interchange between the Beeches and Ice House colonies. Rivers et al. (2006) and Smith (2000) never recorded any interchange between different maternity colonies of Natterer's bats in their studies. The most striking finding was the use of natural cavities in double – leadered Corsican pines as day and maternity roosts by the Beeches and Ice House colonies. Due to the young age of the commercial plantations it is was assumed that there would be virtually no natural tree cavities present. Some populations of Natterer's bats appear highly selective in their choice of tree cavities as roost sites. In a study in Slovakia in parkland, Natterer's bats selected particular types of cavities in ash trees (Kanuch 2005). In this study double –leadered pines were the only type of natural cavity available apart from numerous woodpecker holes. These natural cavities were used 65% of the time compared to 9% for the woodpecker holes by bats of both colonies.

In commercial forests in the U.S.A. woodpecker holes are often favored roost sites (Vonhof 1998), but in Tentsmuir this was not the case, despite the availability of numerous woodpecker holes. Sparkes et al. (2003) reported that bat predation by woodpeckers could be an important source of mortality and both great spotted woodpeckers *Dendrocopos major,* and green woodpeckers *Picus viridus,* are resident in the study area. In Tentsmuir several of the boxes have been damaged by great spotted woodpeckers, which have been widely reported to break into bird boxes to eat the young. This would make the use of woodpecker holes as roosts by bats very risky.

The natural cavities were used significantly more than the bat boxes, however the time spent in them before the bats switched roosts was not significantly different. There could be several different reasons for this, including:

1. The natural roosts might provide a more stable microclimate. The interior cavities can extend >2m and appear to be much more insulated than the bat boxes.
2. They offer greater protection against predators. The bat boxes are liable to attack by great spotted woodpeckers and possibly grey squirrels *Sciurus carolinensis* and the trees offer much greater protection having smaller entrances and much thicker walls. Bats may also be more difficult to locate in a tree roost. The bat boxes are relatively low down and situated on the outside of the tree. It is possible at times to both hear and smell an occupied box from ground level.
3. Since tree cavities are frequently much deeper than bat boxes, the bats will be further away from the droppings where the ectoparisites are most abundant.

5.6.2 Bat box selection

The results of the Generalized Linear Model on bat box selection and site characteristics were only significant for box type and site location. However, the experimental setup was limited both in time and by disturbance. At the start of the project it was believed that the bats were roosting in bat boxes at two locations and that only one type of box (old square wooden) was used. Following systematic checking of the boxes over a summer it was discovered that they were roosting in seven locations in three different types of bat box; old square wooden, old wedge wooden and round woodcrete. It was decided not to disturb any of the boxes (apart from checking) until the winter when a programme of replacement and repair was carried out. All damaged boxes were replaced with either new square wooden types or round or flat woodcrete boxes. The following spring (2004) the Natterer's bats were still using the old wooden square and wedge types and readily took to round woodcrete boxes. The following spring (2005, not included in the analysis) they started to occasionally use the new wooden square boxes. It is quite possible that they prefer wooden boxes that are weathered before using them. The significance of site is more difficult to assess without having any reason why they might prefer one site to another. It was notable that two boxes used extensively in 2003 were not used in 2004 after woodpeckers damaged the boxes. Unknown predation attempts are just one of many possibilities why bats switch/choose different sites. It would seem that the advice of Swift (2004a) is sensible; bat box schemes need to employ a mixture of both wood and woodcrete boxes of several different shapes to achieve optimum occupancy.

5.6.3 Roost switching

In general the findings mirrored that of previous work on Natterer's bats with frequent roost switching occurring (Smith 2000, Smith & Racey 2005). Every individual bat that was radio tracked used the same core foraging areas regardless of where they roosted. This was also recorded by Brigham (1991) who provided evidence that tree roosting big brown bats did not minimize commuting distance by roost switching. Lewis (1995) suggested that could be a factor in roost switching. The natural tree roosts are much greater in size than bat boxes and this might lead to a reduced effect of ectoparasites. However, in Tentsmuir, ectoparasite loadings would appear not to be a factor as there was no significant difference in the amount of time bats spent in either natural roosts or bat boxes. Differences in microclimate between roosts are also difficult to quantify. Smith & Racey (2005) investigated the physical and thermal characteristics of summer roosts of Natterer's bats in an area of mixed pastureland. They found that the type of roost had a marked and significant effect on mean roost temperature. They compared roosts in the attic adjacent to the roof, attic mortises and tree cavities. The tree roosts were the coolest and the authors suggested that temperature is likely to play an important part in day-to-day selection of roost type in summer colonies of Natterer's bats. The temperature differences between bat boxes and natural tree roosts in Tentsmuir Forest were not checked, so it is unknown if this is a factor in roost site selection within the forest.

5.6.4 Conservation

In the U.K. and Europe, bats foraging and roosting habitats are protected by law, however Rancourt et al. (2005) suggested that bat conservation is hindered by a lack of geographic-specific knowledge of the characteristics of roost sites used by reproductive females. This is particularly relevant in the context of roosts in commercial coniferous plantations as they are working forests where trees get felled. This is illustrated clearly in this study where Natterer's bats used natural roosts of a type not described before

The fact that Natterer's bats roost switch on a regular basis demonstrates either that there are numerous suitable roost trees in their home range in Tentsmuir, or that there is a limited number, which are regularly reused. This is difficult to observe because roost trees were only found by radio tracking. There appear to be only a small number of double-leadered pines in Tentsmuir. It can also be seen that only a small percentage of these have developed a natural cavity, which could be used by bats for roosts. Many of the cavities are > 15 meters above ground level, so the only way to find whether they have been used as roosts is to scale the tree and check the cavity with an endoscope. This was not possible in this study. Whether there are numerous roost trees or a limited number we must view both the forest and bat populations from a larger, landscape scale and it is possible that significant areas of forest with appropriate types of trees may have to be preserved if the population is to be sustained. If there are only small numbers of double-leadered Corsican pines present within an area, then perhaps land owners could be persuaded to leave these standing. Crampton & Barclay (1998) proposed that to sustain bat populations in commercial forests in the U.S.A. old stands must be retained and roost sites preserved by managing the forest at the stand or landscape level The problem of monitoring bat populations that roost switch is also difficult. A species that uses only one type of roost is predictable in time and space, therefore monitoring is easier and more reliable. The natural cavities in Corsican pines appear to be widely, but thinly dispersed across the forest, making it difficult to locate, let alone monitor these roosts.

As discussed in Chapter 6 there is the probability that male and females Natterer's bats exhibit different roosting behaviours. There needs to be further research on what the roosting requirements of male Natterer's are. The only previous records of male roosts were by Swift (1997) and no evidence was found in this study. Perkins (1996) suggested that local bat diversity and population size in commercial managed forests are related to interspecific competition for limited roost sites, and to intraspecific division by sex that depends on local population numbers.

Bat boxes are vitally important for bats in commercial coniferous plantations. They provide roosts in an area where there is an abundant food supply but a lack of natural roost sites. It is not only in commercial plantations that the benefits of bat boxes are apparent. In wetland rice paddies in the Mediterranean region a bat box scheme was highly successful in attracting large numbers of soprano pipistrelles *Pipistrellus pygmaeus* (Flaquer et al. 2005). The authors concluded that the study highlights the role of bat boxes as useful alternative management tools for the conservation of bat populations in wetland habitats where few natural roost sites are available. The importance of a) bat box schemes and types of box erected and b) the scale and use of natural cavities in commercial plantations by Natterer's bats need to be urgently incorporated in management plans by relevant landowners.

CHAPTER 6

Survival rates and population size/structure.

6.1 Abstract

Worldwide many species of bats are declining for various reasons, and there is an urgent need to collect ecological data to inform conservation concerns. There is a paucity of information regarding survival rates and how they determine population dynamics in many species of bats; traits that are particularly important in a conservation management context. Natterer's bats are one of the least studied European bats with relatively little known regarding basic ecological parameters. This study investigated two colonies of Natterer's bats that form summer and maternity roosts in bat boxes in Tentsmuir Forest, east Scotland, U.K. Tentsmuir is a commercial coniferous plantation planted predominantly with Scots pine and Corsican pine. A mark-recapture study involving banding the bats has been carried out twice yearly on all bats present in bat boxes since 1998. Annual survival rates of Natterer's bats were estimated as between 0.79-0.87 for adult females and 0.38-0.59 for juveniles. It was impossible to estimate survival of males due to presumed dispersal, higher mortality rates or unknown male roosts. Population densities for the two colonies were estimated at a maximum of 10 bats km^2 and 25 bats km^2 respectively, which is extremely high compared to bats in broad-leafed woodland. 80% of adult females recaptured annually were pregnant; the trend for the study period 1998 -2005 showed no significant difference in numbers of pregnant bats.

6.2 Introduction

Knowledge of a species' life history traits is one of the fundamental requirements of both animal ecology and sound conservation management. These traits include juvenile and adult survival, growth rate, age & size at maturity, number & size of offspring and life span. Capture-recapture studies have been used in estimating abundance and survival rates in animal populations for many years (Pollock et al. 1990, Pollock 1991).

Robust estimates of annual survival are essential for effective conservation because the probability of survival, particularly of adult survival, has the greatest influence on population growth rates of long-lived vertebrates. Survival of juveniles to maturity together with emigration and immigration determines recruitment to reproductive age (Prevot-Julliard et al. 1998, Sandercock 2003, Sendor & Simon 2003). In most species juvenile survival is lower than adult survival, however, there are exceptions e.g. red-winged fairy wrens *Malurus elegan,* (Russell & Rowley 2000) and sociable weavers *Philetairus socius* (Covas et al. 2004) where first year survival is equal to that of adults.

Species that have been studied intensely using mark-recapture include birds (Dobson 1990, White & Burnham 1999), passerines (Baillie & McCulloch 1993, Johnston et al. 1997), ducks (Blums et al. 2003), shorebirds (Morrison et al. 2001), whales (Buckland 1990, Stevick et al. 2003, Larsen & Hammond 2004), seals (Garcia-Aguilar & Morales-Bojorquez 2005) and large herbivores (Coulson et al. 2001, Gaillard 2000). Capture-recapture studies on bats have also been undertaken e.g. New Zealand long tailed bats *Chalinolobus tuberculatus*, (Pryde et al. 2005), common pipistrelles (Sendor & Simon 2003) and ghost bats *Macroderma gigas* (Hoyle et al. 2001). However, in general there have been relatively few such studies.

Previous survival estimates were achieved with relatively simple methods of analysis, which have statistical limitations (Sandercock 2003), e.g. brown long eared bats (Boyd & Stebbings 1989) and common pipistrelles (Gerell & Lundberg 1990).

The dynamics of bat populations are more typical of large than small mammals and require high adult survival rates for populations to persist. This is due to low reproductive rates (1-2 young per year) with long life spans of up to 38 years. A low reproductive rate makes it difficult to reverse downward trends in population, which are then consequently very susceptible to elevated mortality or depressed recruitment (O'Shea & Bogan 2000). Long-term capture-recapture studies would seem well suited to bats because, for their body size, bats live longer than any other order of mammal (Wilkinson & South 2002). Long term monitoring is the only way in which survival parameters can be estimated with any accuracy (Bearhop et al. 2003).

The marking of bats with uniquely numbered metal bands applied to the wing bone or forearm has been ongoing for over 75 years (Baker et al. 2001). It is generally thought that banding has no direct impact on the flight or foraging behaviour of the bats. In the avian world where banding has been carried out much more intensely, Sandercock (2003) stated that ornithologists studying wader populations have not made the best possible use of the statistical tools that are available for estimation of survival and other demographic rates. In most cases, population data have been analysed with relatively simple methods while survival values derived from mark-recapture modelling are better estimates of true survival than return rates (Martin et al. 1995, Sandercock 2003). It is only in the last 15 years that new computer programs, which have improved the rigor and statistical techniques of capture-recapture, have been available e.g. Surge and MARK (Pollock et al. 1991, White 1996, White & Burnham 1999).

6.3 Aims

The aim of this study was to use live-recapture techniques on two colonies of Natterer's bats present in bat boxes in a commercial coniferous plantation in east Scotland, to estimate:

- Survival rates
- Population abundance
- Population structure

6.4 Materials and methods

6.4.1 Data collection

Natterer's bats were first recorded breeding in Kinshaldy stables within Tentsmuir in spring 1985 (Bullock et al. 1986). This coincided with a bat box scheme when approximately 90 boxes were erected in ten separate localities. Four localities were situated on the west side of the forest (known as the Beeches colony) and three on the east side (the Icehouse colony). Bat boxes at two localities were soon holding small numbers of Natterer's bats (Altringham & Bullock 1988, Mortimer 1993). Natterer's bats now roost in bat boxes in seven of these localities. For a full description and history of box placement see Chapter 2.

From 1998 the population found roosting in the bat boxes has been the object of a bat-banding programme (Tables 2.1a, 2.1b). Boxes have been checked twice yearly in May and August (before and after breeding) and any unmarked bats have been fitted with a numbered alloy bat ring (Mammal Society, London) on the forearm (Hatton & Cohen 2000). Bats were sexed and aged as either juvenile (born that year), or adult (>1 year). Aging has been done by whether epiphyses are fused (adults) or unfused (juveniles) (Racey 1974, 1988). Any adult females were checked for pregnancy, state of lactation and whether parous where appropriate using established techniques (Racey 1969). Due to the bats in the Beeches colony (Table 2.1b) moving to previously unchecked bat boxes within the same area in 2000, only data from the Ice House colony have been used in the survival analysis.

The banding data were stratified into four groups: juvenile females, adult females, juvenile males and adult males (Table 6.1). Data were collected bi-annually in May and August from 1998-2005, a total of 16 sampling occasions. Data were also pooled within a year to give eight annual catching occasions.

	Animals captured for the first time				Recaptures		
Year	Ad. Fem	Juv. Fem.	Ad. Male	Juv. Male	Recapture Female	Recapture Male	Total
1998	53	2	1	0	55	1	112
1999	5	4	1	8	34	9	61
2000	6	4	1	5	59	6	81
2001	4	14	0	9	37	10	74
2002	7	6	0	5	53	7	78
2003	8	0	2	0	50	4	64
2004	6	6	2	2	65	7	88
2005	0	7	1	7	73	12	100
Total	89	43	8	36	426	56	658

Table 6.1: Bats banded at Icehouse colony 1998-2005. The totals show how many individuals of each sex and age were banded yearly. The columns for "Recapture Females and Recapture Males" are the number of bats that were previously marked either earlier in that year or in a previous year.

Despite near parity in numbers of females and males being banded as juveniles, only very small numbers of adult males were recaptured in the following years. The numbers were so small (Table 6.2) that no male survival estimates were possible.

Year	Ad. Male	Years recaptured	Juv. Male	Years recaptured
1998	1	0	0	-
1999	1	0	8	7 = 0, 1 = 2003
2000	1	0	5	3 = 0, 1 = 2002, 1 = 2004
2001	0	0	9	8 = 0, 1 = 2002
2002	0	0	5	4 = 0, 1 = 2003
2003	2	1 = 2005, 1 = 2004+2005	0	0
2004	2	0	2	0
2005	1	0	7	-
	8		36	

Table 6.2: Recapture history of males banded as either juveniles or males.

6.4.2 Survival analysis

Survival rates were estimated using capture–recapture models of the Cormack-Jolly Seber (CJS) type as implemented in program MARK (Lebreton et al. 1992, White & Burnham 1999). Models were used to estimate apparent survival (ϕ) and recapture probability (p) varying over time (t) or constant over time (.) for adult females and juvenile females. Age specific differences in survival were investigated through models that estimated first year or first and second year survival separately from adult survival.

The fully time dependent CJS-model ($\phi(t)\ p(t)$) makes some fundamental assumptions: (1) the individuals of the ith sample have the same probability of recapture, (2) the individuals of the ith sample have the same probability of surviving to $i + 1$, (3) marks are not lost or overlooked, and (4) samples are instantaneous and the individuals are released immediately after the sample (Pollock et al. 1990). Of the four assumptions numbers 1 and 2 are sometimes considered problematic. Assumption 3 regarding unknown mark losses are not normally considered an issue with bats (Keen 1988). In estimating direct rates of population growth, Rotella & Hines (2005) state that bias was low and often negligible with low rates of tag loss and high capture probability. Assumptions 1 and 2 are often violated due to extra binomial variation e.g. transience and trap heterogeneity (see below), which has to be accounted for in the structure of the model. Both transience and trap homogeneity were tested for specifically in U-CARE (Choquet et al. 2003).

Transience

A problem with mark-recapture in open populations is distinguishing between individuals that leave the study site and those that die, since this will give biased estimates when dispersal rates are incorrectly included in mortality rates (Kendall et al. 1997, Perret et al. 2003). Transients can be defined as individuals that have a zero probability of recapture after their initial capture (Pradel et al. 1997). Transience can be accommodated in the data selection by removing the initial capture point from the recapture history (Paradis 1993).

Heterogeneity in capture probabilities

Heterogeneity in capture probability is a common problem with mark-recapture studies. The sources of heterogeneity can be split into two categories: methodological e.g. bad survey design and biological e.g. some individuals not having the same capture probability as others (Bearhop et al. 2003). At the start of the banding programme in 1998 the only known summer and maternity roosts were bat boxes. After the start of radio tracking in 2003 it was discovered that natural roosts in Corsican pines were also used extensively (Chapter 5). This had not been recorded before and was unexpected because trees in commercial plantations are normally felled in their prime before natural and rot holes form. Radio tracking showed that some individuals use tree roosts significantly more than the bat boxes and vice-versa (Chapter 5). This may have led to heterogeneity of capture probability as some bats were nearly always present in the bat boxes while other bats were only occasionally found in the boxes.

6.4.2.1 Model fit and model selection

A global model, i.e. the most parameterised model, was tested for goodness of fit (GOF) using parametric bootstrapping. If the proportion of generated values smaller than the observed values was < 0.05 the model was rejected (White & Burnham 1999). Reduced models with fewer parameters were fitted to the data with selection of the most parsimonious model determined by Akaike's information criterion, (AIC_c), (Akaike 1973). If the difference between two models was less than 2 units then Likelihood Ratio Tests (LRT) were used to determine the better model (Burnham et al. 1995a, 1995b). Each selected model was also tested for a lack of fit by calculating the Variance Inflation Factor, ($\hat{c}$), by dividing the observed model deviance by the mean of the deviance of the simulated data obtained from the parametric bootstrapping (Lebreton et al. 1992). If $\hat{c} = 1$ the data are distributed as expected by the model. Values of $\hat{c} < 1$ suggest under dispersion in the data and are not generally considered problematic. Values of $\hat{c} > 1$ indicate over dispersion, but this is not considered problematic unless $\hat{c} > 3$ (Cooch & White 2005). Any $\hat{c}$ values greater than one and less than three were used to adjust the measure of model fit for the over dispersion. If an adjusted $\hat{c}$ was used then the best model was determined by quaisi-AIC values ($QAIC_c$).

6.4.3 Population size estimation

Two colonies of Natterer's bats (Beeches and Icehouse) utilize bat boxes in Tentsmuir. To estimate population abundance the Chapman-modified Petersen estimator was calculated using data from marked bats in the boxes in 2003 /2004. The Petersen estimator is based on the ratio of marked to unmarked individuals within a population and the methodology is:

- Capture, mark and release a sample of animals (n_1)
- Allow population to mix
- Capture a second sample of animals (n_2)
- Determine how many are marked (m_2)
- Equate proportion marked in 2nd sample with proportion marked in population (N)

The population is estimated by:

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

The variance of the estimate is estimated by:

$$var(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2 (m_2 + 2)}$$

In this study all bats were intensively checked for marks in 2003 and 2004 by visiting all bat boxes in both colonies in the same day.

The Petersen estimator has the following assumptions:

- The population under study is closed i.e. there are no births, deaths, immigration or emigration between samples.
- Within a sampling occasion each member of the population has the same probability of being captured.
- Capture does not alter the probability of recapture.

- Marked and unmarked individuals randomly mix between samples.
- Marks are permanent and always recognizable.

The densities of bats in the colonies were estimated as bats per km^2 of the calculated home range size for each colony. Home ranges were calculated using Minimum Convex Polygons (MCP) from radio-tracking data obtained in 2003/2004 (Chapter 3).

6.5 Results

6.5.1 Survival

6.5.1.1 Model goodness of fit

The global models (most parameterised) were tested for goodness of fit (GOF) to determine if the model fitted the data (Table 6.3).

	Sampling period	$\hat{c}$	GOF P value	Transience P value	Trap dependence P value
Adult females	Annual	0.96	0.64	0.97	0.036
	Twice annual	0.87	0.94	0.77	0.59
Juv. Females	Annual	1.38	0.09	0.21	0.81

Table 6.3: Goodness of fit statistics for global survival models.

Cooch & White (2005) suggest that if the GOF probability value is less than 0.05 then the model did not fit the data. The two models for bats banded as adult females had very high GOF probability values, 0.64 and 0.94; however, the model for bats banded as juveniles did not fit so well at $P = 0.09$. As goodness of fit probabilities of < 0.2 may suggest some evidence of a lack of fit, the over dispersion in the model was measured by calculating the variance inflation factor ($\hat{c}$). Table 6.3 shows that there was little evidence for over dispersion in the data. The data were tested for the effects of transience and all models had a non-significant result (Table 6.3). The tests for trap dependence showed that this had a significant effect for adult females with annual pooled data but not when unpooled (Table 6.3). Consequently, it was decided not to investigate trap dependence further.

6.5.1.2 Model selection

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance	
Phi(t) p(t)AGE	159.877	0.00	0.40404	1.0000	9	36.338	**Model 1**
Phi(.) p(t)	161.165	1.29	0.21220	0.5252	8	40.146	
Phi(t) p(t)AGE2	161.436	1.56	0.18522	0.4584	10	35.3081	**Model 2**
Phi(.) p(.)	161.464	1.59	0.18270	0.4522	2	54.241	
Phi(t) p(.)	166.966	7.09	0.01167	0.0289	8	45.947	
Phi(t) p(t)	169.025	9.15	0.00417	0.0103	13	34.677	

Table 6.4: Model selection data for juvenile females sampled annually 1998-2005.

Table 6.4 shows the results of fitting various survival models to data on juvenile females. It can be seen that the best fitting model is **Model 1**, which estimated first year survival separately from all other years. **Model 2,** which estimated first and second year survival separately from all other years, also received considerable support from the data. Given the support for these age-structured models, the models Phi(.) p(t) and Phi(.) p(.) were not considered further.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance	
Phi(.) p(t)	551.416	0.00	0.57808	1.0000	8	107.688	**Model 3**
Phi(t) p(t)	552.046	0.63	0.42190	0.7298	12	97.423	
Phi(.) p(.)	572.155	20.74	0.00002	0.0000	2	140.948	
Phi(t) p(.)	579.806	28.39	0.00000	0.0000	8	136.078	

Table 6.5: Model selection data for adult females sampled annually 1998-2005.

Table 6.5 shows the results of fitting survival models to data on adult females with data pooled over years. The best fitting model (**Model 3**) was where survival was constant over time and capture probability time dependent. However, the Phi(t) p(t) model also received considerable support from the data.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance	
Phi(.) p(t)	904.490	0.00	0.99397	1.0000	16	412.263	**Model 4**
Phi(t) p(t)	914.698	10.21	0.00603	0.0061	29	392.409	
Phi(.) p(.)	1063.621	159.13	0.00000	0.0000	2	601.096	
Phi(t) p(.)	1064.276	159.79	0.00000	0.0000	16	572.050	

Table 6.6: Model selection for adult females sampled twice annually 1998-2005.

Table 6.6 shows the results of fitting survival models to data on adult females with bi-annual data. The best fitting model (**Model 4**) was where survival was constant over time and capture probability time dependent.

6.5.1.3 Survival estimates

Table 6.7 gives the survival estimates for Models 1-4.

Age/sex	Capture occasions	Annual survival	S.E.	Description	Model Number
1st year female	8	0.482	0.104	Age structured model, bats banded as juveniles then recaptured as adults	1
Adult female	8	0.791	0.132		
1st year female	8	0.491	0.088	Age structured model, bats banded as juveniles then recaptured as adults	2
2nd year female	8	0.684	0.151		
Adult female	8	0.875	0.118		
Adult female	8	0.815	0.023	Bats banded as adults	3
Adult female	16	0.804	0.022	Bats banded as adults	4

Table 6.7: Survival estimates from Models 1-4.

For bats banded as juveniles, Model 1 estimated first year survival as 0.482 and adult survival as 0.791. In Model 2, first year survival was estimated at 0.491, second year survival at 0.684 and adult survival at 0.875. The annual survival estimates for bats banded as adult females for Models 3 & 4 were very similar at 0.815 and 0.804 respectively. The standard errors of the survival estimates from Models 1 & 2 are relatively high. The standard errors for Models 3 & 4 are much smaller and suggest that the models fitted the data better.

6.5.2 Population size

Table 6.8 shows the data used to estimate population size.

Year	Colony	No. of bats 1st capture session.(n1)	No. of bats 2nd capture session.(n2)	No of bats already marked 2nd session (m2)
2003/2004	Beeches	103	57	51
2004/2005		57	59	37
2003/2004	Icehouse	42	49	32
2004/2005		49	50	40

Table 6.8: The numbers of individual female bats marked and recaptured for the Beeches and Icehouse colonies in 2003-2005.

Population estimates from all marked female bats are given in Table 6.9. The Beeches colony had nearly double the estimated population of the Ice House colony (Table 6.9). As the Beeches home range is smaller than the Icehouse home range, then the difference in density is even greater, (20.5 - 25.1 bats per km^2 for the Beeches and 9.4-9.9 bats per km^2 for the Icehouse colony).

Colony	Year	Estimated no. females	Variance	Standard error	Home range (km^2)	Density (per km^2)
Ice House	2003/2004	64	9.9	3.15	6.46	9.9
	2004/2005	61	3.3	1.82		9.4
Beeches	2003/2004	115	13.1	3.62	4.43	25.1
	2004/2005	91	27.2	5.22		20.5

Table 6.9: Population numbers and densities of female bats present in Beeches and Icehouse colonies 2003-2005.

6.5.3 Sex ratio and pregnancy rates

Table 6.10 displays the near parity of the sex ratio of juvenile bats banded. However, juvenile recruitment is heavily biased towards females with only 10% of males being recaptured in the colony as adults. A high number of adult females were recorded pregnant each spring (80.3%). The trend for the study period showed no significant difference in number of pregnant bats ($F_{1,5} = 2.8$, $p = 0.16$),(Figure 6.1).

% Juvenile females/male ringed	52% females (71) / 48% males (66)
Juvenile recruitment-subsequently recaptured after at least 1year (pooled)	29.7% females. / 10% males.
Mean % females recorded pregnant > 1 year old	80.3%. +/- 6.7 s.e.
Roost size (adult females)	Mean 13.1 +/- 1.57 s.e., range 1-53.
Roost size (all bats)	Mean 14.8 +/- 1.75 s.e., range 1-54.
Roost size spring	Mean 14.5 +/- 2.59 s.e., range 1-54
Roost size summer	Mean 16.5 +/- 2.53 s.e., range 1-46

Table 6.10: Breeding population dynamics 1998-2005.

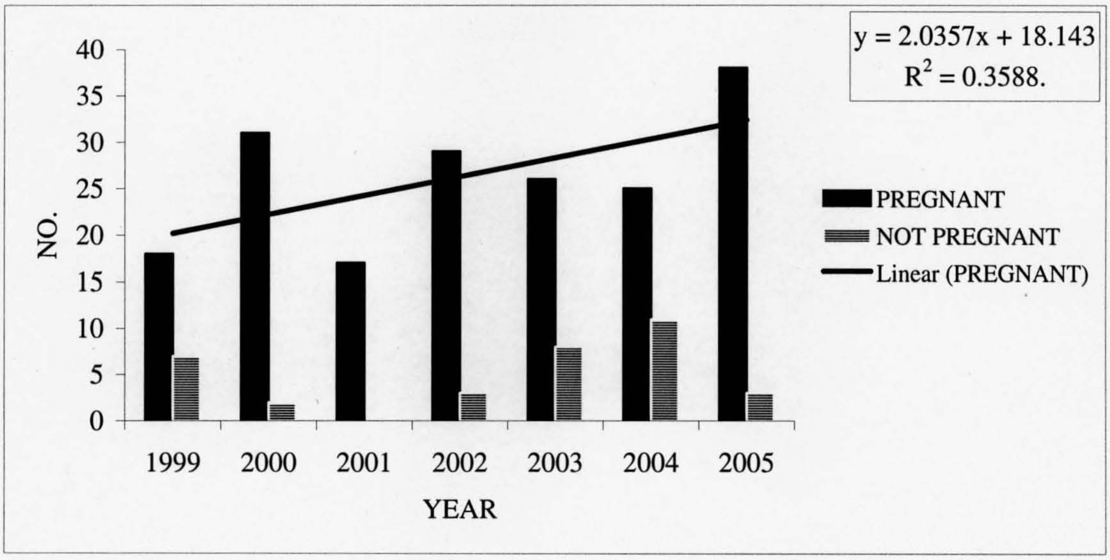


Figure 6.1: Annual pregnancy totals of adult females greater than 1 year old.

The roost sizes recorded showed no significant difference between colonies, before breeding (spring) and after breeding (summer), either in size or sex composition (Table 6.10).

6.6 Discussion

6.6.1 Survival

The study has provided an insight into survival and population dynamics of probably the least studied European bat. Various limitations in collecting the data, length of study, and biological realities all impacted on the model fit. The data from the Beeches colony could not be fully utilized because the bats were found to use previously unchecked bat boxes in the early part of the study. It would be preferable to have collected data over a longer time period than the lifespan of the bats; Schober & Grimmberger (1989) state that Natterer's bats have been recorded living up to 20 years old. Some of the bats ringed as adult females in 1998 are still present and a similar, related species, Brandt's bat has been recorded living up to 38 years in the wild (Wilkinson & South 2002). The use of natural tree roosts (Table 5.5) was unexpected because it was generally assumed that there would be a shortage of natural roosts in commercial plantations (Altringham1988, Boyd & Stebbings 1989). There was a positive significant difference between occupancy in natural roosts and bat boxes (Table 5.5), implying that some individuals may roost in bat boxes preferentially over tree roosts and vice-versa. It is not possible to check the tree roosts, as they are inaccessible. Although there was evidence of trap dependence in the data for Model 3, the survival estimates for both this model and Model 4 were virtually identical. Therefore, it is unlikely that trap dependence had an impact on survival estimates. Despite this, for adult females, the model fitted the data well with a low $\hat{c}$ recorded, and the survival estimates obtained should be robust.

The adult female annual survival estimates of 0.79-0.87 compare well with the figure of 0.86 (0.66-1.00) quoted by Rivers et al. (2006). She states that this figure might be overestimated, as the data did not include juveniles which did not survive the first swarming season. The survival estimates also compare well with figures of 0·80 for common pipistrelle and 0.86 for brown long-eared bat, which are similar sized bats (Boyd & Stebbing 1989, Sendor & Simon 2003). There are differences between the survival estimates of Natterer's bats and the estimate of 0.57-0.77 obtained for ghost bats, a much larger bat at 150g (Hoyle et al. 2001). The adult female survival estimates obtained from Models 1 & 2 had relatively large standard errors, which are probably due to sparse data. The estimates from Models 3 & 4 (0.815 & 0.804) had much smaller standard errors and are therefore more precise. Due to sparse data only rough estimates for juvenile survival were obtained, 0.48, (+/- 0.104 s.e.) and 0.49 (+/- 0.088 s.e.). These are comparable to 0.53 for common pipistrelle and 0.35-0.46 for juvenile female ghost bat. Model 2 indicates that juveniles show greater mortality in their first two years before parity in survival is reached with adults. Other studies on bats have shown survival to vary with age, with adult survival higher than juveniles (Hoyle et al. 2001, Sendor & Simon 2003), and juveniles showing greater mortality in their first two years (Pryde et al. 2005).

Despite near uniformity for juvenile males and females surviving to banding age (Table 6.11) it proved impossible to determine survival estimates for males. Capture and recapture rates for males (Table 6.3) were very low. There are many reasons that could explain why relatively few males compared to females were recaptured. No male roosts

(Swift 1997) were found in the bat boxes and also compared to the findings of Park et al. (1998) there were fewer mixed sex groups, with more than one or two adult males present. It is possible that roost site fidelity varies between males at different locations; e.g. in common pipistrelle, Gerell & Lundberg (1988) found that males were much more vagrant than females, while in brown long-eared bats, Entwistle et al. (1997) showed that high site fidelity and long term use of roosts for both sexes occur. Emlen & Oring (1977) found that social behaviour of a species is not permanent and may differ both geographically and temporally. It is feasible that males use other inaccessible roosts, but there is no way of checking unless radio-transmitters are utilized, which was beyond the scope of this study. There is also the possibility that male survival in Natterer's bats is lower than females as in New Zealand long tailed bats (Pryde et al. 2005). Male-biased dispersal is considered typical for mammals (Fisher 2005), and is well documented in some species e.g. noctule bat (Petit & Mayer 2000), Bechstein's bat (Kerth et al. 2002), long fingered bat, *Miniopterus schreibersii* (Miller-Butterworth et al. 2003) and brown antechinuses, *Antechinus stuartii* (Fisher 2005).

From the data it can be seen that there is much yearly variation, particularly in recapture rates, but the reasons for this are unknown, since data are too sparse to identify specific reasons. Anders & Marshall (2005) found that survival parameters obtained from empirical data on juvenile and adult survival, can vary between landscapes, species, and years within a single population.

6.6.2 Population abundance/density and reproduction

It is difficult to compare many of the recorded bat abundance/densities (Robinson & Stebbings 1977) because many different techniques have been utilized; e.g. ultra sound detectors (Rydell et al. 1994, Kalcounis et al. 1999), visual (Geilsa & Chytil 2002, Moreno-Valdez 2004), radio telemetry (Crampton & Barclay 1994), roost counts (Warren & Witter 2002) and mist netting (Clarke et al. 2005). In other radio tracking and roost count studies, population densities have been found that are much lower than those in this study (9.9 & 25.1 bats per km^2). Smith (2000) estimated that Natterer's bat maternity colonies in open pastureland on the English/Welsh borders had a density of 2.88 bats per km^2. For adult serotine bats an even lower figure, 0.8 per km^2, has been reported (Robinson & Stebbings 1977). The population estimates (Beeches 91-115 adult females, Ice House 61-64 adult females) obtained in this study were unexpectedly high. The assumption that the population was closed was violated in this study. This could have resulted in an inflated population estimate as the proportion of animals marked is diluted in the second sampling occasion. However, Hammond (1986) considers that using a Petersen estimator for pairs of year's model is appropriate in long lived animals where mortality and birth rates are low because bias in estimated population size is small. Over the study period the maximum numbers of bats recorded in a bat box were 59 adult females, with an average of 14 bats. It was only by recording band numbers that it became apparent that there was a large turnover of bats within the boxes, and that more bats were present than expected. This was also a finding of Entwistle et al. (2000) who in a study of marked brown long-eared bats *Plecotus auritus,* found that population estimates were substantially higher than in previous studies with unmarked bats. Due to the size and structure of the majority of commercial coniferous forests, it is not surprising that, if they are good foraging habitats, densities of bats are high. With a few exceptions, broad –leafed woods are much smaller and more fragmented and consequently unable to support high densities of foraging bats.

The numbers of adult females showing signs of pregnancy was recorded yearly. There was no significant overall trend, which would indicate that the population is relatively stable at least in the years of this study. Numbers of young bats ringed yearly did, however, show considerable fluctuation that could be the result of different factors. Poorer juvenile survival in inclement weather could impact on adults' ability to provide adequate food (Sendor & Simon 2003). But it could be due to annual variation in roost use. Tree roosts may provide a more stable environment in periods of cold weather and the bats might simply move their young to safer roosts where they were not recorded. Small numbers of female juveniles were recorded back in roosts in the following year after birth and these were usually pregnant. Juvenile recruitment for Natterer's bats was determined from all juveniles ringed and subsequently recaptured in later years and indicated that a minimum 30% of females were returning compared to 10% of males. These figures can only be used as benchmarks since the tree roosts were inaccessible. The sex-ratio of the juveniles ringed was almost uniform and this concurred with Rivers et al. (2006). She recorded no significant difference in the sex-ratio in juvenile Natterer's bats ringed at summer roosts in Yorkshire, U.K.

Roost size in the bat boxes size displayed no significant difference between spring and summer, or between the two colonies with a mean of 13 adult females present. Due to size limitations of the bat boxes the larger roost numbers associated with buildings and tree roosts were not found. However, roost composition was different; before breeding the roosts were predominately females with only occasional males. After breeding there was a mixture of adult females, juvenile females and males with up to three adult males with a mean of 14 bats per box. The fact that there were no significant differences in numbers of bats found in boxes between the two colonies is interesting. The estimated population for the Beeches colony (91-111 adult females) is almost twice that of the Icehouse colony (61-64 adult females). This, and the fact that roost sizes were not different between spring and summer, when greater numbers of bats are present in the colonies, suggests that lack of roost sites could be a limiting factor in Natterer's bat populations. An average roost size of 14 bats in an estimated population of 111, suggests that approximately 8 active roosts within the colonies home range are active at any one time. However, it is not known if natural tree roosts within Tentsmuir hold similar numbers of roosting bats to the bat boxes.

It is not surprising that different studies on the same species, investigating population and survival dynamics find that results vary. Methodology and data analysis need to be clearly stated otherwise comparisons are difficult to make. In a review of habitat ecology of forest roosting bats, Miller et al. (2003) found that many studies did not clearly define how data were obtained and therefore the reliability of the data on which to base management is uncertain. Despite limitations often found with mark-recapture studies, the results are important in many ways. They provide an insight into survival and population dynamics of one of our least studied bats that will impact on conservation management. They also demonstrate the importance of commercial plantations not only to Natterer's bats but potentially other species as well.

The paradigm that commercial coniferous plantations are an "inferior" habitat needs to be quickly addressed, since it would appear that, for some bat species, landowners of these forests are guardians of some of the richest bat habitat in the U.K. Further research is necessary to establish whether more species of bats are utilizing the forests. At the very least, successful conservation management requires adequate ecological knowledge of foraging, roosting and population dynamics of the bat species involved.

CHAPTER 7

General discussion

7.1 Abstract

The Natterer's bat is one of Europe's least studied bat species, and commercial coniferous plantations are probably the least studied bat habitat in the U.K. Two colonies of Natterer's bats occupying bat boxes in Tentsmuir Forest, a commercial coniferous plantation, were studied to determine foraging ecology, roosting dynamics and survival rates. The study highlighted several exciting findings that are important from both an ecological and conservation perspective. Natterer's bats preferentially foraged in mature Corsican pines, they showed preferential use of particular types of bat box and the use of a particular type of natural roost not previously reported in the literature, and there were extremely high densities of bats present in the forest. These results question the long held paradigm that commercial plantations are an inferior habitat for bats compared to broad leafed woodland. This has far reaching consequences from a conservation perspective, since commercial plantations are the largest area of woodlands in the U.K. Management recommendations on how to improve commercial plantations to benefit bat conservation in the long term are suggested.

7.2 Natterer's bats and commercial coniferous plantations

In the U.K. and Europe, bat foraging and roosting habitats are protected by law, however, Rancourt et al. (2005) suggested that bat conservation is hindered by a lack of geographic-specific knowledge of the characteristics of roost sites used by reproductive females. This study was particularly relevant to this point since we do not know where Natterer's bats forage within commercial coniferous plantations, and the results have increased our knowledge of Natterer's bats, which are the least studied European bat (Smith & Racey 2004). Knowledge of a species' life history traits and basic ecological parameters are one of the fundamental requirements of both animal ecology and sound conservation management. Various other studies on Natterer's bats have looked at foraging dynamics (Siemers et al. 1999, Smith 2000), diet (Swift & Racey 2002), and at roost dynamics (Smith & Racey 2005), however, none of these have been in commercial coniferous plantations. From a landscape perspective on a national scale commercial plantations are the most abundant woodland type in the U.K. (Figure 1.1). The suitability and potential of commercial coniferous plantations as bat habitat has been almost totally overlooked despite several successful bat box schemes scattered throughout commercial plantations in the U.K.

7.3 Foraging and habitat preferences

The two important questions that were answered about foraging Natterer's bats in commercial plantations by this study were; where do they forage and how much of this habitat(s) do they use. The habitat preferences found in this study are different from any previous work and call into question previous generalizations about the foraging habitats used by bats in the U.K. The preferential use of mature Corsican pine habitat (Table 4.3) for foraging was unexpected given previous work on Natterer's bats, which found that broad-leafed deciduous woodland, orchards and pastureland were preferentially chosen (Siemers et al. 1999, Smith 2000). Given the extent of both Corsican pines and commercial coniferous plantations in the U.K., this finding has important implications for conservation management and further detailed research into both the foraging ecology of bats and the invertebrate prey communities of commercial plantations.

The size and extent of individual bats' home ranges were very small compared to those found by Smith (2000) in semi-natural deciduous woodland and pastureland. The use of core areas that did not overlap with other individuals' core areas was similar to Smith's findings. The small home ranges and the structure of commercial plantations have resulted in very high densities of Natterer's bats in Tentsmuir (Table 6.5). These densities are considerably higher than any recorded densities for Natterer's bats and, yet again, demonstrate how important commercial plantations are for Natterer's bats.

7.4 Roost dynamics

Where bats roost, what types of roost they use and how often they change roosts are fundamental questions in their ecology. Without the answers to these questions then conservation management is unlikely to be effective. The use of bat boxes as roosts is well documented in commercial plantations; however there is a paucity of information regarding the most suitable types, size or construction material. The finding of this study that particular box types were important to Natterer's bats was not surprising. The practice of erecting three boxes per individual tree is considered sensible, given bats' sensitivity to microclimate within roosts. As many commercial forests have several bat species present, then in agreement with Swift (2004a), the use of an assortment of box types, sizes and materials is recommended in bat box schemes.

The finding of natural roosts in double-leadered Corsican pines (Figures 5.5 & 5.6) is a major issue with regards to forestry work practices. The "ideal" tree for forestry purposes is straight and tall. Any trees that have deformities are not financially worthwhile and are normally removed by thinning at an earlier age. There needs to be further research into what trees within plantations are used by bats for roosting, and more importantly, how they can be easily identified and preserved by forest managers.

Roost switching is a well-known but relatively poorly understood mechanism used by various bat species. While it is known that Natterer's bats switch roosts (Smith 2000), little was known about the frequency of switching in bats roosting in bat boxes. The finding that Natterer's bats used the natural tree roosts significantly more than the bat boxes is important, as is the fact that there was no difference in the rate of switching between the types of roost (Figure 5.3, Table 5.4). Again, from a conservation aspect, this emphasises the importance of both the natural roosts and the bat boxes in maintaining and increasing populations of Natterer's bats in commercial plantations.

7.5 Survival

Knowledge of a species' life history traits is one of the fundamental requirements of both animal ecology and sound conservation management (Pollock et al. 1990, Pollock 1991). These traits include juvenile and adult survival which have not been recorded before in populations of Natterer's bats present in commercial plantations. The survival estimates for adult females recorded in this study, 0.76-0.87 per year are similar to that found for other bat species (Boyd & Stebbing 1989, Sendor & Simon 2003, Rivers et al 2006) and are probably the most accurate yet recorded for Natterer's bats.

7.6 Diet and invertebrate trapping

The results of the diet analysis as found in faecal samples was relatively similar to the results found by Swift & Racey (2002) with any differences probably reflecting temporal, seasonal and geographical variation in insect abundance as found in e.g. big brown bat (Whitaker 1995). It also shows that Natterer's bats are able to take a wide variety of prey using several different foraging techniques.

Invertebrate trapping methods are known to be subject to a variety of potential biases (Canaday 1987, Duelli & Obrist 1998) and this area of the study threw up some intriguing results. There was no difference in canopy invertebrate diversity or composition (Figure 4.11) as trapped between mature Scots and Corsican pines. Also, there were no differences in invertebrates caught between the different trapping methods. Invertebrate trapping is one area where a more intensive study, with a greater variety of trapping methods, would repay increased effort. The invertebrate composition of commercial plantations is relatively unknown, particularly between different tree species. An understanding of invertebrate prey availability in commercial plantations would undoubtedly help in understanding bat distribution in these forests.

7.7 Forest management proposals

There are at least two distinct types of commercial plantations present in the U.K. These are basically the mixed lowland pine plantations like Tentsmuir and the upland spruce monocultures. To make these more attractive to bats for both foraging and roosting a variety of forest management measures need to be considered. These include recommendations by Humprey (2005) for increasing biodiversity in upland spruce plantations but are also relevant for other types of commercial plantations.

- Areas of old mature trees allowed to develop. A high proportion of large, old trees, multiple age classes and high volumes of fallen and standing deadwood normally characterize these areas in forests. This would increase roost potential, create more foraging areas and increase overall biodiversity.
- Encourage all landowners to be able to identify potential natural roosts in double leadered pines and preserve them wherever possible.
- Where timber production is ongoing then these old-growth stands could be managed by singletree selection or small group-fell silviculture. If clear felling of large areas of trees is essential then enclaves of old growth areas should be retained as refuges and to help dispersal. This should be considered on the landscape scale to ensure an appropriate balance between old growth and other types of woodland and non-woodland habitats (Humprey 2005).
- When new plantations are planted they should be designed to allow access to the interior either/or by provision of rides or by creating gaps and edge effects.
- Thinning of young trees is also essential to allow access to the interior and increase overall biodiversity.
- Plant a mixture of tree species, particularly Corsican and Scots pines and avoid monocultures of spruce.
- Where possible encourage bats by erecting bat box schemes with suitable designs of bat box available. In some forests it is possible that roost sites are the limiting factor.

The above proposals are thought to offer both short and long term advances in bat conservation. The proposals are relatively simple to implement and cost effective and will benefit both bat conservation and overall biodiversity.

7.8 The way forward

This study has clearly illustrated that particular types of commercial coniferous plantations are a valuable roosting and foraging habitat for Natterer's bats. It also raises several ecological questions that are at present unanswered. These include what is the extent of natural roosts in commercial forests, are other tree species involved and are other bat species involved? The further south you travel in the U.K. the more bat species you find present in bat box schemes in commercial plantations. Successful conservation management requires these species to be studied to provide adequate ecological knowledge of foraging, roosting and population dynamics of the bat species involved. This study has found that commercial coniferous plantations are unexpectedly important for Natterer's bats. Similar forests in the U.K. may well be important to the conservation of other bat species. This study has concentrated on adult female Natterer's bats, as these form maternity colonies and are therefore easily accessible. There is virtually nothing known about male Natterer's bats. The same questions can be asked of males that were for the females; where do they forage and roost. Other areas that urgently need baseline research are the effect on bats of changing silvicultural practices (Chapter 1.5.1) that are presently ongoing in commercial plantations, with a swing from open patch clear felling to continuous cover forestry. Patriquin & Barclay (2003) stated that silvicultural methods have different immediate effects on different species of bats and that forest management must take these effects into consideration.

This study has provided some baseline answers regarding Natterer's bat ecology in commercial plantations; however, this must clearly be seen as a springboard for many avenues of future research. The paradigm that commercial coniferous plantations are an "inferior" habitat needs to be quickly addressed, since it would appear that, for some bat species, landowners of these forests are guardians of some of the richest bat habitat in the U.K.

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