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Neyland, Penelope Jane (2011) *Habitat, home range, diet and demography of the water vole (Arvicola amphibious): Patch-use in a complex wetland landscape..* thesis, Swansea University.
http://cronfa.swan.ac.uk/Record/cronfa42744

Habitat, home range, diet and demography of the water vole (*Arvicola amphibius*): Patch-use in a complex wetland landscape

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for the degree of

Doctor of Philosophy

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June 2011

Author's declaration

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree

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Abstract

Water vole (*Arvicola amphibius*) ecology was studied at the National Wetland Centre Wales (NWCW), a National Key Site for water voles, consisting of a diversity of interconnected habitats, including ponds, ditches and reed-beds. A novel method of mapping the vegetation of the wetland landscape was devised, using patches of vegetation classified according to the dominant vegetation type (DVT). The richness and abundance of DVT patches was used as an index of diversity at the habitat level. This provided a basis for describing the matrix habitat, which underpins the study of water vole ecology at the patch-landscape scale. The practical application of the DVT mapping approach allows the stages of wetland succession to be monitored, identifies areas of high biodiversity and provides a baseline on which to monitor the distribution and movements of animal species. Implementation of this method reduces time and the need for specialist field surveyors, thereby facilitating efficient management practices if applied at a national level. An intensive four year study of a metapopulation of water voles on eight adjacent ponds in the NWCW wetland reserve revealed an important insight into the dynamics of wild populations in complex, non-linear habitats. Multi-annual fluctuations in population densities were observed, characterised by a peak density phase and a low density phase. Density dependent juvenile dispersal was characteristic of the water vole population. Female water voles in diverse pond habitats maintained intra-sexually overlapping home ranges, uncharacteristic of this species. During the breeding season, water voles selected the ponds with the highest habitat diversity (assemblage of DVTs) but were typically associated with the least diverse DVT patches within the vegetation mosaic. Temporal plasticity in niche partitioning was observed both between genders and between individual female water voles at NWCW. During the winter, Bramble (*Rubus fruticosus*) was the most important dominant vegetation type, providing a source of cover and protection from predation. Water voles selected 23 plant species (and 3 non-plant species) as food. Soft Rush (*Juncus effusus*) a species with high nitrogen and calorific content was favoured particularly. The physical effects of water vole grazing and burrowing, combined with the large amounts of nitrogen-containing faeces deposited in latrines and underground burrows, has implications for wetland nutrient cycles. The effects of large scale vegetation clearance are described and holistic management recommendations are presented.

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List of animal species mentioned in the text

American mink	*Neovison vison*
Bank vole	*Myodes glareolus*
Barn owl	*Tyto alba*
Beach vole	*Microtus breweri*
Brown rat	*Rattus norvegicus*
Bush cricket	*Metrioptera bicolour*
Common frog	*Rana temporaria*
Common moorhen	*Gallinula chloropus*
Common toad	*Bufo bufo*
Eurasian otter	*Lutra lutra*
Field vole	*Microtus agrestis*
Grass snake	*Natrix natrix*
Great Bittern	*Botaurus stellaris*
Great crested newt	*Triturus cristatus*
Great pond snail	*Limnea stagnalis*
Grey heron	*Ardea cinerea*
Grey squirrel	*Scirius carolinensis*
Hazel dormouse	*Muscardinus avellanarius*
Lemming	*Lemmus lemmus*
Lesser Snow goose	*Chen caerulescens caerulescens*
Meadow pipit	*Anthus pratensis*
Meadow vole	*Microtus pennsylvanicus*
Montane vole	*Microtus montanus*
Muskrat	*Ondatra zebithicus*
Northern water vole	*Arvicola amphibius*
Pocket gopher	*Geomys bursarius*
Rabbit	*Oryctolagus cuniculus*
Red fox	*Vulpes vulpes*
River otter	*Lutra Canadensis*
Root vole	*Microtus oeconomus*
Southern red-backed vole	*Clethrionomys gapperi*
Southern water vole	*Arvicola sadipus*
Stoat	*Mustela erminea*
Townsend's vole	*Microtus townsendii*
Tree shrew	*Tupia belangeri*
Water shrew	*Neomys fodiens*
Water vole	*Arvicola amphibius*
Weasel	*Mustela nivalis*

List of plant species mentioned in the text

Alder, *Alnus glutinosa* (L.)
American Marram grass, *Ammophila breviligulata* (Fernald.)
Bird's-foot Trefoil, *Lotus corniculatus* (L.)
Black Poplar, *Populus nigra* (L.)
Bog Moss, *Sphagnum* sp. (L.)
Bramble, *Rubus fruticosus* (L.)
Broad-leaved pondweed, *Potamogeton natans* (L.)
Bulrush, *Typha latifolia* (L.)
Common Reed, *Phragmites australis* (Cav.)
Common Spike-rush, *Eleocharis palustris* (L.)
Compact Rush, *Juncus conglomeratus* (L.)
Creeping Bent-grass, *Agrostis stolonifera* (L.)
Creeping Buttercup, *Ranunculus repens* (L.)
Duckweed, *Lemna* sp. (L.)
False Fox-sedge, *Carex otrubae* (Podp.)
Field Thistle, *Cirsium arvense* (L.) Scop.
Fleabane, *Pulicaria dysenterica* (L.) Bernh.
Floating Sweet-grass, *Glyceria flutians* (L.)
Galingale, *Cyperus longus* (L.)
Greater Bird's-foot Trefoil, *Lotus pendunculatus* (Cav.)
Greater Pond-sedge, *Carex riparia* (Curtis.)
Greater Spearwort, *Ranunculus lingua* (L.)
Grey Club-rush, *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla.
Jointed rush, *Juncus articulatus* (L.)
Lesser Spearwort, *Ranunculus flammula* (L.)
Perennial Rye-grass, *Lolium perenne* (L.)
Reed Sweet-grass, *Glyceria maxima* (Hartm.) Holmb.
Sea club-rush, *Bolboschoenus maritimus* (L.) Palla.
Sheep's Fescue, *Festuca ovina* (L.)
Soft Rush, *Juncus effusus* (L.)
Stinging Nettle, *Urtica dioica* (L.)
Velvet Bent-grass, *Agrostis canina* (L.)
Water Mint, *Mentha aquatica* (L.)
Water Pepper, *Persicaria hydropiper* (L.) Spach.
Water Plantain, *Alisma plantago aquatica* (L.)
Willow, *Salix* sp. (L.)
Yellow Iris, *Iris pseudacorus* (L.)
Yorkshire Fog, *Holcus lanatus* (L.)

Abbreviations used in the text

ARC	Amphibian and Reptile Conservation
ANOVA	Analysis of Variance
BAP	Biodiversity Action Plan
Bg	Bare ground
C	Carbon
C: N	Carbon to nitrogen ratio
Ca	Calcium
$\mathbf{D_{DVT}}$	DVT Patch diversity
df	Degrees of freedom
Dg	Damp grassland
$\mathbf{D_{pond}}$	Habitat diversity
DVT	Dominant Vegetation Type
***Bm*DVT**	A patch of vegetation dominated by Sea Club-rush (*Bolboshcoenus maritimus)*
***Ca*DVT**	A patch of vegetation dominated by Field Thistle (*Cirsium arvense)*
***Cl*DVT**	A patch of vegetation dominated by Galingale (*Cyperus longus)*
***Cr*DVT**	A patch of vegetation dominated by Greater Pond-sedge (*Carex riparia)*
***Eh*DVT**	A patch of vegetation dominated by Willowherb (*Epilobium hirsutum)*
***Ep*DVT**	A patch of vegetation dominated by Spike-rush (*Eleocharis palustris)*
***Gm*DVT**	A patch of vegetation dominated by Reed Sweet-grass (*Glyceria maxima)*
***Jc*DVT**	A patch of vegetation dominated by Compact Rush (*Juncus conglomeratus)*
***Je*DVT**	A patch of vegetation dominated by Soft Rush (*Juncus effusus)*
***Rf*DVT**	A patch of vegetation dominated by Bramble (*Rubus fruticosus)*
***Tl*DVT**	A patch of vegetation dominated by Bulrush (*Typha latifolia)*
g	Gram
$\mathbf{gg^{-1}}$	Gram per gram
GIS	Geographic Information System
GPS	Global Positioning System
H'	Shannon diversity
Kg	Kilogram
K-S	Kolmogorov-Smirnov
Mg	Magnesium
MNA	Minimum Number Alive

N	Nitrogen
n	Sample size
NCC	Nature Conservancy Council
NH_4^+	Ammonium
nm	Nanometre
NO_3^-	Nitrate
NWCW	National Wetland Centre Wales
ORL	Observed Range Length (home range)
P	Phosphorous
PD	Population density per 100m
PIT	Passive Integrated Transponder
PO_4^{3-}	Phosphate
rpm	Revolutions per minute
SE	Standard Error
Sp.	Species
SWWARG	South and West Wales Amphibian and Reptile Group
UK	United Kingdom
USA	United States of America
v/v	Volume per volume
WWT	Wildfowl and Wetlands Trust
µg	Microgram
$\mu mol\ l^{-1}$	Micromoles per litre

Acknowledgements

This thesis has been the most challenging and rewarding endeavour that I have undertaken, and would not have been possible without the support of numerous people. At Swansea University I am forever indebted to my supervisors Dr Charles Hipkin and Dr Dan Forman. Thank you Charles, for inspiring my love of plant biology, for being patient and for keeping me on the edge of Occam's razor (!) Thank you Dan, for giving me the opportunity to study water voles and for being a constant source of enthusiasm, support, friendly advice and coffee. To my good friend Dr Laura Roberts, who has tread every step of this journey with me, since we started our undergraduate studies in 2003, thanks for advice on statistics, for the endless cups of tea and for knowing what to say and when. Also thanks to Dr Gareth Parry, for useful help and advice whenever necessary. A big thanks to everyone that helped with chemical analysis; Dr Kath Ficken, Dr Ingrid Lupatsch and Dr Purazen Chingombe. Thanks also to Dr Geoff Proffitt, not least for designing the wetland reserve home to the water voles in this study, but also for useful information regarding the site history. The help of Jean Leamon, Maureen Roberts and Sarah Walmsley during laboratory work was indispensible; thanks ladies for access to laboratories, glassware and lessons in filter paper origami (!)

Many thanks to everyone that helped with field work, in particular Dr Clive Hurford and Dan Guest at the Countryside Council Wales, for their assistance with vegetation mapping. Thanks also to Dan Guest for teaching me the joys of Mapinfo and helping me to create the habitat map. I am honoured to have been invited to write a chapter in a book (Conservation Monitoring in Freshwater Habitats) edited by Dr Clive Hurford and Dr Michael Schneider. Writing that chapter kick-started the remainder of this thesis, so I am grateful for the opportunity and the impetus. Thanks also to Dr. Michael Schneider for sending me a copy of his PhD Thesis from Sweden. Thanks to the National Wetland Centre Wales, for supporting this project and allowing continued access to the site. I hope this thesis is useful can be implemented in their future management plans.

I dedicate this thesis to my husband-to-be, Dean, for his continued love and support, for making sure the children were fed, clothed and in school on time, for ensuring water voles were warm in their traps during winter trapping, for all the laughter and for generally keeping me sane. Love and a big thank you to my beautiful daughters, Jordan and Robyn, for their patience during the long years I have spent in the field and writing up and also for asking the right questions (Why *is* bramble so spiky?). This thesis is also for you. Many thanks also to the rest of my family, Mum, for always being there, my sister Lindsay, my brother Ben and sister-in-law Al, for providing welcome distractions when necessary, not to mention wine (!) Finally, I would like to thank the water vole, a most endearing creature with which I have taken the most unforgettable journey. Long live Ratty, and not just on our bookshelves!

Introduction

'As he stared before him into the dark hole, some bright small thing shone and twinkled in it depths, moving towards him. A face grew up around it, a familiar face! Brown and small, with whiskers. Grave and round, with neat ears and silky hair. It was the Water Rat!'

Kenneth Graeme (The Wind in the Willows, 1908)

1. Habitats to Ecosystems

Habitats and plant communities

In most terrestrial habitats, vegetation is the most obvious physical representation of an ecosystem. Major distinctions can be made on the basis of physiognomy (growth form) of the vegetation, with more subtle changes in the landscape evident in variations of colour (reflecting differences in plant species composition) between different areas of vegetation with similar physiognomy (Kent & Coker, 1992). A habitat is the resources and conditions present in an area that produce occupancy for a species (Fischer & Lindenmayer, 2007). Habitats may be described at various levels, as phase 1 broad habitat types (e.g. wetland) or in terms of the phase 2 community types (e.g. S19, *Eleocharis palustris* swamp) that they contain (Rodwell, 1995). Plant communities are dynamic in nature, particularly in seasonal environments. Over time, community composition will change according to the principles of succession, ultimately reaching a climax community, typically dominated by woodland in temperate climates (Kent & Coker, 1992; Cronk & Fennessy, 2001). Since plants (as primary producers) represent the basal component of most ecosystems, they represent the logical place to begin any detailed ecological study (Loreau *et al.*, 2001).

Ecological Wetland Succession

Succession is the continuous change in the species composition of natural communities (Morin, 1999) and is the fundamental process of landscape dynamics (Hutson, 1994). Changes in community structure may occur for a number of reasons, including internal processes of species competition and herbivory or external processes such as natural or anthropogenic disturbances (Cronk & Fennessey, 2001). The hydrarch model of ecological succession describes wetlands as a seral community in the succession of an open water lake to a terrestrial community (Lindeman 1941; Gates 1942; Conway 1949). However, given the propensity of wetlands to periodic flooding, succession can stop short of the upland woodland climax community and, instead, develop into a wet forest (Weller, 1994). This has been observed in glacial lakes (Heinselman 1963; 1975), oxbow lakes (van der Valk & Bliss, 1971), bogs (Damman & French, 1987) and other wetland systems (Mitsch & Gosselink, 2000). Since plants are the dominant organisms on most landscapes, both visually and functionally, plant succession is the dominant biological process that affects landscape patterns of biological diversity (Hutson, 1994).

The importance of scale: from patches to landscapes

The spatial configuration of high quality and low quality habitats creates a mosaic of habitat patterns in natural landscapes (Collins & Barrett, 1997). High quality habitat patches for small mammals include both high quality food resources and adequate vegetative cover (Birney *et al.*, 1976; Ostfeld, 1985; Ims, 1987; Collins & Barrett, 1997). These areas are termed environmental resource patches and are distinct from the surrounding habitat, termed a matrix (Forman & Godron, 1981). The measurement of landscape characteristics is scale-dependent (Levin, 1992). In a patch-landscape scale study, the patch is the experimental unit, but independent variables include landscape structure within a specified neighbourhood distance surrounding the patch (McGarigal & Cushman, 2002). A landscape is a human-defined area ranging in size from c. $3km^2$ to c. $300km^2$ (Fischer & Lindenmayer, 2007). Fragmented landscapes are characterised by a strong contrast between native vegetation patches and their surrounding matrix (Mortelliti *et al.*, 2010).

Europe is one of the most ‘fragmented’ continents in the world, and as a consequence, habitat loss and fragmentation are the greatest threat to European mammals (Temple & Terry, 2009) as well as the main causes of biodiversity loss worldwide (Foley *et al.*, 2005). A recent review (Mortelliti *et al.*, 2010) revealed that progress in the study of the effects of these processes has been hampered for several reasons. These include a large predominance of small-scale field studies of short duration and a lack of meta-analyses due to crucial details not included in the publications, such as information on spatial scales and the landscape context.

Biodiversity and ecosystem functioning

During the last decade, the relationship between biodiversity and ecosystem functioning has emerged as a central issue in ecological and environmental sciences (Loreau *et al.*, 2001). The importance of biodiversity led to the designation of 2010 as the International Year of Biodiversity by the United Nations (Pacheco, 2010). Species diversity consists of both species richness and abundance (Magurran, 1988). Although species richness is easier to measure, a more predictive science might be achieved if more appropriate functional classifications were devised (Hutson, 1994; Grime, 2001). The majority of animal species probably do not perceive landscapes as binary (habitat versus non-habitat) but rather as a continuum of habitats with different levels of suitability (Mortelliti *et al.*, 2010). More effort should be made in applying standard approaches for the measurement of vegetation cover or structure (Hill *et al.*, 2005).

Grazers and ecosystems

Competition and herbivory are two of the main forces shaping plant communities (del Val & Crawley, 2005). Grazers can have important consequences for ecosystem functioning, not least through the direct effects of grazing on plant community structure (McNaughton, 1979; Howe, 2008), but also indirectly through the deposition of nitrogen rich faeces, which has consequences for nutrient cycling (Holland & Detling, 1990; Ben-David *et al.*, 1998; Sirotnak & Huntly, 2000). Disturbances such as herbivory and trampling by mammals may help maintain plant species richness by reducing total plant biomass and preventing competitive exclusion of the less competitive species (Connell, 1978).

2. Rodent Ecology

Cyclic population dynamics

Small mammal populations can sometimes reach plague proportions, after which a population crash is observed. In Britain, microtine rodents such as field voles (*Microtus agrestis*) and bank voles (*Myodes glareolus*) typically show these fluctuations in a cyclical fashion, with periodic peaks at 3 to 5 year intervals and times of decline, relative scarcity and increase in the years in between (Flowerdew, 1993). Many rodent populations show extensive density fluctuations on a multiannual basis (Krebs & Myers, 1974; Hansson, 2002). In simple arctic and boreal ecosystems, cyclic population dynamics are driven by predation (Gilg *et al.*, 2003) and primary production (Ekerholm *et al.*, 2004). In the more complex temperate ecosystems of western Europe, population cycles are influenced by the combined action of a hierarchy of many regulating factors, both spatially and temporally (Lidicker, 2000; Hansson, 2002).

In upland regions of Europe water vole (*Arvicola amphibius*) populations fluctuate widely, where periodic outbreaks move in waves from epicentres, devastating orchards, grasslands and young tree plantations (Giradoux *et al.*, 1997). Population cycles last six to seven years (Weber *et al.*, 2002) with alternating phases of low density and outbreaks, the latter of which can last two to four years (Saucy, 1994) causing severe damage and economic losses (Delattre *et al.*, 2006). Water voles in Western Finland exhibit eight to ten year population cycles, which operate independently from the dominant three year *Microtus* and bank vole cycles in the area (Korpimäki *et al.*, 2005).

Factors that constrain small mammal populations

There are typically two mechanisms that operate to constrain small mammal populations, namely predation and food availability, although both may operate at different levels and times of the year. Climatic factors can also have a strong influence. Predators appear to have at least temporary detrimental effects on small rodent densities at the community level, and the effects of predation can result in synchronisation of the low phases of population cycles of all small mammal species in the community (Korpimäki *et al.*, 2005). Predation can be viewed as a top down control mechanism that constrains numerous vole populations. Indeed, vole cycles in Scandinavia are caused by the interactions between voles and their specialist predators, namely stoat (*Mustela erminea)* and weasel (*Mustela nivalis)* (Hanski *et al.*, 1991; Schneider, 2000). In contrast to these processes, forage availability or habitat quality is a plausible bottom up control mechanism that may contribute to population cycles.

Large scale spatially synchronous population dynamics provide an excellent opportunity for distinguishing between local intrinsic and regional extrinsic mechanisms of population regulation. Large scale survey data and theoretical modelling indicate several plausible synchronising mechanisms; however data on local demographic processes is required to determine the most important processes (Ims & Andreassan, 2000). Intra-specific competition will also have internal effects on population control and knowledge of the effects of these processes will be a valuable contribution to population models. Inter-specific competition may have numerous effects depending on the species concerned. For example, interactions between brown rats and water voles are very different to those between water voles and field voles. A rat may have a negative impact on water voles through direct predation, whereas a field vole may compete for space or even attract other predators, for example avian predators or foxes.

Metapopulations and source-sink dynamics

The term metapopulation is typically applied to a system of local populations, in which even the largest population may be prone to extinction. However, in a dynamic, sustainable metapopulation structure, the rate of extinction is balanced by recolonisation (Levins, 1970; Hanski, 1991). In many applications of the concept, the metapopulation consists of a larger core population that functions as the main source of emigrants to smaller satellite populations. In this instance, source-sink dynamics apply (Pulliam, 1988) which are akin to mainland-island metapopulations (MacArthur & Wilson, 1967; Harrison *et al.*, 1988). Source-sink dynamics are applicable to a large or high quality habitat patch supporting a large population (source) with no extinction risk, while the smaller populations (sink) are dependent on immigration from the source population (Pulliam, 1988).

A metapopulation approach is often adopted in the study of many insect species (e.g. butterflies; Harrison *et al.*, 1988; Hill *et al.*, 1996). Indeed, the importance of the location and size of habitat patches on dynamics of bush crickets (*Metrioptera bicolor)* has been previously illustrated (Kindvall & Ahlen, 1992), whereby patterns of occupancy are directly related to the characteristics of habitat patches (Kindvall, 1996). Water vole population dynamics are governed, typically, by the processes of extinction and recolonisation and therefore a metapopulation approach is appropriate for studying this species (Telfer *et al.*, 2001).

Mammals: territory and home range

Home range is the area, usually around a home site, over which an animal normally travels in search of food (Stoddart, 1979). Territory is the protected part of the home range, be it the entire home range or only the nest. Every kind of mammal may be said to have a home range, stationary or shifting. Only those that protect some part of the home range, by fighting or aggressive gestures, from others of their kind, during some phase of their lives, may be said to have territories (Burt, 1943). All small mammals have a home range which may be communal (with a social hierarchy); individual home ranges which overlap those of others and individual territories which are mutually exclusive and defended areas (Flowerdew, 1993).

The spatial organisation of individuals in populations has important consequences for ecological processes such as population regulation, competition and mating systems. In many mammalian species, females compete with each other for food and space to raise offspring, while males compete for access to females (Wolff & Peterson, 1998). The use of space by small mammals is usually described in two dimensions although it occurs in three dimensions, particularly in species such as the harvest mouse, which makes use of tall plants (Flowerdew, 1993) or indeed the water vole which utilises a three dimensional world of underground burrow systems.

3. Water vole (Arvicola amphibius)

General introduction to water voles

The water vole (*Arvicola amphibius)* (synonym *Arvicola terrestris*, Linnaeus, 1758) is a rodent of the sub-family Arvicolinae, along with all other voles, lemmings and muskrats. Two species of water vole are currently recognised. These include the northern water vole (*Arvicola amphibius*) in Britain and throughout Europe to Russia, and the southern water vole (*Arvicola sadipus*) in SW Europe (Wilson & Reeder, 1993). The water vole is the largest of the British voles, adults weighing 140-350g, with males normally larger than females (Strachan & Moorhouse, 2006). In Britain, water voles were formerly widespread and common, ranging from Cornwall to the extreme NE Scotland. Water voles are absent from the Isle of Man and the Scottish islands, but occur on Anglesey and the Isle of Wight (Corbert & Harris, 1991).

The British distribution of water voles stemmed from two separate colonisation events following the last ice age (Strachan & Moorhouse, 2006). Scottish water vole populations are derived from an Iberian glacial refugium and are genetically similar to water voles in France, Spain and Switzerland. In contrast English and Welsh water voles were derived from a different refugium in Eastern Europe and are genetically similar to water voles in Finland. Consequently, although all British water voles are the same species (*Arvicola amphibius*), Scottish water voles are genetically dissimilar to English and Welsh water voles (Piertney *et al.*, 2005). Further background biology and general characteristics of water voles are outlined in Strachan & Moorhouse (2006).

The water vole displays remarkable ecological plasticity throughout its European range. In stark contrast to their common name, water voles adopt a fossorial (underground dwelling) lifestyle in many regions of mainland Europe, in which the presence of water is not a defining factor in their distribution (Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006). There, water voles inhabit mountainous terrain and grassland habitats and are regarded a serious pest species of vegetable root crops in some regions (Giradoux *et al.*, 1997; Morilhat *et al.*, 2008). In contrast, the distributions of water vole populations in Britain (the species is absent from Ireland), the Netherlands and parts of Spain and France are closely associated with wetland habitats providing suitable opportunity for burrowing and abundant structured riparian vegetation (Woodall, 1993; Carter & Bright, 2003; Strachan & Moorhouse, 2006; Moorhouse *et al.*, 2008).

Alarmingly, over the last 100 years the British water vole population has undergone a dramatic and widespread decline (Jefferies *et al.*, 1989; Strachan & Jefferies, 1993) and the species is currently a priority Local Biodiversity Action Plan (LBAP) listed species of significant conservation concern in Wales, England and Scotland (Strachan, 1998; Strachan & Moorhouse, 2006).

Early history of the water vole in Britain

Historically, water voles were widespread throughout Britain and once regarded as a familiar waterside mammal (Strachan & Jefferies, 1993). Vast quantities of *Arvicola amphibius* teeth discovered among bone-cave deposits among the sub-fossil record imply that this species was formerly extremely abundant (Yalden, 1977, 1982; Andrews, 1990). Fossils of *Arvicola amphibius* dating back to Mesolithic times, suggest early British water voles adopted a more terrestrial lifestyle (Yalden, 2006) similar to their European counterparts (Saucy, 1994; Giradoux *et al.*, 1997). Indeed, it is interesting to speculate that before the arrival of rabbits (*Oryctolagus cuniculus)* by introduction during Norman times c. 900 years ago (Sterry, 2005) and man's domestic livestock, the vole community may have been the dominant grazers in Britain, especially at upland sites (Strachan & Jefferies, 1993).

Recent history of the water vole in Britain

The subsequent history of the water vole in Britain has largely been governed by the activities of man changing and managing the environment (Strachan & Jefferies, 1993). Recently, research undertaken by the Vincent Wildlife Trust (VWT) and the Environment Agency (EA) has clearly shown that the number of sites historically occupied by water voles is reducing significantly in all regions of Britain, with a 94% loss last century (Jefferies *et al.*, 1989; Strachan & Jefferies, 1993). In 1990, the total pre-breeding population of water voles in Britain was estimated at 7.3 million, while the estimate for 1998 suggested a total population of 875,000, a further loss of 88% in less than a decade (Strachan *et al.*, 2000). Surveys during 2002 have suggested that the decline appears to have slowed, but the total population varies between 200,000 and 500,000 across its entire British range (Strachan, 2004). This makes the water vole Britain's most rapidly declining mammal and as such, it has been given a high priority on the conservation agenda.

The factors that have driven this alarming decline, in what was previously a relatively common mammal in Britain, are complex and poorly understood. However, it is generally agreed that modification and loss of wetland habitats, coupled with the active predation of water voles by feral populations of American mink (*Neovison vison*) are significant determining factors in the widespread decline of water voles (Woodroffe *et al.*, 1990a; Macdonald & Strachan, 1999; Strachan & Moorhouse, 2006). Interestingly, during the 1970s and 1980s plagues of brown rats were abundant, particularly along many waterways (Strachan & Jefferies, 1993). This species has previously been reported to predate on juvenile or nestling water voles and even cause local extinctions (Ryder, 1962; Leuze, 1976; Stoddart, 1971). More recently the aversion of water voles to the odours of rats has been studied (Barreto & Macdonald, 1999) however, the effect of rats on water vole populations on ponds or in Wales has never been studied.

Since the plight of the water vole in Britain was recognised and highlighted, significant effort has been invested in the identification and monitoring of local populations by a wide range of statutory and non-statutory organisations (Strachan & Moorhouse, 2006). In addition, a considerable amount of autecological research has been conducted on water voles, predominantly on populations inhabiting linear wetland habitats, such as rivers, ditches and canals. This research has revealed important insights into how water vole populations behave at both the local and the broader landscape level (e.g. Bonesi *et al.*, 2002; Telfer *et al.*, 2003) and into the relationship between water vole distribution, population density, different vegetation community types and American mink (e.g. Woodroffe *et al.*, 1990a; Lawton & Woodroffe, 1991; Rushton *et al.*, 2000; Moorhouse & Macdonald, 2008; Moorhouse *et al.*, 2009). This and other ongoing work is beginning to provide the information and tools necessary to successfully monitor, appropriately manage and safeguard the remaining British populations of water voles, with the ultimate aim of restoring this important species to as much of its former range as possible.

Distribution of water voles in Britain at the landscape level

Distribution is the pattern, or mosaic, of occupation of suitable habitats by a group of individuals, and is a group attribute related to the pattern of overlap of the individual ranges of the members of the group (Stoddart, 1970). Distributional patterns of water voles reflect fundamental ecological processes (Macdonald & Rushton, 2003). Water vole populations in Britain are known to show different levels of fragmentation and one might expect them to be characterised by different dynamics (Bonesi *et al.*, 2002).

Where populations are fragmented as a result of the nature of the habitat, water voles have been shown to be organised as a metapopulation (Aars *et al.*, 2001; Lambin *et al.*, 2004). In other areas, the distribution of water voles is less fragmented and can be clumped (Woodall, 1993) or nearly continuous (Stoddart, 1970; Macdonald & Strachan 1999). Water vole colonies are located along waterways in Britain and are typically sub-divided in discrete colonies comprising a few individuals (Lawton & Woodroffe, 1991). Larger, seemingly continuous populations are also found along some lowland rivers in England where predator control is intense, suggesting that such continuous distribution was more prevalent prior to the recent decline (Aars *et al.*, 2001).

Water vole habitat preferences

On a local scale, the water vole's main requirements are good sources of food including tall grasses, reeds, sedges and aquatic vegetation (Zejda & Zapletal, 1969; Woodall, 1977; Lawton & Woodroffe, 1991; Barreto *et al.*, 1998a; Lambin *et al.*, 1998) and steep banks for burrowing made of uncompacted soils (Zejda & Zapletal, 1969; Lawton & Woodroffe, 1991; Lambin *et al.*, 1998). On a regional scale, the best water vole habitat is found at low altitude on chalk and limestone rivers (Woodall, 1977), typically characterised by suitable vegetation and rich soils (Bonesi *et al.*, 2002). Factors such as rocky or otherwise impenetrable substrates, over-shading by trees and fast flowing or shallow water are inimical to water voles (Strachan & Moorhouse, 2006). In addition to habitat characteristics, the presence of water vole colonies is also associated with predator distribution and the proximity of neighbouring colonies (Lawton & Woodroffe, 1991; Macdonald & Strachan, 1999; Barreto *et al.*, 1998b; Telfer *et al.*, 2001; Bonesi *et al.*, 2002).

Water vole life expectancy and survival

Even in the absence of American mink, water voles typically experience high predation rates and are foraged upon by a variety of mammalian and avian British predators, including red foxes (*Vulpes vulpes*) and barn owls (*Tyto alba*) (Strachan & Jefferies, 1993; Forman, 2005). Their anti-predator behaviour includes running to their tunnel system and diving under water and kicking up a screen of sediment (Strachan & Moorhouse, 2006).

In exceptional circumstances water voles may survive three winters, however, the majority of individuals survive fewer than two (Strachan & Moorhouse, 2006). High over-winter mortality rates (up to 70% of the population) are characteristic of the species (Stoddart, 1970; Macdonald & Strachan, 1999; Carter & Bright, 2003), especially among dispersing juveniles (Strachan & Moorhouse, 2006).

Water vole home ranges

Home ranges of water voles in the majority of habitats in the UK comprise a narrow (1 to 2 metres) width of habitat over a much greater length (Stoddart, 1970; Lawton & Woodroffe, 1991; Barreto *et al.*, 1998a; Macdonald & Strachan, 1999; Strachan & Moorhouse, 2006). Measurements of water vole ranges are therefore often considered in terms of length of occupied habitat, rather than area (Stoddart, 1970) due to the typically linear nature of above ground occupancy in this species (i.e. the activities that we, the observer, can monitor, occur in a linear fashion along the bankside of the water course). Exceptions to this are habitats such as large reed beds, where water vole ranges tend to be more two dimensional, and therefore best described as an area (Strachan & Moorhouse, 2006). The sizes and juxtaposition of home ranges will depend on the availability and dispersion of resources within the landscape and the presence of competitors and predators. Furthermore, home ranges are inevitably dynamic, in that they are determined by variables that are themselves in flux (Macdonald & Rushton, 2003).

Water vole territoriality and social behaviour

Female water voles are territorial with small, non-overlapping ranges, typically intra-sexually aggressive and often arranged in contiguous territories along the bankside (Pelikan & Holisova 1969; Stoddart, 1970; Strachan & Moorhouse, 2006). In contrast, the home ranges of male water voles are larger (Stoddart, 1970; Strachan & Moorhouse, 2006; Moorhouse & Macdonald, 2008), often overlapping with each other and may overlap the range of several females (Stoddart, 1970; Strachan & Moorhouse, 2006; Moorhouse & Macdonald, 2008). Males are typically considered to be non-territorial (Moorhouse & Macdonald, 2005), however sexually mature males can be aggressive and engage in conflict over access to females (Forman & Brain, 2006).

Increasing our understanding of behaviour is likely to prove important in the long-term recovery of any endangered vertebrate species (Gosling & Sutherland, 2000). Data that provide insights into social interactions should be taken into consideration when planning and managing captive breeding and reintroduction programmes, which are increasingly being implemented in England and Wales (e.g. Moorhouse & Macdonald, 2005; 2008; Environment Agency, pers. comm.) in the attempt to restore the water vole to the wider countryside, in accordance with the UK Biodiversity Action Plan (UKBAP). Environmental conditions and social stress can influence patterns of biting attack in water voles. These aspects of water vole ecology clearly require further investigation if refinements to husbandry techniques in this species are to be made in order to promote 'normal' behaviour in individuals destined for reintroduction programmes (Forman & Brain, 2006).

Water vole latrines

The boundaries of water vole territories are demarked with latrines (aggregations of faecal pellets) (Stoddart, 1970; Woodroffe *et al.*, 1990b; Strachan & Moorhouse, 2006) that are regularly maintained by females (Stoddart, 1970) on which males counter-mark scent as a means of communication (Woodroffe *et al*, 1990b; Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006). Water vole droppings (faeces) are a very distinctive field sign. Droppings may be scattered along runways, but most are usually deposited at discrete latrine sites near the nest, at range boundaries and where water voles enter and leave the water.

Latrines are typically maintained throughout the breeding season and consist of flattened piles of older droppings topped with fresh ones (methodology, figure 5). Territory holding females scent-mark latrines by stroking their hind-feet across lateral scent glands (on the flank) and then drumming them on the latrine (Strachan & Moorhouse, 2006). The presence of drum-marked latrines is indicative of breeding females. Woodroffe *et al.* (1990b) estimated approximately six latrines per adult female holding a territory, although this figure was later corrected and Morris *et al.* (1998) suggested an approximate one to one relationship between the number of latrines and the number of water voles.

Water vole foraging behaviour

Water voles have diverse dietary preferences, and in Britain alone they may consume any one of 227 different plant species (Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006). The diversity of the British water vole diet reflects both the wide geographic distribution and broad diversity of habitats once occupied by this species in Britain (Strachan & Jefferies, 1993). Furthermore, the complex plant communities found within riparian habitats provide a wealth of food and shelter for an opportunistic forager such as the water vole (Strachan & Moorhouse, 2006). Water vole foraging behaviour can greatly shape the riparian corridor through the physical action of grazing, reducing competition between plants species thus increasing the biodiversity wetland plant communities

(Forman *et al.*, 2008). Indeed, the water vole may be helpful (where it still persists) in keeping our waterways flowing freely by clearing them of weeds, reeds and rotting vegetation (Ryder, 1962).

One obvious and extremely useful feature of water vole ecology is their regular use of food caches. Water voles actively gather and arrange vegetation in discrete feeding stations (methodology, figure 5). These are usually located in safe places such as under the drooping fronds of tall emergent vegetation, along vole runways or at haul-out platforms along the waters edge. They can be a useful indicator of the presence (but not abundance) of water voles in an area (Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006). Detailed knowledge of water vole diet and foraging behaviours are essential to provide a strong evidence-base to ensure appropriate housing conditions for captive animals, to allow the selection of correct plant species when designing and creating new water vole habitats, and to ensure that sufficient diversities and densities of plants remain available to water voles during the active management of existing habitats (Forman *et al.*, 2008).

Water vole dispersal strategies

Dispersal is the active process of individual movement that results in a change of a population's distribution pattern. It is an important population process influencing the spatial organisation of the group, since any permanent or semi-permanent shift of range by any individual will cause a certain degree of reorganisation of territory tenure within the group (Stoddart, 1970). Dispersal facilitates gene flow and influences both the demography and stability of patchily distributed populations (Hanski & Gyllenberg, 1993) and has important consequences for metapopulation structure. Dispersal may involve short or long distance movements and different mechanisms. It is a fundamental ecological and evolutionary process, the prevalence and scale of which determine colonisation ability and the contribution of immigration to population dynamics (Telfer *et al.*, 2003).

Typically, water voles are sedentary and may displace to the next available habitat (if the necessary habitat corridors are present), however, certain individuals (in Scotland) have been observed to travel several miles (up to 5.2 km) overland (Telfer *et al.*, 2003). Dispersal may occur because the habitat is already saturated and no further territories are available or simply because territorial females drive out juveniles (Forman & Brain, 2006).

A note on American mink

Predation of water voles by American mink (*Neovison vison*) has been widely publicised (Woodroffe *et al.*, 1990a; Strachan & Jefferies, 1993; Barreto & Macdonald, 2000; Aars *et al.*, 2001; Macdonald & Harrington, 2003; Strachan & Moorhouse, 2006). The American mink is an invasive species in the UK and a threat to the endangered water vole (Woodroffe *et al.*, 1990a; Macdonald & Strachan, 1999). Mink control projects have been implemented in certain areas where water vole populations have been impacted (Reynolds *et al.*, 1994). Typically, mink rely on mature willows (*Salix* sp.) and pollarded trees for den sites (Mason & Macdonald, 1986), while water voles prefer areas with low tree cover and high emergent vegetation cover (Lawton & Woodroffe, 1991; Strachan & Jefferies, 1993). Although American mink have been known to devastate water vole colonies, this typically occurs on major river systems. In many areas active mink control is the only possible strategy to promote the conservation of the water vole (DoE 1995; Macdonald & Strachan, 1999).

Since mink tend to operate on main river channels (Strachan & Moorhouse, 2006), water vole populations inhabiting linear wetland corridors are subject to a higher predation pressure. However, the tightrope hypothesis predicts that mink and water voles are more likely to coexist if they are freed from the linear constraint of a narrow swathe of bankside vegetation that characterises many British rivers (Barreto *et al.*, 1998b). For example, water voles and mink are sympatric along the Rivers Kennet and Coln (tributaries of the River Thames, London Basin), where both species co-exist (Birks, 1986). Indeed, large water vole populations have persisted at some reed-bed sites (Stodmarsh National Nature Reserve, Kent) where mink have been present for over 30 years (Carter & Bright, 2003). Healthy populations of water voles also exist in the presence of mink in Tregaron Bog, Cors Caron National Nature Reserve, Wales (Strachan & Jefferies, 1993). Mink were active at NWCW, their presence confirmed by observation of both field signs (scat) and occasional sightings, however, the effect of mink on water voles at NWCW was beyond the scope of this study (chapter 2).

4. Water vole conservation and management

Water voles - threats and conservation measures

One of the major factors responsible for the decline of water voles in the last century is habitat loss, resulting from a change of land use practices (Strachan & Moorhouse, 2006). Prior to 1940, one third of the farmland in the UK was covered by rough semi-natural vegetation used for extensive cattle grazing (Parry *et al.*, 1992). Since then, intensive agricultural practices have progressively subjected the semi-natural vegetation along rivers favoured by water voles, to a change in both land use and intensity (Rushton *et al.*, 2000). Fragmentation of the semi-natural river vegetation through intensification of agricultural land adjacent to rivers has negative effects on water vole populations (Strachan & Jefferies, 1993); Barreto *et al* 1998a).

Recently, numerous habitat enhancement and restoration projects, including the linking of colonies have been undertaken as a response to the widespread loss of water vole populations Britain. In managing flood risks, many watercourses have been modified in the past, in order to improve their capacity to store and carry flood water. Waterway channel, bankside, water level and vegetation management all have consequences for water voles (Strachan & Moorhouse, 2006). With the current plight of the water vole highlighted, and recent legal inclusions enforcing protection to this species, habitats are managed sympathetically, with numerous projects being undertaken nationwide to ensure habitat enhancement and restoration (Kennet and Avon Canal), wetland pond creation and management (River Don, Doncaster), restoration of flows to dry water courses (River Ver, Hertfordshire) and ditch management in the uplands (Peak District) (see Strachan & Moorhouse, 2006).

Across Britain, 16 National Key Sites for water voles have been identified (including the National Wetland Centre Wales, NWCW) and are subject to conservation management (Strachan & Moorhouse, 2006). Due to the high degree of fragmentation of the national water vole population, restoration of this species to the wider countryside has been underpinned by reintroduction of individuals from captive bred populations (Strachan & Moorhouse, 2006). Numerous reintroduction programmes are being undertaken on English river systems and the release cohorts monitored. These provide important information regarding growth and maturation rates of released water voles (Moorhouse *et al.*, 2008) together with the effects of habitat quality on reintroduction success (Moorhouse *et al.*, 2009).

Current techniques used to monitor water vole populations

The most widely used technique to monitor the activity of water voles is the standardised transect survey in which the presence or absence of distinctive field signs (including food caches, burrows, footprints, and perhaps more reliably, faeces and latrines) are recorded over a defined distance of wetland edge (see Strachan 1998, Strachan & Moorhouse 2006). Live capture and release programmes (under controlled and licensed conditions) can also provide an extremely valuable and detailed source of population-level data. These techniques have recently been used by Oxford University to study several water vole introductions (Moorhouse *et al.,* 2008, 2009). Over time this approach can provide information on the number of animals present, their respective range sizes and movement patterns in different water vole populations.

Persistence of extant water vole populations

If a colony of water voles is to survive then it requires habitat corridors providing connectivity to other suitable patches in order for both the dispersal of the offspring of these highly fecund rodents and immigration of new individuals into the colony (Telfer *et al.*, 2001). Gene flow by dispersal influences the genetic structure of populations and consequently modifies the effects of genetic drift and selection (Ims & Yoccoz, 1997; Telfer *et al.*, 2003). This will maintain the genetic diversity and prevent the effects of inbreeding such as population bottlenecks and the founder effect, both of which reduce heterozygosity of the population leading to compromised Darwinian fitness. If the corridors are available or provided between suitable patches then natural recolonisation will occur, assuming there are extant colonies in the vicinity (Telfer *et al.*, 2001).

In addition to these essential habitat corridors, persistence also depends on the integral quality of the habitat. The need for the best obtainable habitats has been highlighted (Moorhouse *et al*, 2009), however we must ask the question what makes the best habitat obtainable? Broad habitat classifications for water voles have already been made, (Lawton & Woodroffe, 1991; Woodall, 1993; Strachan & Moorhouse, 2006); however it is now essential to identify those plant species or vegetation types that can sustain high population densities and a continuous turnover of populations.

Evidence-based conservation

The need for an evidence-based framework to evaluate effectiveness and support decision-making in conservation has been previously highlighted (Pullin & Knight, 2001; Fazey *et al.*, 2004; Sutherland *et al.*, 2004). The problems of environmental change and biodiversity loss have entered the mainstream political agenda. Consequently the need for creating a 'Collaboration for Environmental Evidence' that develops a library of systematic reviews on the effectiveness of conservation and environmental interventions has arisen (Pullin & Knight, 2009). Although manipulative experiments and computer modelling are useful in the study of European mammals, observational studies are essential to maximise inference to the real world, which is crucial if conservation action is necessary (Mortelliti *et al.*, 2010). Map-based approaches are often useful in identification of key areas for both management and monitoring (Hurford, 2010).

Implementation of monitoring data to advise management practices

Over time, wetland habitats occupied by, and linking, water vole populations have slowly been lost or degraded (Barreto *et al.*, 1998a). In many cases this progressive fragmentation has resulted in water vole populations becoming isolated from one another by a variety of physical barriers including roads, railways, residential developments, flood defences and other inhospitable environments. As remaining water vole populations gradually become more isolated from one another, the risk of localised colony extinctions increases and the probability of successful recolonisation from extant populations decreases, ultimately destabilising metapopulation structures (Aars *et al.* 2001; Fahrig, 2003; Telfer *et al.* 2003).

The purpose of this study was not to discuss the effects of habitat loss and fragmentation, as the effects of these processes on water voles have been previously demonstrated. Primarily, and from the outset, the aim of this study was to describe and map the extent of water vole habitat in the NWCW wetland complex, using a novel, vegetation-based sampling approach, which is described in Chapter 1. The remainder of this thesis used this sampling method to focus on the following aspects of water vole ecology; population densities (chapter 2); social behaviour (chapter 3); habitat utilisation (chapter 4); foraging choices and their consequences on the wetland environment (chapter 5). Finally, all these aspects were drawn together to provide a holistic interpretation of water vole ecology at the patch-landscape scale. This allowed the provision of evidence-based recommendations for the future conservation of water voles, including the creation of site-specific condition indicator tables to assess the status of existing water vole habitats and aid in the creation of new habitats. Additionally, management practices currently employed by NWCW were reviewed and future holistic management recommendations are presented (chapter 6).

5. Outline of Chapters

Chapter 1 Habitat

In Chapter 1 the wetland landscape was quantified using a vegetation based sampling approach to create a dominant vegetation type (DVT) map. This provided a basis for describing the matrix habitat which underpins the study of water vole ecology at the patch-landscape scale. Additionally, this allowed ponds to be classified according to their diversity, at both the individual patch (DVT) and the habitat (pond) level. Furthermore, this method of mapping the vegetation, using dominant vegetation types (DVT) offers an alternative to Phase 1 mapping, which adds detail at the patch level, minimises observer variation and can be achieved with minimal botanical knowledge. Details pertaining to the size and extent of each habitat and DVT type are also presented.

Chapter 2 Water vole Population Ecology

Chapter 2 described water vole population densities, survival and recruitment of a metapopulation of water voles on a non-linear wetland pond system, during both the breeding season and the winter. Spatial and temporal variations in habitat occupancy by water voles were identified. Density-dependent effects on juvenile recruitment and dispersal are also discussed. Resident adult water voles that established a home range were identified. The weights of resident adults are also presented.

Chapter 3 Water vole Social Ecology

Chapter 3 determined home range lengths of all resident adult water voles during both the breeding season and the winter in non-linear water vole habitats. The relationship between home range lengths and population densities was explored. The effect of water vole weight on home range length is described. Home range overlaps of water voles on non-linear pond systems are presented. Agonistic behaviour (inferred from bite wound patterns) is also discussed.

Chapter 4 Water vole Habitat Utilisation

Chapter 4 identified vegetation types that were important to water voles during both the breeding season and the over-wintering period. The dominant vegetation types (DVT) that were incorporated into the home range of adult water voles were identified, along with the degree to which each DVT was utilised. The relationship between water vole population densities and habitat size was determined. Additionally the effects of diversity of both the habitat and the individual patch (DVT) on water vole distribution were also determined.

Chapter 5 Water voles - Forage and Function

Chapter 5 used field surveys to describe the foraging strategies employed by water voles inhabiting a non-linear wetland pond system. Energy content and elemental analysis identified the nutritional content of plant species selected as forage. Additionally, field surveys revealed the presence of latrines. Latrine density was related to a variety of parameters including population density and habitat diversity. Elemental analysis of faecal pellets, combined with nutrient analysis of wetland soils provided the first step to quantifying the effects of water vole behaviour on the nutrient cycles of the wetland ecosystem.

Chapter 6 Water vole Habitat Management

Chapter 6 described the effects of localised vegetation clearance (habitat fragmentation and degradation) on resident water voles. The consequences of clearance included an alteration of the DVT matrix, with an associated loss of diversity in a formerly high quality habitat. Additionally, an influx of brown rats into the disturbed area was observed, with negative effects for the resident water vole population. A site-specific Condition Indicator Table is presented and provides clear guidelines for identifying and maintaining optimal water vole habitat at NWCW. Holistic management strategies for the future monitoring and conservation of water populations are also included.

Methodology

'The system of life on this planet is so astoundingly complex that it was a long time before man even realised that it was a system at all and that it wasn't something that was just there'

Douglas Adams (Last Chance to See, 1991)

1. Study site

This project was undertaken at the National Wetlands Centre Wales (NWCW) (grid reference SS 532 984), a National Key Site for water voles in South Wales, United Kingdom, managed by the Wildfowl and Wetland Trust (WWT). The site provides an ideal location in which to study the water vole, as it supports an established metapopulation within a number of diverse, interconnected habitats including ponds, ditches and reed beds, of varying size and complexity. The investigation focused on eight interconnected ponds, ranging from a small pond (40 metres in circumference) to a large complex pond (360 metres in circumference). All ponds were within close proximity of each other, separated by vegetation corridors or wooded areas and some were flanked by paths or wooden bridges that provided access to the public. Numerous water voles captured within the study site used at least two ponds concomitantly and thus ponds were regarded as separate entities and as part of a combined system (metapopulation; chapter 2) when interpreting the results.

1.1 Site history

The NWCW in the Burry Inlet of the Loughor estuary was once a tidal marsh. Two hundred years ago, construction of a sea wall reclaimed the land for low-grade agricultural farming. Eight years ago (2003), the site was developed into the National Wetland Centre Wales, incorporating the millennium wetlands. The wetlands were initially designed as a reserve for twenty bird species, including nationally important species. However, ecological surveys before construction began located two water vole populations on the central ditches, in the area that is now the deep lake, south of the areas studied here (figures 1 and 2). In addition to birds and water voles, otters and Odonata were also considered in the design of the reserve. Both the design and construction of the wetlands were ecologically sensitive, utilising the natural features of the landscape wherever possible. A mosaic of habitats was created, retaining the botanical infrastructure of conservation value. The network of paths follows the old hedgerows, all of which were left intact. The pools and ponds were designed around the areas that typically flooded. These areas were identified by characteristic plant species associated with wet conditions e.g. Soft Rush (*Juncus effusus*). In contrast, areas that were not subject to flooding were typically characterised by dry grassland species e.g. Sweet Vernal-grass (*Anthoxanthum odoratum*). The edges of the ponds and ditches were convoluted and scratched, to encourage seeds and propagules to establish. Construction took eighteen months, however, the site was not opened to the public for another year. A large reed bed (*Phragmites australis*) was planted in the southerly reaches of the site. Trees that were planted include Willow (*Salix* sp.), Alder (*Alnus glutinosa*) and Black Poplar (*Populus nigra*). The ponds and pools were left to vegetate naturally, resulting in the diversity of vegetation observed across site today (G. Proffitt, pers. comm.). NWCW is now one of two Key Sites for water voles in Wales, the other situated on the island of Anglesey (Strachan & Moorhouse, 2006).

Figure 1 Site map showing location of NWCW and surrounding land-use. Red box highlights the eight ponds that were studied. Adjacent land-use includes a road and grazing pasture (to the north), a deep lake, reed bed and tidal estuary (to the south), NWCW centre grounds and zoo bird collection (to the west) and a water treatment centre and a caravan park (to the east) (reproduced from www.googlemaps.co.uk).

1.2. Ponds

Water vole populations were studied on eight ponds (A to H; figure 2) during a forty month trapping period. Depths of the ponds are presented here and in chapter 1. Detailed depth profiles are available in the design plans of the NWCW millennium wetlands or in appendix 10 (figures A10 to A17).

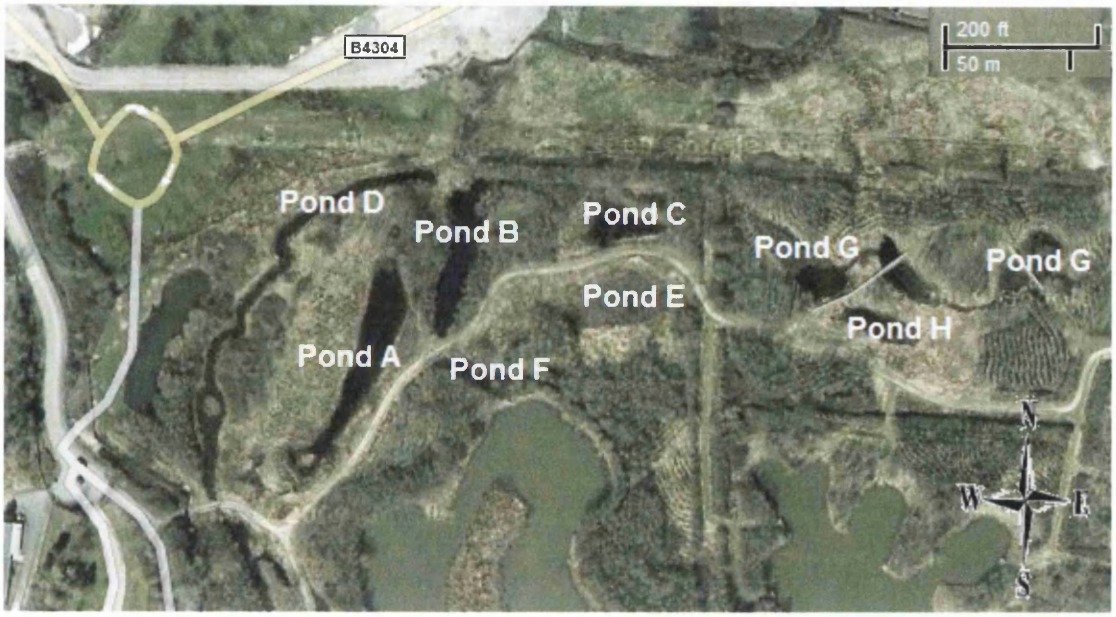


Figure 2 Site map showing location of ponds at NWCW (reproduced from www.googlemaps.co.uk)

1.2.1 Pond A

Pond A consisted of a large shallow water body (depth 1 m) with a circumference of 160 m. The pond substrate was predominantly silt which formed shallow banks which were liable to flooding, but an elevated mound of vegetation, dominated by Field Thistle (*Cirsium arvense*) along 20 m of the western bank, provided a suitable area for burrowing in safety. The perimeter of the pond consisted of dense and species rich vegetation, both bankside and emergent. Greater Pond-sedge (*Carex riparia)* and Bramble (*Rubus fruticosus)* provided a good degree of cover and food, with species such as Galingale (*Cyperus longus)* adding diversity and structure to the bankside vegetation and the water vole diet, as well as representing a locally abundant but nationally scarce species (Jermy *et al*., 2007). A high diversity of emergent species here, such as Water Mint (*Mentha aquatica)* and Common Spike-rush (*Eleocharis palustris)* also contributed to the wide variety of potential forage plants available (see chapter 5). Pond A was flanked by a path and connected to pond

B via trees and bramble and connected to pond D via a broad expanse of Soft Rush (*Juncus effusus)* grassland.

1.2.2 Pond B

Pond B consisted of a deep and steep sided water body (depth 1.5 m) with a circumference of 100 m. This site was considered to be sub-optimal as the surrounding vegetation was predominantly wet woodland, with the field layer dominated by Creeping Buttercup (*Ranunculus repens)* and Stinging Nettle (*Urtica dioica)* and subsequently the habitat structure was fairly limited. Small patches of Great Willowherb (*Epilobium hirsutum)*, *Carex riparia*, *Juncus effusus* and *Rubus fruticosus*, provided cover and a source of food but these were scattered and limited in size and interspersed with wet woodland. Pond B was flanked by a path and connected to pond C via wet woodland with a field layer of *Ranunculus repens, Urtica dioica* and Yorkshire Fog (*Holcus lanatus)*. Pond B was connected to pond D via a patch of damp grassland and also an underground water pipe that water voles were observed to utilise during inter habitat movements. The pond was liable to flash floods as it was situated on the water table. Pond F was located across the path opposite pond B.

1.2.3 Pond C

Pond C consisted of a shallow (depth of 1 m), highly vegetated water body with a circumference of 100 m. The substrate was predominantly silt and 100% of the pond was dominated by Bulrush (*Typha latifolia)* or *Carex riparia*, with small areas of open water between plants. Much of the bankside was densely vegetated with *Juncus effusus* or *Carex riparia*, with the northern bank typically dominated by willow trees (*Salix* sp.). The perimeter of the pond was highly structured providing a good degree of cover but a low diversity of food plants. A row of trees divided the pond from a public path that runs parallel to it. Pond E was located across the path opposite pond C. Pond G was separated from pond C by wet woodland punctuated with small patches of *Rubus fruticosus* and *Juncus effusus*.

1.2.4 Pond D

Pond D consisted of a deep (depth 2 m), steep-sided ditch system approximately 160 m long and 2 m wide, resulting in a long and contorted corridor, similar to the linear habitats inhabited by water voles in other areas of Britain. The pond was constructed in an area of hard rocky substrate, creating steep banks along the circumference. The bankside vegetation was varied, with areas of trees providing poor cover with a sparse herb layer and areas dominated by bramble, providing a good degree of cover but a low diversity of associated species. Swathes of *Juncus effusus* on the northern bank provided continuous cover and an island in the southerly part of the ditch provided increased edge. A large diversity of emergent plants was found throughout the pond, with pockets of *Carex riparia* providing an important source of food and cover, and stretches of Sea Club-rush (*Bolboschoenus maritimus)* towards the middle reaches. This pond represented optimal water vole habitat and continued for 200 to 300 m (beyond the area studied here) joining a large reed bed at the southern coastal reaches which was not included in this study due to time constraints and inability to access without causing structural damage.

1.2.5 Pond E

Pond E consisted of a shallow (depth 80 cm) circular pond with a circumference of 120 m. This pond was dominated by *Typha latifolia* as the emergent vegetation and fringed with *Juncus effusus*, *Carex riparia* and stretches of *Epilobium hirsutum.* All vegetation was dense and a variety of plant species were represented around the perimeter of the pond. Water levels varied according to rainfall, with the pond drying out to a layer of Bog Moss (*Sphagnum* sp.) amongst the extensive stand of *Typha latifolia* in the summer months. The structural nature of the pond vegetation made it difficult to survey this habitat without causing damage, but provided an ideal habitat in which water voles could take refuge from predators. Pond E was located opposite pond C, intersected by a path. Pond E was separated pond F by a broad expanse of wet woodland and *Rubus fruticosus*. A fringe of *Epilobium hirsutum* connected the two ponds along the edge of the path.

1.2.6 Pond F

Pond F consisted of a small, shallow (depth 1 m) pond 40 m in circumference that was only utilised during one breeding season. The water was dominated by Duckweed, *Lemna* sp. This site was considered sub-optimal as it was surrounded by wet woodlands, but a sparse understory with patches of *Juncus effusus*, *Epilobium hirsutum* and *Bolboschoenus maritimus* provided small areas that were utilised when populations were at a peak and other ponds were occupied. This pond was only inhabited by water voles during the breeding season of the first year of the study (2006).

1.2.7 Pond G

Pond G was a large and complex pond system with a circumference of 360 m. It consisted of a large deep area of pond dominated by *Typha latifolia* and open water (depth 1.5 m), connected by a narrow shallow water body (depth 75 cm), dominated by *Eleocharis palustris,* to another large area of shallow pond (depth 1 m). This area had 100% vegetation cover comprised of various dominant species that were not featured as dominants on any other ponds in this study, including, Greater Spearwort (*Ranunculus lingua*), Broad-leaved pondweed, (*Potamogeton natans)* and Grey Club-rush (*Schoenoplectus tabernaemontani).* Additionally, plant community associates that were not present on any other pond (across the area of wetland studied), such as Water Pepper (*Persicaria hydropiper)* were present. Thus, pond G had a high diversity of plant species, both as dominants and associates, with bank-side and emergent vegetation providing a high degree of structural cover. In addition, certain areas of the bank-side were convoluted, which provided an increased surface area for burrowing and vegetation growth. A path and two wooden bridges dissected the pond which was surrounded by wet woodlands. A broad-expanse of *Juncus effusus* separated pond G from pond H.

1.2.8 Pond H

Pond H was a small, shallow pond (depth 1 m) adjacent to pond G and entirely surrounded by *Juncus effusus*, except for an area dominated by Reed Sweet-grass (*Glyceria maxima)* that separated pond H from the bridge over pond G. Bare mud under the bridge distinguished the ponds as two separate entities, yet they were often utilised concomitantly by water voles due to the high degree of cover provided by the connecting expanse of *Juncus effusus.* A path flanked the southern bank of pond H.

2. ***Vegetation surveys and habitat mapping***

Since water voles depend on the vegetation surrounding the water body as both a source of food and cover from predation, it was deemed appropriate to map all of the bank side and emergent vegetation of the ponds together with the surrounding land use (tracks, trees or scrub) (see chapter 1, figure 1.1). This provided the baseline onto which other activities such as trapping events and field signs could be mapped. In effect this was a bottom-up description of habitat utilisation. Homogenous stands of vegetation were identified and drawn onto satellite maps of the site. Each stand or patch of vegetation was labelled according to the dominant vegetation type (DVT). A DVT is defined here as a homogenous patch (stand) of vegetation dominated by a particular plant species after which the DVT is named. For example a patch of vegetation dominated by *Juncus effusus*, was labelled as a *Juncus effusus* DVT (*Je*DVT) on the habitat map (figure 1.1). Plant species associated were also noted as these often feature in the water vole diet, but were not used to define the map. The DVTs were then mapped onto the satellite map using the program Mapinfo Version 8.5 (MapInfo GIS is a product of the MapInfo Inc.) which created colour coded polygons corresponding to individual plant species and provided a clear way to visualise the arrangement of vegetation. The DVTs were the experimental blocks or sampling units (see chapters 1 and 4). DVT classification is particularly appropriate for vegetation description in wetland habitats where plant community patches are often dominated by one (or few) species that are easy to identify.

2.1 Vegetation surveys at the habitat level: ponds

In order to describe movement patterns of water voles in relation to discrete stands of vegetation, it was necessary to identify a set of site-specific vegetation types, defined by the dominant plant species within each stand (patch). These 'dominant vegetation types' (DVTs) were mapped in the field onto recent ortho-rectified aerial photographs at 1:1250 scale and the boundaries subsequently digitised using Geography Information System (GIS) software (Mapinfo). Although open water and bare ground are not a vegetation type *per se*, they were both classified as DVTs as they represent a land use that may or may not be utilised by water voles. Since water voles typically operate within the vicinity of the bankside (Strachan & Moorhouse, 2006) a 5 m boundary beyond the water's edge was used to delineate the ponds (figure 1.1). The DVT patches within this 5 m boundary line were counted for use in statistical analysis of pond diversity (section 2.3). The areas of each DVT patch were noted for use in determining water vole field sign density per unit area (chapter 5).

2.2. Vegetation surveys at the patch level: DVTs

Plant species lists were compiled for each pond and included aquatic, emergent and bankside vegetation (Appendix 1). Plants were identified to species level using the New Flora of the British Isles (Stace, 1997) and the nomenclature used here is based on names given in that flora. Quadrat sampling of ten DVTs ($n = 50$ quadrats) was undertaken during the summer of 2008. Of these, the *Eleocharis palustris* DVT was the only dominant vegetation type sampled that did not contain a water vole trap, since this species typically grows in shallow water and therefore does not provide a suitable substrate. However, this DVT was utilised by water voles (confirmed by the presence of distinctive field signs and activity; chapter 5) and was thus considered to be important. For each DVT, plant species composition and % abundance was recorded, degree of open water or bare mud was determined and the height of the dominant vegetation type was measured. Using a hand held Garmin Vista GPS system (Garmin International Inc., Kansas, USA), a 10 figure Ordnance Survey grid reference was taken at the position of each quadrat and cross referenced with the DVT and aerial maps. Quadrat data was not recorded for DVTs dominated by trees since these were only associated with sporadic capture events and could not be sampled using 1 m^2 quadrats.

2.3 Statistical analysis of vegetation data

The diversity index selected for the determination of both habitat diversity (D_{pond}) and patch diversity (D_{DVT}) was Shannon (H') (Shannon & Weaver, 1949), since this takes species richness and abundance into consideration and is a more powerful measure of diversity than those indices based on species richness alone (Magurran, 1988).

The habitat diversity index (D_{pond}) of each pond was calculated (appendix 2) using habitat data (the number of different DVTs and the total number of DVT patches) and the formula (equation 1):

$$(D_{pond}) = -\sum_{i=1}^{s} p_i \ln p_i \quad \text{--} \text{ Equation 1}$$

where s = the total number of different DVT patches

p_i = the proportion of patches or the abundance of the ith patch expressed as a proportion of total number of patches

ln = log base_n

The patch diversity index of each dominant vegetation type (D_{DVT}) was calculated for each DVT using quadrat data (species and abundance) and the same formula (equation 1), but where:

s = the number of plant species

p_i = the proportion of individuals or the abundance of the ith species expressed as a proportion of total cover

ln = log base_n

Ward's agglomerative cluster analysis (based on Euclidian distances) was used to classify ponds based on their habitat diversity (D_{pond}) and DVT patches on their patch diversity (D_{DVT}). All frequency data sets (number of plant species, DVTs and DVT patches per pond) were analysed using G-tests of homogeneity, with appropriate correction factors where necessary. Linear regression analysis (ANOVA) was undertaken to determine the relationship between habitat diversity (D_{pond}) and both length and area of trapped habitat and the relationship between the number of plant species per pond and the number of DVTs.

3. Live Trapping

Live trapping was conducted under CCW licence (numbers; OTH: SA: 54: 2006; 136: 2007; 197: 2008; 240: 2009). In total, 56 numbered single entry rat cage traps (figure 2) measuring 435 mm x 190 mm x 190 mm (Soloway Feeders Ltd, Kirkcudbright, Scotland, DG6 4QH) were positioned at 20 m intervals in the dense vegetation close to the edge of the ponds (figure 3). Previous trapping studies of UK water voles indicate that that a 20 m grain is small, relative to the mean range lengths of adult males and females (Stoddart, 1970; Moorhouse & Macdonald, 2005). The number of traps positioned in each study pond was restricted by its size. Accordingly, eight traps were placed around pond A; five around pond B, five around pond C, eight along pond D, six around pond E, two around pond F, eighteen around pond G and four traps around pond H. Traps on pond D were initially placed every 20 m on the southern side on the water course (March to December 2006) but were relocated and staggered every 40 m along both sides of pond D (January 2007 to May 2009). Since Pond D was a narrow water course (<5 m) and water voles were observed to swim between both banks, it was assumed that this new arrangement would not confound the results. This relocation provided a more comprehensive view of habitat utilisation and was taken into consideration when analysing the data.

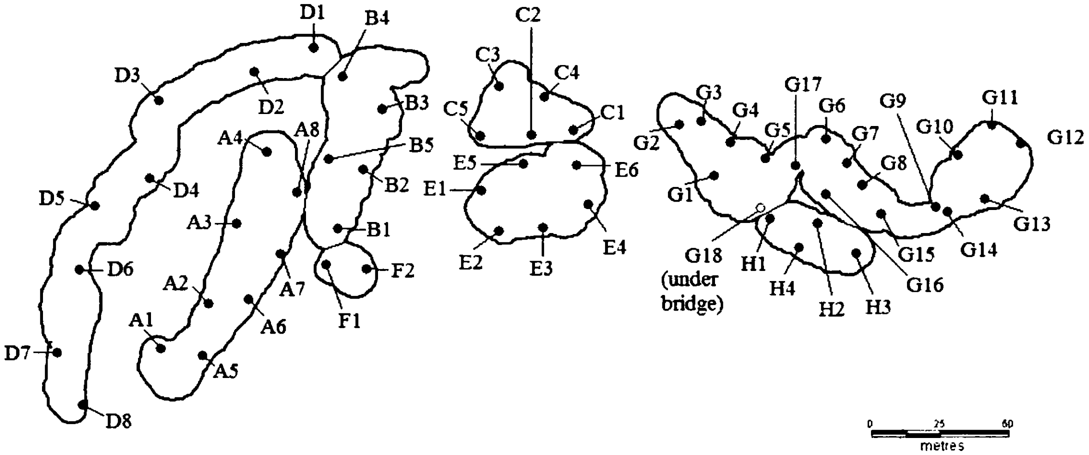


Figure 3 Trap map showing location of water vole traps around the periphery of 8 ponds (A to H), including the 5 m buffer around each water body (see chapter 1, figure 1.1).

All traps were provided with abundant dry hay and circa 150 g of apple. Traps were set for continuous periods of at least five days every month throughout the periods described. During each trapping period, every trap was regularly checked (three times per day) and fresh hay and apple provided as required, as field voles frequently consume apple bait without triggering the trap mechanism. Live trapping occurred on eight interconnected ponds over a period of forty months. The total trapping effort was 10,340 nights.

3.1 Processing captured animals

Water voles that were captured (figure 4) were examined while still in the trap for injuries, parasites and other notable features (including wounds received from agonistic encounters), before being transferred gently to a netting bag. Each vole was then sexed visually and individually tagged using a single Passive Integrated

Transponder (PIT) (MID Fingerprint Ltd, Weymouth, Dorset, DT3 6YH) inserted into the subcutaneous tissue between the shoulder blades (in accordance with Zoo Federation guidelines). All re-captured voles were scanned using a hand held PIT reader to determine the identity of marked animals. All voles were weighed using a 500 g Salter spring balance (Envisage Wildcare, Swindon, SN25 5DC) before release at the point of capture. Water voles weighing > 140 g were classified as adults (appendix 5). The average duration of this procedure was approximately 4 minutes per vole. Faeces (pertaining to the trapped individual) were collected from within the trap and stored on ice for future analysis. Rats were infrequently caught on some ponds. The location of each rat was noted in order to observe the effects of this predator, which has a sympatric distribution with respect to water voles. In order to minimise the potential exposure risks to voles caught in traps, trapping was not conducted in either very hot or cold weather, or during periods of heavy and prolonged rainfall.

Figure 4 Water vole (*Arvicola amphibius)* in trap

3.2 Juvenile water voles

A juvenile water vole was classified as any animal weighing ≤ 140 g. The age and date of birth of all juveniles born into the metapopulation throughout the four year study period was calculated using previous studies undertaken on both wild and laboratory-reared water voles (Stoddart, 1970). The age of all animals weighing less than 120g can be accurately estimated, however beyond this estimates are inaccurate (Stoddart, 1970) and should be treated with caution, especially for those animals caught during winter with weights of 120 to 140 g, as these animals may have already recruited into the adult population then lost weight due to seasonality (low temperatures, low food availability). All juvenile birthdates (Appendix 5) were cross referenced with sexual status of adult females (i.e. pregnant, lactating or perforate) to more accurately predict the boundaries of the breeding season at NWCW.

3.3 Water vole population densities

Population densities are presented as the mean number of individuals per 100 m (±SE) of habitat and calculated separately for each pond (chapter 2). The minimum number of animals alive (MNA) provides the most conservative population estimates (i.e. the least number of water voles on a pond during a given trapping session) and included adults only. Juveniles are discussed separately. MNA was used as the population estimate for the site thus: population density = (MNA / length of trapped habitat) x 100 (Moorhouse & Macdonald, 2008). MNA was determined monthly (Appendix 4) and used to determine mean annual population densities (±SE) per 100 m, together with breeding season (March to October) and winter (November to February) population densities per 100 m. If an animal was not trapped during a particular month the MNA was calculated from recaptures thereafter.

3.4 Recruitment and survival of water voles

In order to identify whether the distribution patterns observed resulted from survival of those adults already present or continual recruitment from source ponds in the vicinity, survival and recruitment graphs were plotted for both males and females per pond (figures 2.5 to 2.20) (after Moorhouse and Macdonald, 2005). The recruitment of water voles was estimated using the numbers of new animals captured at time $t2$ per extant member of the population at time $t1$. The survival of water voles was estimated using the numbers of recaptured (previously tagged) animals at time *t*2 per extant member of the population at time *t*1.

3.5 Statistical analysis of population data

All data was subject to one sample K-S tests to determine normality. No data transformation was required. Mean water vole population densities per 100 m were subject to analyses of variance with *post hoc* Bonferroni multiple comparisons to determine differences between ponds and years, since no *a priori* assumption was made as to which ponds were likely to support the highest population densities. All frequency data sets (number of water voles by gender and age class) were analysed using G-tests of homogeneity, with appropriate correction factors where necessary. Independent samples t-tests were used to compare the weight of male and female water voles. Analysis of variance ANOVA (GLM) was used to analyse variations in weight per pond and gender. The weight of the resident animals (21 males and 33 females) was significantly correlated with the number of times each animal was weighed (Pearson's $p = 0.008$). Thus, the number of times each animal was weighed was entered as a co-variate in the analysis of variance of population density and weight data per gender, pond and season.

3.6 Water vole home range lengths (ORL)

Observed range lengths (ORL) were estimates of minimal water vole range and calculated as the distance between the two furthest capture positions following the contours of the water course on the satellite map (Moorhouse & MacDonald, 2008) (chapter 3). It should be noted that in some instances the two furthest capture points did not necessarily represent range boundaries, but may be the result of displacements. To consider these displacements as part of the home range would give an over estimate of ORL. Home ranges were determined for resident water voles that were captured during at least two trapping sessions ($n = 54$ water voles) (Appendix 6). Those animals that were caught repeatedly in the same trap were assigned an ORL of 15 m. ORLs were determined during both the breeding season (March to October) and non-breeding season (winter; November to February). Although only 54 water voles maintained a home range, there were 68 ORLs maintained altogether (i.e. included in statistical analyses of ORL), since 17 males and 31 females ($n = 48$) maintained an ORL during the breeding season. Certain males maintained an ORL on one pond before displacing to another on which they maintained a second ORL during the breeding season (n = 2). Additionally, 9 males and 9 females (n = 18) maintained an ORL during the winter (total n = 68 ORLs). It should also be noted that 5 of the 9 male water voles and 6 of the 9 female water voles that maintained an ORL during the winter also maintained an ORL in the summer.

3.7 Statistical analysis of water vole home range length (ORL)

Differences in ORL between males and females were determined using independent samples t-tests and unequal variances were assumed. ORLs were regressed against population densities to determine density-dependent effects. Analysis of variance identified differences between ORL per pond and gender. Linear regression analysis was undertaken to determine the relationship between both ORL and population density and ORL and weight of resident animals. The home range lengths (ORLs) of the resident animals (21 males and 33 females; breeding season and winter combined) were significantly correlated with the number of times each animal was captured (Pearson's p = 0.008). Thus, the number of times each animal was captured was entered as a co-variate in the analysis of variance of home range length between gender, pond and season and the effects of population density and individual weight on home range length.

3.8 Water vole home range overlaps

Exclusive use of a length of habitat with lack of overlap of same sex individuals indicated territoriality and individuals were defined as having overlapping ranges when captured within the known range of another individual (Moorhouse & Macdonald, 2008). In addition to the 19 male water vole home ranges (ORLs) that were maintained (by 17 males) during the breeding season (table 3.1; figure 3.1), a further 2 males that were only captured once during the breeding season (but maintained a home range during the winter) were also included in the analyses of breeding season home range overlaps. In addition to the 9 males that maintained an ORL during the winter (figure 3.2; table 3.3), 6 males that maintained an ORL during the breeding season (but only captured once during the winter) were also included in the analyses of winter home range overlap. In addition to the 9 females that maintained an ORL during the winter (figure 3.2; table 3.3), 10 females that maintained an ORL during the breeding season (but only captured once during the winter) were also included in the analyses of winter home range overlaps. Accordingly, 21 male ORLs and 31 female ORLs were included in the analyses of home range overlaps during the breeding season and 15 male ORLs and 19 female ORLs were included in the analyses of home range overlaps during the winter (tables 3.4 and 3.5). All frequency and proportional data sets were analysed using G-tests of homogeneity with appropriate correction factors where necessary.

3.9 Agonistic behaviour

The frequency of bite wounds, together with area of the body that received bites, was recorded for all water voles captured throughout the entire duration of the study. However only resident adult males (n = 21) and females (n = 33) (that maintained a home range) together with all juveniles that were assigned a gender (n = 25), were included in the analyses. Target areas in which bites were received were defined as the head (including numerous eye injuries, leading to blindness or loss of eye), body (including legs, feet and rump) and tail. The number of water voles wounded, together with the number of wounds received was used to determine the relative number of wounds per animal (tables 3.6 and 3.7). Seasonal variations in bite wounds were identified and variations between ponds during both the breeding season (n = 19 males, 31 females) and the winter (15 males and 19 females) were also determined. All frequency and proportional data sets were analysed using G-tests of homogeneity with appropriate correction factors where necessary.

3.10 Habitat utilisation (DVTs and water voles)

The location and movements of individually micro-chipped water voles tracked over forty months were plotted on the vegetation map to describe occupancy per dominant vegetation type (DVT). Temporal and seasonal utilisation of DVTs was examined. Observed range lengths (ORLs) (chapter 3) of resident adult water voles were overlaid onto the DVT map to identify core and peripheral DVTs that featured in their territories or home ranges. It should be noted that animals that were only encountered once may have been dispersing or removed from the population by predation and therefore no longer continued to occupy the aforementioned location. Although each capture incident was only a snap shot in time, it provided an insight into DVTs that corresponded with high capture rates.

However, since it was the resident animals with established home ranges or territories that constituted the breeding population, DVTs that were incorporated into observed range lengths (ORLs) (chapter 3) were examined for both the number of adults and the number of capture events associated with each dominant vegetation type. This provided a measure of the relative importance of each DVT to water voles when selecting suitable habitat and the degree of niche partitioning that occurred between genders and individuals. Each DVT was examined for both the number of resident adults that were associated with it, together with the degree to which it was utilised. Only DVTs associated with more than one resident adult were included in the analyses. Certain ponds had more than one patch of the same DVT, with two or more traps located in similar DVTs, but in separate patches around the circumference of the water body. In order to provide a true reflection of patch preference, all results were adjusted for unequal sample size and effort i.e. catch per unit effort (CPUE). The relative number of resident water voles per DVT was calculated by dividing the number of adults per DVT by the number of traps within each DVT type. The relative degree of DVT utilisation was calculated by dividing the number of captures of residents per DVT by the number of traps within each DVT type.

3.11 Statistical analysis of habitat utilisation data

Analysis of variance identified variations in dominant vegetation type (DVT) utilisation between genders and age classes for all water voles captured. Male and female population densities were regressed against pond size to determine gender-dependent effects. Linear regression of home ranges (ORL) of resident adult water voles against number of DVTs per home range was undertaken for both males and females during both the breeding season and the winter. In order to identify the level of diversity that is important to water voles, including seasonal effects, population densities were regressed against the habitat diversity (D_{pond}) and patch diversity (D_{DVT}) during both the breeding season and the winter. Home range lengths were also regressed against habitat diversities (D_{pond}).

4. Field surveys

Crude field surveying (when setting traps) gave a rough estimate of the location of latrines and food selection on each pond. Intensive field surveys of each habitat were undertaken during spring (March), summer (May) and autumn (September) of 2008 and 2009 to determine the presence of latrines (figure 5), feeding stations (figure 6), burrows (figure 7) and other prominent field signs, such as tumulus excavated from burrows (figure 8) and branching runways through bankside vegetation (figure 9).

Figure 5 A typical water vole latrine containing drum-marked (scent-marked; indicated with an arrow) and unmarked faecal pellets (see introduction, p12)

Figure 6 A typical water vole feeding station – Yellow Iris *(Iris pseudacorus)*

Figure 7 A typical burrow entrance of a water vole with grazed lawn, indicating the presence of a female nursing young

Figure 8 Chewed earth (tumulus) excavated from newly created water vole burrows

Figure 9 A typical water vole runway through bankside vegetation

No field surveys were undertaken during the winter (November to February) due to the sensitivity of the habitat, associated with reduced vegetation cover and the susceptibility of water voles to winter predation. However, during winter trapping sessions, both feeding stations and latrines were encountered during January and February on certain ponds. During intensive field surveys the position of each field sign was plotted onto the DVT map and details were recorded. The proportion of drum-marked latrines was determined. The number and colour of faecal pellets in all latrines were recorded, together with distance from waters edge (cm). A selection of fresh faeces were collected (both from latrines and from occasional pellets encountered in aggregations of > 10) and stored on ice for future analysis of nitrogen content.

Plant material in feeding stations was identified to species level using the New Flora of the British Isles (Stace, 1997). The distance of a feeding station from the waters edge was measured in cm. Representative samples of plants of the same species were collected from the vicinity of the feeding station (preferably with evidence of foraging) and stored on ice for future analysis of nitrogen and energetic content. Occasionally, molluscs and amphibians were encountered in feeding stations. In instances where foraging upon non-plant species was suspected, material was inspected for the occurrence of distinctive incisor marks that would indicate that water voles had consumed the material. Great care was taken in these procedures since both rats (*Rattus norvegicus*) and water shrews (*Neomys fodiens*) were known to make non-plant food caches on pond edges in the NWCW wetland complex (pers. obs.). Obvious burrow entrances and tumulus from burrowing activity were recorded. Predator activity was recorded (otter spraints, mink scat, fox scat and rat pellets). Field vole activity (feeding stations and latrines) was also noted.

4.1 Analysis of field surveys

Replicated intensive field survey data was overlaid onto the DVT map (figure 1.1) to provide a visual representation of habitat utilisation and patch use. Feeding stations of a species other than that which was used to define the DVT (plant species associates) provided an example of foraging selection. The water vole diet varied throughout the year and field surveys undertaken during spring, summer and autumn allowed temporal fluctuations in forage selection to be observed and comparisons between the distribution of field signs and the distribution of water vole populations during the breeding season.

4.2 Statistical Analysis of field survey data (chapter 5)

All frequency data sets (number of feeding stations per pond and year, number of plant species selected as forage per pond and year, number latrines per dominant vegetation type) were analysed using G-tests of homogeneity with appropriate correction factors where necessary. Linear regression analysis was undertaken to determine relationships between (i) the number of plant species present and the number of plant species in feeding stations per pond, (ii) water vole population density and the number of plant species in feeding stations, (iii) number of feeding stations and DVT patch diversity (D_{DVT}), (iv) water vole population density and latrine density per 100m, (v) population density and number of faecal pellets per latrine and (vi) habitat diversity (D_{pond}) and latrine density.

5. Elemental and energy content analysis

Selected plant species that were commonly found in feeding stations throughout the year, together with occasional species that were found in summer, were subject to elemental analysis, to determine their total carbon and nitrogen content and C:N ratio (sections 5.1 and 5.3). Additionally, the energy and mineral content of plant samples was determined by bomb calorimetry. Faecal pellets were also collected and analysed for their nitrogen content (sections 5.2 and 5.3) in order to estimate the amount of nitrogen that could be returned to the wetland ecosystem through the creation of nitrogen rich latrines.

5.1 Plant samples

Representative samples of plant species found in feeding stations were collected during field surveys (see section 4) and freeze dried. Samples were weighed before and after drying to determine their water content (% water = gg^{-1} fresh plant material) (see Chapter 5.2 and Appendix 8). Representative dry samples weighing 0.6 mg were transferred into tin cups for elemental analysis. In order to observe any seasonal effects on the nitrogen content of food plants, samples were taken over a period of months and the species selected were those that featured most heavily in the water vole diet. Analysis of variance identified variation in water content of forage species.

5.2 Faecal samples

Faecal samples were collected from trapped animals (see section 3.1) and during field surveys (see Chapter 5) and freeze dried before weighing out 0.6 mg samples into tin cups for elemental analysis (see section 5.3). Samples were weighed before and after drying to determine their water content (% water = gg^{-1} fresh plant material) (Appendix 8).

5.3 Elemental analysis (Carbon: Nitrogen)

Freeze dried samples of plant and faecal matter were subject to elemental microanalysis to determine the percentage carbon (gg^{-1}) and percentage N (gg^{-1}). Samples of known amount (*ca.* 100 µg C) were weighed into tin cups and combusted on-line at 1000°C over chrome$_{(III)}$ oxide and copper$_{(II)}$ oxide (Elemental Microanalysis, Okehampton, UK) using a PDZ Europa ANCA GSL analyser. Oxides of nitrogen were reduced to nitrogen gas over hot copper and any traces of water present removed by passage through magnesium perchlorate. The resulting nitrogen and carbon dioxide were resolved gas chromatographically using a 0.6 m long GC column packed with Porapak QS. Carbon and nitrogen were determined using a PDZ Europa 20/20 isotope ratio mass spectrometer (Coplen 1995; Craig 1957). Carbon: nitrogen (C: N) ratios are calculated relative to atropine and acetanilide standards of known elemental composition (OAS, Elemental Microanalysis, Okehampton, UK). Analytical precision was typically better than 0.1 per mille (n=15), and 0.1 (%N) and 0.65 (%C) (n=12) based upon replicate analysis of an in-house Sigma cellulose (Sigma Aldrich, UK) and acetanilide OAS standard respectively.

5.4 Bomb calorimetry (energetic and mineral content)

Representative samples of the plant species that were subject to elemental analysis were also subject to bomb calorimetry, in order to determine energetic and mineral content. In addition to those plant species subject to elemental analysis, two further species, Galingale (*Cyperus longus)* and Common Spike-rush (*Eleocharis palustris)* were combusted in order to determine energy content, mineral content and protein content. Dry matter was calculated by weight loss after drying at 105 ^{0}C for 24 h.

Crude protein was measured using the Kjeldahl technique (Stuart, 1936) and multiplying N by 6.25 (Lupatsch & Kissil, 1998; Lupatsch *et al.*, 2003). Ash (mineral content) was calculated from the weight loss after incineration of the samples for 12 h at 550°C in a muffle furnace (Carbolite, Sheffield, UK). Gross energy content was measured by combustion in a Parr 6200 Calorimeter (Scientific and Medical Products Ltd, Cheshire, UK) using benzoic acid as the standard.

5.5 Statistical analysis of elemental and energetic data

Analysis of variance was used to test for any significant differences in carbon, nitrogen, energy and mineral (ash) content of forage species. Independent t-tests were used to compare C: N ratios of forage species. Analysis of variance identified variations in nitrogen content in faecal pellets from varying sources (water voles and latrines) and also seasonal variations in nitrogen content of faecal pellets.

5.6 Nutrient loading of wetland soils

Ten soil samples weighing 20 g (extracted as cores) were collected from the water vole runways on the bank-side of ponds, where latrines were typically found (0 to 2m from the edge of the water body). Samples were taken from historic latrine sites, which had been maintained by water voles patrolling their home ranges for at least one breeding season. Additionally, seven further soil samples weighing 20 g (extracted as cores) were taken from water vole habitats, from areas where no latrines were known to have been created. The seventeen samples were shaken for one hour (100 rpm) with 100 ml 5% glacial acetic acid (v/v). The resultant soil suspensions were filtered and a representative sample (5 ml) analysed with a Seal 2 channel Segmented Flow Autoanalyser with digital colorimeter (Seal Analytical, Fareham, Hants, UK).

Nitrate was measured as nitrite after cadmium / copper reduction (550 nm) (Wood *et al.*, 1967) and phosphate was measured by the phospho-molybdenum method (Johnson 1971). Ammonium was measured using the modified Berthelot reaction (660 nm) (Weatherburn, 1967). Modifications to the Berthelot method include; replacement of phenol with sodium salicyclate; incorporation of a complexing agent to prevent the precipitation of calcium and magnesium hydroxides; and addition of sodium nitroprusside to enhance sensitivity. Additionally, six samples of faecal pellets were also subject to extraction and segmented flow analysis. This provided baseline levels of nitrogenous compounds and phosphate and determined whether there were any compounds in faecal pellets that would give a false positive result.

5.7 Statistical analysis of soil nutrients

All data was subject to one sample K-S tests to determine normality. Phosphate concentrations were not normally distributed and were thus square root transformed. Analysis of variance was used to determine variation between nitrate, ammonium and (square root transformed) phosphate concentrations in latrine and control soils.

Chapter 1

Habitat

'The face of the water, in time, became a wonderful book - a book that was a dead language to the uneducated passenger, but which told its mind to me without reserve, delivering its most cherished secrets as clearly as if it uttered them with a voice. And it was not a book to be read once and thrown aside, for it had a new story to tell every day'.

Mark Twain (Life on the Mississippi, 1883)

1.1 Introduction

Current methods used to map habitats

The recording of broad vegetation types in habitat or land cover maps is often the starting point of ecological investigations of sites and landscapes (Cherill & McClean, 1999). The majority of the land surface in Wales has been surveyed using the Phase 1 method. The Phase 1 survey method requires field surveyors to identify areas of homogenous vegetation and to assign these `parcels' to land cover types defined primarily on the basis of the characteristic plant species. Descriptions of the Phase 1 land cover types are provided by the Nature Conservancy Council (1990). Land cover types include (for example) wet acid heath or marshy grassland and, as such, provide a broad description of the habitats present in an area and indeed highlight areas that may be of ecological significance that may require further (typically Phase 2) investigation.

Reliable information from time-series analyses requires comparable sets of habitat data, collected using similar methods and habitat classification (Stevens *et al.*, 2004). Phase 1 survey (NCC, 1990) provides a tool widely used for this purpose in the UK. However, considerable levels of variation (both observer and spatial) have been found between organisations in the application of the Phase 1 method (Cherrill & McClean, 1995; 1999). Furthermore, the importance of unambiguous, objective definitions in conservation monitoring has recently been highlighted. Subjective interpretation of unclear definitions leads to observer variation and consequently unreliable monitoring, since the monitoring result is an artefact of observer bias (Hurford, 2010).

Why map water vole habitats?

Habitat mapping is a fundamental tool in the methodologies applied by ecologists, environmental managers and conservationists (Cherill & McClean, 1999). Site managers often find it difficult to formally prioritise habitats or species for conservation on their sites, but it is an essential first step in the development of a strategy for conservation and monitoring (Hurford, 2010). It is important to map the vegetation in any habitat that is vulnerable or home to a vulnerable species, such as the water vole, since it allows the natural process of succession to be monitored (see Introduction, p1). This is essential for the management of those habitats, in which the process of succession could have consequences for the persistence of the species, as is the case with the water vole. Data on habitat change over time are useful for setting and revising conservation and other environmental management objectives (Stevens *et al.*, 2004).

Water vole distribution is negatively correlated with the presence of trees (Zejda & Zapletal, 1969) and typically associated with luxuriant vegetation at the water's edge (Gaisler & Zejda, 1974; Strachan & Moorhouse, 2006; Moorhouse *et al.*, 2009) and thus a climax woodland community would have negative consequences for water vole populations. Mapping habitats also allows the mosaic of vegetation to be used as a baseline onto which movements of individual animals can be overlaid and identifies core areas of water vole activity. This facilitates our understanding of those parameters that are important to the persistence of the species in question. Seasonal changes in vegetation structure and abundance are reflected in the behavioural choices implemented by water voles (chapters 3 to 6) and the success and survival of the animals (chapter 2). Having identified the conservation priorities, the best way to achieve a conservation strategy is to adopt a map-based approach, including the current extent of the habitat (or potential habitat) and how much of it meets the criteria for being in good condition. This allows identification of key areas for both management and monitoring (Hurford, 2010).

Water vole habitat requirements

Numerous studies regarding water vole habitat requirements have been undertaken and are outlined in the introduction (p9) and chapter 4. In Britain, the water vole favours rivers with well vegetated banks (Lawton & Woodroffe, 1991; Strachan & Moorhouse,

2006) and emergent vegetation (Strachan & Jeffries, 1993; Strachan & Moorhouse, 2006; Moorhouse *et al.*, 2009).

Rationale

Although occupancy of riverbank habitat can be predicted based upon a combination of several habitat features (Lawton & Woodroffe, 1991), water voles in Britain occupy a range of habitats from upland streams to agricultural ditches and thus there is a gradient in habitat quality, without clear habitat boundaries. Consequently it is necessary to survey a wide range of potential habitats in order to establish the distribution of water voles, however, delineating patch boundaries and hence patch size is difficult (Telfer *et al.*, 2001). In the case of British water voles, reintroduction studies have revealed that it is desirable to target releases at habitats with broader swathes of riparian vegetation and highlight the need to ensure that any habitat selected for release is the 'best obtainable' (Moorhouse *et al.*, 2009). Previous studies have highlighted that the physiognomy of the vegetation is important for water voles (Lawton & Woodroffe, 1991; Woodall, 1993; Moorhouse *et al.*, 2009; Neyland *et al.*, 2010). However, if habitat structure is only a surrogate measure of habitat 'quality' it is possible that the fundamental role of habitat quality in determining distribution patterns may be underestimated (Mortelliti *et al.*, 2010).

Aims

1. To quantify the landscape of the NWCW wetland complex
2. To develop a vegetation based sampling system in which to study water voles
3. To distinguish between different ponds in the wetland complex based on attributes of their vegetation and classify their 'quality' objectively, on the basis of their diversity
4. To provide a baseline habitat map on which to monitor and manage water voles and their habitats
5. To describe a method of habitat mapping that adds more detail than the Phase 1 land cover use method and reduces observer bias by using clear, objective definitions that can be implemented easily and efficiently

1.2 Results

1.2.1 Dominant Vegetation Types (DVT)

A DVT is a homogenous patch (stand) of vegetation dominated by a particular plant species after which the DVT is named. For example a patch of vegetation dominated by Soft Rush (*Juncus effusus*) is labelled as a *Juncus effusus* DVT (*Je*DVT) on the habitat map (figure 1.1 and table 1.1). There were thirty-one different dominant vegetation types (DVTs) across the area of wetland complex studied (figure 1.1), including bare ground, footpaths or bridges and open water. However, only twenty-three of these DVTs were located within the 5 m boundary line around the ponds in the wetland complex and not all the DVTs were present on each pond (table 1.1). Footpaths were present, adjacent to the majority of ponds, with footbridges over pond G (figure 1.1). With the exception of trees, the *Epilobium hirsutum* DVT was the only one to be present on all ponds studied within the wetland complex.

The damp grassland DVTs were so named because typically, they were dominated by graminoids and contained a varied assemblage of plants (none of which were the dominant species). These included Yorkshire Fog (*Holcus lanatus*), Velvet Bent-grass (*Agrostis canina*) or Creeping Bent-grass (*Agrostis stolonifera*), Jointed Rush (*Juncus articulatus*), Greater Bird's-foot Trefoil (*Lotus pendunculatus)*, Creeping Buttercup (*Ranunculus repens)* and Fleabane (*Pulicaria dysenterica)* (table 1.7). Of all the DVTs that contained a water vole trap, the damp grassland DVT and the *Eleocharis palustris* DVT were the only two that did not represent a permanent vegetation type, in that they were absent after senescence and would only provide cover during the summer months. All the other DVTs maintained a constant structural presence (even if they became woody after senescence e.g. *Epilobium hirsutum*). In total there were 205 DVT patches, covering an area of 66,142.24 m^2, however, only 156 of these patches were located within the 5 m boundary line, covering an area of 16,492.95 m^2 (table 1.2).

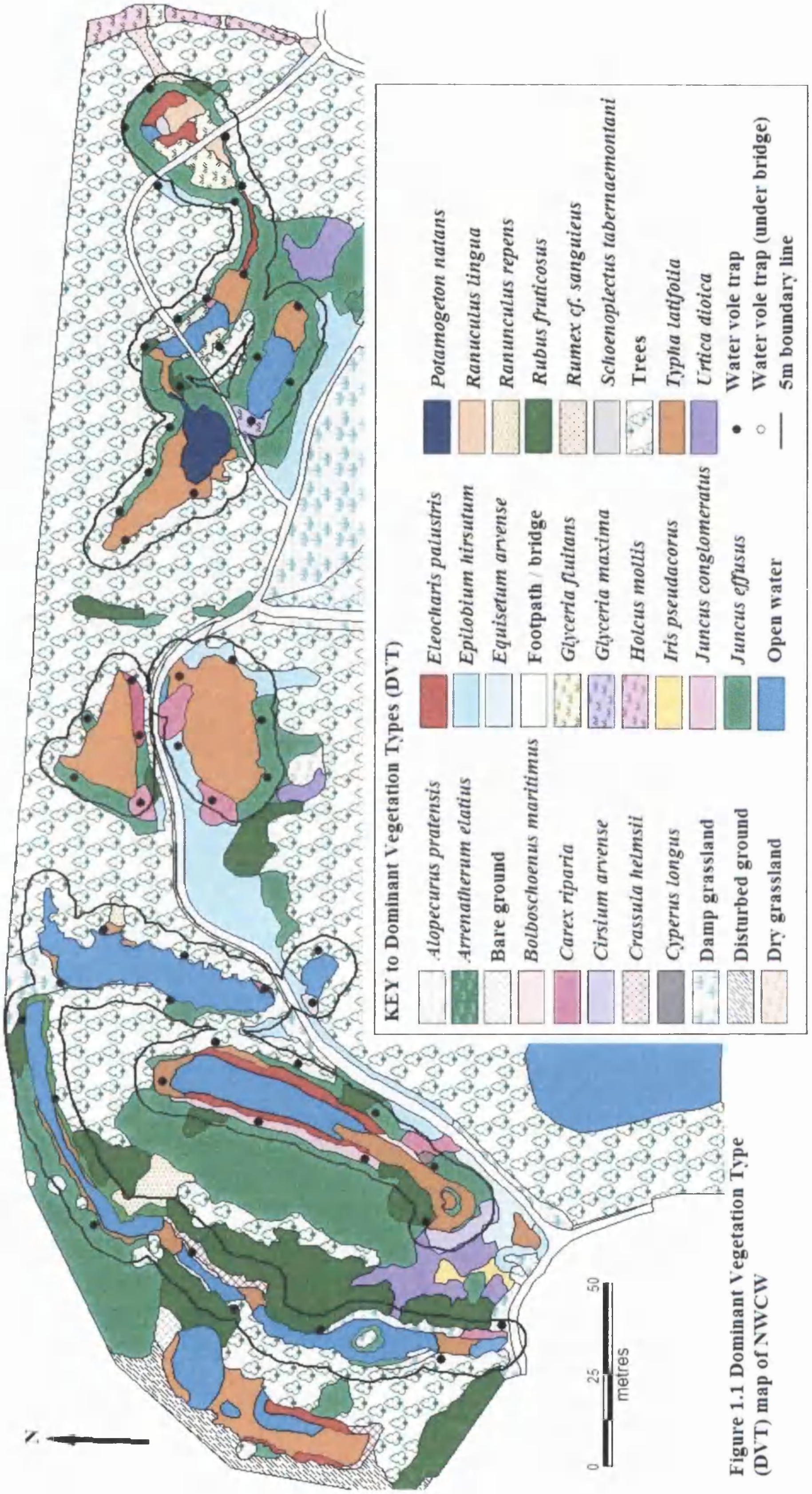


Figure 1.1 Dominant Vegetation Type (DVT) map of NWCW

Table 1.1 Dominant vegetation types (DVTs) per pond that lay within the 5 m boundary line (buffer) of the pond edge. English botanical names for plant species can be found in tables 1.5 to 1.14

		Pond							
Dominant Vegetation Type (DVT)	Abbreviation	A	B	C	D	E	F	G	H
Bolboschoenus maritimus	*Bm*DVT	x			x		x		
Carex riparia	*Cr*DVT	x	x	x	x	x		x	
Cirsium arvense	*Ca*DVT	x							
Crassula helmsii	*Ch*DVT				x				
Cyperus longus	*Cl*DVT	x							
Damp grassland	DgDVT		x	x	x	x	x		
Eleocharis palustris	*Ep*DVT	x						x	
Equisetum arvense	*Ea*DVT	x							
Epilobium hirsutum	*Eh*DVT	x	x	x	x	x	x	x	x
Glyceria fluitans	*Gf*DVT							x	
Glyceria maxima	*Gm*DVT							x	x
Juncus conglomeratus	*Jc*DVT	x	x						
Juncus effusus	*Je*DVT	x	x	x	x	x		x	x
Open water	OwDVT	x	x		x		x	x	x
Potomageton natans	*Pn*DVT							x	
Ranunculus lingua	*Rl*DVT							x	
Ranunculus repens	*Rr*DVT				x				
Rubus fruticosus agg.	*Rf*DVT	x	x		x			x	
Rumex cf sanguineus	*Rs*DVT							x	
Schoenoplectus tabernaemontani	*St*DVT							x	
Trees	TreeDVT	x	x	x	x	x	x	x	x
Typha latifolia	*Tl*DVT	x	x	x	x	x		x	x
Urtica dioica	*Ud*DVT	x			x				
	Total number of DVTs	14	9	6	12	6	5	14	6

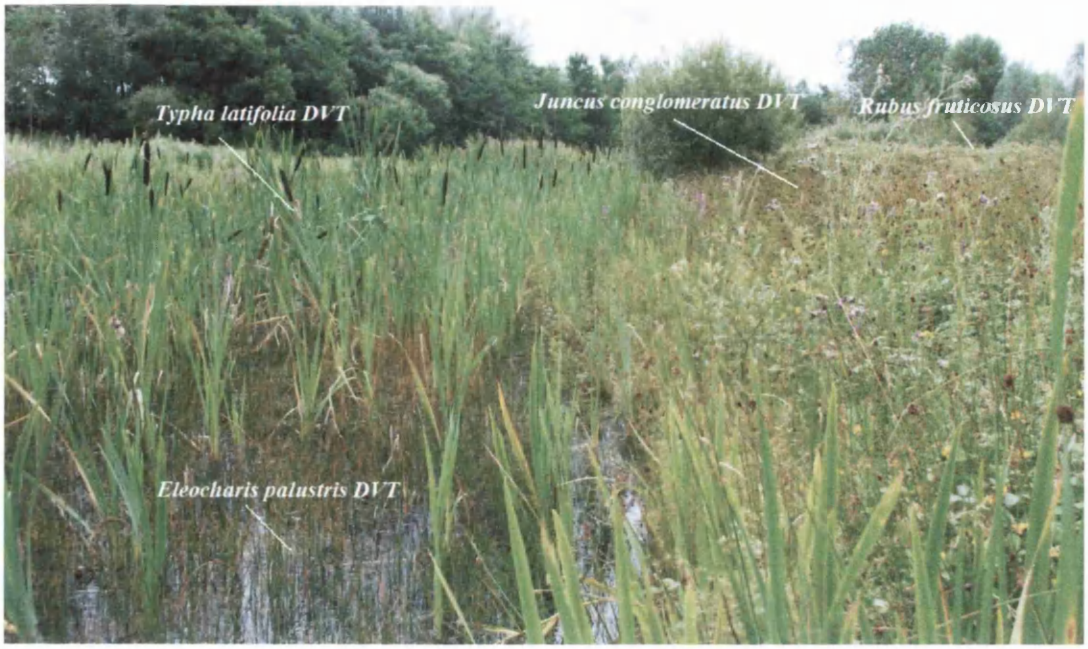


Figure 1.2 Pond A (east bank) with the dominant vegetation types (DVTs)

Figure 1.3 Pond A (west bank, trap A6) with the dominant vegetation types (DVTs)

Figure 1.4 Pond B (north bank, trap B4) with the dominant vegetation types (DVTs)

Figure 1.5 Pond B (south bank, trap B1) with the dominant vegetation types (DVTs)

Figure 1.6 Pond C (south bank, trap C2) with the dominant vegetation types (DVTs). There is no open water *per se*, with the pond itself consisting of a vast *Tl*DVT

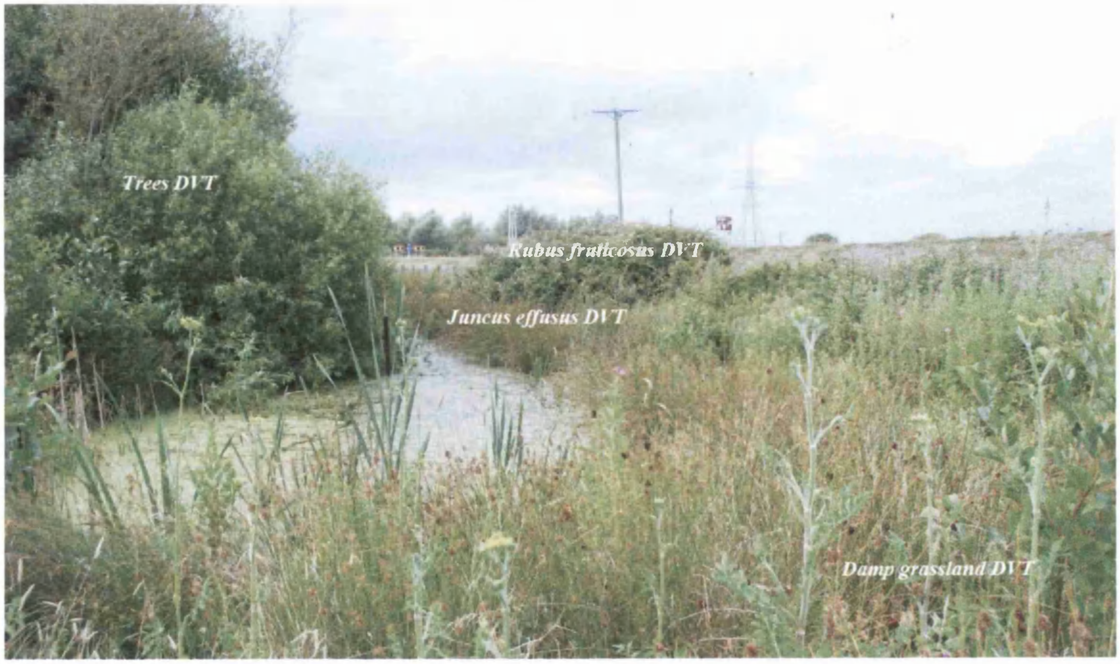


Figure 1.7 Pond D (north bank) with the dominant vegetation types (DVTs). Trap D1 was located in the *Rf*DVT. The DgDVT in the foreground is continuous with that on pond B (figures 1.1 and 1.4)

Figure 1.8 Pond D (south-west bank) with the dominant vegetation types (DVTs) and trap D2. *Holcus lanatus* (Yorkshire Fog) was present as a seasonal DVT plant species associate and was foraged upon intermittently (chapter 5)

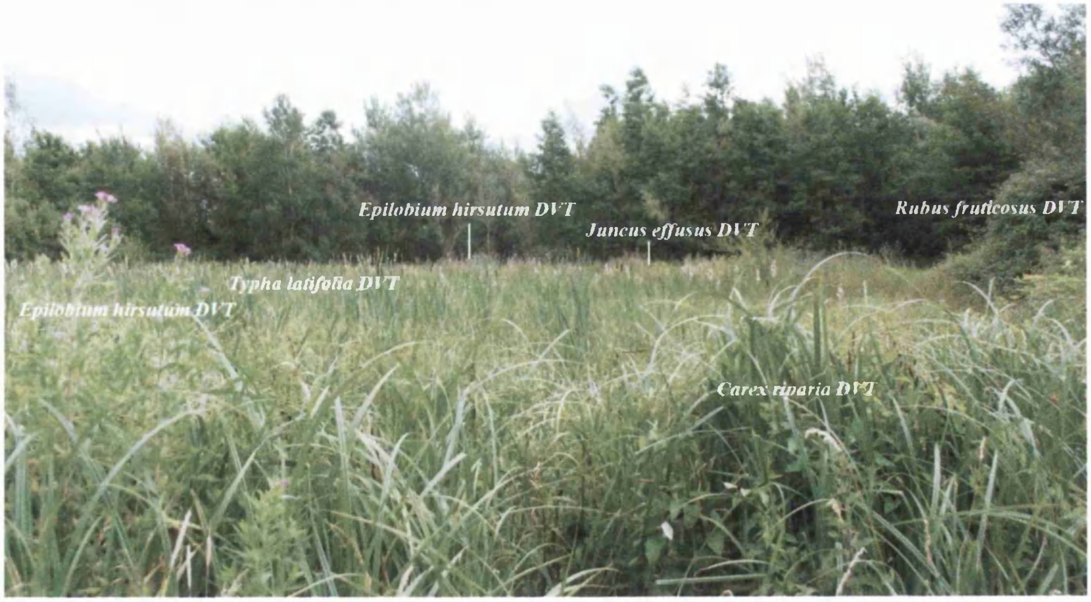


Figure 1.9 Pond E (north west bankside, trap E1) with the dominant vegetation types (DVTs). Pond E was located opposite pond C and was also dominated by a vast *Tl*DVT (figure 1.1)

Figure 1.10 Pond E (north bank, trap E5) with the dominant vegetation types (DVTs). This image illustrates the high diversity of the *Eh*DVT, with DVT plant species associates such as *Glyceria maxima, Filipendula ulmaria, Juncus effusus*, *Lysimachia vulgaris* visible

Figure 1.11 Pond F (view from path) with the dominant vegetation types (DVTs). This pond was dominated by trees, however, the *Bm*DVT was utilised by both male and female water voles during the breeding season in the peak density phase.

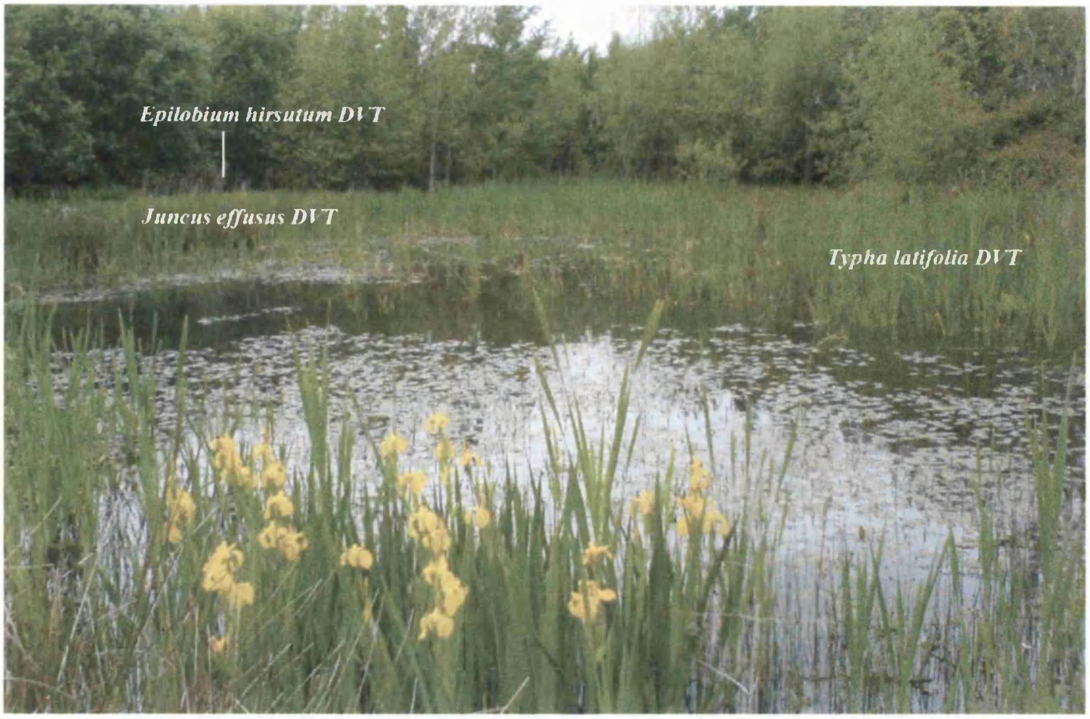


Figure 1.12 Pond G (view west bridge looking west) with dominant vegetation types (DVTs). *Iris pseudacorus* was present as a DVT plant species associate and an important seasonal component of the water vole diet

Figure 1.13 Pond G (view from E bridge looking north east) with the dominant vegetation types (DVTs)

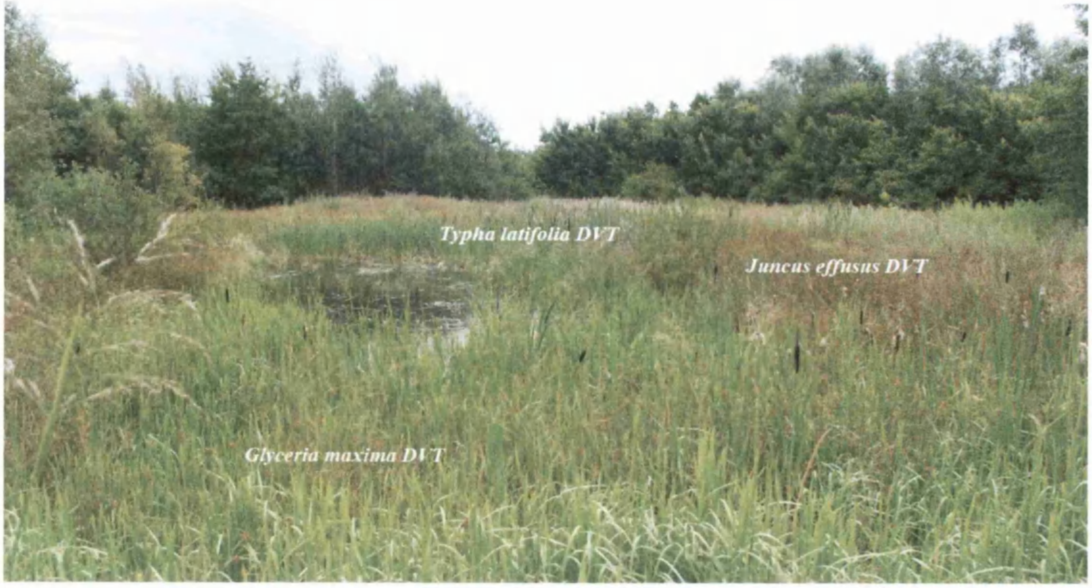


Figure 1.14 Pond H (view from the bridge looking east) with the dominant vegetation types (DVTs)

1.2.2 Length and area

There were 156 DVT patches within the 5 m boundary line, covering an area of 16,492.95 m^2 (table 1.2).

Table 1.2 Perimeter length of each trapped habitat (m) and area (m^2) encompassed by each pond (within the 5 m boundary line). Depth (m) of ponds also presented.

Pond	Perimeter of trapped habitat (m)	Area of trapped habitat (m^2)	Depth of trapped habitat (m)
A	160	2,678.58	1
B	100	3,452.52	1.5
C	100	933.01	1
D	160	3,653.63	2
E	120	1,335.68	0.8
F	40	478.53	1
G	360	3,412.99	0.75 to 1.5
H	80	548.01	1
Total	1,120	16,492.95	N / A

Table 1.3 Total number and area (m²) of Dominant Vegetation Type (DVT) patches (within the 5 m boundary line) across the wetland complex

Dominant Vegetation Type (DVT)	Total number of DVT patches	Total area (m²)	Mean patch area (m²)
Bolboschoenus maritimus	4	66.73	16.68
Carex riparia	8	320.16	40.02
Cirsium arvense	1	96.36	96.36
Crassula helmsii	1	79.42	79.42
Cyperus longus	1	11.33	11.33
Damp grassland	10	340.82	34.08
Eleocharis palustris	5	352.72	70.54
Epilobium hirsutum	12	470.05	39.17
Equisetum arvense	1	2.85	2.85
Glyceria fluitans	4	271.6	67.9
Glyceria maxima	1	56.75	56.75
Juncus conglomeratus	3	143.58	47.86
Juncus effusus	26	2571.37	98.90
Open water	11	2228.06	202.55
Potomageton natans	2	222.22	111.11
Ranunculus lingua	2	77.91	38.96
Ranunculus repens	2	68.11	34.06
Rubus fruticosus agg.	16	992.88	62.06
Rumex cf sanguineus	1	14.44	14.44
Schoenoplectus tabernaemontanii	1	15.88	15.88
Trees	24	5846.4	243.60
Typha latifolia	18	2203.29	122.41
Urtica dioica	2	40.02	20.01
Total	156	16,492.95	105.72

With the exception of trees, the most widespread DVT was the *Je*DVT, with 26 patches covering over 2500 m^2 of the area of wetland studied (within the 5 m boundary line), however, the *Tl*DVT had the largest mean patch area (122.41 m^2) with 18 patches covering approximately 2200 m^2.

1.2.3 DVTs as a measure of diversity at the habitat level (D_{pond})

Since water voles are predominantly patch-based foragers (chapter 5) the number of different plant patches may be an important determinant of their distribution. Due to the spacing of traps (every 20 m around the circumference of each pond) and the variability in patch size of each DVT (table 1.3), it was deemed appropriate to list all DVTs on each pond within the 5 m boundary line, even if they did not contain a trap. This highlighted the ponds that were the most diverse in terms of number of different DVTs, together with those that contained the most number of DVT patches. This provided a measure of habitat diversity (D_{pond}) and was calculated in a similar manner to the Shannon diversity index (Shannon & Weaver, 1949) (see methodology section 2.3).

Table 1.4 Total number of different DVTs, DVT patches and habitat diversity (D_{pond}) of each pond

Pond	Number of DVTs	Number of DVT patches	Habitat diversity (D_{pond})
A	14	26	2.33
B	9	20	2.18
C	6	10	1.70
D	12	38	2.24
E	6	10	1.67
F	5	5	1.60
G	14	40	2.67
H	6	7	1.75

A difference in habitat diversity (D_{pond}) was observed between ponds. Ponds A and G both had the greatest number of different DVTs (14) and the highest habitat diversities (D_{pond}); however, pond G had the greatest number of DVT patches (40) and therefore represented the most heterogeneous habitat. Pond D also represented a diverse habitat, with a large number of DVT patches (38). Pond B had 9 DVTs consisting of 20 DVT patches, however, these were restricted to slender patches entirely flanked by wet woodland. Ponds C and E represent the only two ponds without any open water, with extensive *TI*DVTs. Pond F was the least diverse, with the lowest habitat diversity (D_{pond}), and the least number of DVTs and patches. *G*-tests of homogeneity revealed that there was no significant difference between the total number of different DVTs per pond ($G_7 = 5.243$, $p = 0.608$) however, there was a significant difference in the total number of DVT patches per pond ($G_7 = 32.63$, $p < 0.0001$). Ward's agglomerative cluster analysis (Euclidian distance) clustered ponds based on their habitat diversity (D_{pond}) (figure 1.15). The major division sub-divided the eight ponds into two groups; ponds A, B, D and G in the first cluster were the most diverse habitats and ponds C, E, F and H in the second cluster were the least diverse habitats.

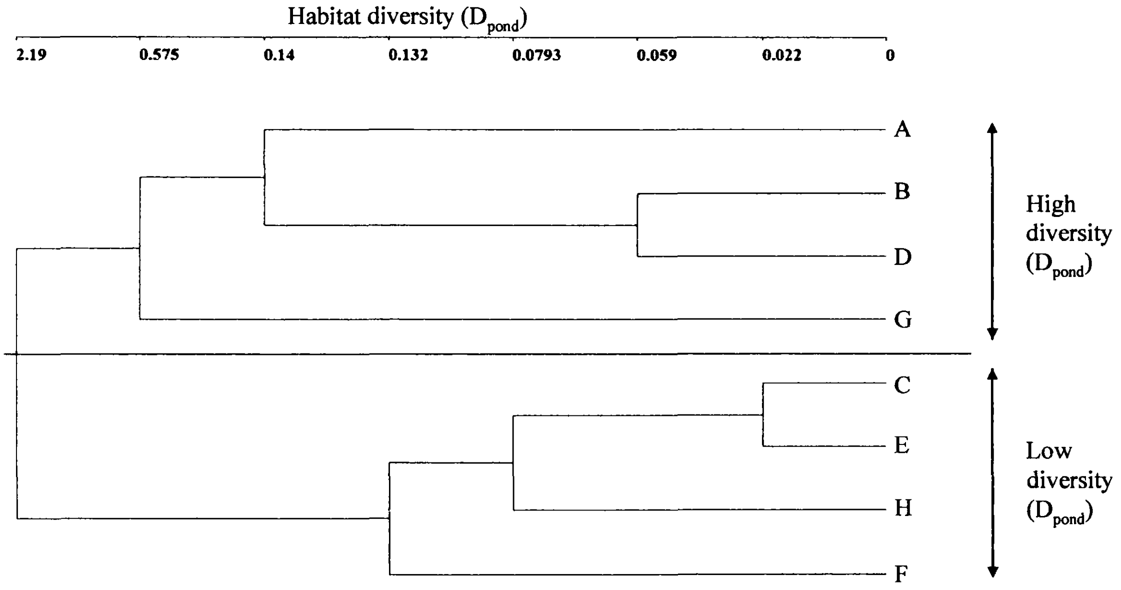


Fig 1.15 Ward's Agglomerative Cluster Analysis (Euclidian distance) of ponds (A to H) based on habitat diversity (D_{pond})

1.2.4 Habitat diversity (D_{pond}) – does size matter?

Linear regression analysis revealed that habitat diversity (D_{pond}) corresponds positively and significantly with the length ($R^2 = 0.714$, $F_{1,7} = 21.74$, $p = 0.003$) (figure 1.16) and area ($R^2 = 0.786$, $F_{1,7} = 15.13$, $p = 0.008$) (figure 1.17) of trapped habitat. Pond F had the shortest circumference, covered the smallest area and had the lowest habitat diversity. In contrast, pond G had the largest circumference and the highest habitat diversity (tables 1.2 and 1.4).

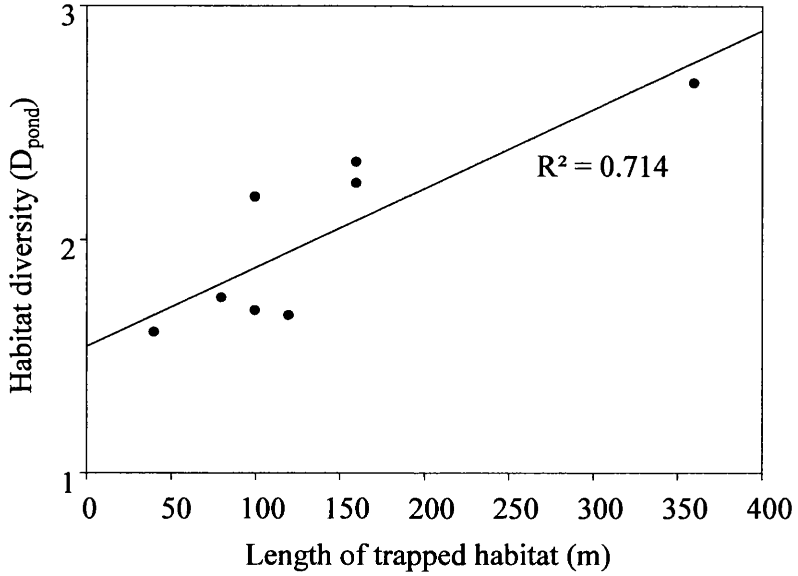


Figure 1.16 Linear regression of habitat diversity (D_{pond}) against length of trapped habitat

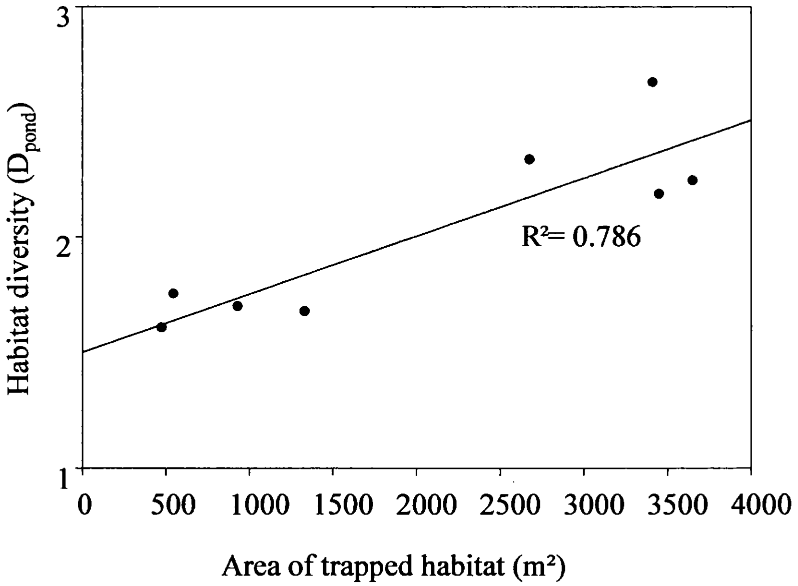


Figure 1.17 Linear regression of habitat diversity (D_{pond}) against area of trapped habitat

1.2.5 How well do DVTs reflect the plant species diversity of the ponds?

Pond D had the greatest number (62) of plant species (figure 1.18). *G*-tests of homogeneity revealed that there was a significant difference between the total number of plant species per pond ($G_7 = 15.06$, $p = 0.035$). A significant positive relationship ($R^2 = 0.845$, $F_{1,7} = 32.735$, $p = 0.001$) was observed between the total number of different DVTs and the total number of plant species present per pond (figure 1.19).

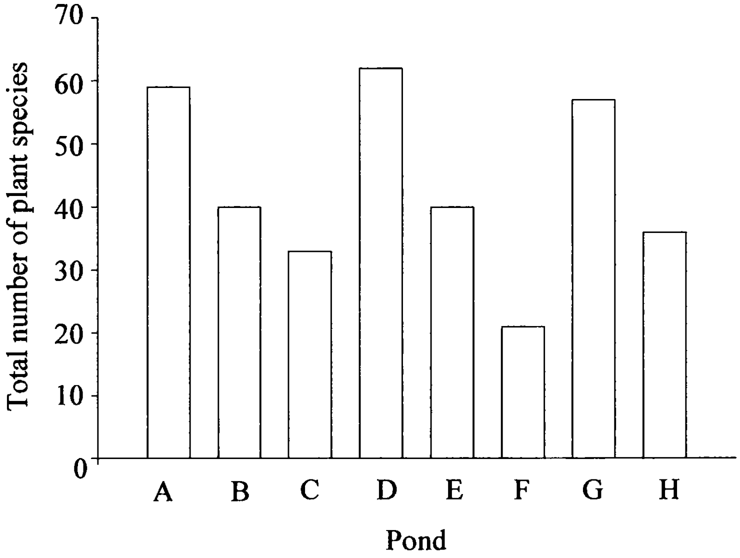


Figure 1.18 Total number of plant species per pond (see appendix for species lists)

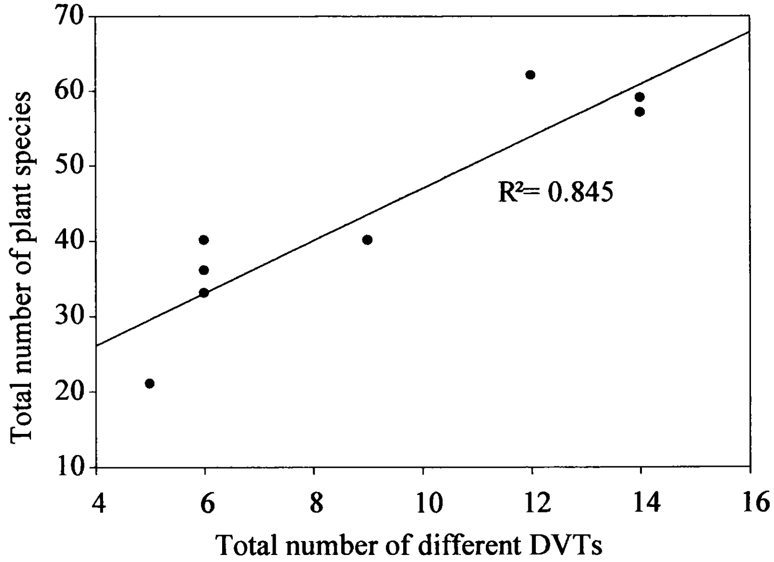


Figure 1.19 Linear regression of total number of plant species against the total number of different DVTs

1.2.6 DVT plant species associates

The DgDVT and the *Eh*DVT had the greatest number of associated plant species (n = 34) (tables 1.7 and 1.8). In contrast the *Rf*DVT had no associated plant species and consisted of 100% cover of the dominant species (table 1.13). The following tables present plant species lists compiled from quadrat sampling (n = 50) of ten different DVTs within the 5 m boundary line. The presence and abundance of these associate plant species were not used to define the DVT map (figure 1.1) (methodology section 4) but were used to calculate the diversity of each DVT (D_{DVT}) (section 1.3.7 and appendix 3) and often featured in the water vole diet (chapter 5).

Table 1.5 Plant species occurring in the *Bolboschoenus maritimus* DVTs

Bolboschoenus maritimus	**Sea Club-rush**
Agrostis stolonifera	Creeping Bent grass
Bolboschoenus maritimus	Sea Club-rush
Carex otrubae	False Fox Sedge
Crassula helmsii	New Zealand Pigmyweed
Epilobium hirsutum	Great Willowherb
Juncus effusus	Soft Rush
Iris pseudacorus	Yellow Iris
Lotus pedunculatus	Marsh Bird's-foot Trefoil
Plantago lanceolata	Ribwort Plantain
Rubus fruticosus	Bramble
Schoenoplectus tabernaemontani	Grey Club-rush
Mean % cover of dominant species	81%
Total number of species	11

Table 1.6 Plant species occurring in the *Carex riparia* DVTs

Carex riparia	**Greater-Pond Sedge**
Calystegia sepium	Hedge Bindweed
Carex riparia	GreaterPond-sedge
Galium palustre	Marsh Bedstraw
Iris pseudacorus	Yellow Iris
Lemna minuta	Least Duckweed
Ranunculus flammula	Lesser Spearwort
Rumex hydrolapathum	Water Dock
Typha latifolia	Bulrush
Mean % cover of dominant species	95%
Total number of species	8

Table 1.7 Plant species occurring in the damp grassland DVTs

Damp grassland	
Achillea millefolium	Yarrow
Agrostis stolonifera	Creeping Bent-grass
Ajuga reptans	Bugle
Arrenatherum elatius	False Oat-grass
Carex otrubae	False Fox-sedge
Cirsium palustre	Marsh Thistle
Cynosurus cristatus	Crested Dog's-tail
Dactylis glomerata	Cock'sfoot
Dactylorhiza praetermissa	Southern Marsh-orchid
Epilobium hirsutum	Great Willowherb
Equisetum arvense	Field Horsetail
Gallium aperine	Cleavers
Gallium palustre	Marsh Bedstraw
Heracleum sphondylium	Hogweed
Holcus lanatus	Yorkshire Fog
Juncus effusus	Soft Rush
Juncus inflexus	Hard Rush
Leucanthemum vulgare	Oxeye Daisy
Lotus corniculatus	Common Bird's-foot-trefoil
Lotus pedunculatus	Marsh bird's foot trefoil
Pastinaca sativa	Wild Parsnip
Plantago lanceloata	Ribwort Plantain
Potentilla anserina	Silverweed
Pulicaria dysenterica	Common Fleabane
Ranunculus acris	Meadow Buttercup
Ranunculus repens	Creeping Buttercup
Rumex obtusifolius	Broad leaved dock
Silene dioica	White Campion
Stellaria media	Common Chickweed
Taraxacum agg	Dandelion
Trifolium pratense	Red Clover
Trifolium repens	White Clover
Urtica dioica	Common Nettle
Viccia sativa	Tufted Vetch
Mean % cover of dominant species	N /A
Total number of species	34

Table 1.8 Plant species occurring in the *Epilobium hirsutum* DVTs

Epilobium hirsutum	**Great Willowherb**
Achillea millefolium	Yarrow
Agrostis capillaries	Common Bent-grass
Alopecurus pratensis	Meadow Fox-tail
Anthoxanthum odoratum	Sweet Vernal-grass
Calystegia sepium	Hedge Bindweed
Carex hirta	Hairy Sedge
Carex otrubae	False Fox-sedge
Chrysanthemum leucanthemum	Oxeye Daisy
Cirsium vulgare	Spear Thistle
Dactylorhiza praetermissa	Southern-Marsh-orchid
Epilobium hirsutum	Great Willowherb
Epilobium palustre	Marsh Willowherb
Epilobium tetragonum	Square-stalked Willowherb
Equisetum arvense	Field Horsetail
Festuca rubra	Red Fescue
Galium aparine	Cleavers
Geranium dissectum	Cut-leaved Crane's-bill
Holcus lanatus	Yorkshire Fog
Juncus effusus	Soft Rush
Juncus inflexus	Hard Rush
Lathyrus pratensis	Meadow Vetchling
Lotus pedunculatus	Marsh Bird's-foot-trefoil
Myosotis scorpioides	Water Forget-me-not
Plantago lanceolata	Ribwort Plantain
Poa trivialis	Rough Meadow-grass
Polygonum lapathifolia	Pale Persicaria
Potentilla anserina	Silverweed
Ranunculus repens	Creeping Buttercup
Rumex crispus	Curled Dock
Rumex obtusifolius	Broad-leaved Dock
Silene dioica	Red Campion
Trifolium repens	Red Clover
Urtica dioica	Common Nettle
Vicia sativa	Common Vetch
Mean % cover of dominant species	49%
Total number of species	34

Table 1.9 Plant species occurring in the *Eleocharis palsutris* DVTs

Eleocharis palustris	**Common Spike-rush**
Agrostis stolonifera	Creeping Bent-grass
Alisma plantago-aquatica	Water-plantain
Azolla filicoides	Water Fern
Callitriche stagnalis	Common Water-starwort
Cardamine pratensis	Cuckooflower
Eleocharis palustris	Common Spike-rush
Galium palustre	Marsh Bedstraw
Glyceria fluitans	Floating Sweet-grass
Hippurus vulgaris	Mare's-tail
Iris pseudacorus	Yellow Iris
Juncus acutiflorus	Sharp-flowered Rush
Juncus articulatus	Jointed Rush
Lemna minuta	Least Duckweed
Lemna trisulca	Ivy-leaved Duckweed
Mentha aquatica	Water Mint
Schoenoplectus tabernaemontani	Grey Club-rush
Typha latifolia	Bulrush
Mean % cover of dominant species	23%
Total number of species	17

Table 1.10 Plant species occurring in the *Juncus effusus* DVTs

Juncus effusus	**Soft rush**
Alopecurus pratensis	Meadow Fox-tail
Callitriche stagnalis	Common Water-starwort
Epilobium palustre	Marsh Willowherb
Galium aparine	Cleavers
Holcus lanatus	Yorkshire Fog
Juncus effusus	Soft Rush
Lemna minuta	Least Duckweed
Lotus pedunculatus	Marsh Bird's-foot-trefoil
Polygonum lapathifolium	Pale persicaria
Ranunculus repens	Creeping Buttercup
Rumex crispus	Curled Dock
Typha latifolia	Bulrush
Urtica dioica	Common Nettle
Mean % cover of dominant species	82%
Total number of species	13

Table 1.11 Plant species occurring in the *Juncus conglomeratus* DVTs

Juncus conglomeratus	**Compact rush**
Agrostis canina	Velvet Bent-grass
Agrostis stolonifera	Creeping Bent-grass
Alopecurus pratensis	Meadow Fox-tail
Cirsium arvense	Creeping Thistle
Cirsium palustre	Marsh thistle
Dactylorhiza praetermissa	Southern Marsh-orchid
Epilobium montanum	Broad-leaved Willowherb
Eupatorium cannabinum	Hemp Agrimony
Gallium aperine	Cleavers
Gallium palustre	Marsh Bedstraw
Holcus lanatus	Yorkshire Fog
Iris pseudacorus	Yellow Iris
Juncus conglomeratus	Compact Rush
Juncus effusus	Soft Rush
Lotus pedunculatus	Marsh Bird's-foot-trefoil
Lycopus europaeus	Gypsywort
Mentha aquatica	Water Mint
Pulicaria dysenterica	Common Fleabane
Ranuculus repens	Creeping Buttercup
Ranunculus acris	Meadow Buttercup
Rubus fruticosus	Bramble
Rumex acetosa	Common Sorrel
Taraxacum agg	Dandelion
Typha latifolia	Bulrush
Mean % cover of dominant species	43%
Total number of species	24

Table 1.12 Plant species occurring in the *Glyceria maxima* DVTs

Glyceria maxima	**Floating Sweet-grass**
Agrostis stolonifera	Creeping Bent-grass
Epilobium palustre	Marsh Willowherb
Epilobium tetragonum	Square-stalked Willowherb
Filipendula ulmaria	Meadowsweet
Galium palustre	Marsh Bedstraw
Glyceria maxima	Reed Sweet-grass
Juncus effusus	Soft Rush
Lemna minuta	Least Duckweed
Lysimachia vulgaris	Yellow Loosestrife
Lythrum portula	Water Purselane
Ranunculus flammula	Lesser Spearwort
Mean % cover of dominant species	81%
Total number of species	11

Table 1.13 Plant species occurring in the *Rubus fruticosus* DVTs

Rubus fruticosus	**Bramble**
Rubus fruticosus	Bramble
Mean % cover of dominant species	100%
Total number of species	1

Table 1.14 Plant species occurring in the *Typha latifolia* DVTs

Typha latifolia	**Bulrush**
Callitriche stagnalis	Common Water- starwort
Cardamine pratensis	Cuckooflower
Eleocharis palustris	Common Spike-rush
Galium palustre	Marsh Bedstraw
Glyceria fluitans	Floating Sweet-grass
Lemna minuta	Least Duckweed
Lemna trisulca	Ivy-leaved Duckweed
Lysimachia vulgaris	Yellow Loosestrife
Mentha aquatica	Water Mint
Schoenoplectus tabernaemontani	Grey Club Rush
Typha latifolia	Bulrush
Mean % cover of dominant species	40%
Total number of species	11

1.2.7 DVT patch diversity (D_{DVT})

The diversity of each dominant vegetation type (D_{DVT}) was determined (see methodology 2.3). The DgDVT was the most diverse dominant vegetation type (34 species, $D_{DVT} = 2.291 \pm 0.059$) (tables 1.7 and 1.15) with *Rf*DVT representing the least diverse DVT (1 species, $D_{DVT} = 0$) (tables 1.13 and 1.15), associated with 100% cover of the dominant species. With the exception of the homogeneous patches of *Rf*DVTs, the *Bm*DVTs and the *Je*DVTs were associated with the lowest patch diversity ($D_{DVT} = 0.677 \pm 0.061$ and 0.714 ± 0.152, respectively). Ward's agglomerative cluster analysis (Euclidian distance) clustered the DVTs according to their patch diversity (D_{DVT}) (figure 1.20). The major division sub-divided the ten DVTs into two groups; with the least diverse DVTs in the first cluster (the *Rf*DVT, the *Bm*DVT, the *Tl*DVT, the *Cr*DVT, the *Je*DVT and the *Gm*DVT) and the most diverse DVTs in the second cluster (the DgDVT, the *Ep*DVT, the *Eh*DVT and the *Jc* DVT) (figure 1.20).

Table 1.15 Diversity of dominant vegetation types (D_{DVT}) per quadrat. Mean (D_{DVT}) ± SE is also presented

DVT	Q1	Q2	Q3	Q4	Q5	Mean (± SE) D_{DVT}
*Bm*DVT	0.765	0.585	0.808	0.741	0.485	0.677 ± 0.061
*Cr*DVT	0.748	0.693	0.798	0.301	0.353	0.579 ± 0.104
DgDVT	2.243	2.51	2.217	2.309	2.176	2.291 ± 0.059
*Ep*DVT	1.253	1.313	1.319	1.746	0.481	1.222 ± 0.205
*Eh*DVT	1.383	0.897	1.906	1.274	1.419	1.376 ± 0.162
*Gm*DVT	1.13	0.306	0.472	0.858	0.994	0.752 ± 0.156
*Jc*DVT	1.748	1.615	1.506	1.555	1.734	1.632 ± 0.048
*Je*DVT	0.691	0.784	1.222	0.287	0.587	0.714 ± 0.152
*Rf*DVT	0	0	0	0	0	0
*Tl*DVT	0.525	0.984	0.673	0.678	0.76	0.724 ± 0.075

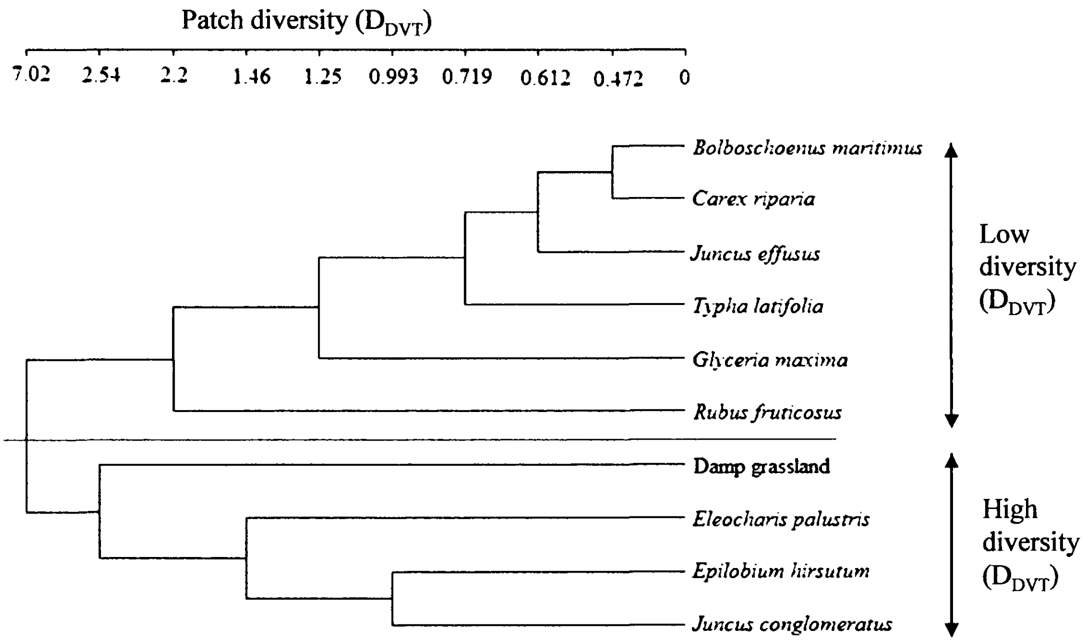


Figure 1.20 Ward's Agglomerative Cluster Analysis (Euclidian distance) of dominant vegetation types (DVTs) based on their patch diversity (D_{DVT})

1.3 Discussion

1.3.1 Dominant vegetation types (DVT)

The data presented in this chapter provide a basis for describing the matrix habitat, which underpins the study of water vole ecology at the patch-landscape scale. Furthermore, this method of mapping the vegetation, using dominant vegetation types (DVT) offers an alternative to Phase 1 mapping (NCC, 1990) which adds detail at the patch level, minimises observer variation and can be achieved with minimal botanical knowledge. Indeed, wetlands often consist of large, homogeneous patches (e.g. distinct beds dominated by rhizomal or clonal reed-like graminoid species or forbs) that occur within the broad Phase 1 habitat, which make them particularly suitable for this type of patch-habitat classification. The area of wetland complex studied at NWCW contained 31 different DVTs, although only 23 of these were located within the 5 m boundary line (buffer) of the ponds. No two ponds contained the same assemblage or arrangement of DVT patches. With the exception of trees, the *Epilobium hirsutum* DVT was the only dominant vegetation type present on every pond (figure 1.1, table 1.1). The variation in utilisation of each DVT by water voles is explored in later chapters (4 and 5).

Habitats are usually defined in terms of the vegetation they contain. Predicting where mammals are with respect to particular habitats depends on an understanding of how they use space. Broadly, space influences animals firstly by providing the base from which they obtain resources and secondly, as the medium through which they have to disperse in order to find new resources (Macdonald & Rushton, 2003). Knowledge of the way in which organisms select habitat is useful for understanding the components that govern ecological systems, but also for predicting changes in community structure that might follow natural or anthropogenic alterations of ecosystems (Dunning *et al.*, 1995). Landscapes are naturally heterogeneous, consisting of a mosaic of various habitat types and most species will thus encounter their preferred habitat as patches embedded in a matrix of less favourable habitats (Forman & Godron, 1981; 1986). The persistence of species living in fragmented environments often depends on the matrix habitat allowing for movement between patches (Hanski & Gilpin, 1997).

1.3.2 Length and area

In this investigation, water voles were studied in a total area of 66,142.24 m^2 (figure 1.1). The area of habitat encompassed by the 5 m buffer around each pond was 16,492.95 m^2, with water vole traps set along a length of just over a kilometre (1120 m) (see methodology). Although this area is not large enough to be classified as a landscape *per se* (Fischer & Lindenmayer, 2007), it does fall within the scale of patch-landscape (McGarigal & Cushman, 2002) that also includes detail of the matrix habitat, which is an important parameter that is often overlooked in studies of European mammals (Mortelliti *et al.*, 2010). The *Tl*DVT (i.e. homogenous patches of vegetation dominated by *Typha latifolia*) was associated with the largest patch areas (mean 122.41 ± 42.15 m^2). This species is known to competitively displace other species as it matures and develops dense foliage (Hewitt & Miyanishi, 1997). However, *Typha latifolia* releases oxygen from its root into the soil facilitating the growth of certain Willow (*Salix* sp.), which alone are unable to tolerate anoxic soil (Callaway & King, 1996). Effectively, the presence of *Typha latifolia* drives the process of wetland succession.

The *Je*DVT was the most widespread, with the greatest number of patches (26) covering the greatest total area (2571.37 m^2). *Juncus effusus* is capable of vegetative reproduction and can form extensive clonal patches due to the growth of rhizomes (Richards & Clapham, 1941; Grime *et al.*, 1990). The expansion of *Juncus effusus* tussocks, as populations become established, can alter the wetland community composition greatly, since shading by *Juncus effusus* affects cover and species richness in the surrounding plant community (Ervin & Wetzel, 2002).

Others, such as the *Cl*DVT occurred in localised areas with only one patch in the study site (pond A), covering an area as little as 11.33 m^2. Due to the small size and location of this DVT, no water vole trap was located in this vegetation type (see methodology). Nevertheless, its importance should not be underestimated since it was utilised by water voles, revealed by the presence of characteristic field signs (chapter 5). *Cyperus longus* is a Red Data List species in Britain (Status: Near threatened) (Cheffings & Farrell, 2005). It is a lowland species of marshy pond margins, ditches and flushes, mainly in coastal areas. It is very local and has decreased in recent years, through drainage of suitable habitats (Jermy *et al.*, 2007).

1.3.3 DVTs as a measure of diversity at the habitat level (D_{pond})

The arrangement of DVT patches within the habitat determined the diversity of the habitat (D_{pond}). A greater number of DVTs indicated a more diverse habitat and the pond with the greatest number of DVT patches represented the most diverse habitat in terms of patch distribution across the vegetation mosaic. Ponds A and G had the greatest number of different DVTs (14), with ponds D and G also having the greatest number of patches (38 and 40 respectively). Consequently these ponds (A, D and G) had the highest habitat diversity (D_{pond}). The relationship between water voles and diversity at the habitat level (D_{pond}) is explored in chapter 4.

1.3.4 Habitat diversity (D_{pond}) - does size matter?

A positive relationship was observed between habitat diversity (D_{pond}) and the size of the habitat (figures 1.19 and 1.20), with larger ponds typically being more diverse. This result may seem unsurprising, since the positive relationship between species richness and area is a fundamental one in ecological theory (MacArthur & Wilson, 1967). However, here it is shown that this relationship can also be applied to habitat area and patch diversity at the patch-landscape scale.

Riparian vegetation provides both shelter and food for water voles (Barreto *et al.*, 1998b; Macdonald & Strachan, 1999; Strachan & Moorhouse, 2006) and so increasing its width over a given length of water course may lead to increased survival rates (Moorhouse *et al.*, 2009) by increasing the abundance and diversity of food (Efford, 1985) and reducing predation risk (Barreto *et al.*, 1998b). Water voles spend the majority of their time within 1 or 2 m of the water's edge, in tall riparian plant communities (Lawton & Woodroffe, 1993; Macdonald & Strachan, 1999; Stoddart, 1970; Strachan & Moorhouse 2006) in an ecotonal habitat representing the transition from dry grassland communities to tall herb, emergent and aquatic vegetation (Moorhouse *et al.*, 2009). Variation in the width of vegetation between sites may translate into differences in forage ability (chapter 5) and demographic rates (chapter 2) in water voles (Moorhouse *et al.*, 2008). Large quantities of vegetation promote higher likelihood of establishment, higher survival rates for established animals and higher population densities (Moorhouse *et al.*, 2009). The rationale underpinning the 5 m buffer around each pond is outlined in chapter 5. This boundary was selected since it affords an additional 3 to 4 m of riparian habitat to the 1 to 2 m of bankside adjacent to the water's edge, where water voles typically operate (Lawton & Woodroffe, 1993; Macdonald & Strachan, 1999; Stoddart, 1970; Strachan & Moorhouse 2006, Neyland *et al.*, 2010). Additionally, water voles were seen to utilise these areas (and beyond) during inter-pond movements and dispersals (chapters 2 to 4).

1.3.5 How well do DVTs reflect the diversity of the ponds?

A strong positive relationship (figure 1.19) was observed between the total number of different DVTs per pond and the total number of plant species present (within the 5 m boundary). Ponds A, D and G had the highest number of plant species present (figure 1.18), the greatest numbers of different DVTs and the highest habitat diversities (D_{pond}) (table 1.4). Thus, these three ponds represent high diversity habitats not only in terms of patch diversity but also in terms of plant species richness. The positive relationship between the total number of different DVTs per pond and the total number of plant species present arises, since each DVT patch is itself a plant community and therefore has an associated suite of plant species (tables 1.5 to 1.14). Increasing the variety of DVTs in a given habitat, increases the likelihood of encountering the differing plant species associated with each DVT. The positive relationship between the total number of DVTs and total number of plant species present adds a practical element to the DVT mapping approach. Firstly, the ability to classify habitats on their quality using methods described here requires only the ability to delimit homogeneous stands of vegetation and to identify the dominant vegetation type in each stand. At NWCW there were only twenty-three different DVTs (within the 5 m boundary line of each pond) and thus even with a limited botanical knowledge it is possible to create both a DVT map and to determine habitat diversity (D_{pond}). This has practical implications for managers both at this site (to monitor both vegetation succession and water vole populations) and other sites (to develop future databases and allow comparisons between sites). The practical application of this approach in relation to monitoring water vole populations is explored in chapter 4. Secondly, a measurement of DVT diversity provides an easy surrogate measure of species diversity.

1.3.6 DVT plant species associates and patch diversity (D_{DVT})

A full species inventory was undertaken for each pond. In total, 129 plant species were identified across the area of wetland complex studied (c.f. only 23 DVTs). Both the DgDVT and the *Eh*DVT had the greatest number of associated plant species (34 species; tables 1.6 and 1.7). In contrast, the *Rf* DVT had no community associates (table 1.12) due to 100% continuous cover of a single species. Ward's cluster analysis (figure 1.20) distinguished the DgDVT as the most diverse (D_{DVT} = 2.291) since it was the least similar to the *Rf*DVT, the latter of which was typically associated with a diversity (D_{DVT}) of zero. Although the DVTs provided both food and cover for water voles, field surveys here revealed that foraging choices did not always reflect the most abundant species in the vicinity (chapter 5) and thus the DVT plant species associates may be equally important to water voles as the DVTs themselves. Furthermore, since it is the variety and abundance of plant species associates that determines the diversity of each DVT patch, these species are an important contribution to the diversity of each dominant vegetation type (D_{DVT}). Additionally, this verifies the contention that both richness and abundance (of plant species, or in this case, DVTs) are important determinants of diversity (Magurran, 1988). The relationship between water voles and the diversity of DVTs at the patch level (D_{DVT}) is explored in chapter 4.

1.3.7 How can the DVT method be implemented practically?

Previous studies of southern red-backed voles (*Clethrionomys gapperi*) inhabiting forests in the southern Appalachian Mountains, USA, revealed that vole presence and abundance were most evident at the high resolution (macrohabitat) scale, with this species utilising and selecting from a discrete portion of the complex landscape (Orrock *et al.*, 2000). This concurs with the findings of this study (chapters 2 to 6). It is likely that voles exploit different portions of the macrohabitat because resource requirements, predation risk and social status vary with sex and age (Nordahl & Korpimäki, 1998). Indeed, it is also possible that scales of habitat selection and utilisation vary among individuals of different sex and age (chapter 4), as each vole's perception of opportunities and subsequent selection may be a function of their position in the social hierarchy (Mihok, 1979; Bondrup-Nielson, 1987). Additionally, macro-habitat data, (or in this case delineating the DVTs) that are useful for predicting vole abundance can be gathered with a minimal investment of field time, as plant communities and site attributes (or in this case the DVT patches) are relatively easy to identify and quantify. In this manner, managers can assess habitats in a hierarchical manner and can identify areas of concern efficiently (Orrock *et al.*, 2000).

The development of site-specific ‘condition indicators’, a protocol which describes a suite of attributes and targets used as evidence for the condition of a habitat (or species), enables the site manager to recognise when the key habitat is in a state of high conservation value (Hurford, 2010). Condition indicators should incorporate knowledge from both research and site-based surveillance, and comprise a target for both the overall extent of the broad habitat and the extent of good quality habitat, together with unambiguous definitions for both the broad and good quality habitats in a concise and transparent form (Hurford, 2010). Since this study was based on a pond system, it provided important information regarding the ecology of water voles on non-linear habitats that may be implemented in future models to predict water vole distribution. In addition, it allowed a condition indicator table to be created (chapter 6), providing clear practical guidance for NWCW managers. It outlines how to maintain areas of good quality habitat and enhance potential areas through habitat creation in accordance with the site-specific conditions outlined in the table. Furthermore, it provided a method of delineating patch boundaries that could be implemented across a range of water vole habitats that would not only offer a standardised method of monitoring habitat utilisation by water voles, but would also allow the process of vegetation succession to be monitored. This is particularly important in wetland habitats that are susceptible to encroachment by trees, or aggressive growth of species that can form large homogenous stands (e.g. *Typha latifolia*) (Cronk & Fennessey, 2001) thereby reducing both species and habitat diversity, and subsequently habitat suitability for water voles. Additionally, the spread of invasive non-native plant species, such as New Zealand Pigmyweed (*Crassula helmsii*) on pond D, can be monitored using the DVT mapping technique. The management of non-native species will play a critical role in the future maintenance of natural biodiversity in wetland habitats.

Summary

- Twenty-three dominant vegetation types (DVTs) were delineated and described within the 5 m boundary of the ponds in the area of NWCW studied
- Ponds D and G covered the largest area in the wetland complex
- With the exception of trees, the *Epilobium hirsutum* DVT was the only one to occur on all ponds across the wetland complex
- Both damp grassland DVTs and *Epilobium hirsutum* DVTs had the greatest number of associated plant species and the highest patch diversities (D_{DVT})
- The *Juncus effusus* DVT was the most widespread DVT
- With the exception of the *Rubus fruticosus* DVT, which had a patch diversity (D_{DVT}) of zero, the *Juncus effusus* DVT had the lowest patch diversity (D_{DVT})
- The *Typha latifolia* DVT had the largest mean patch area and was also associated with lower patch diversities (D_{DVT})
- Ponds A, D and G had the highest habitat diversity (D_{pond})
- There was a significant positive correlation between both the length and area of a pond and the diversity of the habitat (D_{pond})
- There was a significant positive correlation between the habitat diversity (D_{pond}) of each pond and the total number of plant species present
- It follows that habitat diversity (D_{pond}), based on DVT types and patches, not only provides a measure of habitat diversity but also a surrogate measure of total species richness per pond
- The practical application of the DVT mapping approach allows the stages of wetland succession to be monitored, identifies areas of high biodiversity and provides a baseline on which to monitor both the distribution and movements of animal species and the spread of invasive alien plant species
- Implementation of this method will reduce both time and the need for specialist field surveyors, thereby facilitating management practices if applied at a national level

Chapter 2

Population Ecology

'Animals arrived, liked the look of the place, took up their quarters, settled down, spread, and flourished. They didn't bother themselves about the past - they never do; they're too busy'

Kenneth Grahame (The Wind in the Willows, 1908)

2.1 Introduction

Water vole population densities in Europe

Spatial dynamics models (incorporating the use of environmental, habitat and animal population information) have revealed that the most significant predictors of water vole population size in the UK are the carrying capacity of the habitat and the annual number of litters (Macdonald & Rushton, 2003). Even within a suitable habitat, water vole population densities can vary with habitat and season. According to Strachan and Moorhouse (2006), estimates of water vole population densities in linear English habitats have ranged from 2.4 to 14.0 animals per 100 m (table 2.1). Indeed, water vole densities in excess of 200 to 600 animals per hectare have been recorded in France, where this animal is considered a serious agricultural pest and control measures have been implemented to buffer these population 'outbreaks' (Giradoux *et al.*, 1997) (Introduction p3).

Table 2.1 Water vole population density per habitat type (after Strachan & Moorhouse, 2006)

English site	Habitat type	Water vole population density
West Lancashire	Dyke system	2.4 per 100 m
North Yorkshire	Moorland	3.3 per 100 m
Bure Marshes, Norfolk	Fen (ditches)	6.1 per 100 m
Slimbridge WWT	Wetland	14.0 per 10 0m
Redgrave, Suffolk	Fen	25-30 per hectare
Brownsea Island, Dorset	Reedbed	45-50 per hectare

Over-winter survival of water voles in Britain

Life expectancy of water voles is typically three to four months; however, in exceptional cases animals may live up to three years. During the non-breeding, over-winter period, wild water vole populations typically experience a 70% reduction in numbers (Carter & Bright, 2000; Strachan & Moorhouse, 2006). Breeding "colonies" may consist of as few as ten adults, dropping to as little as two or three in the winter (Lawton & Woodroffe, 1991). Studies of survival rates of juvenile water voles in Scotland have shown that only young born early in the breeding season survived and recruited into the adult breeding population the following year; however, young born in the latter half of the breeding season did not survive the winter (Stoddart, 1971). Typically, the water vole breeding season lasts from March to September (Corbert & Harris, 1993). However, water voles at NWCW remained active all year round, where vegetation cover persisted (Forman, 2005; pers. obs.) and juveniles born in October were caught during the winter in this study. Accordingly, winter here was defined as the months outside the breeding season at NWCW, November 1st to February 28th inclusive (see Methodology, section 5.1).

Sex ratios in water voles

Fisher's sex ratio theory states that an even offspring ratio is typically observed (Fisher, 1930). Since this assumes homogenous and panmitic populations, deviations from the 1:1 rule may be expected, depending on the spatial structure of the population, in concert with the specific type of mating system. Moreover, the increasing extent of human disturbances, such as habitat fragmentation, may make the assumption of Fisher even less adequate (Aars *et al.*, 1995). Populations that reproduce within closed demes for some generations before mixing will favour a female-biased offspring production (Hamilton, 1967). In microtine rodents, maternal condition is also an influential factor, with heavier mothers tending to produce female-biased litters (Aars *et al.*, 1995). Conversely the local resource competition hypothesis predicts that mothers with access to poor resources should produce offspring of the sex that is most likely to disperse (males), in order to reduce competition for resources in the natal range (Clark 1978; Silk 1983). There is evidence of natal sex ratio variation among water voles, with food deprivation during pregnancy almost halving the number of weaned young produced by captive female water voles, and litter sex ratios were skewed in favour of males by > 2 : 1 (Bazhan *et al.*, 1996). Radio-tracking of water voles has been shown to result in a stress invoked response, with a substantial decline in female numbers in the radio-collared population, apparently resulting from a male skew in the sex ratios of offspring born to the population (Moorhouse & Macdonald, 2005).

Rationale

This study is the first to measure water vole population demographics in a non-linear wetland habitat, with the exception of Carter & Bright (2000 and 2003) who focused on reed bed habitats in England. There are no published data regarding water vole population densities in Welsh habitats. Typically studies of water populations are conducted during the breeding season only, which is defined as March to September in Britain (e.g. Moorhouse & Macdonald, 2008), but see Carter & Bright (2000 and 2003) for over-winter losses of water voles inhabiting reed beds. This study was conducted continuously over four years, throughout both the breeding season and the over-winter period. As such, it provided an insight into the life history of water voles and important information regarding demography, behaviour and habitat utilisation during these two differing seasons. It is hoped that the results of this study will augment the current knowledge base and be implemented in population modelling for water voles on non-linear systems, such as ponds.

Aims

1. To investigate the response of water voles to live trapping on eight different ponds over four breeding seasons and three winters
2. To determine male and female water vole population densities on non-linear habitats (ponds)
3. To observe temporal and spatial variation in the distribution of water voles
4. To identify density-dependent processes that determine the distribution patterns observed
5. To measure survival and recruitment of individuals per pond
6. To monitor population densities throughout the breeding and non-breeding (over-wintering) season
7. To identify resident adult water voles that maintain a home range (chapter 3)
8. To identify juveniles that recruit into the adult population
9. To use repeat-capture data of resident adults to observe variations in weight between genders and ponds

2.2 Results

2.2.1 Trapping effort and capture success

Throughout the duration of the study, 150 water voles were captured on 492 occasions, (table 2.2). Ponds A to F were studied for 40 months during which time 22 trapping sessions were undertaken, including 4 breeding seasons (March to October) and 3 winters (November to February). Ponds G and H were studied for 29 months, during which time 13 trapping sessions were undertaken, including 3 breeding seasons and 2 winters.

Table 2.2 Total trapping effort expended and percentage occupation of traps by water voles across the area of wetlands studied, throughout the entire duration of the study period

Pond	Trapping nights	Number of water vole captures	Trap success (% occupation)
A	1760	78	4.43
B	1100	54	4.91
C	1100	69	6.27
D	1760	91	5.17
E	1320	73	5.53
F	440	13	2.95
G	2340	90	3.85
H	520	24	4.62
Total	10340	492	Mean = 4.72 ± 0.36

The highest degree of trap occupation was observed on pond C (6.27%) and pond E (5.53%) (table 2.2), despite the fact that both these ponds were unpopulated (according to capture data) for over a year, during the low density phase of the population (see sections 2.2 and 2.5). Pond F was associated with the lowest trap success, however, this pond was only utilised during the breeding season in the peak density phase of the population (2006) (see section 2.5) after which time it remained unoccupied. Of the 150 water voles captured during this study, only 16 (10.66%) were captured on the last day of a given trapping session (table 2.3), suggesting that the duration of the trapping sessions (5 days) was sufficient to capture the majority of the marked population.

Table 2.3 Capture histories of adult water voles (n = 52 males; n = 70 females) at NWCW throughout the entire duration of the study period. (Juveniles are discussed separately; section 2.8)

Capture history	Percentage (%) of males	Percentage (%) of females
Only caught once (transients)	40.38	30.00
Caught >1 within a trapping session	63.46	64.29
Caught during 2 or more trapping sessions	57.69	55.71
Caught on >1 pond	67.31	45.71
Dispersed within the area of wetland studied	28.84	20.00
Maintained a home range	40.38	47.14

Approximately 60% of adult male water voles and 70% of adult female water voles were recaptured after initial capture, with 64% of both males and females recaptured within the same trapping session (5 days) (table 2.3). Additionally, just over half of the adults were recaptured in subsequent (but not necessarily consecutive) trapping sessions (table 2.3). A home range (observed range length; chapter 3) was maintained by 41% of adult males and 47% of adult females (table 2.3). Males and females varied in the degree to which they utilised multiple ponds, with 67% of males and 46% of females encountered on more than one pond (table 2.3), however, these figures include both maintenance of home ranges and displacement events involving animals that did not maintain an observed range length. The social ecology of adult water voles is discussed in chapter 3.

Table 2.4 Other small mammals that occupied traps throughout the duration of the study

Species		Number of captures	% occupation (of a possible 10,340)
Microtus agrestis	Field vole	71	0.67
Rattus norvegicus	Brown rat	23	0.22
Scirius carolinensis	Grey squirrel	1	0.01

Other rodents, particularly field voles (*Microtus agrestis*), brown rats, (*Rattus norvegicus*) and on one occasion a grey squirrel (*Scirius carolinensis)* occupied or set off traps and thus potentially introduced a degree of bias into the results. The small mammal by-catch, however, was less than 1% of the trap occupation (table 2.4) and is therefore unlikely to have influenced the water vole distribution patterns observed (but see chapter 6).

2.2.2 Demography of the water vole meta-population

In total, 122 adult (including 52 males and 70 females) and 28 juvenile water voles were captured throughout the duration of the study across the area of wetland studied. There were significant differences between years ($G_{11} = 48.34$, $p < 0.001$) and between genders and age classes ($G_{11} = 34.92$, $p < 0.001$). More adult males were captured during 2006 than any other year, however, this number declined as the study progressed (figure 2.1). Adult females and juveniles displayed a similar pattern to one another, with the greatest number of both adult females and juveniles captured during 2007 (figure 2.1).

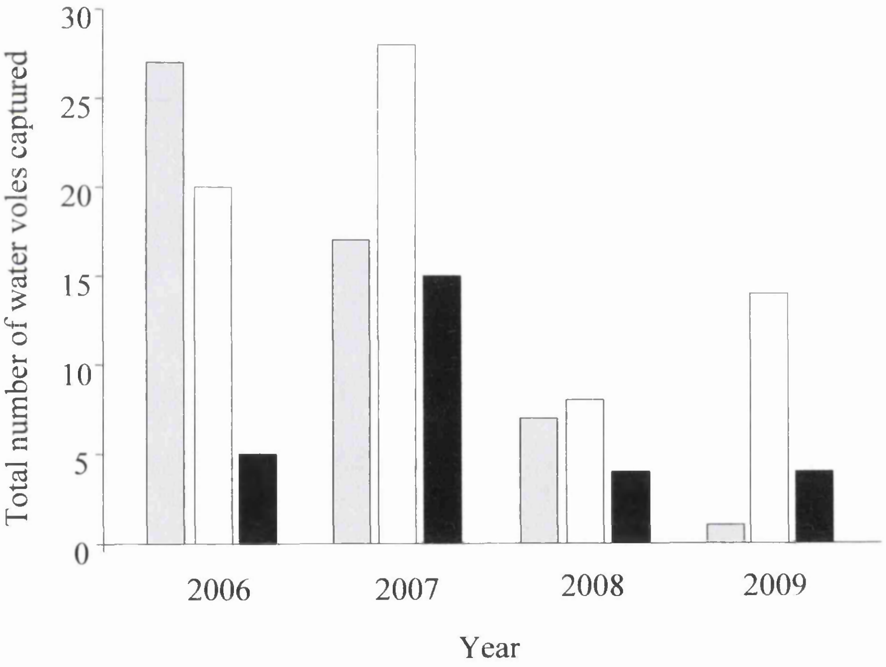


Figure 2.1 Total number of water captured per year across the area of wetland studied (34 traps during 2006; 54 traps thereafter). Adult males (grey bars), adult females (open bars), juveniles (black bars)

2.2.3 *Sex ratio of adult water voles captured*

The sex ratio of newly tagged adult per year appeared skewed during all years of the study, in favour of males during 2006, however, in favour of females during all other years. The mean sex ratio was 1 adult male to 1.35 adult females (table 2.5).

Table 2.5 Number of water voles tagged and sex ratio of adult water voles per year across the area of wetland studied

	2006	2007	2008	2009	Total
Males	27	17	7	1	52
Females	20	28	8	14	70
Male:Female	1.35:1.0	1.0:1.65	1.0:1.14	1.0:14.0	1.0:1.35

Although adult females constituted almost half of the newly tagged population (n = 70), the remainder consisting of both adult males (n = 52) and juveniles (both genders) (n = 28) (see figures 2.1 and section 2.8), there was no significant difference ($p = 0.117$) between the total number of adult males and females throughout the duration of the study. Furthermore, there was no significant difference ($p > 0.05$) between the number of males and females tagged each year during the first 3 years of study (2006 to 2008). However, during 2009 there were significantly more females than males ($G_1 = 12.43$, $p = 0.004$) since only one un-tagged adult male was captured and the sex ratio of adults was 1M: 14F (table 2.5).

2.2.4 *Pooled data: water vole population densities per year*

The mean adult water vole population density (all ponds and seasons combined) over the study period was 0.95 adults per 100 m, comprised of 0.45 males per 100 m (± 0.047, n = 275) and 0.50 females per 100 m (± 0.049, n = 275) (figure 2.2). There were significant differences between mean population densities per year ($F_{3,29} = 15.557$, $p < 0.0001$). *Post hoc* Bonferroni multiple comparisons revealed that population densities during 2006 were significantly higher than in 2008 and 2009 ($p < 0.0001$) but not significantly higher than 2007 ($p = 0.189$). Population densities during 2007 were also significantly higher than 2008 and 2009 ($p = 0.024$). The population densities during the latter two years of study were statistically similar ($p = 1.000$). Accordingly, the first two years of the study are referred to as a 'peak density phase' and the latter two years as a 'low density phase'.

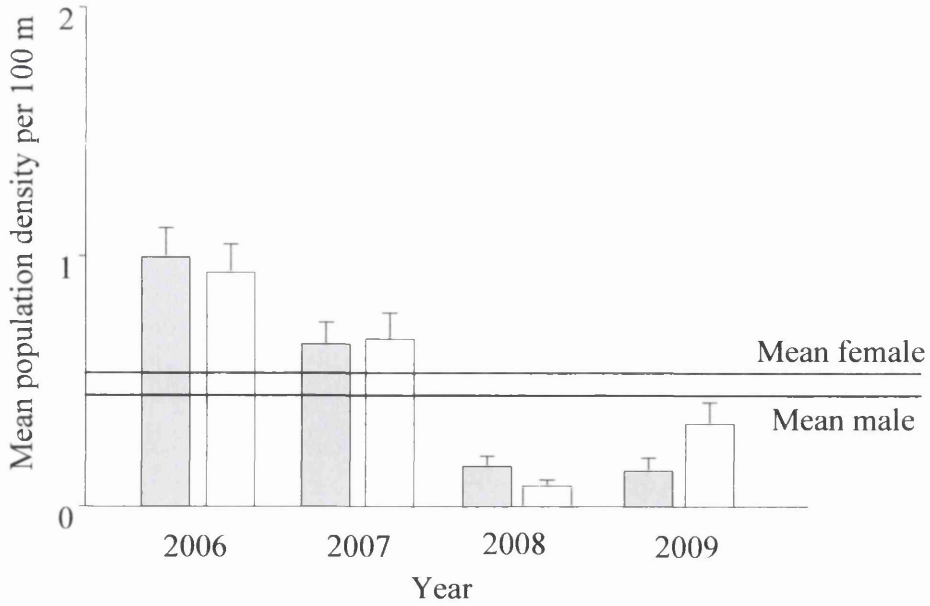


Figure 2.2 Mean (±SE) population densities per 100 m of adult water voles for the area of the wetlands studied, over the entire duration of the study period. Males (grey bars), females (open bars), overall means presented

2.2.5 Water vole population densities per pond

The highest overall mean population density was observed on pond D (1.24 ± 0.55 adults per 100 m) (figure 2.3). The highest mean annual population density occurred on pond E during 2006 (2.5 ± 0.37 adults per 100 m), however, this pond experienced the lowest mean annual density during 2008 (0 per 100 m). In fact no water voles were trapped on pond E between October 2007 and April 2009, until a female migrated into the population from pond C. Despite being empty for eighteen months, pond E still supported the second highest mean density (1.16 ± 0.58 adults per 100 m) (figure 2.3) and the highest peak density (6.6 adults per 100 m) (figure 2.4) observed throughout the metapopulation and the duration of the study. Pond C was also unoccupied during the low density phase (2008) and pond F was only inhabited during the breeding season of the peak density phase (2006). Ponds A, B, D, E and H had a mean population density that exceeded the overall mean observed throughout the wetland area and the duration of the study period (figure 2.3). Despite the variation in population densities observed, there were no significant differences (p = 0.903) between mean populations densities per pond, until the year was divided into breeding season and winter populations (section 2.6).

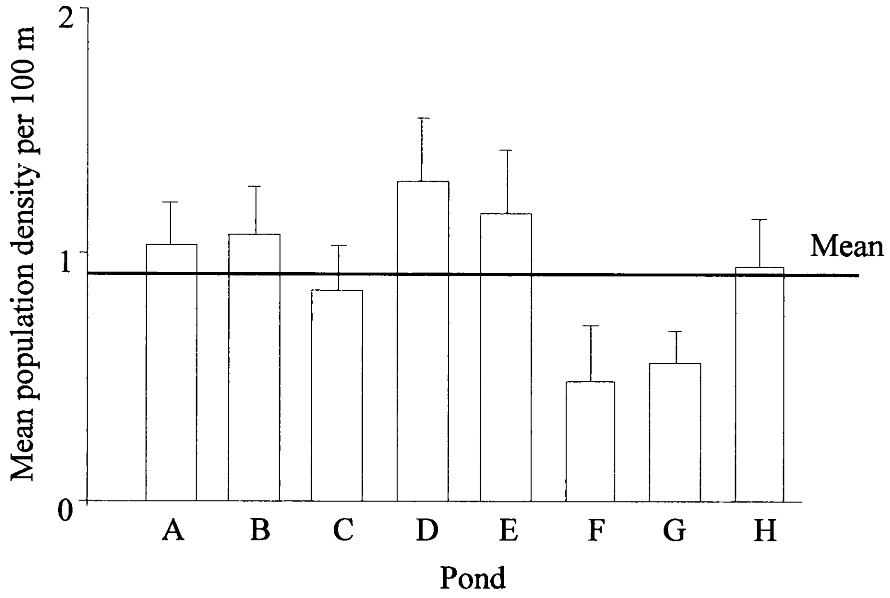


Figure 2.3 Mean (±SE) adult water vole population density per 100 m per pond over the entire duration of the study period. Overall mean presented for comparison

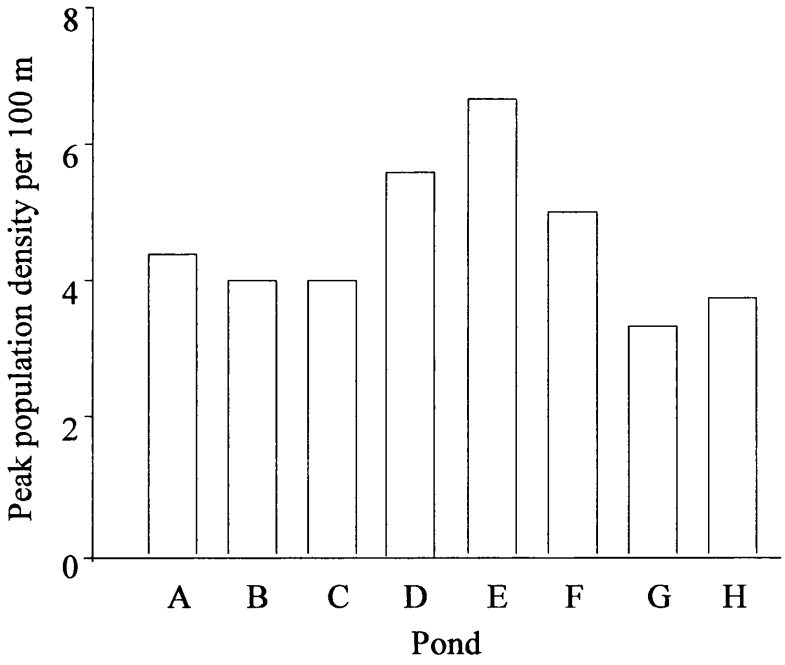


Figure 2.4 Peak adult water vole population density per 100 m per pond throughout the entire duration of the study period

Analysis of variance revealed that there was no significant difference between peak populations densities per pond ($p = 0.433$) however, there was a significant difference ($F_{3,29} = 10.273$, $p < 0.0001$) between peak population densities per year.

Post hoc Bonferroni multiple comparisons are similar to those observed for mean population densities per year. Peak densities during 2006 were significantly higher than in 2008 and 2009 ($p = 0.006$) but not significantly higher than 2007 ($p = 1.000$). The latter two years of study were also statistically similar in terms of peak population densities ($p = 1.000$). As expected this follows a similar trend to the mean population densities. It is interesting to note, however, that a significant difference between years implies a significant difference between the timing of population peaks (occurring during different months each year). All peak population densities were observed during the breeding season (March to October), with the exception of pond E, when a peak population of 6.6 water voles per 100 m was observed during the winter (non-breeding) season, in January 2007 (table 2.6).

Table 2.6 Months during which peak population densities (figure 2.4) occurred throughout the study

Pond	Date
A	July 2006
B	April and September 2007
C	July 2006
D	September 2006 and April 2007
E	January 2007
F	June, July and August 2006
G	March 2007
H	March and April 2007

2.2.6 Seasonal water vole population densities

Surprisingly, mean breeding season population densities of adult water voles (0.99 ± 0.08 adults per 100 m) were not significantly higher ($F_1 = 3.347$, $p = 0.084$) than those observed during the winter (0.77 ± 0.19 adults per 100 m) (table 2.7). Nevertheless, spatial variation was observed between seasons, with certain ponds being utilised more during the winter than the breeding season. A significant difference ($F_{1,15} = 3.045$, $p = 0.01$) in mean population densities was observed per pond. Although there was no significant effect of gender on population density ($p = 0.802$), males and females utilised ponds to varying degrees and there was a significant interaction observed between pond and gender ($F_{1,7} = 2.817$, $p = 0.044$).

Table 2.7 Mean (±SE) water vole population densities per 100 m per pond during the breeding season (March to October) and winter period (November to February). Data is presented separately for adult males and adult females and excludes juveniles

	Male population density per 100 m		Female population density per 100 m	
Pond	Breeding season	Winter	Breeding season	Winter
A	0.45 ± 0.12	0.05 ± 0.05	0.75 ± 0.13	0.57 ± 0.26
B	0.62 ± 0.19	0.83 ± 0.30	0.38 ± 0.16	0.42 ± 0.26
C	0.39 ± 0.12	0.33 ± 0.14	0.55 ± 0.14	0.33 ± 0.14
D	0.60 ± 0.17	0.57 ± 0.25	0.69 ± 0.19	0.73 ± 0.19
E	0.60 ± 0.15	0.69 ± 0.30	0.40 ± 0.14	0.83 ± 0.40
F	0.26 ± 014	0	0.43 ± 0.18	0
G	0.35 ± 0.08	0.07 ± 0.05	0.36 ± 0.11	0.11 ± 0.05
H	0.71 ± 0.16	0.63 ± 0.24	0.36 ± 0.18	0
Mean	0.50 ± 0.06	0.40 ± 0.12	0.49 ± 0.05	0.37 ± 0.11

The highest mean male population density recorded was on pond B during the winter (0.83 ± 0.30 males per 100 m) (table 2.7). Pond B was also an important pond for males during the breeding season, however, during this time the highest male population density was observed on pond H (0.71 ± 0.16 males per 100 m) (table 2.7). In contrast, the highest mean female population density during the breeding season was recorded on pond A (0.75 ± 0.13 females per 100 m) (table 2.7), while Pond E supported the highest mean female population density during winter (0.83 ± 0.40 females per 100 m. Indeed, pond E was an important overwintering site for water voles, with mean adult densities of 1.53 ± 0.67 adults per 100 m (table 2.7) and a peak population density of 6.6 adults per 100 m during January 2007 (figure 2.4; table 2.6). However, pond D supported the highest mean (breeding season) population density of 1.29 ± 0.33 adults per 100 m (table 2.6). These results are consistent with the mean annual population densities (ponds A, B, D, E and H had the highest mean annual population densities (figure 2.3), however, dividing the year into breeding season and winter allowed identification of ponds that were important during these different seasons (table 2.7). Additionally, observing variations between male and female population densities allowed gender specific distribution patterns to be identified (table 2.7).

2.2.7 *Survival and recruitment of adult water voles*

The variations in population densities between ponds and seasons (table 2.6) were reflected in the varying recruitment and survival of adult water voles per pond (figures 2.5 to 2.20). Additionally, seasonal preferences in pond occupation were observed, with a spatial separation between genders. Ponds B, D and E were important habitats for male water voles, particularly during the winter; reflected in the mean population densities (table 2.7) and survival rates of adult males (figures 2.7, 2.9, 2.11), most notably during the peak density phase (2006 to 2007). Females were typically associated with ponds A, D and E (table 2.6), in particular pond A, the only pond to be continually occupied throughout the duration of all breeding seasons during the study. Certain ponds were occupied only during the breeding season (pond F) or during the peak density phase (ponds C, E and F), reflected in their lower mean population densities (table 2.7) and their reduced survival and recruitment rates during the low density phase (2008 to 2009). Water vole populations on ponds G and H were only studied for the latter three years and thus mean densities may underestimate actual numbers during peak years of the study. Furthermore, widespread vegetation clearance and an influx of brown rats (*Rattus norvegicus*) during Autumn 2007 influenced population densities on pond G (chapter 6) and thus results may not reflect true distribution patterns and processes in the absence of disturbance (chapter 6). Nevertheless, the highest mean male population density was observed on pond H (0.71 ± 0.16 males per 100 m) (table 2.7), reflected in the increasing recruitment and survival (figure 2.19) of male water voles on pond H at the close of the study.

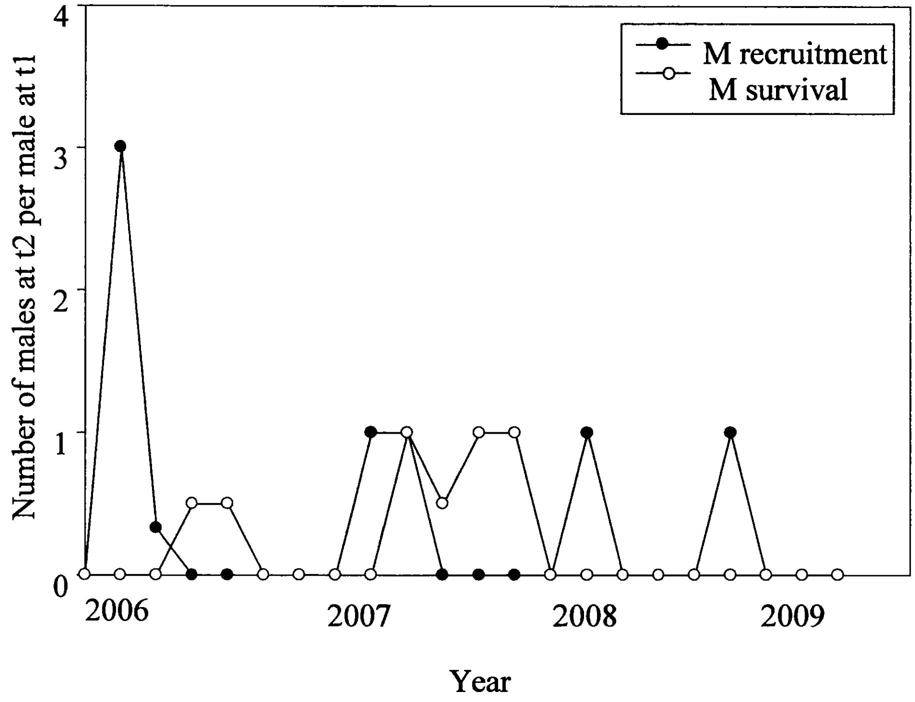


Figure 2.5 Male recruitment and survival on pond A throughout the entire duration of the study

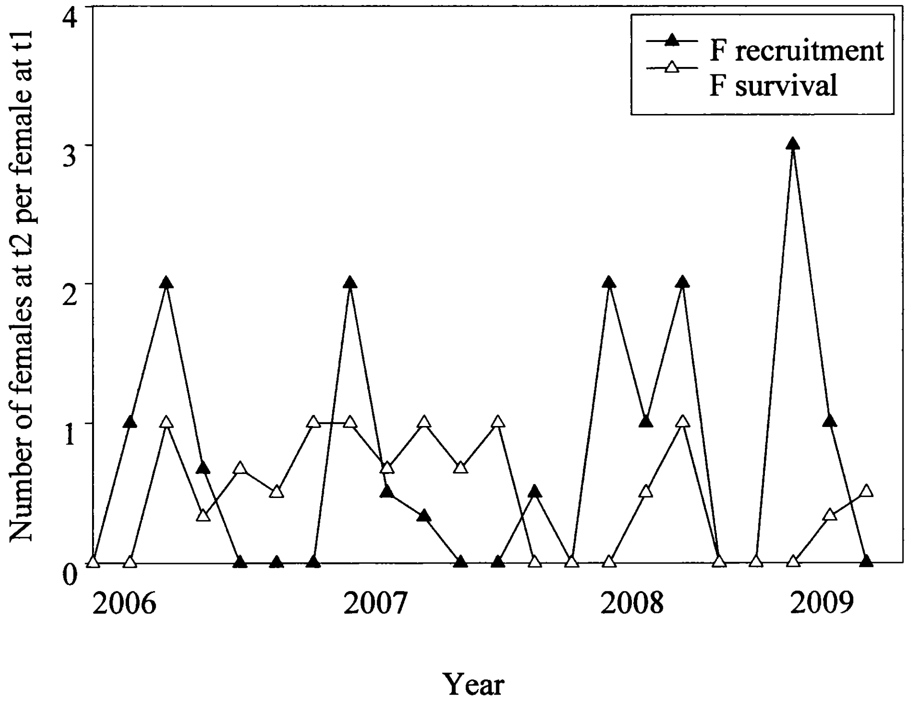


Figure 2.6 Female recruitment and survival on pond A throughout the entire duration of the study

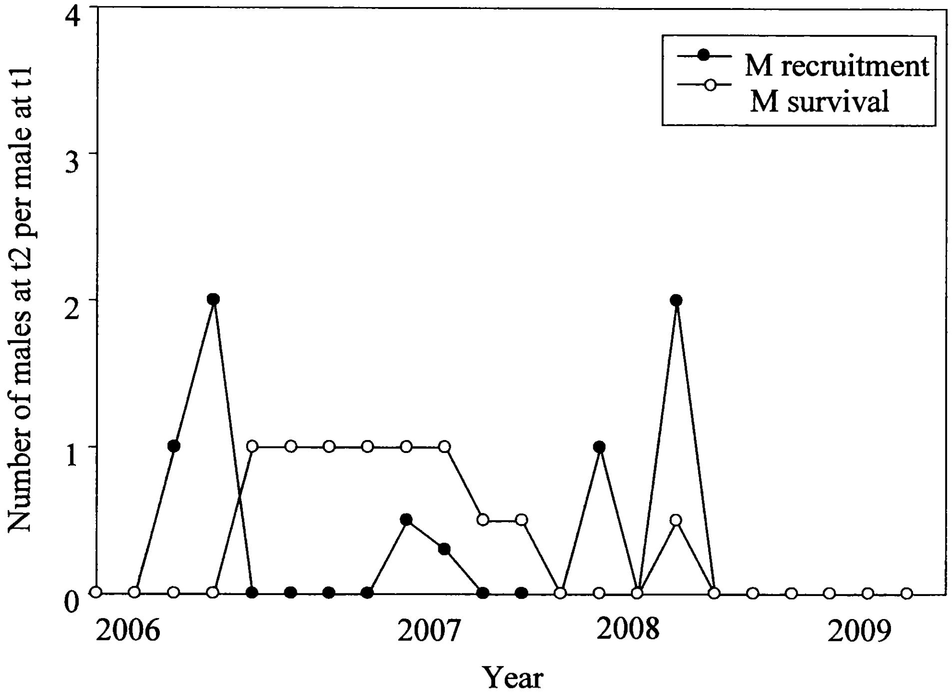


Figure 2.7 Male recruitment and survival on pond B throughout the entire duration of the study

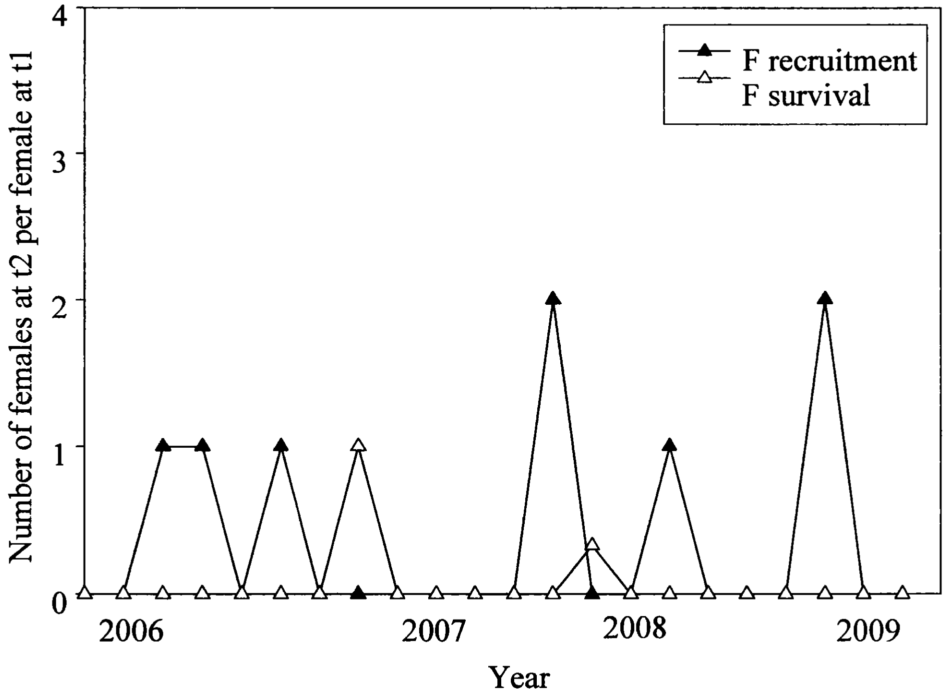


Figure 2.8 Female recruitment and survival on pond B throughout the entire duration of the study

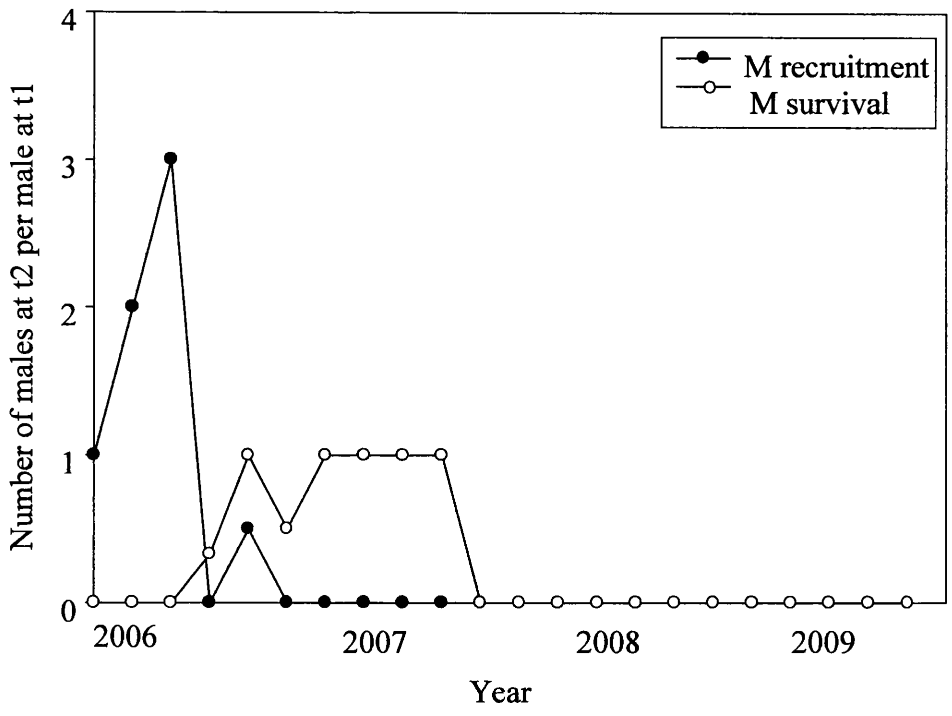


Figure 2.9 Male recruitment and survival on pond C throughout the entire duration of the study

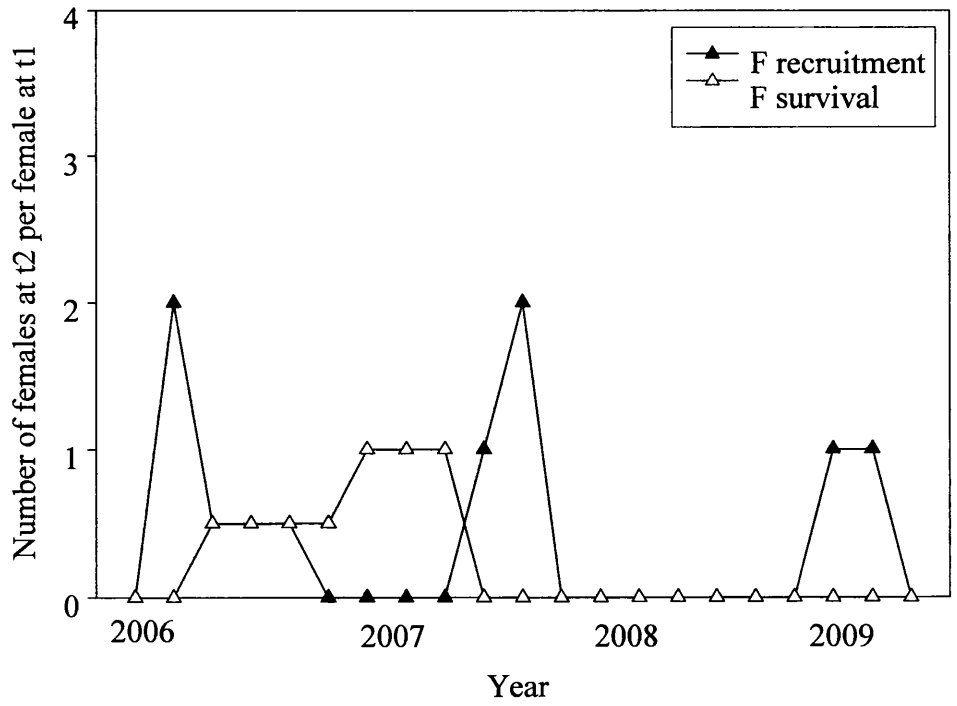


Figure 2.10 Female recruitment and survival on pond C throughout the entire duration of the study

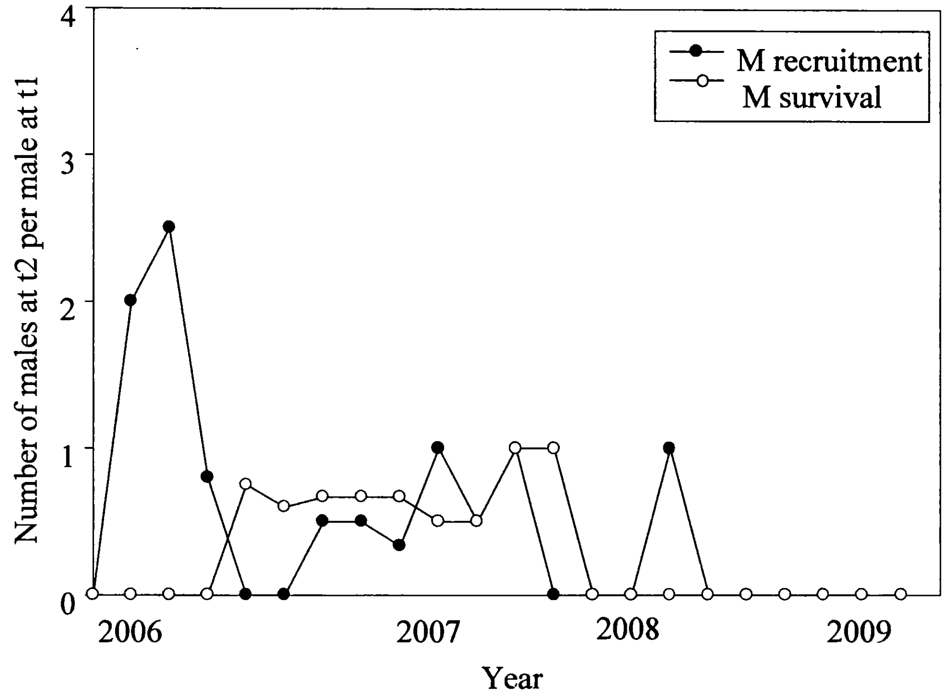


Figure 2.11 Male recruitment and survival on pond D throughout the entire duration of the study

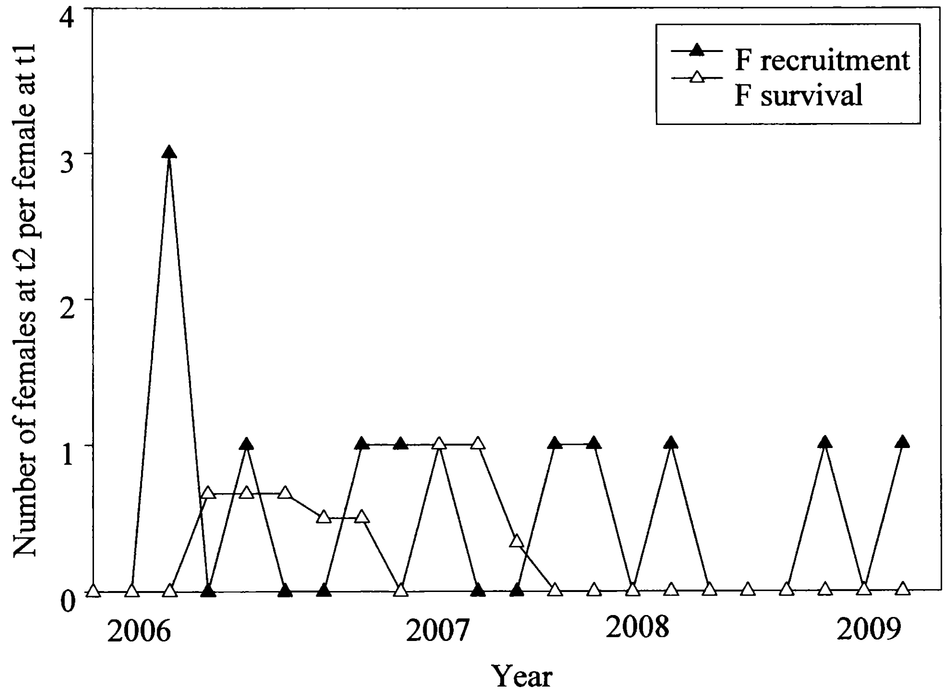


Figure 2.12 Female recruitment and survival on pond D throughout the entire duration of the study

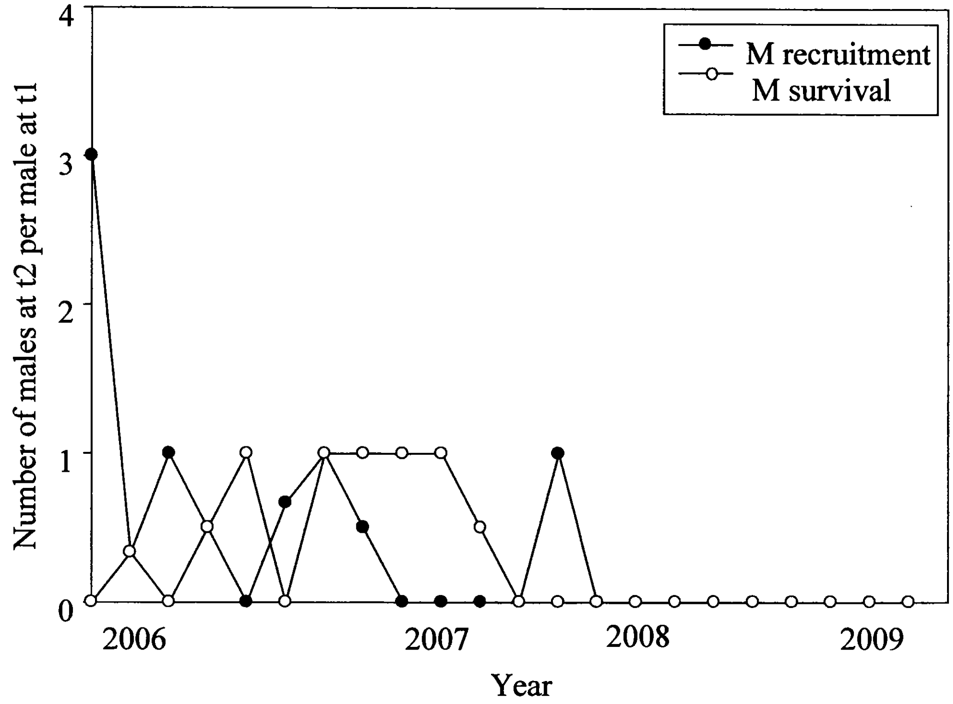


Figure 2.13 Male recruitment and survival on pond E throughout the entire duration of the study

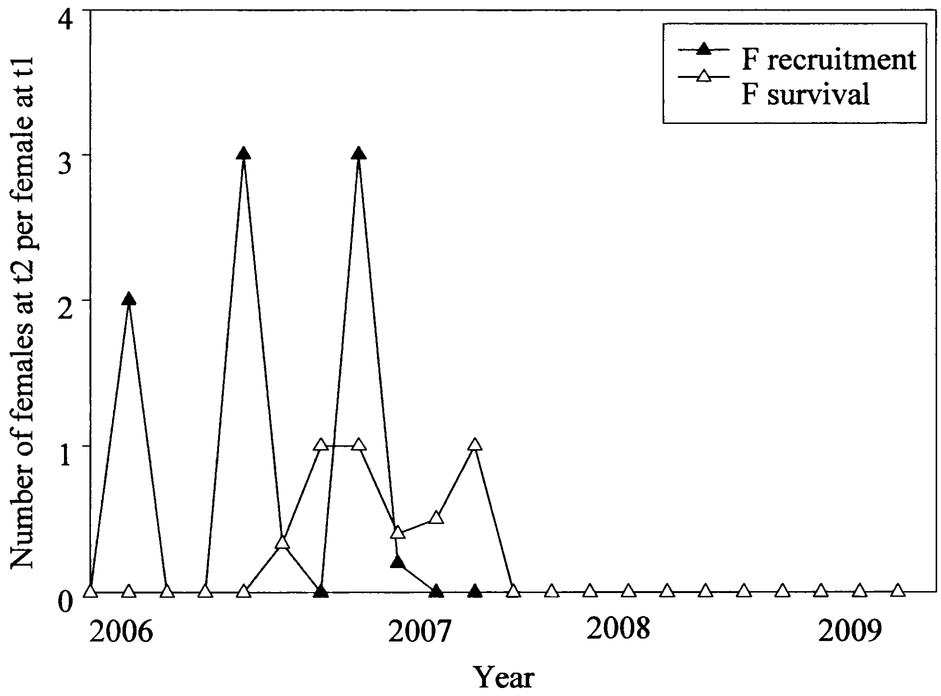


Figure 2.14 Female recruitment and survival on pond E throughout the entire duration of the study

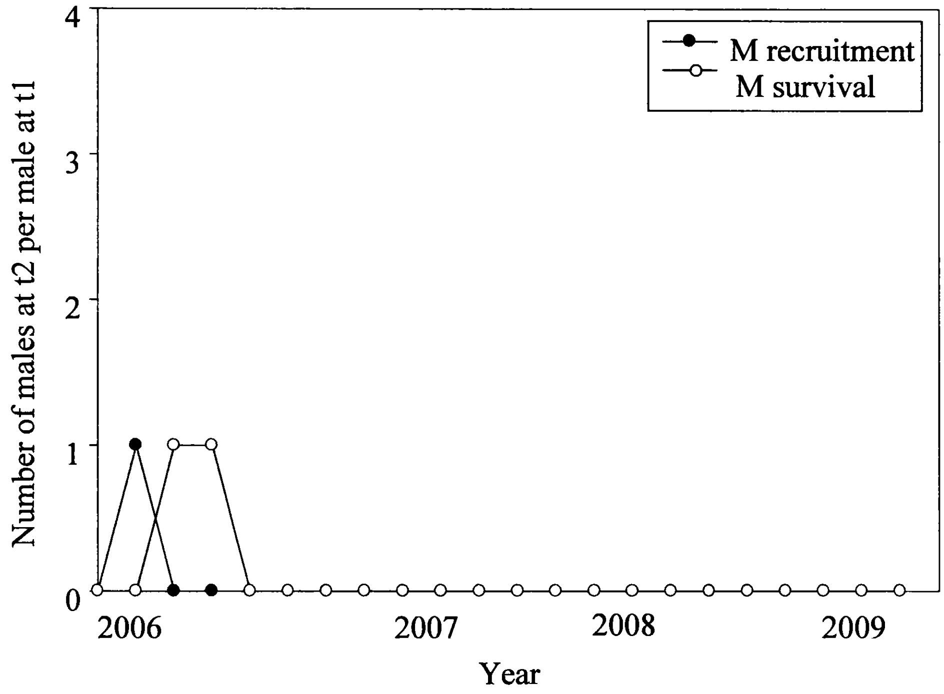


Figure 2.15 Male recruitment and survival on pond F throughout the entire duration of the study

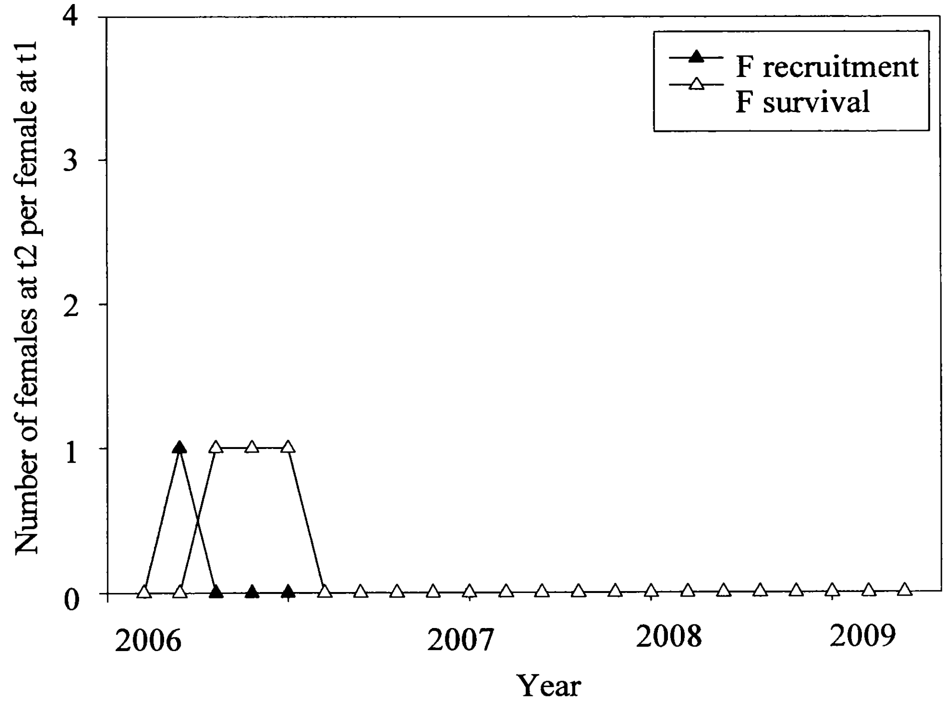


Figure 2.16 Female recruitment and survival on pond F throughout the entire duration of the study

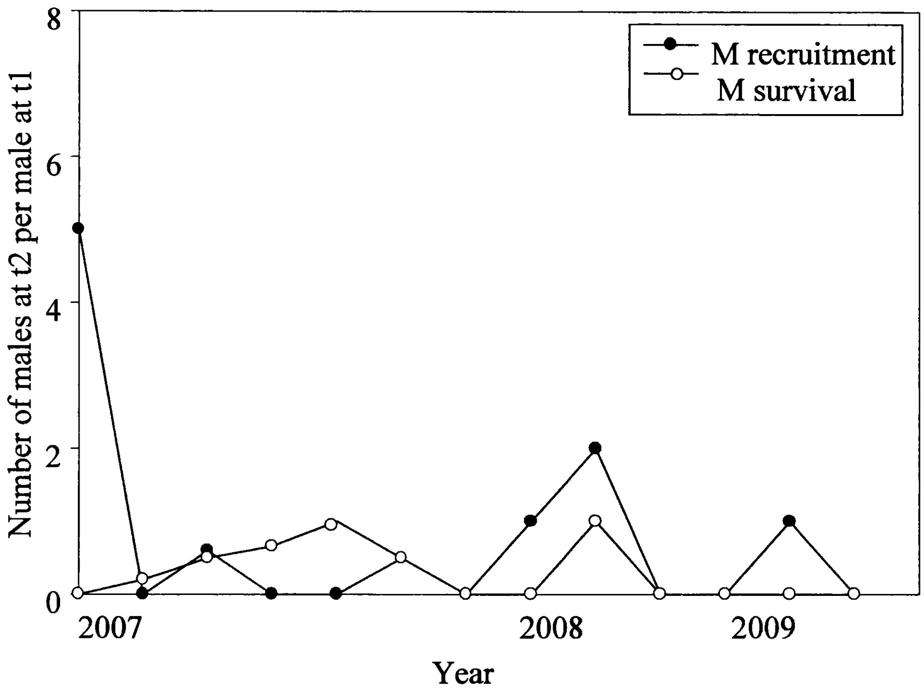


Figure 2.17 Male recruitment and survival on pond G throughout the entire duration of the study (commencing February 2007)

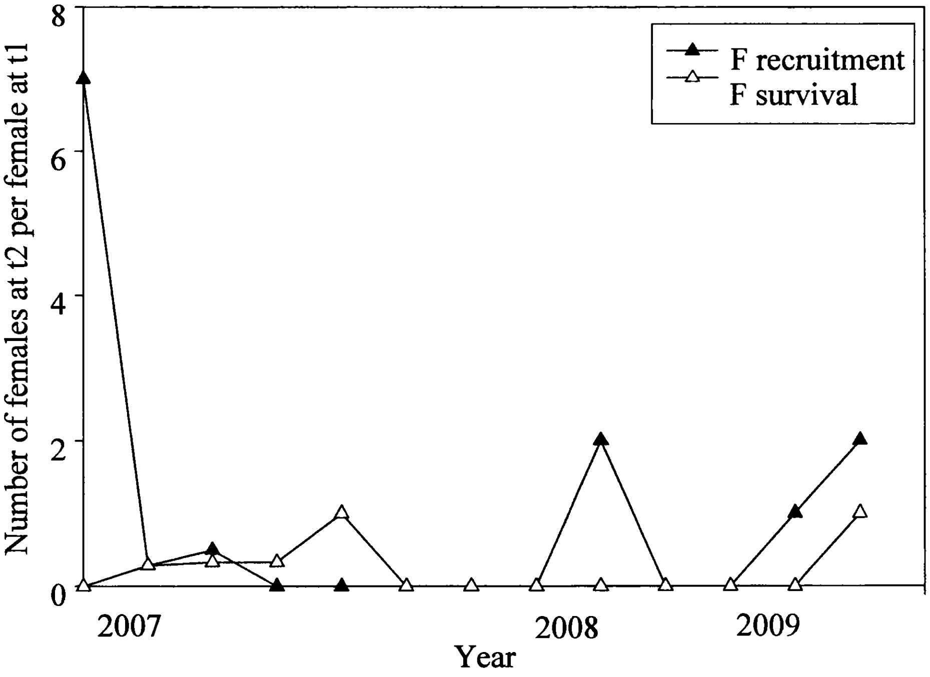


Figure 2.18 Female recruitment and survival on pond G throughout the entire duration of the study (commencing February 2007)

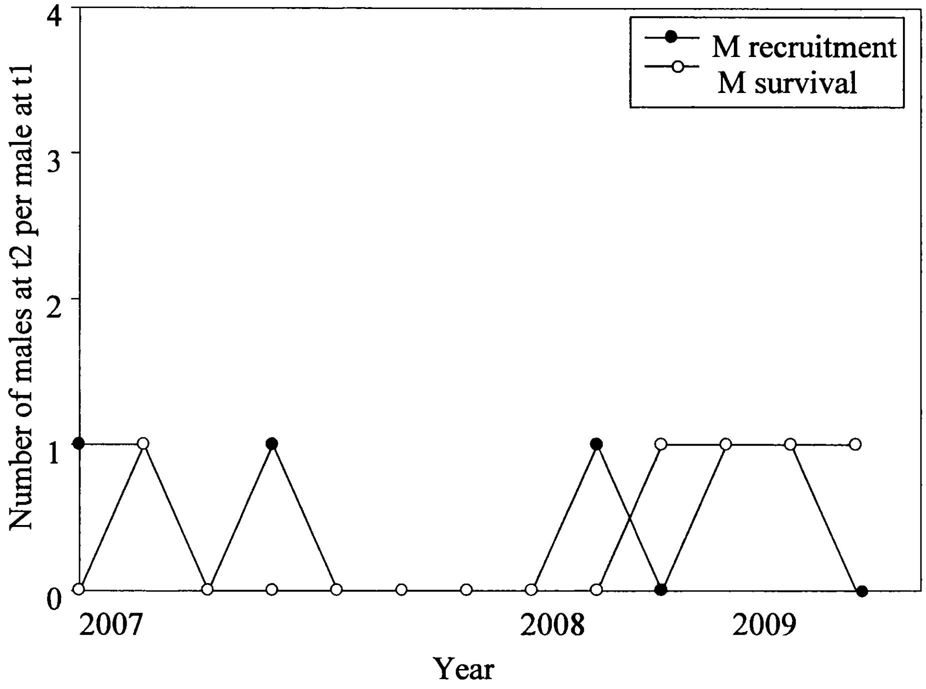


Figure 2.19 Male recruitment and survival on pond H throughout the entire duration of the study (commencing February 2007)

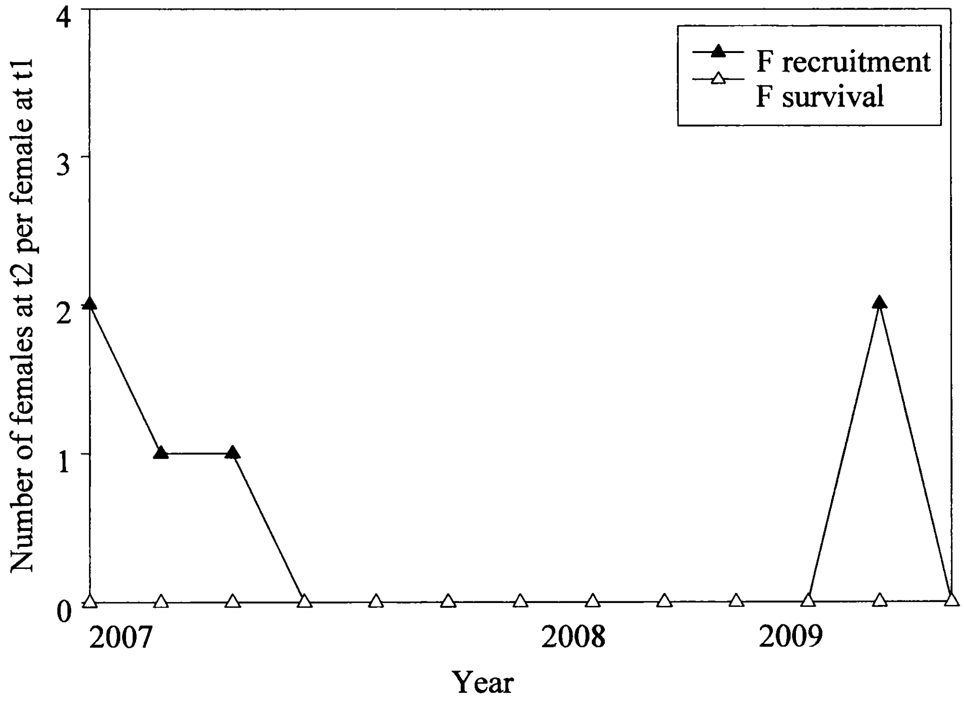


Figure 2.20 Female recruitment and survival on pond H throughout the entire duration of the study (commencing February 2007)

2.2.8 Over-wintering water voles

Only 16 (13.11%) adult water voles survived over the winter period and were recaptured during the following season, representing mean over-winter losses of 85%, throughout the 4 year study period (table 2.8). However, 14 water voles were tagged during the first breeding season and survived the first winter period (ponds A to E only). These 14 individuals were members of the first year population of 47 animals (27 males and 20 females). In total, 8 males (29.63%) and 6 females (30%) survived the winter during the peak density phase (2006), representing over-winter losses of 70% for both genders.

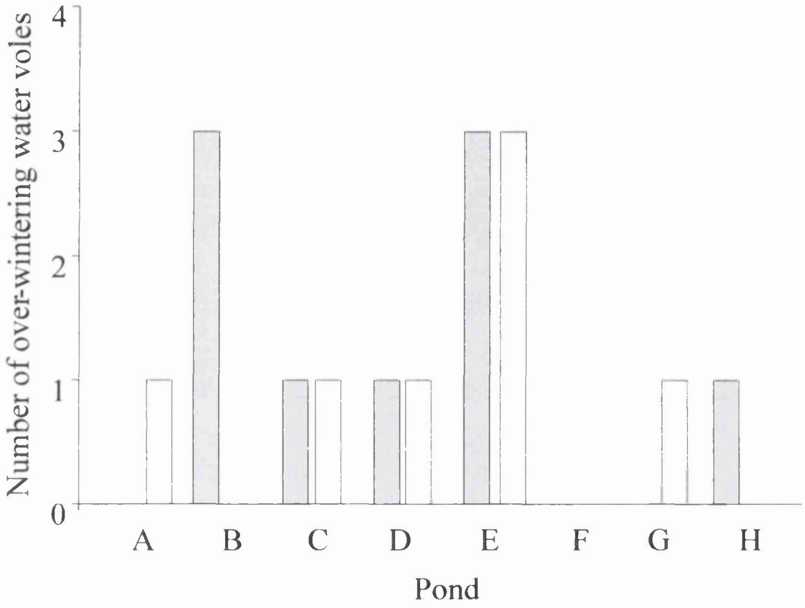


Figure 2.21 Number of water voles that were tagged the previous season and survived the winter period throughout the entire duration of the study. Males (grey bars), females (open bars).

Table 2.8 Percentage survival of water voles that were tagged the previous season and survived the winter period throughout the entire duration of the study

	Percentage (%) survival	
Over-winter period	Males	Females
2006-2007	29.6	30.0
2007-2008	0	0
2008-2009	14.3	12.5
Mean	14.6	14.2

Beyond the winter of 2006 – 2007, no water voles (tagged the previous season) survived the overwinter period on ponds A to E. The remaining two individuals were tagged during the breeding season of 2008 on ponds G and H and overwintered to be recaptured the following season; however, neither of these adults established a home range during the breeding season (table 2.8).

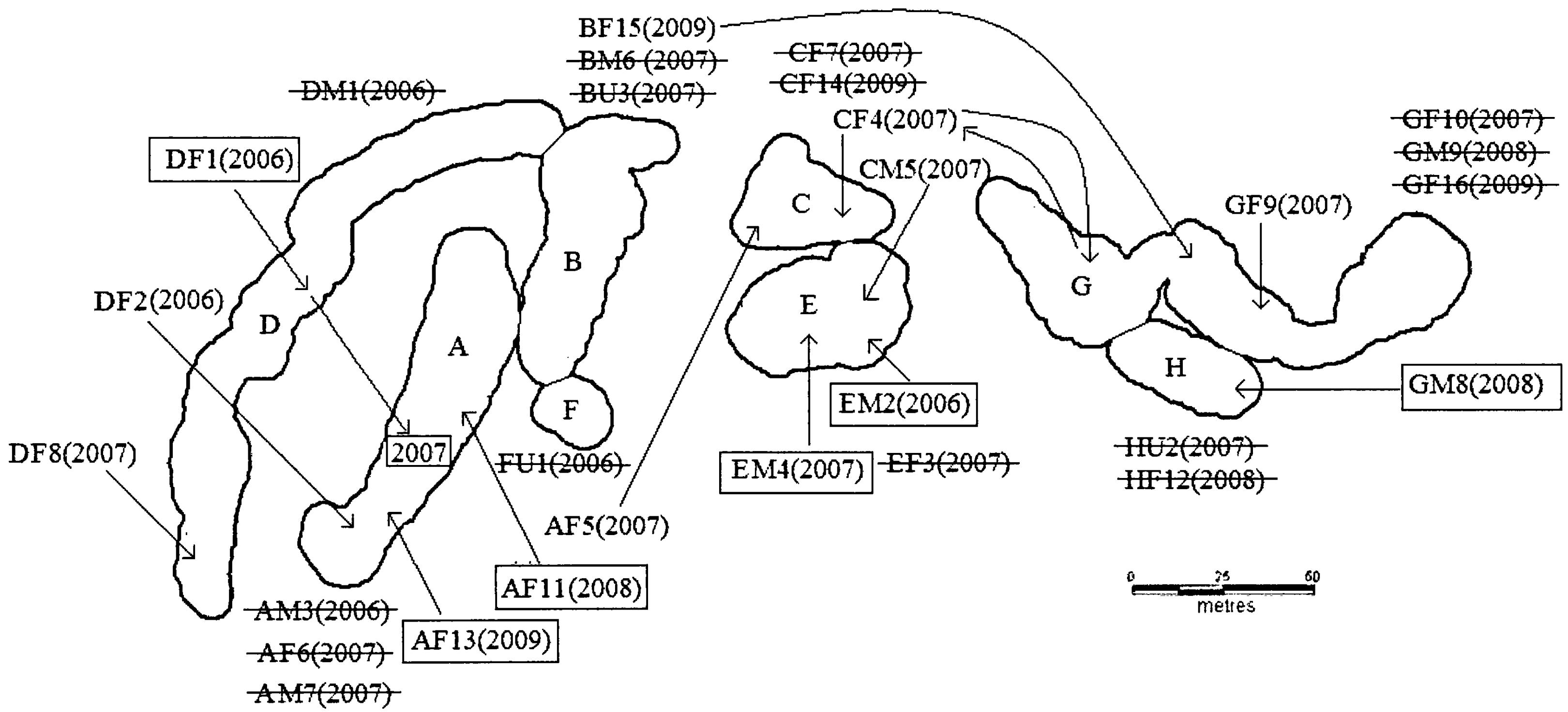
2.2.9 Juvenile water voles

Juvenile water voles were encountered on all ponds at least once throughout the duration of the study (table 2.9); however, spatial and temporal variations were observed in both the source and destination ponds (figure 2.22; juvenile sources and sinks).

Table 2.9 Total number of juvenile water vole captured per pond throughout the entire duration of the study.

Pond	Number of juvenile water voles
A	6
B	3
C	4
D	4
E	3
F	1
G	5
H	2

Of the 28 juveniles captured (9 male, 16 female and 3 unknown gender), 14 were born before July 1st (early breeding season) and 14 were born after July 1st (late breeding season). The greatest number of juveniles were captured on pond A (n = 6) (table 2.7; figure 2.21). Over half of the juveniles (n = 15) were only captured once; their fates are unknown (dispersed to other ponds not studied here, or predated upon). Of the remaining 13, 6 (46.2%; 2M, 4F) were born early in the season (before July 1st) and 7 (53.8%; 2M, 5F) were born late in the season (after July 1st). However, only 6 juveniles (21%) recruited into the adult water vole population (in the area of wetland studied) and established a home range (chapter 3). Of these, 2 (33%; 1M, 1F) were born in the early breeding season and 4 (67%; 2M, 2F) were born in the late breeding season. Only juveniles first captured on ponds A, D, E and G became established adults (in the area of wetlands studied).



Boxes denote juveniles that recruit into the adult population and establish a home range (n = 5)
Strikethrough denotes juveniles that were only captured once (n = 15)
The remainder were recaptured at least once but did not establish an adult home range (n = 8)

A to G denotes pond of first capture
MFU denotes gender (males, females and unknown)
1-16 denotes juvenile animal number (9M, 16F, 3U)

Figure 2.22 Juvenile water voles: Annual sources and sinks

Although a skewed sex ratio (female bias) was observed (on first capture), equal recruitment into the adult population was observed; 3 juvenile females and 3 juvenile males maintained a home range as adults. However, spatial variation was observed between genders, with juvenile females only recruiting into the adult population on ponds A and D, whereas male juveniles only recruited into the adult population on ponds E and G. Furthermore, juvenile female recruitment (onto the natal pond) was a density-dependent process; recruitment only occurred when population densities were low. During the peak density phase (2006 to 2007), juvenile females captured on pond A were displaced (figure 2.21); however, during the low density phase (2008 to 2009), the two juvenile females both recruited into the adult population on pond A and maintained a home range (chapter 3). The one juvenile female that recruited into the adult population on pond A dispersed from pond D during 2007 (DF1; figure 2.22), however, entered the population on pond A as an adult, after over-wintering on pond D. Juvenile male recruitment was also density-dependent, but in contrast to juvenile females; 2 juvenile males recruited into the adult population and overwintered on pond E at a time when peak population densities were observed (table 2.6).

2.2.10 Life histories from repeat captures

Of all 122 adult water voles captured, the mean male weight was 218 g (± 2.67g) (n = 50 males) and mean female weight was 205 g (± 2.34g) (n = 72 females). Adult male water voles were significantly heavier than their female counterparts (t_{121} = 2.034, p = 0.043). In order to identify factors that may influence the weight of resident water voles per pond, transient animals were removed from the analyses. Of the 122 water voles captured, 48 (17 males; 31 females) adults maintained a home range (over two or more trapping sessions) during the breeding season and 18 (9 males; 9 females) maintained a home range during the winter (chapter 3). These resident water voles provided repeat capture life history data for established adults. The mean weights of individual residents by gender and season were clustered per pond (figures 2.23 to 2.26).

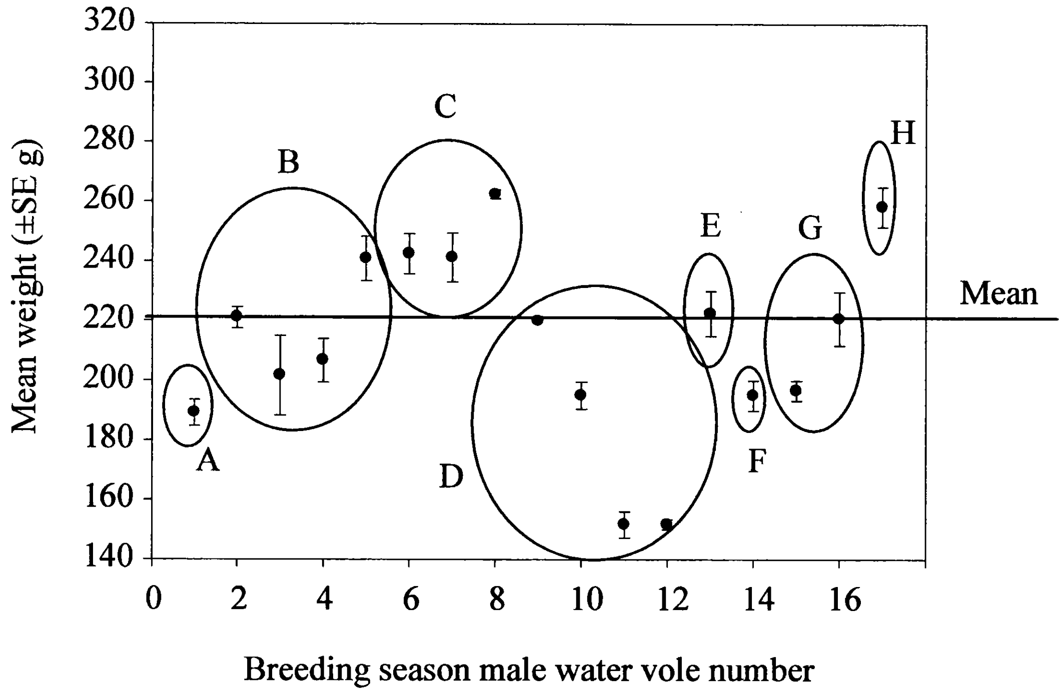


Figure 2.23 Mean weight (g ±SE) per pond of the 17 resident adult, male water voles that maintained a home range during the breeding season in the area of wetland studied (Overall mean = 221.38 ± 3.34 g; n = 94 captures)

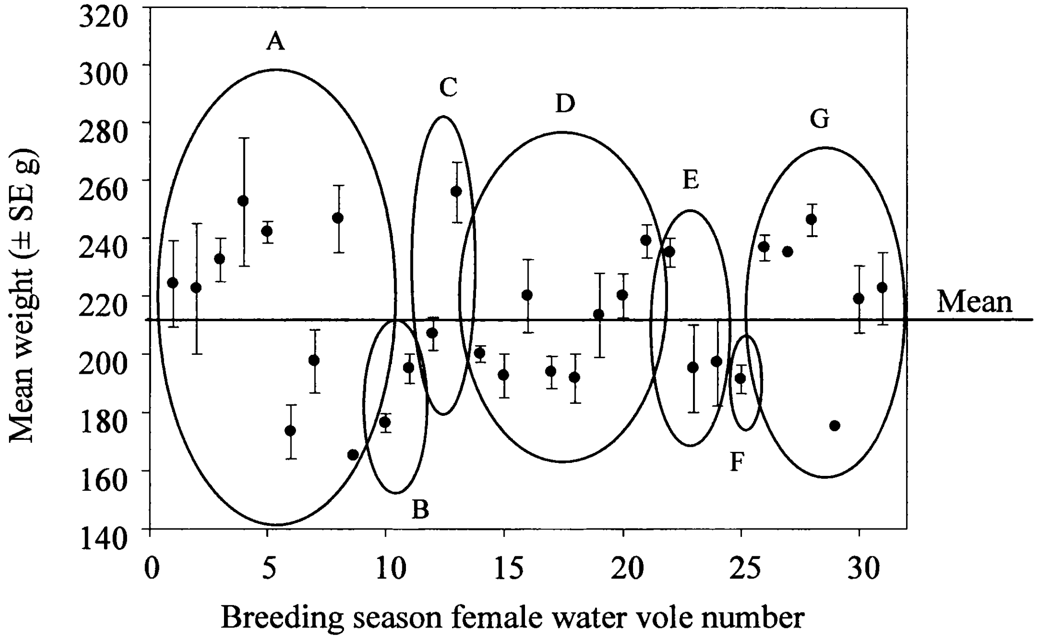


Figure 2.24 Mean weight (g ±SE) per pond of the 31 resident adult, female water voles that maintained a home range during the breeding season in the area of wetland studied (Overall mean = 213.78 ± 3.06 g; n = 111 captures)

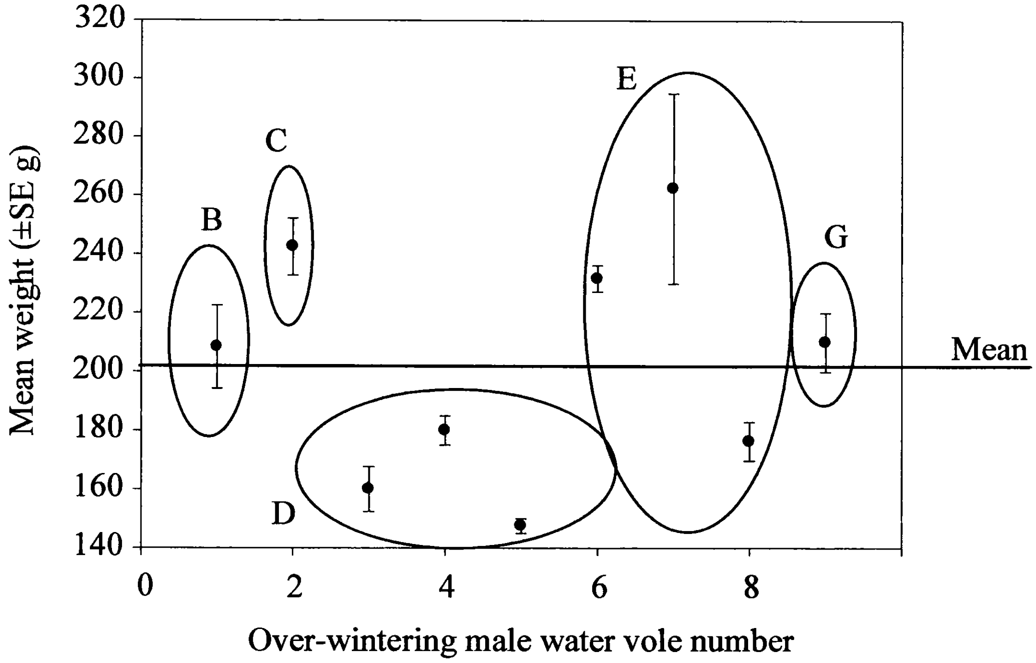


Figure 2.25 Mean weight (g ±SE) per pond of the 9 resident adult, male water voles that maintained a home range during the winter in the area of wetland studied (Overall mean = 203.00 ± 7.78 g; n = 25 captures)

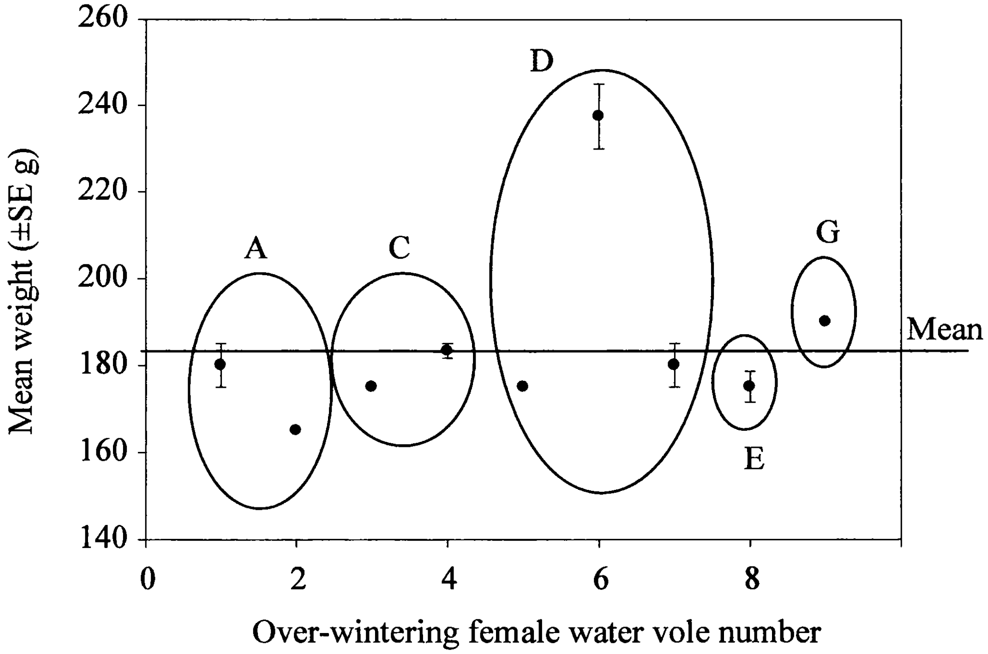


Figure 2.26 Mean weight (g ±SE) per pond of the 9 resident adult, male water voles that maintained a home range during the winter in the area of wetland studied (Overall mean = 183.10 ± SE 4.27 g; n = 21 captures)

Interestingly, there was no significant difference in weight between genders of resident adult male and female water voles that maintained a home range ($t_{44.72} = 0.781$, $p > 0.05$). However, there was a significant difference between weight of adults between seasons ($t_{27.18} = 0.27$, $p < 0.05$), with water voles captured during the breeding season significantly heavier than those captured during the winter. Additionally, there was a significant difference between the mean weight of resident adults per pond ($F_{1,7} = 2.323$, $p = 0.043$) and a significant interaction between pond and gender ($F_{1,6} = 2.690$, $p = 0.027$). The heaviest females maintained a home range on ponds A, C, D and G (figure 2.24), while the heaviest males maintained a home range on ponds B, C, E and H (figure 2.23). However, no significant relationship ($F_{1,7} = 0.270$, $p = 0.605$) was observed between the mean weight of resident water voles and the mean adult population density.

2.3. Discussion

2.3.1 Trapping effort and capture success

Of the 122 adult water voles captured throughout the entire duration of the study, 60% of the males and 70% of females were recaptured within a given trapping session and over half of the water voles in the NWCW metapopulation were captured in a subsequent trapping session (at least one month later). Males and females both displayed a similar response; however, this may be for different reasons. Male water voles maintain longer home ranges (Strachan & Moorhouse, 2006; Moorhouse & Macdonald, 2008; chapter 3) and were more likely to utilise multiple ponds. However, since the majority of nearby ponds were also subject to trapping, the likelihood of recapturing males within their home range was maximised (assuming all males have equal trappability). In contrast, females maintain limited ranges (Strachan & Moorhouse, 2006; Moorhouse & Macdonald, 2005; chapter 3) and it is this that defined their likelihood of recapture on a subsequent occasion. Provided they were not displaced or predated, the majority of females were relatively sedentary and typically remained in the same area, maintaining a territory of 20 m or less (chapter 3).

Both ponds C and E were associated with the highest degree of trap occupation, yet were both unoccupied for a year during 2008, before recolonisation by dispersing water voles in 2009. Pond E was an important overwintering site and associated with high adult densities during 2006 and 2007. Pond C was inhabited by a breeding male and female, both captured repeatedly throughout the breeding season and winter of the peak density phase.

2.3.2 Multi-annual fluctuations in water vole population densities

Over the duration of the study, multi-annual fluctuations in water vole population densities became evident, as the study progressed. These were characterised by high population densities at the start of the study (2006 to 2007), a population crash (2008) and the onset of an increase phase (2009). During the early part of the study (2006 to 2007) population densities were significantly higher than the latter two years (2008 to 2009). However, during 2009, ponds that were empty during 2008 (ponds C and E) were recolonised by adult water voles. Furthermore, mean population densities across site were still increasing at the close of study. Although the four years over which this study was conducted identified peak and trough years, it was not possible to identify a population cycle *per se* that characterises many vole populations (Southern, 1979). However, it is tempting to speculate that the water vole populations at NWCW are cyclic since the pattern (high densities, to population crash, to onset of increase phase) (figure 2.2) appears to be operating on a similar timescale to those observed for water voles in Western Europe, suggesting that at there are at least five years between successive population peaks (Weber *et al*, 2002). Further studies over a longer time period (eight to ten years) are likely be required in order to identify whether a water vole population cycle is actually operating at NWCW and to determine the time lag between successive peaks and troughs.

Multiannual microtine cycles are a well documented and exhaustively studied area of population ecology (e.g., Elton 1924; 1942; Krebs & Myers, 1974; Stenseth & Ims, 1993; Begon *et al.*, 1996; Krebs 1996; Lambin *et al.*, 1998; 2000). Indeed, many *Microtus* populations show extensive density fluctuations on a multiannual basis (Krebs & Myers, 1974; Hansson & Henttonen, 1988). Some populations exhibit a female-biased recruitment in years of increase (Myllymäki, 1977; Hansson, 1978, *Microtus agrestis*) and a male bias in peak years (Chelkowska, 1978; Jannett, 1981, *Microtus montanus*). This is consistent with the findings of this study, where male population density only exceeded female population density during the peak year (2006), characterised by an even sex ratio. A female skew in sex ratios was observed for all other years, particularly in 2009, when population densities were increasing after the 2008 crash and all juveniles trapped were female.

2.3.3 Water vole population densities

The mean population density of adult water voles across the area of wetland studied at NWCW was 0.95 water voles per 100 m, lower than those observed in England (Lawton & Woodroffe, 1991; Strachan & Moorhouse, 2006). However, population densities during 2006 (2.5 water voles per 100 m during the peak density phase) were comparable with those of West Lancashire dyke systems (Strachan & Moorhouse, 2006). It is worth noting that since live trapping was continuous (i.e. occurred throughout the winter as well as the breeding season) then mean population densities may be lower than those observed elsewhere. Other studies focus primarily on the breeding season and do not take account of lower winter population densities or the effects of multi-annual fluctuations (e.g. Moorhouse & Macdonald, 2008;

Moorhouse *et al.*, 2009). Temporal variations between breeding season and winter (non-breeding) populations are discussed (sections 2.3.5 and 2.3.6).

Pond D supported the highest mean density of water voles (1.24 adults per 100 m) and represented the optimal habitat at this site (chapter 4), where monthly densities of 5 and 5.6 water voles per 100 m was observed during July and September respectively, during the peak density phase (2006). These peaks coincided with the first and second wave of juveniles entering the population and are comparable with water vole densities observed at the Bure Marshes, Norfolk (Strachan & Moorhouse, 2006).

Pond E supported the second highest mean density of water voles (1.16 per 100 m) and the highest peak density (6.6 per 100 m) during January 2007. This reduced to 4.2 water voles per 100 m in February and 3.3 water voles in March as the onset of the breeding season drives territorial females to spread out and establish their ranges (Strachan & Jeffries, 1993; Forman & Brain, 2006; Strachan & Moorhouse, 2006) (chapter 3). The high density of water voles on pond E (during dry winters) reflected the importance of this pond as an overwintering refuge in the beginning (peak density phase) of the study. However, heavy rainfall in 2007 flooded out the numerous moss burrows associated with the extensive stands of Bulrush (*Typha latifolia)* on this pond (see chapter 4 for habitat associations). The wet winter of 2007, together with subsequent wet summers appeared to negatively impact the population on pond E, which was uninhabited during 2008 (according to capture data) and not recolonised until May 2009. In light of the predicted increase in rainfall associated with climate change (McMichael *et al.*, 2006) the prognosis for water voles inhabiting shallow, lowland ponds and rivers that may be liable to flooding is worrying.

Pond A represented an important habitat in the wetland complex, particularly for females. It is thought the topography of this area contributed to its suitability for water voles (chapter 4). Lawton & Woodroffe (1991) characterised core water vole sites as those located on steep banks. The mean population density on pond A (1.03 per 100 m) exceeded the mean across site, with this pond representing the only location that continually sustained water voles throughout the four year period. The continued occupation was associated with density dependent survival and recruitment (sections 2.3.7 to 2.3.9).

Pond B represented sub-optimal habitat (chapter 4) characterised by a high-turnover of individuals, receiving a number of dispersing animals before they relocated to an alternative habitat. During the peak density phase the densities on this pond were among the lowest on site; however, beyond 2007, this pond became an important winter refuge for males and a net receiver for water voles displaced from neighbouring pond D following adjacent land development (see chapter 6).

Of the ponds occupied for more than one breeding season, Pond C had the lowest overall population density (0.86 per 100 m), yet was still an important component of the metapopulation and was only unoccupied during the low density phase (2008). The regional dynamics of water vole populations in lowland Scotland are governed by the processes of extinction and recolonisation. Occupancy in the previous year was the single most important factor determining current occupancy and persistence tended to be higher for larger populations (Telfer *et al.*, 2003). This was not always the case at NWCW, with smaller populations on ponds A and B being the most persistent, and ponds D and E which supported the highest mean density overall, being completely unoccupied for at least a year at a time. The high degree of connectivity between ponds in the NWCW contributed to persistence of the metapopulation in this study (chapter 4).

2.3.4 Distribution of water voles - the NWCW metapopulation

Water voles at NWCW, occupying non-linear habitats (ponds) exhibited a metapopulation structure (Introduction p5). Certain ponds (A, B and D) were continuously inhabited by a turnover of populations. Other ponds (C, E and F) that previously supported high densities during peak years (2006 to 2007) were empty during the low density phase (2008) but (with the exception of pond F) recolonised during the increase phase (2009). In the uplands of Scotland, metapopulation structure appears to be a fundamental feature of water vole populations. Much of the fragmented distribution of water voles there can be attributed to lack of available habitat, with colonies scattered along the waterway network. Colonies in upland Scotland, occupy only a fraction of the available habitats each year, with a substantial turnover rate facilitated by dispersal and immigration (Aars *et al.*, 2001). A similar scenario is observed in the uplands of Yorkshire (Lawton & Woodroffe, 1991), the lowlands of Scotland (Telfer *et al.*, 2001) and in southern England

(Macdonald & Strachan, 1999). The observations of this study are consistent with these findings, despite the non-linear nature of the wetland system described here.

The spatial organisation of individuals in a population has consequences for ecological processes such as population regulation, competition and mating systems (Moorhouse & Macdonald, 2008). At a low level degree of population fragmentation (typical of water voles before their decline started), water vole distribution is determined by three environmental factors; presence of freshwater, adequate food and cover (Bonesi *et al.*, 2002) and population dynamics are determined by home range requirements (Moorhouse & Macdonald, 2009) and the number of litters produced each year (Macdonald & Rushton, 2003). However, at intermediate to high levels of fragmentation the dynamics of water vole populations are determined by dispersal ability and stochastic processes (Rushton *et al.*, 2000). Distribution of water voles along the River Thames is highly clustered, most particularly for adult females, followed by juveniles and least for adult males (Woodall, 1993). These results are similar to those found in this study, despite the non-linear nature of the habitats at NWCW. However, this differs from the observations of Stoddart (1970) who found that water voles were more evenly distributed along a stream in Scotland, probably due to a more uniform, linear habitat (chapter 4).

Throughout the duration of the study, pond F was utilised during only one breeding season (2006), when adjacent habitats were already saturated with adult water voles, during the peak population phase. One adult male and female occupied pond F from June to September and a juvenile water vole was captured in the vicinity. The fate of the juvenile is unknown; however, it did not recruit into the adult population in the area of NWCW studied. After the breeding season of 2006, both the adult male and female displaced to adjacent pond E, where the male maintained a home range (chapter 3). The female was only captured once on pond E, after which she was not captured for four months (over winter), until the following March, after dispersal to pond G. After this time her fate is unknown, since she was displaced from pond G by the large dominant females that were maintaining home ranges in this area (chapter 3). Nevertheless, this individual was the only female water vole to be captured on three ponds, providing important information pertaining to dispersal capacity and habitat selection. Beyond the breeding season of 2006, no water voles were ever captured on pond F, possibly due to the fact that this pond represented sub-optimal habitat (dominated by trees; see chapter 4). Nevertheless, this habitat was an important component in the persistence of the water vole metapopulation at this site, throughout the progression of the study.

Numerous ponds in the area of wetland studied here were observed to remain empty for a number of breeding seasons, yet were subsequently recolonised by water voles when population densities increased (e.g. ponds C and E). This highlights two important points; i) the need for proximity of nearby habitats that can act as a sink for dispersing animals when population densities increase and ii) the necessity of repetitive surveys over a number of breeding seasons in order to determine whether water voles are present. The absence of water voles during the breeding season of one year does not imply that the area is not an important habitat component for the persistence of the metapopulation. Indeed, the function of sub-optimal habitat within a metapopulation context should not be underestimated, particularly when monitoring species that undergo multi-annual fluctuations.

Further studies over a longer time scale would reveal whether empty ponds would be recolonised by water voles when populations reach another peak. These studies would identify the whether the water vole populations in non-linear lowland systems such as those in Wales are indeed cyclical and the timescale over which these cycles operate. This is an important parameter that should be incorporated into population and habitat models for this species, particularly as animals expand into sub-optimal habitat when populations reach peak densities (Pulliam, 1988). Furthermore, unless other studies take multi-annual fluctuations into account, the water vole population densities recorded in different habitats and locations elsewhere in Britain (table 2.1 after Strachan & Moorhouse, 2006) are not comparable or representative of true densities. Large fluctuations in population densities can be expected between peak and trough years (Saucy 1994); other studies that occur over the short term will fail to identify multi-annual fluctuations or cyclic populations and may underestimate or overestimate population densities, particularly if the stage of the population cycle during which the studies were conducted is not identified. Indeed, these fluctuations should be taken into consideration when undertaking water vole surveys, particularly in areas that may be subject to development.

2.3.5 Seasonal water vole population densities

No significant differences in population densities per pond were observed until annual data was divided into the breeding and non-breeding (winter) population densities. Interestingly, the mean adult population density (0.99 ± 0.08 per 100 m) during the breeding season was not significantly different from the winter population density (0.77 ± 0.17 per 100 m). This was influenced by the peak population density of 6.6 water voles per 100 m observed on pond E during the first winter of the study. Gender dependent pond utilisation was observed between adult water voles maintaining home ranges (chapter 3), with some habitats utilised more than others. Males were associated with ponds B, C, E and H and females associated with ponds A, D and G. Pond A was an important female site throughout the year, reflected in the high female population densities during the breeding season, high female survival and large number of juvenile water voles encountered on this pond. Pond D was also associated with higher densities of females. Males over-wintered on pond B, where no female water voles were observed to maintain a winter home range (chapter 3).

2.3.6 Over-wintering animals

Although 18 water voles were observed to maintain a home range throughout the winter (chapter 3), only 16 water voles that were tagged during the previous breeding season (or during early winter) survived to be recaptured during the following breeding season. This represents a mean of 85% (± 8.7%) over-winter losses to a metapopulation of water voles throughout a multi-annual population study and exceeds estimates for water voles elsewhere (typically 70% losses) (Carter & Bright, 2000; 2003; Strachan & Moorhouse, 2006). The majority of the survivors were members of the peak density phase cohort (tagged during 2006) and survived the dry winter of 2006. Although large over-winter losses were observed over the duration of the study, the peak density phase was characterised by 70% over-winter losses, comparable to estimates of over-wintering densities in reed-beds (Carter & Bright, 2000; 2003) and on river habitats (Stoddart, 1970; Strachan & Moorhouse, 2006). Again, it is important to note the similarity in the results of this study to those of previous studies, despite the non-linear nature of the habitats here.

Pond E was associated with the greatest number of overwintering animals. Indeed over half of the females that survived the first winter inhabited pond E. It is plausible that the physiognomic characteristics of this pond, dominated by dense stands of bulrush (*Typha latifolia*) are synonymous with those observed in reed-beds (*Phragmites australis*) the latter of which are a known refuge for over-wintering water voles, provided a respite from rising water levels is available (Carter & Bright, 2000). Habitat associations of water voles during the critical winter period are discussed in chapter 4. No water voles survived the winter of 2007. This was the largest loss observed and may be associated with the cold and wet winter of that year. The consequences of these losses may be reflected in the low mean population density observed during 2008, with three of the eight ponds remaining unoccupied throughout this year (C, E and F) and water voles only present on pond D during March.

Rodents in seasonal environments may overshoot the equilibrium set by winter food availability, after which they quickly crash (Oksanen, 1990) (chapter 6). However, it is generally agreed that small mammal population cycles are controlled by the top down process of predation (Hanski *et al.*, 1991; Schneider, 2000; Gilg *et al.*, 2003; Korpimäki *et al.*, 2005). Unfortunately the effects of predation were beyond the scope of this study. However, water voles have been shown to be an important component of the diet of two common predators at this locality; the red fox (*Vulpes vulpes)* and the grey heron (*Ardea cinerea)* (Forman, 2005). Other potential predators at this locality included barn owls (*Tyto alba*), brown rat (*Rattus norvegicus*), stoat (*Mustela erminea)*, weasel (*Mustela nivalis),* polecat (*Mustela putorius*) and American mink (*Neovison vison*). The small mustelids (e.g. stoat, weasel and female mink) and brown rats are burrow predators, while others are active during the day (e.g. fox and heron) or during the night (e.g. barn owl).

It is worth noting that even in the presence of American mink; water vole populations (in non-linear habitats) continue to persist at NWCW, a similar situation to that observed on (non-linear) reed beds (Carter & Bright, 2000; 2003) and (non-linear) Tregaron Bog, Wales (Strachan & Jefferies, 1993). In light of this, non-linear water vole habitats should be the focus of water vole conservation, rather than directing all efforts towards mink control (Reynolds *et al.*, 2004) and re-introduction of captive bred water voles (Moorhouse *et al.*, 2008, 2009). Management and monitoring of the NWCW water vole metapopulation, including the effects of rats on water vole distribution and activity, are discussed in chapter 6. Further studies would be required in order to identify the effects of these predators on the multi-annual fluctuations in water vole population densities observed at NWCW.

2.3.7 Survival and recruitment of adult water voles

Gender dependent occupation was observed between habitats at NWCW. 'High quality' optimal habitats were characterised by a high diversity of vegetation as a source of forage and cover (chapter 4). Such habitats were associated with higher densities of female water voles and characterised by high survivorship e.g. Ponds A and D. In contrast, males were typically associated with 'low quality' or sub-optimal habitats, characterised by low diversity of vegetation or less available cover due to homogeneous vegetation or the presence of trees e.g. ponds B and C (chapter 4). This gender dependent habitat utilisation has implications for understanding the social ecology (chapter 3) and for predicting habitat occupancy (chapter 4) for the species. Indeed, studies of California voles (*Microtus californicus*) in grassland habitats have revealed that high quality (heterogenous) habitat patches are characterised by higher peak densities, female-biased sex ratios, higher juvenile recruitment rates and longer individual residency and persistence (Ostfeld *et al.*, 1985; chapter 4).

Pond A was the only pond to be continually occupied by water voles throughout the duration of the study, in particular adult females (section 2.2.7). During the peak density phase of the multi-annual fluctuations (2006 and 2007), female population densities on pond A were maintained by retention of resident females, rather than recruitment of new individuals. (Indeed, juvenile recruitment on pond A was a density dependent process; section 2.3.8). In contrast, during the low density phase (2008 and 2009), female population densities on pond A were maintained by recruitment of both juveniles and adults into the population, rather than survival of those adults already present. Pond A was initially frequented by male water voles, however, no male maintained a home range here beyond 2008.

The opposite scenario was observed on pond B, which was an important site for males (but not females) in the peak density phase, during which time adult males were recruited and overwintered, leading to the sustained survival rates of males on pond B. Despite recruitment of adult females onto pond B during all years of study, female survival rates were very low (figure 2.8). Spatial dynamics of populations can influence water vole distribution. When carrying capacity is reached, intra-specific competition is high and water voles are expected to expand into sub-optimal habitat (Pulliam, 1988). The males that survived on pond B also incorporated ponds A and D into their home ranges (chapter 3), which provided access to the high female densities on these two ponds. It is plausible that the gender separation observed in survival per pond was associated with territorial females excluding males from their home ranges (Forman, 2005). The availability of space facilitates the distribution patterns of water voles observed at NWCW. The non-linear nature of the habitats, coupled with large inter habitat areas (figure 1.1) allowed males and females to establish home ranges, without the effects of crowding that are typically associated with the linear constraints of river or canal habitats, characteristic of many water vole populations elsewhere in Britain.

Pond C was inhabited by a dominant adult male and female who co-existed in close vicinity over two breeding seasons and one winter during the peak density phase (July 2006 to April 2007). This behaviour is not typical of the species (Strachan & Moorhouse, 2006). After this time an influx of juveniles displaced the adult male to pond G (approximately 100 m away; figure 1.1 DVT map) and the female was displaced from the population (dispersed beyond the study area or was predated).

Pond D supported the highest mean population densities and was an important habitat for both males and females, during both the breeding season and the winter of the peak population phase. Survival on pond D was lower during the low density phase (2008), but was also affected by development and adjacent habitat loss (chapter 6). Despite this, at the end of the study (July 2009), female water voles were still recruiting into the adult population on pond D and maintaining home ranges on the northern reaches, adjacent to pond B (figure 1.1; DVT map).

Survival of water voles on pond E was characterised by high densities during the winter of the peak density phase (2006 to 2007), however they were displaced by rising water levels associated with increased rainfall (section 2.3.6). No water voles inhabited this area during the low density phase (2008), yet this area was recolonised as population densities began to increase again (2009) (section 2.3.4).

Ponds G and H were not studied until 2007. Pond G was initially characterised by active recruitment and retention of resident water voles. In contrast, although water voles recruited onto pond H, survival was low, possibly due to the small size of this pond (80m circumference) and associated lower habitat diversity (chapter 4). Populations of water voles on ponds G and H were affected by large scale vegetation clearance during October 2007, with obvious effects on both the recruitment and survival of water voles in this area, during the subsequent winter and following breeding seasons (chapter 6).

2.3.8 Juvenile water voles

Correlations between the first capture locations of juveniles and adult females were observed since young juveniles can be expected to remain in their natal area for some time before dispersing (Woodall 1993). Interestingly, the ponds considered to be optimal habitats (ponds A, D and G) provided the most floristically and structurally diverse habitats at NWCW (chapters 1 and 4) and all exhibited a female bias in juvenile sex ratios. A similar observation has been reported in studies of the effects of habitat heterogeneity, space use, and demography in a population of California voles (Osfeld *et al.*, 1985). In contrast a male bias in juvenile sex ratios was observed on the less diverse pond E, during the peak density phase. Female root voles, (*Microtus oeconomus*) typically restrict their range to a single habitat patch or fragment. The absence of other females (within the fragment) in the week of delivery (but not the week of conception) resulted in a female-biased offspring sex ratio (Aars *et al.*, 1995). Local resource competition resulting from a patchy environment may also affect litter sex ratios (Clark, 1978), as individuals of the philopatric sex may suffer reduced fitness due to intra-sexual competition (Greenwood, 1980). Female-biased litter sex ratios produced by solitary breeding female *Microtus oeconomus* are consistent with a local resource enhancement effect when the local density is low, however, if the local density of reproductive mothers is high, competition will rise and a situation of local resource competition may develop (Aars *et al*, 1995). A similar situation has been observed in this study. Adult female water voles associated with the most diverse habitats (chapter 4) produced more juveniles.

Additionally, recruitment of juvenile female water voles into their natal ponds was a density dependent process, influenced by the distribution of adult females (section 2.3.10). Litter sex ratios of Townsend's vole (*Microtus townsendii*), vary according to season and population density, with female-biased litters prevalent when resource enhancement was expected to be high relative to local resource competition. Spring litters are typically female-biased, in contrast to male-biased autumn sex ratios, consistent with the shift in balance between resource enhancement and resource competition (Lambin, 1994).

2.3.9 Recruitment of juvenile water voles

Only 21% of the juvenile water voles recruited into the adult population and established a home range in the area of wetland studied. Juvenile female recruitment was a density-dependent process. Juvenile females were only permitted to recruit onto their natal ponds when female population densities were low. Stoddart (1970) found that young water voles born early in the season contribute to the breeding population the following year, possibly as these animals stand a better chance of filling vacancies in the vole societies, than those born later in the season. Young born later in the season tend to disappear during the winter; however, these animals may have dispersed as a response to increasing densities. This was not the case in this study, with juveniles born at any time during the season experiencing an equal recruitment rate. This may be explained by the amount of available space at NWCW (in contrast with linear habitats) and by the increased amount of vegetation cover (sedges, rushes and bramble) that persists throughout the winter on this site (chapter 4), providing increased protection from predation. Typical water vole habitats are characterised by a high percentage of grasses (Lawton & Woodroffe, 1991) which senesce during autumn, leaving no vegetative cover in the winter months. The importance of vegetation structure and composition on water vole conservation and management is discussed in chapter 6.

2.3.10 Dispersal of juvenile water voles

During the low density phase of the multi-annual population fluctuations (2008 to 2009), juvenile females recruited onto their natal ponds. In contrast, during peak years (2006 to 2007), juvenile females dispersed to adjacent, lower quality habitats (chapter 4). This suggests intra-specific territoriality and competition between mothers and daughters is temporally fluctuating and density dependent on non-linear habitats. Retention of juveniles is high during the low density phase, however, dispersal is pronounced during peak years. Local and metapopulation dynamics are influenced by population heterogeneity in dispersal characteristics and heritable changes in dispersal propensity occur on timescales short enough to impact population dynamics (Hawkes, 2009).

Female dispersal minimises maternal conflicts. Post-weaning conflict over access to resources often occurs between mothers and their offspring (Triviers, 1974). Dominant females drive out their daughters when demand for resource is high

(Clark 1978; Silk 1983; Forman & Brain, 2006). In Scottish water vole metapopulations, natal dispersal accounts for most movements between colonies, with local populations linked by high rates of juvenile dispersal but much lower levels of adult dispersal (Telfer *et al.*, 2003). Only one (male) juvenile dispersed within the study site to be recaptured as an adult established on a neighbouring pond; however, this age class is likely to suffer the highest predation rates (Macdonald *et al.*, 1997). Additionally, one juvenile female on pond D recruited into the adult population on her natal pond but did not disperse until the following spring. Males tend to disperse at 4 months of age, whereas females disperse in the spring (Macdonald *et al.*, 1997). Indeed, the longest dispersal observed by a juvenile at NWCW was approximately 200m, when a young female was driven out of her natal pond (A) by a dominant and long established female during the breeding season in the peak density phase. In Scottish metapopulations, the median natal dispersal distance for individuals that reached breeding status was 180 m for both males and females; however, a maximum dispersal distance of 5.2 km overland was recorded for a female water vole (Telfer *et al.*, 2003). The scale of this study was such that large distance movements are unlikely to have been recorded. Additionally, the high availability of optimal water vole habitat in the area of wetland studied, together with broad inter-pond areas of *Juncus effusus* (chapters 4) reduced the necessity for long term dispersals.

2.3.11 Dispersal corridors at NWCW

Dispersal of water voles is not exclusive to water ways (Telfer *et al.*, 2003). Indeed the majority of dispersal events observed at NWCW appeared to occur overland. During dispersal water voles utilised inter-habitat areas of soft rush pasture in dispersal (between ponds A and D, G and H) together with sub-optimal habitats and wooded areas, (between B and C, C and G) (see figure 1.1 and chapter 4). The complex nature of the landscape in the wetland pond system allowed multidirectional dispersal provided vegetative cover was present. Water voles are generally considered poor dispersers (Stoddart, 1970). For species like the water vole, dispersal may be restricted to movement in wetland habitats, which are unusually long and variously contorted river stretches (Macdonald & Rushton, 2003), however, overland dispersals have been observed in Scotland, with recolonised areas typically closer to their nearest neighbour overland than via waterways (Telfer *et al.*, 2003).

Dispersing voles have been shown to actively select habitat on the basis of its quality (Telfer *et al.*, 2001). Indeed a number of dispersing animals moved from ponds C and E to the more diverse pond G (chapter 4), a distance of approximately 100 m. These ponds were separated by seemingly inhospitable habitat (wet woodlands and concrete paths); however, small patches of *Rubus fruticosus* and *Juncus effusus* may have facilitated these dispersals (figure 1.1 and chapter 4). Cyclic vole populations in Northern Europe exhibit a higher frequency of risky dispersal movements in slowly growing populations that accelerate predation rates. Dispersal may induce a feedback-loop between predation and population growth that enhances synchrony (Ims & Andreassen, 2000).

2.3.12 Habitat connectivity and synchrony of multi-annual fluctuations

The ponds at NWCW were typically small and within close proximity of one another. Overlaps of the 5 m riparian buffer zone occurred between all ponds with at least one other pond (chapter 1, figure 1.1). Numerous water voles were observed to move between ponds utilising overlapping buffer zones within the same day or week (recorded by trap data). These movements often involved crossing inhospitable areas such as concrete paths, with evidence of burrowing at either side of the path, (an inhospitable substrate in which to create underground burrows connecting ponds) that may only be crossed overland. These movements were not classified as dispersal events, and occurred as adult water voles patrolled their home ranges (chapter 3). Females were observed to maintain territories between the northern reaches of ponds B and D, males were observed to patrol home ranges across multiple ponds at a time (A,B and D). Both males and females were observed to move back and forth between ponds C and E. This indicates that the populations were not arranged around individual ponds, rather in patches that occupied areas of bankside composed of two (or more) ponds, depending on the degree of connectivity (chapter 4). Furthermore, synchrony in population densities and occupancy between ponds connected by buffer zones was evident. Populations on ponds A and B fluctuated similarly throughout the duration of the study, while ponds C and E were both unoccupied simultaneously during the low density phase (2008), until the increase phase (2009) when both became occupied again and dispersal (in both directions) was observed between ponds.

Without effective demographic connectivity between numerous colonies, small clusters of colonies would be greatly exposed to both within-patch demographic and between patch extinction-recolonisation stochasticity (Aars *et al.*, 2001). At NWCW more movements were observed between ponds connected by suitable vegetation corridors, than those separated by unsuitable landscape. However, dispersal events assumed to have occurred across seemingly unsuitable habitat (trees or paths) were occasionally recorded (by capture data), especially between ponds B and C; C and E; C and G; E and G and were usually density dependent.

2.3.13 Life histories from repeat captures

Of the 122 water voles captured throughout the duration of the study, males were significantly heavier than females, typical for this species (Strachan & Moorhouse, 2006). However, no significant difference in weight was observed between genders of the 17 males and 31 females that maintained a home range (chapter 3) during the breeding season and thus yielded repeat (weight) data. It is likely that mean female weight also included pregnant females and thus skewed the analysis. Indeed, those adult captured during the breeding season were significantly heavier than those captured during winter. In addition to maintaining a non-breeding status, over-wintering animals are more likely to lose weight throughout this critical period, due to extreme temperature conditions and a reduction in available (above ground) food resources. Although resident males were not significantly heavier than resident females, a gender separation was observed between ponds (section 2.3.7). The heaviest females maintained home ranges on ponds A, C, D and G with the heaviest males occupying ponds B, C, E and H. However, no significant relationship was observed between the mean weight of resident water voles and the mean adult population density. The relationship between water vole weight and observed range length and habitat diversity are further explored in chapters 3 and 4, respectively.

Summary

- 150 water voles were captured on 8 ponds, on 492 occasions, over 40 months (4 breeding seasons and 3 over-wintering periods)
- 60% of adult males and 70% of adult females were recaptured
- Multi-annual fluctuations in water vole population densities were identified, with population densities during the peak density phase (2006 and 2007) significantly higher than the low density phase (2008 and 2009)
- Pond D had the highest overall mean population density (1.24 ± 0.55 adults per 100 m); pond E had the highest annual mean population density (2.5 ± 0.37 adults per 100 m)
- A peak density of 6.6 water voles per 100 m was observed on pond E during the peak density phase
- Pond A was the only pond to be continually occupied throughout the duration of the study, particularly by female water voles, characterised by survival (retention) of residents during the peak density phase and recruitment of juvenile females during the low density phase
- Ponds C, E and F were unoccupied for long periods of time (years), yet were still important components of the metapopulation
- The mean breeding season population density (0.99 ± 0.08 adults per 100 m) was not significantly higher than the mean winter population density (0.77 ± 0.17 adults per 100 m)
- Larger populations did not necessarily have a higher chance of persistence and during wet years, were adversely affected by rainfall and flooding, particularly in habitats with shallow bank-sides where no islands or vegetated mounds were present to provide respite from rising water levels
- 21% of juvenile water voles recruited into the adult population; recruitment of juvenile water voles was gender specific and density dependent

Chapter 3

Social Ecology

'For the female of the species is more deadly than the male'

Rudyard Kipling (The Female of the Species, 1911)

3.1 Introduction

Water vole home ranges and territoriality

Typically, female mammals compete with each other for food and space to raise offspring, whereas males compete with each other for access to females (Wolff & Peterson, 1998). Territoriality of females comprises defence of habitat related resources (Moorhouse & Macdonald, 2005). Heterogeneous habitats offer areas of varying quality, where patches that support good nesting sites or high levels of forage represent defendable resources (Ostfeld, 1985; 1990). Water vole home ranges and territoriality are also outlined in the Introduction (p10 to 11).

What limits water vole home range size?

Rodent home range sizes are affected by variations in population densities and food resources (Ostfeld, 1990; Wolff & Peterson, 1998). In the case of water voles, the length of territory varies between 30 m to 150 m for females and home range from 60 m to 300 m for males and is strongly influenced by overall population density, season and habitat quality (Strachan & Moorhouse, 2006). In linear habitats, home ranges of male water voles are smaller at higher population densities, with heavier males maintaining longer ranges than their lighter counterparts (Moorhouse & Macdonald, 2008). Radio-tracking of female water voles in linear habitats revealed that females exhibit density-dependent drifting territoriality (where the geographical position of the territory continually shifts over time), with less flexibility observed at higher population densities (Moorhouse & Macdonald, 2005).

This flexibility of water vole home range lengths, both within and between genders, has consequences for niche occupancy (chapter 4). The typical definitions of the niche focus on the ecological interactions of a population or species as a whole (Schoener 1989; Chase & Leibold 2003). However, since the niche is an emergent property of the individual, the population's niche is thus an aggregate of the biotic or abiotic interactions experienced by potentially heterogeneous individuals (Bolnick *et al.*, 2010).

Agonistic behaviour in water voles

In order to survive and increase their relative fitness, individuals must compete with others for scarce resources such as food, territories and mates. Individuals must make economic behavioural choices and will employ particular strategies in order to attain the resource in question (Krebs & Davies, 1993). Evolutionary stable strategies are those in which costs are minimised and gains are maximised. Intraspecific conflicts are usually limited involving inefficient weapons or ritualised tactics that seldom cause injury to either contestant (Maynard-Smith, 1982).

In contrast, agonistic behaviour is typically associated with intraspecific conflict in water vole populations (Strachan & Moorhouse, 2006), the extent of which is determined by seasonality; females become territorial during the breeding season and an increased incidence of aggressive encounters often occurs. Previous patterns of bite topography and agonistic behaviour in this species seem to reflect competitive interactions between individuals, particularly between territorial females and their female offspring, over access to essential resources (Forman & Brain, 2006).

Rationale

The home range length and movement patterns of water voles inhabiting non-linear habitats (such as ponds) have not been previously described. The three-dimensional nature of the pond habitats at NWCW (associated with topography and bankside structure) may allow male and female water voles to maintain shorter home ranges than their counterparts on linear habitats. Moreover, the structure of the landscape may facilitate a greater degree of intra-sexual range overlaps between females in areas associated with continuous cover of available habitat between ponds (chapter 1). Current knowledge suggests that adult females exclude same sex individuals from their range during the breeding season, but overlap with males (Strachan & Jefferies 1993, Strachan & Moorhouse 2006). However, female water voles at NWCW maintained intra-sexually overlapping ranges on certain ponds, during both the breeding season and the winter (section 3.2.3).

The plasticity in social behaviour observed between water voles on non-linear habitats such as those at NWCW and their counterparts on linear river habitats may be attributed to habitat structure (chapter 4) and has implications for niche occupancy. This aspect of water vole ecology has important consequences for furthering our understanding of the species requirements and should be taken into consideration during the design of new habitats. Additionally, agonistic behaviour in a metapopulation of water voles has not previously been studied (but see Forman & Brain, 2006). Population densities of water voles at NWCW were observed to vary between pond and season (chapter 2). The relationship between water vole home range length, weight and population density has been described on linear habitats (Moorhouse & Macdonald, 2005, 2008) however, has not been previously studied on ponds. Increasing our understanding of water vole social behaviour on pond systems will not only add to the current knowledge base, but will augment future conservation measures, particularly if restoration of water vole habitat includes pond construction. Additionally, improving our understanding of social interactions and agonistic behaviour will complement refinement to husbandry techniques of housing captive bred water voles, prior to release in reintroduction programmes.

Aims

1. To determine the number of adult water voles that maintain a home range per pond at NWCW
2. To assess water vole home range length (ORL) during the breeding season
3. To assess water vole home range length (ORL) during the winter
4. To record variations in home range between genders and ponds during both the breeding season and the winter
5. To investigate the effect of population densities on home range length
6. To investigate the effect of weight on water vole home range length per individual
7. To assess the degree of intra- and inter-sexual overlap of home ranges between males and females during both the breeding season and the winter
8. To record the degree of agonistic behaviour in the form of bite wound patterns in resident adults and also juveniles, during both the breeding season and the winter

3.2. Results

3.2.1 Water vole ORL during the breeding season

Observed range lengths (ORL) were determined for 17 males and 31 females during the breeding season. Adult water voles maintained a home range on all ponds in the area of wetlands studied for at least one breeding season throughout the duration of the study. However, no females maintained a home range on pond H (according to trapping data; but see chapter 5) (table 3.1). Of the 17 males, 2 maintained a home range on one pond, before being displaced to another pond, where they maintained a new home range during the same breeding season. Accordingly, 19 male ORLs were included in the analyses on mean male ORL during the breeding season (table 3.1, figure 3.1). Males maintained a significantly longer home range than females during the breeding season ($t_{23.59} = 2.531$, $p = 0.018$). The mean ORL during this time was 59.74 ± 10.17 m for males and 32.10 ± 3.97 m for females. A number of water voles, particularly males (n = 6; 35%) but also females (n = 2; 6%), were observed to maintain an ORL over two or more ponds during the breeding season (table 3.2).

Table 3.1 Number of water vole home ranges (ORL) observed per pond during the breeding season (numbers in brackets indicate male water voles that maintained an ORL on a different pond in the area of wetland studied, before displacing to maintain a new ORL on the pond specified)

Pond	Number of male water voles	Number of female water voles
A	1	9
B	4	2
C	3	2
D	4	8
E	1 (+1)	3
F	1	1
G	2 (+1)	6
H	1	0
Total	17 (+2)	31

Table 3.2 Number of water voles that maintained a home range (ORL) over more than one pond during the breeding season

Home pond	Number of males	Other ponds included in ORL	Number of females	Other ponds included in ORL
A	1	B and D	0	-
B	3	A and D	1	D
C	1	A and D	0	-
D	0	-	1	B
E	0	-	0	-
F	0	-	0	-
G	0	-	0	-
H	1	G	0	-
Total	6	-	2	-

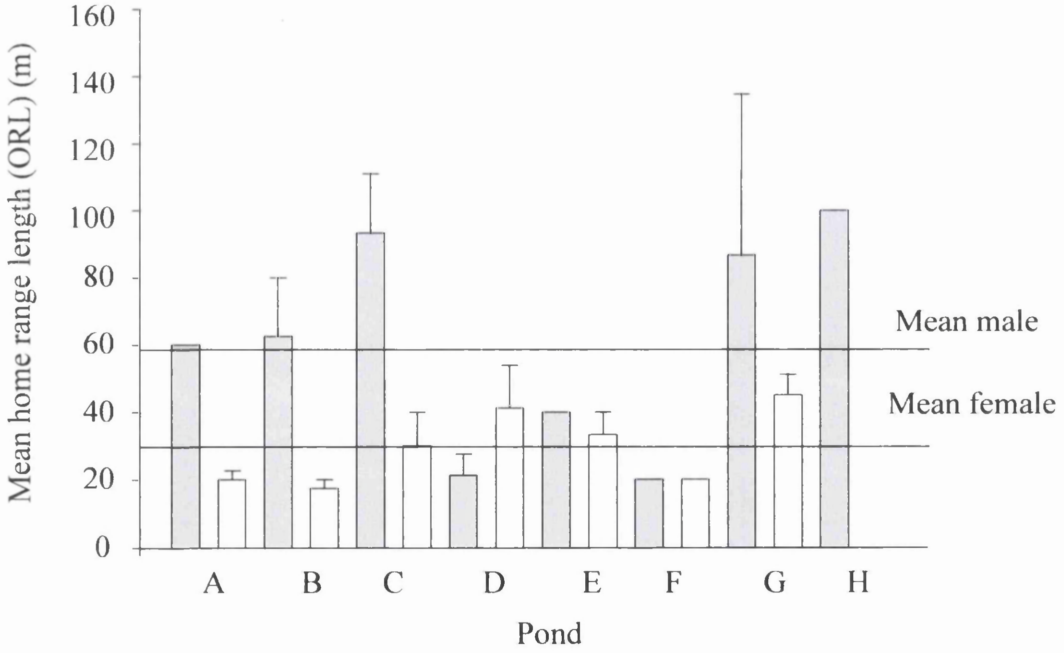


Figure 3.1 Mean (±SE) breeding season home range length (ORL) (m) of resident adult water voles per pond, across the area of wetland studied. Males (n = 19) (grey bars), females (n = 31) (open bars). Overall means also presented.

Although male water voles typically maintained longer home ranges than females, no significant differences in mean home range length per pond were observed during the breeding season (figure 3.1), ($F_{1,15}$ = 1.443, p =0.223) and no interaction was observed between pond and gender ($F_{1,6}$ = 1.291, p = 0.288). However, in contrast to all other ponds, males on pond D appeared to maintain shorter home ranges than their female counterparts (figure 3.1).

3.2.2 Water vole ORL during the winter

Observed range lengths were determined for 9 males and 9 females during the winter (table 3.3). Winter home ranges were not normally distributed and were thus square root transformed for the analyses. Males maintained a significantly longer home range than females during the winter ($t_{11.72}$ = 3.224, p = 0.008).

Table 3.3 Number of water voles that maintained a home range (ORL) per pond during the winter (numbers in brackets indicate resident water voles that maintained a breeding season home range but were only captured once during the winter and thus could not be assigned an exact winter ORL)

Pond	Number of male water voles	Number of female water voles
A	0	2 (+4)
B	1 (+3)	0 (+2)
C	1	2
D	3 (+2)	3 (+1)
E	3	1 (+1)
F	0	0
G	1 (+1)	1 (+2)
H	0	0
Total	9 (+6)	9 (+10)

The mean ORL during the winter was 48.50 ± 8.13 m for males and 20.00 ± 2.64 m for females. This represented an over-winter home range contraction of 17% for males, however, there was no significant difference in male home range length between seasons ($t_{26.62}$ = 0.863, p = 0.396). However, only 1 male (n = 1; 11%) (resident on pond B) was observed to utilise more than one pond during winter, incorporating pond A into his home range. In contrast, a significant range contraction was observed for females in the winter, with a 38% reduction in their home range length ($t_{36.05}$ = 2.537, p = 0.016). There was no significant difference observed between home range length per pond during the winter (figure 3.2) ($F_{1,10}$ = 1.206, p = 0.431).

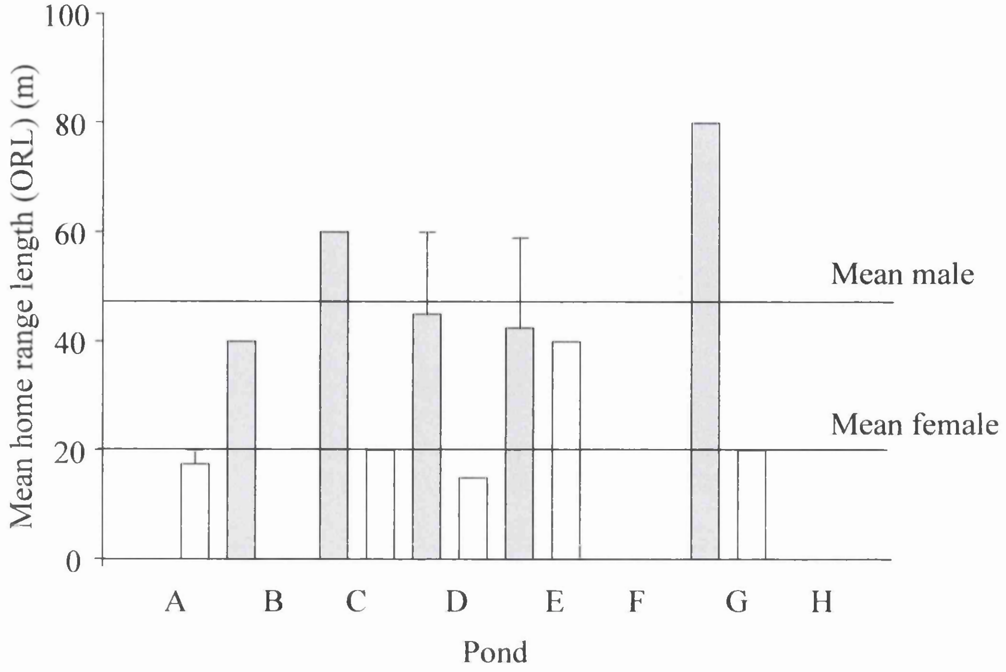


Figure 3.2 Mean (±SE) winter home range length (ORL) (m) of resident adult water voles per pond across the area of wetland studied. Males (n = 9) (grey bars), females (n = 9) (open bars).

In addition to the 18 water voles that maintained a home range during the winter, a further 16 water voles (6 males, 10 females; table 3.3) over-wintered, but were only captured once during the winter. Although these animals provided information regarding over winter survival (chapter 2) and winter habitat utilisation (chapter 4) per pond, they were not included in the analyses of winter range length (methodology 3.6) however, they were included in the analyses of home range overlaps (section 3.2.4).

3.2.3 What influences water vole ORL during the breeding season?

Male water vole home range length on the ponds was not significantly influenced by total adult population density ($F_{9,18}$ = 0.764, p = 0.653, R^2 = 13%) or by female population density ($F_{9,18}$ = 0.755, p = 0.659, R^2 = 14%) during the breeding season. Furthermore, male weight had no significant influence on male home range length ($F_{9,18}$ = 3.408, p = 0.171, R^2 = 67%) during the breeding season. Additionally, female home range length showed a similar response to males in the effect of population densities. Female home range length was not significantly influenced by total adult population density ($F_{12,30} = 0.664$, $p = 0.779$, $R^2 = 16\%$) or by female population density ($F_{14,30} = 0.478$, $p = 0.914$, $R^2 = 32\%$) during the breeding season. However, female home ranges of water voles inhabiting non-linear systems were significantly influenced by the weight of individuals ($F_{27,30} = 9.215$, $p = 0.046$, $R^2 = 88\%$). Heavier female water voles maintained longer home ranges during the breeding season than their lighter counterparts across the area of wetland studied.

3.2.4 Water vole home range overlaps

Many water vole home ranges were overlapped with those ranges of other individuals, during both the breeding season and the winter. Interestingly, intra-sexual home range overlaps (male-male and female-female) were as frequent as inter-sexual (male-female) home range overlaps (table 3.4) during the breeding season ($G_2 = 4.08$, $p = 0.13$). Furthermore, the only significant differences were observed during the winter ($G_2 = 6.33$, $p = 0.042$), when the majority of home range overlaps were inter-sexual, observed between males and females.

Table 3.4 Number of water vole home range overlaps that occurred per year during the breeding season and the winter. (M-M male-male; M-F male-female; F-F female-female).

	Breeding season ORL overlaps			Winter ORL overlaps		
Year	M-M	M-F	F-F	M-M	M-F	F-F
2006	5	6	1	0	3	0
2007	4	6	3	2	3	1
2008	0	0	1	0	0	0
2009	0	0	1	0	0	1
Total overlaps	9	12	6	2	6	2
Total animals	11M	6M 10 F	10F	2M	6M 5F	4F

During the breeding season, 6 males (31%) and 10 females (32%) maintained 12 inter-sexually overlapping ranges (table 3.4). Males were intra-sexually overlapping, with 9 male-male home range overlaps observed between over half (11; 58%) of the resident adult males, particularly on pond D. All intra-sexual female overlaps involved only 2 females, whereas males were observed to overlap with up to 3 other males or females. Nevertheless, apparent male territoriality was evident on certain ponds, with males on ponds C and G excluding other males from their home ranges. However, both male-male and male-female overlaps were density dependent, occurring only during the peak density phase (2006 to 2007) (table 3.4 and see chapter 2).

Interestingly, in contrast to other studies, intra-sexual home range overlaps were observed for female water voles during both the breeding season and the winter, particularly on pond A (table 3.4). A third (10; 32%) of the resident adult female water voles were observed to maintain intra-sexually overlapping home ranges during the breeding season across the area of wetland studied. Furthermore, 8 (4 pairs) of the 9 females that maintained a home range on pond A were involved in (4 of the 6) home range overlaps. Moreover, female intra-sexual overlaps were not density dependent, with one pair of females maintaining overlapping home ranges during every breeding season on pond A, even throughout the low density phase (2008 to 2009) (table 3.4 and see chapter 2). In contrast, the pairs of females on ponds D and E that maintained (2 of the 6) female-female overlaps, only did so during the peak density phase (2006 to 2007), associated with higher population densities (chapter 2) and associated loss of vacant habitat (chapter 4).

3.2.5 Agonistic behaviour in water voles

In total, 82 wounds were recorded on adult water voles that maintained a home range throughout the area of wetland studied, with juveniles receiving a total of 16 wounds (tables 3.5 and 3.6). There were significant differences in the total number of bite wounds recorded between gender and age classes ($G_3 = 82.68$, $p < 0.001$) and between the areas of the body that received bites, with the tail receiving significantly more bites than any other area of the body ($G_3 = 51.86$, $p < 0.001$). Although adult males and females received a similar relative number of wounds (table 3.5), seasonal differences were observed (table 3.6).

Table 3.5 Summary of the number of resident adult water voles and juveniles that sustained bites in relation to three areas of the body. Total number of animals and wounds and relative number of wounds per animal are presented (breeding season and winter combined)

	Body area bitten					
Gender / age class	Head	Body	Tail	total voles	total wounds	Relative number of wounds per vole
Adult male	3	2	12	21	31	1.48
Adult female	10	1	19	33	51	1.54
Juvenile male	1	0	2	9	6	0.67
Juvenile female	1	1	6	16	10	0.63

Table 3.6 Seasonal occurrence of bite wounds sustained by resident adult male and female water voles in relation to three areas of the body. Total number of animals and wounds and relative number of wounds per animal are presented per season.

		Body area bitten					
Gender	Season	Head	Body	Tail	total voles	total wounds	Relative number of wounds per vole
Male	Breeding	3	2	6	19	16	0.84
	Winter	0	0	6	15	15	1.00
Female	Breeding	8	1	19	31	46	1.48
	Winter	2	0	3	19	5	0.26

Significantly more bite wounds were received by females during the breeding season, than during the winter ($G_1 = 113.94$, $p < 0.001$). During the breeding season 68% of adult females received a total of 46 wounds, whereas only 16% of females received a total of 5 wounds during the winter (tables 3.6 and 3.7). In contrast, no significant difference in the number of wounds received by adult males was observed between seasons ($G_1 = 0.097$, $p = 0.755$). Adult males received a similar number of wounds during the breeding season (33% of males; 16 wounds) as during the winter period (40% of males; 15 wounds) (tables 3.6 and 3.7).

Table 3.7 Total number (and proportion) of resident adult water voles that sustained bite wounds per pond and season

	Breeding season		Winter	
Pond	Males	Females	Males	Females
A	0	5 (0.63)	0	1 (0.17)
B	1 (0.25)	1 (0.5)	2 (0.5)	2 (1.0)
C	2 (0.67)	1 (0.5)	0	0
D	1(0.25)	7 (0.88)	1 (0.25)	1 (0.33)
E	1 (0.5)	3 (1.0)	3 (1.0)	0
F	0	0	0	0
G	2 (0.67)	4 (0.67)	0	0
H	0	-	-	-
Total	7 (0.33)	21 (0.68)	6 (0.40)	3 (0.16)

Ponds F and H were the only habitats where no resident adult water voles were wounded (table 3.7), however, both these ponds were associated with the lowest numbers of resident adults (chapter 2). There was no significant difference in the proportion of wounded males per pond ($G_7 = 1.985$, $p = 0.960$) or females per pond ($G_7 = 2.352$, $p = 0.937$) during the breeding season. Since only 6 resident males and 3 resident females were wounded during the winter period (table 3.8), the small sample size precluded them from statistical analysis of wounded animals per pond. Nevertheless, the ponds sustaining wounded animals during the winter period were associated with higher densities of overwintering water voles. Indeed, all resident males on pond E were wounded during the winter, when the highest peak density of water voles was recorded throughout the entire duration of the study (chapter 2).

3.3 Discussion

3.3.1 Water vole home range length (ORL) during the breeding season

Adult water voles inhabiting a complex pond system maintained shorter observed range lengths than their Scottish and English counterparts on linear river systems (Strachan & Jefferies, 1993; Telfer *et al.*, 2001; Moorhouse & Macdonald, 2008). During the breeding season at NWCW, males maintained a mean home range length (60 m) significantly longer than the mean female home range length (32 m), a trend which is typical of this species (Stoddart, 1970; Strachan & Jeffries, 1993; Strachan & Moorhouse, 2006). Males were also observed to travel further than females, maintaining a maximum home range length of 180 m and 100 m respectively. Radio-tracking studies of water voles have observed movements of more than 100 m in an hour (Moorhouse & Macdonald, 2005) and up to 800 m in a single day (Macdonald & Strachan, 1999). Females can traverse their entire territory in a day (Moorhouse & Macdonald, 2005), visiting important latrines twice and peripheral latrines once in a 24h period (Stoddart, 1970) (chapter 5).

The range lengths observed at NWCW were typically much shorter than those recorded elsewhere (Moorhouse & Macdonald, 2005; 2008; Strachan & Jefferies, 1993; Telfer *et al.*, 2001), possibly due to the non-linear nature of the wetland complex at this site. Numerous adult water voles, both males and females were observed to maintain discrete home ranges as short as 20m or less, representing static territoriality (Moorhouse & Macdonald, 2005). Furthermore, many of these home ranges were maintained between two water bodies (e.g. between ponds B and D) or on ponds with islands (e.g. ponds A and D), particularly by females. Both of these strategies increased the amount of available edge (that may be utilised for foraging and nesting) maintained over a shorter territory length (chapter 4). Indeed, field surveys revealed both latrines and food piles on islands (chapter 5), confirming their utilisation by resident adults. This three-dimensional habitat utilisation may contribute to the reduced range lengths observed at this site (chapter 4).

3.3.2 Water vole home range length (ORL) during the winter

During winter, adult male water voles maintained a mean home range length (49m) significantly longer than their female counterparts (20m), typical for this species (Stoddart, 1970; Strachan & Jeffries, 1993; Strachan & Moorhouse, 2006) and also a similar response to that observed at NWCW during the breeding season.

Interestingly no significant differences were observed between male home range length during the breeding season and winter, with males maintaining above ground activity throughout the year. Nevertheless, only one male used more than one pond during the winter, whereas males used up to three ponds during the breeding season. In contrast to males, female water voles significantly contracted their home range in the winter; however, above ground activity was still maintained, albeit over a shorter range length.

Below ground, overwintering water voles may spend long periods in their nest chambers and there may be very little sign of above ground activity (Strachan & Moorhouse, 2006). However, at NWCW, water voles were active all year round where above ground cover persisted (Forman, 2003; pers. obs). Indeed, during milder winters (such as 2006 to 2007) latrines were established during January (chapter 5) substantiating the fact that territories were established beyond the boundaries of the breeding season at this site. Furthermore, pregnant females were trapped during February. During this time much above ground activity in the form of burrows, runways and feeding stations were also recorded (chapter 5).

It is plausible that water voles maintain latrines throughout the year. However, if their movements are restricted to underground burrows during winter (particularly in colder years) then it is possible that latrine creation occurs in underground burrows that we are unable to detect. Further studies are required in order to determine the degree to which water voles create latrines beyond the boundaries of the 'typical' breeding season (i.e. March to September; Strachan & Jefferies, 1993). Indeed, since we do not understand the range of chemical and olfactory signalling associated with the production of scent marked latrines (chapter 5), we are unable to fully understand the role latrines play in communication, or indeed what signals are portrayed, particularly beyond the boundaries of the breeding season. Furthermore, we do not understand the degree to which social structure or below ground range lengths are maintained during periods of time spent over-wintering in underground burrows. Nevertheless, agonistic behaviour was apparent above-ground during winter at NWCW, with males receiving a similar number of bites during this time as during the breeding season. This indicated continual intra-specific conflict, most likely from interactions with dominant females, but potentially between dominant males.

3.3.3 What influences water vole home range length during the breeding season?

The effects of both water vole population density and individual weight on ORL were examined for both male and female water voles. The only significant relationship was observed between female home range length and individual weight. Heavier females maintained longer home ranges during the breeding season than their lighter counterparts. Larger animals may have larger ranges if larger body weights conferred greater competitive ability (Nelson, 1995). A similar result was observed for male water voles on linear habitats, where heavier males maintained longer home ranges (Moorhouse & Macdonald, 2008). However, no significant relationship was observed between male weight and home range length at NWCW. Furthermore, in contrast to previous studies, no significant relationship was observed between home range length of males or females and population density (Moorhouse & Macdonald, 2008). Despite this, pond D was the only location where males maintained a shorter range than their female counterparts, perhaps in response to the high density of females in this locality.

Numerous studies of many vole species reveal that home range sizes are smaller at high population densities (Nelson, 1995; Ostfeld & Canham, 1995; Bond & Wolff, 1999; Moorhouse & Macdonald, 2008). Previous studies (largely conducted on linear habitats in England) suggest that, depending on overall population density, season and habitat quality, the length of territory for female water voles varies between 30 m to 150 m for females and home range from 60 m to 300 m for males (Strachan & Moorhouse, 2006; Moorhouse & Macdonald, 2008). In Scotland, during the breeding season, males occupy ranges of up to 500 m and breeding females up to 300 m in length at low population densities, reducing to 180 m and 90 m for males and females respectively at high population densities (Leuze, 1976). It is plausible that the non-linear nature of the wetland pond system at NWCW accounts for the lack of relationship observed between population densities and home range lengths.

Numerous areas of habitat in between ponds were utilised by water voles during both dispersals and maintenance of home ranges at this locality. These areas were beyond the 5 m boundary around the edge of ponds (figure 1.1) and therefore were not subject to trapping. However, these areas provided an excess of unoccupied habitat between ponds (up to 50 m wide in some areas) and were utilised by water voles, confirmed by the presence of field signs (chapter 5). Active intra-habitat movements, coupled with competition for resource monopolisation, may increase the risk of encounter between males, and to a lesser extent, females (Forman & Brain, 2006). It is likely that this availability of vacant habitat ensured that no pond was ever saturated with water voles, even during the peak density phase. Further studies are required to identify the response of water vole home range lengths to increasing population densities on non-linear pond habitats.

3.3.4 Water vole home range overlaps

Both male and female water voles displayed remarkable plasticity in their social behaviour at NWCW, with both male and female behaviours recorded that contradict previous observations on linear habitats in Britain (Stoddart, 1970; Moorhouse & Macdonald, 2005; 2008). Male water voles employed varying degrees of territoriality during the breeding season at NWCW, implying the presence of a social hierarchy. Intra-sexual male overlaps only occurred during the peak density phase on ponds associated with higher population densities (chapter 2). Male water voles on all other ponds appeared to exclude other males from their home ranges. This contradicts previous studies in Britain, where typically male water voles are considered to be non-territorial, with large ranges that overlap those of several other males and females (Stoddart, 1970; Leuze, 1976; Strachan & Moorhouse, 2006). However, in grassland and marsh habitats outside the UK, females represent a clumped, defendable resource and male water voles respond by becoming territorial and maintaining non-overlapping ranges (Jeppson, 1990).

At NWCW, various mating strategies were adopted. Apparently monogamous females lived on pond A (territorial male with numerous females), pond C (male and female pair that co-existed for at least 12 months) and pond F (male and female pair that co-existed for one breeding season). In contrast, polygamous adults with numerous inter-specific range overlaps lived on both pond D (linear), pond E (complex) and pond G (complex). The spatial arrangement of ponds in the wetland system has consequences for both range overlaps and mating systems. Water voles have flexible social and mating systems, being predominantly monogamous in linear habitats such as rivers and streams (Stoddart, 1970), but polygamous in more complex habitat types such as reed bed systems (Forman, pers. comm.).

Female water voles maintained intra-sexually overlapping home ranges during the breeding season at NWCW. This contradicts previous observations for this species (Stoddart, 1970; Leuze, 1976; Moorhouse & Macdonald, 2005; Strachan & Moorhouse, 2006). However, it should be noted that the majority of intra-sexual female overlaps occurred on pond A, where the topography and structural diversity of the habitat (chapters 1 and 4) permitted overlaps, with a reduced likelihood of interaction with conspecifics. Intra-sexual female overlaps on pond A were not density-dependent, occurring during both the peak density phase (2006 to 2007) and low density phase (2008 to 2009). However, during the low density phase, these overlaps occurred between established adult females and juveniles that recruited onto their natal ponds. This is in contrast with the peak density phase when juveniles were forced to disperse to other ponds in the vicinity (chapter 2).

With the exception of pond A, females were typically territorial and excluded other females from their home range, unless high population densities induced overlaps through lack of available space (ponds D and E during the breeding season). Temporal patterns of range use in water voles results in individual females' territories overlapping in time and space (Moorhouse & Macdonald, 2005). This seasonal feature of habitat exploitation increases the likelihood of female-female territorial encounters as individuals strive to defend or retain important resources (Kapusta & Marchleweska-Koj, 1998). Pond D supported the highest mean population density throughout the study (chapter 2). The structure of the habitat on pond D (figure 1.1) is similar to that of lowland linear systems studied elsewhere (Strachan & Moorhouse, 2006; Moorhouse & Macdonald 2005; 2008). Indeed, females on pond D maintained discrete contiguous home ranges, arranged in a manner comparable to those on linear English systems such as canal habitats or ditch systems (Moorhouse & Macdonald, 2005). Females on pond D were highly territorial, typically excluding other females and also males from their home ranges. Water voles have a limited capacity for mutual avoidance, and any interactions between individuals are likely to directly affect range sizes (Moorhouse & Macdonald, 2008). Minimising overlap between each other in turn minimises territorial conflicts and associated loss of fitness (Forman & Brain, 2006).

3.3.5 Agonistic behaviour in water voles

Significantly more wounds were recorded on female water voles on the ponds during the breeding season than the winter, implying seasonal territoriality. Moreover, male water voles were as likely to be wounded during the breeding season as during the winter. This concurs with the findings of previous studies of wild water voles on this site (Forman & Brain, 2006). Juvenile water voles suffered less than their adult counterparts; however, on pond D the majority of juveniles were wounded. Both juvenile males and (particularly) juvenile females suffered the highest incidence of bites in this locality, particularly to vulnerable areas of such as the head and body, associated with offensive attack (Brain, 1981; Pellis, 1997). The high population densities on pond D may have contributed to this observation.

Post-weaning conflict over access to resources often occurs between mothers and their offspring (Trivers, 1974). Patterns of bite topography and agonistic behaviour in this species reflect competitive interactions between individuals, particularly between territorial females and their female offspring (Forman & Brain, 2006) and are typically density dependent. Pond A was the only pond on which adult females were resident during all years of study. Interestingly, during the peak density phase, juvenile daughters on pond A dispersed (to pond C), however, during the low density phase, juvenile daughters were permitted to stay and their ranges overlapped with resident adult females. Juvenile females displaying bite wounds were not encountered on pond A until 2009, when they overlapped their ranges with dominant females, during periods of low population density. Permission to remain in the natal pond is only granted if resource competition is also low. It is likely agonistic encounters occur even when daughters are permitted to establish within their mother's territory, if the outcome is only to inform the juvenile offspring of her position within the social hierarchy. Agonistic interactions between adult females and their daughters are typically much longer than both intra- and inter-specific encounters between adults (Forman & Brain, 2006).

Both adult males and (particularly) females received head wounds and several individuals (both male and female) lost an eye as a result of agonistic encounters. Previous studies of wild water voles (within NWCW but not in the area under study here) revealed that water voles show no inhibition in targeting bites to vulnerable body areas (namely the head and tail) (Forman & Brain, 2006). The results of this study substantiate this finding. This contrasts with previous studies of rodents where competitive forms of attack largely avoid these sensitive areas. During territorial encounters, individuals generally direct bites towards the back of conspecifics (Blanchard & Blanchard, 1977; Pellis & Pellis, 1989; Pellis *et al.*, 1992). Inter-male combat involves offensive attack but a clear inhibition of biting vulnerable regions (Brain, 1981). In contrast, potentially lethal defensive attacks between resident non-receptive females and male intruders are often targeted at vulnerable areas (Blanchard & Blanchard, 1981). Indeed, interactions between males and reproductively active females in the field show that the females often bite males on their heads during pre-copulation interactions (Forman & Brain, 2006). However, this study clearly shows that the vast majority of bites occurred on the tail of conspecifics. Water voles may drive defeated animals away by targeting bites to the tail area (Forman & Brain, 2006). Agonistic encounters in tree shrews (*Tupia belangeri*) often result in retreating animals being bitten on the rump (Blanchard *et al.*, 2001). Both adults and juveniles were significantly more likely to suffer bites to the tail than any other area; however, juveniles were more likely to retreat during agonistic encounters with dominant adults, particularly during the peak density phase.

In light of the results of this study and previous studies (Forman & Brain, 2006), it is apparent that social interactions between individual water voles are often agonistic and can result in wounding of conspecifics. It is important to increase our understanding of this range of animal behaviours, particularly since numerous individuals are destined for captive breeding and reintroduction programmes (e.g. Moorhouse & Macdonald, 2005; 2008). It is essential to ensure refinements to husbandry techniques in this species are to be made in order to promote 'normal' behaviour in such individuals (Forman & Brain, 2006). Captive bred animals are frequently underweight and immunologically compromised (Moorhouse *et al.*, 2007) and if not provided with appropriate housing conditions and proper husbandry are likely to incur stress through agonistic conflicts associated with overcrowding. This will further compromise their fitness, and therefore likelihood of survival, post-release (Gelling & Macdonald, 2010).

Summary

- Males maintained significantly longer home ranges than females during both the breeding season and the winter
- Water vole home ranges at NWCW are substantially shorter than those recorded in linear habitats in England or Scotland
- Females exhibit significant range contraction during the winter however no significant difference in male home range length was observed between seasons
- In contrast to previous studies, population densities did not affect home range length of water voles
- Heavier females maintained longer ranges than their lighter counterparts, however no relationship between weight and home range length of males was observed
- Intra-sexual female overlaps were as common as intra-sexual male overlaps and intersexual overlaps, implying male territoriality and a lack of female territoriality
- The structure of the wetland habitat potentially contributed to the reduced home range lengths and increased intra-sexual female home range overlaps (chapter 5)
- Females were more likely to be wounded during the breeding season, implying female territoriality
- Males were just as likely to be wounded during the breeding season as during the winter, implying both males and females maintain inter-sexual aggression beyond the boundaries of the breeding season
- Juvenile females suffered a higher degree of wounding on pond D than any other pond, associated with high population densities and competition for resources

Chapter 4

Habitat Utilisation

'Variety is the spice of life.'

William Cowper (The Task, 1785)

4.1 Introduction

Water vole habitat

The large size of the British water vole (up to ten times greater than that of the field vole) may preclude it from using vegetation as cover except in those localities, such as rivers, where the vegetation grows very dense and remains so for the rest of the year (Woodall, 1993). Water vole habitat preferences and requirements are outlined in the Introduction (p9). Typically, water voles inhabit sites with slow flowing water and wide swathes of riparian vegetation, which provide food and shelter (Strachan & Moorhouse, 2006).

Water vole distribution and activity is strongly related to a variety of habitat parameters, particularly vegetation structure and composition (Lawton & Woodroffe, 1991; Woodall 1993; Strachan & Moorhouse, 2006; Neyland *et al.*, 2010). On English river systems, 'core' areas for water voles (supporting breeding colonies and marked with latrines) reflect sites actively selected for their specific characteristics. These include a high percentage of grass, steep bank angles and relatively high layering of the vegetation (Lawton & Woodroffe, 1991). Further studies went on to classify environmental correlates that have a positive relationship with water voles. These include a water depth greater than 100 cm and the presence of specific plant species; Stinging nettle (*Urtica diocia)*, Common Reed *(Phragmites australis)* and an unidentified grazed graminoid species (Woodall, 1993). The importance of reed beds (*Phragmites australis*) as a refuge from predators has also been demonstrated (Carter & Bright, 2003).

Most recently the effects of habitat quality upon reintroduction success have been investigated. Those sites supporting abundant vegetation increase the likelihood of long term survival and likelihood to colonise further areas, thus highlighting the need to ensure that any habitat selected for reintroduction is the best obtainable (Moorhouse *et al.*, 2009).

Current water vole conservation measures

Much of the focus of current conservation measures has been on reintroduction of captive bred water voles (Moorhouse *et al.*, 2008, 2009) and control of feral American mink populations (Reynolds *et al.*, 2004). Although these approaches have localised success, the wider picture must be considered. In addition to the current conservation measures, conservation management should also focus on increasing habitat suitability in areas where reintroductions are occurring.

Although numerous studies have identified important habitat characteristics and plant species positively associated with water voles (Lawton & Woodroffe, 1991; Moorhouse *et al.*, 2008; Strachan & Moorhouse, 2006; Woodall, 1993) these studies were primarily on river habitats. The vegetation on pond systems in relation to water vole populations in lowland Wales has not been studied previously. Identification of plant species that are intrinsic to optimal habitats for water voles within complex wetland landscapes is required. Since NWCW represents one of the nationally important Welsh Key sites, it was deemed appropriate to map all of the pond and bank side vegetation, together with the areas between ponds that water voles utilised during dispersals and inter pond movements.

Rationale

Population density data (chapter 2) revealed that pond D supported the highest mean population density of water voles; however, pond A was the only pond to be continually occupied throughout the duration of the study. Additionally, certain ponds in the metapopulation (ponds C and E) were unoccupied for over a year during the low density phase, before recolonisation as population densities increased. The purpose of this chapter was to identify habitat characteristics that determined the distribution patterns observed.

With the exception of water vole in reed-beds (Carter & Bright, 2003), little information is available describing the population size, movement patterns and other ecological aspects of water vole populations occupying non-linear habitats such as ponds. It was anticipated that this study would provide a detailed assessment of the local movements of a water vole population in distinct plant patches. This study builds upon previous live capture and release techniques used to monitor water vole populations, by implementing a new method of studying the movement patterns of water voles in relation to discrete stands of vegetation (dominant vegetation types;

DVTs, chapter 1). In turn, this could assist in the construction of empirically derived models that could be used to predict water vole population densities under different ecological conditions. This study and the approach it describes should augment the knowledge required for the effective monitoring and management of pond systems containing water voles and provide useful comparative data on the species' ecology.

Aims

1. To determine the degree to which different dominant vegetation types (DVT) (figure 1.1) were utilised by water voles
2. To determine the dominant vegetation types incorporated into the home ranges of resident adult water voles
3. To observe seasonal variation in utilisation of DVTs
4. To determine the dominant vegetation types associated with over-wintering water voles (chapter 2)
5. To investigate the relationship between pond size and population density (chapter 2)
6. To investigate the relationship between water vole populations and diversity at both the habitat (D_{pond}) and patch (D_{DVT}) level (chapter 1)
7. To determine the relationship between home range length (ORL; chapter 3) and habitat diversity (D_{pond})

4.2 Results

It was assumed that the location of each trapped animal reflected habitat selection and that all water voles had an equal chance of being captured. Thus, if a water vole was captured in a specific location, this represented a specific behavioural choice that has been made, i.e. occupying a particular location that offers a particular requirement such as food, shelter or access to mates (Woodall, 1993). Surveys that revealed the presence of characteristic field signs including latrines, food piles and burrows (see chapter 5) indicated that areas of activity typically corresponded with high trap incidence and thus it can be assumed that the trapped population usually (but not always) reflected true distribution effects.

4.2.1 Water vole occupancy per Dominant Vegetation Type (DVT)

There were thirty different dominant vegetation types (DVTs) across the area of wetland studied (see figure 1.1; DVT map), however, not all DVTs were present on each of the eight ponds. Twenty-three DVTs were present within the 5 m boundary line around the edge of the ponds (chapter 1). However, only eleven DVTs (including bare ground) contained a trap (table 4.1) due to the spacing of traps (approximately 20 m apart; methodology section 3). The bare ground DVT that contained a water vole trap was located under the bridge on pond G (figure 1.1). No water voles were ever captured in this trap, despite the fact that animals were observed to move between ponds G and H (chapter 3). Certain ponds had duplicate numbers of DVTs, with two or more traps located in similar DVTs at different points around the circumference of the water body. All results were adjusted for unequal sample size and effort to represent true effects (methodology section 5.5). Of the 150 water voles captured throughout the duration of the study, adult water voles occupied significantly different DVTs from juveniles. Analysis of variance revealed a significant difference in DVT occupancy observed between age classes ($F_{3,29}$ = 6.058, p = 0.007). *Post hoc* Bonferroni multiple comparisons showed that the greatest difference in DVT occupancy was observed between males and juveniles (p = 0.008), however, females also occupied significantly different DVTs than juveniles (p = 0.032). No significant difference was observed between adult males and females (p = 0.836). Despite this, variations in DVT utilisation between genders and seasons were observed for those adults that established a home range (sections 4.2.3 to 4.2.4).

Table 4.1 List of all dominant vegetation types (DVTs) that contained traps with abbreviations (used in graphs) and English botanical names (after Stace, 1997; see Methodology section 2 and chapter 1)

DVT name	DVT abbreviation	DVT botanical name
Bare ground	BgDVT	N/A
Bolboschoenus maritimus	*Bm*DVT	Sea Club-rush
Carex riparia	*Cr*DVT	Greater Pond-sedge
Damp grassland	DgDVT	N/A
Epilobium hirsutum	*Eh*DVT	Great Willowherb
Glyceria maxima	*Gm*DVT	Reed Sweet-grass
Juncus conglomeratus	*Jc*DVT	Compact Rush
Juncus effusus	*Je*DVT	Soft rush
Rubus fruticosus	*Rf*DVT	Bramble
Trees	TreeDVT	N/A
Typha latifolia	*Tl*DVT	Bulrush

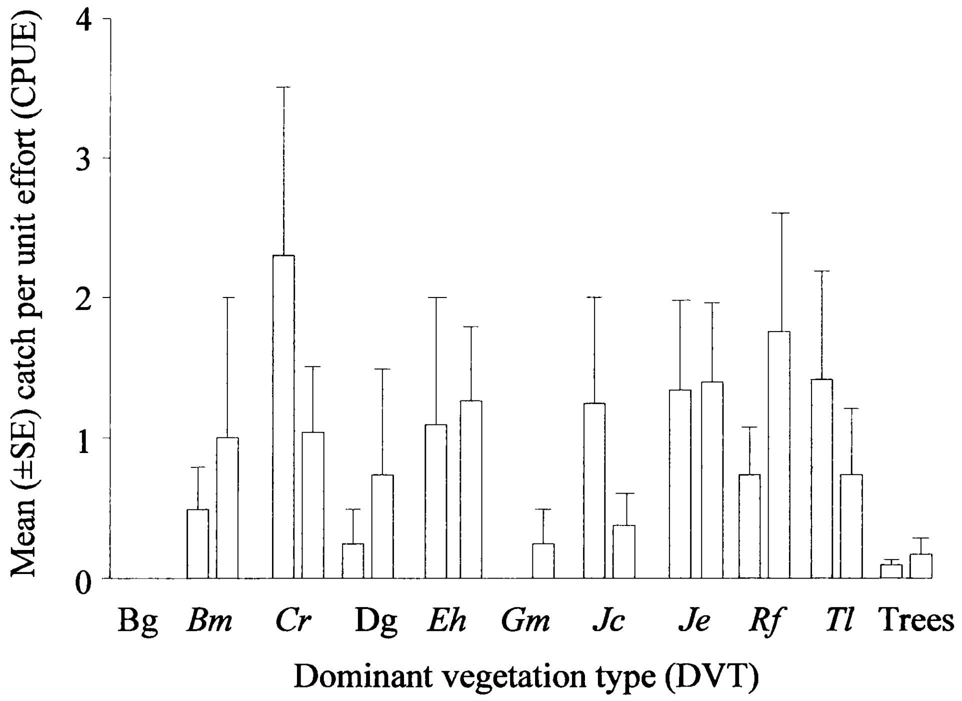


Figure 4.1 CPUE: Mean relative number (± SE) of adult water voles captured per dominant vegetation type (DVT) across the area of wetland studied, throughout the entire duration of the study period. Males (grey bars; n = 52), females (open bars; n = 70)

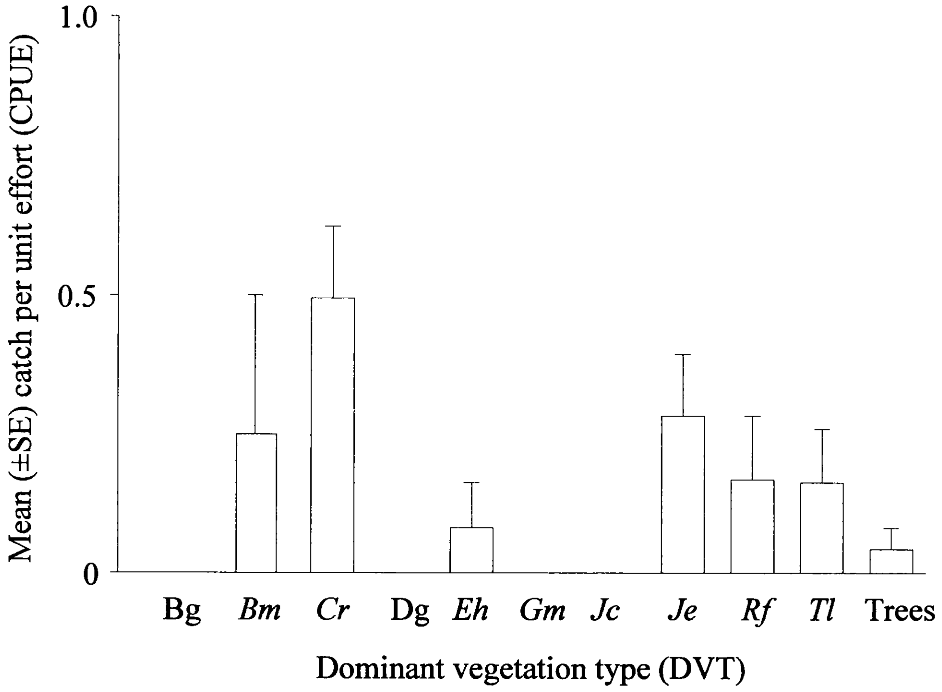


Figure 4.2 CPUE: Mean relative number (± SE) of juvenile water voles captured per dominant vegetation type (DVT) across the area of wetland studied, throughout the entire duration of the study period. (Genders combined; n = 28)

Females occupied ten DVTs (figure 4.1) however, relatively more females were associated with the *Rf*DVT than any other DVT type. The *Eh*DVT and the *Je*DVT were also of significant importance to females. Males utilised only nine DVTs (figure 4.1), (with the exception of the *Gm*DVT) and showed a strong association with the *Cr*DVT, although the *Tl*DVT and the *Je*DVT were also utilised regularly. Juveniles were associated with the least amount of DVTs (seven; figure 4.2), most significantly with the *Cr*DVT.

4.2.2 Annual fluctuations in DVT utilisation

All eight ponds supported at least one breeding pair of adult water voles, during at least one breeding season throughout the duration of this study, with both sub-optimal and optimal habitats utilised during peak population densities (chapter 2). It was assumed that during the low density phase (2008), resident water voles were at liberty to select optimal habitats or DVTs, due to the availability of empty habitats. Indeed during this time ponds C, E and F were unoccupied, with populations located on ponds A, B, D, G and H. During this low density phase, the *Rf*DVT was the most heavily utilised by both genders, particularly females. This observation reflects the importance of this vegetation type as a component of the water vole habitat at NWCW. However, analysis of variance revealed that there were no significant differences in DVT utilisation between gender or age class ($F_{2,22} = 1.455$, $p = 0.257$) or between the species of DVTs utilised ($F_{8,22} = 0.408$). The small sample size during the low density phase (2008 and 2009) may have influenced this result. Accordingly, transient animals (chapter 2) were removed from the analyses and only DVT utilisation by water voles that established home ranges (ORLs; chapter 3) were included. Furthermore, data from all years was pooled and then divided into the breeding season and the over-wintering period, to examine the seasonal variation in DVT occupancy and utilisation (section 4.2.3 and 4.2.4).

4.2.3 Breeding season DVT utilisation by resident water voles

DVT utilisation was determined for male and female water voles that maintained a home range (ORL) during the breeding season (n= 19 male ORL and 31 female ORL; chapter 3). Additionally, 2 males that maintained a winter ORL, but were only captured once during the breeding season (and therefore unable to be assigned a breeding season ORL) were also included in the analyses of breeding season DVT utilisation. Accordingly, 21 males and 31 females were included in the following analyses. Individual males were associated with the greatest number (4) of DVTs, whereas individual females were typically restricted to one or two DVTs (figure 4.3). A significant positive relationship between home range length (ORL) and the number of DVTs incorporated into the home range for both males ($F_{1,20} = 10.316$, $p = 0.005$, $R^2 = 39.2\%$) and females ($F_{1,30} = 21.605$, $p \leq 0.001$, $R^2 = 42.5\%$) was observed during the breeding season. Of the 23 water voles (6M and 17F) that that maintained a limited range (15 m) and therefore only utilised one DVT type during the breeding season (figure 4.3), 5 (83%) males and 4 (24%) of females were captured in the *Rf*DVT; 1 (17%) male and 1 (6%) female were captured in the *Cr*DVT; the remaining 12 (70%) females were captured in the *Je*DVT. These three DVT types had the lowest patch diversity (D_{DVT}) (see section 1.3.7 and section 4.2.7) but provided an important source of cover (and food; chapter 5) for water voles.

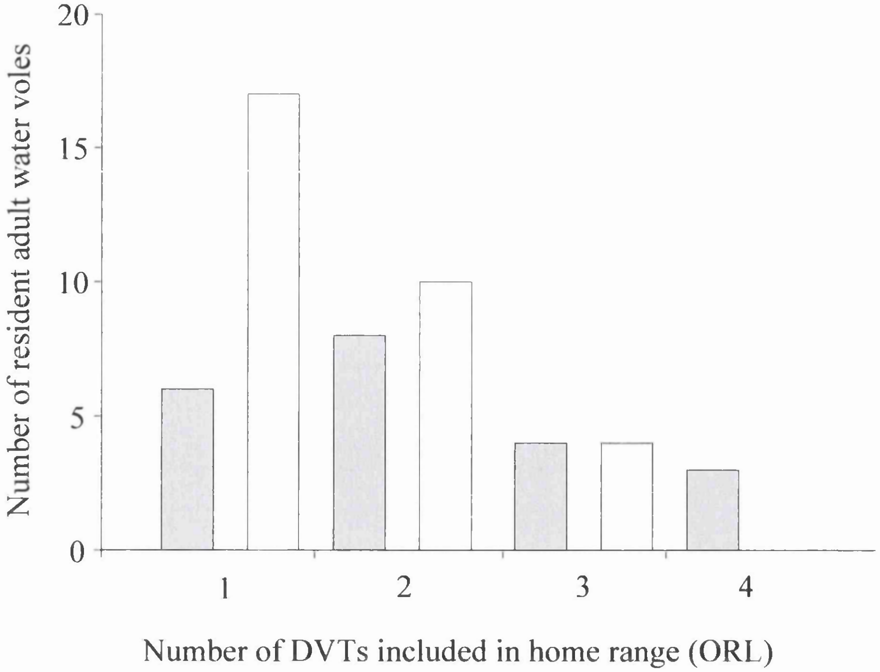


Figure 4.3 Number of different DVTs included in the home range of resident adult water voles across the area of wetland studied, throughout the breeding seasons of the study period. Males (grey bars; n = 21), females (open bars; n = 31)

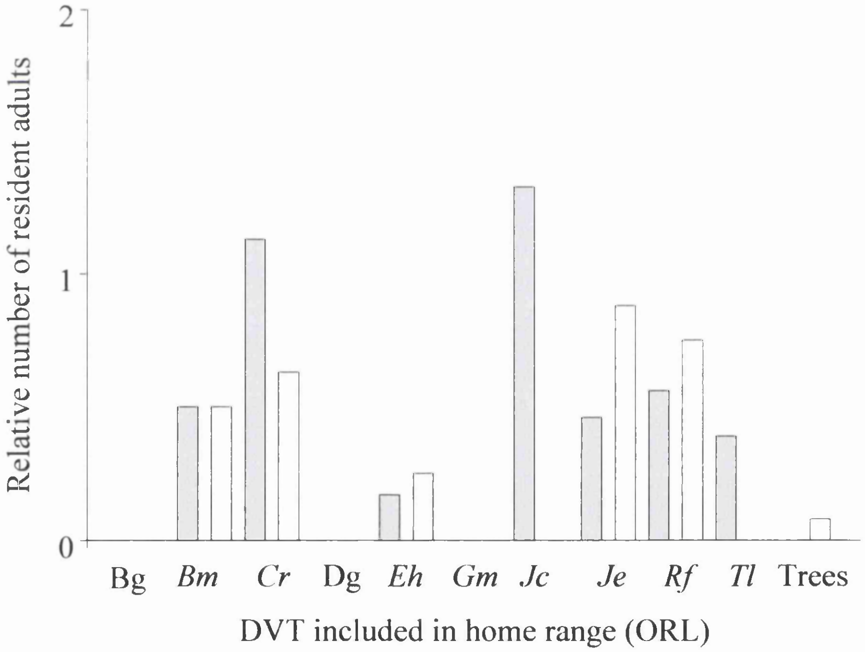


Figure 4.4 Relative numbers of resident adult water voles that incorporated each DVT type into their home range across the area of wetland studied, throughout the breeding seasons of the study period. Males (grey bars; n = 21), females (open bars; n = 31)

The DVTs were ranked in order of importance according to both the relative number of resident adults that incorporated each DVT type into their home range (figure 4.4) and the relative degree of utilisation of each DVT type by resident adults maintaining a home range (figure 4.5) during both the breeding season and the over winter period (section 4.2.4). Accordingly, during the breeding season, males used 7 different DVT types (figures 4.4 and 4.5); however, the most important DVT types for male water voles were the *Jc*DVT and the *Cr*DVT. In contrast, during the breeding season, females used 6 different DVT types (figures 4.6 and 4.7); no females were associated with the *Jc*DVT, however, two females incorporated the treeDVT into their home ranges. Relatively more females were associated with the *Je*DVT and the *Rf*DVT than any other DVT type, although the highest degree of utilisation (relative number of captures) of a DVT was observed for females in the *Je*DVT and the *Bm*DVT.

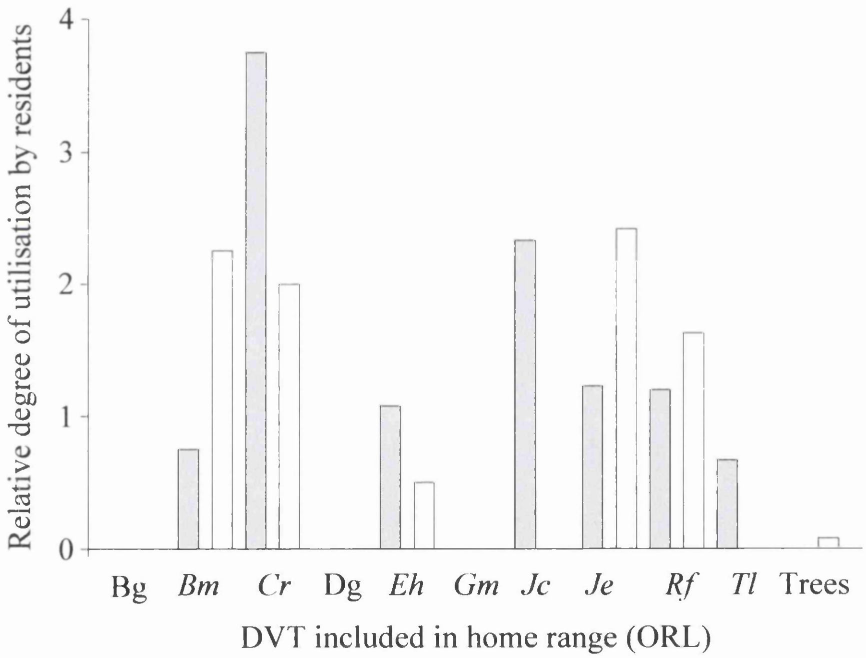


Figure 4.5 Relative degree of utilisation of each DVT by resident adult water voles that maintained a home range across the area of wetland studied, throughout the breeding seasons of the study period. Males (grey bars; n = 122 captures), females (open bars; n = 135 captures)

4.2.4 Over-winter DVT utilisation by resident water voles

Since it was the over-wintering water voles that constituted the breeding populations in the following year (assuming survival), it was important to identify the plant types (DVTs) favoured by water voles during the winter period. Observed range lengths were determined for 9 males and 9 females (chapter 3) that overwintered. Numerous adult residents were observed to contract their home ranges (chapter 3) and reduce their above ground activities during the winter. However, a number of water voles were only captured once during the winter period and therefore were not included in the analyses of winter range lengths (chapter 3). Nevertheless, these animals provided information regarding DVT utilisation during the winter period. Accordingly, 15 males and 19 females were included in the analyses (figures 4.6 and 4.7).

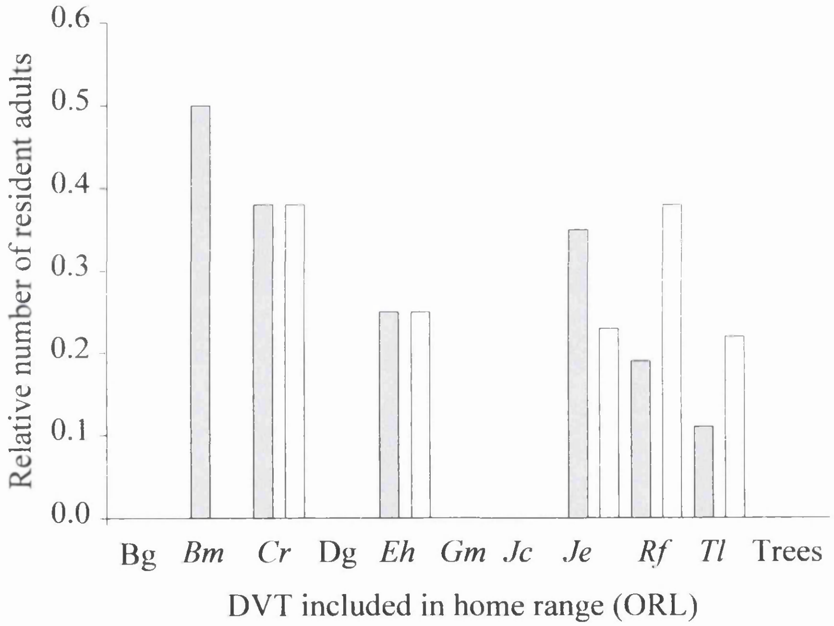


Figure 4.6 Relative numbers of resident adult water voles that incorporated each DVT type into their home range across the area of wetland studied, throughout the winters of the study period. Males (grey bars; n = 15), females (open bars; n = 19)

In addition to the breeding season, a significant positive relationship between home range length (ORL) and the number of DVTs incorporated into the home range for both males ($F_{1,8}$ = 9.030, p = 0.02, R^2 = 75.1%) and females ($F_{1,8}$ = 21.913, p = 0.002, R^2 = 87.1%) was also observed during the winter. However, both males and females utilised less DVTs (6 and 5 respectively) during the winter than during the breeding season (figures 4.4 to 4.8). Throughout the winter the *Bm*DVT and the *Cr*DVT were associated with the highest relative number of resident male water voles (figure 4.6), with the *Cr*DVT being utilised the most (figure 4.7). The *Cr*DVT was therefore the most important component of the water vole habitat to over-wintering male water voles. This DVT was also important to adult males during the breeding season (figures 4.4 and 4.5) however, it is interesting to note the seasonal variation in DVT utilisation. For instance, the *Jc*DVT was frequented by adult males during the breeding season (figures 4.4 and 4.5), but never utilised during the winter (figures 4.6 and 4.7).

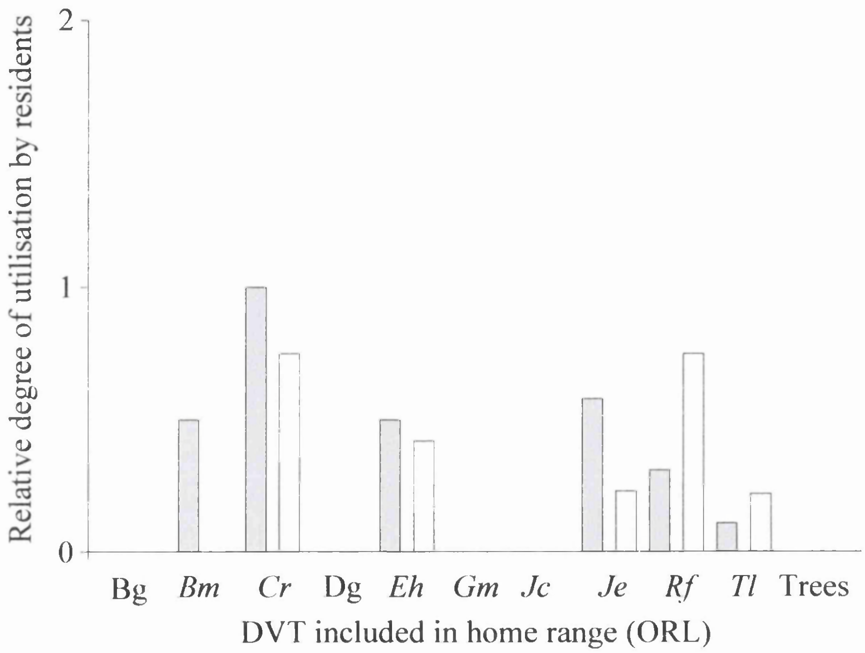


Figure 4.7 Relative degree of utilisation of each DVT by resident adult water voles that maintained a home range across the area of wetland studied, throughout the winters of the study period. Males (grey bars; n = 40 captures), females (open bars; n = 36 captures)

During the winter, both the *Rf*DVT and the *Cr*DVT were the most important DVT types for resident female water voles. Both these DVT types were associated with the highest relative number of females (figure 4.6) and were utilised to a greater degree than any other DVT types by females during the winter period (figure 4.7). Seasonal variations in DVT utilisation by females were also observed. For example, the *Eh*DVT was more important to resident females during the winter (figures 4.6

and 4.7) than during the breeding season (figures 4.4 and 4.5). Indeed, the *TI*DVT was not incorporated into the home range of any adult females during the breeding season, however, was associated with 4 (21%) overwintering resident adult females.

4.2.5 Does pond size influence water vole population density?

A gender specific response was observed between pond size and population density. Larger ponds supported higher mean female population densities than smaller ponds (figure 4.8). A significant positive relationship was observed between the length of the trapped habitat and the mean female water vole population density ($F_{1,6} = 34.825$, $p = 0.02$, $R^2 = 87.5\%$). Conversely, male population densities per 100 m did not correspond with pond size ($F_{1,6} = 0.421$, $p = 0.545$, $R^2 = 7.8\%$).

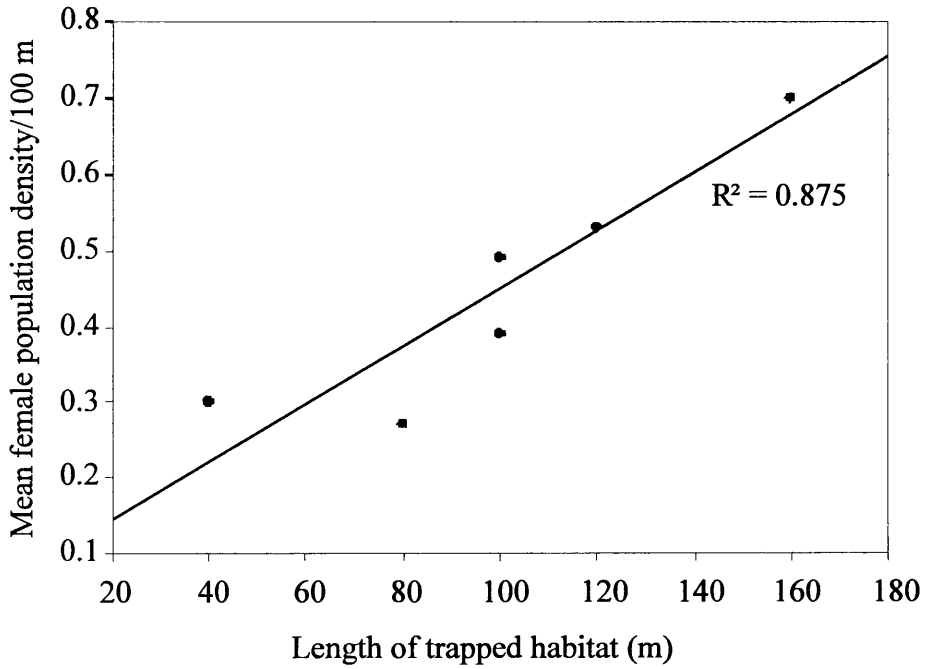


Figure 4.8 Linear regression of mean female water vole population density per 100 m against length of trapped habitat (m). Note that the regression includes 7 ponds; mean female population density/100 m = 0.7 and pond size = 160 m for both ponds A and D. The population density on pond G was influenced by vegetation clearance and the presence of brown rats and was thus omitted from the regression analysis

4.2.6 How does habitat diversity (D_{pond}) influence water vole distribution?

The diversity of each pond (D_{pond}) was determined in chapter 1. A significant positive relationship was observed between habitat diversity (D_{pond}) and mean adult population densities during the breeding season (figure 4.9) ($F_{1,6} = 7.020$ $p = 0.045$, $R^2 = 58.4\%$). The greater the diversity of DVT types (patches) across the vegetation mosaic, the more diverse the habitat (chapter 1). Ponds A and D were the most diverse habitats (D_{pond}) and supported the highest water vole population densities during the breeding season (chapter 2). Thus, during the breeding season, water voles selected ponds on the basis of their diversity at the habitat level (chapter 1). In contrast, during the over-winter period there was no significant relationship observed between habitat diversity and adult water vole population densities ($F_{1,6} = 0.659$ $p = 0.454$, $R^2 = 11.4\%$).

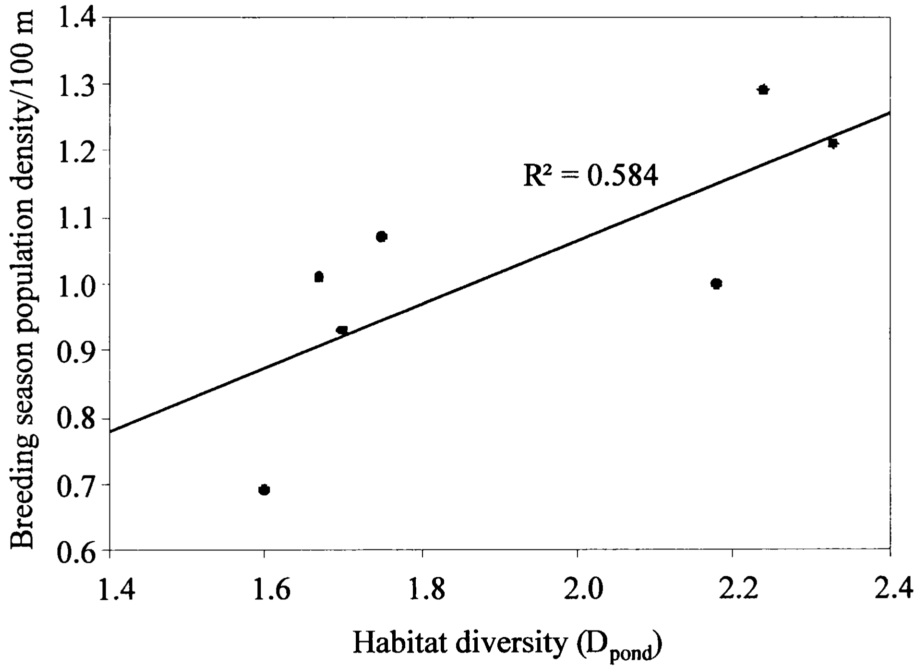


Figure 4.9 Linear regression analysis of mean adult population density per 100 m during the breeding season against habitat diversity (D_{pond}). The population density on pond G was influenced by vegetation clearance and the presence of brown rats and was thus omitted from the regression analysis

4.2.7 How does patch diversity (D_{DVT}) influence water vole distribution?

Water voles select habitat on the basis of its diversity, however, they typically operate within the least diverse patches within the chosen habitat. Although water vole population densities were positively correlated with diversity at the habitat level (D_{pond}) during the breeding season (section 4.3.5), the DVT types incorporated into the home ranges of adults included some of the least diverse patches (figures 1.20, 4.4 and 4.5). There was no significant relationship between the total number of resident adults per DVT type and the patch diversity (D_{DVT}) ($F_{1,8} = 2.7$, $p = 0.144$, $R^2 = 27.8\%$). With the exception of the *Jc*DVT, all the DVTs integral to the home ranges of adult males and females during the breeding season were associated with the lowest patch diversity (D_{DVT}) (chapter 1). Indeed, some of the least diverse DVTs such as the *Rf*DVT ($D_{DVT} = 0$) were incorporated into the majority of adult home ranges and heavily utilised by resident adults.

4.2.8 How does habitat diversity (D_{pond}) influence water vole home range length?

Although habitat diversity (D_{pond}) had a significant effect on adult population density during the breeding season, no significant relationship was observed between male home range length ($F_{7,30} = 1.474$, $p = 0.225$, $R^2 = 10\%$) and habitat diversity or between female home range length (chapter 3) and habitat diversity ($F_{8,18} = 1.1$, $p = 0.435$, $R^2 = 4\%$) during the breeding season. Nevertheless a significant positive relationship was observed between home range length and the number of DVTs incorporated into the home range for both males and females (sections 4.2.3 and 4.2.4).

4.3 Discussion

4.3.1. Water vole occupancy per Dominant Vegetation Type (DVT)

DVT occupancy was examined for every water vole captured (n = 150 animals) in the area of wetlands studied. Over half (n = 67) of these water voles were considered transient, since they were only encountered once because of dispersal or predation (chapter 2). However, the DVT occupancy by all animals was determined, as this provided a more detailed picture of water vole requirements, even if short lived. No water voles were ever captured in the trap situated in the bare ground DVT, due to the lack of cover, the susceptibility of water voles to predation (Forman, 2005; Strachan & Moorhouse, 2006) and their ability to perceive this risk when cover is reduced (Carter & Bright, 2000).

Female water voles were associated with ten types of DVT that contained a trap; however, more females were encountered in the *Rf*DVT than any other DVT type. *Rubus fruticosus* has also been shown to be of importance to bank voles, (Flowerdew & Ellwood, 2001). The structural nature of the *Rf*DVT and the protective spines associated with this species provided a safe environs for the water vole in which to take refuge, from both predators and aggressive encounters with conspecifics. *Rubus fruticosus,* however, was not utilised a regular source of food at this site, encountered in less than 1% of food piles (chapter 5). The *Je*DVT was also associated with more female captures than other DVTs, with this dominant providing a source of food, in addition to cover. This observation contradicts previous studies on English river habitats, where *Juncus effusus* was negatively correlated with adult female captures (Woodall, 1993). Two DVTs (the DgDVT and the *Gm*DVT) were associated with female captures, but not incorporated into the home range of resident adult females.

Male water voles were encountered in nine DVTs and were most strongly associated with the *Cr*DVT; this DVT supported the highest amount of total captures (including adults and juveniles of both genders). The *Cr*DVT was an important source of both food (chapter 5) and cover (associated both with the sharp edged blades that characterise the leaves and the continuous green cover this species provides throughout the year) and it is likely that water voles utilised both aspects of this vegetation type. *Carex riparia* often forms large stands around ponds and has far creeping rhizomes and thick roots. This species is a lowland plant, most frequent in S and E England and mainly restricted to coastal areas in Wales (Jermy *et al.*, 2007).

Juvenile water voles were only associated with seven of the eleven DVTs most notably the *Cr*DVT and the *Je*DVT. Typically, juvenile water voles operate in the vicinity of mothers and can be expected to remain in their natal area for some time before dispersing (Woodall, 1993); however, juvenile dispersal was a density-dependent process at this locality (see chapter 2). It is worth noting that male and juvenile DVT utilisation may not reflect habitat selection *per se*, since it was the females that were predominantly territorial (Forman & Brain, 2006; Strachan & Moorhouse, 2006). Males and juveniles could only occupy the areas that were not incorporated into the home range of the resident females (unless they were receptive to breeding).

4.4.2 Annual fluctuations in population densities and DVT utilisation

Although no significant differences in DVT occupancy were observed between years, certain DVTs were unoccupied during some years and heavily utilised during others. This was particularly true for females and was also dependent on population densities. The higher the population density of water voles the greater the number of different DVTs utilised. During the peak density phase (2006 to 2007) both habitat and DVT patch utilisation were determined by social interactions as numerous dominant females competed for territories. When carrying capacity is reached, intra-specific competition is high and water voles are expected to expand into sub-optimal habitat (Pulliam, 1988). Pond F was only occupied during the peak density phase and only during the breeding season, representing an important receiving habitat when population densities increase. Consequently, at this time the *Bm*DVT was heavily utilised by a breeding female, however, this pond was dominated by trees (figure 1.1) and was therefore considered to be sub-optimal.

Water vole distribution is typically negatively correlated with the presence of trees (Zejda & Zapletal, 1969; Lawton & Woodroffe, 1991; Strachan & Moorhouse, 2006). Indeed, the treeDVT was only associated with water vole captures during peak population densities. Furthermore trees were only incorporated into the home range of two adult female water voles. This occurred during the peak density phase and reflected density-dependent, rather than active habitat selection.

Annual variations in DVT utilisation were particularly evident for the *Rf*DVT. For example, on pond A, no female was encountered in the *Rf*DVT until January 2007, after which time this DVT became an important and defendable resource. The *Rf*DVT provided a homogenous stand of vegetation with no associated plant species to provide a source of food. Nevertheless, it provided protection from the numerous predators that operate in the vicinity, including foxes and herons. The importance of cover to *Microtus* populations has been previously demonstrated by numerous authors (Eadie, 1953; Mossman, 1955; Ogilvie & Furman, 1955; Zimmerman, 1965; Hanson 1971). In grassland habitats, site-dependent threshold levels of cover are necessary to allow microtine populations to increase in numbers sufficiently to undergo multiannual cycles. Levels of cover above the threshold may support resident breeding populations; however, levels of cover above the threshold may influence the amplitude, duration and synchrony of Microtus cycles (Birney *et al.*, 1976). The protection afforded by the *Rf*DVT (i.e. increased level of continuous cover) may also have contributed to the higher population densities observed on ponds A and D, where this species occurs in numerous and extensive patches (figure 1.1; DVT map).

The lag observed in *Rubus fruticosus* occupation (unoccupied until January 2007) may be associated with the lag response of predators to their prey cycle, with an increase in the number of predators typically observed as a response to peaks in microtine cycles. Activity levels of predators are normally higher in more productive habitats (Oksanen & Schneider, 1995). Ponds A and D were highly productive in terms of prey, with these areas supporting the highest population densities. It is possible that these two ponds were subject to the heaviest predation pressures, resulting in the dispersion of the water vole populations in these areas centred within the *Rf*DVTs.

Population densities influence population social structure with intrasepcific competition contributing to habitat selection and occupation. Presumably when densities are low and intraspecific competition is reduced, water voles are presented with a greater number of available habitats and thus a greater opportunity to occupy the desired optimal habitat. DVT occupancy during the last two years of study reflected active habitat selection unconstrained by social pressures associated with increased population densities. During this time DVT selection reflected the typical trends observed throughout the study (section 4.3.1).

4.4.3 Breeding season DVT utilisation by resident water voles

The relationship between water vole capture events and DVT occupancy focused on all animals, including transients. This provided an insight into the differing dominant vegetation types that were utilised by water voles. However, in order to distinguish those DVTs that were important for the maintenance of this metapopulation, transient animals were removed from the analysis and from this point forward only those animals maintaining home ranges (ORLs) over two or more trapping sessions were considered. That is not to say that these animals were more important than transients, since transient animals that are not lost to predation are important colonisers of empty habitats (Telfer *et al.*, 2001) and thus of great significance to the persistence of the metapopulation. However, focusing on data collected from animals with repeat capture histories provides vital information regarding the ecology and behavioural choices of this species in a metapopulation pond complex, including observed range lengths and the degree of range overlap within and between genders (chapter 3).

Water voles maintaining longer home ranges incorporated more dominant vegetation types into those home ranges, than their sessile counterparts. A significant positive relationship was observed between home range length (ORL) and the number of DVTs included in the ORL for both males and females. Adult males had significantly longer ORLs than females (60 m and 32 m respectively, during the breeding season at this site; chapter 3). Consequently, adult males included more DVTs in their home ranges than females, particularly as a number of males maintained a home range over three ponds (A, B and D). Typically, adult males show less habitat selectivity than females (Woodall, 1993), associated with their larger home ranges (Stoddart, 1970; Strachan & Moorhouse, 2006; Moorhouse & Macdonald, 2008) as they move over a wider range of habitats (Woodall, 1993). Nevertheless, almost a third of resident adult males maintained a limited home range (15 m) associated with one DVT, most notably the *Rf*DVT.

Resident female water voles also showed a strong positive correspondence with presence of the *Rf*DVT during both the breeding season and the winter (section 4.4.4). The *Jc*DVT was important to resident male water voles during the breeding season. However, no female home range included the *Jc*DVT during the breeding season and thus males utilising this DVT did not exploit it for access to females. It is likely that males may be forced to occupy areas that are left after females have defined their territories, since female water voles that are unreceptive to breeding will exclude males from their territory (Forman, pers. comm.). Furthermore, the *Jc*DVT was adjacent to a *Rf*DVT (associated with numerous female capture events) (figure 1.1). The *Cr*DVT was an integral component of adult water vole home ranges, particularly males. The *Cr* DVT has been shown to be important for both males and females, and was utilised wherever present, even if only in small discrete patches, and often contained evidence of foraging, (see chapter 5). This species occurred in large patches on ponds C and E, with both leaves and underground rhizomes utilised as a food source by water voles in this locality (chapter 5).

The *Je*DVT was the most important vegetation type for female water voles during the breeding season. This contradicts previous studies of water voles on English river systems that actively avoid *Juncus sp.*, (Woodall, 1993). The majority of water vole food piles at NWCW consisted of *Juncus effusus* (see chapter 5), which not only provided continuous cover but also an important source of high energy food (see chapter 5). The pith of *Juncus effusus* was also frequently utilised by females to line their nests during the breeding season with numerous food piles consisting of the stripped remains of this plant (pers. obs.). Females with established ranges at NWCW were never associated with the DgDVT, however, at this site, rushes and sedges dominated vast areas and damp grassland was typically restricted to small, slender patches. These results differ from those seen elsewhere, with water vole breeding colonies on English river systems characterised by a high percentage of grasses, usually > 70%, with a minimum of 66% (Lawton & Woodroffe, 1991). However, numerous grass species were associated with a number of DVTs. Furthermore, certain grass species (e.g. *Holcus lanatus, Glyceria maxima*) were observed in food piles (chapter 5) and thus were a component of water vole diet on this site, even if they were not typically associated with capture events.

Water voles in English river habitats prefer to inhabit areas of *Phragmites australis* and *Urtica dioicia* (Woodall, 1993). Of these two species, an *Ud*DVT separated pond A from pond D and numerous movements between these two ponds were observed. It is likely that the *Ud*DVT was utilised as a source of cover during both dispersal events and maintenance of home ranges by patrolling male water voles. Furthermore, *Urtica dioicia* was a frequent associate on pond B, which may have contributed to the utilisation of this habitat by water voles, particularly males (chapter 2). Common reed, (*Phragmites australis)* was not present as a DVT or as an associate species in the area of wetland studied, however, a vast reed bed inhabited by water voles was present at the western end of the wetland complex, but was not studied here.

4.4.4 Over-winter DVT utilisation by resident water voles

Rubus fruticosus was the most important dominant vegetation type to overwintering water voles that maintained above ground activity during the winter at NWCW. Since overwintering water voles spend the majority of the winter in underground burrows they are less vulnerable to larger avian and mammalian predators (Macdonald & Strachan, 1999). Those water voles that operate above ground during the winter tend to do so in DVTs that provide a high level of cover and protection, most notably the *Rf*DVT. Indeed, *Rubus fruticosus* provided important cover for water voles and was utilised as a protection from both avian and mammalian predators at this study site. Red foxes (*Vulpes vulpes*) and grey heron (*Ardea cinerea*) are known to regularly prey upon water voles at this location (Forman, 2005). Barn owls (*Tyto alba*) also operated at NWCW (pers. obs) and are known to prey upon water voles (Strachan & Jefferies, 1993). Studies at Wytham Woods, near Oxford, from 1949 to 1999, indicated that a significant reduction in bank vole numbers occurred as a result of observed changes in the woodland vegetation, including a significant reduction in the ground cover of bramble (*Rubus fruticosus agg.*) (Flowerdew & Ellwood, 2001).

This study is the first to observe water vole behaviour beyond the boundaries of the breeding season in Wales (but see Carter & Bright (2000 and 2003) for overwintering mortality in English reed beds). The survival of water voles over winter, throughout the peak density phase in NWCW, was comparable to that recorded in other habitats (Leuze, 1976; Woodroffe *et al.*, 1990; Carter & Bright, 2000, 2003) (chapter 3). The DVTs utilised during winter reflected reduced social pressures, associated with the breakdown of territoriality beyond the boundaries of the breeding season (Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006). Indeed, during winter numerous females overlapped their home ranges on ponds where high densities of adults overwintered e.g. pond E (chapter 3). Additionally, nutritional requirements of water voles in winter were very different from those in summer. During the breeding season there was a requirement for nitrogen associated with the production of a litter, with both males and females requiring a higher calorific intake in order to maintain territories (females) and search for mates (males). During winter both males and females contracted their home ranges and much activity was confined to below ground burrows. Here, access to food stores and underground roots and rhizomes of the *Cr*DVT and the *Tl*DVT minimised the predation risk associated with reduced above ground vegetation cover. In winter water voles feed largely on roots, rhizomes and bulbs from within their burrow systems (Carter & Bright, 2000). The *Cr*DVT and the *Je*DVT were also important DVTs throughout the winter months, providing a continuous source of both above ground cover and green food during this harsh time.

Interestingly, the *Eh*DVT was utilised more during the winter than the breeding season. At NWCW, ***Epilobium hirsutum*** was regularly foraged upon early in the year (late January and throughout spring) as soon as fresh growth appeared (pers. obs.). Since female water voles were observed to maintain home ranges above ground during the winter, latrines were established by February (chapter 5) as females prepared for the onset of the breeding season. ***Epilobium hirsutum*** is associated with high nitrogen levels (see chapter 5), a requirement of breeding females (Strachan & Moorhouse, 2006). In addition to its utilisation as a forage species, ***Epilobium hirsutum*** also provided cover during the breeding season and during winter, although it became woody after senescence.

4.3.5 Does pond size influence water vole population density?

A significant positive relationship was observed between the female water vole population density and pond size. Female home range length during the breeding season (32 m) was less than the size of the smallest pond (40 m) and indeed, all ponds were utilised at least once by a breeding female throughout the duration of the study period. However, larger ponds supported higher densities of female water voles per 100 m than smaller ponds, during the breeding season. Although, this result should be treated with caution since it may be an artefact of the positive correspondence between pond size and habitat diversity (chapter 1) and the positive correspondence observed between water vole population density and habitat diversity (section 4.4.6).

Since no correspondence was observed between male water vole population density and pond size, it is likely male population density was influenced by the distribution of females rather than by the size of the ponds. Furthermore, males are known to range over larger areas than females (Stoddart, 1970; Strachan & Moorhouse, 2006; Moorhouse & Macdonald, 2008) and at this locality over two or more ponds (chapter 2). Larger ponds provided a greater diversity of vegetation (both plant species and DVTs) (chapter 1). Indeed, vegetation abundance can have clear effects on the probability of recapturing water voles (released during reintroductions), with over 70% success of female recaptures observed on sites with the highest vegetation abundance (Moorhouse *et al.*, 2009).

Ponds A and D were both diverse and adjacent to one another, separated by a large expanse of *Juncus effusus*, together with a *Rf*DVT and patches of *Urtica diocia* (figure 1.1). The importance of these species to water voles has been previously demonstrated (see section 4.4.4). Moreover, the large area between ponds A and D was utilised in numerous dispersal events and also by males patrolling between ponds during the breeding season. Although this area was beyond the 5 m boundary of the ponds it was indeed utilised by water voles, not just in dispersal or movements, but also in the construction of burrows (evident from field signs; chapter 5). With the exception of this area and ponds B and D (N reaches separated by a DgDVT; figure 1.1), ponds E and F (separated by an *Eh*DVT; figure 1.1) and ponds G and H (separated by a *Je*DVT; figure 1.1), inter-pond areas were typically dominated by trees (figure 1.1), which are typically negatively correlated with the presence of water voles (Zejda & Zapletal, 1969).

Not only was the size of the pond an important determinant of female water vole population density, but the matrix habitat between ponds must also be considered (Mortelliti *et al.*, 2010). This is particularly important for species (such as the water vole) that are threatened by habitat loss and fragmentation (Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006), since habitat loss and fragmentation are landscape scale processes (Fahrig, 2003) which by definition require a landscape scale approach to study (Mortelliti *et al.*, 2010).

4.3.6 How does habitat diversity (D_{pond}) influence water vole distribution?

This study provides evidence that water vole population density corresponds positively with the diversity of the habitat (D_{pond}) during the breeding season. Habitats with diverse vegetation mosaics provided a greater diversity of available forage (chapter 1). The amount of forage availability is an important determinant of habitat selection. Numerous studies of small mammals have demonstrated higher population densities in populations where food resources have been manipulated (artificially increased) (Andrzejewski 1975; Cole & Batzli 1978; Gilbert & Krebs 1981; Taitt & Krebs 1981; Abdellatif *et al.*, 1982; Taitt & Krebs 1983; Desy *et al.*, 1990; Koskela *et al.*, 1998; Jonsson *et al.*, 2002). The more diverse the habitats, the more likely they are to support higher population densities and a continuous presence of individuals. The diverse mosaic on the south and east banks of pond A is an example of habitat heterogeneity and numerous water voles, particularly females were associated with this locality. More homogenous ponds such as C, E and F were observed to be empty during troughs in the Microtine cycle, suggesting that less diverse habitats at this site are only utilised when population densities are high and competition for space is increased.

The extent of habitat is a major driver of the occurrence and abundance of species and the richness and composition of assemblages (Andrén, 1992; Bennett & Ford, 1997; Fuller *et al.* 1997; Boulinier *et al.* 1998; Trzcinski *et al.* 1999; Villard *et al.* 1999; Pino *et al.* 2000; Bailey *et al.* 2002; Olff and Ritchie, 2002; Radford *et al.* 2005). Additionally, the spatial configuration of habitats has significant effects on the occurrence or incidence of species and the richness and composition of assemblages (Fuller *et al.* 1997; Villard *et al.* 1999; Smith *et al.*, 2001; Millán de la Peña *et al.*, 2003; Weibull *et al.*, 2000, 2003; Luoto *et al.*, 2004). However, in most landscapes, the spatial configuration and the extent of habitat are significantly correlated (Fahrig, 2003). Untangling the relative effects of these components is important because it has practical relevance for identifying priority areas for conservation and the efficient allocation of resources for landscape restoration (Bennett *et al.* 2006).

It has been demonstrated that habitat heterogeneity or diversity of elements often corresponds positively with the richness of taxonomic assemblages and enhances faunal diversity (Pino *et al.,* 2000; Tews *et al.,* 2004; Weibull *et al.,* 2000, 2003). However, the majority of these studies occurred within the fragmented agricultural landscape and none looked at the effects of landscape diversity on the density of a mammal population. In Britain, birds and butterflies are the taxonomic groups most frequently studied (Sparks & Parish, 1995; Fuller *et al.,* 1997; Chamberlain *et al.*, 1999; Gates & Donald, 2000; Smith *et al.*, 2001). The diversity of landscape elements has been shown to be the strongest determinant of total species richness of both butterflies (Sparks & Parish, 1995) and birds (Chamberlain *et al.,* 1999). Few studies have looked at the effects of landscape diversity on mammals (but see Bailey *et al.* 2002; dormouse) or on population densities (but see Smith *et al.*, 2001; meadow pipit densities). This study is the first to relate habitat diversity at the patch-landscape scale to demographic parameters of an endangered mammal, the water vole. Determining the relationship between the diversity of habitats within the wetland landscape and the effects on demographic parameters provides evidence based data that can be implemented in the conservation and creation of water vole habitats. This is a priority for the persistence of this highly endangered mammal in Britain, where continued development of floodplain and riparian areas drives habitat creation, through essential mitigation and restoration in accordance with the UKBAP.

4.3.7 How does patch diversity (D_{DVT}) influence water vole distribution?

In contrast to habitat diversity (section 4.3.6), no relationship was observed between the relative number of water voles per DVT type and the diversity of the patch (D_{DVT}) during the breeding season. Moreover, the least diverse DVTs were the most important components of resident adult home ranges, particularly females. Indeed, the *Rubus fruticosus* DVT was associated with a patch diversity of zero (due to 100% continuous cover of a single species). Nevertheless *Rubus fruticosus* was an integral component of the water vole habitat at NWCW during both the breeding season and the winter. Water vole populations respond to diversity at the habitat, but not the individual patch level. Water voles are known to select habitat on the basis of its quality (Telfer *et al.*, 2001). At NWCW during the breeding season, water voles selected the ponds with the highest diversity (at the habitat level), but were most active within the least diverse patches within the vegetation mosaic. This has very important consequences, both for water vole habitat creation and for the management of existing habitats (chapter 6).

4.3.8 Topography or habitat diversity?

Of all ponds in the NWCW, pond A was the only pond to sustain a continuous turnover of populations. However, a female bias was observed on this pond, particularly in the last two years of study. Of the available DVTs, two in particular were the most heavily utilised; the *Rf*DVT and the *Je*DVT. These two DVT were separated from one another by 20 m and a *Ca*DVT.) Pond A was associated with more juveniles (n = 6) than any other pond studied, all of which were captured in the vicinity of the *Ca*DVT. Previous studies have observed a negative correlation between juvenile water voles and *Cirsium arvense*, (Woodall, 1993). Numerous females were observed to operate in the vicinity of the *Cirsium arvense* DVT, many with overlapping ranges. The topography of this area of the pond (see figure 1.2) included a tall bund of earth that provided an increased area for the creation of burrows at varying heights and a retreat from increasing water levels associated with elevated rainfall. Steep banks are advantageous because water voles construct extensive burrow systems at a number of levels, moving to chambers higher up the banks during high spates (Lawton & Woodroffe, 1991). In addition to this, a small island (containing a *Tl*DVT and a *Je*DVT; see figure 1.1) provided an increased area of edge on which territories could be established (where field surveys substantiated the utilisation of this area; see chapter 5).

Pond D was associated with the highest mean population densities during the breeding season and was a highly diverse habitat (D_{pond}; chapter 1). An island was also present on pond D (figure 1.1), however, the deep water associated with the steep banks of pond D restricted surveying in this area. The importance of islands to water vole populations (particularly during winter) has previously been demonstrated in studies of water voles on English reed bed systems. Islands (or dykes), with steep banks for burrowing provide a refuge for water voles living in reedbeds when water levels rise (Carter & Bright, 2000).

Pond E provided the most important over-wintering site for adult water voles in the area of wetland studied (chapter 2), however, this pond was on the water table and there were no islands present. Although there was no open water *per se*, the extensive *Tl*DVT was associated with a vast expanse of *Sphagnum* sp. moss. During dry summers and winters (such as those observed during the peak density phase), water voles were observed to utilise the three-dimensional network of tunnels created by their movements through the carpet of moss. This provided a refuge from the numerous predators known to operate in this locality (Forman, 2005). A large *Rf*DVT was adjacent to pond E, and although this was beyond the 5 m boundary of the pond (figure 1.1), water vole runways were observed to enter and leave the *Rf*DVT (chapter 5). It is likely that the presence of *Rubus fruticosus* in the vicinity contributed to the suitability of pond E as an overwintering site, during dry seasons. Due to its propensity to flooding, however, pond E become unsuitable for occupation due to the heavy rainfall observed throughout the latter winters of the study. The dense *Tl*DVTs that occupied the majority of both ponds C and E were also sensitive to flooding with a subsequent loss of available bankside. Consequently water voles became restricted to the periphery of the ponds, where predators regularly patrol (pers. obs). The lack of islands or bunds of earth in ponds C and E reduced their suitability for water voles during years of heavy rainfall, resulting in both ponds C and E being unoccupied during the low density phase.

4.3.9 Water vole habitat requirements at NWCW

When actively seeking habitats water voles require three important components, namely access to food, shelter and mates. Females establishing territories are likely to play a greater role in habitat selection than their male counterparts, locating areas that provide a high degree of forage and shelter, while minimising conflicts with other territorial females. Males on the other hand are more likely to select a habitat that provides access to females, although when females are unreceptive then males may be forced to occupy areas that are not favoured by females. This has been observed with males occupying DVTs such as the *Jc*DVT or the *Tl*DVT, which are not favoured by females and are therefore selected by males for other reasons, namely as forage or shelter. *Rubus fruticosus* has been shown to provide excellent cover for both males and females, but is rarely used as a source of forage. *Juncus effusus* and *Carex riparia* on the other hand are selected for both cover and forage, both species providing a relatively high source of nitrogen (see chapter 5).

Recruitment rates of reintroduced water voles on English river systems were not correlated with vegetation abundance, indicating that increased quantities of vegetation offered increased protection from predation, as opposed to influencing population densities through increasing food resources for breeding (Moorhouse *et al.*, 2008). The most important goal of successful reintroductions is maximising the survival of the release cohort. It is therefore desirable to target releases at broader swathes of riparian vegetation (i.e. habitats with a larger width of available bankside per unit length), as this potentially increases the likelihood of long term survival and opportunity to colonise further areas (Moorhouse *et al.*, 2009). The data presented here allow us to distinguish the broad species required to ensure persistence of water voles in Welsh pond complexes, particularly *Rubus fruticosus, Carex riparia*, and *Juncus effusus,* but also *Juncus conglomeratus, Bolboschoenus maritimus* and

Epilobium hirsutum. Additionally, habitat restoration or creation should aim to incorporate diversity at the patch-landscape level, by creating habitats that incorporate a mosaic of patches of these species.

Summary

- Female water voles were associated with more (ten) dominant vegetation types (DVTs) than males (nine) and juveniles (seven)
- No water voles were ever captured on bare ground
- More DVTs were utilised at higher population densities
- The damp grassland DVT and the *Glyceria maxima* DVT were utilised by transient animals, but were not incorporated into the home range of adult males or females
- More DVTs were incorporated into the home ranges of adult residents during the breeding season than during the winter
- A significant positive relationship was observed between home range length (ORL) and the number DVTs included in the ORL for both males and females during both the breeding season and the winter
- Gender dependent niche portioning was evident, with males and females maintaining portions of their home ranges in different DVTs
- The *Rubus fruticosus* DVT was an important refuge for both males and females during both the breeding season and the winter
- The *Juncus effusus* DVT was the most heavily utilised by resident female water voles, providing food, cover and nesting material
- A positive relationship was observed between pond size and female population density
- Diversity at the habitat level (D_{pond}) corresponded positively with water vole population densities during the breeding season; more diverse ponds supported higher population densities
- Diversity at the patch level (D_{DVT}) did not correspond with the number water vole captures; the least diverse DVTs were incorporated into the majority of home ranges
- Water voles perceive the ‘quality’ of their habitat at a grain greater than that of their home range size and select habitats on the basis of their diversity at the patch-landscape scale, rather than the diversity of the patches themselves

Chapter 5

Forage and Function

> *'The little lives of earth and form, of finding food, and keeping warm, are not like ours, and yet a kinship lingers nonetheless: We hanker for the homeliness of den, and hole, and set. And this identity we feel - perhaps not right, perhaps not real - will link us constantly; I see the rock, the clay, the chalk, the flattened grass, the swaying stalk, and it is you I see.'*
>
> Philip Larkin (The Little Lives of Earth and Form, 1977).

5.1 Introduction

The role of water voles in nutrient cycling

The effect of mammalian grazers on the environment is a subject area of considerable interest and focus in conservation biology, applied ecology and adaptive biology, particularly in grassland ecosystems (Huntly, 1991; Augustine & Frank, 2001; Augustine *et al.*, 2003; Bardgett & Wardle, 2003; Frank, 2005; Waldram *et al.*, 2008). Herbivory changes the structure and spatial heterogeneity of vegetation (Waldram *et al.*, 2008). Herbivores can directly increase nitrogen mobility by increasing the quality and quantity of organic matter entering the decomposition cycle, but they may also decrease nitrogen mobility by decreasing the biomass of high-nitrogen species in the plant community (Sirotnak & Huntly, 2000). Free-ranging mammalian grazers have been seen to accelerate nutrient cycling in natural ecosystems in a way that enhances their own carrying capacity. Grazers promote nitrogen availability in soils resulting in higher plant-available nitrogen levels in soils of highly grazed sites (McNaughton *et al.*, 1997).

Rationale

Water voles are potentially very important ecological engineers. The foraging behaviour of water voles is outlined in the introduction (p11). Water voles ingest an impressive volume of food (93% of their body weight per day) (Saucy *et al.*, 1999), equivalent to 186 g of plant matter per 200 g vole per day. Additionally, water voles produce significant amounts of faeces (100-200 pellets per animal per day in captivity) (Woodall, 1977). As water voles maintain above and below ground latrines containing nitrogen-rich faeces and cache food in discrete piles (feeding stations) within their ranges, they may also play an important (and as yet unrecognised) functional role in the recycling of nutrients and organic matter within wetland and adjoining terrestrial ecosystems (Forman *et al.*, 2008).

Aims

1. What plant species do water voles select as forage?
2. In which dominant vegetation types (DVT) are feeding stations located?
3. Is habitat diversity reflected by the diversity of species selected as forage?
4. Is there a relationship between water vole population density and the diversity of plants selected as forage?
5. Why do water voles select particular plant species as forage?
6. How does diet vary seasonally?
7. How do nitrogen and energetic content of food items vary seasonally?
8. On which ponds and in which DVTs are latrines created?
9. Can latrine density be used as a proxy indicator of population density in non-linear habitats?
10. Does the location of latrines correspond with home ranges of adult females?
11. What is the nitrogen content of faecal pellets?
12. What are the nitrogen contents of wetland soils associated with historical latrine sites?
13. Could the removal of vegetation and the input of faeces accelerate the turnover of nutrients in the wetland soils?
14. Do water voles compliment the functioning of a healthy wetland ecosystem?

5.2 Results

5.2.1 Water vole diet at NWCW

Juncus effusus was the most important source of food selected by water voles as forage throughout both the breeding season and the winter. Additionally, *Typha latifolia*, *Carex riparia*, *Epilobium hirsutum,* were also important food plants; however their utilisation varied throughout the year. Together, these four plant species represented the main (above ground) forage species of the water vole at NWCW. During three years of field surveys, the plant composition of 415 feeding stations was identified and content classified to species level. The vast majority (99%) of water vole feeding stations were composed of a single plant species. Of the 129 plant species available across the wetland complex, only 23 (18%) species were foraged upon (table 5.1) and water vole foraging choices varied both between ponds and years (tables 5.1 to 5.3). The maximum number of plant species eaten on a given pond (pond D) or during a given year (2007 and 2008) was 14, equivalent to 23% of the total plant species available on this pond and 11% of the total plant species available across the area of NWCW studied. *Juncus effusus* was the species most frequently selected, representing 38% of the 415 feeding stations. *Typha latifolia* and *Carex riparia*, were also important components of the water vole diet, representing 20% and 15% of feeding stations respectively (table 5.1). *Epilobium hirsutum* was encountered in 7.5% of feeding stations, and was typically foraged upon during the winter and early spring prior to the onset of the breeding season.

Other than the four main forage species, all other plant species in feeding stations were encountered only occasionally (table 5.1) and represented seasonal associates to the water vole diet. The greatest number of plant species in feeding stations (14) was found on Pond D (table 5.2) equivalent to 23% of the plant species on this pond (table 5.3 and figure 5.3). A large diversity of plant species in feeding stations was also observed in feeding stations on pond A, with 12 species cached in feeding stations over the three years of survey, equivalent to 20% of the plant species on this pond. However, numerous plant species cached in feeding stations on pond A were not foraged upon on any other ponds at NWCW, including, *Cyperus longus, Eleocharis palustris, Juncus articulatus, Juncus conglomeratus* and *Mentha aquatica.* Feeding stations were not found on pond F, which was only occupied by water voles during the breeding season of 2006 (chapter 2), during which time no field surveys were undertaken.

Table 5.1 Total number of feeding stations and their constituent plant species found across the area of wetland studied (2007-2009)

Plant species	Number of feeding stations			Total	Percentage (%)
	2007	2008	2009		
Alisma plantago-aquatica	0	2	0	2	0.48
Carex otrubae	0	2	0	2	0.48
Carex panacea	0	1	0	1	0.24
Carex riparia	14	9	39	62	14.94
Ceratophyllum demersum	1	0	0	1	0.24
Cirsium arvense	4	2	0	6	1.45
Cyperus longus	5	0	7	12	2.89
Eleocharis palustris	0	0	6	6	1.45
Epilobium hirsutum	14	6	11	31	7.47
Glyceria fluitans	0	3	0	3	0.72
Glyceria maxima	0	2	1	3	0.72
Holcus lanatus	8	0	0	8	1.93
Iris pseudacorus	11	2	2	15	3.61
Juncus articulatus	1	0	0	1	0.24
Juncus conglomeratus	5	0	0	5	1.2
Juncus effusus	34	62	63	159	38.31
Juncus inflexus	0	1	0	1	0.24
Mentha aquatica	0	0	1	1	0.24
Persicaria hydropiper	0	6	0	6	1.45
Ranunculus lingua	1	0	0	1	0.24
Ranunculus repens	1	3	1	5	1.2
Rubus fruticosus	2	0	0	2	0.48
Typha latifolia	20	30	32	82	19.76
Total feeding stations	121	131	163	415	
Total plant species	14	14	10	23	
Total non plant species	2	0	1	3	

With the exception of pond F, pond E had the lowest number ($n = 16$) (table 5.2) and the least diverse feeding stations ($n = 4$ species) (table 5.3) equivalent to only 10% of the plant species on pond E. Field surveys undertaken over three years revealed a significant difference between the total number of water vole feeding stations per pond ($G_7 = 283.04$, $p < 0.001$) and per year ($G_2 = 13.68$, $p = 0.001$). There was also a significant difference between the total number of different plant species in water vole feeding stations per pond ($G_7 = 26.01$, $p < 0.001$). However, no significant difference between the total number of plant species in feeding stations between years was observed ($G_2 = 1.68$, $p = 0.975$). Nevertheless, annual variations in plant species selected as forage were observed. For example, *Carex otrubae* and *Juncus conglomeratus* were only present in feeding stations during 2007; *Glyceria flutians*, *Alysma plantago aquatica* and *Persicaria hydropiper* were only present in feeding stations during 2008; *Mentha aquatica* and *Eleocharis palustris* were only present in feeding stations during 2009.

Other species were consumed during all years, including *Juncus effusus*, *Typha latifolia*, *Epilobium hirsutum*, *Carex riparia*, *Iris pseudacorus* and *Ranunculus repens*. Additionally, seasonal variations were observed; *Epilobium hirsutum* was only encountered in feeding stations during the winter and early spring. In contrast, *Iris pseudacorus* was only encountered during the summer months. *Carex riparia* was present in feeding stations throughout the breeding season (spring to autumn). *Juncus effusus* and *Typha latifolia* were cached in feeding stations throughout both the breeding season and the winter. Of the 23 species selected as forage (in feeding stations) by water voles at NWCW, 19 were encountered only occasionally, in 3% or less of feeding stations (table 5.1). Interestingly, three non plant species were discovered in feeding stations during this study, two of which were amphibians, encountered during the end of winter, at the onset of the breeding season (figures 5.1 and 5.2). During February 2007 a frog (*Rana temporaria)* was found in a feeding station on pond G (figures 5.1 and 5.2). The remains of a toad (*Bufo bufo*) were also found on pond B during February 2009, cached by a water vole inside a regularly utilised open (un-set) trap. Great Pond-snails (*Limnea stagnalis*) were found in a water vole feeding station on pond D during September 2007.

Table 5.2 Total number of water vole feeding stations on each pond throughout the area of wetland studied (2007-2009)

Pond	2007	2008	2009	Total
A	27	15	56	98
B	11	2	10	23
C	11	0	13	24
D	37	41	40	118
E	11	0	5	16
F	0	0	0	0
G	20	66	25	111
H	4	7	14	25
Total	121	131	163	415

Table 5.3 Number of different plant species in water vole feeding stations on each pond in the wetland complex (2007-2009)

Pond	2007	2008	2009	Total	Percentage of plant species (%)
A	10	5	8	12	20.34
B	4	2	3	5	12.50
C	4	0	3	5	15.15
D	11	8	5	14	20.97
E	4	0	2	4	10.00
F	0	0	0	0	0
G	4	7	3	7	12.28
H	4	3	3	4	11.11
Total	14	14	10	23	17.83

Figure 5.1 February 2007 feeding station (pond G). The remains of a frog discovered within the territory of a pregnant female water vole and positively identified as a water vole food source by the presence of discernable incisor marks and water vole faeces

Figure 5.2 Two days later, further consumption, more incisor marks and water vole droppings reaffirm the frog as a water vole food item

5.2.2 Water vole foraging in dominant vegetation types (DVT)

During the latter half of the study, field surveys overlaid onto the DVT map (figure 1.1) revealed that 294 feeding stations consisting of 17 plant species (table 5.4) were encountered in 11 different dominant vegetation types (table 5.5).

Table 5.4 Plant species in water vole food-piles per dominant vegetation type (DVT) (2008-2009) (see table 1.1 for key to DVTs)

Plant species in feeding station	Number of DVTs containing plant species in feeding station	DVT
Alisma plantago-aquatica	2	*Cr, Tl*
Carex otrubae	1	Dg
Carex panacea	1	Dg
Carex riparia	1	*Cr*
Cirsium arvense	1	*Eh*
Cyperus longus	1	*Cl*
Eleocharis palustris	1	*Ep*
Epilobium hirsutum	2	*Eh, Je*
Glyceria fluitans	1	*Gf*
Glyceria maxima	1	*Gm*
Iris pseudacorus	2	*Cr, Dg*
Juncus effusus	6	*Jc, Je, Eh, Gf, Rf, Tl*
Juncus inflexus	1	*Je*
Mentha aquatica	1	*Ep*
Persicaria hydropiper	2	*Eh, Je*
Ranunculus repens	1	*Je*
Typha latifolia	3	*Eh, Je, Tl*

Of the 23 DVTs (within the 5 m boundary line; figure 1.1), 5 were considered unsuitable environs on which to create feeding stations, including open water and aquatic species such as Broad-leaved Pondweed (*Potomageton natans)*, Greater Spearwort *(Ranunculus lingua)* and Lesser Spearwort *(Ranunculus flammula).* The remaining 18 DVTs were more suitable foraging patches (i.e. provided a solid substrate for at least part of the year) and were utilised variably by water voles creating feeding stations (table 7.5). It should be noted that although Floating Sweet-grass (*Glyceria fluitans*) is an aquatic species, feeding stations of this species were found occasionally, cached on top of the dense floating mats of this DVT.

Table 5.5 Dominant vegetation types (DVTs) (within 5 m boundary line; figure 1.1) and the total number of different plant species in water vole feeding stations (n = 294) per DVT (2008-2009). See table 1.1 for key to DVTs and table 5.4 for key to plant species

DVT	Total number of feeding stations	Percentage (%) of total feeding stations	Total number of plant species in feeding stations
*Bm*DVT	0	0	0
*Cr*DVT	50	17.01	3 (*Cr, Je, Ip*)
*Ca*DVT	0	0	0
*Ch*DVT	0	0	0
*Cl*DVT	7	2.38	1 (*Cl*)
DgDVT	3	1.02	3 (*Co, Cp, Eh*)
*Ep*DVT	7	2.38	3 (*Ep, Ma, Tl*)
*Eh*DVT	16	5.44	5 (*Eh, Ca, Je, Ph, Rr, Tl*)
*Ea*DVT	0	0	0
*Gf*DVT	4	1.36	2 (*Gf, Je*)
*Gm*DVT	3	1.02	1 (*Gm*)
*Jc*DVT	3	1.02	1 (*Je*)
*Je*DVT	132	44.90	7 (*Je, Co, Eh, Ip, Ji, Ph, Rr, Tl*)
OwDVT	0	0	0
*Pn*DVT	0	0	0
*Rl*DVT	0	0	0
*Rr*DVT	0	0	0
*Rf*DVT	3	1.02	1 (*Je*)
*Rs*DVT	0	0	0
*St*DVT	0	0	0
TreeDVT	0	0	0
*Tl*DVT	66	22.45	3 (*Tl, Apa, Je*)
*Ud*DVT	0	0	0

Table 5.6 Number, percentage and location of feeding stations of the major forage species included in the water vole diet at NWCW (2008-2009)

	Plant species in feeding station			
	Carex riparia	*Epilobium hirsutum*	*Juncus effusus*	*Typha latifolia*
Number of feeding stations of the dominant plant species in the DVT	48	4	105	56
Percentage of feeding stations of the dominant plant species in the DVT (%)	100	24	84	90
Number of feeding stations of the associate plant species in the DVT	0	13	20	12
Percentage of feeding stations of the associate plant species in the DVT (%)	0	76	16	10

Of the 18 available DVTs, 11 (61%) were utilised for caching food. *Je*DVT provided the most important source of food, with 6 plant species associates of this DVT occurring in feeding stations located in this vegetation type. *Eh*DVT, DgDVT and *Tl*DVT also provided a diversity of associated plant species utilised by water voles as forage species (table 7.5). Water voles at NWCW employed selective patch-based foraging. Of the 17 species in feeding stations, 6 (35%) were encountered in more than one DVT (table 5.5) (i.e. were actively gathered where available) and 11 (65%) were selectively chosen (i.e. the plant species in the feeding station was not the dominant species of the DVT in which the feeding station was located). Additionally, 8 (47%) species in feeding stations were the dominant species of the DVT in which the food-pile was located. These included *Cyperus longus, Eleocharis palustris, Glyceria fluitans* and *Glyceria maxima,* all of which were only foraged upon occasionally, found in less than 3% of all feeding stations (table 5.1) and the four main forage species (discussed below).

The majority (90%) of feeding stations consisted of the four main forage species; *Carex riparia, Juncus effusus, Epilobium hirsutum* and *Typha latifolia.* In the case of *Carex riparia,* all feeding stations containing this species were encountered in *Cr*DVT (table 5.6), with an additional 2 species also cached in feeding stations in this DVT (table 7.5). *Juncus effusus* represented the dominant forage species, with 105 (84%) of the 125 feeding stations of this species occurring in a *Je*DVT (table 5.6). Although only 16% of *Juncus effusus* feeding stations were encountered in DVTs that were not dominated by this species, these comprised the greatest variety of DVTs (5) including; *Jc*DVT, *Eh*DVT, *Gf*DVT, *Rf*DVT *and* *Tl*DVT, (table 5.4). *Je*DVTs were associated with the highest diversity of cached plant species, with 7 plants selected by water voles from this DVT (table 5.5). *Epilobium hirsutum* as a forage species was only encountered in 5% of the total feeding stations during 2008 and 2009. However, 76% of these feeding stations were located in a DVT that was not dominated by the plant species in the feeding station, indicative of selective foraging (table 7.6). Additionally, the *Eh*DVT provided a high diversity of associate plant species, 5 of which were selected by water voles (table 7.5). There was no significant difference between the number of plant species cached in feeding stations per DVT ($G_{16} = 5.158$, $p = 0.995$) or between the total number of different DVTs containing feeding stations ($G_{10}= 3.175$, $p = 0.977$). However, there was a significant difference between the total number of feeding stations per DVT ($G_{10}= 80.37$, $p < 0.001$), the majority of which were encountered in the *Je*DVT.

5.2.3 Plant species diversity and water vole foraging behaviour

A significant positive correspondence was observed between the total number of plant species in feeding stations and the total number of plant species available per pond ($R^2 = 0.849$, $F_{1,7} = 33.716$, $p = 0.001$) (figure 5.3).

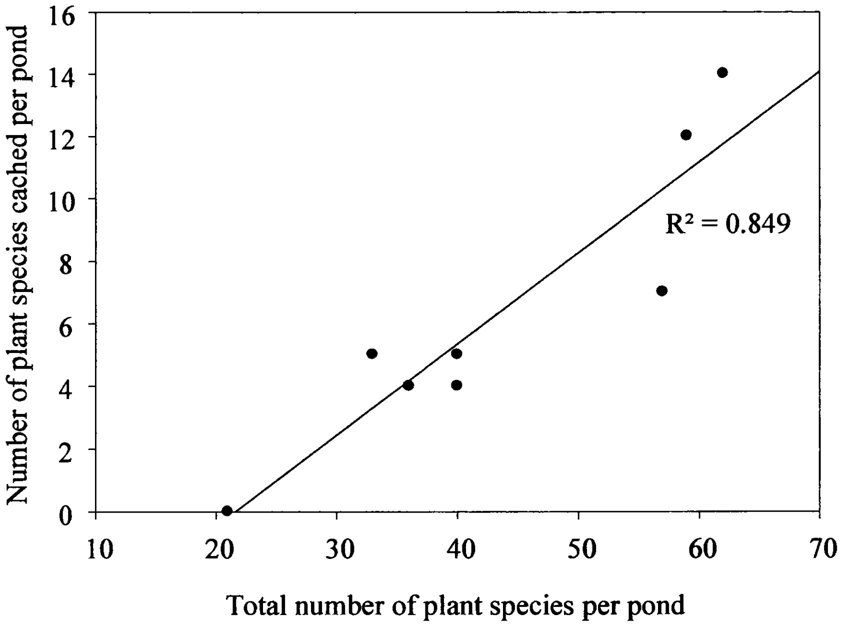


Figure 5.3 Linear regression of total number of plant species cached in feeding stations and the total amount of plant species available per pond

5.2.4 The effects of water vole population density on foraging choices

Variations in female population density were reflected in the number of plant species selected by water voles as forage. A significant positive correspondence between female population density per 100 m and the total number of plant species in water vole feeding stations was observed (figure 5.4) ($R^2 = 0.622$, $F_{1,7} = 9.893$, $p = 0.020$). In contrast there was no relationship between male population density per 100 m and the total number of plant species in feeding stations ($R^2 = 0.020$, $F_{1,7} = 0.0120$, $p = 0.740$).

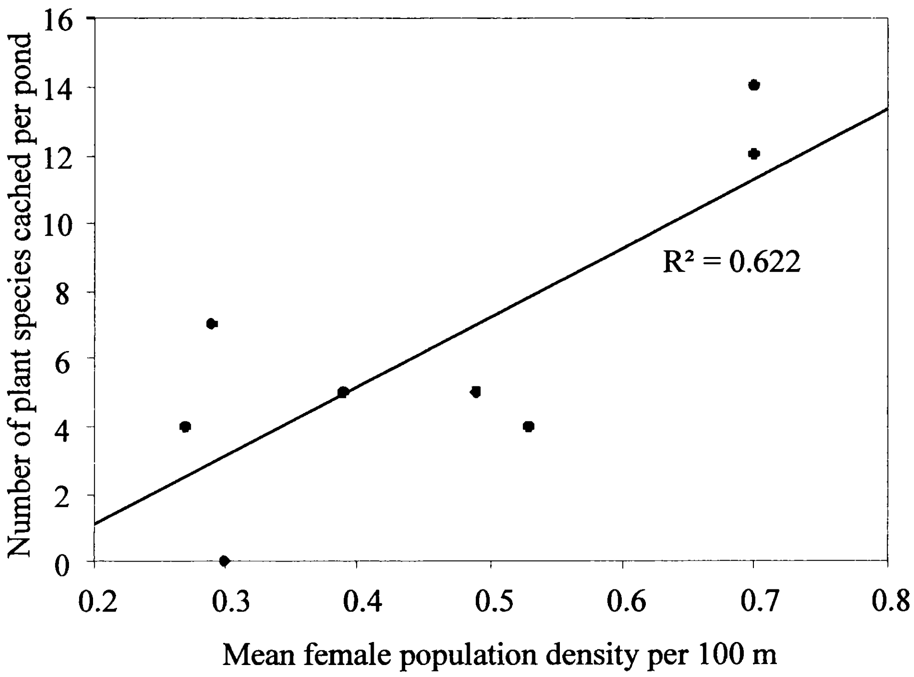


Figure 5.4 Linear regression of mean female population density per 100 m and the total number of plant species cached in feeding stations per pond

5.2.5 Water content of forage species

The plant species foraged upon by water voles varied significantly in water content ($F_{36} = 4.828$, $p = 0.001$) (table 5.7). *Juncus effusus* contained the lowest mean water content (65.06 ± 1.98%) and *Typha latifolia* contained the highest mean water content (87.39 ± 1.8%) per mass of fresh plant material (gg^{-1} fresh weight*100). These figures were used to calculate the total amount of nitrogen, carbon, energy and other minerals per gram of wet plant material (see table 5.10).

Table 5.7 Mean (±SE) water content (percentage water per mass of fresh plant material) of plant species included in the water vole diet

Plant species	Botanical name	Mean water content (%=gg^{-1} wet weight *100)	± SE
Malus domestica	Braeburn apple	85.02	0
Carex riparia	Greater Pond-sedge	71.07	4.21
Cirsium arvense	Field Thistle	81.35	0
Cyperus longus	Galingale	82.58	1.75
Eleocharis palustris	Common Spike-rush	76.90	0
Epilobium hirsutum	Great Willowherb	85.62	2.85
Glyceria maxima	Reed Sweet-grass	76.13	0
Iris pseudacorus	Yellow Iris	81.89	0
Juncus effusus	Soft Rush	65.06	1.98
Persicaria hydropiper	Water Pepper	79.52	3.19
Ranunculus repens	Creeping Buttercup	84.27	0
Typha latifolia	Bulrush	87.39	1.80

5.2.6 Forage nutritional quality – elemental content

The nitrogen content of plant species foraged upon by water voles differed significantly between species ($F_{73} = 5.051$, $p < 0.001$). *Epilobium hirsutum* had the greatest mean nitrogen content (3.1 ± 0.31%) (gg^{-1} dry weight*100) of all plant species, significantly more than *Carex riparia* ($p < 0.001$), *Juncus effusus* ($p < 0.001$) and *Cyperus longus* ($p = 0.004$) (table 7.5). Significant differences between the carbon content of forage species were also observed ($F_{69} = 3.316$, $p = 0.003$). *Persicaria hydropiper* and *Juncus effusus* had the highest carbon contents (46.36 ± 1.19% and 44.66 ± 0.55% respectively) (gg^{-1}dry weight*100); significantly more than *Cirsium arvense* ($p = 0.003$ and $p = 0.009$ respectively) (table 5.8). *Juncus effusus* had a significantly higher C:N ratio (31:1) than all other forage species selected by water voles ($t_9 = 11.053$, $p < 0.001$) (table 5.8).

Table 5.8 Mean (± SE) carbon and nitrogen content (% = gg^{-1}dry weight*100) and C:N ratios of plant species included in the water vole diet. Overall means (± SE) are presented for comparison and exclude Braeburn apple (*Malus domestica*)

Plant species	n	Mean (% ± SE) carbon content	Mean (% ± SE) nitrogen content	Mean C:N
Malus domestica	2	40.61 ± 4.29	0.28 ± 0.07	148:1
Carex riparia	14	43.23 ± 0.59	1.53 ± 0.16	28:1
Cirsium arvense	2	37.91 ± 0.25	2.16 ± 0.18	18:1
Cyperus longus	2	-	0.66 ± 0.31	-
Eleocharis palustris	2	-	1.49 ± 0.04	-
Epilobium hirsutum	12	42.70 ± 0.76	3.10 ± 0.31	13:1
Glyceria maxima	2	43.48 ± 0.75	1.65 ± 0.20	26:1
Iris pseudacorus	2	42.61 ± 0.15	2.81 ± 0.17	15:1
Juncus effusus	12	44.66 ± 0.55	1.47 ± 0.13	30:1
Persicaria hydropiper	4	46.36 ± 1.19	2.53 ± 0.14	18:1
Ranunculus repens	2	41.61 ± 0.59	2.56 ± 0.67	16:1
Typha latifolia	20	42.39 ± 0.59	2.21 ± 0.20	19:1
Overall mean		43.11 ± 0.31	2.07 ± 0.11	

5.2.7 Seasonal variations in elemental content of the four main forage species

Carex riparia, Epilobium hirsutum, Juncus effusus and *Typha latifolia* constituted the majority of (above ground) food-piles in the water vole diet (table 5.1). The four species differed significantly in their nitrogen content ($F_{3,57} = 11.545$, $p < 0.001$). *Epilobium hirsutum* had the highest nitrogen content, particularly during the spring. Although differences in nitrogen content were observed between seasons (figure 5.5), these seasonal variations were not significant ($F_{1,2} = 1.451$, $p = 0.234$). In contrast, the carbon content of the major forage species remained fairly constant (figure 5.6) and did not vary significantly between species or season (species $F_{1,57} = 2.763$, $p = 0.051$; season $F_{1,2} = 2.749$, $p = 0.103$).

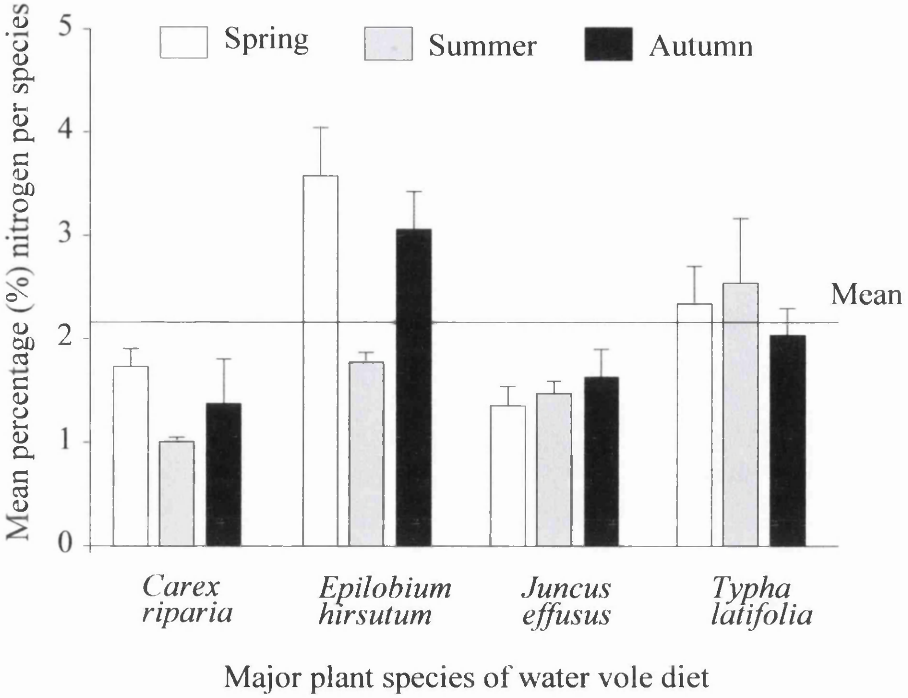


Figure 5.5 Seasonal variations (± SE) in mean nitrogen content (% = gg^{-1} dry weight*100) of the main plant species included in the water vole diet (n = 58 and includes leaf and shoot material). Mean line included for comparison

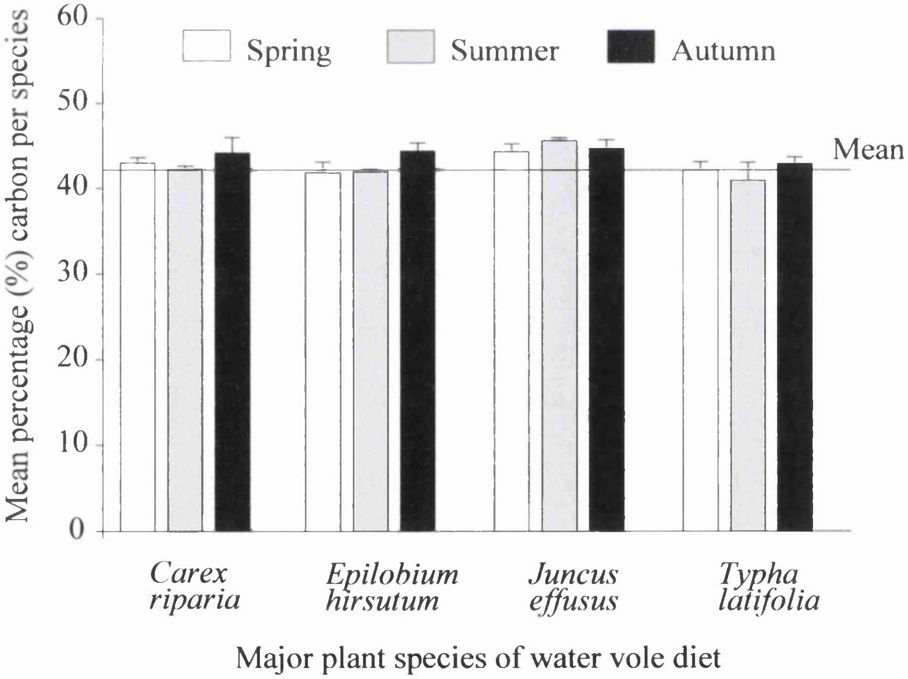


Figure 5.6 Seasonal variations (± SE) in mean carbon content (% = gg^{-1} dry weight*100) of the main plant species included in the water vole diet (n = 58 and includes leaf and shoot material). Mean line included for comparison

5.2.8 Forage nutritional quality - energetic and mineral content

A significant difference in mean energy content (kjg^{-1}) was observed between plant species ($F_{1,36}$ = 4.006, p = 0.002). *Iris pseudacorus* had the highest energy content (18.07 kjg^{-1}) of all plant species selected by water voles as forage (table 5.6). This species was a seasonal component of the water voles diet, consumed sporadically during the summer months and represented only a minor part of the diet (1%; table 5.1). Of the 4 plant species that formed the majority of the diet, *Juncus effusus* had the highest mean energy content 17.45 ± 0.27 kjg^{-1} and constituted 38% of feeding stations (table 5.1). There was a significant difference in energy content between the 4 main forage species ($F_{1,3}$ = 5.579, p = 0.006). Although seasonal variations were observed between the energy content of the four species, these were not significant (p = 0.189, $F_{1,3}$ = 1.847). Since the nitrogen content of forage species was predetermined using elemental analysis (section 5.3.7), the difference between the ash content and the nitrogen content represented the mineral proportion of the plant material (including phosphorous, calcium, potassium, copper, zinc sulphur, magnesium, molybdenum, boron and other essential elements) (table 5.9).

Table 5.9 Mean (± SE) energy (kjg^{-1}), ash (minerals plus nitrogen) and mineral content (% = gg^{-1} dry weight*100) of plant species included in the water vole diet

Plant species	Mean Energy (± SE) (kJg^{-1})	Mean (% ± SE) ash (minerals plus N)	Mean (% ± SE) minerals
Malus domestica	14.94 (± 0)	1.65 (± 0)	1.37 (± 0)
Carex riparia	16.62 (± 0.18)	6.57 (± 0.42)	5.05 (± 0.37)
Cirsium arvense	15.00 (± 0)	11.37 (± 0)	9.21 (± 0)
Cyperus longus	16.75 (± 0.28)	6.42 (± 1.11)	5.76 (± 0.8)
Eleocharis palustris	16.14 (± 0)	6.26 (± 0)	4.73 (± 0)
Epilobium hirsutum	15.90 (± 0.48)	7.66 (± 1.56)	4.82 (± 1.32)
Glyceria maxima	15.41 (± 0)	6.28 (± 0)	4.63 (± 0)
Iris pseudacorus	18.07 (± 0)	3.11 (± 0)	0.20 (± 0)
Juncus effusus	17.45 (± 0.27)	4.40 (± 0.39)	2.85 (± 0.28)
Persicaria hydropiper	16.45 (± 0.08)	6.66 (± 0.29)	4.42 (± 1.04)
Ranunculus repens	16.20 (± 0)	10.40 (± 0)	7.84 (± 0)
Typha latifolia	16.38 (± 0.13)	8.86 (± 0.52)	6.53 (± 0.46)

A significant difference was observed between the ash content of the plant species selected as forage by water voles ($F_{11,32} = 4.515$, $p = 0.001$). *Cirsium arvense* had the highest ash content (11.37%) (table 5.10) and a nitrogen content of 2.16% (table 5.9). The difference (9.21%) represents the mineral content of this species and is significantly higher than all other forage species ($F_{1,31} = 4.529$, $p = 0.002$). However, this species was only foraged on intermittently and constituted < 1% of feeding stations (table 5.1). Of those plant species that formed the majority of the diet, *Typha latifolia* had the highest ash content (8.86 ± 0.52%) and the highest mineral content (6.53 ± 0.46%) (table 5.9).

5.2.9 Nutritional value of dietary choices

The plant species selected as forage by water voles varied significantly in water content (table 5.7). Additionally, the carbon, nitrogen (table 5.8), energy and mineral content were measured per gram of dry plant matter (table 5.9). Consequently, fresh plant material containing a low water content (e.g. *Juncus effusus*) contains more carbon, nitrogen and minerals per wet weight of plant matter than fresh plant material containing a high water content (e.g. *Typha latifolia*). The following calculations provide an idea of the nutritional value of varying diets and are based on an adult water vole weighing 200 g. With the assumption that adult water voles consume 93% of their body weight per day (Saucy *et al.*, 1993), a 200 g water vole consumes 186 g of wet plant material per day. Although the proportions of each plant species eaten by an individual vole are not known, for simplicity it was assumed that only a single species was consumed. Data are presented based on strict individual diets of the four main forage species (table 5.10). Since no significant difference was observed between seasons (section 5.2.7), the mean values for the species (tables 5.7 to 5.9) were used in the calculations.

Table 5.10 Daily nutritional value of varying water vole diets based on consumption of a single plant species with a wet weight of 186 g (fresh leaf and shoot material)

	Plant species selected as forage			
	Carex riparia	*Epilobium hirsutum*	*Juncus effusus*	*Typha latifolia*
Water content (%)	71	86	65	87
Dry weight (g)	53.94	26.05	65.1	24.18
Carbon (g ± SE)	23.32 ± 0.26	11.12 ± 0.20	29.07 ± 0.25	10.25 ± 0.25
Nitrogen (g ± SE)	0.83 ± 0.09	0.81 ± 0.08	0.96 ± 0.08	0.53 ± 0.05
Minerals (g ± SE)	2.72 ± 0.20	1.25 ± 0.34	1.86 ± 0.18	1.58 ± 0.11
Energy (Kj ± SE)	896.48 ± 9.70	414.20 ± 12.50	1136.00 ± 17.58	396.07 ± 3.14

A diet consisting of 100% *Juncus effusus* had significantly more carbon (g) ($F_{1,3}$ = 20255.73, $p < 0.001$), nitrogen (g) ($F_{1,3}$ = 5979.67, p = 0001) and energy (Kj) ($F_{1,3}$ = 19280.25, $p < 0.001$) than strict diets consisting of 100% of the other three main forage species (table 5.10). In contrast, a diet consisting of 100% *Carex riparia* contained significantly more minerals (g) ($F_{1,3}$ = 10161.00, $p < 0.001$) than the other three main forage species (table 5.10).

5.2.10 Water vole social behaviour – latrines as a measure of habitat utilisation

During three years of field surveys (2007 to 2009), 186 latrines were encountered (table 5.11). Latrine counts were standardised per 100 m to allow for differing circumference of ponds and for comparison with population densities per 100 m (section 5.2.12). The majority of latrines (90%) were encountered in the breeding season, during which time 20% were drum marked. Nevertheless, on ponds D and G, latrines were established in winter (as early as January) during the peak phase (2007). The highest (above ground) mean latrine density per 100 m was encountered on pond D (12.09 ± 2.05) (table 5.11). There was a significant difference in latrine density per 100 m between ponds ($F_{1,7}$ = 4.724, p = 0.006) however, no significant difference was observed between years (F_1 = 1.314, p = 0.270). The mean latrine density for the site was 4.39 ± 0.88 latrines per 100 m.

Table 5.11 Total number of latrines per pond per year throughout the area of wetland studied

	A	B	C	D	E	F	G	H	Total
2007	14	8	1	21	3	0	21	4	72
2008	5	2	0	24	1	0	34	2	68
2009	10	2	7	13	1	0	2	5	40
Total	29	12	8	58	5	0	57	11	186

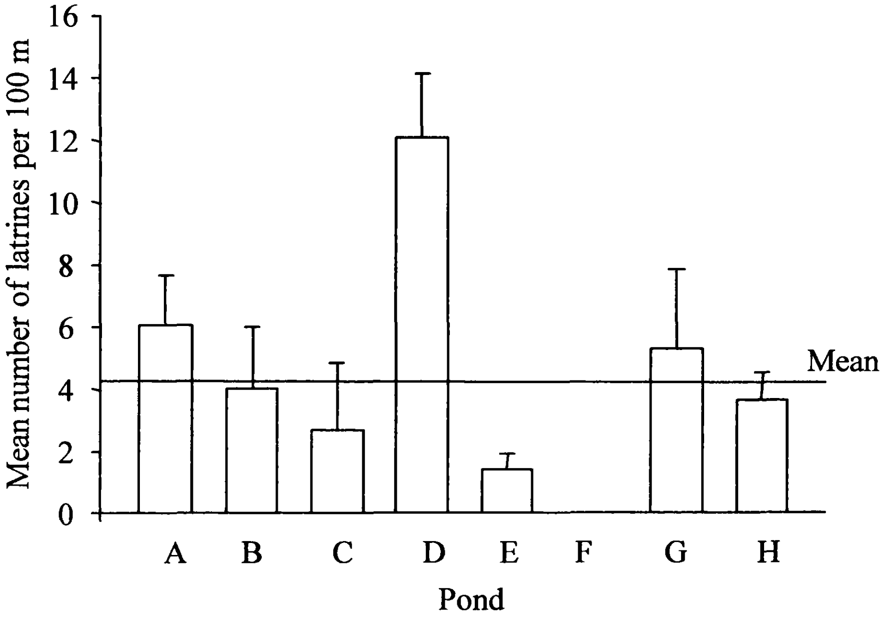


Figure 5.7 Mean latrine density per 100 m (± SE) per pond throughout the duration of the study. Mean line included for comparison

5.2.11 Population density and water vole latrines

In contrast to previous studies (Woodroffe *et al.*, 1990; Morris *et al.*, 1998), water vole population density did not influence the number of latrines per 100 m. Since latrine density was only determined during 2007 to 2009, population density data from 2006 was not included in the regression analyses. No obvious relationship between the mean population density and the mean latrine density was observed ($R^2 = 0.202$, $F_{1,7} = 1.520$, $p = 0.264$). Since females create latrines at range boundaries (Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006), the mean female population density was also regressed against the mean latrine density, however, no significant correspondence was observed ($R^2 = 0.308$, $F_{1,7} = 2.671$, $p = 0.153$).

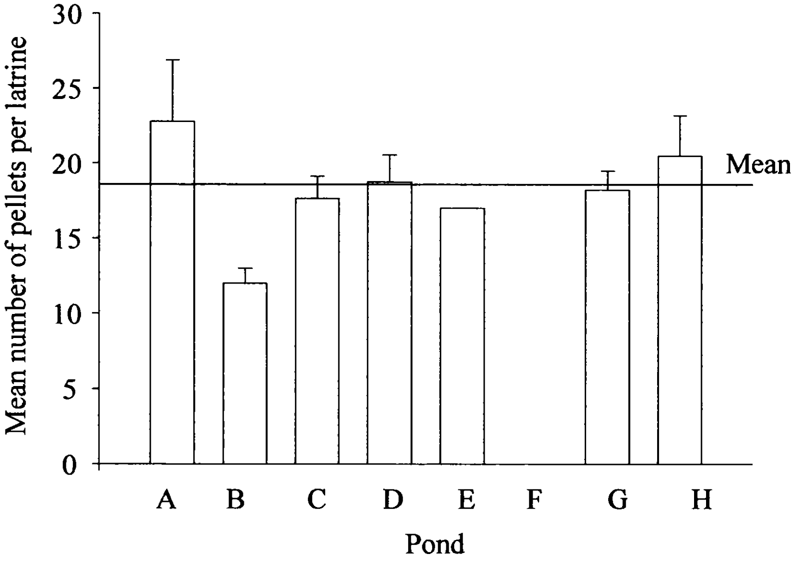


Figure 5.8 Mean number of faecal pellets per water vole latrine per pond

Although female population density did not influence latrine density (figure 5.7), it had a significant effect on the number of faecal pellets per latrine (figure 5.8). Ponds supporting higher female population densities had significantly more faecal pellets per latrine ($R^2 = 0.531$, $F_{1,7} = 6.799$, $p = 0.040$). Moreover, a seasonal effect was observed. During spring there were significantly more pellets per latrine (21.42 ± 1.31 pellets; figure 5.9) than during both summer and autumn ($F_{2,107} = 3.244$, $p = 0.008$). However, thorough field surveys that included pellet counts were only undertaken during the low density phase (2008 to 2009) and thus results should be treated with caution.

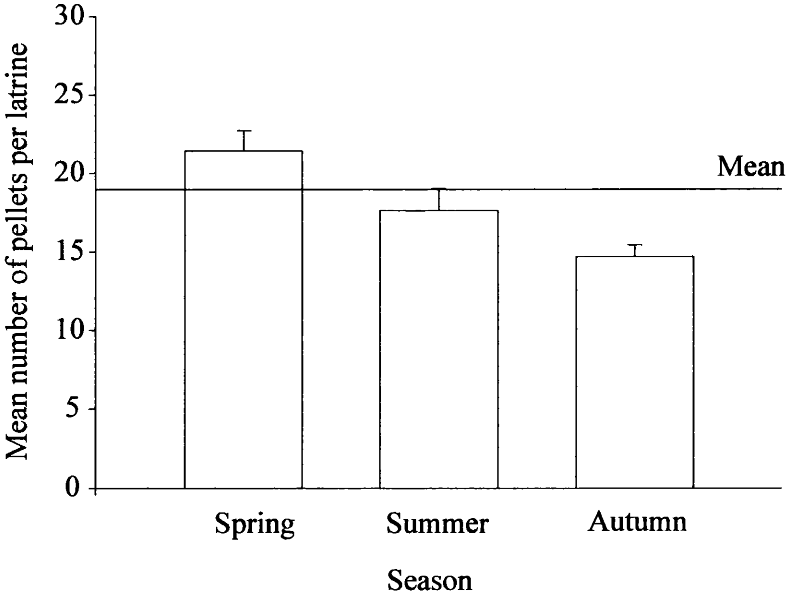


Figure 5.9 Mean number of faecal pellets per water vole latrine per season

5.2.12 Habitat diversity (D_{pond}) and latrine density

There was no significant relationship between the mean latrine density per 100 m per pond and the habitat diversity (D_{pond}) of the ponds ($R^2 = 0.427$, $F_{1,7} = 4.466$, $p = 0.079$) (figure 5.10), until the outlier (pond D) was removed from the analyses.

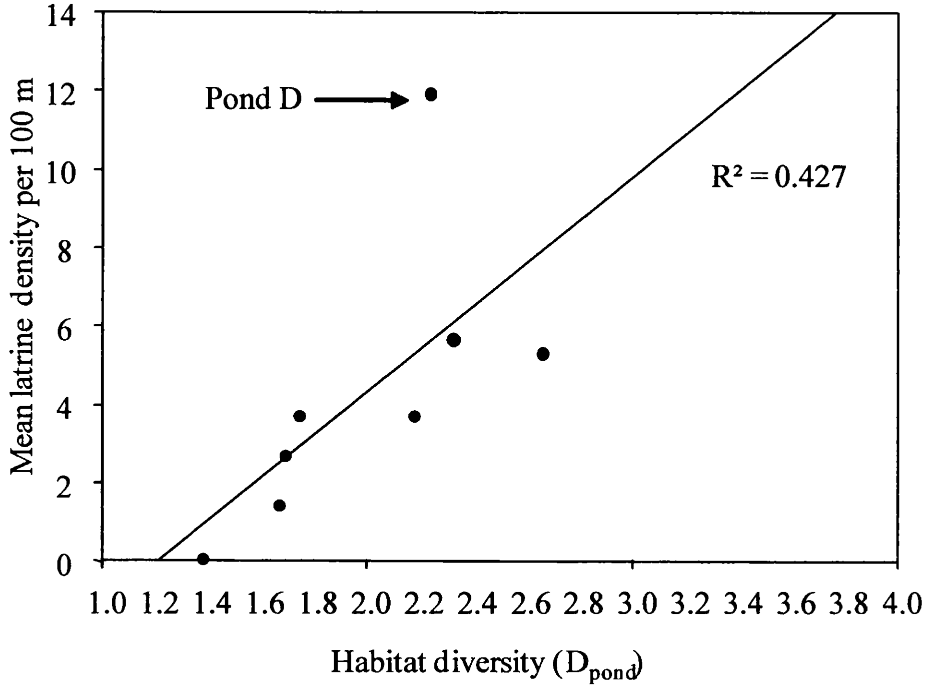


Figure 5.10 Linear regression of mean latrine density per 100 m per pond against habitat diversity (D_{pond}) per pond

Pond D had the highest mean latrine density (11.88 ± 2.25 per 100 m) and represented an outlier in the regression analysis (figure 5.10). However, removing pond D from the analysis corrected the model and revealed a strong positive relationship between the habitat diversity (D_{pond}) and the mean latrine density ($R^2 = 0.801$, $F_{1,6} = 20.09$, $p = 0.007$). More diverse habitats typically had a higher density of latrines. Reasons for omitting pond D are discussed in section 5.3.9.

5.2.13 Water vole latrines and Dominant Vegetation Types (DVT)

The following analyses incorporate field survey data (n = 108 latrines) from 2008 and 2009 only, since the exact location of latrines was only mapped for the latter half of the study. During 2007, field surveys assigned latrines to ponds but not to exact DVTs and thus data from this year was excluded from the following analyses. Of the

23 DVTs (within the 5 m boundary line; figure 3.1), 6 were considered to unsuitable environs on which to create latrines, such as open water, and aquatic plants including Broad-leaved pondweed (*Potomageton natans)*, Floating Sweet-grass (*Glyceria fluitans)*, Greater Spearwort (*Ranunculus lingua)* and Lesser Spearwort *(Ranunculus flammula*). The remaining 17 DVTs were typically non-aquatic species, provided a solid substrate (for at least part of the year) and were utilised variably by water voles creating latrines (table 5.12).

Table 5.12 Total number of water vole latrines and percentage of latrines that were drum-marked per dominant vegetation type (DVT) during field surveys across the area of wetland complex studied (2008-2009)

Dominant Vegetation Type (DVT)	Number of latrines	Percentage (%) of latrines drum-marked
*Cr*DVT	17	23.5
*Cl*DVT	3	0
*Eh*DVT	7	42.9
*Jc*DVT	1	100
*Je*DVT	62	16.1
*Rf*DVT	6	50
*Tl*DVT	12	8.3
Total	108	20.4

Water vole latrines were encountered in 7 (41%) DVTs, particularly the *Je*DVT, which had significantly more latrines than any other DVT ($G_6 = 104.03$, $p < 0.001$). Approximately one fifth (20.4%) of latrines were drum-marked. There were no significant differences observed in the proportion of drum-marked latrines per DVT ($G_6 = 1.758$, $p = 0.941$). However, approximately half of the latrines in the *Rf*DVT and the *Eh*DVT were drum-marked (table 7.9), representing important DVTs for female water voles maintaining territories. The distribution of latrines in the 7 DVTs was plotted onto the DVT map (appendix 10, figure A18).

5.2.14 DVT patch diversity (D_{DVT}) and degree of utilisation

Water voles utilised DVTs for both foraging and communicating via latrine sites. During the latter two years of the study, 11 DVTs were used for the creation of feeding stations (table 5.5); however, only 7 of these were used for the creation of latrine sites (table 5.12). Moreover, water voles caching vegetation in feeding stations typically operated within the least diverse DVT patches, with the greatest number of feeding stations per patch observed in the *Cr*DVT and the *Je*DVT. With the exception of the *Rf*DVT, (associated with zero diversity due to 100% cover of the dominant species) the *Cr*DVT and the *Je*DVT had lowest DVT patch diversities (D_{DVT}) (chapter 1). A significant negative relationship between the number of feeding stations per DVT patch and the diversity of the patch (D_{DVT}) was observed (figure 5.11) ($F_{1,7}$ = 14.519, p = 0.009, R^2 = 0.708). However, no obvious relationship was observed between the number of latrines per patch and the diversity of the patch (D_{DVT}) ($F_{1,4}$ = 3.714, p = 0.150, R^2 = 0.553).

Table 5.13 Feeding stations per DVT patch and per m^2 of the area of wetland studied (within the 5 m boundary; figure 1.1). The number and area of patches are detailed in chapter 1 (table 1.3)

Dominant Vegetation Type (DVT)	Total feeding stations	Feeding stations per patch	Feeding stations per m^2
*Cr*DVT	50	6.25	0.16
*Cl*DVT	7	7	0.62
DgDVT	3	0.3	0.01
*Ep*DVT	7	1.4	0.02
*Eh*DVT	16	1.33	0.03
*Gf*DVT	4	1	0.01
*Gm*DVT	3	3	0.05
*Jc*DVT	3	1	0.04
*Je*DVT	132	5.08	0.05
*Rf*DVT	3	0.19	0.01
*Tl*DVT	66	3.67	0.03
Total	294	Mean = 1.88	Mean = 0.02

The *Je*DVT had the greatest number of latrines per patch (2.39) (table 5.13). However, due to the broad expanses of this DVT across all ponds, this only equated to 0.02 latrines per m^2, equivalent to 1 latrine per 50 m^2. Almost half (44.9%) of the 294 feeding stations created during 2008 and 2009 were located in the *Je*DVTs (tables 5.1 and 5.5). This equated to 5.08 feeding stations per patch, 0.05 feeding stations per m² or 1 feeding station per 20 m² (table 5.10). Additionally, the highest diversity of plant species in feeding stations was observed in the *Je*DVTs, with 7 plant species selected by water voles in this DVT (table 5.5). The distribution of feeding stations in the 11 DVTs was plotted onto the DVT map (appendix 10, figure A18).

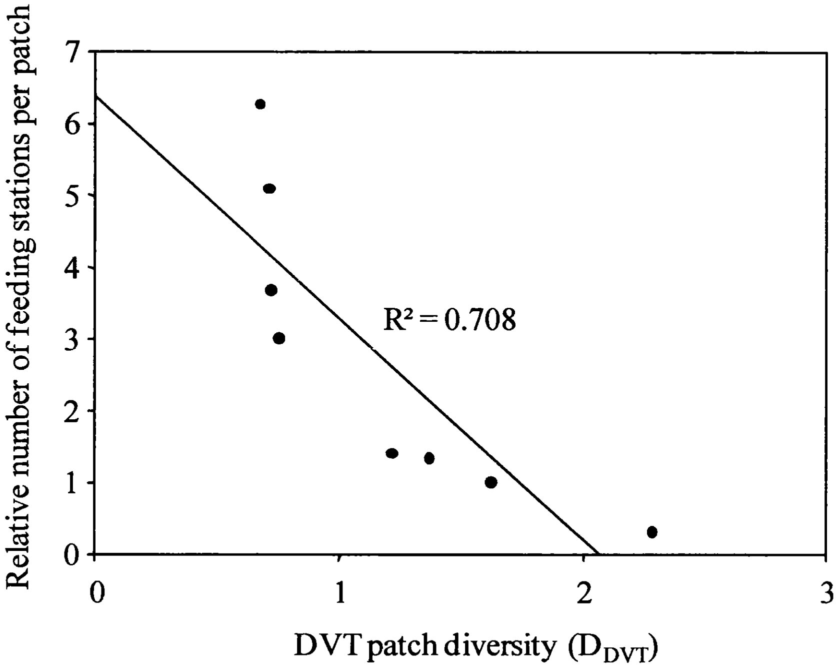


Figure 5.11 Linear regression of number of water vole feeding stations per DVT patch and the DVT patch diversity (D_{DVT})

The *Cr*DVT had 2.13 latrines and 6.25 feeding stations per patch, equating to 0.05 latrines and 0.16 feeding stations per m² or 1 latrine per 20 m² and 1 feeding station per 6.25 m² (tables 5.13 and 5.14). Interestingly, the highest latrine and feeding station density was observed in the *Cl*DVT, with 3 latrines and 7 feeding stations occurring in one small patch (11.33 m²), equivalent to 1 latrine per 3.78 m² and 1 feeding station per 1.62 m². There were 4 DVTs in which only feeding stations were present (however latrines were absent), but were only foraged in occasionally. These included the DgDVT, the *Ep*DVT, the *Gf*DVT and the *Gm*DVT. Traps were located in both the DgDVT and the *Gm*DVT, however, neither DVT was incorporated into home range of resident adult water voles (chapter 3). No traps were located in the *Ep*DVT or the *Gf*DVT.

Table 5.14 Latrines per DVT patch and per m^2 of the area of wetland studied (within the 5 m boundary; figure 1.1)

DVT	Total latrines	Latrines per patch	Latrines per m^2
*Cr*DVT	17	2.13	0.05
*Cl*DVT	3	3	0.27
DgDVT	0	0	0
*Ep*DVT	0	0	0
*Eh*DVT	7	0.58	0.02
*Gf*DVT	0	0	0
*Gm*DVT	0	0	0
*Jc*DVT	1	0.33	0
*Je*DVT	62	2.39	0.02
*Rf*DVT	6	0.38	0.01
*Tl*DVT	12	0.67	0.01
Total	108	Mean = 0.69	Mean = 0.007

5.2.15 Faecal loading of wetland soils

Field surveys revealed that latrines contained an average of 18.66 ± 0.82 faecal pellets. The mean latrine density across the area of wetland studied (based on 2007 to 2009 surveys) was 4.88 ± 0.33 latrines per 100 m. There appeared to be no relationship between latrine density and population density, however, a positive relationship was observed between female population density and the number of pellets per latrine (section 5.3.12). Moreover, population densities and latrine counts can be used to predict the amount of faecal loading occurring on each pond based on previous studies of captive water voles. Since water voles produce between 200-300 faeces per day (in captivity, Woodall, 1977) and assuming a wet weight of 0.36 g per pellet, an average vole produces (as a conservative estimate) 72 g faeces per day (based on producing 200 faeces). One animal will produce 26.28 kg of faecal pellets per year. Consider pond A which in March 2009 had a population density of 1.88 animals per 100 m and a latrine density of 1.88 per 100 m. Since pond A had a circumference of 160 m, this equated to 3 water voles and 3 latrines. If the average water vole produced 200 faeces per day, then 3 water voles potentially contributed 600 pellets to pond A per day. Since only 3 latrines were observed (containing 55.98 pellets; based on a mean value of 18.66 pellets per latrine), this leaves a deficit of approximately 544 pellets (91% of predicted faecal loading) that are unaccounted for. Similarly pond A in May 2009 had a population density of 1.25 water voles per 100 m and a latrine density of 3.13 per 100 m. This equated to 2 water voles (contributing 400 pellets per day) and 5 latrines (containing 93.3 pellets), leaving a deficit of approximately 307 pellets (77% of predicted faecal loading).

5.2.16 Nitrogen content of water vole latrines

The mean nitrogen content (%N = gg^{-1} dry faecal material) per water vole pellet was 1.82 ± 0.06 % and there was no significant difference in the nitrogen content of faecal pellets between genders, age classes or those collected from latrines (figure 5.12) ($F_{3,63}$ = 2.102, p = 0.122). Furthermore, no significant differences were observed between seasons (figure 5.13) (source of pellets $F_{1,3}$ = 1.278 p = 0.290; season $F_{1,2}$ = 2.238, p = 0.140).

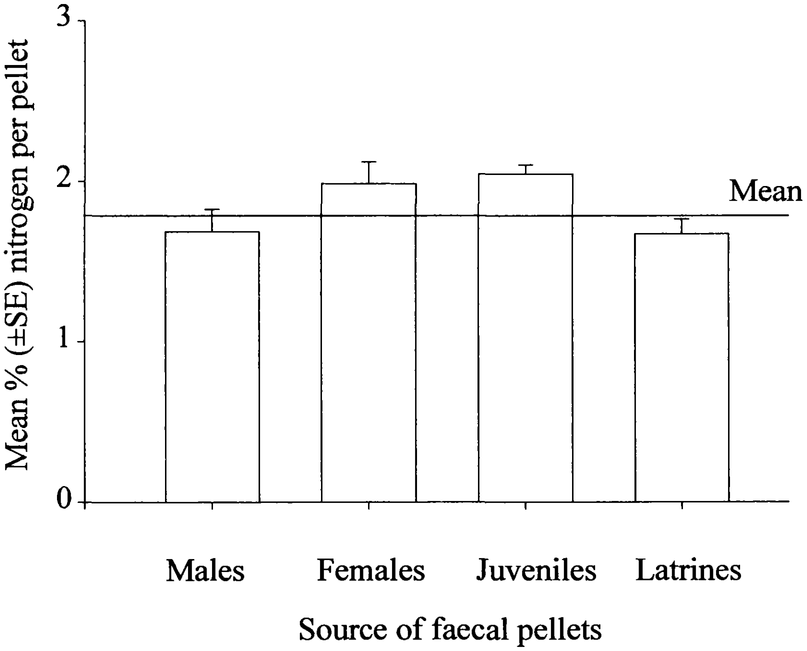


Figure 5.12 Mean (±SE) nitrogen content of water vole faecal pellets collected from trapped animals and latrines

Elemental analysis revealed that each 0.36 g pellet (n = 66) contained between 1.08 and 3.53% total N (mean 1.82 %). A 0.36 g pellet contained a mean moisture content of 66.81% (see appendix 8), the remaining 33.19% was dry matter, which is equivalent to 0.12 g. Thus one pellet containing 0.12 g of dry matter contained 2.18

mg N per fresh pellet. Taking Woodall's lower estimate (Woodall, 1977) each water vole produces 200 faeces per day, equivalent to 72 g of faeces containing 436mg (0.436g) of nitrogen per day. Assuming full survivorship, one animal could contribute 26.3 kg of faeces containing 155.22 g of N per year to the habitat. The total water vole population at NWCW (including areas not covered in this study) is conservatively estimated at 400 animals (Forman, pers. comm.). In one day these animals contribute 28.8 kg of pellets containing 174.4 g of N to the wetland habitat. Assuming full survivorship, this equates to 10.51 metric tonnes of faeces containing 63.66 kg of N annually. A pre-breeding population of 41,000 water voles in Wales (Harris *et al.*, 1995) can contribute (in one day) a total of 8,200,000 faecal pellets, weighing 2.95 metric tonnes, containing 17.88kg of nitrogen to the wetland habitat in Wales per day. Assuming full survivorship of these animals, this equates to an impressive 1076.75 metric tonnes of faeces containing 6.52 metric tonnes of nitrogen deposited annually in riparian or wetland areas that are home to water voles in Wales.

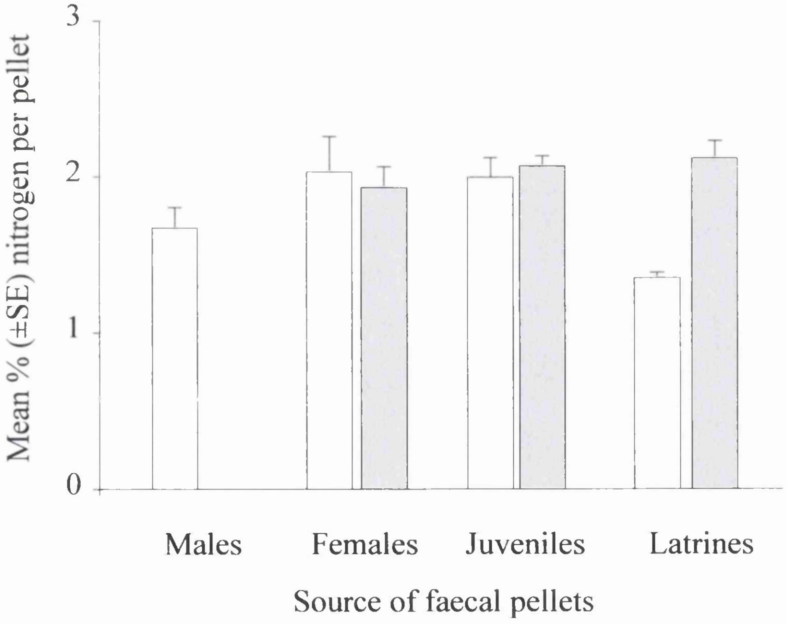


Figure 5.13 Seasonal variation in mean (±SE) nitrogen content of water vole faecal pellets collected from trapped animals and latrines. Spring (open bars), Autumn (grey bars).

5.2.17 Do water vole latrines contribute to the nutrient status of wetland soils?

Variations in nutrient concentrations (µmol l^{-1}) were observed between soil samples (figure 5.14). Soil cores removed from latrines sites had a similar amount of nitrate to those removed from non-latrine sites ($F_{1,16} = 0.123$, $p = 0.731$). However, latrine soil cores had higher ammonium concentrations and lower phosphate concentrations than their non-latrine counterparts. Despite the variations observed, there was no significant difference in ammonium concentration ($F_{1,16} = 1.318$, $p = 0.269$). Phosphate concentrations were not normally distributed and were thus square root transformed, however, no significant differences in transformed phosphate concentrations were observed between soils ($F_{1,16} = 2.607$ $p = 0.127$).

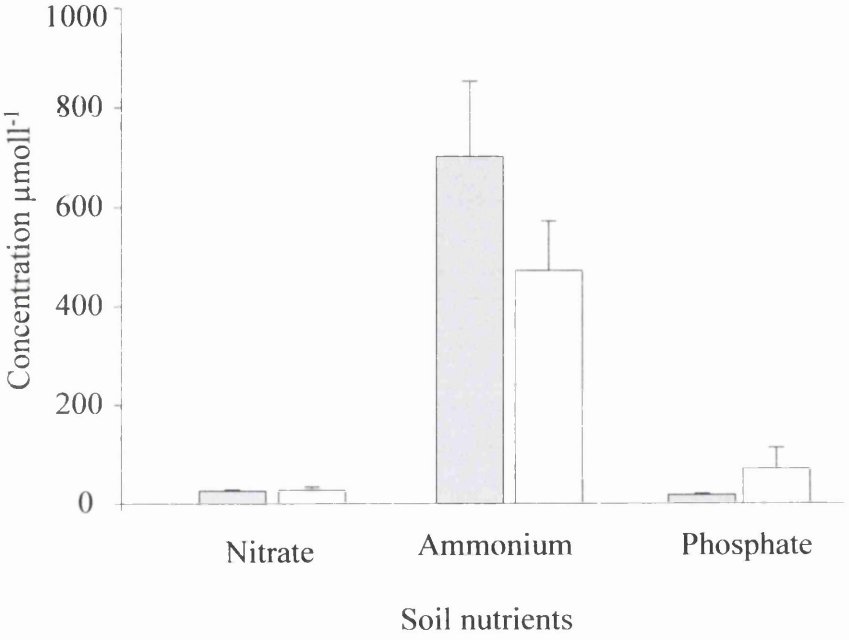


Figure 5.14 Concentration of nutrients in soil extractions from latrine and non-latrine (control) soils. Latrine soil (grey bars), control soil (open bars). Faecal pellet concentrations (µmol l^{-1}); $NO_3^- = 61.98 \pm 18.54$; $NH_4^+ = 1568.64 \pm 870.08$; $PO_4^{3-} = 2078.01 \pm 212.31$

5.3 Discussion

5.3.1 Water vole diet at NWCW

The majority of the (above ground) water vole diet at NWCW was dominated by rushes and sedges, consumed during both winter and the breeding season. In contrast to previous studies (Lawton & Woodroffe, 1991; Strachan & Jefferies 1993; Woodall, 1993), grass did not constitute a major component of the water vole habitat at NWCW. Grasses were foraged on only occasionally and only during the breeding season, and represented less than 5% of the total feeding stations. *Juncus effusus* was the plant species most frequently encountered in feeding stations and was consumed throughout the year. *Juncus effusus* is known to be eaten by water voles (Holisova, 1965, 1970; Howes, 1979) and was reported to occur frequently in water vole feeding stations during a nationwide survey (Strachan & Jefferies, 1993). However, water voles have also been negatively associated with this species in the past (Woodall, 1993). *Juncus effusus* represented one of the most important components of the water vole ecosystem at this site, constituting a major part of the water vole diet. In addition to providing a source of nutritional food (sections 5.2.7 to 5.2.10) *Juncus effusus* provided a continuous source of cover from predation, the importance of which has been previously demonstrated (Carter & Bright, 2003; Strachan & Moorhouse, 2006). Additionally, during the breeding season water voles at NWCW stripped the *Juncus effusus* stems to access the soft pith that was utilised as nesting material. A similar behaviour was also observed for field voles at this site (pers. obs.).

Carex riparia and *Typha latifolia* were also important forage species, cached in feeding stations during both the breeding season and the winter at this site. Both these species have been reported as *occasional* sources of forage for water voles during winter and spring (Strachan & Jefferies, 1993). However, they were *frequently* encountered in feeding stations at this locality. This contrasts with the findings of Boyce (1991) who found that water voles most frequently consumed reeds (*Phragmites* sp.) which were clearly preferred over other emergent macrophytes such as *Typha* sp. Although *Phragmites australis* was present at NWCW, it was not present in the area of wetland studied and therefore the importance of this species to water voles at this site cannot be determined. *Epilobium hirsutum* was encountered in less than 10% of water vole feeding stations. However, this species was still considered to be one of the four most important sources of forage for water voles at this locality due to its seasonal exploitation by water voles. The leaves of *Epilobium hirsutum* were frequently found in feeding stations from February and throughout the early part of the breeding season. This was one of the first herbaceous species to put forth new growth after the winter and was cached in feeding stations on all ponds on which it occurred at this site. Young leaves contain less fibre and more protein than older leaves (Polisini & Boyd, 1972).

Certain plant species were exploited only during the summer by water voles at NWCW, classified as seasonal associates of the water vole diet. These included herbaceous species, such as *Ranunculus repens*, (including flower buds), aquatic species, such as *Iris pseudacorus*, and various rushes and sedges, all of which have been previously reported to be components of the water vole diet (Strachan & Jefferies, 1993). It has been reported that pregnant water voles selectively eat flowers for their protein rich pollen (Strachan, 1997).

Of all the plant species encountered in feeding stations, *Cyperus longus* and *Cirsium arvense* were the only two that were not included in the list of 227 species consumed by water voles reported in the nationwide survey, however, other species of thistle were reported to be consumed occasionally (Strachan & Jefferies, 1993). *Cirsium arvense* was foraged upon infrequently and is not typically utilised by water voles as a food source, perhaps because of its armour of protective spines (Woodall, 1993). *Cyperus longus*, a species of conservation concern in Britain (Cheffings & Farrell, 2005) has decreased in recent years, through drainage of suitable habitats (Jermy *et al.*, 2007). It is likely that this species was not present in the water vole habitats included in the nationwide survey (Strachan & Jefferies, 1993) since it typically has a coastal distribution (Jermy *et al.*, 2007). Nevertheless, *Cyperus longus* appears to be of importance to water voles at this locality. Since only above ground habitat utilisation was studied, one should be cautious in the inference of water vole dietary choices from the field survey results, as many food caches (and sources of food) were located underground. Frustratingly, our inability to study them limits our understanding of their significance (Neyland *et al.*, 2010).

5.3.2 Non-plant elements of the water vole diet

In addition to the 23 plant species consumed by water voles, 3 non-plant species were cached in water vole feeding stations throughout the duration of this study. On one occasion the remains of Great pond snails (*Limnea stagnalis)* were encountered.

This species has been recorded on rare occasions in water vole feeding stations (Strachan & Jefferies, 1993). Water voles have been observed to augment their diet with freshwater molluscs and crayfish, presumably as a rich source of protein during pregnancy (Strachan, 1997).

Additionally, water voles at NWCW occasionally foraged on amphibians during the winter. It is not known whether the voles actively predated the frog or opportunistically fed upon its carcass, however, the latter is more likely. Although water voles in the past have been reported to feed on carrion (dead fish) (Ryder, 1962), this study provides the first evidence that amphibians are utilised as a water vole food source (reported in Forman *et al.*, 2008). The frog was cached in a feeding station (with *Juncus effusus* and water vole droppings) and foraged upon over a number of days. Furthermore, the frog was cached within the home range of a pregnant adult female during February. The early onset of breeding observed during 2007 could be associated with the mild winter of the previous year. It is likely that non-plant items were used as a source of protein during the winter, or at the onset of the breeding season, when availability of forage remained low until the growing season began. In addition to non-plant species, water voles typically augment their diet with bark and underground rhizomes during the winter (Strachan & Jefferies, 1993). No evidence of foraging upon woody species during the winter was observed at NWCW, however, the rhizomes of *Carex riparia* were occasionally utilised as a food source.

5.3.3 Water vole foraging in dominant vegetation types (DVT)

Capture data overlaid onto the habitat map (figure 1.1) provided information regarding the dominant vegetation types (DVT) incorporated into the home ranges of resident adults (chapter 4). With the exception of the *Rf*DVT, the *Bm*DVT and trees, the DVTs that were incorporated into the majority of adult water vole home ranges reflected the species usually selected as forage; *Cr*DVT, *Je*DVT, *Eh*DVT and *Tl*DVT. In addition to the dominant plant species, between two and six other species associated with these DVTs were also cached in water vole feeding stations in these DVT types. As well as providing a diversity of food, these four DVTs were also exploited by water voles as cover, associated with the high-layering of the vegetation, which permits water voles to remain hidden, particularly from avian predators, while foraging out of the water (Lawton & Woodroffe, 1991). In addition to grasses, stands of *Epilobium* sp. are associated with the best water vole sites in Britain (Strachan & Moorhouse, 2006).

The *Je*DVT was the most important DVT for resident females during the breeding season as determined by both capture data (chapter 4) and field survey data. Combining the distribution of water vole home ranges and the distribution of distinctive field signs (including feeding stations and latrines) across the available area of habitat not only highlighted the degree to which each DVT was utilised, but also added important information that could not be gained from live trapping alone (chapter 2). Water voles created feeding stations in eleven DVTs; however, only eight DVTs were incorporated into the home ranges of adult water voles at NWCW. Food-piles were created in both the DgDVT and the *Gm*DVT, although these two DVTs were not incorporated into the home ranges of any resident adult water voles (as inferred from capture data; chapters 2 to 4).

During the breeding season feeding stations were created in the *Ep*DVT, illustrating that this vegetation type was utilised by water voles, albeit infrequently. Moreover, feeding stations of this species were usually encountered in the vicinity of juveniles. It is plausible to speculate that *Eleocharis palustris* was foraged upon by juvenile water voles, since it is typically smaller and less fibrous than *Juncus effusus* and thus may be easier for younger animals to manipulate and digest. The allometry of herbivore food selection notes that herbivores of differing body sizes select plants with differing characteristics (Belovsky, 1997). No traps were located in the *Ep*DVT since it was typically associated with shallow water and therefore unsuitable for the placement of traps, due to the risk associated with flooding. The *Cl*DVT occurred in one localised patch on pond A, the only pond to be continually inhabited throughout the four year study (chapter 2) and was incorporated into the home ranges of numerous females (chapters 3 and 4), representing an integral component of the water vole ecosystem at NWCW.

Interestingly, during the breeding season, only male water voles were observed to maintain a home range in the *Tl*DVT, however, numerous feeding stations of this species were encountered in this DVT during this time. It is plausible that the *T. latifolia* feeding stations encountered during the breeding season were created by males. Additionally, occasional feeding stations were also created in the *Jc*DVT, another component of male home ranges that was not utilised by females. Radio-telemetry of meadow voles (*Microtus pennsylvanicus*) revealed that reproductively active females maintained small exclusive territories, forcing males to forage in the interstices of their territories (Madison, 1980).

5.3.4 Plant species diversity and water vole foraging behaviour

Water voles at NWCW cached 23 different plant species in feeding stations over the duration of the study. The number of plant species selected as forage by water voles reflected the species richness of the pond. The greatest number of plant species cached in food-piles (n = 14) was observed on pond D, which represented the most species rich (n = 62) habitat at this locality. Furthermore, ponds supporting larger or continuous populations throughout the study were associated with a more diverse habitat (chapters 1 and 4) and a greater diversity of plants selected as forage. Water voles are known to select habitat on the basis of its quality (Telfer *et al.*, 2001).

Previous authors have inferred that food availability influences water vole distribution and choice of habitat (Holisova, 1965; Pelikan, 1974; Howes, 1979). Under a low degree of population fragmentation (such as the one that was probably typical of water voles before their decline started) water voles' distribution is mainly determined by three environmental factors: presence of freshwater, adequate food, and cover (Bonesi *et al.*, 2002). Less diverse ponds were associated with a low diversity of species selected as forage, with water vole feeding stations on ponds B, C, E and H containing 5 species or less. Additionally, a significant negative relationship was observed between patch diversity (D_{DVT}) and the number of feeding stations per DVT. Water voles creating feeding stations tended to do so within DVT patches of lower diversity. This observation is consistent with the habitat selection inferred from capture data (chapters 2 to 4); during the breeding season, water voles selected the ponds with the highest diversity (at the habitat level), but typically operated within the least diverse patches within the vegetation mosaic.

5.3.5 Does water vole foraging behaviour influence habitat diversity?

Soft rush (*Juncus effusus*) was the most important component of the water vole diet at NWCW. *Juncus effusus* is densely tufted and can form large patches. It is abundant in Britain, associated with marshes, ditches, bogs, wet meadows, rivers, lakes and damp woodlands, mostly on acid soils (Stace, 1997). *Juncus effusus* is a dominant macrophyte and can rapidly expand to fill a wetland area, however, experimental manipulation reducing shading in tussocks, increases plant species richness and diversity (Ervin & Wetzel, 2002).

Other than *Juncus effusus*, *Typha latifolia* was most frequently cached in feeding stations, representing the second most important forage species for water voles at NWCW. Muskrats (*Ondatra zebithicus*) have been shown to influence plant species richness of American marsh communities, through disturbance of the dominant macrophyte, lesser bulrush (*Typha angustifolia*) allowing non-*Typha* species to establish, through the creation of light openings, addition of nutrients or seed dispersal (Hewitt & Miyanishi, 1997). In marsh habitats, not only can wetland plants establish on the openings around muskrat dens, but after depletion of their forage species (*Typha angustifolia*), muskrats disperse to other areas of the marsh, allowing re-growth of disturbed areas (Weller, 1981).

Experimental studies on the effects of vole herbivory on vegetation indicate that preferred food plants may persist through their capacity to quickly recover during periods of low vole density (Howe, 2008). Mammalian herbivores frequently alter the species composition of plant communities upon which they feed (Huntly, 1991; Olff & Ritchie, 1998). It is plausible that grazing of *Juncus effusus* and *Typha latifolia* by water voles may influence the diversity of these DVTs and indeed shape both the structure and diversity of their wetland plant communities. Plant species richness is related to grazing pressure, but responses to grazing regimes are determined by the nutrient status of the ecosystem; nutrient-poor ecosystems exhibit significantly lower species richness under high grazing than under low grazing, in contrast nutrient-rich ecosystems show significantly higher species richness under high grazing than under low grazing (Proulx & Mazumder, 1998). Indeed, field studies of lemmings (*Lemmus lemmus*) in Norway revealed that the cyanogenic phenotypes of Bird's-foot Trefoil (*Lotus corniculatus)* were more frequent in areas of high lemming densities, suggesting a link between the dynamics of fluctuating rodent populations and changes in the proportions of cyanogenic *Lotus* plants (Compton *et al.*, 1983).

5.3.6 The effects of water vole population density on foraging choices

A greater diversity of plant species were cached in water vole feeding stations on ponds that supported higher female water vole population densities. Female water voles require a diversity of food items to support the energetic demands of reproduction and often augment their diet with various sources of protein during pregnancy (Strachan, 1997). In small mammal populations, demographic rates and food resources are intrinsically linked (Ostfeld, 1985). An increase in the abundance of food may influence demographic rates via increased reproductive success and immigration (Taitt & Krebs, 1981; 1983).

In contrast to female population density, no relationship was observed between the diversity of species selected as forage and male population density per pond. Indeed, due to the exclusion of males from female home ranges (unless receptive), males typically operated in different dominant vegetation types to females at this site. These included the *Typha latifolia* DVT, which had a low patch diversity (D_{DVT}), associated with only 10 other species, the majority of which were aquatic species that did not appear to be dietary components at this locality. Moreover, since males range over a larger area (Stoddart, 1970; Leuze, 1976; Moorhouse & Macdonald 2005; 2008) and during the breeding season may maintain a home range over up to three ponds at NWCW, they are likely to forage in a number of locations as they move over a greater variety of habitats.

Studies of water voles in France have revealed that at a patch-spatial scale (area approximately 1ha) populations may be regulated by primary production (Saucy, 1988, Kopp 1993). However, it is likely that these habitat patches are influenced by farming practices, with a positive correlation observed between the addition of organic nitrogen and the early increase in *Arvicola terrestris* populations in the patches, associated with nitrogen induced primary production of plants (Morilhat *et al.*, 2007). Recent studies of water voles in England revealed that the demography of wild populations of small mammals can be regulated (in part) by a feedback mechanism deriving from the effects of forage availability (and therefore maturation rates), through variation of range sizes (and therefore available forage) in response to population density (Moorhouse *et al.*, 2008).

5.3.7 Why do water voles select particular plant species as forage?

Water voles selected plant species on the basis of their availability and nutritional quality. *Epilobium hirsutum* contained the highest nitrogen content (3 g / 100 g dry plant material) and was an important spring component of the water vole diet at NWCW. *Iris pseudacorus*, a summer component of the water vole diet, contained the highest energy content (kjg^{-1} dry plant material). *Cirsium arvense* was infrequently cached in water vole feeding stations, but had the highest mineral content (9 g / 100 g dry plant material). Carbohydrates make up a large proportion of the dry weight of vascular plants (Wicks *et al.*, 1991). However, caution is advised when inferring nutritional quality of food items from elemental and energetic content of dry plant materials, since significant variations in water content were observed between species. Although *Epilobium hirsutum* had the highest nitrogen content (dry weight), the water content of this species (86%) translates into 14 g of dry plant material per 100 g of wet material i.e. 0.42 g of nitrogen per 100 g of fresh plant material. In contrast the dominant forage species soft rush, *Juncus effusus* had a low nitrogen content (1.5 g per 100 g dry plant material) but also the lowest water content (65%). This equates to 35 g of dry plant material per 100 g of wet material i.e. 0.53 g of nitrogen per 100 g of fresh plant. Thus, a water vole feeding on *Juncus effusus* would attain more nitrogen (gram per gram of fresh plant material) than if feeding on *Epilobium hirsutum*. Previous studies on wetland macrophtyes have revealed that *Juncus effusus* has a higher nitrogen content than *Typha latifolia* (Polisini & Boyd, 1972).

Laboratory studies of captive water voles have revealed that a typical 200 g water vole requires a daily intake of 0.28 gNday^{-1}; however, the nitrogen requirements of reproductive female water voles (and young growing animals) are likely to be considerably higher (Woodall, 1977). Indeed, *Juncus effusus* had significantly more carbon, nitrogen and energy (gram per gram of fresh plant material) than the other three main forage species (*Carex riparia, Epilobium hirsutum* and *Typha latifolia*); however, *Carex riparia* had the highest mineral content. Mineral deficiencies cause a seasonal decline in reproduction in wild mammalian herbivores (Batzli, 1986). Resource limitation is a significant factor in vole population dynamics (Ford & Pitelka, 1984). Feeding experiments have shown that differences in quality of available food in different habitats translate into differences in the demography and density of microtine rodents in these habitats (Cole & Batzli, 1979; Krohne, 1980). Supplemental feeding of microtine rodents results in increased reproduction and survivorship and greater densities than non-supplemented populations Cole & Batzli, 1978; Ford & Pitelka, 1984). The reproductive success and population densities of natural populations of herbivorous mammals are influenced by the nutritional quality of the available food (Cole & Batzli, 1979; Batzli, 1983; Ford & Pitelka, 1984). The nutritional requirements of female mammals increase dramatically during reproduction (Maynard *et al.*, 1979). Reproduction of wild herbivores appears to be timed so that young can be raised in a nutrient rich environment (Batzli, 1986).

Of the four main forage species (*Carex riparia, Epilobium hirsutum, Juncus effusus* and *Typha latifolia*), ***Epilobium hirsutum*** had the highest nitrogen content during the spring. Water voles readily selected this species where available, as soon as fresh growth appeared, however, as the breeding season progressed this species was only infrequently encountered in feeding stations. The main food plant of the beach vole (*Microtus breweri*) is American Marram grass (*Ammophila breviligulata)* the leaves of which are preferred in the spring and early summer when the overall nutritional content (N, P, Mg, Ca) of the blades is high (Goldberg *et al.*, 1980). The potential of a plant species as food must be considered in estimates of animal feeding strategies (Polisini & Boyd, 1972). Many rodents are herbivorous and the plant substrates they consume are rich in cellulose but poor in protein nitrogen (Belov *et al.*, 2002). Taste, odour and physical characteristics of plant tissues are important in determining the diets selected by animal species. Additionally, plant materials may be unpalatable or even toxic to herbivores (Polisini & Boyd, 1972). Optimal foraging theory predicts that herbivores may use two criteria in maximising their nutritional intake when confronted with a range of food resources: minimum digestibility (dependent on plant chemical characteristics) and minimum cropping rate (dependent on the density and mass of plant items) (Belovsky, 1997).

In addition to their nutritional content, the four dominant forage species at NWCW were all widespread, with at least one DVT of the four species occurring on every pond in the area of wetland studied. Furthermore, both the structure of *Juncus effusus* tussocks and the broad-leaves associated with *Carex riparia* and *Typha latifolia* minimise the handling time during foraging, facilitating the creation of water vole feeding stations. Selective foraging of rabbits (*Oryctolagus cuniculus*) reveal preferences for the broader-leaved Perennial Rye-grass, (*Lolium perenne)* are associated with structural nature of the blades, such that broad leaves are easier to select than the intertwined, narrow-leaves of Sheep's Fescue (*Festuca ovina)* (Iason *et al.*, 2002).

5.3.8 Does water vole population density influence latrine density?

No apparent relationship between water vole population density and (above ground) latrine density was observed at NWCW. This contrasts with previous studies where estimates have varied between six latrines per territory holding female (Woodroffe *et al.*, 1990) to later estimates of one latrine per water vole (Morris *et al.*, 1998). Caution is advised when inferring water vole population densities from latrine counts, since numerous activities occur in underground burrow systems (Strachan & Jefferies, 1993). It is likely that the underground portion of the home range is also defended by females, however, our inability to observe latrine creation underground limits our understanding of this aspect of water vole ecology. Morris *et al.* (1998) suggests that the one to one relationship between water voles and latrines may not be applicable to habitats with larger populations. Moreover, this relationship may not be applicable to water vole populations that appear to exhibit cyclic periodicity, such as the population studied here.

Although latrine density did not correspond with population density, the number of faecal pellets per latrine was a function of female water vole densities; habitats supporting a higher density of females had significantly more faecal pellets per latrine than on habitats associated with lower female densities. The boundaries of water vole territories are often actively mediated by overt aggression (Leuze, 1976) and passive exclusion via creation of latrines (Stoddart, 1970, Woodroffe *et al.*, 1990). Many vertebrate species mark their territories with excretory products such as urine or faeces, which can modify behavioural and physiological functions among individuals of the same population (Brown 1979). As female densities increase, the need for communication between females is increased, particularly in a species such as the water vole, known to be highly territorial (Stoddart, 1970; Leuze, 1976; Moorhouse & Macdonald, 2005). Furthermore, seasonal effects were observed, with spring latrines containing a greater number of faecal pellets than latrines maintained in summer or autumn. This was associated with the establishment of territories by females at the onset of the breeding season (Stoddart, 1970; Strachan & Moorhouse, 2006).

5.3.9 Does habitat diversity (D_{pond}) influence latrine density?

Biodiversity and ecological functions in terrestrial ecosystems are closely linked (Hooper *et al.* 2005). More diverse habitats were characterised as valuable resources, associated with a higher latrine density than more homogenous habitats. Pond D represented diverse optimal water vole habitat at NWCW, associated with the highest latrine density and the highest mean population density over the duration of the study (chapter 2). During the latter part of the study, the population was in the low density phase. Concomitantly, development of a road adjacent to the site (methodology figure 1 and chapter 6) resulted in the loss of swathes of vegetation in the vicinity of pond D and a subsequent displacement of numerous water voles that moved through this area in search of suitable habitats. In response to this influx, water voles that were resident on pond D when construction began had to constantly reinforce their range boundaries and consequently numerous additional water vole latrines were created. In view of this, the number of latrines on pond D may not be a true reflection of water vole behaviour in undisturbed habitats and thus pond D was removed from the regression analyses. With the exception of pond D, ponds with the highest habitat diversity (D_{pond}) had a higher latrine density. Territoriality of females comprises defence of habitat related resources (Moorhouse & Macdonald, 2005). In this instance, diversity at the habitat level is a defendable resource. In contrast, no relationship was observed between patch diversity (D_{DVT}) and latrine density.

5.3.10 Water vole latrines and Dominant Vegetation Types (DVT)

The DVTs dominated by the four main forage species (*Carex riparia, Epilobium hirsutum, Juncus effusus* and *Typha latifolia*) were also associated with the highest density of latrines. All of the DVTs in which latrines were created were also associated with the creation of feeding stations (section 5.3.3). However, latrines were only created in seven dominant vegetation types (DVT), in particular the *Je*DVT. The importance of this species to water voles has been demonstrated throughout this study. However, the broad expanses of *Juncus effusus* across site, equate to only one latrine per 50 m² of *Je*DVT. The highest density of latrines was observed in the *Cl*DVT with one latrine per 4 m². This result should be treated with caution, since this species only occurred in one small localised patch (pond A; figure 1.1). Nevertheless, it was considered a defendable resource, utilised by water voles as a food source and incorporated into the home range of numerous adult females that operated within the vicinity.

The *Rf*DVT was incorporated into the home range of numerous adult water voles throughout the year and represented an integral component of the habitat at

NWCW (chapter 4). This species was not regularly used as a source of food, however, represented a defendable resource and was used for the creation of latrines. *Rubus fruticosus* has also been shown to be of importance to bank voles (Flowerdew & Ellwood, 2001). The structural nature of the *Rf*DVT and the protective spines associated with this species provided a safe environs for the water vole in which to take refuge. However, the structure of *Rubus fruticosus* also impaired surveying (under large patches of this species) and it is possible that the number of field signs located in the *Rf*DVT were underestimated.

5.3.11 Do water vole latrines contribute to the nutrient status of wetland soils?

The mean nitrogen content of faecal pellets was 2.18 mg per fresh pellet. This is equivalent to approximately 0.5 gN per 200 pellets, deposited by the average water vole per day (Woodall, 1977) or 17.88 kg of nitrogen deposited by a pre-breeding population of 41,000 water voles in Wales to their wetland habitats per day (Harris *et al.*, 1995). Mammals can influence plant communities through addition of available nutrients in their waste (Hewitt & Miyanishi, 1997; Belov *et al.*, 2002). No significant differences were observed in nitrogen content of pellets collected from various sources (adult males and females, juveniles and latrines) although it is likely that the water voles that produced the pellets had varying diets. Woodall (1977), found that even on varying diets, the nitrogen content of water vole faecal pellets remained fairly constant, and any excess nitrogen ingested was excreted as urine. It was inappropriate to collect urine from animals in this study, due to the nature of the habitat and therefore it was impossible to quantify the effects of water vole urinary products on their environment in this study.

Soil sampling revealed that historic latrine soils had more ammonium and less phosphate than soils that were never associated with the creation of latrines, however, the differences were not significant. It is likely the small sample size affected the results and further studies are required to determine the influence that water voles may have on their environment through the creation of latrines. Furthermore, it is likely that rain washes soluble nitrogen from the droppings (Bazely & Jefferies, 1985).

Voles in grasslands redistribute nutrients at a very fine scale, returning small amounts to many plants, in contrast to cattle, which create a few very rich patches and remove nutrients from most of the vegetation (Bakker, 2003). Scent marking behaviour of river otters (*Lutra canadensis*) fertilises terrestrial vegetation on the shore line, resulting in elevated levels of nitrogen in grasses and mosses at latrine sites (Ben-David *et al.*, 1998). Previous studies on nitrogen transformation in soils, revealed that microtine rodents influenced processes of the nitrogen cycle in the soil of their colonies, particularly on runways, where excrement of animals and residues of plant food were always present (Belov *et al.*, 2002).

A major consequence of grazing, is that plant tissue, rather than accumulating as live biomass or litter, is converted into herbivore biomass or faeces (Bazely & Jefferies, 1985). Previous studies of lesser snow geese (*Chen caerulescens caerulescens*) grazing on graminoid salt marsh species, have revealed that their grazing activities induce a positive feedback on the ecosystem, with grazed shoots containing significantly more total nitrogen content than ungrazed swards (Cargill & Jefferies, 1984). The addition of mobile nitrogen from faeces results in enhanced growth of the graminoid species and better quality (high N) forage, sufficient to enhance production of the birds' preferred forage species in a nitrogen-deficient environment (Bazely & Jefferies, 1985).

Soil organic matter and nitrogen are not only the important components of wetland soils, but also the ecological factors of the wetland ecosystem that greatly influence its productivity (Mitsch & Gosselink, 2000). Nitrogen is often the most limited nutrient in flooded soils (Downing *et al.*, 1999). Nitrates (NO_3^-) are not easily adsorbed by soil particles with negative charges and are easily leached in soil profiles (Bai *et al.*, 2005). In addition to leaching, nitrogen loss from wetland soils is caused by plant uptake, immobilisation, denitrification and ammonia volatilisation (Delaune *et al.*, 1998). The growth characteristics of wetland macro-plants are greatly influenced by nutrient retention in wetland soils (Stefan *et al.*, 1994). River otters transfer marine-derived nitrogen (from foraging behaviour) into the terrestrial vegetation in coastal forests, through the creation of spraint sites (latrines), fertilising the terrestrial vegetation in the terrestrial marine-interface (Ben-David *et al.*, 1998). Nitrogen-containing excretory products of voles have been shown to reduce nitrogen fixation but increase denitrification as they accumulate in the soils of vole colonies (Belov *et al.*, 2002). By the production of faeces alone, vertebrate herbivores greatly impact on both above- and belowground components of tundra ecosystems and in doing so manipulate their own food supply (van der Wal *et al.*, 2002).

It should be noted that soil analysis may only provide a crude estimate of nutrient loading to a wetland ecosystem inhabited by water voles. There are numerous interacting processes that contribute to the nitrogen cycle and one important component that may be overlooked is the activity of soil bacteria. Any nitrates or ammonium released from faecal pellets (in a wild situation) may be immediately sequestered and assimilated and therefore will be undetectable. Results should be treated with caution since bacteria may act in a matter of hours or days, sequestering N from the soil pool and making it immeasurable by the means described here. Despite the basic nature of this analysis, it provides a first step towards quantifying the effects of water vole behaviour on the nutrient cycles of their wetland habitats.

5.3.12 Water vole runways and burrows modify the wetland landscape

Water voles were observed to create numerous branching runways throughout the bankside vegetation, leading to latrine sites and food caches (Strachan & Moorhouse 2006). During years of peak population density, microtine rodents in grasslands can destroy as much as 20% of the vegetation in the act of runway construction (Ford & Pitelka, 1984). In addition to the deposition of faecal matter, burrowing rodents can influence the physical properties, microtopography and plant cover of disturbed soils (Grant & McBrayer, 1981; Huntly & Inouye, 1988). Indeed, burrowing pocket gophers (*Geomys bursarius*) are agents in soil formation, estimated to deposit at least 8000 tonnes at the soil surface per year in Yosemite National Park (Grinnell, 1923). By creating a mosaic of soil patches of varying successional age, gopher mounds potentially increase plant diversity, allowing different plant species to co-exist (Hobbs & Hobbs, 1987).

It is plausible that the diversity of habitats that have established at NWCW (over the eight years since it was created) have in part been influenced by the water vole populations that those habitats support. Indeed, it is interesting to speculate that the relationship observed between water vole population density and habitat diversity (chapter 4) may not be the result of water voles selecting higher quality habitat (Telfer *et al.*, 2001). Rather, the influence of high densities of water voles may indeed shape the diversity of the habitats in which they reside, through behaviours that are known to influence plant species richness and diversity (foraging, defecating and burrowing) (Grant & McBrayer, 1981; Hobbs & Hobbs, 1987; Huntly & Inouye, 1988; Ben-David *et al.*, 1998).

5.3.13 Rationale underpinning the 5 m boundary line on ponds

Of the 294 feeding stations encountered during thorough field surveys (2008 to 2009), the mean distance from the water was 18.93 ± 1.83 cm and the maximum was 3m. Of the 108 latrines observed during this time, the mean distance of a latrine from the waters edge was 24.03 ± 3.82 cm and the maximum was 3 m. Runways through vegetation were evident around the perimeter of all ponds at a distance of approximately 1m from the waters edge. Pond E provided an increased area available for the creation of feeding stations and latrines during drier summers, when numerous burrows and networks of runways were created throughout the dense layer of moss associated with the *Typha latifolia* that dominated this pond. Due to the sensitivity of the habitat it is likely that the number of feeding stations and latrines may have been under-estimated, since surveying was restricted to the periphery of the pond. However, in wetter seasons these extensive runways are flooded out and vital areas of habitat are lost, leading to a temporal extinction of the water vole population in this area, until recolonisation occurred the following year (chapter 4). Excavated tumulus (soil) from the creation of burrows was evident up to 5 m away from the waters edge on some ponds. A boundary line around each pond was therefore delineated at 5 m (figure 1.1), encompassing all DVTs implemented by water voles in the creation of these conspicuous field signs, evident of their choices of habitat selection and utilisation.

Summary

- 23 plant species and 3 non-plant species (amphibians and molluscs) were utilised as a food source by water voles at NWCW
- Soft rush (*Juncus effusus)* was the plant species most frequently cached in water vole feeding stations
- Greater Pond-Sedge (*Carex riparia*) Bulrush (*Typha latifolia)* and Great Willowherb (*Epilobium hirsutum)* were also important dietary components
- Feeding stations were created in 11 dominant vegetation types (DVT)
- The DVTs dominated by the four main forage species were associated with the most number of feeding stations
- In addition to the dominant species, 5 associate species were foraged upon in the *Je*DVT
- The greater the species richness of the habitat, the greater the richness of plant species cached in feeding stations
- Higher female densities were associated with a greater diversity of plant species cached in feeding stations
- A negative relationship was observed between patch diversity (D_{DVT}) and the number of feeding stations; water voles foraged in the least diverse patches
- Due to the low water content of the plant tissues, fresh *Juncus effusus* contained significantly more carbon, nitrogen and energy content than the other 3 main forage species
- Fresh *Carex riparia* had significantly more minerals than the other 3 main forage species
- Water voles produce significant amounts of nitrogen containing faeces
- Water vole population density did not correlate with latrine density however did influence the number of faecal pellets per latrine
- Latrines were created in 7 DVTs
- No significant differences in nutrient concentrations were observed between historic latrine soils and control soils

Chapter 6

Habitat Management

'A little knowledge that acts is worth infinitely more
than much knowledge that is idle'
Kahlil Gibran (The Prophet, 1923)

6.1 Introduction

Management of water vole habitats

In managing flood risks, many watercourses have been modified in the past to improve their capacity to store and carry flood water. Waterway channel, bankside, water level and vegetation management all have consequences for water voles (Strachan & Moorhouse, 2006). With the current plight of the water vole highlighted and recent legal inclusions enforcing protection to this species, habitats, typically, are managed sympathetically. Additionally, numerous projects are being undertaken nationwide to ensure habitat enhancement and restoration (Kennet and Avon Canal), wetland pond creation and management (River Don, Doncaster), restoration of flows to dry water courses (River Ver, Hertfordshire) and ditch management in the uplands (Peak District) (Strachan & Moorhouse, 2006).

Numerous reintroduction programmes are being undertaken on English river systems and the release cohorts monitored (Moorhouse *et al.*, 2008; 2009). Habitat management at NWCW usually involves tree or scrub clearance across site and routine cutting of *Typha latifolia*. Management of *Typha* in order to retain areas of open water is necessary, since this species can spread aggressively, causing ponds to dry out (Cronk & Fennessy, 2002).

Water voles and predators

Potential native predators on this study site included; brown rats (*Rattus norvegicus*), red foxes (*Vulpes vulpes)*, Eurasian otters (*Lutra lutra*), weasels (*Mustela nivalis*), grey herons (*Ardea cinerea)* and barn owls (*Tyto alba)*; their presence confirmed by sightings (rat, fox, weasel, heron and barn owl) or observation of field signs (otters) (pers. obs.). Otters in South Wales typically feed on small bottom dwelling fish such as blennies (Parry, 2010) and on site observation of otter spraints indicated that the majority of otters at NWCW were foraging offshore, upon coastal estuarine fish (Forman, pers. comm.) Water vole predation by barn owls has been shown to be significant in areas where vegetation has been extensively cleared (Howes, 1979) and although certain ponds were once subject to wide scale vegetation clearance (see section 6.2), no evidence of barn owl pellets was found in this area and thus the effects of clearance upon barn owl predation rates were immeasurable. Predation of water voles by red foxes and grey herons has already been previously investigated at NWCW, with water voles contributing significantly to the diet of both these British predators in this locality, particularly during the winter (Forman, 2005).

After consideration it was deemed appropriate to monitor the effects of rat predation on water voles, since this area of water vole ecology has received little attention in the past (particularly in a wild situation), and knowledge of this process may contribute significantly to increasing the distribution and persistence of water vole populations in the future. As well as possibly preying on water vole pups, rats may be aggressive intraguild competitors of adult water voles, in which case they may displace water voles from an area (Barreto & MacDonald, 1999). Since rats that were captured were not individually marked, densities of rats could not be directly estimated; however, crude numbers and distribution of rats were inferred from capture data (appendix 9).

Water voles at this study site did not appear constrained by mink predation (one spraint and one unconfirmed observation in four years) and since the effects of mink predation have been previously demonstrated by numerous authors (Woodroffe *et al.*, 1990; Strachan & Jefferies, 1993; Barreto *et al.*, 1998; Aars *et al.*, 2001; Strachan & Moorhouse, 2006), this aspect of water vole ecology was not explored further in this study.

Monitoring and condition indicators

Reliable monitoring projects require a clear focus (Hurford, 2010). The need for an evidence-based framework to evaluate effectiveness and support decision making in conservation has been previously highlighted (Pullin & Knight, 2001; Fazey *et al.*, 2004; Sutherland *et al.*, 2004). Site-specific condition indicators describe the suite of attributes and targets used as evidence for the condition of the habitat (or species). Furthermore they allow recognition of when the key habitat is in a state of high conservation value and should be applied at the management unit level (Hurford, 2010).

Rationale

Although the effects of development and vegetation clearance on water vole habitats were not the initial focus of this study, populations on three of the eight ponds were affected by management or development throughout the duration of this study. This chapter does not present data *per se*, rather a description of the outcome of the management techniques employed and recommendations for future monitoring and management. Unfortunately in both instances there were obvious negative effects on the resident water vole populations, associated with reduction or total loss of water voles from the area affected. Nevertheless, long term observation of populations through live trapping and surveying allowed the effects of these processes to be monitored and in turn the ability to advise best practice, if such events were to occur.

Aims

1. To describe the effects of large scale habitat development on adjacent water vole populations
2. To describe the effects of vegetation clearance on resident water voles
3. To discuss the influx of rats associated with widespread vegetation clearance
4. To describe the effects of rats on water voles
5. To monitor the time taken for the habitat to recover from clearance
6. To monitor the time taken for water voles to recolonise disturbed habitats
7. To provide a site-specific condition indicator table
8. To outline recommendations for the creation and management of optimal water vole habitats at NWCW
9. To provide guidelines outlining how to undertake vegetation clearance in water vole habitats
10. To discuss the necessity for sensitive and holistic habitat management

6.2. Results

6.2.1 Observations of the effects of large scale habitat development

Commencing in September 2007 and throughout the duration of 2008, development of a new road (B4304) outside the wetland complex, but adjacent to pond D (approx 50m; methodology figure 1), caused a disturbance to the resident water vole population. Numerous resident water voles were observed to displace (their fates are unknown). Furthermore, numerous water voles temporarily dispersed into the population before displacing again. During this time additional latrines were created, as resident animals strove to reinforce home range boundaries (chapter 5). Although 2008 was characterised by low water vole densities across the wetland complex (chapter 2), only two water voles were encountered on pond D during 2008. These individuals were only captured during March and did not establish a home range in this area.

Throughout the development process a section of the *Je*DVT on the north bank of pond D was lost, however, another pond was created (figure 1.1). Although this new pond is now entirely vegetated (January, 2011), the species present are not optimal for water voles and the pond is in close proximity to the road. The heavy machinery implemented in the creation caused vibrations in the soil which was amplified down the water vole burrows. Since completion, the road continues to receive a high density of traffic (particularly lorries) which again causes a certain degree of disturbance in terms of noise and vibrations. Two female water voles were encountered on pond D during 2009, one of which was a transient animal (chapter 4) and the other a resident who maintained a home range for at least two months (chapter 5) along the NE reaches of pond D across to the NW reaches of pond B. No animals had re-established home ranges on the mid to southerly reaches of this pond after completion of the development (chapter 5) until trapping ceased in July 2009. However, pond D still supported the highest mean water vole population density, due to the high densities observed during the peak phase, prior to development.

6.2.2 Observation of the effects of widespread vegetation removal

During October 2007, a routine clearance of *Typha latifolia* was undertaken on two of the ponds (G and H) in the area of the wetland studied. Water vole populations on these two ponds were impacted by this large scale vegetation clearance that, in addition to habitat loss and fragmentation, resulted in an influx of rats into the disturbed habitat. Pond G was the most diverse pond in the area of the wetland studied (chapter 1) and connected to pond H via large swathes of vegetation (mainly *Juncus effusus*). In addition to its importance as a food source (chapter 5) the *Je*DVT provided protection and connectivity, allowing juveniles to disperse (chapters 2 and 4) and adults to move within and between areas of both ponds in relative safety (chapter 3).

Since the NWCW was created (2001) the site has undergone natural succession and many ponds appeared to be 'overcrowded' with tall vegetation including *Typha latifolia*. While the structure of such a system can provide suitable environs for the water vole (Lawton & Woodrofe, 1991; Carter & Bright, 2003) it greatly reduces the amount of open water available to dragonflies and management determined that the ponds required opening up. This management technique was implemented with the help of a team of local (c. 20) volunteers. Patches of riparian vegetation were removed from two areas on pond G (either side of the eastern footbridge) (figures 6.1 and 6.2) and from pond H (figure 6.3), together with a large swathe of vegetation between the two ponds to provide access for volunteers (figure 6.4).

6.2.3 Observations of the effects of the loss of water vole habitat

On pond G, patches of *Eh*DVT and *Je*DVT were removed from the bankside. This allowed volunteers access to the centre of the pond in order to cut down *Typha latifolia*. The cut area visible in the centre of the pond (figure 6.2) was a *Gf*DVT, with *Typha latifolia* growing as a community associate. Cut *Typha* was piled up on the far bank, creating further disturbance to the water vole habitat by breaking up the continuous bankside cover, allowing easy access to predators. All aquatic vegetation in the far eastern reaches of pond G was cut down, as an attempt to remove the *T. latifolia*, despite this species only growing as a DVT associate (with *Ep*DVT, *St*DVT *Gf*DVT and *Rl*DVT) and not a dominant in this area (figure 1.1). The *Je*DVT between ponds G and H, continuous with that on the north bank of pond H, was also cut down to provide access to the pond. *Typha latifolia* was cut down in the eastern reaches of pond H and piled up in the adjacent wooded area (tree DVT) (figure 1.1).

Figure 6.1 Pond G (eastern reaches; traps G11 and G12) immediately after vegetation clearance. (Image taken October 2007)

Figure 6.2 Pond G (eastern reaches; traps G9, 10, 13 & 14) immediately after vegetation clearance. (Image taken October 2007)

Figure 6.3 Pond H (north bank) immediately after vegetation clearance. (Image taken October 2007)

Figure 6.4 A path cut through the centre of the *Juncus effusus* DVT (between ponds G and H) allowed volunteers to access the north bank of pond H. (Image taken October 2007)

6.2.4 Short and long term effects of vegetation clearance

Vegetation clearance compromised the quality of the habitat for the resident water vole population through trampling of inter habitat areas and removal of large swathes of riparian vegetation which previously provided both food (chapter 5) and cover and an important corridor for both dispersal (chapters 2 and 4) and maintenance of home ranges (chapter 3). Optimal habitat (chapter 1) (May 2007) was replaced by a suboptimal habitat (figures 6.1 to 6.4), which was rapidly colonised by rats. This had an immediate effect on the water vole population, resulting in a substantial loss of resident water vole activity. All female water voles and the majority of males were displaced. A number of rats were trapped within the site (previously not active there) and a large increase in rat field signs including droppings and food caches were evident. Water voles that have been trapped since the clearance were severely wounded from rat encounters with large bites seen on atypical areas and portions of tail missing. Additionally, the remains of a water vole (and a grass snake) were cached in a rat feeding station, in an open trap. Although the density of rats was not determined (since they were not marked), 5 different rats were captured in one day in this area immediately following clearance, with rats captured on 12 occasions in total (see appendix 9). Moreover, the rats continued to operate in this locality up to 8 months after the vegetation clearance. The water voles that were captured during the following breeding season (2008) were also atypically wounded, after which they immediately displaced. No water voles were encountered in this area between July 2008 and May 2009, until a male and female established a home range in this area (table 6.1). Their fates are unknown since trapping ceased in July 2009.

Table 6.1 Number of adult water voles that were captured and that maintained a home range (resident) on ponds G and H before and after large scale vegetation clearance

		Prior to clearance (2007)	1 year after clearance (2008)	2 years after clearance (2009)
Males	Number captured	11	3	2
	Number resident	3	1	1
Females	Number captured	13	2	5
	Number resident	3	0	1

In addition to the effects of rats and the predation risk associated with loss of cover, large scale vegetation clearance can impact water vole populations by reducing the diversity and abundance of dominant vegetation types (DVT). Consequently this reduces the habitat diversity (D_{pond}) which is a function of the species richness and abundance of DVT patches (chapter 1). Prior to clearance pond G consisted of 40 DVT patches, which consisted of 13 different dominant vegetation types, and contained the highest habitat diversity ($D_{pond} = 2.67$) of all the ponds studied across the wetland (table 6.2). Immediately after clearance, removal of patches resulted in a reduction in both the number and type of DVT patches. Two years following clearance, although the vegetation has recovered structurally (figure 6.5) and provides a source of cover and food (chapters 4 and 5) for water voles, the integrity of the habitat has been compromised. During 2009 the overall diversity remained lower than it was prior to clearance, with pond G consisting of 36 DVT patches, comprised of 12 different dominant vegetation types, and a reduced habitat diversity ($D_{pond} = 2.24$) (table 6.2).

Table 6.2 The effects of vegetation clearance on the number of different dominant vegetation types (DVT) and DVT patches and the habitat diversity (D_{pond}) of pond G

Habitat status	Number of different DVTs	Number of DVT patches	Habitat diversity (D_{pond})
Prior to clearance	13	40	2.67
Immediately after clearance	11	33	2.16
2 years after clearance	12	36	2.24

Figure 6.5 Pond G (eastern reaches). *Typha latifolia* DVT plus open water replaced the *Glyceria fluitans* DVT and the *Ranunculus lingua* DVT that were present prior to clearance. (Image taken June 2009)

6.2.5 Condition Indicators for the water vole habitat at NWCW

The following Condition Indicator Table (table 6.3) describes the conditions under which the water vole habitat at NWCW is considered to be in a favourable condition for water voles and is based on data collected from eight ponds over four years at this National Key Site.

Table 6.3 Condition Indicator Table for the water vole habitat at the National Wetland Centre Wales (modified from Neyland *et al.*, 2010)

Basic vegetation components of water vole habitat	**Water vole habitat in the NWCW will be in a favourable condition when**	
	Lower limit	**In each pond**
Water body		Circumference > 100 m, with convoluted edges and steep banks or islands
Vegetation cover		>5% of the total pond area is open water with or without submerged macrophytes (e.g. *Potomageton natans*) At least 95% of the bankside is vegetated (no more than 5% bare ground or mud)
Vegetation type		>50% of the pond edge vegetation should be dominated by *Juncus effusus* and >5% of *Typha latifolia* – with at least one DVT present of *Epilobium hirsutum* (>3.5% of the pond edge) and one DVT of *Carex riparia* (>5% of the pond edge) or one DVT of *Rubus fruticosus* (3.5 to10% of the pond edge) Where *Rubus fruticosus* occurs it should not be cleared below a level of <3.5% of the pond edge
Habitat diversity		At least 10 different DVT types and 20 different DVT patches across the water body and pond edge
Proximity of nearby ponds		At least one more pond present no further than 50 m away and connected with suitable habitat corridors (e.g. DVTs that provide cover for dispersing water voles)
Site-specific definitions		
Pond edge		Area of habitat within 5 m of open water with or without submerged macrophytes (e.g. *Potomageton natans*) or with emergent vegetation (e.g. *Juncus effusus, Typha latifolia, Carex riparia, Eleocharis palustris, Iris pseudacorus, Bolboschoenus maritimus)*
DVT		Dominant Vegetation Type – Homogenous stands of vegetation labelled according to the dominant plant species

6.2.6 Recommendations for creation and management of water vole habitats

The following table (table 6.4) highlights habitat components of significant importance that should be considered when managing or creating water vole habitats at NWCW.

Table 6.4 Habitat components of significant importance to be considered when creating or managing water vole habitat at NWCW

Habitat components	**When creating or managing water vole habitat at the National Wetland Centre Wales (NWCW) the following factors are of significant importance**
Available pond edge	Increase the amount of available pond edge by providing convoluting 'fingers' of land that jut out into the water body and / or bunds of earth around the bankside that provide a three-dimensional area in which burrows can be created. Alternatively islands can be created within the existing water body (Carter & Bright, 2000).
Bank angle	Steeper banks are more suitable than shallow ones as the latter are more prone to flooding (Lawton & Woodroffe, 1991; Carter & Bright, 2000) and the former allow a larger population to exist along a given circumference of water body.
Pond system structure	A series of small interconnected ponds can sustain a larger population than one large pond, provided there are suitable habitat corridors (above or below ground) between water bodies to allow the dispersal of individuals (Strachan & Moorhouse, 2006).
Bankside vegetation	Ensure that the habitat has dense and diverse bankside vegetation that will persist throughout the winter months. See condition indicator table for the basic habitat components, together with a variety of seasonal associates that add diversity to the diet.
Breeding requirements	Rushes and sedges are the dietary staples, but flowering species (e.g. *Epilobium hirsutum*) are important seasonal associates. *Juncus effusus* is the most important forage species at this site, utilised as nesting material as well as food and cover.
Habitat corridors	Linking up of occupied areas to previously occupied areas is essential if populations are to persist and will allow new water vole populations to establish. These are highly fecund rodents with the potential to reproduce rapidly. If corridors are provided to new suitable areas then water voles will expand their occupancy accordingly (Telfer *et al.*, 2001, 2003)
Clearance	Remove young trees as these are negatively associated with water voles and once established drive the succession of the wetlands, removing important water vole habitat. Widespread clearance of woody species or scrub vegetation along bankside habitat can lead to an encroachment of predatory species including rats, reducing the chances of persistence of the water vole population (see table 6.5).

6.2.7 Recommendations for vegetation clearance in water vole habitats

The following table (table 6.5) highlights factors of significant importance that should be considered when undertaking vegetation clearance in water vole habitats at NWCW.

Table 6.5 Factors to be taken into consideration when undertaking vegetation clearance in water vole habitats at NWCW

Factors	**When managing water vole habitat at the National Wetland Centre Wales (NWCW) the following factors are of significant importance**
Bramble, *Rubus fruticosus*	Control but do not remove completely. This species provides important protection from predators particularly during the winter. Brambles can be pruned sympathetically in Spring and Autumn, avoiding the breeding season.
Patch-based management	Focus on areas of habitat 10 m^2 or less at a time. Stagger areas over time to allow the habitat to respond to the clearance.
Seasonality	During the breeding season water voles may be underground in burrows raising litters. Never disturb breeding females (look for burrows with 'plugged up' entrances) and undertake the necessary clearance during the winter (unless the clearance involves removal of bramble).
Continuity and Connectivity	Do not create gaps in bankside vegetation. Water voles are exposed when crossing open areas which may be created within their range, leaving them vulnerable to aerial predators such as birds as well as terrestrial predators including otters, polecats, mink and rats.
Disturbance	Minimise disturbance by always entering and leaving the pond by the same path, otherwise numerous gaps will be created in the bankside which will break up the home ranges of all animals on the pond. This will force them to forage in sub-optimal areas with at least some degree of cover that may decrease their chances of predation but will compromise their breeding success.
Trampling	Minimise trampling by using no more than two people per pond, spread volunteers out across the site. A major factor in loss of populations is due to overgrazing of bankside vegetation and the crushing of burrows underfoot by cattle; humans are likely to crush burrows too, particularly in large numbers.
Sympathetic management for multiple species	Think holistically and consider other species. For example moorhens may be nesting in the Bulrushes or grass snakes may be hibernating. Different species are sensitive at different times of the year.

6.3 Discussion

6.3.1 The effects of large scale habitat development

Although water voles have recolonised pond D at the close of field work (2009), the creation and subsequent use of the road has had a negative impact on the water vole metapopulation at NWCW, since this pond represents the most heterogeneous, species rich habitat of all the ponds studied here and was home to high densities of water voles at the start of the study. Furthermore, the female otter that regularly foraged in this area was unfortunately killed attempting to cross the road during 2008. Development of large scale projects so close to vulnerable habitats has severe consequences for all resident wildlife. Although there is no evidence that any water voles were actually harmed or killed during this process, the long term effects are still obvious. Mitigation in the form of pond creation will only have a chance of success if the correct vegetation is encouraged in the new habitats, however, proximity of the new pond to the road may preclude it from ever being an optimal habitat again.

6.3.2 Vegetation clearance: Recovery of disturbed habitats

Two years after large scale vegetation clearance (2009), secondary succession allowed the vegetation in all areas to recover structurally. At the time of writing (2011) bankside vegetation and inter-pond areas were continually vegetated, thereby reducing the predation risk associated with open areas (Carter & Bright, 2003). However, the integrity of both ponds has been compromised, with pond G experiencing a shift in DVT arrangement, together with a loss of numerous DVTs including the *St*DVT, the *Ep*DVT and the *Gf*DVT. Furthermore, the reduced number of DVTs leads to a reduced habitat diversity (D_{pond}), which also has negative consequences for water vole populations, in particularly female water vole densities which correspond positively with habitat diversity at this site (chapter 4). Moreover, the *Typha latifolia* that was growing only as an associate species prior to clearance is now a dominant vegetation type (figure 6.5 and 6.6), suggesting that the clearance was unsuccessful in the long term.

Dominant homogeneous patches are likely to encroach further and accelerate the process of succession through the drying up of ponds and subsequent encroachment by trees (Morin, 1999; Cronk & Fennessey, 2006), thus exacerbating the situation. Habitat destruction or patch removal reduces the number and proportion of patches occupied by the superior competitor, but can result in an increase in the number of patches occupied by the inferior competitor (Nee & May, 1992). On pond H, unsympathetic habitat management in the form of removal of the superior competitors, *Typha latifolia* (pond) and *Juncus effusus* (bankside) resulted in an empty patch that was quickly recolonised by the inferior competitor, *Glyceria maxima*, previously restricted to one small patch (approximately 57m^2). Recolonisation by *Glyceria maxima* filled the vacant patch (approximately 30m^2), resulting in a continuous bankside cover, however, this species was only associated with transient capture events and was never incorporated into the home ranges of resident adult water voles (chapter 4). Although pond H gained a new patch of *Glyceria maxima*, ultimately increasing habitat diversity (D_{pond}) due to increased number of DVT patches, the replacement of an area of *Je*DVT with a patch of *Glyceria maxima* has negative consequences for water voles. In contrast *Typha latifolia* and *Juncus effusus* were both important plant types for males and females respectively (chapter 6). Effectively, the quality of the habitat for water voles was reduced, even if the structure of the vegetation appeared to be restored.

6.3.3 Vegetation clearance: Recovery of water vole populations

Water voles have since recolonised ponds G and H, however, only in low numbers and the far eastern reaches of pond G are still devoid of resident water voles (chapter 2). It is not necessary to destroy all patches to extinguish a metapopulation that persists by virtue of a balance between local extinctions and recolonisations in a mosaic environment (Lande, 1987). Fortunately, at NWCW the large number of neighbouring habitats and vegetated corridors connecting ponds allowed recolonisation of ponds G and H by water voles. Nevertheless, it took almost two years before an adult female was recaptured on the eastern reaches of pond G; even then she failed to establish a territory in this area and either dispersed or was predated upon.

Macro-habitat integrity is essential for vole abundance. When interpreting a landscape, managers must consider changes in patches at high resolution to predict population-level impacts of management on voles. Alteration of macro-habitat is likely to alter population structure, even if dispersal allows colonisation of disturbed habitat (Orrock *et al.*, 2000). Landscape effects include decreased fitness due to increased costs of foraging both in time and increased predation risk (Morris, 1987).

The importance of vegetative cover to microtine populations has been previously demonstrated, since all voles living in low cover habitat are highly vulnerable to predation. There is a threshold level of vegetative cover necessary for a microtine population to increase in numbers sufficiently to under go a multi-annual cycle (Birney *et al*, 1976) such as the one observed at NWCW (chapter 4). Levels of cover above this threshold may influence the amplitude, duration and synchrony of microtine cycles, however, it should be noted that cover is only one index of the environment in which voles live and it is what cover provides, not cover alone that is important (Birney *et al*, 1976). Indeed, the degree of cover can influence social behaviour. Fighting and mortality of crowded captive meadow voles (*Microtus pennsylvanicus)* increases in the absence of cover (Warnock, 1965) since individuals are more likely to make contact when cover is less dense (Krebs *et al.*, 1971).

6.3.4 The effect of rats on water voles

The results of this study reveal that rats can influence the distribution of water voles. The two ponds supporting the highest water vole densities (ponds A and D) were not associated with rats (according to capture and field survey data), whereas ponds with rats present had lower vole densities (ponds B, C and E). During trapping sessions when rats were encountered, water voles were typically absent. Ponds G and H suffered an influx of rats after vegetation clearance, and a number of male water voles received serious injuries associated with direct rat predation. Female water voles on the affected ponds were completely displaced after vegetation clearance and rat colonisation (although it is not known which of these factors led to their displacement; it is likely to be a combination of both). Mortality in water voles is highly variable but is typified by high juvenile mortality (Macdonald *et al.*, 1997). It is important to know the relative importance of different population regulating mechanisms (Oksanen & Schneider, 1995). Predators can have profound effects on prey populations and predation has been suggested as a proximate factor threatening the survival of many endangered species (Schneider, 2000). Grazers are typically regulated by predation, with grazer communities being structured by apparent competition (Holt, 1977).

Rats tend to have distributions that are sympatric with water voles and may have a greater negative impact on water vole populations than was previously thought. In Britain, water voles were not in contact with brown rats until the 18th century, when the latter arrived (Barreto & Macdonald, 1999). These versatile animals typically occur along hedgerows, fields and semi-urban or urban areas, and concentrate their movements near food sources such as barns or other farm buildings (Macdonald & Fenn, 1995). During cage experiments where the odours of predators were simulated, water voles were observed to actively avoid the smell of rats, perceiving the smell as a threat (Barreto & Macdonald, 1999). In the past, water voles have been observed to avoid rats that have colonised their habitat by adopting a more diurnal activity pattern, to avoid encounters with the predominantly nocturnal brown rat (Knight, 1975). Preliminary studies involving trap-timers at NWCW revealed that the average time that water voles were active was 6.21 a.m., whereas rats were caught at an average time of 3.52 a.m. (pers. obs.). There are many anecdotal reports of brown rat colonisation being detrimental to water vole survival. For instance when rats colonised Brownsea Island (Poole Harbour) in 1998, a colony of water voles was almost eradicated until the rats were controlled (for the conservation of nesting birds) (Strachan, pers. comm.). Previous studies reveal that one of the criteria used to select the water vole population under study was its freedom from brown rats (*Rattus norvegicus*) (Stoddart, 1970). Brown rats are versatile animals with an impressive ability to disperse and reproduce (Knight, 1975). Ancient remains of water voles have revealed that this species might once have been more terrestrial (akin to its European counterparts) (Yalden, 2006) and it is possible that brown rats played a role in displacing water voles to the aquatic habitats where they occur today (Jewell, 1959).

In order for extant water vole colonies to persist or future reintroduction programmes to be successful, it is essential to ensure that predators are controlled. It would be naïve to think that mink eradication will ensure the persistence of the colony, without rat control. However, control should involve live trapping and not poisoning, since the latter will have negative impacts on water vole colonies, as well as all other animals in the habitat. Accidental poisoning of water voles has occurred in the past when attempting to control rats or through misidentification, whereby water voles have been confused with rats, and poisoned accordingly (Strachan & Moorhouse, 2006).

6.3.5 Condition Indicators for water vole habitat at NWCW

The Condition Indicator Table describes the basic habitat components that need to be present to in order to classify the habitat in a state of high conservation value (Hurford, 2010) for water voles. These include a water body at least 100m in circumference with convoluted edges to provide increased edge for the creation of water vole home ranges. Additionally, the presence of another pond no further than 50m away and connected via suitable habitat corridors is very important. This provides a sink habitat for dispersing water voles (Pulliam, 1998). Furthermore the presence of neighbouring colonies is essential for the persistence of the water vole metapopulations (Bonesi *et al.*, 2002). The dominant vegetation types listed in the table include those species that were the most heavily utilised as a source of both food and cover during the breeding season (in particular *Juncus effusus,* but also *Carex riparia, Typha latifolia* and *Epilobium hirsutum*) and as winter refuge (*Rubus fruticosus*) by water voles at NWCW. The DVTs should also contain associate plant species that compliment the water vole diet e.g. *Iris pseudacorus.* A diversity of DVTs should be present as a number of small patches (e.g. 30m^2) producing a diverse mosaic of vegetation. This is more beneficial than large homogeneous stands (i.e. one continuous patch covering a large area) since these reduce habitat diversity and thus water vole population density. Water voles select habitat on the basis of its quality (Telfer *et al.*, 2001) and more diverse habitats support higher water vole population densities at NWCW.

6.3.6 Recommendations for the management of water vole habitats

These recommendations are based on the best available data and techniques at the current time and are specific to the water vole habitats at NWCW. Water voles occupy the interface between terrestrial and wetland habitats, residing on the edge of water bodies. The presence of steep banks (Lawton & Woodroffe, 1991) and islands (Carter & Bright, 2000) are beneficial to water voles as they provide an increased area, allowing the habitat to support more water voles per linear metre. Furthermore they provide a refuge from elevated water levels that occur after heavy rainfall (Lawton & Woodroffe, 1991; Carter & Bright, 2000).

Since water voles are patch-based foragers, maintaining relatively short home ranges at this site (approximately 60m and 32m for males and females respectively) (chapter 3) they would respond better to patch-based management, rather than widespread clearance. The appropriate unit of management is the DVT patch, however, patch sizes vary between species and ponds (chapter 1). If vegetation clearance is necessary, each pond should be considered individually. Control of *Typha latifolia* is necessary, since this species is a dominant macrophtye and can rapidly expand to fill wetland areas (Cronk & Fennesey, 2001) however, sensitive clearance undertaken by one or two people is recommended. Furthermore, bankside vegetation should be left intact as lack of cover comprises habitat integrity and has negative consequences for water voles (Lawton & Woodroffe, 1991; Carter & Bright, 2000, Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006).

Bramble and scrub clearance typically enhances floral diversity (Gardiner & Vaughn, 2009) however, removal of bramble has negative consequences for vole populations (Flowerdew & Ellwood, 2001). Bramble control at NWCW is recommended where necessary, but where present this species should not be cleared below a level of 3.5% of the bankside vegetation of water vole habitats at NWCW. Moreover, the timing of vegetation is essential since bramble clearance is typically a winter activity (Gardiner & Vaughn, 2009). Water voles rely on bramble for protection from predators throughout the year, particularly during the winter and therefore winter clearance could have devastating effects on resident water voles. Furthermore, if an area is home to a vulnerable or protected species, such as the water vole, then there is a legal obligation to implement sympathetic management. This is particularly true for isolated populations. Unless there is a source habitat in the locality then recolonisation is highly unlikely once a population is lost, and local extinctions will occur (Bonesi *et al.*, 2002).

6.3.7 The necessity for sensitive and holistic management

Although widespread vegetation clearance had negative effects on the water voles and their habitat, it still provided a framework on which to base future management decisions to ensure that future vegetation clearance is controlled and sympathetic. A combination of many factors, including habitat loss, has led to the continuing demise of the water vole across Britain (Lawton & Woodroffe, 1991; Strachan & Jefferies, 1993; Strachan & Moorhouse, 2006). Further habitat destruction and poor habitat management will only exacerbate this situation and it is crucial that future conservation management decisions are evidence-based (Pullin & Knight 2001, 2009) and take into consideration the dynamic competitive interactions between different species within a given habitat (Nee & May, 1992). In addition to dead water voles, the remains of a grass snake (*Natrix natrix*) were found in a rat cache, suggesting that unsympathetic large scale vegetation removal also affected other important wetland vertebrates. It was not clear whether the rats actually predated the cached voles or whether they were scavenged, however, atypical wounding observed on a number of adults suggests that there was direct conflict between rats and water voles.

Unfortunately this single species approach is often the underlying cause of habitat mismanagement as it does not take into account the effect such clearance may have on other resident species. Like water voles, moorhens (*Gallinula chloropus)* make extensive use of the macrophytes removed by riparian engineering works and so provide a supporting parallel for losses of water vole sites (Taylor, 1984). Moreover, Great Bittern (*Botaurus stellaris)*, a rare wetland species, utilises similar habitats to the water vole and since there have been winter records of this species at this site (NWCW pers. comm.) this too should be considered when undertaking clearance work. Conservation and management must be approached holistically, particularly in the case of vulnerable declining species such as the water vole, the future of which still hangs precariously in the balance.

Overall Discussion

'Come forth into the light of things, let nature be your teacher'

William Wordsworth (The Tables Turned, 1798)

Dominant Vegetation Types (DVT) as a tool for conservation of water voles

How animals use space is a long-standing theme in ecology (Stoddart, 1970; Ostfeld *et al.*, 1985; Bowers *et al.*, 1996; Martin & McComb, 2002; Moorhouse & Macdonald, 2005, 2008). Mapping stands of vegetation according to the dominant vegetation type (DVT) provides a basis for describing the matrix habitat, which underpins the study of water vole ecology at the patch-landscape scale (McGarigal & Cushman, 2002). Additionally, it provides important quantitative data on the matrix habitat, a parameter that is often overlooked (Mortelliti *et al.*, 2010). As an alternative to the widely adopted Phase 1 method (NCC), the DVT approach minimises observer variation (Cherrill & McClean, 1995; 1999) and uses clear unambiguous definitions (Hurford, 2010). This method of mapping can be achieved with minimal botanical knowledge and is particularly appropriate for wetland habitats where vegetation units are often dominated by easily recognised graminoid and/or forb species, which largely determine the overall physiognomy. This adds a practical element which can be implemented by site managers.

Furthermore, the DVT map can be used as a baseline against which the spread of invasive species at NWCW can be monitored. These include alien plant species, such as New Zealand Pigmyweed (*Crassula helmsii)* (pond D) or native tree species that can encroach into wetlands and drive the process of ecological succession (Cronk & Fennessey, 2001), thus making the habitat unsuitable for water voles (Zejda & Zapletal, 1969; Lawton & Woodroffe, 1991; Strachan & Moorhouse, 2006). Additionally, the DVT mapping approach identifies areas of high biodiversity and provides a baseline from which to monitor the distribution and movements of animal species. Implementation of this method will reduce both time and the need for specialist field surveyors, thereby facilitating management practices if applied at a national level.

Multi-annual water vole population densities – is there a population cycle?

Water vole populations at NWCW were characterised by a peak density phase and a low density phase, with populations still actively recruiting at the close of study.

Further studies over a longer time-scale would be required to verify whether the water vole population at NWCW was characterised by a multi-annual population cycle, such as those typical of microtine rodents (Krebs & Myers, 1974; Hansson & Henttonen, 1988; Lambin *et al.*, 2000; Lidicker, 2000; Hansson, 2002). Although the four years of field studies were not sufficient to determine whether water vole populations at NWCW were truly cyclical, or indeed the periodicity, it is interesting to speculate that if present, the water vole population cycle is operating similarly to those of water voles in Europe, which last six to seven years (Weber *et al*, 2002). There, population cycles are characterised by alternating phases of low density and outbreaks, the latter of which can last two to four years (Saucy, 1994). Throughout the study, two ponds were unoccupied for a year at a time, during the low density phase. Additionally, one pond was only occupied for one breeding season, during the peak density phase. The multi-annual population fluctuations at NWCW were characterised by high densities and occupation of both optimal and sub-optimal habitats during peak years (Pulliam, 1988).

Although multi-annual cycles are well documented in microtine rodents (Krebs & Myers, 1974; Cole & Batzli, 1979; Erlinge *et al.*, 1983; Hansson & Henttonen, 1988; Lambin *et al.*, 2000; Lidicker, 2000; Turchin & Hanksi, 2001; Hansson, 2002) and fossorial water vole populations in Europe (Saucy, 1994; Giradoux *et al.*, 1997; Weber *et al.*, 2002), they are not mentioned in recent studies of water vole populations in either England (e.g. Lawton & Woodroffe, 1991; Moorhouse & Macdonald, 2008) or Scotland (e.g. Stoddart, 1971; Telfer *et al.*, 2001) nor in the conservation guidelines for this species (Strachan & Moorhouse, 2006). However, Telfer *et al.* (2003) speculate that the low levels of genetic diversity characterising water vole populations on Scottish Islands may be partly the result of multi-annual bottlenecks. Aars *et al.* (2001) also suggest that (in the absence of mink) causes of such regional variation in extinction and colonisation rates in Scottish water vole populations, and the processes leading to synchrony within regions (but not between them), may be part of multi-annual fluctuations such as those reported for fossorial populations in Europe.

The utilisation of seemingly unsuitable habitats by water voles during peak years has important consequences for the conservation of the species. Moreover, the potential multi-annual cycle of water vole populations in Britain clearly requires further investigation and should be taken into consideration particularly when undertaking surveys for the presence of water voles. Unoccupied habitat may only be utilised by water voles during peak years of the population cycle (Pulliam, 1988) provided that neighbouring colonies within dispersal distance are present (Rushton *et al.*, 2000; Telfer *et al.*, 2001; Bonesi *et al.*, 2002) and thus repetitive surveying over at least 4 consecutive years is necessary. Repetitive surveys will identify whether the habitat in question is an important component of the metapopulation which is unoccupied because the water vole population is in the low density phase, or if the area is actually unsuitable. This is particularly important in areas that may be affected by development, or areas that are monitored under the National Water Vole Surveys (e.g. by the Vincent Wildlife Trust). Additionally, the multi-annual fluctutations should be incorporated into water vole population models (e.g. Rushton *et al.*, 2000; Macdonald & Rushton, 2003). Models are not throw-away tools, but powerful instruments that should be the subject of progressive refinement and adaptation (Mortelliti *et al.*, 2010).

Water vole demography and dispersal on wetland ponds

Population density, survival and recruitment of water voles varied between habitats, ponds and seasons at NWCW. Pond D supported the highest mean population density per 100 m and peak monthly densities (during the breeding season of the peak density phase; 2006 to 2007) comparable to those observed in linear English habitats (Strachan & Moorhouse, 2006). The structure of this habitat was similar to that of typical water habitats, in that it was a linear ditch with highly-layered vegetation (Lawton & Woodroffe, 1991). All other ponds within the area of wetland studied were non-linear, with pond A representing the most important component of the wetland system at this locality; these provided an insight into the population dynamics of wild water voles in non-linear habitats. Pond A was the only habitat that sustained a continuous turnover of populations throughout the duration of the study and provided an important source of juveniles.

Numerous dispersal events (both adult and juvenile) were observed at NWCW. The necessity of neighbouring colonies for the persistence of water vole populations has been previously documented (Telfer *et al.*, 2001; Bonesi *et al.*, 2002). Without effective demographic connectivity between numerous colonies, small clusters of colonies would be greatly exposed to both demographic stochasticity within patches and extinction-recolonisation stochasticity between patches (Aars *et al.*, 2001). Correlations between the locations of juveniles and adult females are expected, since young juveniles can be expected to remain in their natal area for some time before dispersing (Woodall 1993). However, dispersal of juvenile water voles at NWCW was a density-dependent process. Juvenile dispersal to neighbouring ponds was observed during the peak density phase (2006 to 2007), whereas juveniles recruited into the adult population on their natal pond during the low-phase (2008 to 2009).

Water vole home range length and social behaviour on wetland ponds

Male and female adult water voles on wetland ponds in NWCW maintained shorter home ranges (60 m and 32 m respectively, but many 20 m or less) than those inhabiting linear habitats elsewhere in Britain (typically 60 to 300 m for males and 30 to 150 m for females) (Stoddart, 1970; Moorhouse & Macdonald, 2005; 2008; Strachan & Moorhouse, 2006). Female water voles maintaining home ranges on the linear ditch habitat (pond D) behaved in a similar manner to their English counterparts, maintaining contiguous non-intra-sexually overlapping territories (Stoddart, 1970; Moorhouse & Macdonald, 2005; Strachan & Moorhouse, 2006) (chapter 3). Interestingly, males on pond D maintained shorter home ranges (c.20 m) than their female counterparts (c. 30 m) in this locality, during both the breeding season and the winter. The restricted movements of males may be due to i) high female densities on pond D reduce the need for males to travel long distances in order to encounter a mate or ii) territorial females excluding males from their home ranges, unless receptive to breeding.

Additionally, female water voles were observed to maintain intra-sexually overlapping home ranges, during the breeding season and the winter of both the peak density phase and low density phase on pond A. This contradicts all previous studies of female water voles, which are typically intra-sexually territorial (Pelikan & Holisova, 1969; Stoddart, 1970; Leuze, 1976; Moorhouse & Macdonald, 2005; Strachan & Moorhouse, 2006). It is plausible that the three-dimensional nature of the wetland pond reserve at NWCW (scattered ponds within close proximity, often used concomitantly by both males and females), together with the presence of islands, tall vegetated mounds of earth and convoluted pond edges, contributed to the reduced home range lengths and intra-sexual female range overlaps observed at this locality. The presence of islands and tall bunds of earth within reed beds has shown to be of significant importance to water voles with respect to survival rates (Carter & Bright, 2000; 2003), but here it is demonstrated that these topological features also influence social behaviour in this species.

Water vole habitat requirements on wetland ponds

In addition to the topological aspects discussed previously, optimal water vole habitats at NWCW were characterised by a diverse assemblage of dominant vegetation type (DVT) patches including stands of *Juncus effusus*, *Carex riparia*, *Epilobium hirsutum*, *Rubus fruticosus* and *Typha latifolia*. This study is the first to identify *Rubus fruticosus* as an important component of the ecosystem for water voles, although its importance to microtine rodents has been demonstrated previously (Flowerdew & Ellwood, 2001). *Rubus fruticosus* was an integral component of male and female water vole home ranges during both the breeding season and winter. This species provides important protection from predators, particularly during the winter when above-ground vegetative cover is reduced. *Rubus fruticosus* can grow aggressively and clearance of this species is often undertaken (during the winter) to increase floristic diversity (Gardiner & Vaughn, 2009). It is essential that this does not occur on a large scale in water vole habitats, since reduced cover will increase the susceptibility of water voles to predation (Carter & Bright, 2000; Forman, 2005; Strachan & Moorhouse, 2006).

DVTs of *Juncus effusus*, *Carex riparia* and *Epilobium hirsutum* were included in the home ranges of numerous males and females during the breeding season, with males also incorporating the *Typha latifolia* DVT into their home ranges. All of these species provided a source of cover and food for water voles at NWCW; particularly *Juncus effusus*, the most heavily utilised plant species by female water voles at this locality. This contradicts previous studies on linear habitats where this species was negatively correlated with the presence of water voles (Woodall, 1993) and highlights the need to survey numerous water vole populations in varying habitat types before inferring the importance of various plant species. *Juncus effusus* provided both nutritious food, nesting material and continuous cover for water voles throughout the year at NWCW.

At what level does diversity influence water voles?

At NWCW during the breeding season, water voles selected the ponds with the highest habitat diversity (assemblage of dominant vegetation types; D_{pond}) but were most active within the least diverse DVT patches within the vegetation mosaic. Knowledge of the way in which organisms select habitat is useful for understanding the components that govern ecological systems, but also for predicting changes in community structure that might follow natural or anthropogenic alterations of ecosystems (Dunning *et al.*, 1995).

This study provides evidence that water vole population density corresponds positively with the diversity of the habitat (i.e. richness and abundance of DVT patches) during the breeding season. High diversity may translate into high layering of the vegetation, which is important for water voles (Lawton & Woodroffe, 1991). Habitat diversity also corresponds positively with the total number of plant species per pond, with more diverse habitats offering a greater selection of forage items. Increased food abundance is known to increase population densities of microtine rodents (Andrzejewski 1975; Cole & Batzli 1979; Gilbert & Krebs 1981; Taitt & Krebs, 1981; 1983; Desy *et al.*, 1990; Koskela *et al.*, 1998; Jonsson *et al.*, 2002). Moreover, female population density corresponds positively with the number of plant species selected as forage.

Additionally, more diverse habitats were associated with higher survival rates and a greater number of juvenile water voles, particularly females. Females inhabiting suboptimal territories may benefit by differentially producing more males, since they are more likely to disperse (Clark 1978; Silk 1983; Julliard 2000). Perhaps the high diversity of optimal habitats at NWCW contributed to the number of females produced and the female-skew observed towards the end of the study. A similar response has been reported for microtine rodents in heterogeneous habitats (Ostfeld *et al.*, 1985; Bowers *et al.*, 1996). Furthermore, maternal condition is also an influential factor, with heavier mothers tending to produce female-biased litters (Aars *et al.*, 1995). The most diverse ponds associated with the highest productivity of juveniles, particularly females (e.g. ponds A and D) were characterised by heavier females maintaining home ranges than their lighter counterparts on less diverse ponds, the latter of which were typically characterised by a lower number of juveniles and a male-skew in the juvenile population (e.g. pond E).

Habitat diversity, home range and patch use

In the case of small mammals, the standard measure of how individuals utilise space is termed the home range. Home ranges are operationally simple to define, and are one of the most commonly measured variables in animal ecology today (Bowers *et al.*, 1996). Variation in home range size has been used to make inferences about food availability, habitat quality, breeding condition, and social organisation (Bowers *et al.*, 1990). The home ranges of water voles studied here were overlain onto the dominant vegetation type (DVT) map and provided an insight into patch use in non-linear wetland habitats. Habitat diversity showed a significant positive relationship with water vole population density. Furthermore, the most diverse ponds habitats (high D_{pond}) were associated with higher female densities, more juveniles and female-biased juvenile sex-ratios. A similar response has also been observed for female California voles (*Microtus californicus*) in heterogeneous habitats (Ostfeld *et al.*, 1985). Additionally, gender specific utilisation was observed, both between ponds, and between DVT patches within the same ponds. Although both male and female water voles at NWCW overlapped their home ranges in certain DVT patches (e.g. the *Cr*DVT, the *Je*DVT and the *Rf*DVT), males and females also maintained home ranges in different DVTs. For example, during the breeding season, males utilised the *Jc*DVT and the *Tl*DVT, whereas females were never associated with these DVTs at this time. Additionally, during winter, males maintained a home range in the *Bm*DVT, which was only utilised by females during the breeding season.

Habitat heterogeneity is hypothesised to have wide-reaching effects on the behaviour and population dynamics in microtine rodents (Ostfeld, 1992). Habitat diversity is an important determinant of female distribution (Ostfeld *et al.*, 1985; Bowers *et al.*, 1996), which in turn determines male distribution through competition for access to females (Wolff & Peterson, 1998; Bond & Wolff, 1999). Patterns of space use and social behaviour of females are highly responsive to the abundance and distribution of food and cover (Osfeld *et al.*, 1985). Female water voles are typically intra-sexually aggressive, maintaining contiguous territories (Pelikan & Holisova 1969; Stoddart, 1970; Moorhouse & Macdonald, 2005; Strachan & Moorhouse, 2006). The non-linear nature of the wetland habitat at NWCW provided additional space for the establishment of home ranges, in a three-dimensional landscape, particularly in habitats with convoluted bank-sides, raised banks and islands (e.g. ponds A and D). In addition to maintaining intra-sexually overlapping home ranges on some ponds, females (unless receptive) also excluded males from portions of their home ranges, evident in the distribution of males and females in different DVT patches.

Previous studies have revealed that patch richness, pattern and composition are key landscape features that influence the distribution of small mammals inhabiting forest landscapes (Martin & McComb, 2002). Bowers *et al.* (1996) document an edge effect in response to habitat heterogeneity for female meadow voles (*Microtus pennsylvanicus*) inhabiting experimental grassland plots; those maintaining home ranges on patch edges have greater body weights, higher persistence times and reproduce more frequently than those with home ranges in patch interiors or the continuous habitat landscape. They suggest that edge habitats may represent higher quality home range sites than interior habitats, due to the quality of forage being higher on and adjacent to patch edges, than in patch interiors, despite the increased risk of predation associated with occupation of edge habitats (Donovan *et al.*, 1997). Indeed, other studies of microtine rodents have shown home range size in females to be more sensitive to habitat quality than to defence costs (Ostfeld & Klosterman 1986; Ims 1987).

Manipulative experiments on the effects of habitat fragmentation (i.e. increasing the number of patches, with its positively associated edge-effects) have been shown to increase female densities of meadow voles (*Microtus pennsylvanicus*). This in turn influences female meadow vole social structure, including differences in home range size and habitat use between sexes, serving as a population regulatory mechanism (Collins & Barrett, 1997). The diversity and arrangement of DVT patches within the wetland ponds at NWCW provided continuous cover (and in most instances, food) for water voles. However, different DVTs were associated with different physiognomy.

Consider the structure of the five major habitat components of the water vole habitat at NWCW; *Rubus fruticosus* and *Epilobium hirsutum* (typically damp grassland or bankside), *Carex riparia* and *Juncus effusus* (typically shallow water or bankside) and *Typha latifolia* (typically open or shallow water). These five species are structurally very different from one another, are associated with different substrates, grow to different heights and are exploited by water voles for different reasons. Furthermore, the plant species associated with each DVT differ both in abundance and composition between DVTs, thereby providing varying degrees of available forage for water voles. The gradation between DVT patches is usually distinct and may represent an edge effect (Bowers *et al.*, 1996). Provided adjacent DVT patches of different species still afford continuous cover from predation (albeit of different heights or physiognomy), each patch and associated patch edges may offer the diversity of associate forage species required to sustain an adult female water vole. Indeed, numerous females were observed to maintain a home range of 15m or less, in just one distinct DVT patch (ponds A, B and D).

Maintaining habitat heterogeneity has been proposed as a means of conserving species richness in habitats threatened by human activities (McGarigal & McComb, 1992). In the case of the water vole, maintaining habitat heterogeneity has positive consequences for both the size and persistence of populations, facilitated by an increased niche width (Bolnick *et al.*, 2010). Higher habitat diversities in turn provide a greater availability of patches, exploited as resource of forage or territory (home range) for both male and female water voles. The spatial organisation of water voles in varying habitats (i.e. linear versus non-linear), together with gender separation between vegetation types, has consequences for social interactions, both intra-sexually (i.e. contiguous versus overlapping territories) and inter-sexually (i.e. seasonal exclusion of males from DVTs preferred by females). The plasticity of these behaviours observed between both genders and habitat types should also be taken into consideration in future population modelling and habitat monitoring for the species.

Gender dependent ecological niche partitioning

Ecologists are becoming increasingly aware of the role of spatial heterogeneity in population and community dynamics (e.g., Ricklefs, 1987; Karieva, 1990; Levin, 1992; Diffendorfer *et al.*, 1995). Recognising the scale at which animals perceive environmental heterogeneity is essential for understanding community structure (Cramer & Willig, 2005). The habitat heterogeneity hypothesis proposes that an increase in the number of habitats leads to an increase in species diversity in a landscape (MacArthur & MacArthur, 1961) through an expansion in the number of partitionable niche dimensions (Cramer & Willig, 2005). The niche width of a species reflects a balance between the diversifying effects of intra-specific competition and the constraining effects of inter-specific competition (Bolnick *et al.*, 2010). Many apparently generalist species are in fact composed of individual specialists that use a small subset of the population's resource distribution (Bolnick *et al.*, 2002).

The water vole is typically considered to be a generalist herbivore (Strachan & Jefferies, 1993), associated with a gradient of habitat types without clear habitat boundaries (Telfer *et al.*, 2001). This study provides the first real evidence that male and female water voles inhabiting non-linear wetland ponds, maintain portions of their home range within exclusive vegetation types. Additionally, a significant positive relationship was observed between female population density and the number of different plant species selected as forage. This implies that, in addition to niche partitioning between genders, individual variation between female water voles was also evident (Bolnick *et al.*, 2002). As more females occupied a pond, a greater diversity of plant species were selected as forage. This may be due to the variation in DVT occupancy by females maintaining contiguous (e.g. pond D) or partially overlapping (e.g. pond A) home ranges, within the diverse matrix of vegetation types in a single pond. Since different DVTs offer different associated plant species, a female maintaining a home range within the *Je*DVT will encounter a different suite of associated plant species to a female maintaining a home range in, for example, the *Eh*DVT or the *Cr*DVT. It is therefore plausible that each female may indeed exploit different plant species as forage. The absolute niche width of the water vole at NWCW is an aggregate of the interactions experienced by potentially heterogeneous individuals (Bolnick *et al.*, 2010) and is determined by the combination of individual water voles exploiting various portions of the wetland landscape as sources of food and cover.

Do water voles influence their wetland ecosystem?

Water voles influence their ecosystem by grazing (i.e. cutting vegetation) and creating feeding stations, burrows, runways in vegetation and latrines containing nitrogen-rich faeces. Grazing converts plant tissue into herbivore biomass or faeces, i.e. it doesn't accumulate as live biomass or litter (Bazely & Jefferies, 1985) and this accelerates the nutrient cycle. The production of significant amounts of nitrogen-containing faeces by water voles (Woodall, 1977) could potentially influence the nutrient cycle of the wetland ecosystem. At a national level, 18 kg of nitrogen contained in faecal pellets is deposited by a pre-breeding population of 41,000 water voles to the wetland habitat in Wales per day (Harris *et al.*, 1995).

Although preliminary experiments indicated that the soil samples derived from historic latrines sites had a similar concentrations of nitrate, ammonium and phosphate as control non-latrine soils; these measurements may have been compromised by the small sample size and problems related to dilution and wash-out resulting from inundation of soils by rain and flood water. Further studies are required to verify the effects of latrines created by water voles. Herbivores can directly alter ecosystem components and in turn manipulate their own food supply (van der Wal *et al.*, 2002) and increase the floristic diversity of their habitats (Hobbs & Hobbs, 1987; Proulx & Mazumder, 1998). It is plausible to speculate that selective grazing, burrowing and latrine creation by water voles maintains the diversity of their wetland habitat.

Evidence-based water vole conservation

Since this study took place over a long period of time, it adds important autecological details to the existing knowledge base regarding water voles, particularly the observation of the multi-annual fluctuations in water vole densities. The need for an evidence-based framework to evaluate effectiveness and support decision-making in conservation has been previously highlighted (Pullin & Knight, 2001; Fazey *et al.*, 2004; Sutherland *et al.*, 2004).

Creation of the site-specific Condition Indicator Table for the water vole habitat at NWCW (chapter 6) describes the suite of attributes and targets used as evidence for the condition of the habitat and allows recognition of when the key habitat is in a state of high conservation value (Hurford, 2010). It is recommended that water vole ponds should be at least 100 m in circumference with convoluted edges and islands (Carter & Bright, 2000), comprised of at least 10 different dominant vegetation types (DVT) and 20 DVT patches across the water body and pond edge (within 5 m of the water's edge). As the circumference is increased, the richness and abundance of DVTs should be increased accordingly. The DVTs themselves do not necessarily need to be characterised by high patch diversity (D_{DVT}), but should be combined to create a diverse mosaic of vegetation patches (D_{pond}). The DVTs should reflect those selected by water voles as food, including; *Juncus effusus, Carex riparia, Typha latifolia* and *Epilobium hirsutum,* and cover, including; *Juncus effusus, Carex riparia, Typha latifolia* and *Rubus fruticosus.*

The Million Ponds Project

The Million Ponds Project was recently launched, aiming to reverse a century of pond loss by creating an extensive network of new ponds across the UK. This project involves a collaboration of land owners and land managers including the Environment Agency (EA), Countryside Council Wales (CCW) and the Forestry Commission and wildlife organisations or groups such as the Royal Society for the Protection of Birds (RSPB), the Amphibian and Reptile Conservation (ARC) and the South and West Wales Amphibian and Reptile group (SWWARG). The first phase (2008-2012) aims to create 5,000 clean water ponds in England and Wales, 25% of which will be targeted to support some of the 80 pond species that are national priority for conservation action under the UK Biodiversity Action Plan (BAP). In Wales these include rare plants, insects, amphibians, reptiles, birds and mammals including bats, water voles and otters (www.pondconservation.org.uk/million ponds).

The problems encountered with re-introduction of captive-bred water voles

Reintroductions are an important tool in conservation biology but frequently fail (Fischer & Lindemayer, 2000; Moorhouse *et al.*, 2009). Reintroduction attempts are frequently unsuccessful for a number of reasons (Lyles & May, 1987; Griffith *et al.*, 1989; Fischer & Lindemayer, 2000). Failures to implement adequate measures to control predators at the release site (Short *et al.*, 1992) or address inadequacies of habitat quality (Burgman & Lindemayer, 1998) are examples. Reintroductions of captive bred water voles are becoming more common and sometimes fail, unless American mink are controlled (Moorhouse *et al.*, 2009).

Studies of reintroduced populations of water voles have provided important autecological information, including the responses of water vole home range lengths to variations in population density on linear habitats (Moorhouse & Macdonald, 2008) and the effects of habitat quality upon reintroduction success (Moorhouse *et al.*, 2009). However, captive bred animals are frequently underweight and immunologically compromised (Moorhouse *et al.*, 2007). Most recently, a study of reintroduced water voles revealed that four months after release, 43% of reintroduced captive-bred water voles (particularly females) had been exposed to leptospirosis, whereas only 6% of wild water voles were host to the disease (Gelling & Macdonald, 2010). It has been suggested that reintroduction of captive bred individuals is necessary to restore the water vole to the wider countryside, because in many areas water vole populations are so highly fragmented that even areas where good quality habitat persists are unlikely to become colonised by natural dispersal (Strachan & Moorhouse, 2006). However, if the released animals are essentially 'too clean' to tolerate the natural environment because of their susceptibility to disease (Moorhouse *et al.*, 2007; Gelling & Macdonald, 2010) and suffer an increased likelihood of predation associated with domestication (Roberts, 2010) reintroductions are likely to be unsuccessful in the long term.

The future for water vole conservation

In the light of the results presented here, water vole conservation should be directed towards non-linear habitats such as reed beds (Carter & Bright, 2000) and wetland pond systems. Holistic joined-up thinking between various conservation bodies would augment the conservation of water voles in Britain. Pond creation should include clusters of ponds in various localities, rather than single ponds (Strachan & Moorhouse, 2006). These should preferably be created in the vicinity of wild populations to allow natural recolonisation (Bonesi *et al.*, 2002), rather than reintroduction of compromised captive animals (Moorhouse *et al.*, 2007; Gelling & Macdonald, 2010). This would allow water voles to exist as a metapopulation, as they do in this study. This offers protection from the effects of the tightrope hypothesis (Barreto *et al.*, 1998), while providing a number of source and sink habitats from which recolonisation can occur (Pulliam, 1988) following stochastic events that may have devastating effects on single isolated populations (Aars *et al.*, 2001; Telfer *et al.*, 2001). Furthermore, ponds with a diverse mosaic of vegetation patches will support higher population densities of water voles.

Creating diverse water vole habitats not only compliments the International Year of Biodiversity (Pacheco, 2010) and the National Environment Framework for Wales, but also has supporting parallels for many species. These include UKBAP species such as the common toad (*Bufo bufo)* and the internationally important great crested newt (*Triturus cristatus),* both priority species of conservation concern in Britain (Inns, 2009). Applying the results of this study in both the management of existing habitats and the creation of new ponds will contribute to the persistence of water vole populations at NWCW. Furthermore, the results of this study could be implemented in the restoration of the water vole to the wider countryside in accordance with the UK Biodiversity Action Plan.

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'If we do not develop a strong theoretical core that will bring all parts of ecology back together, we shall all be washed out to sea in an immense tide of unrelated information' Kenneth Watt (1971)

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APPENDIX

1. Plant species lists

Table A1 Total plant species present on each pond (within the 5m boundary line) across the area of wetland studied

	Pond								
Plant species	A	B	C	D	E	F	G	H	Total
Achillea millefolium	x	x		x		x	x	x	6
Agrostis capillaris	x			x			x	x	4
Agrostis stolonifera						x	x		2
Ajuga reptans					x				1
Alnus glutinosa		x		x			x		3
Alopecurus pratensis	x	x	x			x			4
Alisma plantago aquatica	x		x	x		x		x	5
Anthoxanthum odoratum	x						x	x	3
Apium graveolens					x				1
Arrhenatherum elatius								x	1
Azolla fillicoides							x		1
Bellis perennis				x					1
Berula erecta	x						x		2
Betula pubescens								x	1
Bolboschoenus maritimus	x			x		x	x		4
Callitriche stagnalis	x	x	x		x		x	x	6
Calystegia sepium		x	x		x				3
Cardamine flexuosa		x							1
Cardamine pratensis	x	x		x	x				4
Carex hirta							x		1
Carex otrobae				x	x	x			3
Carex ovalis								x	1
Carex panicea	x			x					2
Carex paniculata		x			x				2
Carex pendula							x		1
Carex riparia	x	x		x	x		x		5
Centaurea nigra						x			1
Cerastium fontanum	x		x			x			3
Ceratophyllum demersum				x					1
Chamerion angustifolium					x				1
Chrysanthemum leucanthemum			x	x					2
Cirsium arvense	x			x	x		x		4
Cirsium palustre	x			x	x		x		4
Cortaderia selloana				x					1
Corylus avellana	x	x					x		3
Crassula helmsii				x					1
Crataegus monogyna			x	x					2
Cynosaurus cristatus	x			x	x			x	4
Cyperus longus	x								1
Dactylorhiza praetermissa			x				x	x	3
Deschampsia caespistosa				x					1
Dryopteris filis-max	x								1
Eleocharis palustris	x	x	x	x	x		x		6

Table A1 (continued) Total plant species present on each pond (within the 5m boundary line) across the area of wetland studied

	Pond								
Plant Species	A	B	C	D	E	F	G	H	Total
Elodea canadensis				x			x		2
Epilobium hirsutum	x	x	x	x	x	x	x	x	8
Epilobium palustre	x	x	x	x	x		x	x	7
Epilobium parviflorum				x			x		2
Epilobium tetragonum					x		x		2
Equisetum arvense	x	x							2
Eriophorum angustifolium	x								1
Eupatorium cannabinum					x				1
Festuca rubra	x	x					x		3
Filipendula ulmaria					x		x	x	3
Galium aperine	x	x	x		x				4
Gallium palustre	x		x	x	x		x	x	6
Geranium dissectum				x		x			2
Geranium robertianum				x					1
Glyceria fluitans					x		x		2
Glyceria maxima					x		x	x	3
Heracleum sphondylium				x					1
Hippuris vulgaris	x			x			x		3
Holcus lanatus	x		x	x			x	x	5
Hydrocharis morsus-ranae				x					1
Iris pseudacorus	x			x			x		3
Juncus acutiflorus					x				1
Juncus articulatus	x				x				2
Juncus conglomeratus	x				x				2
Juncus effusus	x	x	x	x	x	x	x	x	8
Juncus inflexus		x	x	x	x	x			5
Lathyrus pratensis							x	x	2
Lemna minor	x			x					2
Lemna minuta	x	x		x		x			4
Lolium perenne								x	1
Lotus pedunculatus					x	x		x	3
Lychnis flos-cuculi	x	x	x	x				x	5
Lycopus europaeus	x	x		x			x		4
Lysimachia vulgaris							x	x	2
Lythrum salicaria				x			x	x	3
Mentha aquatica	x			x	x		x		4
Myosotis discolor			x						1
Myosotis scorpiodes	x		x	x			x	x	5
Nasturtium officinale			x						1
Pastinaca sativa ssp. Sativa		x							1
Peplis portura	x						x		2
Persicaria hydropiper							x	x	2
Persicaria maculosa	x	x		x					3
Phleum pratense					x				1
Plantago lanceolata		x		x	x	x		x	5
Poa trivialis		x					x	x	3
Polygonum lapathifolium							x		1
Populus alba				x					1
Populus tremula		x					x		2

Table A1 (continued) Total plant species present on each pond (within the 5m boundary line) across the area of wetland studied

	Pond								
Plant Species	A	B	C	D	E	F	G	H	Total
Potamogeton natans			x	x			x		3
Potentilla anserina	x								1
Prunus spinosa				x					4
Pulicaria dysentarica	x		x	x					3
Quercus petraea				x					1
Ranunculus acris	x			x					2
Ranunculus aquatilus		x							1
Ranunculus flammula							x		1
Ranunculus lingua				x			x		2
Ranunculus repens	x	x	x	x		x	x		6
Raphunus maritimus	x								1
Rosa arvensis					x				1
Rubus fruticosus	x	x	x	x	x	x	x	x	8
Rumex acetosa	x	x			x				3
Rumex conglomeratus			x		x			x	3
Rumex crispus				x					1
Rumex hydrolapathum	x			x	x				3
Rumex obtusifolius							x		1
Rumex cf sanguineus							x		1
Salix aurita	x		x						2
Salix caprea		x							1
Salix cinerea	x	x	x	x	x	x	x	x	8
Salix fragilis		x							1
Schoenoplectus tarbernaemontani				x			x		2
Scutellaria galericulata	x				x				2
Silene dioica		x							1
Solanum dulcamara	x	x	x			x	x	x	6
Sparganium erectum				x					1
Stellaria uliginosa	x						x		2
Thelycrania sanguinea			x						1
Trifolium pratense	x			x					2
Trifolium repens	x	x		x					3
Typha latifolia	x	x	x	x	x	x	x	x	8
Urtica dioica	x	x	x	x	x	x	x	x	8
Veronica catanata							x		1
Vicia cracca	x							x	2
Vicia sativa	x	x	x	x	x		x	x	7
Total species	59	40	33	62	40	21	57	36	129

2. Habitat diversity index (D_{pond})

Table A2 Pond A: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Bolboschoenus maritimus	1	0.038	-3.270	-0.124
Carex riparia	1	0.038	-3.270	-0.124
Cirsium arvense	1	0.038	-3.270	-0.124
Cyperus longus	1	0.038	-3.270	-0.124
Eleocharis palustris	2	0.077	-2.564	-0.197
Epilobium hirsutum	1	0.038	-3.270	-0.124
Equisetum arvense	1	0.038	-3.270	-0.124
Juncus conglomeratus	1	0.038	-3.270	-0.124
Juncus effusus	7	0.269	-1.312	-0.353
Open water	1	0.038	-3.270	-0.124
Rubus fruticosus	3	0.115	-2.159	-0.248
Trees	1	0.038	-3.270	-0.124
Typha latifolia	4	0.154	-1.872	-0.288
Urtica dioica	1	0.038	-3.270	-0.124
Total	26			-2.33

$D_{pond} = \Sigma p_i \ln p_i = 2.33$

Table A3 Pond B: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Carex riparia	1	0.050	-2.996	-0.150
Damp grassland	3	0.150	-1.897	-0.285
Epilobium hirsutum	2	0.100	-2.303	-0.230
Juncus conglomeratus	2	0.100	-2.303	-0.230
Juncus effusus	2	0.100	-2.303	-0.230
Open water	1	0.050	-2.996	-0.150
Ranunculus repens	1	0.050	-2.996	-0.150
Rubus fruticosus	1	0.050	-2.996	-0.150
Trees	4	0.200	-1.609	-0.322
Typha latifolia	3	0.150	-1.897	-0.285
Total	20			-2.181

$D_{pond} = \Sigma p_i \ln p_i = 2.18$

Table A4 Pond C: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Carex riparia	2	0.200	-1.609	-0.322
Damp grassland	1	0.100	-2.303	-0.230
Juncus effusus	3	0.300	-1.204	-0.361
Rubus fruticosus	1	0.100	-2.303	-0.230
Trees	2	0.200	-1.609	-0.322
Typha latifolia	1	0.100	-2.303	-0.230
Total	10			-1.696

$D_{pond} = \Sigma p_i \ln p_i = 1.7$

Table A5 Pond D: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Bolboschoenus maritimus	2	0.053	-2.944	-0.156
Carex riparia	1	0.026	-3.638	-0.095
Crassula helmsii	1	0.026	-3.638	-0.095
Damp grassland	6	0.158	-1.846	-0.292
Epilobium hirsutum	1	0.026	-3.638	-0.095
Juncus effusus	4	0.105	-2.251	-0.236
Open water	4	0.105	-2.251	-0.236
Ranunculus repens	1	0.026	-3.638	-0.095
Rubus fruticosus	5	0.132	-2.028	-0.268
Trees	7	0.184	-1.692	-0.311
Typha latifolia	5	0.132	-2.028	-0.268
Urtica dioica	1	0.026	-3.638	-0.095
Total	38			-2.241

$D_{pond} = \Sigma\ p_i \ln p_i = 2.24$

Table A6 Pond E: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Carex riparia	2	0.182	-1.705	-0.310
Damp grassland	1	0.091	-2.398	-0.218
Epilobium hirsutum	3	0.273	-1.299	-0.355
Juncus effusus	1	0.091	-2.398	-0.218
Trees	3	0.273	-1.299	-0.355
Typha latifolia	1	0.091	-2.398	-0.218
Total	11			-1.674

$D_{pond} = \Sigma\ p_i \ln p_i = 1.67$

Table A7 Pond F: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Bolboschoenus maritmus	1	0.166	-1.386	-0.230
Damp grassland	1	0.166	-1.386	-0.230
Epilobium hirsutum	1	0.166	-1.386	-0.230
Open water	1	0.166	-1.386	-0.230
Trees	2	0.332	-1.386	-0.460
Total	5			-1.590

$D_{pond} = \Sigma\ p_i \ln p_i = 1.60$

Table A8 Pond G: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Carex riparia	1	0.025	-3.689	-0.092
Eleocharis palustris	3	0.075	-2.590	-0.194
Epilobium hirsutum	2	0.050	-2.996	-0.150
Glyceria fluitans	4	0.100	-3.689	-0.369
Glyceria maxima	1	0.025	-3.689	-0.092
Juncus effusus	7	0.175	-1.743	-0.305
Open water	2	0.050	-2.996	-0.150
Potamogeton natans	1	0.025	-3.689	-0.092
Ranunculus lingua	2	0.050	-2.996	-0.150
Rumex cf. sanguineus	1	0.025	-3.689	-0.092
Rubus fruticosus	3	0.075	-2.590	-0.194
Schoenoplectus tabernaemontani	1	0.025	-3.689	-0.092
Trees	9	0.225	-1.492	-0.336
Typha latifolia	3	0.100	-3.689	-0.369
Total	40			-2.674

$D_{pond} = \Sigma\ p_i \ln p_i = 2.67$

Table A9 Pond H: Richness and abundance of dominant vegetation types (patches) used to determine habitat diversity (D_{pond})

Dominant Vegetation Type (DVT)	number of patches	pi	ln pi	pi ln pi
Epilobium hirsutum	1	0.143	-1.946	-0.278
Glyceria maxima	1	0.143	-1.946	-0.278
Juncus effusus	1	0.143	-1.946	-0.278
Open water	1	0.143	-1.946	-0.278
Trees	2	0.143	-1.946	-0.278
Typha latifolia	1	0.286	-1.253	-0.358
Total	7	0.143	-1.946	-1.750

$D_{pond} = \Sigma\ p_i \ln p_i = 1.75$

3. Water voles Minimum Number Alive (MNA)

The MNA was used as the population estimate (after Moorhouse & Macdonald 2008): Population density per 100m = (MNA / length of trapped habitat)*100

Table A10 Minimum number of water voles (MNA) on pond A during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2006	March	0	0	0
	April	0	0	0
	May	3	1	0
	June	1	0	0
	July	4	3	0
	August	2	3	0
	September	1	2	0
	October	0	1	0
	November	0	2	0
	December	0	2	1
2007	January	0	4	0
	February	1	3	0
	March	1	2	0
	April	2	3	0
	May	1	2	2
	June	1	2	0
	July	1	0	0
	August	1	0	0
	September	1	1	0
	October	0	0	0
	November	0	0	1
	December	0	0	0
2008	January	0	0	0
	February	0	0	0
	March	1	1	1
	April	0	2	0
	May	0	2	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	1	0	0
	November	0	0	0
	December	0	0	0
2009	January	0	0	0
	February	0	0	0
	March	0	3	1
	April	0	2	0
	May	0	2	0
	June	0	1	0
	July	0	1	0

Table A11 Minimum number of water voles (MNA) on pond B during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2006	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	1	0
	August	2	1	0
	September	1	0	0
	October	1	0	0
	November	1	1	0
	December	1	1	0
2007	January	2	0	0
	February	3	0	0
	March	3	0	0
	April	4	0	0
	May	2	0	0
	June	1	0	0
	July	1	0	0
	August	1	0	0
	September	1	3	2
	October	0	3	0
	November	0	3	0
	December	0	0	0
2008	January	2	0	0
	February	1	0	0
	March	1	1	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2009	January	0	0	0
	February	0	0	0
	March	0	2	0
	April	0	0	0
	May	0	1	0
	June	0	1	0
	July	0	1	1

Table A12 Minimum number of water voles (MNA) on pond C during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2006	March	1	0	0
	April	1	0	0
	May	1	2	0
	June	0	1	0
	July	2	2	0
	August	1	2	0
	September	2	1	0
	October	1	1	0
	November	1	1	0
	December	1	1	0
2007	January	1	1	0
	February	1	1	0
	March	1	1	0
	April	1	1	0
	May	0	1	2
	June	0	2	1
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2008	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2009	January	0	0	0
	February	0	0	0
	March	0	1	1
	April	0	0	0
	May	0	1	0
	June	0	0	0
	July	0	0	0

Table A13 Minimum number of water voles (MNA) on pond D during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2006	March	0	0	0
	April	0	0	0
	May	2	0	0
	June	0	0	0
	July	5	3	2
	August	0	2	0
	September	4	5	1
	October	3	2	0
	November	3	2	0
	December	3	2	0
2007	January	3	2	0
	February	2	3	0
	March	3	3	0
	April	3	6	0
	May	2	3	0
	June	2	1	0
	July	1	0	0
	August	1	0	0
	September	1	0	1
	October	0	2	0
	November	0	2	0
	December	0	1	0
2008	January	0	1	0
	February	0	1	0
	March	1	1	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2009	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	1	0
	June	0	0	0
	July	0	0	0

Table A14 Minimum number of water voles (MNA) on pond E during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2006	March	3	0	0
	April	1	0	0
	May	2	2	0
	June	1	0	0
	July	2	2	0
	August	2	0	0
	September	2	2	0
	October	1	1	0
	November	2	2	1
	December	3	1	0
2007	January	3	5	2
	February	2	3	0
	March	2	2	0
	April	2	1	0
	May	2	1	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	1	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2008	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2009	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	3	0
	June	0	0	0
	July	0	0	0

Table A15 Minimum number of water voles (MNA) on pond F during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2006	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	1	1	0
	July	1	1	0
	August	1	1	0
	September	0	1	1
	October	0	1	0
	November	0	0	0
	December	0	0	0
2007	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2008	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2009	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	0	0	0
	July	0	0	0

Table A16 Minimum number of water voles (MNA) on pond G during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2007	February	5	7	0
	March	5	7	0
	April	1	4	0
	May	3	3	0
	June	2	1	0
	July	2	1	0
	August	2	1	0
	September	1	0	0
	October	2	0	0
	November	1	0	2
	December	0	1	0
2008	January	0	1	0
	February	1	1	0
	March	1	1	0
	April	1	1	0
	May	1	1	0
	June	3	2	2
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2009	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	1	1	0
	June	1	1	0
	July	0	3	1

Table A17 Minimum number of water voles (MNA) on pond H during each month throughout the duration of the study.

Date		Males	Females	Juveniles
2007	February	1	2	0
	March	1	2	0
	April	2	1	0
	May	0	1	0
	June	1	0	1
	July	0	0	0
	August	0	0	0
	September	0	0	0
	October	0	0	0
	November	0	0	0
	December	0	0	0
2008	January	0	0	0
	February	0	0	0
	March	0	0	0
	April	0	0	0
	May	0	0	0
	June	0	0	1
	July	1	0	0
	August	1	0	0
	September	1	0	0
	October	1	0	0
	November	1	0	0
	December	1	0	0
2009	January	1	0	0
	February	1	0	0
	March	1	0	0
	April	1	0	0
	May	0	2	0
	June	1	0	0
	July	1	0	0

4. Weight of adult water voles

The following box and whisker plots show the median and inter-quartile weight of all adult water voles captured and includes both resident animals that maintained a home range and transient animals (only captured once or within one trapping session).

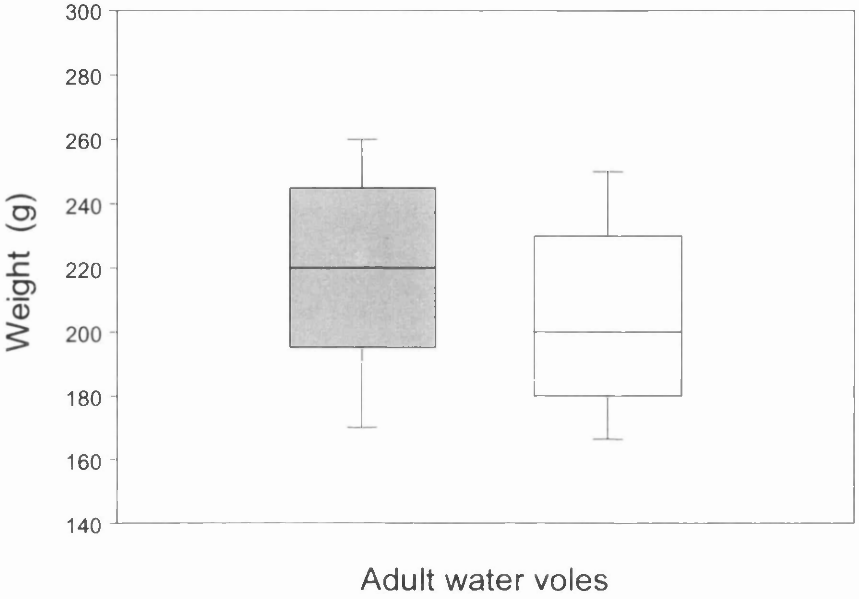

Figure A1. Box and whisker plot of water vole weight (g ±SE) (all ponds and years combined). Adult males (dark bars), adult females (open bars) (n = 122 water voles, 360 weights)

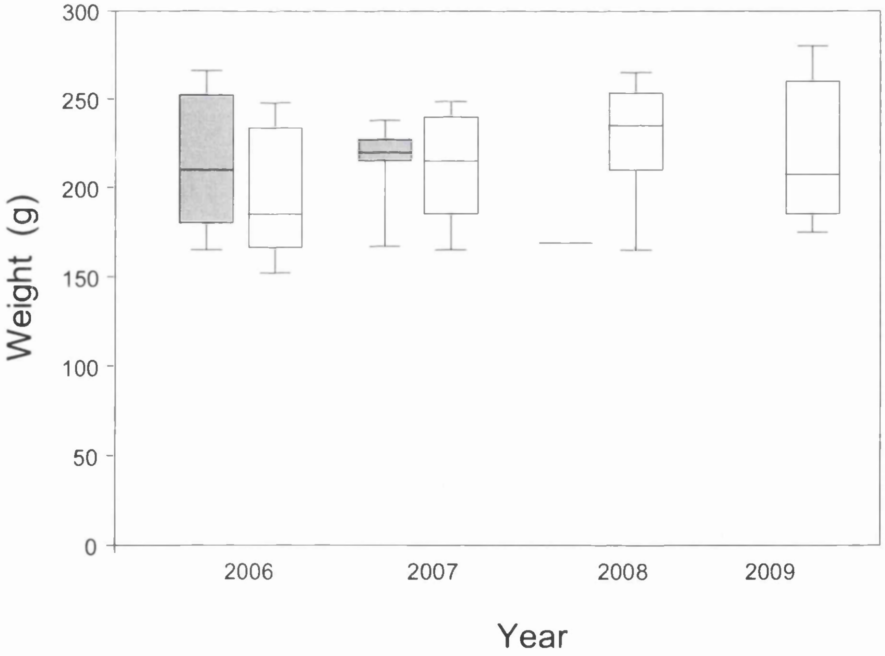

Figure A2 Pond A: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

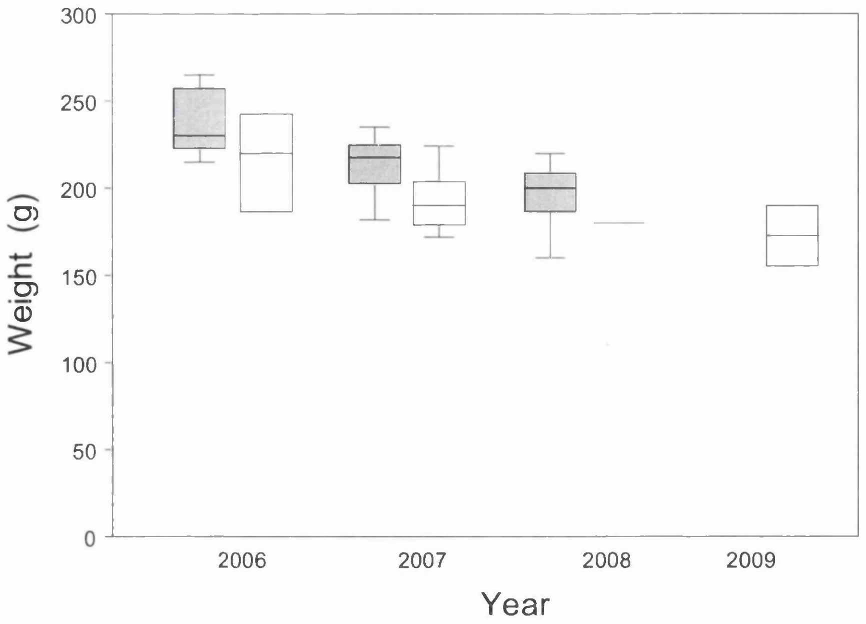

Figure A3 Pond B: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

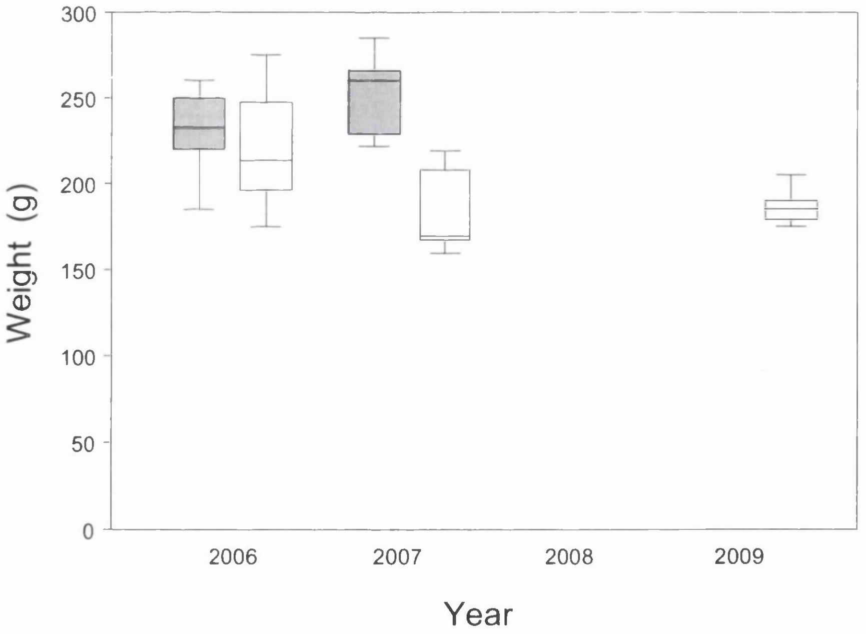

Figure A4 Pond C: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

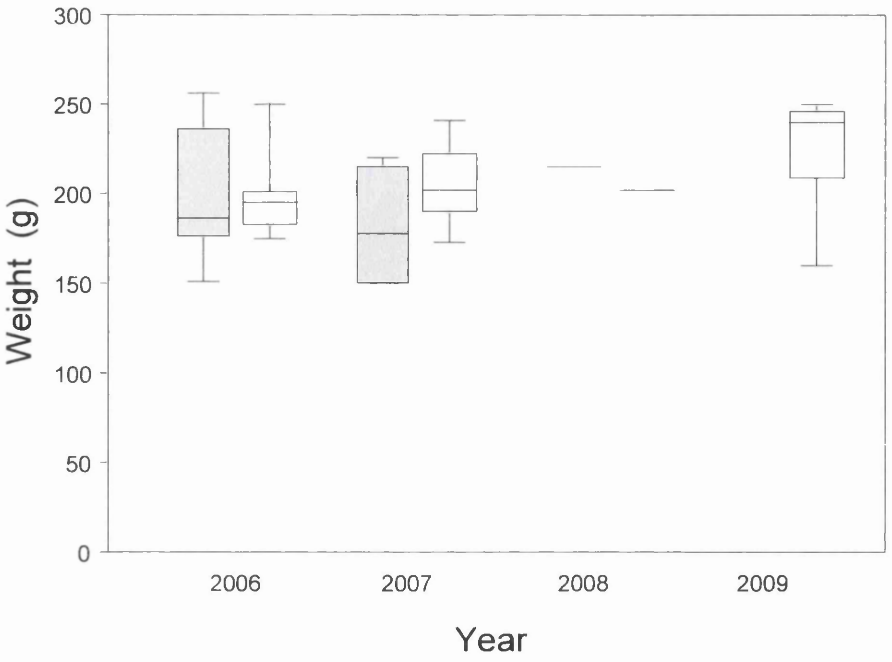

Figure A5 Pond D: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

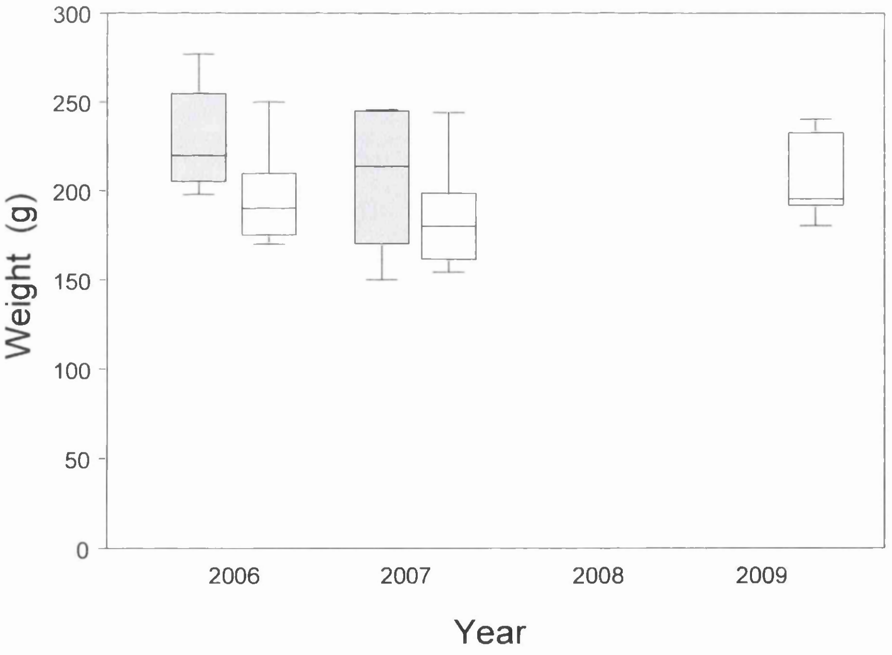

Figure A6 Pond E: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

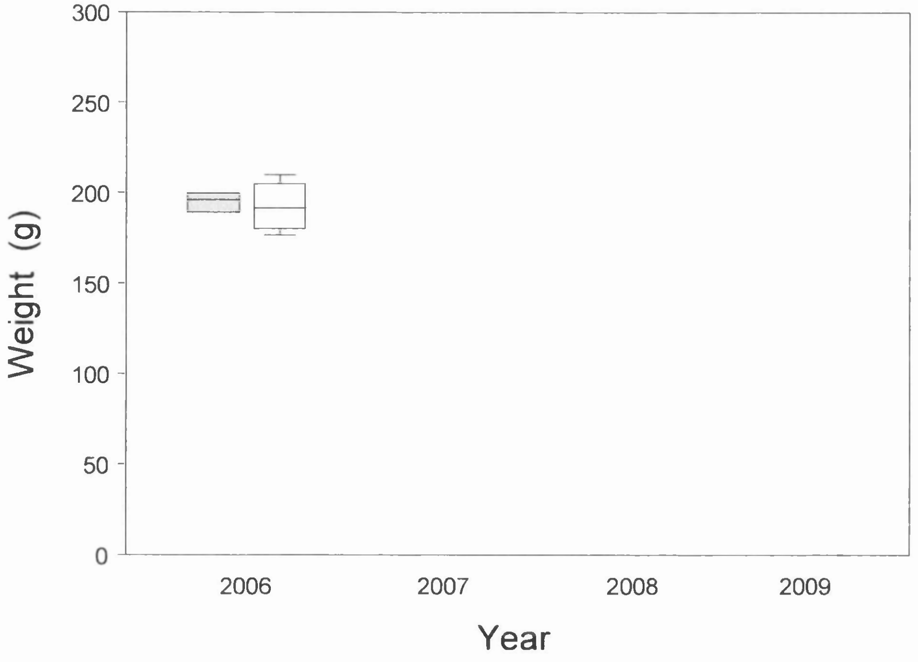

Figure A7 Pond F: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

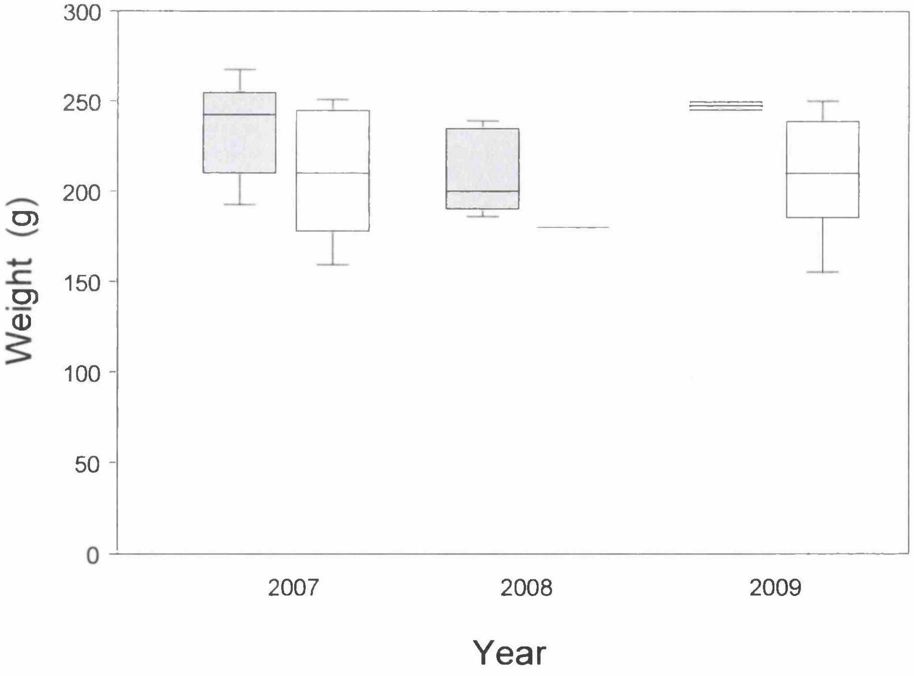

Figure A8 Pond G: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

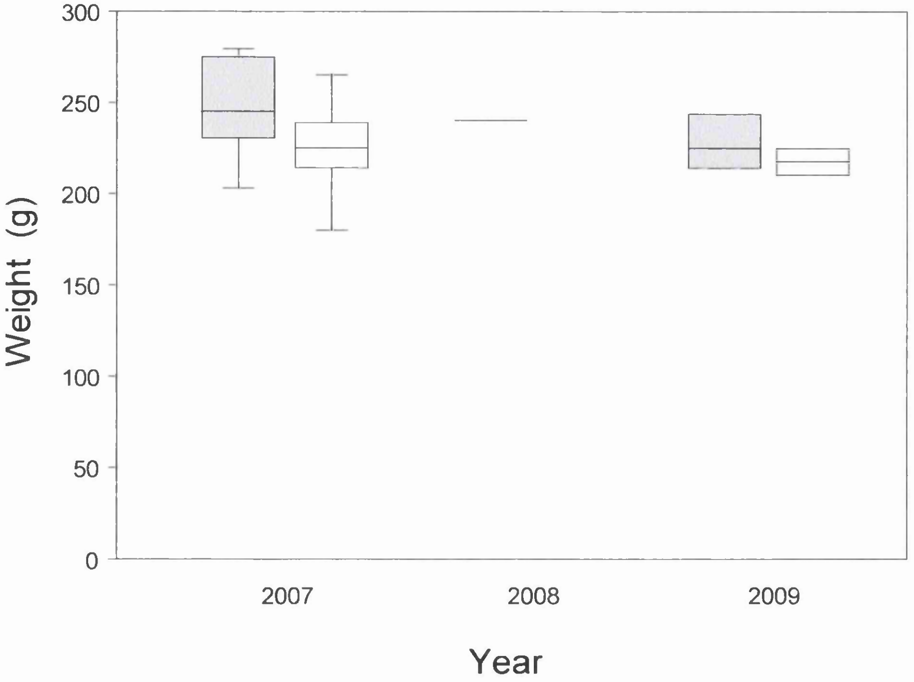

Figure A9 Pond H: Box and whisker plot of water vole weight (g ±SE) per year. Adult males (dark bars), adult females (open bars)

5. *Juvenile water voles*

The weight of juveniles at the time of first capture was used for determination of approximate dates of birth of juveniles, however is only accurate for those juveniles weighing 110g or less (Stoddart, 1971). For those juveniles weighing 120 – 140g, month of birth is estimated (table A18).

Table A18 Date, location, gender, weight and estimated birth dates of the 28 juvenile water voles captured throughout the duration of the study

Date	Trap	PIT	Sex and number	Weight (g)	Estimated Age(days)	Estimated date born
06/07/2006	D2	652AC50	M1	140	> 55	April - May 06
26/07/2006	D4	66AC071	F1	70	34	23/06/2006
01/09/2006	F1	65977B0	U1	70	34	29/07/2006
26/09/2006	D8	65AOAF5	F2	130	> 55	July - August 06
02/11/2006	E6	65A01DA	M2	115	53	11/09/2006
14/12/2006	A5	659DF32	M3	140	> 55	September – October 06
24/01/2007	E1	66AD6AD	M4	130	> 55	October - November 06
24/01/2007	E1	659CB34	F3	135	> 55	October - November 06
15/05/2007	C2	69B4B8E	F4	110	52	25/03/2007
16/05/2007	C3	69DEEEA	M5	135	> 55	February - March 07
17/05/2007	A1	69DD66B	F5	135	> 55	February - March 07
18/05/2007	A6	69B2990	F6	110	52	28/03/2007
29/06/2007	C1	69DC375	F7	100	49	12/05/2007
29/06/2007	H4	69B2549	U2	80	37	24/05/2007
27/09/2007	B5	69DD8A6	M6	140	>55	June - July 07
27/09/2007	B3	69DDD70	U3	85	39	20/08/2007
27/09/2007	D6	69DC4B4	F8	125	> 55	July - August 07
08/11/2007	A5	69DEDIC	M7	140	> 55	August - September 07
22/11/2007	G7	69B2B3D	F9	135	> 55	August - September 07
23/11/2007	G7	69DC8D3	F10	135	> 55	August - September 07
18/03/2008	A1	69DEF4B	F11	115	53	15/01/2008
04/06/2008	G8	69DC353	M8	105	51	15/04/2008
04/06/2008	H4	69DD4DE	F12	125	> 55	March - April 08
05/06/2008	G2	69542FA	M9	100	49	16/04/2008
27/02/2009	A5	69DF024	F13	135	> 55	November - December 08
28/02/2009	C5	69DEE6A	F14	135	> 55	November - December 08
02/07/2009	B5	69DE893	F15	120	54	May 09
09/07/2009	G5	69DD077	F16	135	> 55	April - May 09

6. Observed Range Lengths (ORL)

Observed range lengths (ORL) were estimates of minimal water vole range and calculated as the distance between the two furthest capture positions following the contours of the water course on the satellite map (Moorhouse & MacDonald, 2008). During the breeding season (March 1st to October 31st), home ranges were maintained by 17 males (table A19) and 31 females (table A20). The number of captures was included as a co-variate in the statistical analyses. Additionally 9 males (table A21) and 9 females (table A22) maintained a home range during the winter (November 1st to February 28th). Note that the ORL and number of captures refers only to that season (breeding season or winter), however the dates captured show the total length of time over which the animal was observed to maintain a home range.

Table A19 Observed range lengths (m) (ORL) of the 17 male water voles that maintained a home range (n = 19) during the breeding season.

Dates captured	Male number	PIT ID	Pond	ORL (m)	Number of captures
Mar 06 – Jul 06	1	65A08CF	C	120	6
Mar 06 – May 06	2	65A3790	C	60	6
Jun 06 – Aug 06	3	659B0AB	F	20	3
Aug 06 – Sep 06	3	659B0AB	E	20	2
Jul 06 – Apr 07	4	659D70B	C	100	18
Jul 06 – Sep 06	5	65A1C3D	A	60	6
Jul 06 – May 07	6	65857F6	E	40	10
Aug 06 – Aug 07	7	66AAB65	B	50	14
Aug 06 – Sep 06	8	6527A3B	D	15	4
Sep 06 – Mar 07	9	65A0345	D	15	3
Sep 06 – Nov 06	10	659FF7C	D	40	4
Jan 07 – May 07	11	695C895	B	80	11
Jan 07 – Sep 07	12	6696B6A	D	15	3
Feb 07 – Oct 07	13	65A06DB	G	180	7
Feb 07 – Apr 07	14	6957686	B	100	4
Mar 07 – Apr 07	15	6956CBA	H	100	6
May 07 - Aug 07	4	659D70B	G	60	7
Jan 08 – Mar 08	16	69DF928	B	20	3
Feb 08 – Jun 08	17	69B5F7F	G	20	3

Table A20 Observed range lengths (m) (ORL) of the 31 female water voles that maintained a home range (n = 31) during the breeding season.

Date	Female number	PIT ID	Pond	ORL (m)	Number of captures
May 06 – Jul 06	1	659D411	C	40	6
Jun 06 – Sep 06	2	6693DAD	F	20	8
Jul 06 – Sep 06	3	6694D59	D	80	4
Jul 06 – Apr 07	4	669AF3A	C	20	8
Jul 06 – Aug 06	5	6586B64	A	15	6
Aug 06 – Sep 06	6	659CE8C	A	20	3
Sep 06 – Nov 06	7	65A3AE5	D	15	2
Sep 06 – Mar 07	8	659CEF0	E	40	3
Sep 06 – Aug 07	9	65A3503	A	20	7
Feb 07 – Apr 07	10	659DE88	D	20	4
Feb 07 – Mar 07	11	6955889	G	40	2
Feb 07 – Apr 07	12	66AC071	A	20	2
Feb 07 – May 07	13	6955F55	D	100	4
Feb 07 – May 07	14	695554B	E	40	5
Feb 07 – Oct 07	15	65A0F06	G	60	5
Feb 07 – Apr 07	16	6956BC4	G	40	4
Apr 07 – Jun 07	17	69DECA8	A	20	4
Mar 07 – Apr 07	18	69556C8	D	15	3
Apr 07 – May 07	19	69DE53A	D	15	3
Apr 07 – Jun 07	20	69DC1F3	D	15	3
Apr 07 – May 07	21	6955B91	G	60	4
May 07 – Aug 07	22	69B5240	G	20	4
Sep 07 – Nov 07	23	69DCE90	B	20	4
Sep 07 – Nov 07	24	69B3E72	B	15	2
Mar 08 – May 08	25	69B4083	A	15	4
Mar 08 – May 08	26	69DEF4B	A	15	2
Feb 09 – May 09	27	69DF024	A	15	4
Feb 09 – Jul 09	28	69DF1E6	A	40	4
Mar 09 – May 09	29	69DECCF	E	20	3
May 09 – Jul 09	30	69DE9ED	D	70	6
May 09 – Jul 09	31	69DF0A5	G	50	3

Table A21 Observed range lengths (m) (ORL) of the 9 male water voles that maintained a home range during the winter (November to February)

Date	Male number	PIT ID	Pond	ORL (m)	Number of captures
Jul 06 – Apr 07	4	659D70B	C	60	6
Jul 06 – May 07	6	65857F6	E	15	4
Jan 07 – May 07	11	695C895	B	40	3
Jan 07 – Sep 07	12	6696B6A	D	60	3
Feb 07 – Oct 07	13	65A06DB	G	80	4
Sep 06 – Dec 06	18	659D7BF	D	15	2
Nov 06 – Dec 06	19	659D259	E	60	2
Nov 06 – Feb 07	20	65A01DA	E	80	6
Dec 06 – Jan 07	21	65A043E	D	60	3

Table A22 Observed range lengths (m) (ORL) of the 9 female water voles that maintained a home range during the winter (November to February)

Date	Female number	PIT ID	Pond	ORL (m)	Number of captures
Jul 06 – Sep 06	3	6694D59	A	15	3
Jul 06 – Apr 07	4	669AF3A	C	20	2
Sep 06 – Nov 06	7	65A3AE5	D	15	2
Sep 06 – Mar 07	8	659CEF0	B	40	5
Feb 07 – Apr 07	10	659DE88	D	15	3
Feb 07 – Mar 07	11	6955889	G	20	2
Mar 09 – May 09	29	69DECCF	B	20	3
Nov 06 – Jan 07	32	659DOD1	D	15	4
Jan 07 – Feb 07	33	66C722D	A	20	2

7. *Dominant Vegetation Types (DVT) and trapping data*

Table A23 Pond A: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	Dominant Vegetation Type (DVT)	Males	Females	Juveniles	Total
A1	*Rubus fruticosus*	2	21	2	25
A2	*Juncus conglomeratus*	4	0	0	4
A3	*Juncus conglomeratus*	6	3	0	9
A4	*Typha latifolia*	5	2	0	7
A5	*Juncus effusus*	5	20	4	29
A6	*Juncus effusus*	4	1	1	6
A7	Trees	0	0	0	0
A8	Trees	0	0	0	0
	Total captures	26	47	7	80

Table A24 Pond B: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	Dominant Vegetation Type (DVT)	Males	Females	Juveniles	Total
B1	*Carex riparia*	11	3	1	15
B2	Trees	0	0	0	0
B3	*Typha latifolia*	2	1	1	4
B4	*Epilobium hirsutum*	14	10	0	24
B5	*Juncus effusus*	4	3	2	9
	Total captures	31	17	4	52

Table A25 Pond C: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	Dominant Vegetation Type (DVT)	Males	Females	Juveniles	Total
C1	*Carex riparia*	3	3	1	7
C2	*Carex riparia*	6	9	3	18
C3	*Juncus effusus*	3	4	0	7
C4	*Juncus effusus*	3	0	0	3
C5	*Carex riparia*	15	12	1	28
	Total captures	30	28	5	63

Table A26 Pond D: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	DVT	Males	Females	Juveniles	Total
D1	*Rubus fruticosus*	8	10	1	19
D2	*Juncus effusus*	14	9	1	24
D3	*Juncus effusus*	4	8	0	12
D4	*Bolboschoenus maritimus*	7	1	1	9
D5	*Rubus fruticosus*	0	3	0	3
D6	*Rubus fruticosus*	4	3	0	7
D7	Trees	0	1	1	2
D8	Damp grassland	1	3	0	4
	Total captures	38	37	4	80

Table A27 Pond E: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	Dominant Vegetation Type (DVT)	Males	Females	Juveniles	Total
E1	*Carex riparia*	13	3	1	17
E2	*Juncus effusus*	6	3	0	9
E3	*Juncus effusus*	6	12	1	19
E4	*Epilobium hirsutum*	3	4	0	7
E5	*Epilobium hirsutum*	0	5	1	6
E6	*Typha latifolia*	6	4	1	11
	Total captures	34	31	4	69

Table A28 Pond F: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	Dominant Vegetation Type (DVT)	Males	Females	Juveniles	Total
F1	*Bolboschoenus maritimus*	2	7	1	10
F2	Trees	1	2	0	3
	Total captures	3	9	1	13

Table A29 Pond G: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	Dominant Vegetation Type (DVT)	Males	Females	Juveniles	Total
G1	*Typha latifolia*	2	0	1	3
G2	*Juncus effusus*	1	1	0	2
G3	*Juncus effusus*	4	6	1	11
G4	*Juncus effusus*	6	7	0	13
G5	*Juncus effusus*	2	0	1	3
G6	*Rubus fruticosus*	6	5	0	11
G7	*Juncus effusus*	4	2	3	9
G8	*Carex riparia*	4	1	4	9
G9	*Juncus effusus*	2	3	0	5
G10	*Epilobium hirsutum*	0	1	0	1
G11	*Juncus effusus*	4	4	0	8
G12	*Juncus effusus*	0	0	0	0
G13	*Juncus effusus*	5	4	0	9
G14	*Juncus effusus*	0	0	0	0
G15	*Typha latifolia*	1	2	0	3
G16	Trees	0	0	0	0
G17	*Rubus fruticosus*	0	0	0	0
G18	Bare mud	0	0	0	0
	Total captures	41	36	10	87

Table A30 Pond H: Dominant Vegetation Type (DVT) per trap and associated number of water vole captures including adults (transients and residents) and juveniles

Trap number	Dominant Vegetation Type (DVT)	Males	Females	Juveniles	Total
H1	*Glyceria maxima*	0	1	0	1
H2	*Juncus effusus*	3	4	0	7
H3	*Typha latifolia*	7	3	0	10
H4	*Juncus effusus*	1	3	1	5
	Total captures	11	11	1	23

8. Water content of forage species and water vole faecal pellets

Table A31 Water content of plant species selected as forage by water voles (as inferred from freeze drying)

Sample	Plant species	Date collected	Wet weight (g)	Dry weight (g)	Water content (g)	water content (%)
1	*E. hirsutum*	14/03/09	3.325	0.463	2.862	86.08
2	*C. riparia*	14/03/09	2.681	0.344	2.337	87.17
3	*T. latifolia*	14/03/09	3.885	0.595	3.290	84.68
4	*C. riparia*	25/09/08	2.314	0.758	1.556	67.24
5	*T. latifolia*	14/03/09	5.522	0.199	5.323	96.40
6	*J. effusus*	14/03/09	2.924	1.057	1.867	63.85
7	*E. hirsutum*	14/03/09	3.078	0.254	2.824	91.75
8	*C. palustre*	25/09/08	2.772	0.051	2.721	98.16
9	*C. riparia*	14/03/09	3.925	0.766	3.159	80.48
10	*P. hydropiper*	25/09/08	4.776	0.838	3.938	82.45
11	*T. latifolia*	25/09/08	6.016	1.187	4.829	80.27
12	*J. effusus*	25/09/08	5.283	1.529	3.754	71.06
13	*T. latifolia*	25/09/08	7.044	0.455	6.589	93.54
14	*T. latifolia*	25/09/08	2.598	0.472	2.126	81.83
15	*P. hydropiper*	25/09/08	3.880	0.963	2.917	75.18
16	*P. australis*	01/05/09	11.060	1.700	9.360	84.63
17	*C. riparia*	12/05/09	4.770	1.110	3.660	76.73
18	*E. hirsutum*	12/05/09	4.630	0.690	3.940	85.10
19	*J. effusus*	12/05/09	1.510	0.440	1.070	70.86
20	*T. latifolia*	12/05/09	3.830	0.630	3.200	83.55
21	*R. repens*	12/05/09	4.260	0.670	3.590	84.27
22	*I. pseudacorus*	12/05/09	3.700	0.670	3.030	81.89
23	*G. maxima*	12/05/09	2.430	0.580	1.850	76.13
24	*J. effusus*	25/09/08	2.797	1.087	1.710	61.14
25	*P. hydropiper*	25/09/08	5.784	1.539	4.245	73.39
26	*C. riparia*	25/09/08	5.070	1.895	3.175	62.62
27	*T. latifolia*	25/09/08	6.479	0.973	5.506	84.98
28	*E. hirsutum*	25/09/08	2.091	0.363	1.728	82.64
29	*E. hirsutum*	25/09/08	2.189	0.563	1.626	74.28
30	*T. latifolia*	25/09/08	6.002	0.850	5.152	85.84
31	*P. hydropiper*	25/09/08	4.261	0.551	3.710	87.07
32	*E. hirsutum*	25/03/08	0.929	0.057	0.872	93.86
33	*C. riparia*	25/03/08	3.282	1.491	1.791	54.57
34	*C. riparia*	25/03/08	3.082	0.966	2.116	68.66
35	*J. effusus*	25/03/08	4.079	1.646	2.433	59.65
36	*J. effusus*	25/03/08	1.195	0.433	0.762	63.77
37	*T. latifolia*	25/03/08	13.808	1.700	12.108	87.69
38	*T. latifolia*	25/03/08	2.207	0.108	2.099	95.11
39	*E. palustris*	17/05/09	3.754	0.867	2.887	76.90
40	*C. longus*	17/05/09	12.121	1.900	10.221	84.32
41	*C. longus*	17/05/09	3.078	0.590	2.488	80.83
42	*M. domestica*	01/09/08	14.682	2.199	12.483	85.02

Table A32 Water content of faecal pellets collected from water voles and latrines (as inferred from freeze drying)

Sample	Source	Date	Wet weight (g)	Dry weight (g)	Water content (g)	Water content (%)
1	Female	7/11/07	0.207	0.051	0.156	75.34
2	Male	29/1/08	0.116	0.050	0.065	56.44
3	Male	20/11/07	1.144	0.275	0.869	75.96
4	Female	20/3/08	0.142	0.075	0.067	47.22
5	Male	18/10/07	0.104	0.060	0.044	42.14
6	Juvenile	17/10/07	0.230	0.097	0.133	57.78
7	Female	20/3/08	0.242	0.072	0.170	70.15
8	Male	20/3/08	0.324	0.087	0.237	73.19
9	Female	20/3/08	0.249	0.077	0.173	69.21
10	Male	18/3/08	0.093	0.047	0.046	49.27
11	Male	19/3/08	0.093	0.047	0.046	49.27
12	Female	19/3/08	0.193	0.068	0.125	64.55
13	Male	18/3/08	0.179	0.053	0.126	70.52
14	Female	18/3/08	0.348	0.128	0.220	63.23
15	Juvenile	8/11/07	0.146	0.072	0.075	51.09
16	Male	18/3/08	0.313	0.145	0.168	53.64
17	Female	7/11/07	0.167	0.065	0.102	61.15
18	Male	30/1/08	0.273	0.104	0.170	62.10
19	Male	17/10/07	0.158	0.068	0.090	57.23
20	Juvenile	18/3/08	0.123	0.062	0.062	49.90
21	Female	7/11/07	0.146	0.078	0.068	46.34
22	Latrine	25/3/08	0.390	0.081	0.309	79.22
23	Latrine	25/3/08	0.785	0.141	0.644	82.09
24	Latrine	25/3/08	0.372	0.076	0.296	79.63
25	Latrine	25/3/08	0.659	0.127	0.532	80.70
26	Latrine	25/3/08	0.336	0.086	0.250	74.27
27	Latrine	25/3/08	0.502	0.106	0.397	78.99
28	Latrine	25/3/08	0.409	0.087	0.322	78.64
29	Latrine	25/9/08	0.548	0.109	0.438	80.03
30	Latrine	25/9/08	0.654	0.128	0.526	80.36
31	Latrine	25/9/08	0.737	0.129	0.608	82.51
32	Latrine	25/9/08	0.583	0.127	0.456	78.22
33	Latrine	25/9/08	0.970	0.151	0.819	84.44
				Mean water content (%)		66.81

9. Rats

Table A33 Spatial and temporal variation in the number of brown rats (*Rattus norvegicus*) captured throughout the duration of the study

Pond / Year	A	B	C	D	E	F	G	H	Total
2006	0	0	0	0	0	0	-	-	0
2007	0	1	1	0	0	0	5	1	8
2008	0	3	2	0	0	0	3	0	8
2009	0	0	2	0	2	0	3	0	7
Total	0	4	5	0	2	0	11	1	23

10. Pond depth profiles

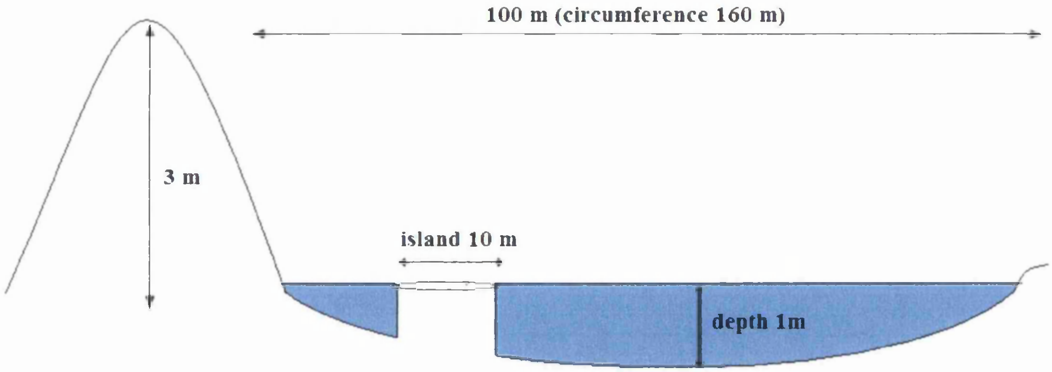

Figure A10 Depth profile of pond A (not to scale)

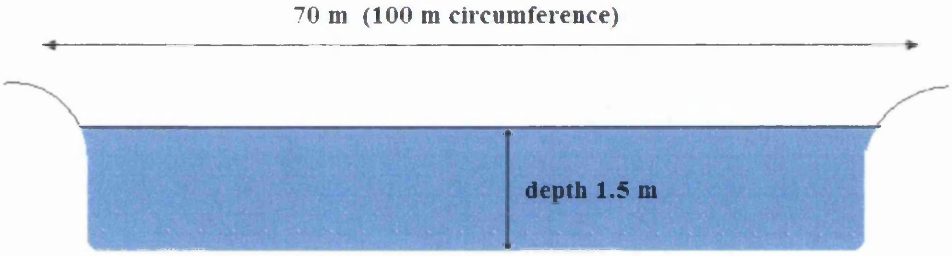

Figure A11 Depth profile of pond B (not to scale)

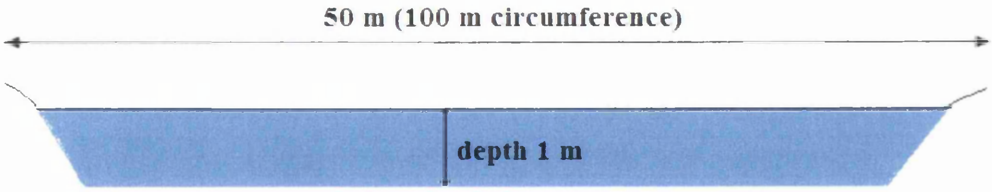

Figure A12 Depth profile of pond C (not to scale)

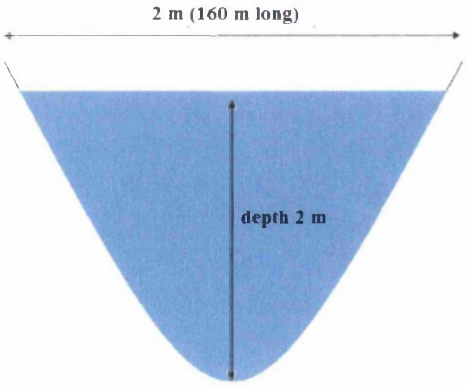

Figure A13 Depth profile of pond D (not to scale)

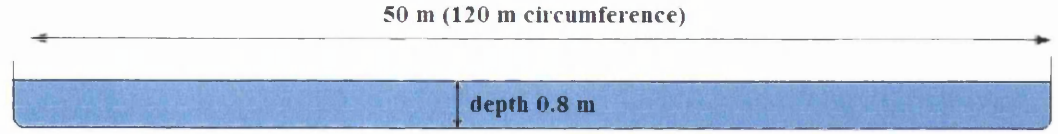

Figure A14 Depth profile of pond E (not to scale)

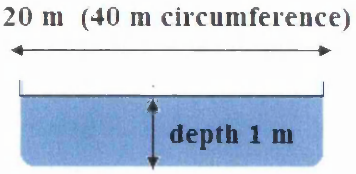

Figure A15 Depth profile of pond F (not to scale)

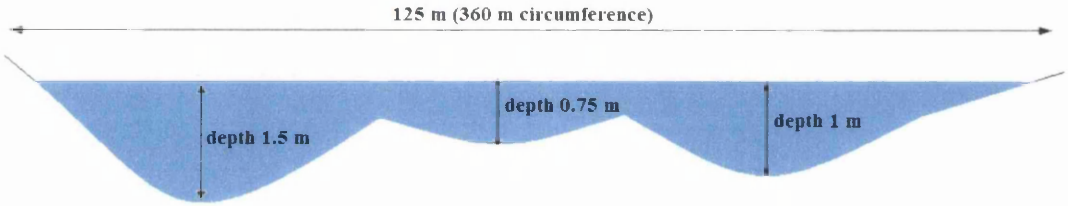

Figure A16 Depth profile of pond G (not to scale)

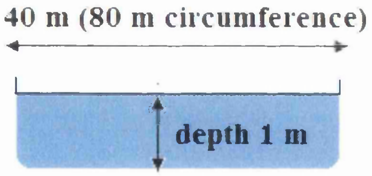

Figure A17 Depth profile of pond H (not to scale)

11. Distribution of feeding stations and latrines per DVT

The map overleaf indicates the distribution of feeding stations (F) and latrines (L) per dominant vegetation type (DVT). The locations of areas in which these field signs were created are highlighted. See chapter 5 for the number of feeding stations and latrines per DVT.

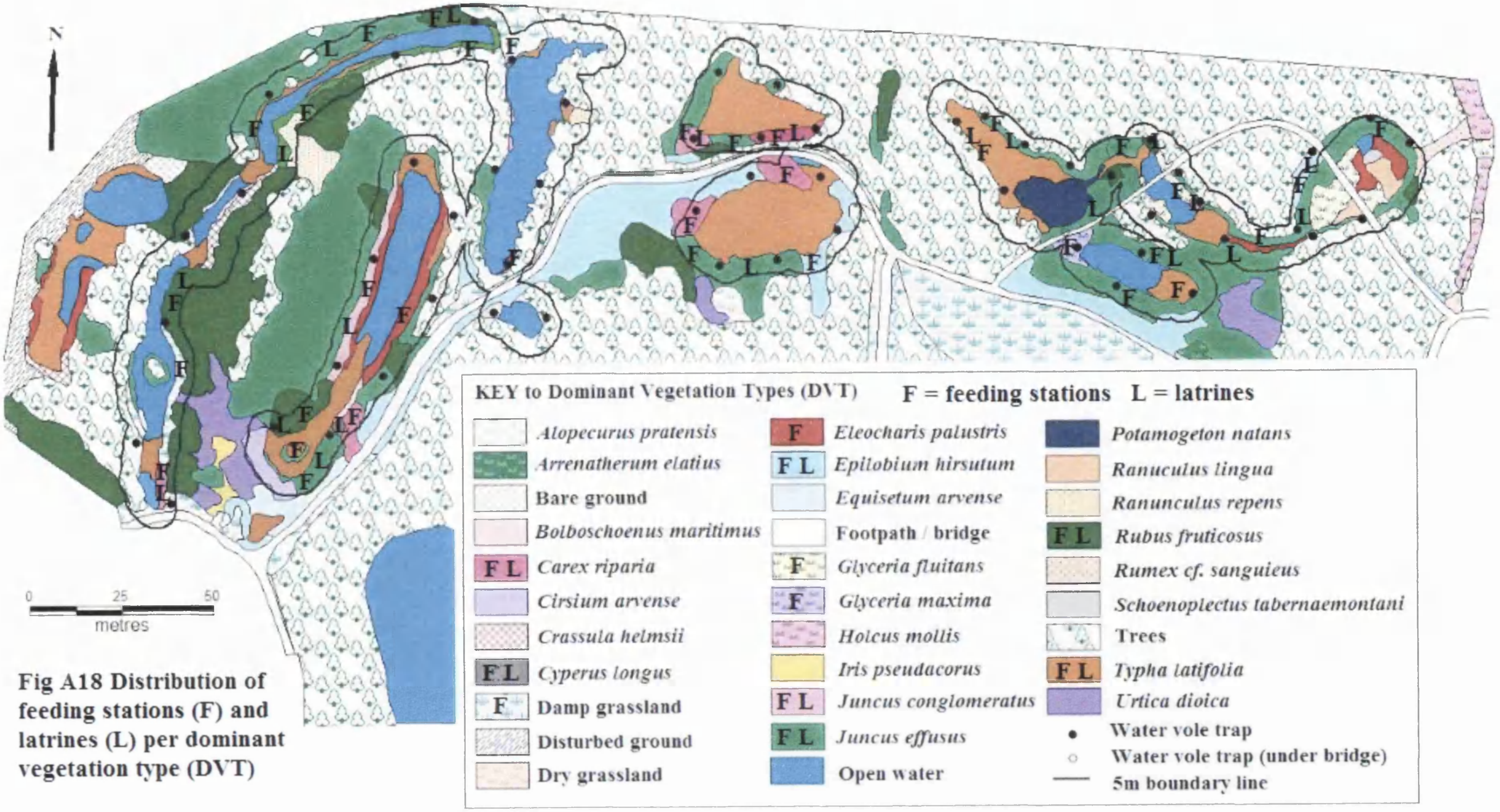

Fig A18 Distribution of feeding stations (F) and latrines (L) per dominant vegetation type (DVT)