Analyses of the Eurasian otter (<italic>Lutra lutra</italic> L.) in South Wales: Diet, distribution and an assessment of techniques.

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How to cite:

Parry, Gareth Stephen (2010) *Analyses of the Eurasian otter (<italic>Lutra lutra</italic> L.) in South Wales: Diet, distribution and an assessment of techniques..* thesis, Swansea University.
http://cronfa.swan.ac.uk/Record/cronfa42984

Analyses of the Eurasian otter (*Lutra lutra* L.) in South Wales: Diet, distribution and an assessment of techniques

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Submitted to the University of Wales in fulfilment of the
requirements for the Degree of Doctor of Philosophy

Swansea University

September 2010

THESIS SUMMARY

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Full title of thesis: Analyses of the Eurasian otter in South Wales: Diet, distribution and an assessment of techniques

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Summary:

The ecology of otters (*Lutra lutra* L.) was studied at a number of locations to investigate specific aspects of carnivore behaviours and trophic niche breadth. Otter inhabiting the Gower Peninsular, in South Wales, ate freshwater fish (58.7%), marine fish (24.6%), non-fish (16.2%) and unidentified prey (0.6%). Bullhead was the core prey on Gower, although eel, stickleback, flatfish, brown trout and amphibians were also important dietary components. There was significant temporal and spatial variation in the composition of otter diet on Gower. A year long study of otters on the Pembrokeshire coast found that diet was composed of marine fish (56%), freshwater fish (29%) and non-fish prey (15%). Otter diet was very diverse on Gower and the Pembrokeshire coast, with slow swimming demersal fish the most frequent prey items. A systematic meta-analytical review of otter dietary studies demonstrated that otters have a very broad trophic niche across Europe ($H' = 0.77$) and suggested that otters are facultative foragers. There was no evidence of latitudinal or Mediterranean trends in trophic diversity. Variation in trophic diversity and dietary composition appeared to be driven at the habitat level. A rigorous assessment of the techniques used to monitor otter populations and investigate otter diet was also undertaken. The standard 600 m transect used to determine otter distribution was inadequate at detecting otters on small lowland rivers, due to a high rate of type II error. Increasing transect size, making repeat visits and surveying additional sites improved the detection power of otter surveys. Five different spraint analysis methods produced dietary data with a low level of comparability. Potential limitations of volumetric analysis in highly diverse diets were identified. Molecular tools and new technologies need to be applied in carnivore dietary studies to advance theories of foraging, competition and life-history strategies.

Declaration

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Acknowledgements

The fact that I have undertaken this study and produced this thesis is, in no small part, down to the support and kindness shown to me by many people and for that I'm truly grateful. Here I will attempt to acknowledge and thank everyone as best I can.

I grew up in the remarkable natural beauty of "The Island", and if it is possible to thank a land mass I am indebted for the interest it sparked in me. My friends there played a big role in shaping my character, and therefore my ability to complete this study. In particular, Danny, Andrew, Mitch, Tom and Luke. In Wales, I have been fortunate to meet some exceptional people. I'm considerably obliged to everyone who lived at "number 20" and "126", particularly for tolerating the faeces and assorted dead things which frequented our freezers. Much gratitude to Fraser and Macky (and the Barry boys) for being first class mates, providing entertainment and humility as and when needed. Thanks to everyone at Vivaldi for employing an average waiter and providing him with delicious meals. It has been a privilege to work alongside the lovely people of CERTS, certainly a force for good in this world. Thanks to Wendy and Penny for their support and making our lab such a good environment to be in, and also to Carolyn for her support and immense common sense. I have been accompanied in the field by many enthusiastic volunteers whom I would like to thank; Hannah, Jess, Chris, Emma, Mark, Adam, Nicola, Ellen, Owen, Gael, Rachael and Felicity, and dam all of you who saw the otters which eternally evade me! A particular mention goes to Waylie whose assistance and company brightened up many surveys otherwise blighted by the Welsh climate. I would like to thank the landowners of Gower for allowing me to traipse through their fields and gardens to collect otter spraints. The Fairy Hill hotel were especially accommodating in this respect. I must also thank all of the volunteers who collected otter spraints on Pembrokeshire, and the Pembrokeshire Marine SAC group for allowing me to use the data I obtained from those spraints. In particular, I would like to thank Sue Burton, Bethan Cox, Blaise Bullimore and Lynne Ferrano for co-ordinating the project and ensuring the spraints reached me. I'm considerably indebted to GIS adivice of Tim Fearnside and the statistical knowledge of Owen Bodger and Mike Gravenor. A number of otter workers from around the world supplied papers and data that made the review possible and for that I am indebted.

Finally I would like to thank a small group of people, without whom this thesis (and my sanity) would not exist. My supervisor Dan has been an incredible inspiration, doing a fantastic job of keeping me positive, focused and stocked with weird and wonderful music. I probably haven't said it enough, but thank you for everything, and I only hope this is the start of our work together. I'd like to thank Jason for been an amazing brother and helping to keep the wolves from the door. To my beautiful girl Shona, you are the most important thing in my life. I'm sorry if at times it felt like this thesis was my "other girlfriend". I love you. Lastly, I would like to thank my parents, for the sacrifices you made for your children and for making us believe we could achieve anything if we tried hard enough. This thesis is dedicated to both of you.

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Acronyms

ANCOVA = Analysis of Covariance

ANOVA = Analysis of Variance

AONB = Area of Outstanding Natural Beauty

BAP = Biodiversity Action Plan

BOD = Biochemical Oxygen Demand

CAP = Community Analysis Package

CITES = Convention on International Trade in Endangered Species

ELISA = Enzyme-linked immunosorbant assay

FO = Frequency of Occurrence

GPS = Global Positioning System

HCT = Herpetological Conservation Trust

IOSF = International Otter Survival Fund

IUCN = International Union for the Conservation of Nature

KMO = Kaiser-Meyer-Olkin

KS = Kolmogorov-Smirnov

KW = Kruskal Wallis

LNR = Local Nature Reserve

LSD = Least Significant Difference

MANOVA = Multiple Analysi of Variance

NGO = Non-Government Organisation

NNR = National Nature Reserve

NVH = Niche Variation Hypothesis

OFT = Optimal Foraging Theory

PCA = Principal Component Analysis

PW = Percentage Weight

RFN = Relative Frequency of Numbers

RFO = Relative Frequency of Occurrence

RHS = River Habitat Survey

RWP = Relative Weight Percentage

SAC = Special Area of Conservation

SD = Standard Deviation

SE = Standard Error

SPA = Special Protection Area

SPSS = Statistical Package for the Social Sciences

SRH = Scheirer-Ray-Hare

SSSI – Site of Special Scientific Interest

SW = Shannon-Wiener

UK = United Kingdom

UKBAP = United Kingdom Biodiversity Action Plan

WWT = Wildfowl and Wetland Trust

List of species mentioned in the text

Common Name	**Taxonomic name**
American mink	*Mustela vison*
Atlantic cod	*Gadus morhua*
Atlantic salmon	*Salmo salar*
Ballan wrasse	*Labrus bergylta*
Bank vole	*Myodes glareolus*
Bass	*Dicentrarchus labrax*
Black bream	*Spondyliosoma cantharus*
Brill	*Scophthalmus rhombus*
Brook lamprey	*Lampetra planeri*
Brown rat	*Rattus norvegicus*
Brown trout	*Salmo trutta*
Bullhead	*Cottis gobio*
Butterfish	*Pholis gunnellus*
Canadian lynx	*Lynx canadensis*
Chub	*Leuciscus cephalus*
Common bream	*Abramis brama*
Common carp	*Cyprinus carpio*
Common cormorant	*Phalacrocorax carbo*
Common frog	*Rana temporaria*
Common goby	*Pomatoschistus microps*
Common shrew	*Sorex araneus*
Common smooth-hound	*Mustelus mustelus*
Common toad	*Bufo bufo*
Coyote	*Canis latrans*
Dab	*Limanda limanda*
Elk	*Cervus elaphus*
Ethiopian wolf	*Canis simensis*
Eurasian badger	*Meles meles*
Eurasian otter	*Lutra lutra*
European eel	*Anguilla anguilla*
European hake	*Merluccius merluccius*
European pine marten	*Martes martes*
European polecat	*Mustela putorius*
Fifteen-spined stickleback	*Spinachia spinachia*

Five-bearded rockling	*Ciliata mustela*
Flounder	*Platichthys flesus*
Four-bearded rockling	*Enchelyopus cimbrius*
Genet	*Genetta genetta*
Geoffroys cat	*Felis geoffroyi*
Golden-ringed dragonfly	*Cordulegaster boltonii*
Goldfish	*Carassius auratus*
Grass snake	*Natrix natrix*
Great-crested newt	*Triturus cristatus*
Great pipefish	*Syngnathus acus*
Grey gurnard	*Eutrigla gurnardus*
Grey heron	*Ardea cinerea*
Grey thick-lipped mullet	*Chelon labrosus*
Grizzly bear	*Ursus arctos horribilis*
Herring	*Clupea harengus*
Harbour seal	*Phoca vitulina*
Iberian lynx	*Lynx pardinus*
John dory	*Zeus faber*
King penguin	*Aptenodytes patagonicus*
Lesser sand eel	*Ammodytes tobianus*
Lesser weever fish	*Echiichthys vipera*
Lion	*Panthera leo*
Little egret	*Egretta garzetta*
Lumpsucker	*Cyclopterus lumpus*
Mackerel	*Scomber scombrus*
Minnow	*Phoxinus phoxinus*
Moose	*Alces alces*
Montagu's blenny	*Coryphoblennius galerita*
Mountain lion	*Puma concolor*
Neotropical river otter	*Lontra longicaudis*
North American river otter	*Lontra canadensis*
Palmate newt	*Triturus heleveticus*
Pike	*Esox lucius*
Pipefish	*Sygnathidae*
Plaice	*Pleuronectes platessa*
Pogge	*Agonus cataphractus*

Polar bear	*Ursus maritimus*
Polecat	*Mustela putorius*
Rabbit	*Oryctolagus cunniculus*
Red fox	*Vulpes vulpes*
Roach	*Rutilus rutilus*
Rock goby	*Gobius pagonellus*
Rudd	*Scardinius erythrophthalmus*
Saithe	*Pollachius virens*
Sea cat	*Lutra feline*
Sea lamprey	*Ptromyzon marinus*
Sea otter	*Enhydra lutris*
Sea scorpion	*Taurulus bubalis*
Scad	*Trachurus trachurus*
Slow worm	*Anguis fragilis*
Smooth-coated otter	*Lutra perspicillata*
Smooth newt	*Triturus vulgaris*
Snow Leopard	*Panthera uncial*
Snowshoe hare	*Lepus americanus*
Sole	*Solea solea*
Stella sea lion	*Eumetopias jubatus*
Stone loach	*Noemacheilus barbatulus*
Three-bearded rockling	*Gaidropsarus vulgaris*
Three-spined stickleback	*Gasterosteus aculeatus*
Tiger	*Panthera tigiris*
Water shrew	*Neomys fodiens*
Water vole	*Arvicola terrestris*
Weasel	*Mustela nivalis*
Whiting	*Merlangius merlangus*
Wildcat	*Felis selvestris*
Wolf	*Canis lupus*
Wood mouse	*Apodemus sylvaticus*
Viviparous eelpout	*Zoarces viviparus*

Chapter 1

Introduction

"The river's swollen up with rusty cans and

the trees are burning in your promised land"

Leonard Cohen (Diamonds in the Mine, 1971, Columbia Records, Nashville)

1.1 The concept of an Ecological Niche

The position of an organism within its environment is described as its niche (Elton, 1927). An ecological niche is a concept that tries to encapsulate how an organism utilises resources and interacts with its environment and community. An organism's niche is essentially a multidimensional entity describing many factors, such as habitat, diet and activity patterns (Hutchinson, 1957). The niche occupied by an organism depends upon its phenotype and the surrounding environment (Whittaker *et al.* 1973). All organisms function within a niche which lies along a continuum of variation between specialist and generalist (Hutchinson, 1957). Specialists have narrow tolerances and patterns of resource use, whereas generalists have a broader tolerance to environmental conditions and more diverse resource use (Futuyma and Moreno, 1988). The degree of specialisation may not be correlated between different ecological traits (Cody, 1974), so each trait should be considered separately. There is normally an optimal niche, which is linked to an optimal phenotype and associated with higher fitness values (Levins, 1962). Consequently, selection favours individuals occupying niches closer to the optimal state (Maynard Smith, 1962). An organism's niche is therefore the most fundamental unit of study in ecology and has numerous applications.

The full range of resources and conditions that an organism can potentially tolerate or utilise is defined as its fundamental niche, which is a manifestation of the organism's genetic properties (Futuyma and Moreno, 1988; Sargeant, 2007). Fundamental niches can be used to investigate the constraints on a species distribution (Hirzel *et al.* 2002), predict species invasions (Peterson, 2003) and model the response to changes in environmental and climatic conditions (Martínez-Meyer *et al.* 2004). As fundamental niche has a genetic basis it can be used to study the ecological divergence of different lineages (Wiens, 2004). Field studies generally observe the realised niche, which is a reduction of the fundamental niche caused by interactions with other organisms and environmental factors (Hutchinson, 1957; Krebs, 2001). The realised niche defines the relationship between species or individuals within a given community (Whittaker *et al.* 1973), forming the basis of major concepts including competition and predator-prey interactions.

1.2 Predators as shapers of community structure and ecological diversity

A carnivore is an organism that consumes animals to obtain the energy it requires for its biological functions (Krebs, 2001). Carnivore populations are characteristically small, have low densities and reproductive rates, which make them vulnerable to extinction (Gittleman *et al.* 2001). Carnivores are of significant ecological interest as they influence the structure and function of ecosystems (Schmitz *et al.* 2000; Ives *et al.* 2005). Predation has a fundamental role in the trophic interactions of food webs exerting a strong top-down selective pressure on prey populations (Leibold, 1996; Miller *et al.* 2001). Predators tend to remove weak and young individuals thereby maintaining the fitness of prey populations (Kruuk and Turner, 1967; Brodie and Brodie, 1999). Predation drives the selection of phenotypes (Lardener, 1998) and behaviours (Hunter and Skinner, 1998) that reduce predation risk, and can affect the spatial organisation of prey populations (Joshi *et al.* 1995). Some carnivores function as keystone predators, a concept defined by Paine (1969) as species having an influence over a community or ecosystem that is disproportionate to their own abundance. Keystone predators may promote diversity within prey communities by enabling the co-existence of competing species (Leibold, 1996) or by regulating the populations of species that alter habitat structure (Power *et al.* 1996). Due to the impact keystone species have on ecosystems, they are of significant concern to environmental managers and policy makers (Power *et al.* 1996). Carnivores are charismatic species making them ideal flagship species to focus conservation action e.g. Polar bear *Ursus maritimus*, Tiger *Panthera tigiris* and Lion *Panthera leo* (Clucas *et al.* 2008). Many carnivores have large ranges, so they can serve as conservation umbrella species, protecting other species within their range (Gittleman *et al.* 2001).

1.3 Trophic niche theory and key indices

An organism's utilisation of food resources is termed its trophic niche, which describes its role in transferring energy within a community (Begon *et al.* 1996; Krebs, 2001). The need to obtain sufficient energy for survival, growth and reproduction is at the core of ecology; therefore, trophic niche is an integral component of the overall niche occupied by an individual or species. There are several different characteristics of trophic niche that can be measured (see Table 1.1).

Table 1.1 Different trophic niche characteristics that can be measured as defined by Sargeant (2007).

Trophic niche characteristic	Definition
Niche evenness	Describes the relative use of each food category
Niche richness	The number of different food categories being utilised
Niche width	Summarises the diversity of an individual's niche, often in terms of the proportion of the resources utilised from different food categories

Carnivores with a more specialised trophic niche (see section 1.1) take a low diversity of prey, whereas generalists take a high diversity of prey. The optimal forgaing strategy may vary according to changes in food resources, competition and environmental conditions (see sections 1.5 and 1.6). It may be beneficial to function as a specialist when one prey type is particularly abundant and conditions are predictable. However, when prey resources and environmental conditions are unpredictable a generalist strategy should be favoured (Krebs and Davies, 1993; Bolnick *et al.* 2003; Tinker *et al.* 2008). Studying trophic niche can provide valuable information on life history strategies related to resource use, changes in environmental conditions as well as interspecific and intraspecific interactions (Krebs, 2001). Dietary studies usually assess the realised trophic niche rather than the fundamental trophic niche (for definition see section 1.1), as they observe the food resources utilised. Diet determines the amount of energy available for an individual to devote to territorial defence and reproductive behaviours (Krebs, 2001). Diet directly influences recruitment to a population affecting birth rate, litter size, neonate survival and immigration (Fuller and Sievert, 2001). Conversely, diet also affects the loss of individuals from a population through starvation and dispersal when food resources are scare. Predator prey relationships are discussed further in section 1.4 and examples of the relationship between prey and consumer population dynamics are provided in section 1.8.2. The relationship between diet and population ecology means a clear understanding of trophic ecology is essential for the successful conservation of any species.

1.4 Predator-prey concepts

Carnivore diet is a particularly important area of ecological research as carnivores have an important influence on ecosystem structure and function (see section 1.2). The dynamics of predator and prey populations are interlinked and predation has a strong influence on community stability (Oaten and Murdoch, 1975), which is the tendency for a community to return to its original state following disturbance (Begon *et al.* 1996). Generalist predators tend to stabilise prey populations, whereas specialist predators tend to cause instability (Krebs, 2001). Predators also apply top down regulation on the populations of prey species, which may restrict their distribution or abundance (MacArthur, 1955; Paine, 1969; Post *et al.* 2000).Conversely, as prey is a fundamental resource for predators, fluctuations in prey populations have a bottom up regulatory effect on predator populations. Carnivore dietary studies help ascertain community stability and viability by identifying foraging strategy and the diversity of prey required to sustain a breeding predator population. The first model of a single predator prey interaction was provided by the Lotka-Volterra equations (Lotka, 1925; Volterra, 1926). More complex models are now available, which take into account the consumption of multiple prey groups and the influence of predator prey ratios (Arditi *et al.* 1991). Predation exerts a strong selective pressure on prey populations driving the predator prey arms race (Dawkins and Krebs, 1979). Many of the morphological, behavioural and physiological characteristics observed in species are adaptations related to predation (Krebs, 2001, see section 1.8.2 for examples). Therefore, dietary studies provide an insight into the evolutionary significance of different life-history strategies.

1.5 Optimal Foraging Theory

Optimal Foraging Theory predicts that an organism will use strategies to maximise energy intake over time as this increases fitness (Macarthur and Pianka, 1966; Stephens and Krebs, 1986). Carnivores are frequently limited by food resources (Fuller and Sievert, 2001) and feeding on mobile prey requires significant energy expenditure (Sih and Christensen, 2001), thus, optimising prey selection and foraging strategy is pivotal. Optimising foraging efficiency increases fitness and enables predators to survive in areas with lower prey densities (Krebs, 2001). The optimal strategy depends upon energetic requirement and factors affecting prey availability and capture (Stephens and Krebs, 1986). Optimal foraging models suggest that predators should be more selective where prey is abundant (Macarthur and Pianka, 1966; Pyke *et al.* 1977) gradually adding less profitable items as long they increase the overall rate of energy gain (Begon *et al.* 1996). However, obtaining food involves a complex sequence of behaviours; location, capture, subjugation, handling and consumption (Krebs and Davies, 1993; Begon *et al.* 1996) each of which is associated with respective costs and benefits. Predators have to strive to minimise costs and maximise benefits. These foraging behaviours are extremely difficult to measure which hinders studies of foraging strategy. Studies also have to consider the influence of physiological factors, such as differential prey digestion rates (see section 1.10.3). Trophic specialisation (see section 1.3) may occurs if there is a high benefit to cost ratio associated with a particular prey type, but this strategy could destabilise predator and prey populations (for examples see section 1.8.2), increasing the risk of predator extinction (Krebs, 2001). Predators can respond to changes in the profitability of a foraging habitat or prey type by utilising switching behaviour (Oaten and Murdoch, 1975). For example, sea otter *Enhydra lutris* diet includes more crabs and clams when the abundance their preferred prey (sea urchins) declines (Ostfeld, 1982). Prey switching can be driven by changes in prey abundance, behaviour or environmental factors (Begon *et al.* 1996), and may be facilitated by switching between prey types or foraging in different habitats containing predictable prey communities (Ostfeld, 1982; Carss *et al.* 1998). Prey switching is important in an evolutionary context, as it helps stabilise fluctuations in prey populations, which in turn stabilises predator populations (Krebs, 2001).

1.6 Trophic partitioning causes and consequences

Optimal Foraging Theory (see section 1.5) predicts that within a given area one diet would be energetically optimal (Macarthur and Pianka, 1966; Stephens and Krebs, 1986). However, the differental utilisation of food resources (trophic partitioning) has been observed within populations (e.g. Svanbäck and Persson, 2004; Svanbäck and Bolnick, 2007; Araújo *et al.* 2008). Trophic partitioning within populations and communities can be driven by several factors, notably differences in foraging ability (Heggberget and Moseid, 1994; Watt, 1993) and competition (Svanbäck and Bolnick, 2007; Araújo *et al.* 2008). Prey resources may be partitioned according to size (McDonald, 2002), type (Svänback and Bolnick, 2007; Araújo *et al.* 2009) or a combination of the two (Tinker *et al.* 2008). Several recent studies have identified trophic partitioning as a major evolutionary driver, maintaining variation in morphological and behavioural characteristics (Bolnick *et al.* 2003; Bolnick 2004; Svänback and Bolnick 2007; Tinker *et al.* 2008). Variation is essential for the processes of evolution and speciation as it provides the traits for natural selection to act upon. Adaptive phenotypic plasticity has lead to the success of organisms in novel habitats and can expand the evolutionary potential of a species (Agrawal, 2001). Foraging strategies that prove advantageous will increase fitness (Krebs, 2001) and thus favour a genotype. Trophic partitioning also enables continued growth in a density dependent population that is limited by prey resources (Van Valen, 1965; Ehlinger, 1990).

1.7 The implications of competition for food

Competition is one of the major interactions occurring between organisms, exerting a selective pressure on individuals, populations and species (Gause, 1934; Abrams, 1987). Competition can occur with individuals of other species (interspecific) or with individuals of the same species (intraspecific) (Krebs, 2001). Ecological niche overlap describes the degree of shared resource use (Sargeant, 2007) and can be used to identify potential areas of competition. Niche overlap in a single trait does not necessarily signify competition, as niche is a multifaceted entity (see section 1.1) and organisms may be relatively segregated in other areas of their ecology (Lack, 1945). Competition requires that an overlap in resource use results in a negative effect (Wiens, 1989b). Competitive ability is an important life history strategy governing the outcome of interactions with other organisms (Krebs, 2001). Carnivores tend to be K-strategists (Gittleman *et al.* 2001), characterised by a low reproductive output but a larger investment in parental care and consequently a lower rate of offspring mortality (Pianka, 1970). Populations of K-strategists are generally subject to higher levels of competition and density dependent regulation (MacArthur and Wilson, 1967). Prey availability is one of the most important factors limiting carnivore populations (Sinclair and Pech, 1996; Abrams and Ginzburg, 2000; Fuller and Sievert, 2001), hence, when prey resources become limited competition can occur. Potential competitors can avoid competition by diverging resource use, a phenomena known as character displacement (Krebs, 2001). Character displacement leads to the utilisation of alternative prey resources, expanding the population's trophic niche (Bolnick, 2004) (for an example of trophic niche expansion see section 1.8.1). Trophic niche expansion can reduce dietary overlap and therefore reduce competition (Svanbäck and Bolnick, 2007).

Trophic competition is important as it can influence population dynamics and the evolution of life history traits. For example, trophic niche expansion enables population growth in a density dependent population (see section 1.6).Competition reduces the fitness of the most common phenotype, so it becomes advantageous to use a subset of the population trophic niche (Bolnick, 2004). This results in disruptive selection of extreme phenotypes, which increases variation within a population and may eventually lead to evolutionary divergence (Bolnick, 2004; Araújo *et al.* 2009). The model organism in this thesis is an apex predator (see section 1.12.4), so intraspecific competition is likely to have a larger influence on diet than interspecific competition. Although, trophic diversification serves to reduce intraspecific competition for food resources it could lead to interspecific competition, due to increased dietary overlap with other species. Furthermore, trophic diversification in predator populations could affect community stability, as it increases the number of predator prey interactions.

1.8 Variation in carnivore trophic ecology

1.8.1 What influences diet and trophic niche breadth in carnivores

Carnivore diet can vary spatially, temporally and between individuals (Iriarte *et al.* 1990; Virgós *et al.* 1999; Elmhagen *et al.* 2000; Prugh *et al.* 2008). Seasonal dietary variation is common in many carnivores (see section 1.8.2) and can be driven by dynamic changes in prey availability or competition. For example, Eurasian otters *Lutra lutra* typically consume a significantly higher proportion of amphibians during winter and spring due to predation on amphibian spawning aggregations (López-Nieves and Hernando, 1984; Weber, 1990; Clavero *et al.* 2005). Similarly, competition with wolves *Canis lupus* caused a significant shift in cougar *Puma concolor* diet from Elk *Cervus elaphus* to deer and sheep (Kortello *et al.* 2007). Carnivores often have large ranges and wide distributions (Gittleman *et al.* 2001), so it is not surprising that geographical dietary trends have been recorded in many species (Virgós *et al.* 1999; Goszczyński *et al.* 2000; Lozano *et al.* 2006; Iverson *et al.* 2006). Several factors influence spatial and temporal variation in carnivore diet. The causes and consequences of trophic partitioning (see section 1.6) and influence of competition on diet (see section 1.7) have been discussed previously. The following sections discuss other factors that influence variation in carnivore diet. Examples are provided from the trophic ecology of the model organism and a range of other carnivore species.

1.8.2 Prey abundance, density and behaviour

Changes in prey availability have a strong influence on carnivore diet (Nachman, 2006). Like most predator prey interactions (see section 1.4) prey availability is a complex entity, which is very difficult to measure as it is influenced by many factors, including prey abundance, prey density, anti-predation behaviour, predator ability, previous experience and prey size (Griffiths, 1975; Li and Li, 1979). Prey availability is also influenced by habitat structure (Kunkel and Pletscher, 2000), which is discussed further below (see section 1.8.3). Temporal and spatial variations in carnivore diet have been shown to reflect changes in prey abundance in several species; Eurasian otter (Heggberget and Moseid, 1994) Red fox *Vulpes vulpes* (Leckie *et al.* 1998), Harbour seal *Phoca vitulina* (Hall *et al.* 1998) and Polar bear (Iverson *et al.* 2006), but these studies did not measure other factors that influence prey availability. The importance of scale in dietary studies is discussed in section 1.8.5. Variation in prey availability affects carnivore diet on a range of temporal and spatial scales. Broad-scale geographical patterns in the diet of genets *Gennetta genetta* (Virgós *et al.* 1999) and wildcats *Felis silvestris* (Lozano *et al.* 2006) have been attributed to differences in prey availability. The distribution of prey patches can drive fine scale spatial variation in diet (Iwasa *et al.* 1981) and influence optimal foraging strategy (see section 1.5). Seasonal dietary trends (e.g. Hall *et al.* 1998; Sidorovich, 2000; Begg *et al.* 2003; Rosalino *et al.* 2005) and long-term shifts in carnivore diet (Elton and Nicholson, 1942; Preston *et al.* 2007) have both been shown to reflect temporal changes in prey abundance.

Predation exerts a selection pressure on prey, leading to behavioural, physiological and morphological adaptations to avoid predation (see section 1.4). The availability of an abundant prey type may be reduced if it has an effective escape response. Birds that show flocking behaviour are less vulnerable to predation than non-flocking birds (Cresswell, 1994), and caudal autonomy is a common anti-predation mechanism in lizards (Clause and Capaldi, 2006). During winter eels respond to decreasing water temperatures by burying into the mud and entering a state of torpidity (Jenkins and Harper, 1980). This life history trait reduces their availability to otters; hence, they are consumed less frequently during this period (Jenkins *et al.* 1979; Brzeziński *et al.* 1993; Watt, 1995). Foraging ability also affects prey availability and is usually related to the size, age and experience of the predator (see section 1.8.4). It is difficult to measure how anti-predation mechanisms and predator ability affect the availability of different prey types, but they have a role in determining the optimal diet (see section 1.5).

The impact of changes in prey availability on predator populations depends upon foraging strategy and how predictable the variation is. Populations of specialist predators typically have a strong cyclical relationship with their prey, such as between the Canadian lynx *Lynx canadensis* and the Snowshoe hare *Lepus americanus* (Elton and Nicholson, 1942). Generalist carnivores have a broader trophic width, and as such, their population dynamics are not as strongly influenced by the abundance of one prey type (Fox, 2005). Generalists tend to respond to changes in prey abundance by utilising switching behaviour, which helps stabilise their populations (see section 1.5). For example, red foxes in Scandinavia switch to roe deer *Capreolus capreolus* fawns when the abundance of voles decreases (Kjellander and Nordström, 2003). Generalist carnivore populations may still suffer losses at times when fewer prey resources are available, but behavioural plasticity enables them to adapt their diet.

1.8.3 Environment, habitat structure and climate

Variation in environmental factors, such as climatic conditions and habitat structure can affect the physiology and behavioural patterns of prey. If this alters their availability it could cause a shift in carnivore diet. One example is the effect of water temperature on the availability of fish. The vast majority of fish species are poikilothermic, so a decrease in water temperature results in a reduction in swimming speed (Beamish, 1978; Lee *et al.* 2003). Changes in water temperature may affect the vulnerability of fish to predation. Piscivorous carnivores appear to preferentially select slow swimming fish (Erlinge, 1968; Trayler *et al.* 1989), as this probably represents a more efficient foraging strategy (See section 1.5). Some species have behavioural adaptations to conserve energy at lower temperatures, which also reduces their availability to predators (e.g. eels, see section 1.8.2). Seasonal fluctuations in rainfall can drive dietary variation in carnivores, leading to prey switching and trophic diversification (Molsher *et al.* 2000; Clavero *et al.* 2003). Rainfall may affect the foraging strategy of riparian carnivores by increasing the energetic cost of foraging in rivers due to increased river flow and turbidity (Lanszki and Sallai, 2006; Prigioni *et al.* 2006a). Climate can also affect prey availability by altering habitat structure. At more northerly latitudes water bodies become frozen during winter, reducing access to fish prey (Sulkava, 1996; Roche, 2001). In Mediterranean climates many small water bodies dry up during summer (Prenda *et al.* 2001) and this coincides with a decreased consumption of fish by Eurasian otters (López-Nieves and Hernando, 1984). Changes in habitat structure can influence prey vulnerability. For instance, moose *Alces alces* are less susceptible to wolf predation in areas with higher tree cover, so moose may represent a less efficient foraging strategy in forests (Kunkel and Pletscher, 2000). Pollution incidents may cause unpredictable changes in prey assemblages, forcing organisms to alter their trophic niche (Eeva *et al.* 1997). The diet of the model organism in this thesis is particularly susceptible to climatic and pollution induced changes in prey populations (see section 1.12).

1.8.4 Innate and learnt predator behaviour

Diet can be affected by innate (genetic) or learnt behaviours. Sexual trophic partitioning may have a genetic base, due to differences in morphology or energetic requirements. For example, in sexually dimorphic species the larger sex tends to take larger prey items (Birks and Dunstone, 1985; Begg *et al.* 2003). Foraging strategy and trophic niche may differ in lactating females due to their high energetic requirements (Powell and Leonard, 1983; Heggberget and Moseid, 1994). Ability and experience has an important influence on foraging strategy as it affects the capture, subjugation and handling stages of predation (see section 1.5).

Prey capture and handling abilities develop gradually, so juveniles and sub-adults are usually less efficient foragers, and may occupy a different trophic niche to adults (Morrison *et al.* 1978). Information such as the location of foraging patches or how to obtain particular prey types may be maternally inherited (Kitchener, 1999). Previous experience may affect prey switching ability (see section 1.5), as predators are more likely to accept alternative prey if they have previously encountered it (Oaten and Murdoch, 1975). As a predator becomes familiar with an area they learn the parameters that affect prey availability, such as the stability of prey patches, enabling them to exploit prey more efficiently (McNamara and Houstan, 1987). Defending a territory would be advantageous if familiarity with an area improves foraging efficiency. Territory quality is likely to reflect social status, with dominant animals holding the best foraging habitat (Schneider, 1984). Low ranking individuals may show trophic diversification to reduce competition with dominants (see section 1.7). Changes in population demography, size and density may increase or reduce competition (Begon *et al.* 1996), leading to changes in the population trophic niche. If a species is subject to interspecific competition diet may be affected by changes in the population of competing species. There is considerable dietary overlap between several Mustelid species (Sidorovich, 2000) meaning changes in the population of one species may affect the diet of another through interspecific competition (see section 1.7).

1.8.5 Spatial scale

Ecological patterns and life history traits often vary with scale, so it is important to study species at a range of scales (Bowyer and Kie, 2006). Patterns in diet that occur at different scales may have unique causes and consequences (Levin, 1992), so the sampling scale should be linked to the study objectives (Kie *et al.* 2002). Carnivore diet can vary on a range of spatial scales (see section 1.8.2), but most studies collect data from a specific area reflecting the realised trophic niche (see section 1.1) of a relatively small proportion of a species global distribution. The information obtained from localised studies is useful as factors limiting individuals within a population, such as prey, often limit the population as a whole (Begon *et al.* 1996). However, this information should be complemented with data collected on a scale more representative of a species' range. At the population level diet is affected by competition (see section 1.7) and local prey assemblages (see section 1.8.2). Therefore, it provides a poor indication of fundamental trophic niche (see section 1.1.) and the evolutionary adaptations of a species (see section 1.9). It is important that investigations of broad spatial trends also expand the temporal scale, as local heterogeneity and sampling bias affect the interpretation of patterns on short time scales (Wiens, 1989a). Seasonal dietary patterns are common in many carnivore species (see section 1.8.2), so recording diet over a short time period could lead to an inaccurate understanding of trophic niche. Furthermore, long-term studies of diet are likely to sample a larger proportion of the population, and thereby, are less prone to idiosyncratic dietary bias. The causes and consequences of dietary patterns could be misinterpreted by sampling at the wrong scale. For example, trophic niche expansion (see section 1.7) at the population level may be due to dietary diversification in a small number of individuals (Svanbäck and Bolnick, 2007; Araújo *et al.* 2008). In the absence of individual dietary data this pattern may be viewed as a population-wide trend, altering models of predator-prey interactions (see section 1.4) and increasing perceived dietary overlap with other species. Amalgamating information collected on a range of scales will provide a more reliable indication of species wide trends in trophic ecology, which can be formulated into models.

1.9 Why is the study of carnivore diet important?

Carnivore dietary studies generate important information for several areas of ecology. They provide insights into the evolutionary processes underlying adaptations to predation, such as bite strength (Christiansen and Wroe, 2007) and muscle type (Munoz-Garcia and William, 2005). It advances the understanding of ecological theories, particularly those related to foraging (see section 1.5), competition (see section 1.7), community regulation (see section 1.2), and predator-prey interactions (see section 1.4). Robust theories supported by empirical data collected in the field are essential for accurate ecological modelling (Austin, 2002). Models are verbal or mathematical statements that attempt to predict the outcome of complex ecological hypothesis (Krebs, 2001). Models can be used to predict the consequences of interspecific competition for prey resources on carnivore populations (Powell and Zielinski, 1983), or the affect changes in carnivore populations will have on community structure, regulation and diversity (Leibold, 1996). These models require an accurate understanding of carnivore diet and trophic interactions. An interdisciplinary application of carnivore dietary data is in the management of economically important prey species. Conflict frequently occurs where carnivores and humans share food resources, such as in marine fisheries (Wickens *et al.* 1992; Freitas *et al.* 1997) or when carnivores predate livestock (Treves *et al.* 2004). Carnivores may predate species that have economical importance for human recreational activities, such as angling (Derby and Lovvorn, 1997; Jacobsen, 2004) or game hunting (Reynolds and Tapper, 1996). Accurate carnivore dietary data is important in order to produce effective management strategies for shared resources, and reduce human-carnivore conflict (Latour *et al.* 2003).

Long-term studies of carnivore diet, providing up to date dietary data are needed to investigate the functional response to changing prey resources and environmental conditions. The potential size of a population is largely dependent on the resources available, and for carnivores food is the usually the most important resource controlling density, distribution, reproductive success, mortality, fitness and behaviour (Fuller and Sievert, 2001). Knowledge of foraging strategy is important, as specialist carnivores may struggle to adapt to environmental change, making them more vulnerable to extinction (see sections 1.1 and 1.5). Trophic partitioning is an important concept (see section 1.6) particularly if a vital group, such as breeding females, occupies a different trophic niche to the rest of the population. Evidence of this has been observed in otters (Heggberget and Moseid, 1994) and Pinnipeds (Reid and Arnould, 1996). Studying and understanding how carnivore populations respond to environmental change at global and local scales is important for ecosystem level conservation, due to the regulatory role of predation (see section 1.2). Future changes in the Earth's climate could substantially alter both aquatic and terrestrial communities (Walther *et al.* 2002; Stuart *et al.* 2004). This may force carnivores to modify their trophic niche, which could affect biodiversity, community structure (see section 1.2) and competition (see section 1.7).

1.10 Techniques for studying vertebrate carnivore diet

1.10.1 Difficulties associated with studying carnivore diet

Vertebrate carnivores are often elusive, have large ranges and live at low densities (Gittleman *et al.* 2001; Gese, 2001; Wilson and Delahay, 2001). Many species are also predominantly nocturnal (Waser, 1980; Carss, 1995; Virgós *et al.* 1999; Ray and Sunquist, 2001). The Ethiopian wolf *Canis simensis* and the snow leopard *Panthera uncial* provide good examples, as they have large ranges in mountainous terrain, live at low densities and forage individually (Oli *et al.* 1993; Sillero-Zubiri and Gottelli, 1995). These characteristics make it difficult to study carnivore trophic ecology. Numerous techniques developed to overcome these challenges (see sections 1.10.2-1.10.5), but the data and conclusions drawn from dietary studies are only as reliable as the techniques used to obtain them. Diet can be assessed directly through visual observations of feeding or prey carcass records (see section 1.10.2). Alternately, diet can be assessed using various indirect techniques (see section 1.10.3). The merits and drawbacks of different techniques are discussed below.

1.10.2 Direct methods of diet and trophic niche assessment

Direct observations of predation events have been used to study diet in a number of carnivores including Felids, Canids, (Kruuk and Turner, 1967) Hyenas (Van Valkenburgh, 1996), and Mustelids (Kruuk and Moourhouse, 1990). Visual observations of feeding provide useful information regarding foraging behaviour (Watt, 1993; Van Valkenburgh, 1996), competition (Haywood, 2006) and trophic partitioning (Tinker *et al.* 2008). However, visual observations of predation by elusive carnivores are rare particularly in nocturnal species. Only 20 observations were made during a three year study of Geoffroy's cat *Felis geoffroyi* undertaken by Johnson and. Franklin, (1991). Even in areas where carnivores are diurnal, visual observations are often made from a distance (Watt, 1993; Kruuk *et al.* 1987), which can hinder prey identification. Kruuk and Moorhouse (1990) observed 3595 predation events in Eurasian otters, but could only identify 57% of prey items. Diet can also be studied directly by examining prey carcasses, a technique that has been used to study the feeding habits of wolves (Boyd *et al.* 1994; Jędrzejewski *et al.* 2000), Polar bears (Derocher *et al.* 2002) and several species of felid (Hart *et al.* 1996; Radloff and Du Toit, 2004). Examining prey carcass can be used to estimate the mass of flesh consumed (Jędrzejewski *et al.* 2000; Derocher *et al.* 2002), providing insights into foraging strategy and energetics (see section 1.5). Determining the size, age, sex and condition of the prey carcass provides useful information on prey selection and predator-prey interactions (Radloff and Du Toit, 2004). Assessing diet through direct visual observations of feeding or by examining prey carcasses is very time consuming, often relying on opportunistic events (Van Valkenburgh, 1996). It takes a significant amount of time, money and effort to obtain a comprehensive record of a population's diet using either technique. These direct methods of assessing diet rarely provide comparable sample sizes to indirect techniques (see section 1.10.3).

1.10.3 Indirect methods of diet and trophic niche assessment

Most carnivore dietary studies assess trophic niche using indirect methods. This usually involves the identification of undigested prey remains present in pellets, stomachs or faeces. Stomach content analysis has been used to study diet in a range of carnivores including wolves (Cuesta *et al.* 1991), Eurasian otters (Britton *et al.* 2006) and King penguins *Aptenodytes patagonicus* (Adams and Klages, 1987). Dietary studies using stomach contents can link data to sex and age (Cuesta *et al.* 1991; Lanszki *et al.* 2008), providing information on trophic partitioning within carnivore populations (see section 1.6). The main drawback of stomach analysis is that obtaining sample material often requires the death of the study organism

(Hyslop, 1980; Cuesta *et al.* 1991; Britton *et al.* 2006), which is highly undesirable especially in studies of endangered species. In mammalian carnivores, this has been overcome by opportunistically collecting carcasses that have died naturally or been killed accidentally (Simpson and Coxon, 2000; Lanszki *et al.* 2008), and if used carefully, stomach pumps can induce regurgitation in seabirds without causing fatality (Wilson, 1984). The sample size of dietary studies using stomach analysis (e.g. Adams and Klages, 1987; Cuesta *et al.* 1991; Lanszki *et al.* 2008) tend to be much smaller than those analysing pellets or faeces (e.g. Beja, 1991; Zijlstra and van Eerden, 1995; Leckie *et al.* 1998).

Faecal and pellet collection does not require invasive procedures or the death of the study organisms, so it can be used to study the diet of rare species e.g. Snow leopard (Oli *et al.* 1993) and common species e.g. Red fox (Leckie *et al.* 1998). Faeces and pellets are easy to collect in large numbers and are a relatively cheap method of obtaining dietary data, as although analysis can be time-consuming very little equipment is required (Carss, 1995; Carss and Parkinson, 1996; Trites and Joy, 2005). Pellets are produced by many predatory birds and consist of regurgitated undigested prey remains (Duffy and Jackson, 1986). Pellet analysis is frequently used to study bird diet, investigating topics such as foraging strategy in owls (Bull *et al.* 1989), trophic competition in raptors (Gerstell and Bednarz, 1999) and the impact of cormorants *Phalacrocorax carbo* on marine fisheries (Leopold *et al.* 1998). Faecal analysis is frequently used to obtain dietary data from mammalian carnivores and has been used to study many aspects of trophic ecology in Pinnipeds (e.g. Dellinger and Trillmich, 1988; Burns *et al.* 1998; Staniland, 2002), Mustelids (e.g. Jenkins *et al.* 1979; Lodé, 1993; Sidorovich, 2000; Van Dijk *et al.* 2007), Cannids (e.g. Leckie *et al.* 1998; Reynolds and Aebischer, 1998; Ciucci *et al.* 2004) and Felids (e.g. Oli *et al.* 1993; Lozano *et al.* 2006). Many carnivores use faeces as scent marks, depositing them in predictable locations (Roper *et al.* 1986; Hutchings and White, 2000; Barja *et al.* 2005). This provides a useful source of material for researchers increasing the ease of dietary studies that would otherwise be difficult to undertake.

Similar methods are used to express the dietary data obtained from stomachs, pellets and faeces, but pellet and stomach analysis produce more reliable data as prey remains are less digested (Jobling, 1987).There are several key issues associated with hard part analysis, regardless of the source of the material, notably that it relies on the presence of hard remains in order to identify prey, and therefore, underestimates soft bodied prey (Reeder, 1951; Duffy and Laurenson, 1983; Carss and Parkinson, 1996; Burns *et al.* 1998). Several studies have questioned whether the frequencies of undigested prey remains accurately reflect the frequency of consumption (Dellinger and Trillmich, 1988; Carss and Parkinson, 1996;

Redpath *et al.* 2001). The rate and extent of digestion may differ with prey type and size (Furness *et al.* 1984) meaning the consumption of some prey items is overestimated, whilst other prey items are completely destroyed during digestion (Duffy and Laurenson, 1983). Physiological variables such as activity level also influence the extent of digestion, with a higher proportion remains recovered following periods of activity (Carss *et al.* 1998).

1.10.4 Molecular approaches to investigating diet

A range of molecular tools are available to help elucidate predator diets (Symondson, 2002). Stable isotope analysis is the most frequently used technique, which has the advantage of detecting soft-bodied prey (Kelly, 2000) However, this technique requires tissue to produce longitudinal data, is associated with numerous biases (Gannes *et al.* 1997) and produces dietary data with a lower resolution than hard-part analysis data (Burns *et al.* 1998). Advances in molecular techniques have enabled identification of prey DNA in faeces, overcoming some of the core restrictions of hard part analysis (Deagle *et al.* 2005). In the future molecular techniques may supersede traditional hard part analysis but currently they remain expensive, which limits sample size and application.

1.10.5 Remote bio-loggers

The difficulties associated with studying carnivore diet (see section 1.10.1) are epitomised in marine species, as foraging usually occurs underwater or in remote areas (Wilson *et al.* 1986). This challenge is ubiquitous throughout marine vertebrate ecology, which led to the development of remote bio-logging devices (Kooyman *et al.* 2004). At first only basic data could be collected, such as dive profiles (Kooyman, *et al.* 1976), but technological advances have enabled more detailed data to be collected, leading to studies of foraging behaviour, foraging strategy and prey mass intake (Pütz *et al.* 1998; Wilson *et al.* 2002). Currently, it has not been possible to accurately determine dietary composition using bio-loggers, but the development of devices such as the inter-mandibular angle sensor (IMASEN) suggest that this may be possible in the future (Ropert-Coudert *et al.* 2004; Liebsch *et al.* 2007). Bio-logging devices hold huge potential for the study of elusive terrestrial carnivores, but few studies have used them. One device that has been successfully deployed on terrestrial species is the Daily Diary, which records detailed information regarding an animal's location, movement, behaviour, energy expenditure and characteristics of the surrounding environment (Wilson *et al.* 2008). Although, there are ethical considerations associated with the use of bio-loggers, (Wilson and McMahon, 2006), they could greatly advance our understanding of trophic ecology in elusive terrestrial carnivores.

1.11 Monitoring populations of elusive carnivores

1.11.1 The function of monitoring programs

For any species the ability to measure and monitor populations is pivotal to understanding their ecology. Determining the distribution, size, demography, fecundity and growth of a population is the basis of conservation biology and paramount to management policies (Gese, 2001). For vulnerable species, determining population distribution and size is an essential step towards successful conservation (Ruiz-Olmo *et al.* 2001). Monitoring can help detect a population decline or failure to reproduce, enabling prompt action to be taken (Eppley and Rubega, 1990). Longitudinal population monitoring data can be used to detect meaningful declines and elucidate potential causes (Hawkins *et al.* 2006). It is important to monitor carnivores as they fill an important ecological role (see section 1.2) and have a high public profile stimulating interest in biodiversity conservation. However, many carnivores are very difficult to monitor due to their population structure, nocturnal behaviour and elusive nature (see section 1.10.1). These traits are typified in the model organism of this thesis (see section 1.12.4). The sensitivity of monitoring schemes should match their objectives and take into account the ecology and status of the species in question (Gese, 2001). Monitoring populations at a broad a level may overlook small declines, which for an endangered species may be critical (Belovsky *et al.* 1994). Conversely, monitoring at too fine a scale may misinterpret natural fluctuations in a population as a more significant trend (e.g. Canadian lynx and snowshoe hare see section 1.8.2). When interpreting the data generated from monitoring schemes the accuracy, power, sample size and statistical power associated with the survey methodology must be taken into account (Macdonald *et al.* 1998; Gese, 2004). It is important to validate the methodology and understand the limitations of monitoring schemes as the data generated has a direct impact on management policy. For example, the recovery in otter populations detected by national monitoring schemes across Western Europe over the last two decades (see section 1.12.1) resulted in the IUCN status of the otter recently being downgraded from 'vulnerable' to 'near threatened' (Reuther and Hilton-Taylor, 2004).

1.11.2 Techniques for monitoring elusive species

As sightings of elusive species are rare (see section 1.10.2) monitoring schemes are often based on identifying indirect but indisputable field signs (e.g. Kohn, 1982; Mason and MacDonald, 1986; Cavallini, 1994). The advantages of indirect survey methods are that they can be undertaken relatively easily in a range of habitats and they are less invasive and cheaper than direct methods (Sadlier *et al.* 2004). Surveys based on indirect field signs are a reasonable method of monitoring distribution, but are less reliable when it comes to estimating population size and growth (Kruuk *et al.* 1986). Faeces are a key field sign used to designate positive sites, but the relationship between faecal density and population size is complex and has only been validated in a few species (Wilson and Delahay, 2001; Sadlier *et al.* 2004). Difficulties arise as in many species faeces function as a scent mark (see section 1.10.3), with a diverse range of functions including; mate attraction (Ferkin and Johnston, 1995), territorial defence (Roper *et al.* 1986), intrasexual competition (King and Gurnell, 2007) and maintenance of social hierarchies (Ishida and Shimizu, 1998). The density and location of faecal marks may be affected by their ecological function.

There are a number of alternative methods of monitoring populations of elusive species. Long-range vocalisation behaviour can be exploited to measure distribution and produce abundance estimates (Maddock *et al.* 1996). Remote cameras have been used to monitor carnivore populations (Kucera *et al.* 1995), but high expense and slow trigger speed currently inhibit widespread use. Wild carnivores can be very wary of novel objects in their environment (Harris and Knowlton, 2001), which impairs population monitoring schemes using cameras, traps and scent stations. In recent years molecular techniques have been developed to monitor populations of elusive species (e.g. Woods *et al.* 1999; Hauer *et al.* 2002; Palomares *et al.* 2002). Molecular methods produce more accurate estimates of population size and have the added advantage of providing information on genetic diversity (Randi *et al.* 2003), sex (Dallas *et al.* 2003) and relatedness (Zedrosser *et al.* 2007). However molecular tools are expensive, which is currently limiting their application in large scale and long-term monitoring programs.

1.12 The Eurasian otter

1.12.1 Distribution and status

The Eurasian otter *Lutra lutra* L.1758 (hereafter referred to as the otter) is a semi-aquatic carnivore belonging to the Mustelidae family. Otters have one of the widest distributions of any carnivore species (Figure 1.1). There have been several major declines in otter populations throughout history (MacDonald and Mason, 1994; Randi *et al.* 2003; Hájková *et al.* 2007). The widespread declines of the mid-twentieth century were primarily caused by the use of organochlorine pesticides (Chanin and Jefferies, 1978) and fragmented many populations, something exacerbated by habitat destruction. Following the population declines otters became protected by British and international law, listed under annexes II and IV of the European Habitat Directive and by schedules 5 and 6 of the Wildlife and Countryside Act 1981. The otter is classified as 'near threatened' by the International Union for the Conservation of Nature (IUCN) (Ruiz-Olmo *et al.* 2008) and is listed in appendix 1 by the Convention on International Trade in Endangered Species (CITES). In the United Kingdom otters are a priority species of the UK Biodiversity Action Plan (UKBAP).

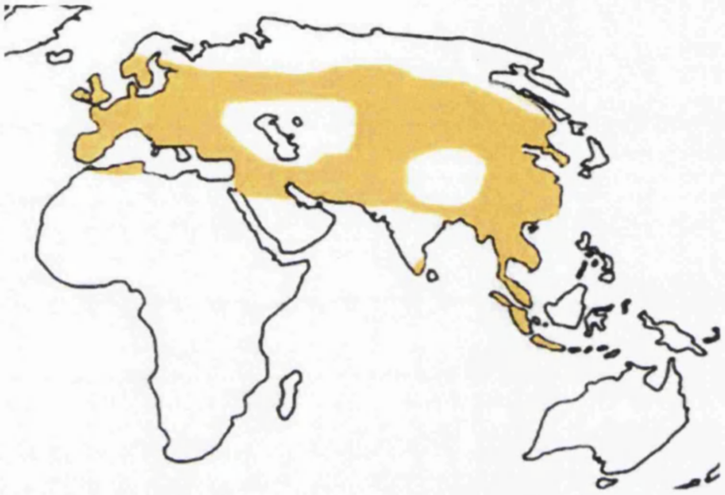


Figure 1.1 Worldwide range of the Eurasian otter *Lutra lutra* (map produced by the IOSF)

1.12.2 Potential threats

Otters face a number of threats including pollution (Erlinge, 1972; Chanin and Jefferies, 1978), habitat destruction (Reuther and Hilton-Taylor, 2004), habitat degradation (Tüzün and Albayrak, 2005), road mortality (Philcox *et al.* 1999), anthropogenic disturbance (Barbosa *et al.* 2003), persecution (Georgiev, 2007), disease (Simpson, 2000) and severe winters (Kruuk and Conroy, 1991). In many areas of Western Europe otter populations are now recovering (Ruiz-Olmo *et al.* 2008), but the effective population size of otters is believed to be very low in many parts of their range, so they remain highly vulnerable to violent demographic changes (Hájková *et al.* 2007).

1.12.3 Gaps in Knowledge

Although a large amount of research has been carried out on otters it has predominantly centred on Western European populations and across much of their range little information is available (Tüzün and Albayrak, 2005).Otters are re-colonizing areas where in many cases prey communities and habitat structure have changed considerably during their absence, and the factors contributing to the success or failure of otters to re-colonise areas are poorly understood (Roche, 2001). In the UK otter conservation is frequently based on information obtained from a small number of Scottish populations over 15 years ago (e.g. Jenkins *et al.*, 1979; Jenkins, 1980; Kruuk *et al.* 1987; Kruuk and Moorhouse, 1990; Weber, 1990; Watt, 1993). A lack of up to date information, particularly in the UK, undermines conservation efforts and our understanding of otter ecology. The significant ecological and evolutionary role of trophic partitioning is now being realised (see section 1.6). The recovery of otter populations in Western Europe (see section 1.12.1), means the likelihood of trophic partitioning occurring within populations is increasing. Otters show clear sexual dimorphism with the larger males having higher growth rates and energetic requirements than females (Heggberget and Moseid, 1994). So it is perhaps no surprise that males tend to take larger prey than females (Kruuk and Moorhouse, 1990; McDonald, 2002). Little is known about the role of intraspecific competition, trophic partitioning and idiosyncratic variation in otter populations, but it may influence social organisation and regulate interspecific competition within the Mustelidae. Similarly, the process and functional significance of olfactory communication signals is poorly understood.

1.12.4 General ecology and life history

Otters inhabit a broad range of wetland, riparian and coastal habitats (Kruuk, 2006). They are of particular ecological interest, being one the few terrestrial predators to have evolved the ability to actively swim and forage in water (Oliveira *et al.* 2008). Otters are an apex predator with important keystone functional role (see section 1.2) within their ecosystems (Bifolchi and Lodé, 2005). Across much of their range otters are elusive and predominantly nocturnal (Carss, 1995), so most knowledge of otter ecology has been obtained indirectly using non-invasive but biased techniques (see sections 1.10.3, 1.11.2 and 1.13). Otters are territorial (Kruuk and Hewson, 1978) and subject to density dependent regulation (Sulkava *et al.* 2007; Hauer *et al.* 2002). However, they have a flexible social structure allowing them to adopt a looser spatial organisation and tolerate increased densities when changes in resource availability necessitate (Erlinge, 1972; López-Nieves and Hernando, 1984; Prenda *et al.* 2001).

Olfactory communication is the most important mechanism for transferring information between and within otter populations (Trowbridge, 1983; Kruuk, 1992). Otter faeces (spraints) are a combination of undigested food remains and glandular secretions, which function as a scent mark (Kruuk, 1992). Spraints are typically deposited on prominent positions on topographical features (Gormally *et al.* 1983; Chanin, 1985; Hutchings and

White, 2000). Otter workers have taken advantage of this easily available resource, hence, most scientific studies of otters use spraints as a sampling unit. Spraints have been used to study many aspects of otter ecology, in particular distribution (e.g. Crawford *et al.* 1979; Strachan and Jefferies, 1996; Jones and Jones, 2004), diet (e.g. Stephens, 1957; Webb, 1975; Jenkins *et al.* 1979; Beja, 1991) and genetic diversity (Hauer *et al.* 2002; Randi *et al.* 2003). Otter ecology and behaviour is subject to considerable variation across its range, something that has enabled it to survive in a wide range of habitats and climates (Kruuk *et al.* 1994; Jacques, 1998; Conroy and Chanin, 2000; Reuther and Dolev, 2000; Dubinin, 2002). This makes it an ideal model for studying the factors affecting carnivore dietary variation at different temporal and spatial scales.

1.12.5 Determining the trophic niche of otters

It is important to identify the trophic niche of otters as it is a species of conservation concern (see section 1.12.1), for which starvation is the biggest cause of mortality (Kruuk and Conroy, 1991; Sulkava *et al.* 2007; Lanszki *et al.* 2008). As an apex carnivore otters have a strong influence on community structure (see sections 1.2 and 1.4). Otter dietary studies have investigated areas such as foraging behaviour (Kruuk and Hewson, 1978; Watt, 1993) prey selection (Carss *et al.* 1990; Heggberget and Moseid, 1994; Lanszki *et al.* 2001), breeding requirements (Kruuk *et al.* 1987; Heggberget and Christensen, 1994; Beja, 1996), interspecific competition (Bonesi *et al.* 2004) and conflict with commercial fisheries (Kloskowski, 2005a). There are currently four basic ways of assessing otter diet; 1) spraint analysis 2) gut content analysis 3) visual observations 4) prey remains found in the field. All of these methods have their benefits and drawbacks (for more information see sections 1.10.2 and 1.10.3). The main difficulty with studying otter diet is that direct observations are rare across much of their range (Carss, 1995).

Spraint analysis is the method most frequently used to study otter diet, but there is no consistent method of interpreting the results (Carss and Parkinson, 1996). Additionally, there are numerous small differences in protocol which contribute to a lack of standardisation between dietary studies. Lack of standardisation is a key problem with otter dietary studies. It is difficult to make comparisons between studies, as a perceived difference in diet may be an artifact of the biases associated with the different methods used. Spraint analysis is subject to the fundamental limitations of faecal dietary analysis (see section 1.10.3). There has been a considerable amount of debate concerning the accuracy of spraint analysis, which is well covered in previous papers (e.g. Carss and Parkinson, 1996; Carss and Elston, 1996; Jacobsen and Hansen, 1996) and discussed further in chapter four. Some studies have expressed their results using several methods (Murphy and Fairley, 1985b; Sulkava, 1996; Kingston *et al.* 1999), which is a useful approach as it increases both the comparability of data and the reliability of conclusions drawn.

1.12.6 Studying prey selection and foraging strategy in otters

It has been suggested that otters prefer or avoid certain prey items (Copp and Roche, 2003; Blanco-Garrido *et al.* 2008), but observed preferences in terms of prey size or type are compounded by a number of factors related to the accuracy of spraint analysis (see section 1.12.5) and prey sampling techniques (Carss and Elston, 1996). There are major limitations with studies of prey selection by otters as most prey sampling methods are biased and few studies attempt to measure the populations of non-fish prey. Fish traps and electro fishing are highly size selective, and thus, give biased interpretations of fish populations (Heggberget and Moseid, 1994; Jacobsen, 2004).Using a range of different sampling techniques can reduce the error, but this is destructive and unethical. Prey selection and foraging strategy are affected by a multitude of factors governing the behaviour of the otter and its prey (see section 1.8) and the interactions between them (see section 1.4).Predation is a complex sequence of events (see section 1.5) and different prey types have different susceptibilities to predation (see section 1.8.2). For example, fast swimming fish such as whiting *Merlangius merlangus* and mackerel *Scomber scombrus* are rarely recorded in otter diet, although, they are often very abundant within coastal foraging areas (Kingston *et al.* 1999). Abundant prey items that are difficult to handle may also be avoided (Beja, 1997; Kingston *et al.* 1999). It is not possible to investigate prey selection or foraging strategy without considering all of the variables that may influence the sequence of predation.

1.12.7 Otter foraging behaviour

Diurnal activity is atypical in otter populations, in many areas they are largely nocturnal or crepuscular (Green *et al.* 1984; Carss *et al.* 1990; Beja, 1991; Lanszki *et al.* 2001; Ruiz-Olmo *et al.* 2001). Many predators are highly active during the crepuscular period as this is a time when both diurnal and nocturnal prey are active, thus making both groups vulnerable (Helfman, 1986). Otters repeatedly use small foraging patches (Kruuk *et al.* 1990) and foraging is expensive energetically (Kruuk and Carss, 1996) so they are under pressure to optimise their strategy. Most information regarding otter foraging behaviour has been derived from studies of captive otters (Erlinge, 1968) or observations of diurnally active wild otters in

Scotland (Kruuk *et al.* 1987; Kruuk and Moorhouse, 1990; Watt, 1993). The data provided by these studies may not be an accurate reflection of foraging behaviour in wild animals. For example, the diving behaviour and activity patterns of free living American Mink *Mustela vison* were measured by Hays *et al.* (2006) using Time-Depth Recorders (TDRs), and were found to be remarkably different from those recorded in captivity and through visual observations of wild animals.

1.12.8 Otter trophic niche

Otters are strongly associated with aquatic environments so naturally fish constitutes a large proportion of their diet (Kruuk, 2006). However, otters are by no means obligate piscivores as a wide range of prey groups have been recorded in their diet, including Amphibia (Weber, 1990), Crustacea (Watson, 1978), Aves (Lanszki and Molnar, 2003), Mammalia (Jurajda *et al.* 1996), Reptilia (Adrian and Delibes, 1987) and Insecta (Harris *et al.* 2007). Otters forage in freshwater (López-Nieves and Hernando, 1984), marine (Watson, 1978) and terrestrial habitats (Lanszki *et al.* 2001). They are generally perceived to be either freshwater or marine foraging, but as demonstrated by Beja (1991) in some areas otters alternate between the two. There are indications that foraging in estuaries is the most efficient strategy, as areas with access to coastal and inland habitats contain a high diversity and abundance of prey (Beja, 1991; Clavero *et al.* 2004).

Otters predominantly feed on slow bottom living or littoral fish species with comparatively few hard parts (López-Nieves and Hernando, 1984; Watt, 1995; Geidezis, 1996; Kingston *et al.* 1999 Lanszki *et al.* 2001). Fish between 10 and 20 cm appear to dominate diet in most areas, with larger fish taken less frequently (Erlinge, 1968; Jenkins *et al.* 1979; Arca and Prigioni, 1987; Taastrøm and Jacobsen, 1999; Lanszki and Sallai, 2006). In coastal areas rockling, gobies, flatfish and blennies are typical prey items (Watson, 1978; Heggberget, 1993; Beja, 1991; Watt, 1995; Kingston *et al.* 1999). In freshwater habitats eels, salmonids, cyprinids and cottids are the most important prey (e.g. Jenkins and Harper, 1980; Carss *et al.* 1990; Durbin, 1997; López-Nieves and Hernando, 1984; Brzeziński *et al.* 1993; Prigioni *et al.* 2006a). Non-fish prey is often discounted as being of secondary importance (Roche, 2001). However, non-fish prey strongly associated with aquatic habitats, notably amphibians, are frequently recorded and often form an important seasonal component of diet (López-Nieves and Hernando, 1984; Weber, 1990; Kožena *et al.* 1992; Lanszki *et al.* 2001; Clavero *et al.* 2005).

1.12.9 Spatial and temporal variation in otter diet

Significant temporal and spatial variation has been recorded in otter diet throughout its range. Many studies have recorded seasonal variation in otter diet (e.g. Watson, 1978; Watt, 1995; Ruiz-Olmo and Palazón, 1997; Kingston *et al.* 1999) and diet can shift considerably over long periods of time in response to broad scale changes in the structure and composition of prey communities (Preston *et al.* 2007). Otter diet varies on both fine (Clavero *et al.* 2004) and broad spatial scales (Jędrzejewska *et al.* 2001; Clavero *et al.* 2003) and trophic diversity is generally higher in Mediterranean habitats (Clavero *et al.* 2003; Ruiz-Olmo and Jiménez, 2009). The primary cause of otter dietary variation is thought to be fluctuations in the availability of prey populations (Carss, 1995), which is affected by abundance, behaviour, anti-predation mechanisms and predator ability (see section 1.8.2). Habitat plays a significant role and large scale spatial patterns in otter diet occur in parallel to landscape characteristics, strongly reflecting the environmental complexity of an area (Clavero *et al.* 2004). This is probably due to the association between habitat structure and biodiversity (Gaston, 2000; Sala, 2000; Jeanneret *et al.* 2003). For instance, water clarity (López-Nieves and Hernando, 1984) and seasonal increases in aquatic vegetation (Fairley and Murdoch, 1989; Kingston *et al.* 1999) affect prey availability. The factors underlying variation in otter diet on a large geographic scale have been investigated by two studies which came to largely conflicting conclusions; Jędrzejewska *et al.* (2001) found that the main variable influencing otter diet was habitat, whereas Clavero *et al.* (2003) found that latitude explained most of the variation in diet.

1.12.10 Are otter's generalists or specialists?

Otters take an extremely wide range of prey types (see section 1.12.8), many studies have recorded over 15 types of fish and non-fish prey in diet (e.g. López-Nieves and Hernando, 1984; Beja, 1997; Roche, 2001; Clavero *et al.* 2004) and in some cases over 35 prey types have been recorded (Sulkava, 1996). This indicates a broad fundamental trophic niche (see section 1.1), typical of a generalist carnivore (see section 1.3). However, some workers describe otters as specialist foragers due to their high reliance on fish (Mason and Macdonald, 1986; Bonesi *et al.* 2004; Pedroso and Santos-Reis, 2006). Most studies agree that otters are opportunistic foragers taking prey roughly according its availability (Heggberget, 1993; Watt, 1995; Taastrøm and Jacobsen, 1999; Lanszki *et al.* 2001), but several dietary studies have observed that the most abundant prey type is not the most captured (Watson, 1978; López-Nieves and Hernando, 1984; Roche, 2001). This suggests that otters may follow a facultative foraging strategy becoming more or less specialised depending on prey availability and competition (Glasser, 1982, 1984; Mitchell, 1990).

1.13 National Otter Surveys

In the UK National Otter Surveys are now regularly carried out, by the Environment Agency in Wales and England, the Environment and Heritage Service in Northern Ireland and by Scottish Natural Heritage in Scotland, in order to monitor the distribution of otter populations (Green and Green, 1980; Strachan and Jefferies, 1996; Jones and Jones, 2004). The National Surveys used a standard survey methodology based on the identification of indirect but indisputable signs of otters such as spraints and footprints, with the presence of signs denoting a positive site and the absence a negative site (Crawford *et al.* 1979; Lenton *et al.* 1980; Mason and MacDonald, 1986). Within each site a 600 m section of bank is typically checked for signs of otters (Mason and MacDonald, 1986). Perhaps the greatest problem with the standard survey method is that the absence of signs does not necessarily imply the absence of otters. It has been suggested that the confirmed non-detection of otters in an area over time indicates that they are absent from the area (Ruiz-Olmo *et al.* 2001), but National Survey sites are generally only visited once or twice (Jones and Jones, 2004) meaning that there is a high probability of false negatives occurring as a consequence of otter behaviour, climatic conditions or surveyor ability (Ruiz-Olmo *et al.* 2001; Brzeziński and Romanowski, 2006; Evans, 2006). Furthermore, the National Survey data can not be used to produce population estimates, as there is no clear relationship between spraint density and population size (Kruuk *et al.* 1986; Ruiz-Olmo *et al.* 2001).

Non-detection is more prevalent in areas that are within the home range but outside of the core area, such as corridors used for dispersal or moving between core areas (Ruiz-Olmo *et al.* 2001). The movement of transient animals may give a positive result in an atypical area that is not particularly suitable for otters (Ruiz-Olmo *et al.* 2001). Conversely, areas where otters have regularly been observed in the past can give negative results based on standard survey methods (Liles, 2003a). Otters are capable of undertaking lengthy journeys overland, particularly in areas where water bodies are poorly connected (Reuther and Dolev, 2000). The National Surveys are linked to water bodies, so overland movements are rarely recorded and the use of corridors and non-linear habitats, which aren't associated with wetlands, represents an unknown aspect of otter biology. A lack of standardisation in the application of surveys between areas and countries has also been noted, which is primarily due to specific circumstances requiring modification of the technique (Ruiz-Olmo *et al.* 2001).

Several attempts have been made to test the validity of the standard survey technique (e.g. Mason and Macdonald, 1987; Ruiz-Olmo *et al.* 2001) and the results of these studies are discussed in chapter three.

1.14 Distribution and ecology of otters in Wales

Otters appear to have been abundant in many areas of Wales up to the 1950s (Stephens, 1957) but, as with other areas in the UK, sightings became less frequent thereafter (Henshilwood, 1981). The areas of Wales which were most affected by the widespread population declines were predominantly centred in the more urbanised south (Jones and Jones, 2004). The first National Otter Surveys, carried out in the 1970s found that 20% of sites surveyed in Wales were positive for otters (Crawford *et al.* 1979). The most recent National Surveys found that 71% of sites were positive in Wales (Jones and Jones, 2004), compared to 34% in England (Crawford, 2003) and 92% in Scotland (Strachan, 2007). In the mid 1980s the otter population in Wales was estimated to consist of 400 individuals (350 in England and 6600 in Scotland), but the reliability of these figure is low and numbers are likely to have increased substantially since then (Harris *et al.* 1995). Wales contains a rich variety of freshwater and coastal habitats which provide highly suitable habitat for otters (Jones and Jones, 2004). The impact of anthropogenic activity is likely to low in many areas of Wales, as the human population density is 141 per km^2 (c.f. England 380 per km^2) (Office of National Statistics, 2002). Despite this only a modicum of work has been carried out on otters in Wales, with very little published data (e.g. Henshilwood, 1981; Liles, 2003a) and no long-term studies have been undertaken.

1.15 Study aims

Through a long-term assessment of diet at two locations, this study will investigate the trophic ecology of otters in Wales an important, yet poorly studied, stronghold for otters in the UK and one of the few countries where marine activity has been recorded. Population monitoring programs generate information that underlies our understanding of population biology, and feeds directly into conservation biology, as such, it is essential to validate monitoring techniques (see section 1.11). This study will determine the probability of detecting otters in a wild population, using the standard survey methodology employed by the National Otter Surveys, and investigate the optimal survey approach for a range of objectives. Spraint analysis is widely used to study the trophic ecology of otters, estimate their influence on ecosystem structure and their impact on commercial fish stocks (see section 1.12.5). This study investigates the implications that a lack of standardisation in spraint analysis protocols has for the comparability of data sets. A systematic review and meta-analysis of otter dietary studies will be undertaken to investigate the factors underlying variation in the trophic ecology of a density dependent carnivore across its range. This will further enable investigation into the scale dependence of dietary variation in carnivores. The specific hypothesis addressed by each of the studies will be stipulated within each chapter.

Chapter 2

Materials and Methods

2.2 Study area

2.1.1 Gower Peninsula

The Gower peninsula (latitude 51°59'64"N, longitude 4°14'47"W) is located to the west of Swansea in South West Wales (Figure 2.1). In 1956 it became the first designated Area of Outstanding Natural Beauty (AONB) in the United Kingdom (UK). The Peninsula (Figure 2.2) is approximately 20 km long and 12 km wide covering an area of 188 km^2. It contains a great diversity of habitats including; rocky shores, sandy shores, mud flats, heath land, salt marsh, agricultural grassland, coniferous and deciduous woodlands. The Gower peninsula is relatively small, but it is an area rich in biodiversity and incorporates four Special Areas of Conservation (SAC), 24 Sites of Special Scientific Interest (SSSI), three National Nature Reserves (NNR), three Local Nature Reserves (LNR), one Special Protection Area (SPA) and one wetland site designated as being of international importance by the Ramsar convention criteria. It is, without doubt, a very important area for both flora and fauna (Mullard, 2006).

There are numerous small streams and rivers on Gower, the largest of which are the Burry Pill, the Pennard Pill and the River Morlais. The River Clyne is situated closer to Swansea on the eastern boundary of Gower. Most of the streams are shallow, between 2-3 m wide and less than 3 km in length however, the larger rivers are approximately 5-7 m wide and 5-7 km in length. In addition to the rivers and streams, there is an abundance of ponds and lakes of varying sizes, many of which are privately owned and contain coarse fish. The purpose of this research was to investigate diet, distribution and sprainting activity of otters on Gower, so four study river systems were selected where otters are thought to be present and sufficient access was confirmed by pilot surveys. The rivers included in this study were; Burry Pill, Pennard Pill, Bishopston Pill and the River Clyne, all of which rise from aquifers. A breeding population of otters is thought to be active on the River Morlais (Forman and Parry *unpub. data*), but access to this river is limited as much of it runs through restricted access land, so it was not included in the study. A summary of the habitat features at each study site is provided below but a more in-depth description, including habitat survey results, can be found in chapter 3.

Figure 2.1 Location of Pembrokeshire and the Gower peninsula in the UK (generated using MapInfo Professional© from an OS map obtained from EDINA©).

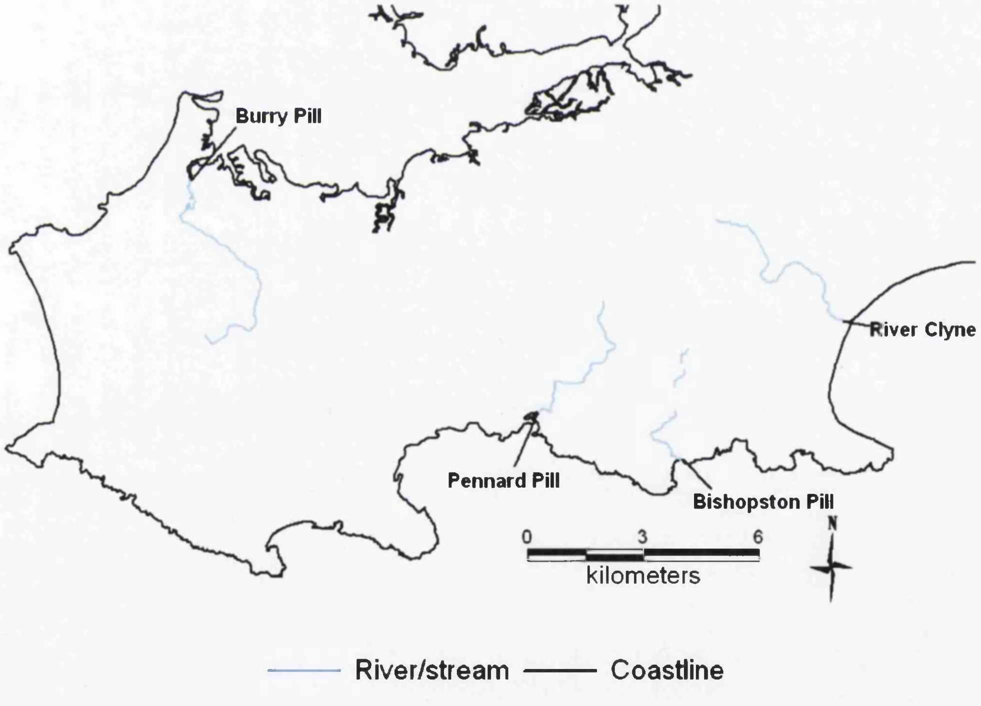


Figure 2.2 The Gower peninsula study sites (generated using MapInfo Professional© from an OS map obtained from EDINA©).

Following the widespread otter population declines of the mid 20th century (see section 1.12.1) a number of reports suggested that otters had returned to Gower by the late 1980s, and three otters were found dead at Barlands quarry around this time (Sian Musgrave *pers. com.*). It is thought that otters recolonised Gower either via the Loughor estuary or the River Tawe (Liles, 2000). The third National Survey of Wales (Andrews *et al.* 1993) found one otter spraint at Oxwich marsh, confirming the presence of otters on Gower. During the 1990s spraints were found at several locations on Gower and otter road casualties were also recorded (Liles, 2000). An audit carried out by Liles (2000) found that otters were widespread on Gower and found evidence of breeding at two sites, suggesting that the signs were due to an established population rather than transient animals. There was evidence of high otter activity at Pennard Pill, Nicholaston Pill, Oxwich marsh, Burry Pill and the River Morlais, with lower levels of activity on the River Clyne, Bishopston Pill and Llangennith moors (Liles, 2000). Five potential breeding sites were found on the Burry Pill, and evidence of breeding was recorded at Oxwich marsh (Liles, 2000).

The Gower peninsula is a popular destination with locals and tourists, which poses a number of threats to the otter population. Many of the larger watercourses are bordered by footpaths regularly used by dog walkers and ramblers. Otters can tolerate moderate levels of disturbance (Copp and Roche, 2003; Tüzün and Albayrak, 2005), but as otter activity is predominantly nocturnal on Gower and there are several relatively undisturbed habitats, this is unlikely to be a major issue in most cases. A more serious threat is that posed by the roads, which although small can become very busy, particularly during summer. Many of the watercourses pass under roads, and although culverts are present at some locations the rivers on Gower are small and prone to spate, often rendering the culverts unusable (Forman and Parry *pers. obs.*). In the last 10 years at least eight otters have been killed on the roads of Gower (Dan Forman *unpub. data*). Other potential threats are habitat alteration and destruction particularly due to pollution and the clearance of bank-side vegetation.

2.1.2 Gower study sites

The four study rivers in the Gower study can all be classified as subtype BVc, small, lowland, impoverished sand/clay rivers, mainly flowing over limestone and sandstone (Holmes *et al.* 1999). The plant communities are dominated by liverworts, ferns and filamentous algae (Holmes *et al.* 1999). The populations of freshwater fish are low on all of the Gower rivers, but particularly on the River Clyne (Swansea County Council, 2002). MapInfo Professional © (Pitney Bowes Software Inc, New York, USA) was used to create maps of each study site showing the distribution of roads, watercourses, residential areas and woodland (Figures 2.3 - 2.6).

2.1.3 River Clyne

The River Clyne (latitude 51°35’57”N, longitude 3°59’48”W) is located on the Eastern boundary of the Gower peninsula (Figure 2.2). The River Clyne flows through an asymmetric valley. The river is 7.4 km in length, of which approximately 4.5 km (61%) could be surveyed. The source of the River Clyne is close to Priors meadow, west of Dunvant, and the mouth opens into Swansea Bay (Figure 2.3). The river flows through a short section of agricultural land, close to the source, before entering the Clyne Valley Country Park, which is a deciduous woodland containing many small ponds.

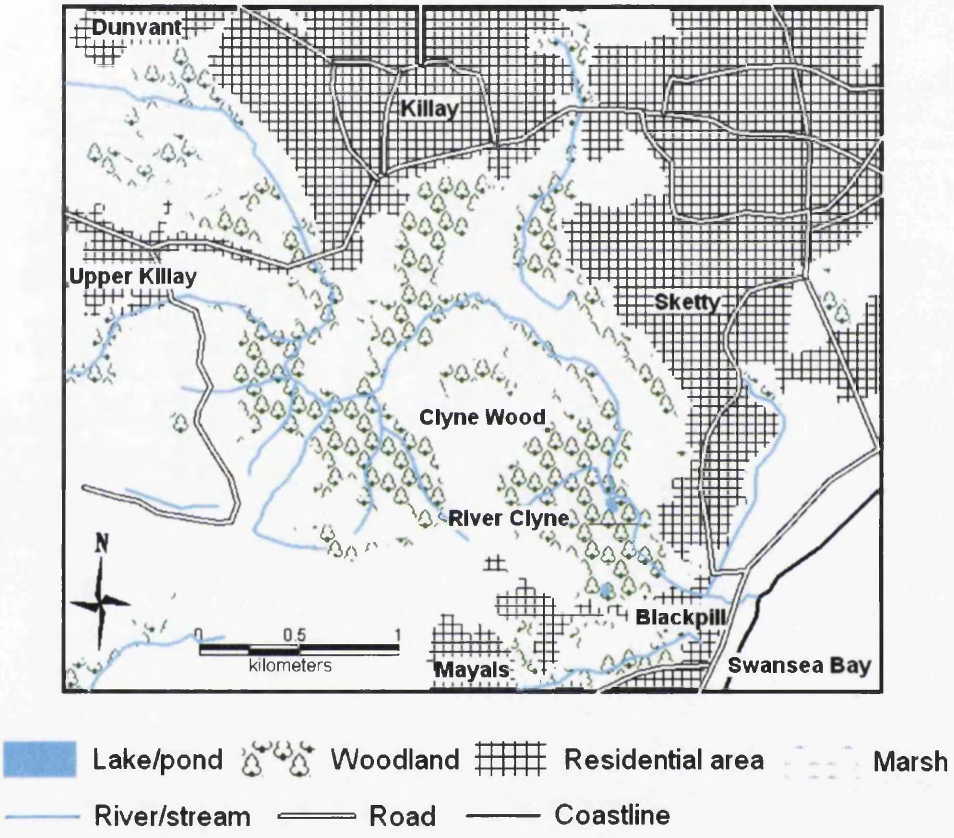


Figure 2.3 The River Clyne showing roads, watercourses, woodland and residential areas.

The Clyne valley is popular with dog walkers, cyclists and tourists and is probably the site subject to the heaviest human disturbance. On two occasions during the study period, significant bank-side construction work took place. The first case occurred in 2005 due to the installation of a pipeline, and involved significant earth movement, heavy machinery and clearance of bank-side vegetation along a 700 m section of the river close to the entrance of the valley. The second case occurred in spring 2008 and affected a 200 m section just downstream from the first case. This was due to the installation of levees around residences close to the entrance of the valley and involved the removal of bank-side vegetation and heavy machinery. A major pollution incident occurred on the River Clyne in 2002, as the result of sewage discharge from a pumping station in Killay. This had disastrous effects on the prey populations, particularly those of eel, bullhead and trout, with an estimated 3000 fish being killed (Environment Agency *pers. com.*). Several sections of the river contain litter with pools particularly susceptible to accumulating plastic waste. The banks are approximately 1 m high with a bank-full width of 5.5 m and a water width of 4 m. The banks predominantly consist of earth and clay and in several places there is evidence of erosion where the banks are undercut. The water depth at the time of the habitat survey was 9 cm and the flow was smooth or rippled, but this varied during the study as the river was observed to enter spate quickly following heavy or prolonged rainfall. The channel is relatively free from vegetation and the predominant substrate is pebble. The bank-side vegetation is complex and a mixture of tall herbs and mixed woodland. There are a relatively large number of large bank-side trees that have root complexes which enter the channel.

2.1.4 Burry Pill

The Burry Pill (latitude 51°37'21"N, longitude 4°14'31"W) is located in North West Gower (Figure 2.2). The Burry Pill flows through an asymmetric valley. The river is 8.6 km in length of which approximately 6.5 km (76%) could be surveyed. The first 1.4 km upstream from the mouth flows through salt marsh and agricultural land (Figure 2.4). In this section the river is bordered by 2 metre high vertical banks and there are no mid-channel features on which to spraint, so it seems safe to assume that if the otters did defecate here it would be directly into the water. No spraint sites were found on this section during the pilot study and, as it was deemed highly unlikely that any spraints would be left here, the section wasn't included in the survey. If the first section is excluded the total length of the river, with the potential for sprainting sites recalculates to 7.2 km, of which (90%) was surveyed.

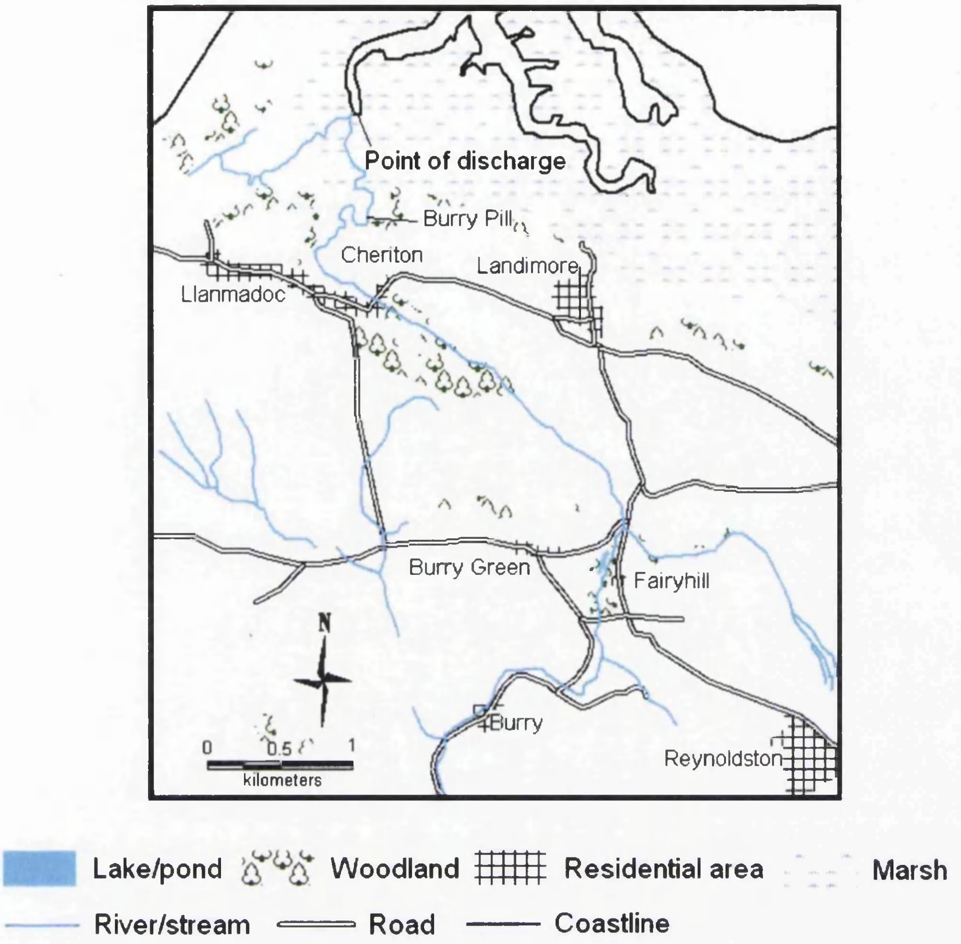


Figure 2.4 The Burry Pill showing roads, watercourses, woodland and residential areas.

The source of the Burry Pill is an aquifer close to the village of Burry, although it is fed by two main tributaries one rising in Kingshall and one at Crow well. The Burry Pill flows through agricultural land bordered by scrub for most of its course, but it does move through two wooded areas; a copse within the gardens of the Fairy Hill hotel and Cheriton woods, before entering the sea through salt marsh at the Burry inlet. A footpath runs adjacent to some sections of the river, but it is infrequently used and many other sections are bordered by private land. In general, the Burry Pill is subject to lower levels of human disturbance than the other sites and the river is relatively free from litter. The banks of the Burry Pill are approximately 0.8 m high with a bank-full width of 6.1 m and a water width of 4.6 m. The banks are vertical or steep and predominantly consist of earth and clay. A small amount of poaching is present in sections bordered by agricultural land. The water depth at the time of the habitat survey was 25 cm and the flow was rippled for most of its course, but this varied depending on rainfall. The channel is relatively free from vegetation and the predominant substrate is pebble, although sections of silt and bedrock are also present. The bank-side vegetation is complex and adjacent land-use is a mixture of deciduous woodland and rough pasture, although it should be noted that a section of the river flows through the gardens of a hotel. There are numerous large bank-side trees with root complexes that enter the water.

2.1.5 Pennard Pill

The Pennard Pill (latitude 51°34'26"N, longitude 4°06'44"W) is located in South Gower (Figure 2.2). The Pennard Pill flows through a shallow v-shaped valley. The river is 5.9 km in length, of which 5.1 km (86%) could be surveyed. The river is ephemeral flowing, as a 0.8 km section of the river between Parkmill and Ilston usually dries up during the summer. During the pilot study spraints were found on the dry river bed, so this section was included in the surveys. The Pennard Pill rises from two sources; Kitchen well spring north of Parkmill and an aquifer close to Moorlakes wood. The river is bordered by deciduous woodland for most of its course, moving through a small residential area and section of agricultural land shortly before entering the sea at Three Cliffs Bay (Figure 2.5).

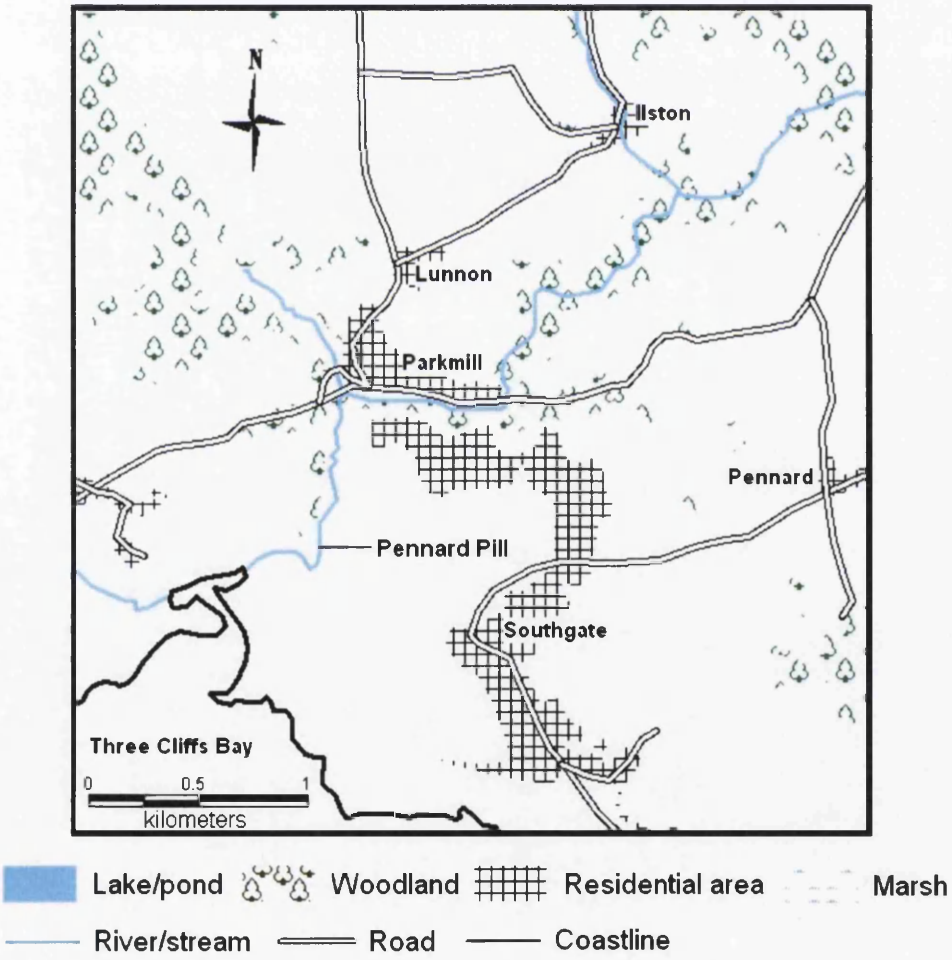


Figure 2.5 The Pennard Pill showing roads, watercourses, woodland and residential areas.

There is a footpath running along the river bank, which is regularly used by dog walkers and locals. During summer, Three Cliffs Bay is a popular destination and the footpath next to the river is busy at this time, but there is relatively little littering on the Pennard Pill. The banks are approximately 0.8 m high with a bank-full width of 5.9 m and a water width of 5.7 m. The water depth at the time of the habitat survey was 19 cm and the flow is generally smooth with unbroken standing waves forming in shallower regions, which was observed to vary depending on rainfall. The channel substrate is a mixture of pebble and cobble, containing a small amount of submerged and emergent vegetation. The banks of the Pennard Pill are predominantly vertical or steep and in places are undercut. The banks are formed from a range of substrates over the course of the river including earth, clay, gravel, cobble and boulders. There is a small amount of erosion present, as the result of poaching by livestock and humans. The bank-side vegetation is mainly simple and adjacent land-use is a mixture of deciduous woodland and rough pasture, although, for around 1 km the river flows through gardens adjacent to a road. Throughout the course of the river there are numerous large bank-side trees with root complexes that enter the water. There are small sections close to residential areas where the banks have been heightened and reinforced with concrete.

2.1.6 Bishopston Pill

The Bishopston Pill (latitude 51°33'56"N, longitude 4°03'25"W) is located in South Gower to the east of the Pennard Pill (Figure 2.2). The Bishopston Pill flows through a shallow v-shaped valley. The river is 4.2 km in length, of which 3.4 km (81%) could be surveyed. A 1.1 km section towards the source of the river was usually dry and only flowed ephemerally after heavy rainfall. However, spraints were found on the dry river bed during the pilot study so this section was included in the surveys. The source of the Bishopston Pill is close to Hams wood, north of Kittle but it flows underground for approximately 1 km before surfacing in the valley. The river flows through the valley, bordered by deciduous woodland, before reaching Pwll du bay (Figure 2.6).

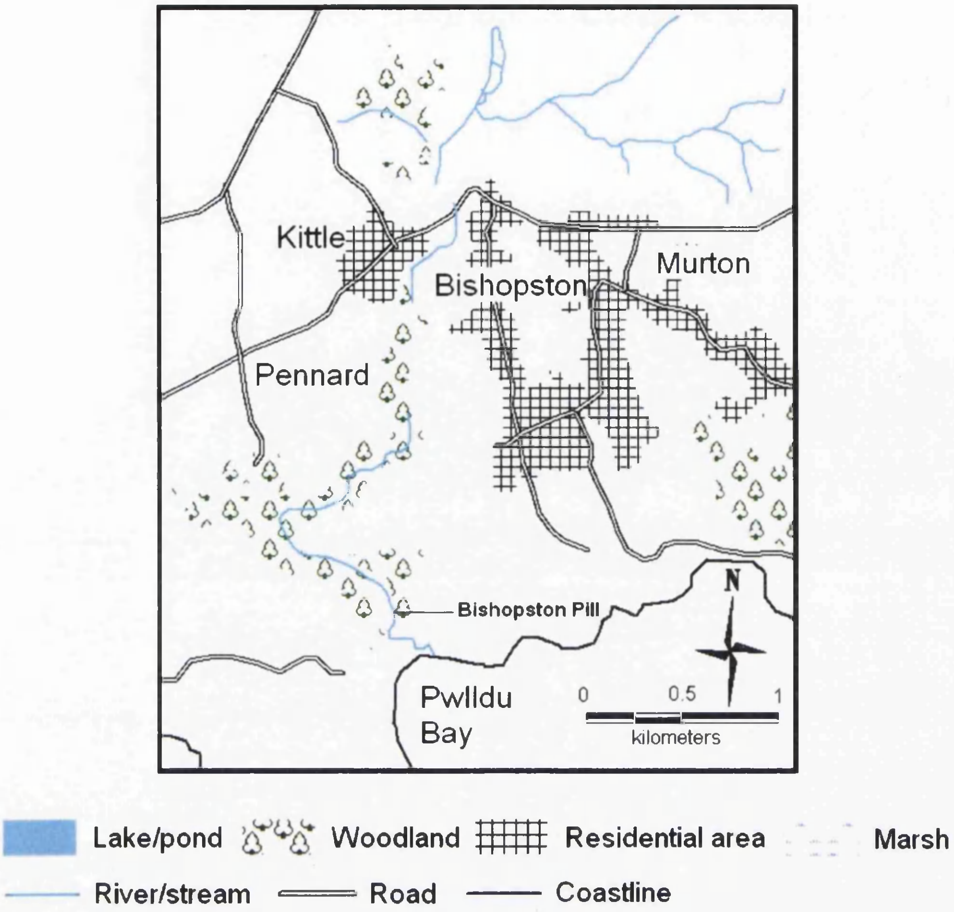


Figure 2.6 The Bishopston Pill showing roads, watercourses, woodland and residential areas.

A pebble bar prevents the river from flowing directly into the sea unless in spate. There is a footpath that runs alongside the Bishopston Pill, which is used frequently during summer but sporadically at other times of the year. The level of human disturbance on the Bishopston Pill is low outside of the summer months and there is very little littering. The banks are approximately 1.5 m high with a bank-full width of 4.7 m and a water width of 4.5 m. The water depth at the time of the habitat survey was 28 cm and the flow is generally smooth or rippled, but as with the other study rivers this varied significantly depending on rainfall. The channel is relatively free from vegetation and the substrate is a mixture of pebble and silt. The banks are predominantly vertical or steep and are formed from a range of materials including earth, clay, cobble and bedrock. There is a small amount of erosion present as the result of poaching by humans. The bank-side vegetation is complex and adjacent land-use is predominantly deciduous woodland, although, some sections flow through rough pasture. Throughout the course of the river there are numerous large bank-side trees with root complexes that enter the water. There are short sections where the banks have been reinforced with concrete bags.

2.2 Pembrokeshire study sites

The Pembrokeshire coast national park covers 416 km of coastline and contains the Pembrokeshire Marine Special Area of Conservation (SAC) encompassing a Marine Nature Reserve and many Sites of Special Scientific Interest (SSSI). Two of the sampling sites fell within the St David's Peninsula Coast Special Protection Area (SPA). The Pembrokeshire coastline is heterogeneous including rocky shores, sandy shores, sub-tidal reefs, mudflats, estuaries, lagoons and salt marsh. In places there are steep cliffs and coastal caves. Many rivers and small streams discharge into the sea along the breadth of the Pembrokeshire coast, most of which are less than 2 km long (Liles, 2003a). The Pembrokeshire coast also contains a number of large shallow inlets and bays, which slope out gradually from the coast providing a shallow foraging habitat for otters. A number of sampling sites were located within the Milford Haven waterway, which is also a part of the Pembrokeshire marine SAC. Pembrokeshire, like Gower, is a picturesque and a popular tourist destination also used by walkers, surfers and coastal orienteering, Milford Haven is a busy port used for both industry and leisure purposes. The presence of cold water reefs off the Pembrokeshire coast may provide a reliable source of prey, but it is not clear whether the otters are foraging on them or not.

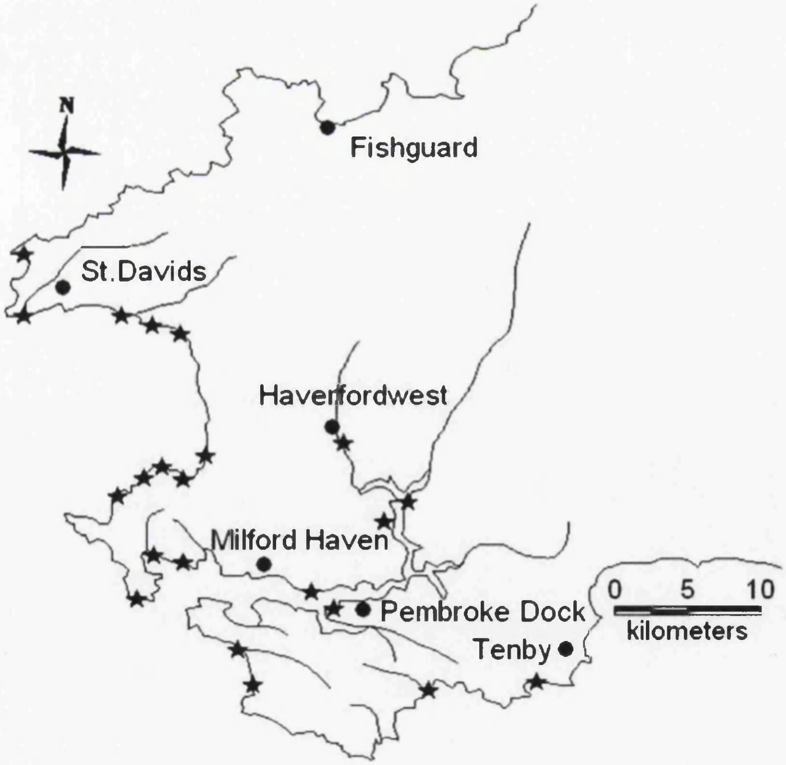


Figure 2.7 The Pembrokeshire coast with stars indicating sampling sites (Produced using MapInfo© using an OS map from EDINA©).

2.3 Surveys and spraint collection

2.3.1 Gower surveys and spraint collection

Where necessary, permission for access to the study sites was gained from landowners. The study sites were surveyed fortnightly for a period of two years between July 2005 and June 2007. Pilot surveys were carried out at all of the sites in the last week of June 2005. During the pilot surveys as much of the river was walked as possible and all located spraints were removed. This determined the standard route used for all subsequent surveys carried out during the study. The length of the rivers and the proportion surveyed were determined using MapInfo Professional©. At all of the study sites, surveys began at the mouth and moved upstream. Both banks and mid-channel features, such as rocks and tree roots, were searched for spraints. All located spraints were collected and placed into individual, sealed and labelled polythene bags. A spraint site was defined as a single feature (rock, root, stump, grass mound etc). At each spraint site a GPS reading was taken using a 12 channel eTrex© device (Garmin Europe Ltd, Southampton, UK). In the instance that two spraints were in relatively close proximity, but on different features, they were recorded as two separate sites. Some sites had multiple spraints on them and in this situation all spraints were given the same GPS reading. The GPS points for each spraint site were mapped onto an Ordinance Survey base map using MapInfo Professional©.

To investigate the selection of spraint sites by otters several measurements were recorded at each site. It is acknowledged that this is subject to bias, as some spraints may not have been located. The substrate the spraint was deposited on was defined as: rock, wood, mud, grass, moss, shingle, sand, leaf, artificial or a twist of vegetation that had clearly been manipulated by the otter. The height (cm) and length (cm) of each spraint from the water was recorded using a 10 m tape measure. The position of the spraint site in relation to the channel was recorded, defined as right bank, left bank or mid-channel. Where possible, surveys were not carried out during or after a period of heavy rainfall, as this can reduce the number of spraints available (Brzeziński and Romanowski, 2006). Due to prolonged periods of rainfall this was not always possible, so it was noted whether it rained on the survey day or on the day preceding the survey. Additional useful observations were also recorded, including the level of human disturbance, sightings of potential prey species or those of other piscivores and carnivores. Any changes to the habitat of the study sites due to human activities were also noted to investigate if they affected sprainting activity. At the end of each survey all spraints were taken to Swansea University and stored at – 17°C until dietary analysis was undertaken.

Photo 2.1 Otter spraint on a rock on the River Clyne (Gareth Parry).

2.3.2 Pembrokeshire spraint collection

Spraint collections were undertaken on Pembrokeshire by a team of volunteers co-ordinated by the Pembrokeshire marine SAC relevant authorities group. The aim was to visit a total of 21 sites (Figure 2.7) every month between July 2007 and June 2008. During each monthly visit the volunteers were instructed to search the site for otter spraints and collect up to three spraints for analysis. In some cases this meant that only a sub-set of the available spraints were analysed, however, in many cases less than three spraints were present. Spraints were placed into individual, sealed and labelled bags and sent to Swansea University where they were stored at – 17°C until dietary analysis was undertaken. Volunteers were given training by the Pembrokeshire Marine SAC group to help them identify and collect spraints. All spraint bags returned were checked by the author to confirm that they contained otter spraints. In the event of rejected samples the reason was recorded (see section 6.4.1)

2.4 Gower habitat survey

A habitat survey was carried out at all of the study sites during October 2007. The habitat survey followed the standard method outlined by the River Habitat Survey in Britain and Ireland (Environment Agency, 2003). This method measures the complexity and extent of channel and bank-side vegetation as well as recording physical features, such as bank structure, channel substrate and land use adjacent to the channel. May and June are the most suitable months for carrying out River Habitat Surveys, but it was felt that the conditions during

October were suitable, as channel features were not obscured by emergent vegetation, but seasonal bank-side and aquatic plants were still present.

2.5 Climate data

Monthly climate data recorded at Mumbles head, situated at the western tip of Swansea Bay, from 2005-2007 was kindly provided by the Met office. This included mean, maximum and minimum temperatures (°C), mean rainfall (mm) and mean wind speed (m/s).

2.6 Prey availability

No formal study of prey availability was undertaken for reasons that are detailed elsewhere (see sections 1.12.6 and 5.5.4). However, a list of potential prey species were recorded during the surveys and information on fish species present in the study areas was obtained from local anglers. A limited amount of electro-fishing data collected in August 2005 from the Pennard and Burry Pills was kindly provided by the Environment Agency.

2.7 Dietary analysis

All spraints were subjected to dietary analysis through the identification of hard prey remains. Prior to analysis spraints were soaked individually in 250 ml beakers, containing a saturated solution of biological detergent, for a period of at least 24 hours. The spraints were then gently rinsed through a 420 µm sieve to remove excess mucus and grit and turned out onto a sheet of blue roll, with care taken to ensure all remains were removed from the sieve. The spraint remains were wrapped up in the blue roll and left to dry for a period of at least 24 hours before analysis. All spraints were analysed using an Olympus SZ40© dissection microscope (Olympus UK ltd, Watford). Fish, mammal, bird, amphibian and invertebrate remains were identified using published keys (Day, 1966; Watson, 1978; Teerink, 1991; Miranda and Escala, 2002; Conroy *et al.* 2005; Cham, 2007) and a reference collection containing vertebrae and mouth parts from 39 fish species, three amphibian species and two reptile species (Table 2.1).Where possible remains were identified to family or species level. As this study aimed to investigate the comparability of spraint analysis studies, five different techniques were used.

Table 2.1 List of species contained in the reference collection of hard remains.

Common Name	Taxonomic name
Atlantic cod	*Gadus morhua*
Ballan wrasse	*Labrus bergylta*
Bass	*Dicentrarchus labrax*
Black bream	*Spondyliosoma cantharus*
Brill	*Scophthalmus rhombus*
Brown trout	*Salmo trutta*
Bullhead	*Cottis gobio*
Chub	*Leuciscus cephalus*
Common frog	*Rana temporaria*
Common goby	*Pomatoschistus microps*
Common smooth-hound	*Mustelus mustelus*
Common toad	*Bufo bufo*
Dab	*Limanda limanda*
European eel	*Anguilla anguilla*
European hake	*Merluccius merluccius*
Fifteen -spined stickleback	*Spinachia spinachia*
Five-bearded rockling	*Ciliata mustela*
Flounder	*Platichthys flesus*
Four-bearded rockling	*Enchelyopus cimbrius*
Goldfish	*Carassius auratus*
Grass snake	*Natrix natrix*
Great pipefish	*Syngnathus acus*
Grey gurnard	*Eutrigla gurnardus*
Grey thick-lipped mullet	*Chelon labrosus*
Herring	*Clupea harengus*
John dory	*Zeus faber*
Lesser sand eel	*Ammodytes tobianus*
Lesser weever fish	*Echiichthys vipera*
Lumpsucker	*Cyclopterus lumpus*
Mackerel	*Scomber scombrus*
Montagu's blenny	*Coryphoblennius galerita*
Plaice	*Pleuronectes platessa*
Pogge	*Agonus cataphractus*
Rudd	*Scardinius erythrophthalmus*
Saithe	*Pollachius virens*
Sea scorpion	*Taurulus bubalis*
Scad	*Trachurus trachurus*
Sole	*Solea solea*
Slow worm	*Anguis fragilis*
Smooth newt	*Triturus vulgaris*
Three-spined stickleback	*Gasterosteus aculeatus*
Three-bearded rockling	*Gaidropsarus vulgaris*
Viviparous eelpout	*Zoarces viviparus*
Whiting	*Merlangius merlangus*

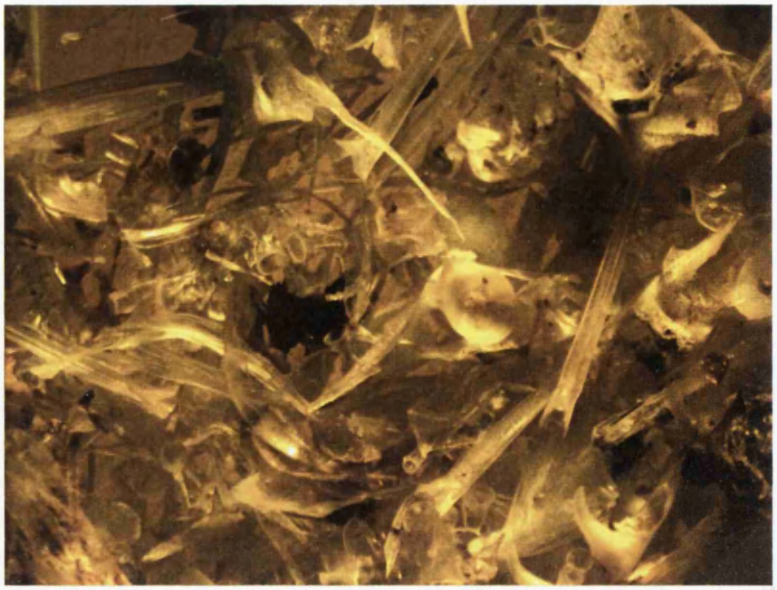


Photo 2.2 Contents of an otter spraint after soaking in detergent (Gareth Parry).

2.7.1 Equation 1. Frequency of occurrence

$$\text{FO} = \frac{\text{Number of spraints containing a prey type}}{\text{Total number of spraints}} \text{ X } 100$$

Frequency of occurrence is one of the oldest and most easily applied methods (e.g. Stephens, 1957; Erlinge, 1968; Jenkins *et al.* 1979). This describes diet as the proportion of spraints containing a particular prey item. One occurrence is defined as the presence of a prey type in a spraint regardless of the number of remains. All frequency based methods tend to overestimate small prey with a large number of hard parts and underestimate large prey or prey with a small number of hard parts (Erlinge, 1968; Wise, 1980).

2.7.2 Equation 2. Relative frequency of occurrence 1

$$\text{RFO 1} = \frac{\text{Number of occurrences of a prey type}}{\text{Sum occurrences of all prey type}} \text{ X } 100$$

Relative frequency of occurrence is probably the most frequently used method (e.g. Watson, 1978; López-Nieves and Hernando, 1984; Watt, 1995). It determines the relative frequency at which prey remains occur in respect to other prey. This method defines the presence of a prey type in a spraint as one occurrence regardless of the number of remains. Relative frequency of occurrence is subject to the same major biases as frequency of occurrence (Erlinge, 1968; Carss and Parkinson, 1996) and other studies have suggested that there is a lack of independence with relative frequencies that affects the interpretation of dietary variation (Clavero *et al.* 2004) However, feeding studies on captive otters have found that this method gives a reasonably accurate interpretation of diet (Erlinge, 1968; Jacobsen and Hansen, 1996).

2.7.3 Equation 3. Relative frequency of occurrence 2

$$\text{RFO 2} = \frac{\text{Number of occurrences of a prey type in each spraint}}{\text{Total number of all prey items identified in the spraint}} \times 100$$

An adaptation of the standard relative frequency method (equation 1) is described by Yoxon and Yoxon (2000). All of the bones are identified in every spraint, and the frequency of each species in that spraint determined as a proportion of the total number of prey remains. This method is thought to be more descriptive than the other relative frequency method as it does not assume that the presence of a prey type represents only one individual.

2.7.4 Equation 4. Relative dry weight percentage

$$\text{RWP} = \frac{\text{Dry weight of remains of a prey type in spraint}}{\text{Sum of dry weights for all prey types}} \times 100$$

Feeding studies on captive otters have suggested that analytical methods based on the bulk of the prey remains give a more reliable indication of diet (Bekker and Nolet, 1990; Jacobsen and Hansen, 1996). Measuring the bulk of the prey remains is less likely to overestimate small prey with a large number of hard parts and provides a more accurate reflection of the biomass intake (Bekker and Nolet, 1990). Several different bulk based methods have been used, but the one of Kingston *et al.* (1999) is the most descriptive and easiest to apply to spraints from wild populations.

2.7.5 Equation 5. Relative frequency of numbers

$$\text{RFN} = \frac{\text{Number of individuals of a prey type}}{\text{Total number of all prey individuals}} \text{ X } 100$$

This estimates the actual number of individual prey items consumed and aims to overcome the assumption that one occurrence represents one individual, which limits relative frequency of occurrence. This method has been used by Bekker and Nolet (1990) and Heggberget (1993) and uses minimum estimates of individuals consumed based on characteristic remains, such as otoliths, maxillas, atlases and pharyngeal bones.

2.8 Systematic review and meta-analysis

2.8.1 Literature search and data collection

A systematic review of otter diet was undertaken, following the data acquisition protocol laid out by Pullin and Stewert (2006). This method summarises research by objectively locating relevant data from published and unpublished sources. Meta-analytical reviews are more comprehensive and less biased than conventional reviews, but must follow strict guidelines. A number of search terms are defined to locate literature related to the subject of the review (Pullin and Stewert, 2006). In this study 19 search terms were defined (Table 2.2). These terms were used to search for literature in electronic databases, professional networks, government bodies, non-government organisations (NGO) and citations from relevant papers. Not all databases have full Boolean search capacity, so where necessary it was important to change the word order of the search terms to ensure that all relevant information was located.

Table 2.2 Search terms, databases and other sources used to locate literature related to Eurasian otter diet in the meta-analytical review.

Search terms	Online information databases	Other Sources
Bulk analysis	Biome	Countryside Council for Wales (CCW)
Eurasian otter	BioMed Central	Natural England
European otter	Blackwell Synergy	Environment Agency
Faeces	Elsevier	Interlibrary Loans
Feeding	Google Scholar	Academics with history of otter research
Fish prey	ISI Web of Science	
Fish vertebrate	JSTOR	
Frequency of occurrence	Pub Med	
Prey selection	Science Direct	
Lutra lutra	Wiley Interscience	
Otter		
Otter behaviour		
Otter diet		
Otter foraging		
Prey remains		
Relative frequency		
Scat analysis		
Spraint		
Spraint analysis		

2.8.2 Inclusion criteria and data extraction

All of the articles located by the initial search process were screened to extract ones which met the pre-set criteria and contained information relevant to otter diet. The criteria for inclusion are determined by the question of the study and must be set prior to the literature search, in order to prevent bias. The review question in this case was: "*How does the composition and diversity of otter diet vary temporally and spatially across its European range?* Six criteria for inclusion used in this study were;

1. Studies should use spraints as the sampling unit,

2. Data should be expressed as Relative frequency of occurrence (see equation 2, section 2.7.2) or convertible to it.

3. Fish prey should be described to a minimum of family level,

4. Sample size must be a minimum of 59

5. The study should investigate general diet and not focus on one prey type.

6. The sampling period should cover a minimum of one year

The minimum sample size of 59 spraints per study was the baseline set, as this was found to be the minimum number of faecal sample required to identify principal prey groups in carnivore diet (Trites and Joy, 2005). A large sample size also lowers the chance of type I errors occurring (Dytham, 2003). The minimum sampling period was set as one year because known seasonal variations in otter diet could bias the results if data from a limited number of seasons was included. Relative frequency of occurrence (RFO %) (see equation 2, section 2.7.2) was used, as this standardized the bias to that of one method, and this is the most frequently used method in the literature. If frequency of occurrence data was presented in conjunction with the numbers of spraints collected then data was converted to RFO 1 (Watson, 1978) using the following equation.

2.8.3 Equation 6. Determining number of prey occurrences from FO % data

$$\text{Relative frequency of occurrence} = \frac{n}{100} \times \text{FO \%}$$

n = Number of spraints collected

FO % = Original frequency of occurrence value for prey

The number of occurrences for each prey type was calculated using equation 6 and the values used to determine the Relative frequency of occurrence for each prey type using equation 2 (see section 2.7.2). In all cases the values produced were back-checked to the original FO% values to ensure their accuracy. This was done by dividing the number of prey occurrences calculated by the total number of spraints (see section 2.7.1, equation 1), and comparing the result to the original FO % value. Where a study collected data from multiple sites these sites were considered separately in the analysis, provided that they met the inclusion criteria. The reason this approach was adopted is that otter diet can vary on small spatial scales. This was not felt to bias the information, as the effect of trends that existed at one site would be softened compared to more general trends that existed at multiple sites.

To investigate the undying cause of dietary variation it was necessary to identify factors that could contribute towards it. In this study 19 such variables were identified; Shannon-Weiner niche breadth, latitude, longitude, access to a marine environment, biogeographic region, broad habitat type, number of prey types, number of fish families, RFO% of the most frequently occurring freshwater fish, marine fish and non-fish prey types. Data were extracted from the studies, selected during the screening process, and subjected to statistical analysis in order to identify which of the factors explained most of the variation in otter diet. An investigation of variation in otter diet between biogeographic regions was made between data collected from central Europe, the Iberian Peninsula and The UK/Ireland. To classify as central Europe a study had to be undertaken in a landlocked area of continental Europe with no access to the marine environment. Studies were assigned to one of four broad habitat types; riparian, lake/pond, estuarine and coastal, using information provided by the studies. Access to the marine environment was defined as within 50 km of the coast, a conservative figure based on the mean range size of otters in freshwater habitats calculated by Kruuk (2006). Mediterranean studies were defined as having been undertaken in a region with a Mediterranean climate (e.g. Spain, Portugal), using information provided by the studies.

2.9 Statistical analysis

All analyses (apart from where stated) were conducted using the Statistical Package for Social Sciences (SPSS) version 13.0 (SPSS Inc, Chicago, USA). Prior to analysis, the distribution of all data were assessed using a Kolmogorov-Smirnov test and the equality of variance tested using a Levene's test (Dytham, 2003). Significance (*p*) was set at 0.05. Parametric tests were used where the assumptions were met, where the assumptions were not met non-parametric tests were used.

2.9.1 Spraint distribution data

The GPS points from spraint sites were mapped using MapInfo Professional©. A Kolmogorov-Smirnov test was used to determine if the distribution of spraints, between seasons and sites, differed from a random Poisson distribution. A negative binomial regression model was used to investigate temporal and spatial variation in sprainting activity. MapInfo Professional© was used to split the rivers into 50 m sections and then to determine the presence or absence of spraints on each section during each survey. A binomial vector of 50 m river sections was constructed for each survey, with 1 denoting a section that contained at least one spraint and 0 denoting a negative section. This data was used to determine the probability of detecting otters associated with different survey approaches (see section 2.9.3).

2.9.2 Meteorological data

Spearman's rank correlation was also used to investigate the relationship between meteorological factors and sprainting activity. All p values were corrected using the Bonferroni method to account for the impact of making multiple correlations (Dytham, 2003).

2.9.3 Assessing the power of different otter survey designs

The power of different otter survey designs was defined as the probability of detecting otters where they are present. As otters were regularly recorded on all of the study rivers, throughout the two year study period (see section 3. 4.1), the rivers were considered to be positive for otters. Therefore, surveys which failed to detect otter presence on the rivers were considered to have recorded a false negative result. The power of different survey designs was investigated by systematically resampling within binary vectors constructed for each survey (see section 2.9.1). Otter survey design was modified by vaying transect length, the number of survey sites and the number of survey visits. Each 50 m interval was treated as a separate survey starting point and the probability of detecting otters was determined at every starting point, using different survey designs. To reduce the influence of individual river characteristics on the probability of detecting otters, the systematic resampling was undertaken on a pooled matrix of vectors from all four study rivers. Each survey design was systematically appiled to every starting point in the pooled vector data. For each suvery design the prevalence of positive 50 m sections was calcualated for every starting point, using equation 7. The proability of detecting otters using different length transects was determined by calculating the mean prevalence of positive 50 m sections at all starting points. When the number of survey sites and/or survey visits was increased, the probability of detecting otters was determined by calculating the binomial distribution probability of recording a positive result.The power associated with each survey design was then calculated using equation 8 which is an adaption of the equation $q = (1-p)$, used to calculate the occurrence of false negatives by Brewer *et al.* (2002) and outlined in detail by Strachan (2007). The probability of detecting otters was also stratified by season, in order to investigate seasonal variation in the power of different survey designs.

2.9.4 Equation 7. The prevalence of positive results associated with an otter survey design

$$p = \frac{nP}{(nP + nN)}$$

p = Prevalence of positive 50 m sections

nN = Number of starting points which were negative for otters

nP = Number of starting points which were positive for otters

2.9.5 Equation 8. The power of an otter survey design

$$P = (1-q)$$

q = probability of recording a false negative

2.9.6 Otter dietary data from Gower and Pembrokeshire

The Relative frequency of occurrence values, calculated using the method described by Watson (1978) (see equation 2, section 2.7.2) were used to calculate Shannon-Wiener niche breadth (see equation 10, section 2.9.7), and to investigate temporal and spatial trends in otter diet on Gower and Pembrokeshire. An in depth analysis of diet was undertaken to investigate temporal and spatial patterns in niche breadth, dietary composition and the relative contribution of marine fish, freshwater fish and non-fish prey. Different methods were used to analyse patterns in the dietary data in chapters 5 and 6 due to differences in the study aims, collection protocols (see section 2.3) and data set properties. Therefore, the statistical methods used to analyse the dietary data are detailed separately within each chapter (see section 5.3 and 6.3.2).

2.9.7 Equation 9. Renkonen's index of percentage similarity

$$P = \Sigma \text{ minimum } (P_{1i} P_{2i})$$

P = Percentage of similarity between sample 1 and 2

P_{1i} = Percentage of species in community 1 sample

P_{2i} = Percentage of species in community 2 sample

The effect of using different analytical methods was investigated using Renkonen's index of percentage similarity (see equation 9), which measures the degree of similarity in the dietary data produced by the different spraint analysis methods (Krebs, 1989). Renkonen's index has previously been applied to the results of feeding studies on captive otters (Jacobsen and

Hansen, 1996) and was used here in order to enable comparison with the results of this previous study. Renkonen's index was also used to compare the composition of diet between the Gower study sites.

2.9.8 Correction to account for sampling bias

Differences in in sample size between sites and seasons could influence the interpretation of variation in the diet of the otter population on Gower. For, example if a seasonal sample contains a large proportion of spraints from one site, a prey item frequently consumed at that site may appear to be of greater seasonal importance to the population than it actually is. To account differences in sample size between sites the RFO % values were corrected using the method described by Kingston *et al.* (1999). This adjusts the data by multiplying the occurrence of a prey type by a factor reflecting the overall number of spraints from an area/season as a proportion of all the spraints analysed e.g. if total spraints = 1510, and 407 are collected from one site, then the correction factor is 407/1510 = 0.2695 (Kingston *et al.* 1999). The correlation between the adjusted and obtained RFO % was investigated using a Spearman's rank correlation test to determine if difference in sample sizes significantly affected the interpretation of temporal and spatial variation in otter diet.

2.9.9 Equation 10. Shannon-Wiener niche breadth

$$\text{Shannon-Wiener niche breadth} = -\Sigma\, P_j \log_e P_j$$

Pj = Proportion of individuals found in or using a resource states

Niche breadth was calculated using the Shannon-Wiener standardised measure (*H'*) as it gives more weight to rare prey items (Krebs, 1989),which may be of seasonal importance to otter diet.

2.9.10 Review data

Statistical analysis of the review data was carried out using SPSS© and Community Analysis Package© (CAP) 4 (Pisces Conservation Ltd, Lymington, UK). A Kruskal-Wallis test was used to investigate if otter trophic niche varied temporally, spatially or with habitat type. Where significant results occurred Dunn's *post hoc* tests were undertaken using Graph Pad Prism 5© (GraphPad Software Inc, USA), to determine pairwise differences. Pearson's correlation was used to determine if otter trophic niche breadth was related to latitude or longitude. PCA was used to explore trends in the composition of otter diet across its European range. The PCA was undertaken on a matrix of RFO % values for the top three marine and freshwater fish families, and the top five non-fish prey classes, recorded in otter diet across their European range. Variation within these prey types were considered important as they form the largest proportion of otter diet across Europe, and including minor prey types may generate unimportant trends (Field, 2007). Spearman's rank correlation was used to identify prey types, which were significantly associated with the scores for the first two components extracted from the PCA. Spearman's rank correlation was also use to investigate if the scores for the first two components were related to variation in latitude or longitude. In all instances where multiple comparison tests were undertaken the Bonferroni method was used to reduce the critical level of significance.

A SRH test was used to determine if variation in the composition of otter diet, summarised in the first two principal components, was affected by differences in broad habitat type. A Kruskal-Wallis test was used to investigate the variation in the diversity and composition of otter diet between three biogeographic regions; the Iberian Peninsular, UK/Ireland and Central Europe, and between habitat types. Dunn's tests were carried out to investigate the nature of any significant variation in dietary composition between the biogeographic regions or habitat types. CAP 4 was used to conduct a TWINSPAN analysis on the dietary data from all studies included in the review, based on the presence/absence of all prey types. TWINSPAN is a multi-variant descriptive method included in CAP 4, which was used to separate dietary studies in order to explore clusters in the dietary data.

Otter foraging strategy, across Europe, was investigated using two methods. Firstly, a Kendall concordance correlation coefficient (K) was calculated to determine the agreement of prey occurrences between the study sites. The K-coefficient generates a statistic ranging from 0 to 1, values closer to zero indicates a generalist opportunistic species, whereas more specialised species will have a value close to 1 (Siegal and Castellan, 1988). The second method used a Spearman's rank correlation to determine if the RFO % of any major prey types were negatively associated with trophic niche breadth. Where negative associations were detected, a SRH test was then applied to determine if trophic niche richness was affected by presence of that prey type. To investigate whether otters behaved opportunistically, variation in the RFO % of important prey items, between habitat types, was investigated using a Kruskal-Wallis-test followed by Dunn's tests on significant results.

Chapter 3

Distribution of otter spraints on Gower and an evaluation of the effectiveness of the 600 m survey transect on small lowland river systems

"If ignorance is bliss, then knock the smile off my face"

Zach de la Rocha (Settle for nothing, 1992, Epic Records, New York)

Summary

1. Monitoring programs for many carnivore species rely on the identification of indirect signs such as faeces. The absence of signs does not necessarily denote the absence of a species, thus, the ability to determine presence/absence is susceptible to type II error. Otter population monitoring programs are typically based on surveying 600 m transects for spraints. This approach is widely used to inform conservation management on a range of spatial scales. There has, however, been no validation of the ability of the 600 m transect survey to detect otters at small spatial scales.
2. Fortnightly catchment-level otter surveys were undertaken on four lowland rivers in South Wales, over a period of two years. Temporal and spatial variation in the spraint distribution was investigated. Binary vectors were constructed for each survey, denoting the presence/absence of otters at each 50 m section of river. Pooled vectors from all of the study rivers were systematically resampled using different survey designs. This information was used to produce optimal survey designs for a range of different purposes.
3. There was significant spatial variation in spraint density and spraint distribution was clustered on all rivers. The mean probability of detecting otters based on a single 600 m transect survey was low (0.26 ± 0.01 SE). The most efficient approach to obtaining a detection power of 0.8 was to undertake three repeat surveys at two separate sites. The transect length required to achieve a detection power of 0.8 varied seasonally.
4. *Synthesis and Applications*. This study demonstrates the low detection power of the standard 600 m transect survey on small lowland rivers, revealing seasonal and scale sensitivity in the National Otter Survey design. This emphasises the importance of standardising detection power by designing otter field surveys according to the study

objectives, habitat and season. Optimal survey designs are suggested for a range of objectives in small lowland river habitats. Increasing in the number of visits and study sites was a more efficient route of improving detection power than increasing transect length alone, which contributes to the general understanding of carnivore survey methodology.

3.1 Introduction

The standard otter survey was designed in the late 1970s with the objective of determining the broad scale distribution of otters in the UK (Crawford *et al.* 1979; Lenton *et al.* 1980; Mason and Macdonald, 1986). It has since been used to monitor otter populations across the UK and mainland Europe (e.g. Mason and MacDonald, 1994; Cortés *et al.* 1998; Prigioni *et al.* 2007), and to survey other species of otter (e.g. Chehebor, 1985; Gonzalèz and Utrea, 2001; Nel and Somers, 2009). The standard otter survey methodology requires that searches are conducted on a specified section of river bank, lake shore or coast for otter signs. The most important field sign, and often the only one used, is spraint (Kruuk *et al.* 1986; Mason and Macdonald, 1987). Importantly, the absence of spraints does not necessarily imply an absence of otters (Kruuk *et al.* 1986). The standard survey technique is particularly susceptible to type II errors, where the null hypothesis (that the site is negative) is falsely accepted (Dytham, 2003). The standard transect size used for otter population surveys is 600 m (Mason and MacDonald, 1986), but the reliability of the 600 m transect size has frequently been questioned (e.g. Kruuk *et al.* 1986; Kruuk and Conroy, 1987; Ruiz-Olmo *et al.* 2001). The 600 m transect was originally validated by Mason and Macdonald (1987) using a linear regression model. This model predicted that 88-94 % of sites, confirmed positive after surveying 1 km, would be designated positive within the first 600 m. However, linear regression assumes that the relationship between cause (transect size) and effect (positive site), is linear (Dytham, 2003). There is considerable evidence that spraint distribution is spatially clustered (Kruuk *et al.* 1986; Prenda and Granado-Lorencio, 1996; Thom *et al.* 1998), which would make standard linear regression an unsuitable model. Furthermore, the study of Mason and Macdonald (1987) could not determine the proportion of negative sites, which would have proved positive, had transects in excess of 1000 m been surveyed.

It has been argued that the level of error associated with the standard survey method is acceptable, as it was designed to identify widespread distribution, rather than locate every otter population (Mason and Macdonald, 1987). Yet otter conservation programs are undertaken on many spatial scales, the most frequent being small scale local authority implemented schemes. Local authorities are required to monitor local otter populations for the UK Biodiversity Action Plan (UK Biodiversity Steering Group, 1995). The standard survey design is also freqently used to detect the presence or absence of otters in small areas designated for development (e.g. O'Hara, 2006; Dudley, 2008; Spedding, 2009). Monitoring the status of specific local otter populations, or determining the presence/absence of otters at a site, requires a higher level of resolution than broad species level conservation programs. Therefore, it is important to determine the reliability of the standard otter survey design at smaller spatial scales, to validate the information being used to make conservation and development decisions. No information has been obtained regarding survey accuracy on short watercourses, which are an important otter habitat in many areas (Brzeziński *et al.* 1993; Prenda and Granado-Lorencio, 1996; Kruuk *et al.* 1998; Lanszki *et al.* 2009). Surveying the entire length of a watercourse, coast or lakeside gives the greatest chance of detecting otter presence. Undertaking comprehensive catchments-level surveys are not always logistically or economically practical. It is therefore, desirable to investigate the optimal approach to otter surveys, to identify the most efficient method of obtaining a high power of detection. Both local level studies and broad-scale reviews of species status will be improved by devising an optimal otter survey methodology, which determines the presence/absence of otters at individual sites with a defined level of power.

3.2 Aims

There has been no comprehensive long-term study of otter activity on Gower. This study aims to provide an in-depth description of the Gower otter population over two years, investigating temporal and spatial variation in sprainting activity. The small size of the rivers on Gower, and the duration and frequency of the study period, made it possible to investigate the probability of detecting otters through spraint surveys. This enables an assessment of the probability of detecting otters using different survey designs, including the 600 m standard transect survey currently used by the UK National Otter Surveys (see section 3.1) The study also investigates the influence of meteorological factors on spraint density. This study had three key aims;

a) To monitor temporal variation in the presence/absence of otters on the four study rivers.

b) To determine the optimum approach to otter spraint surveys that provides 80% confidence in an assessment of otter presence/absence on small lowland rivers.

c) On small lowland rivers that are positive for otters, what distance from a proposed development site should be considered as potentially being used by otters?

These aims were addressed through six questions

1. What is the temporal and spatial occurrence of spraints on each river?
   Null Hypothesis: There is no temporal or spatial variation in the occurrence of spraints on each river on Gower.

2. How frequently do surveyors need to conduct a survey on small lowland rivers to detect the presence of otters or have an 80 % confidence of absence?

3. To improve the confidence of detecting the presence/absence of otters is it better to increase transect length, increase the number survey sites or undertake repeat surveys?

4. To improve the confidence of detecting the presence/absence of otters is it better to conduct repeat surveys at the same transect or at different transects?

5. Does the detection probability associated with otter transect surveys of size *x* vary seasonally?

6. What is the average distance from any random point on a small lowland river to a site where otter activity has been recorded?

3.3 Materials and methods

3.3.1 Spraint Surveys

Fortnightly surveys were carried out between July 2005 and June 2007, as described previously (see section 2.3.1). All located spraints were collected, so the numbers were indicative of the detectable monthly sprainting activity. It could not be assumed that all of the terrestrially deposited spraints were collected. However, the surveyor and survey routes stayed the same, throughout the study period, thereby, standardising and minimising observer error over the entire duration of field sampling.

3.3.2 Mapping spraint data

The GPS points for each spraint site were mapped using MapInfo Professional © (see section 2.3.1). The number of spraints collected from each specific site, during the study, were calculated and incorporated into the maps. Weather conditions affected the accuracy of the GPS readings, so a small number of the GPS points were not placed on the river channel by the mapping software. During the field work, notes describing the location of sprainting sites were taken when the accuracy reading, provided by the GPS device, was less than 15 metres. Anomalous GPS points were re-mapped to their correct locations using these notes; however, this was not possible for a small number of points and the number of affected points is detailed in the results. Such points were moved in a straight line to the closest section of river, and it is acknowledged that this introduces a small amount of error. However, no point would be more than 15m from its actual position, and in context of the study aims this level of error is not important.

3.3.3 Spatial and temporal variation in spraint occurrence

Temporal and spatial variation in spraint occurrence and the influence of meteorological factors was investigated following the procedure outlined in section 2.9.2.

3.3.4 Probability of detecting otters using different survey designs

Binary vectors were constructed for all of the surveys undertaken on all of the study rivers. The vectors denoted the presence (1) or absence (0) of otter spraint at 50 m sections of river (for a full description of this approach see section 2.9.1).Vectors from all of the study rivers were pooled and systematically resampled to determine the probability of detecting otters with different survey designs (see section 2.9.3). Otter survey design was varied by altering transect length, the number of survey sites and the number of survey visits. The probability of detecting otters associated with each survey design was considered to represent its power (see section 2.9.3). The power of different survey designs was investigated, in order to identify the optimal approach to determine the presence or absence of otters on small lowland rivers. Seasonal variation in the probability of recording a false negative also was investigated.

3.4 Results

3.4.1 Occurrence of otters and variation in sprainting activity on Gower

In total, 2651 spraints were collected on the Gower peninsula between July 2005 and June 2007, confirming otter activity on all of the study rivers. The total number of spraints collected appeared to fluctuate seasonally, with a pronounced peak in spring 2007 (Figure 3.1). The median number of spraints collected per km month was 1.5, but there was considerable variation both between and within sites (Table 3.1). Median values were used as the spraint data from Bishopston Pill was not normally distributed (Kolmogorov-Smirnov: $z = 1.4$, $p = 0.03$, $n = 25$).

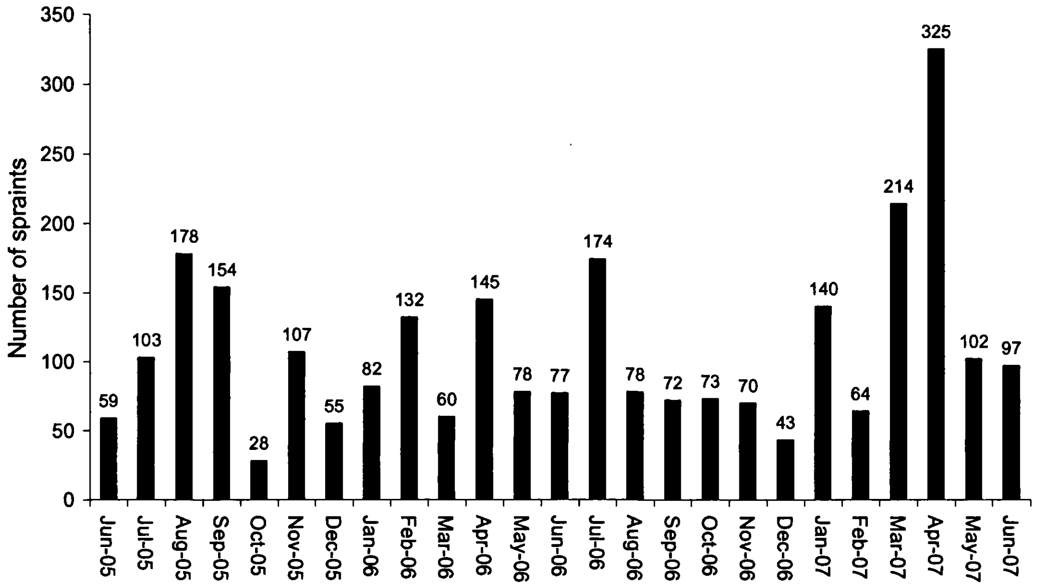


Figure 3.1 The observed temporal variation in the total number of spraints collected on the Gower peninsula between July 2005 and June 2007 (n = 2651 spraints).

Table 3.1 The total, median, minimum and maximum density of otter spraints per km collected on each study river during positive surveys between July 2005 and June 2007.

Study River	Total sprains collected	Median spraints/km	Minimum spraints/km	Maximum spraints/km
River Clyne	470	4	0	10.2
Burry Pill	1504	8.4	2.6	21.9
Pennard Pill	602	3.9	0	22.4
Bishopston Pill	75	0.4	0	7.4
Overall Gower	2561	1.5	0	17.5

A negative binomial regression model was constructed to predict the number of spraints located per km by using study site and season as categorical predictors. The model was statistically significant (likelihood ratio chi-square = 16.0, $p = 0.01$, df =6), but only study site had a significant influence on the model predictions (Likelihood ratio = 11.9, $p < 0.01$, df =3), so the model was repeated with site as the only predictor variable. The second model was also significant (likelihood ratio chi-square = 15.6, $p < 0.01$, df =3) and Akaike's Information Criterion (AIC) confirmed that it was an improvement on the first model. The parameter estimates obtained in the second model indicated that the expected count for spraints/km was higher on the Burry Pill than on the Bishopston Pill (Mean difference = 10.7 ± 7.1, $p = 0.03$).

3.4.2 Distribution and occurrence of otter spraints on the study rivers

The proportion of positive surveys varied between rivers (Table 3.2). Following mapping a number of spraint sites had anomalous GPS positions; these were Clyne six, Burry four, Pennard four and Bishopston four. Some of the anomalous sites could be correctly re-positioned using field notes; these were Clyne three, Burry two, Pennard none and Bishopston three. The spatial pattern of spraint distribution differed between the four rivers (Figures 3.2-3.5). There was an absence of spraints located at the mouth on all of the rivers, but the most frequently used sites were not at equivalent distances upstream from the mouth. The distribution of spraints differed significantly from a Poisson distribution on all of the study rivers (Table 3.2), indicating that the distribution of spraints was spatially clustered. The most frequently used spraint sites on the Burry Pill and Pennard Pill were at confluences and the most frequently used site on the River Clyne was in close proximity to a confluence. No site was used with particularly high frequency on the Bishopston pill. Two of the study rivers (Bishopston and Pennard) were ephemeral, but otters continued to mark dry sections during summer.

Table 3.2 The proportion of full surveys that returned a positive result for otters on each study river between July 2005 and June 2007.

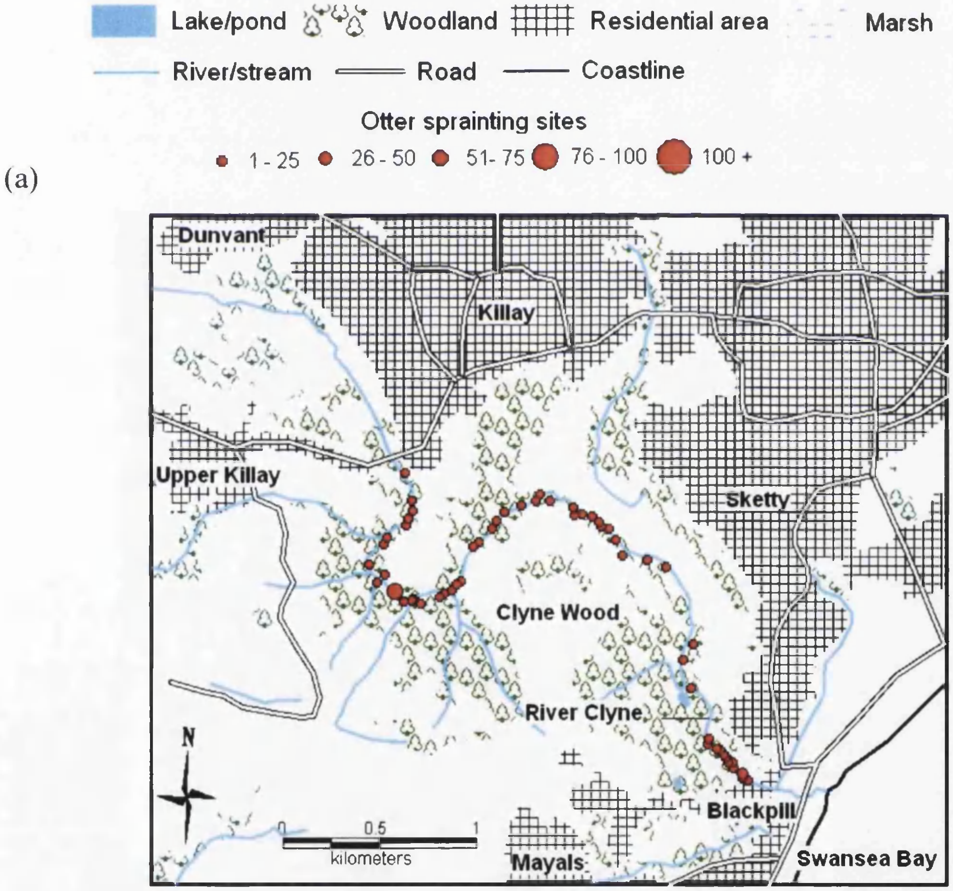
Study River	Proportion of positive surveys %
River Clyne	81.3 (39/48)
Burry Pill	85.4 (41/48)
Pennard Pill	64.6 (31/48)
Bishopston Pill	27.1 (13/48)

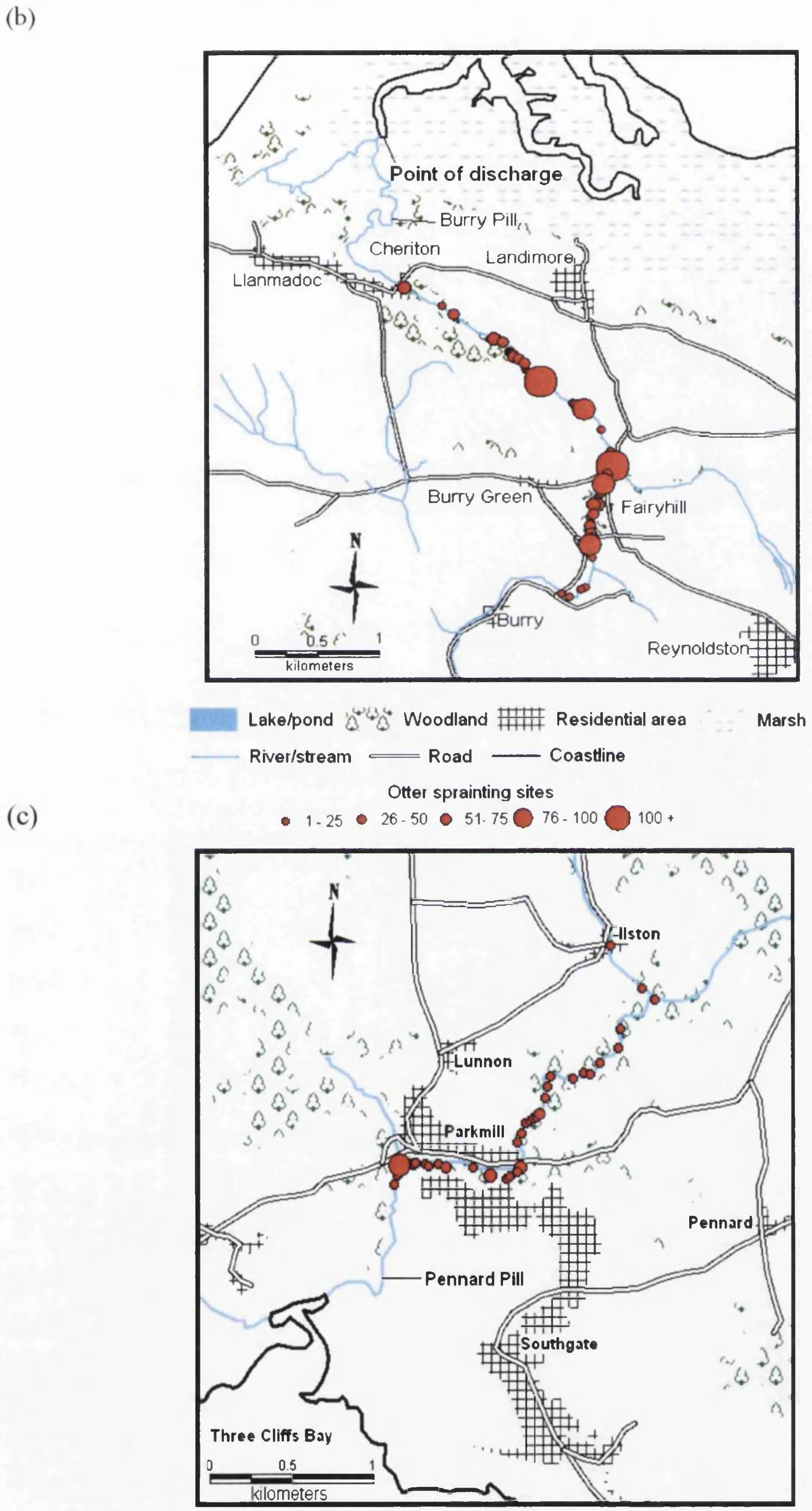
Table 3.3 Kolmogorov-Smirnov (KS) goodness-of-fit test to determine whether the observed distribution of spraint sites on the four study rivers differed from a random Poisson distribution.

Study site	Observed *z*
River Clyne	7.7*
Burry Pill	14.4*
Pennard Pill	5.8*
Bishopston pill	4.0*

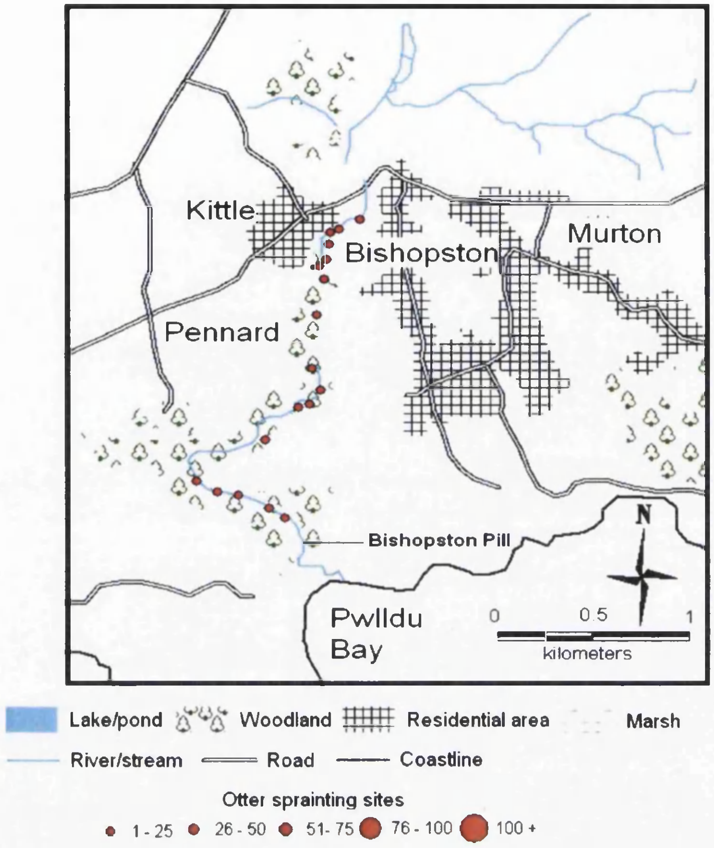
$*p < 0.01$

Figure 3.2 The distribution and relative occurrence of otter spraint sites on (a) River Clyne (b) Burry Pill (c) Pennard Pill (d) Bishopston Pill, between July 2005 and June 2007. The legend shows the relative number of spraints deposited at each site during study.




(b)
Point of discharge
Burry Pill
Cheriton
Landimore
Llanmadoc
Burry Green
Fairyhill
Burry
Reynoldston
N
0
0.5
1
kilometers
Lake/pond
Woodland
Residential area
Marsh
River/stream
Road
Coastline
Otter sprainting sites
1 - 25
26 - 50
51- 75
76 - 100
100 +
(c)
N
Ilston
Lunnon
Parkmill
Pennard
Pennard Pill
Southgate
Three Cliffs Bay
0
0.5
1
kilometers

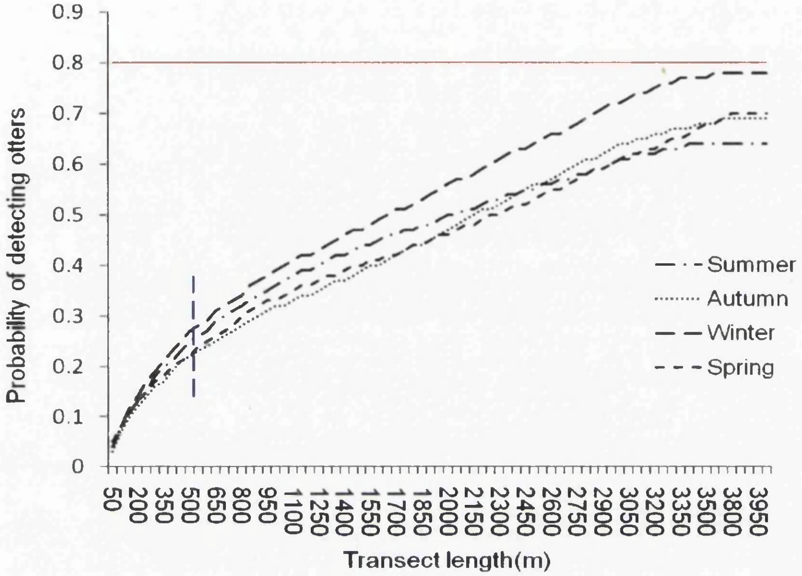
(d)



3.4.3 The probability of detecting otters on small lowland rivers

Systematic resampling of the pooled matrix of survey vectors demonstrated that if otters are present on small lowland rivers, a two year period of fortnightly surveys would record otter activity within a mean distance of 1062.5 m (± 433.7 SE) from every 50 m interval on the river. This indicates that when the overall river is positive for otters, there is likely to be otter activity within 1062.5 m of any random point. The standard error associated with this value is quite large and the minimum distance was 350 m, whilst the maximum distance was 2300 m. When undertaking a single transect survey the probability of detecting otters increased with transect length (Figure 3.3). Otter activity was recorded in all seasons on all of the study rivers (see appendix table 1), but the probability of detecting otters varied between seasons and was highest during winter. The systematic resampling approach demonstrated that a single transect survey did not provide an 80% probability of detecting otters in any season, even with a transect length of 4 km. The overall mean detection power associated with a single 600 m transect survey was 0.26 (± 0.01 SE).

Figure 3.3 Seasonal variation in the probability of detecting otters on the Gower study rivers, by conducting a single spraint survey along a continuous transect of varying length (m). The red horizontal line marks the 0.8 level of power and the vertical blue dashed line marks the detection probability associated with a standard 600 m transect survey.



3.4.4 The affect of increasing the number of sites and repeat surveys on the probability of detecting otters on small lowland rivers

Undertaking repeat surveys, separated by a period of two weeks, improved the probability of detecting otters associated with surveying a single continuous transect (Figure 3.4). Based on two visits, the mean transect length required to detect otters with a power of 0.8 was 2662.5 m (± 94.4 SE). If three visits were undertaken, a mean transect length of 2050 m (± 139.9 SE) would detect otters with a power of 0.8. However, as the distribution of spraints sites was clustered (Table 3.3), no spraints were located on some sections of river over the two year study period (Figure 3.2). For example, if a single 600 m transect was subject to 15 discrete repeat surveys, the mean probability of detecting otters was still under 0.8, so the affect of increasing the number of survey sites was investigated. Surveying two transects separated by 500 m of river bank increased the probability of detecting otters (Figure 3.5). Otters could not be detected with a power of 0.8, if two separate transects were surveyed on only one occasion. Based on two visits, otters could be detected with a power of 0.8 by surveying two separate transects of mean length 1100 m (± 73.6 SE). Based on three visits otters could be detected with a power of 0.8 by surveying two separate transects of mean length 812.5m (± 65.7 SE). To achieve a detection power in excess of 0.8, using a 600 m transect survey design, required six discrete repeat surveys of two separate transects (power = 0.82 ± 0.01 SE).

Figure 3.4 The mean probability of detecting otters on the Gower study rivers by repeatedly surveying one site using a continuous transect of varying length (m)The red horizontal line marks the 0.8 level of power and the vertical blue dashed line marks the detection probability associated with a standard 600 m transect survey.

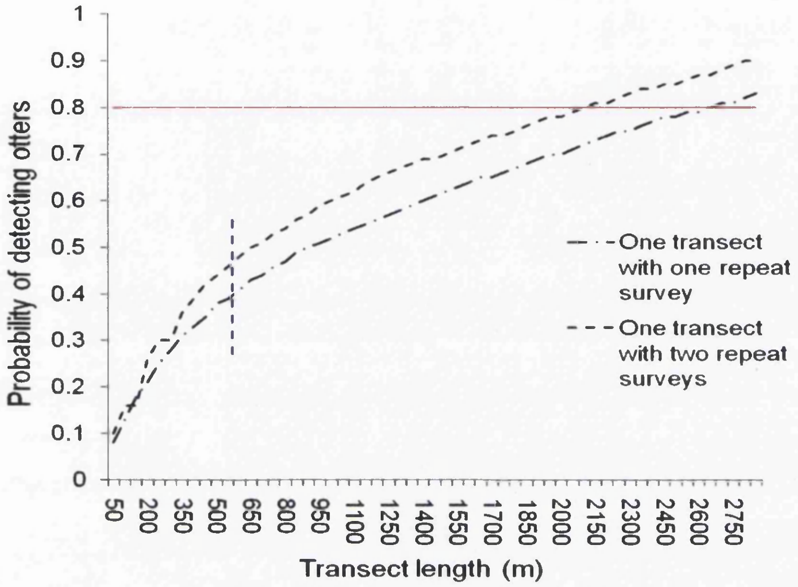
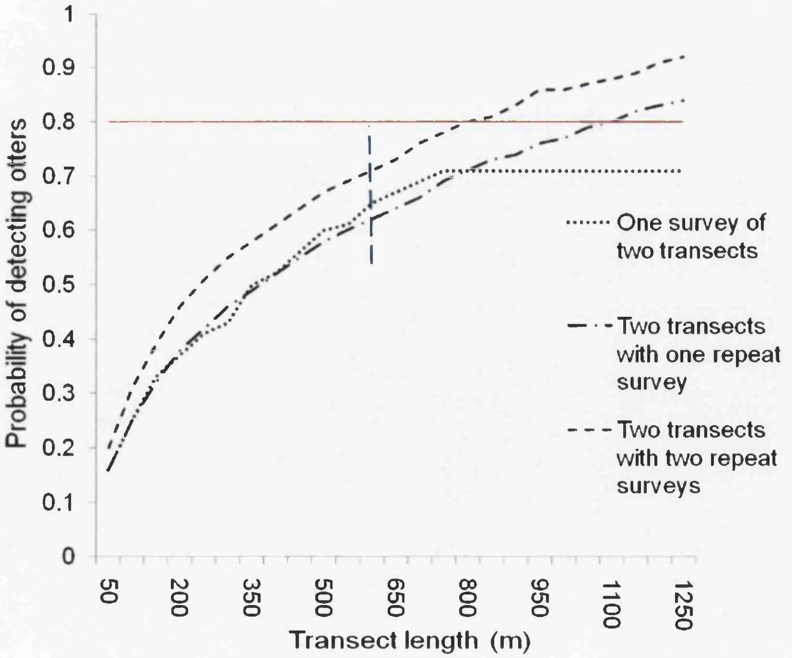


Figure 3.5 The mean probability of detecting otters on the Gower study rivers by repeatedly surveying two sites, separated by 500 m of river bank, using transects of varying length (m)The solid red line marks the 0.8 level of power and the vertical blue dashed line marks the detection probabilities associated with a standard 600 m transect survey.



3.4.5 Seasonal variation in the optimal approach to otter surveys on small lowland rivers

Otters were poorly detected on small lowland rivers by a single visit survey (see section 3.4.2). Of the approaches tested in this study, the most effective method of detecting otter presence on small lowland rivers, was to undertake three repeat surveys of two transects on separate sections of the river. There was seasonal variation in the transect length required to detect otters with a power of 0.8 (Table 3.4). A longer transect survey was required to detect otters with a power of 0.8 in autumn, compared to the other seasons.

Table 3.4 Seasonal variation in the individual transect length required to detect otters on small lowland rivers with a power of 0.8, based on three repeat surveys of two transects on separate sections of the river. Dashed lines mark the detection power of a 600 m transect survey and the mimum transect length required to achieve a 0.8 power of detection is shown in bold.

Transect length (m)	Probability of detecting otters			
	Summer	Autumn	Winter	Spring
50	0.21	0.16	0.2	0.24
100	0.31	0.25	0.32	0.35
150	0.4	0.32	0.41	0.44
200	0.47	0.37	0.46	0.51
250	0.52	0.41	0.54	0.56
300	0.55	0.45	0.58	0.6
350	0.59	0.48	0.62	0.64
400	0.62	0.51	0.65	0.68
450	0.65	0.54	0.68	0.7
500	0.67	0.57	0.7	0.72
550	0.69	0.6	0.75	0.74
600	0.71	0.63	0.75	0.76
650	0.73	0.65	0.77	0.78
700	0.75	0.68	0.79	**0.8**
750	0.78	0.7	**0.81**	0.82
800	**0.8**	0.72	0.83	0.83
850	0.82	0.75	0.85	0.85
900	0.83	0.77	0.86	0.86
950	0.85	0.78	0.88	0.88
1000	0.86	**0.8**	0.89	0.89

3.4.6 The influence of meteorological factors on spraint occurrence

There was no relationship between temperature or wind speed, and the number of spraints collected. The overall number of spraints collected per month on Gower was not associated with the total monthly rainfall. When each study site was considered individually there was a strong negative correlation between the numbers of sprints collected and total monthly rainfall on the River Clyne (r_s = 0 .44, $p = 0.01$, $n = 24$). Thus, it seems that rainfall strongly influenced the number of spraints collected on the River Clyne, but played no role in the number of spraints collected at the other study sites.

Photo 3.1 Confluence on the River Clyne regularly marked by otters (Gareth Parry).

3.5 Discussion

3.5.1 Occurrence and variation in sprainting activity on Gower

There was no significant temporal variation in sprainting activity on Gower. However, there was significant spatial variation in sprainting activity, so the null hypothesis associated with aim two was rejected. Spraint density per km was significantly higher on the Burry pill than on the Bishopston Pill. It could not be determined whether this result was due to differences in the number of otters using the two rivers, as sprainting activity is not a reliable indicator of population size (see section 1.13). Similarly, the size of the otter population on Gower could not be determined. Otters were, however, present on all four study rivers throughout the year, and there was evidence of breeding on the Burry Pill, Pennard Pill and River Clyne. In riparian habitats, large variations in sprainting activity can be used as a rough index of area use (Mason and MacDonald, 1987; Prenda and Granado-Lorencio, 1996; Strachan and Jefferies, 1996). This study presents two years of data, based on full surveys in similar habitats, so it can be postulated that the observed differences in spraint density indicate a higher level of otter activity on the Burry Pill, than on the Bishopston Pill. Areas with higher levels of sprainting activity are likely to contain better resources (Prenda and Granado-Lorencio, 1996; Prigioni *et al.* 1996), and therefore, be important to the population. Areas with lower level of sprainting activity may still be important to the population, if they contain seasonally important prey resources or good breeding habitat.

The lack of temporal variation in sprainting activity on Gower is in contrast to many previous studies, which have observed seasonal peaks in sprainting activity (Jenkins and Burrows, 1980; Macdonald and Mason, 1987; Ottino and Giller, 2004). It has been suggested that seasonal variation in sprainting activity is related to the reproductive cycle (Prigioni *et al.* 1995). Breeding was confirmed on the Burry and Pennard Pills (see sections 3.4.3 and 3.4.4), so the lack of seasonal variation in sprainting activity on Gower was not due to an absence of breeding. Very little is known about the role of spraints in olfactory communication (see 1.12.3). In other species scent marking serves multiple functions (Moran and Sorensen, 1986; Lewis, 2006), which vary with ecological and social context (Miller *et al.* 2003), and this is probably also the case in otters. Many factors are thought to contribute to variation in sprainting activity, including the number and sex of otters, habitat structure, breeding status, prey resources and weather conditions (Gormally *et al.* 1983; MacDonald and Mason, 1986; Prenda and Granado-Lorencio, 1996; Roche, 2001). The relative influence of different stimuli on sprainting activity is poorly understood, thus, the complexity of otter sprainting behaviour is likely to explain the lack of seasonal variation in sprainting activity on Gower.

3.5.2 Spatial distribution of spraint sites on Gower

The spatial distribution of spraints was clustered on all of the study rivers. Previous work has found that otter marking activity tends to decrease in the higher reaches of rivers, and increase downstream (Green and Green, 1980; Prenda and Granado-Lorencio, 1996). In the current study, there was a low level of sprainting activity in higher reaches of rivers, but spraints were absent from sections closest to river mouths, probably due to the influence of tides removing spraints. It is unlikely that the clustered distribution of spraints is driven by the physiological effect of feeding. Although, an increase in food intake causes an increase in defection rate (Smith, 1964; Helm, 1984) otters exert considerable effort to mark and remark specific sites (Kruuk, 1992).Furthermore, otters regularly cover many km per day (Green and Green, 1984; Durbin, 1998; Ruiz-Olmo *et al.* 2001), and the mean otter gut transit time is 67 minutes (Carss *et al.* 1998), so it is unlikely that sprainting at foraging areas is driven by physiological factors. The distribution of spraint clusters is likely to be determined by their function as an olfactory communication signal (see section 1.12.4).

This study did not investigate the function of spraints or the significance of spraint clusters, but a number of sites on each of the study rivers were regularly re-marked between surveys, and these sites may hold significance to the population as sites of communication. North American river otters *Lontra canadensis* also actively investigate and mark certain sites within their ranges (Olson *et al.* 2005), and there is evidence that this behaviour conveys information regarding breeding condition (Mills, 2004). Further research is needed to identify the gender of individuals at spraint sites to determine if spraint marking has a role in reproduction. The territories of otters on Gower were not defined, but on three of the study rivers the most frequently used spraint site was at a confluence, or in close proximity to one. Furthermore, on all of the rivers, the first section marked upstream from the mouth contained a cluster of regularly remarked spraint sites. These sites may represent territory boundaries, and therefore, marking in these areas could serve a territorial function. This is the case in another Mustelid the Eurasian badger *Meles meles* where faecal marks are used to defend breeding females and burrow systems (Roper *et al.* 1993).

Marking at confluences, where several routes converge, has been shown to facilitate information transfer within carnivore populations, enabling mutual avoidance and maintaining social structure (Ahlborn and Jackson, 1988). Sprainting at such focal points, such as confluences, may be a more efficient marking strategy, and spraint distribution may be clustered according to the location of these communication focal points. Some spraint sites, on Gower, were only marked once during the study period, signifying that they are unlikely to mark an important resource, territory boundary or communication focal point. Some otters release a large proportion of spraint in water (Kruuk *et al.* 1986) and for sub-adults a reduction in terrestrial marking, or the avoidance of major spraint sites, may help evade confrontation with social dominants. This provides a possible explanation as to why some sites were only marked once or twice, during the study.

3.5.3 Relationship between environmental factors and otter sprainting activity

The relationship between habitat quality and otter sprainting activity is not fully understood. Some studies have found a positive correlation between sprainting intensity and habitat features such as bank-side vegetation cover (Jenkins and Burrows, 1980; Mason and MacDonald, 1986; Rodriguez *et al.* 1988) and low disturbance (Prenda and Granado-Lorencio, 1996: Prenda *et al.* 2001). Very few spraints were recovered from a section of the

River Clyne, where bank-side vegetation had been removed entirely during construction work in 2005 (see section 2.1.3). Despite the availability of many potential sprainting sites, the otters did not mark this section at all during 2006, and only a small number of spraints were recorded on this section during 2007, although sprainting continued both upstream and downstream. This agrees with the findings of Gormally *et al.* (1983) who found a similar trend where bank-side vegetation was removed. The absence of bank-side vegetation along the majority of a watercourse does not prevent sprainting (MacDonald and Mason, 1983). However, it seems that given a choice otters usually mark where bank-side vegetation is present, and that the sudden removal of vegetation may lead to avoidance of the affected area.

Rainfall is thought to be the most important meteorological factor affecting the disappearance of spraints (Brzeziński and Romanowski, 2006). In this study, rainfall was negatively correlated with the number of spraints collected on one study river and also influenced the position and substrate on which spraints were collected. It is difficult to determine whether this is a deliberate behavioural response or simply because spraints deposited within the river channel are washed away following rainfall. Spraints are believed to be the longest-lasting scent mark (Trowbridge, 1983; Brzeziński and Romanowski, 2006), so the loss of spraints due to rainfall and rising water levels probably coincides with the loss of all scent marks along a watercourse. This means that following heavy rain otters may need to expend extra energy renewing scent marks, or adopt an alternate more efficient marking strategy.

3.5.4 Evaluating the standard 600 m otter transect survey on small lowland rivers.

This is the first study to evaluate the application of the standard otter survey design to small spatial scales. The clustered distribution of spraints demonstrated in this and other studies (e.g. Prenda and Granado-Lorencio, 1996; Thom *et al.* 1998), confirms that standard linear regression is an unsuitable method of validating otter transect surveys. This study found that a single 600 m transect survey detected otters on small lowland rivers with a mean probability of 0.26, which is considerably lower than the 0.8 level of power recommended for protected species monitoring programs (Kendall *et al.* 1992). Therefore, the standard 600 m transect survey design is not suitable for determining otter presence/absence, or for monitoring otter populations, on small lowland rivers. Consequently, the current distribution of otters on small lowland rivers may be underestimated and changes in distribution poorly detected. Recent studies have questioned the reliability of standard survey approaches in other Mustelid species

(Birks *et al.* 2005; Harrington *et al.* 2010), and the current study further emphasises the need to improve Mustelid survey techniques.

It has been argued that a high level of error at individual survey sites is acceptable, if the aim is to detect and monitor otter distribution at broad scales, such as the catchment level (Mason and MacDonald, 1987). Clearly, when monitoring otter distribution on a broad scale, such as within 10 km squares (Cortés *et al.* 1998; Strachan, 2007; Prigioni *et al.* 2007), the presence of multiple survey sites reduces the overall probability of recording false negative results. However, the last National Otter Survey assessed just one 600 m transect on each of the study rivers (Jones and Jones, 2004), an approach that is frequently replicated on small lowland rivers elsewhere in the UK (Crawford, 2003; Jones and Jones, 2004; Strachan, 2007). The detection power of a single 600 m transect survey was very low. Even if two separate sites were surveyed, the overall power still fell below the recommended level of 0.8 (Figure 3.5). This demonstrates that surveying small lowland rivers on a single occasion, using the 600 m transect survey design, can falsely designate entire river catchments as negative for otters. It can therefore be argued that UK National Otter Survey data for small lowland rivers is not reliable and should not be used to establish the absence of otters from this habitat. This may have serious implications for otter conservation management, as local level development planning and conservation decisions are often based on data obtained by applying the standard 600 m transect survey to small spatial scales (see section 3.1). Research is required to determine if the standard 600 m otter transect survey always has a low detection power at small spatial scales, regardless of habitat structure.

Studies of otter ecology and conservation may be undermined by the low detection power of the 600 m transect survey on small lowland rivers. Non-detection affects the ability to determine population status or to detect colonisation and extinction events (Mackenzie, 2005). This makes it difficult to detect changes in distribution and to identify factors contributing to local extinctions or the failure of otters to re-colonise areas, which are poorly understood (see section 1.12.3). Non-detection can introduce significant bias into models of wildlife-habitat relationships (Gu and Swihart, 2003; Tyre *et al.* 2003) and studies of interspecific competition (Mackenzie *et al.* 2004). This can lead to inappropriate habitat management and inaccurate perceptions regarding the spatial organisation of species, and the interactions occurring between them. The bias introduced by non-detection can be addressed by incorporating detection probabilities into studies of species-habitat relationships and interspecific competition (Gu and Swihart, 2003; Mackenzie *et al.* 2004). The current study defines the detection probabilities for a range of otter survey designs in small lowland rivers, an important habitat for otters across their European range (see section 3.1). These could benefit studies investigating otter habitat preferences or competitive interactions, with species such as the American mink *Mustela vison*.

3.5.5 The optimal otter survey design for a range of objectives on small lowland rivers

Field surveys should be designed to minimise the occurrence of false negatives, as they introduce a bias that limits the ability to effectively study and conserve species (Moilanen, 2002). The optimal survey design requires consideration of the study objectives, the biology of the target organism, and what is logistically practical (Mackenzie and Royle, 2005). Otter surveys undertaken at small spatial scales often have very different objectives to those undertaken at broad spatial scales (see section 3.1). The evidence provided by this study suggests that the standard National Otter Survey design is not effective at smaller spatial sales (see section 3.5.4). It also identifies seasonal variation in the probability of detecting otters (Figure 3.3 and table 3.4) despite a lack of variation in sprainting rate (see section 3.4.2). This suggests that environmental factors, such as bank-side vegetation, may affect the probability of detecting otters. The probability of detecting otters on small lowland rivers was highest in winter and spring, which is in contrast to the current advised survey period of May-September (Mason and MacDonald, 1987; Jones and Jones, 2004). Otter surveys should be designed and validated for their specific purpose, taking into account that the probability of detecting otters may vary with spatial scale and season.

A key argument for the continued use of the 600 m transect design by the National Otter Surveys, is that it enables direct comparison with previous surveys (Crawford, 2003; Jones and Jones, 2004; Strachan 2007). Fundamentally, when comparing species distributions between different areas and habitats, it is important to standardise detection probabilities (Mackenzie *et al.* 2002; Gu and Swihart, 2003; Tyre *et al.* 2003). The failure of the standard National Otter Survey design to determine the absence of otters on small lowland rivers, with an acceptable level of confidence, is of significant concern. This suggests that the National Survey data has poor resolution. This study demonstrated that six repeat 600 m transect surveys are required to declare the absence of otters on small lowland rivers, with a level of confidence in excess of 80%. But repeat visits are rarely undertaken by the National Otter Surveys unless rainfall was deemed to have significantly affected the initial survey (Jones and Jones, 2004). Ruiz-Olmo *et al.* (2001) found that three 600 m transect surveys gave 100% detection of otters on small rivers in Spain. The evidence provided by this study and that of

Ruiz-Olmo *et al.* (2001) confirms that undertaking a single 600 m transect survey cannot detect otters on small rivers with sufficient power. The reliability of the National Otter Surveys could be significantly improved, by conducting repeat surveys at sites that were initially negative and visiting a minimum of two sites on each river. This would increase the power of the survey design without altering the 600 m transect. Thus, comparisons with previous surveys would still be possible by only considering the result of the first visit. Logistically it may not be viable to make repeat surveys of multiple sites on all small lowland rivers. Therefore, additional effort should be prioritised to areas believed to have small, threatened or declining populations.

One-off transect surveys undertaken at a single site had the lowest probability of detecting otters on small lowland rivers. Several different survey designs were able to determine otter presence/absence with a power of 0.8. The optimal design depends on whether it is more practical to increase transect length, undertake repeat surveys, or increase the number of survey sites. Increasing transect length improved the probability of detecting otters, but this alone was not sufficient to achieve a power of 0.8 (Figure 3.3). Repeat surveys improved the probability of detecting otters, but to obtain a 0.8 detection power by repeatedly surveying one site required a considerable increase in transect length (see appendix table 2). For example, repeatedly surveying a 600 m transect on 15 occasions provided a detection power of just 0.64. Increasing survey effort at one site does little to improve the detection power when the distribution of signs is low (Mackenzie and Royle, 2005). Adding additional survey sites increased the probability of detecting otters (Figures 3.4 and 3.5), as the clustered distribution of spraints (see section 3.5.4) meant that some sections were always negative for otters (Figure 3.2). However, surveying a large number of sites may be less efficient than surveying fewer sites more often, particularly when detection power is low (Tyre *et al.* 2003). The analysis undertaken in the current study supports this view, indicating that the most efficient survey design, to determine the presence/absence of otters on small lowland rivers, is three repeat surveys of two sites. The sites should be at least 500 m apart and the surveys separated by at least two weeks. Based on this design, the transect length required to achieve a detection power of 0.8 varies with season, from 700 m in spring to 1000 m in autumn (Table 3.4).

Otters have a large home range, estimated to be 38.8 (± 23.4) km in some riparian systems (Kruuk, 2006). Consequently, all developments undertaken on small lowland rivers are liable to fall within the area used by otters, if they are present on the river. It is important to determine whether a proposed development falls within an area that is currently being used by otters, and therefore, likely to have a greater impact on the population. This study revealed that the maximum distance from any point on a river, to a site used by otters during the two year study was 2.3 km. If otters are already known to be present on a river, survey effort can be focussed to a 2.3 km radius of a development site. This will determine whether otters are active within a relevant distance of the site, prior to a development commencing. Surveying 2.3 km upstream and downstream of a development site on one occasion would not detect otters with power of 0.8. Undertaking a repeat survey of this area, at least two weeks after the initial survey, would achieve a detection probability in excess of 0.8 in all seasons (Mean = 0.88 ± 0.03 SE).

3.5.6 Limitations of the study

The detection power of the standard 600 m transect survey has previously been estimated as 0.77, based on data obtained through a single repeat survey (Bonesi *et al.* 2006). The current study systematically re-sampled a comprehensive data set, obtained by repeatedly surveying four rivers over a period of two years, and therefore, provides a more robust assessment of the power associated with different otter survey designs. The study rivers are typical examples of small, impoverished lowland rivers (Holmes *et al.* 1999), so the detection probabilities can be cautiously applied to surveys undertaken on similar rivers, elsewhere in the UK. Comparative studies, carried out on rivers of a range of lengths, would be useful to help verify the figures provided here. The standard survey technique uses spraints, footprints and resting sites to confirm otter presence (Crawford *et al.* 1979; Lenton *et al.* 1980), whereas spraints were the only field sign used in this study. Spraints are very distinctive, making them the field sign most frequently used to designate positive sites (Crawford *et al.* 1979; Mason and Macdonald, 1986; Jones and Jones, 2004; Strachan, 2007). Even experienced surveyors frequently misidentify footprints (Evans, 2006) and very few footprints were recorded on the study rivers, due to a lack of suitable substrate, which is also an issue in other areas (Henshilwood, 1981; Beja, 1996). Resting sites could be due to the activity of European polecat *Mustela putorius* or American mink, both of which are present on Gower. Using spraints reduced the probability of falsely designating sites as positive for otters (Type I error), through misidentification of footprints and resting sites.

The other potential source of error stemmed from the removal of spraint, for dietary analysis. This study surveyed, and removed, spraints every fortnight, but the study of Jenkins and Burrows (1980) found that the mean duration of spraints, on riparian systems, was 21 days. The removal of spraint could have increased the probability of recording false negatives in future surveys. A study undertaken on the River Clyne, found that most spraints disappeared within two weeks (Hill *et al. unpub. data*). Another study found that all of the rivers were regularly remarked within three days of removal (Parry *et al. unpub. data*). It is acknowledged that spraint removal affected the independence of the surveys. However, the high rate of spraint disappearance, coupled with regular remarking, suggests that the impact of removal, on the occurrence of false negatives, was likely to be negliable.

3.5.7 Conclusions and Implications for population monitoring

It could be argued that in the UK the application of the standard otter survey has changed, following the recovery of otter populations. The National Otter Survey looks at distribution on broad geographical scale (Crawford, 2003; Jones and Jones, 2004; Strachan, 2007); false negative results are highly unlikely over such large areas, due to the large number of survey sites. However, the standard survey technique developed for the National Otter Surveys is routinely used to detect otters in smaller areas, for the purpose of conservation and development planning (see section 3.1). The standard 600 m transect survey is also routinely used by studies investigating various aspects of otter ecology, including habitat preference and interspecific competition (Prenda and Granda-Lorencio, 1996; Bonesi *et al.* 2004; McDonald *et al.* 2007). This current study demonstrates that the standard 600 m transect survey design is unsuitable for addressing these objectives on small lowland rivers, due to its low detection power. This may have consequences for monitoring programs in other otter species, which also using the standard otter survey design (see section 3.1).

The lowest survey effort required to achieve a detection power of 0.8 was found to be three repeat surveys of two separate sites. The repeat surveys should be separated by at least two weeks and the survey sites by at least 500 m. The optimal approach, however, depends on the study objectives, and whether it is more efficient to increase the number of survey sites or the number of repeat surveys. It is important to have equal detection power between different areas and habitats. The probability of detecting otters varies seasonally with the lowest survey effort required in winter and spring. In order to maintain equal power of detecting otters between different seasons it is necessary to modify the survey design by adjusting transect length. This study reveals scale sensitivity in the detection power of otter transect surveys. Further research is required to investigate the scale sensitivity of otter transect surveys in different habitats and how landscape affects detection probabilities.

Otters regularly marked dry river beds on Gower, and sprainting was recorded in the woodland around Pennard Pill. This highlights a significant gap in our knowledge of otter ecology, as surveys are usually conducted in linear habitats tied to water bodies (see section 8.3). Current planning regulations take no account of otter activity occurring away from water. A different survey approach would be necessary to monitor the terrestrial activity of otters. Modifying the transect survey technique, to reduce the level of error, is currently the best option to improve otter population monitoring. A range of other survey methods are available, but they all have restrictions preventing their widespread application (see section 1.11.2). Using molecular tools to assign individual identification to faeces could significantly increase the benefit and utility of carnivore field surveys (see section 8.4).

Chapter 4

A comparison of otter dietary analyses methods

"Habit is stronger than reason"

George Santayana (c1863-1952)

Summary

1. Most knowledge concerning the diet of elusive carnivores has been obtained by analysing prey remains recovered in faeces or pellets. There has been considerable debate regarding the accuracy of this approach, which has resulted in the development of a large number of different analysis methods. The comparability of dietary data produced by different methods is integral to the ability to compare different studies. This study represents the first investigation of the comparability of different faecal hard-part analysis techniques in a wild carnivore population with a highly diverse diet.
2. The level of comparability between dietary data produced different analysis methods was relatively low (43.5%-80.2%), particularly between frequency of occurrence and volumetric based methods.
3. Volumetric methods produced higher estimates for non-fish prey and frequency of occurrence methods produced higher estimates for fish prey.
4. *Synthesis and Applications.* This study demonstrates that that a lack of standardisation in the methodology of otter dietary studies has reduced the capacity for comparison between studies. Recommendations for standardisation are provided to help improve the comparability of future studies. Finally, it is demonstrated that the dietary data obtained through faecal hard-part analysis is influenced by trophic diversity. Thus, feeding trials evaluating the accuracy of hard-part analysis need to provide diets that reflect the trophic diversity of wild populations.

4.1 Introduction

The identification of undigested prey remains in faeces, pellets or stomachs, has long been used to investigate diet in a diverse range of species (see section 1.10.3). Faecal sampling is relatively easy to undertake and non-destructive (Trites and Joy, 2005), which makes it particularly useful for studying the diet of endangered and elusive species. Faecal analysis can identify prey that may not be recorded during visual observations of feeding (Moreno-Black, 1978), but relies on the presence of hard remains, in order to identify prey. Hence, soft bodied prey is underestimated, and the consumption of prey with a large number of hard parts tends to be overestimated (Erlinge, 1968; Bruggerk, 1993; Carss and Parkinson, 1996; Tollit *et al.* 1997; Burns *et al.* 1998). Data from hard-part analysis are typically expressed as frequency of occurrence values for each prey type (e.g. Watson, 1978; Van Aarde, 1980; Lønne and Gullikson, 1989; Reid and Arnould, 1996; Schley and Roper, 2003), but due to acknowledged limitations with frequency of occurrences methods, numerous alternative methods have been developed (Corbett, 1989; Bekker and Nolet, 1990; Jacobsen and Hansen, 1996; Zabala and Zuberogoitia, 2003). Much of our knowledge of otter diet has been obtained through the analysis of spraints (see section 1.12.5). Several feeding studies have been undertaken on captive otters to investigate the relationship between the results of different spraint analysis techniques and actual diet (see section 1.12.5). There is still however, a lack of standardisation in the methods by which spraints are analysed (Carss and Parkinson, 1996), which reduces both the robustness and comparability of the data produced.

The ability to compare dietary studies could be undermined if there is a low level of agreement between data produced by different methods. Observed differences between two studies could be little more than artefacts of the different methods employed. Most spraint analysis methods assess either the frequency or volume of occurrence for each prey type. It has been argued that volumetric carnivore dietary analysis methods produce meaningful data, as they indicate the relative importance of prey types (Zabala and Zuberogoitia, 2003). Nevertheless, the vast majority of otter dietary studies have used frequency of occurrence methods (e.g. Watson, 1978; Adrian and Delibes, 1987; Weber, 1990; Beja, 1991; Brzeziński *et al.* 1993; Watt, 1995; Kingston *et al.* 1999; Yoxon, 1999; Clavero *et al.* 2004; Lanszki and Molnar, 2003). Determining the comparability of dietary data produced by different methods is important if volumetric methods are to be advocated in future studies, due to suggestions that this approach is more accurate than frequency based methods (Jacobsen and Hansen, 1996; Zabala and Zuberogoitia, 2003). Previous studies have measured the comparability of volumetric and frequency data in diets containing a small number of prey types (Jacobsen and Hansen, 1996; Corbett, 1989; Zabala and Zuberogoitia, 2003; Van Dijk *et al.* 2007). This study focuses on a carnivore with a highly diverse diet, comparing frequency of occurrence and volumetric methods of faecal analysis using data collected from a wild population.

4.2 Aims

This study investigates the comparability of different spraint analysis methods on a large data set from a long-term study of wild otters on Gower. The aims addressed were;

1) To investigate the comparability of dietary data produced by five different spraint analysis techniques.

2) To recommend a standardised protocol for spraint collection and analysis.

4.3 Materials and methods

Sprains were collected and stored as described in section 2.3. The Gower spraints were subjected to five frequently used dietary analysis methods (see equations 1-5), which are described in detail in section 2.7. Renkonen's index of percentage similarity (see section 2.9.7 equation 9) was used to determine the comparability of dietary data produced by the different analysis methods. Percentage frequency of occurrence could not be included in the comparison as Renkonen's index, like other indices of similarity, requires the use of relative abundances where the sum of the different species is to equal 100 (Krebs, 1989). Prey types that occurred in less than 1% of spraints were considered to be unimportant and excluded from further analysis. Spearman's rank correlation was used to investigate the comparability of prey rankings produced by the different spraint analysis methods.

Equation 1. Frequency of occurrence (FO)

$$\text{FO} = \frac{\text{Number of spraints containing a prey type}}{\text{Total number of spraints}} \text{ X } 100$$

Equation 2. Relative frequency of occurrence 1 (RFO 1)

$$\text{RFO 1} = \frac{\text{Number of occurrences of a prey type}}{\text{Sum occurrences of all prey types}} \text{ X } 100$$

Equation 3. Relative frequency of occurrence 2 (RFO 2)

$$\text{RFO 2} = \frac{\text{Number of occurrences of a prey type in each spraint}}{\text{Total number of all identifiable prey items in each spraint}} \text{ X } 100$$

Equation 4. Relative dry weight (RWP)

$$\text{RWP} = \frac{\text{Dry weight of remains of a prey type in spraint}}{\text{Sum of dry weights for all prey types}} \text{ X } 100$$

Equation 5. Relative frequency of numbers (RFN)

$$\text{RFN} = \frac{\text{Number of individuals of a prey type}}{\text{Total number of all prey individuals}} \text{ X } 100$$

4.4 Results

4.4.1 Comparability of dietary analysis methods

The results produced by the five spraint analysis methods were remarkably different (Table 4.1 and 4.2). The relative dry-weight method (RWP) produced higher estimates for the proportion of non-fish prey than either of the Relative frequency of occurrence methods. Conversely, the occurrence of fish prey tended to be lower using RWP, compared to the frequency of occurrence methods. The highest level of similarity in the dietary data was between relative frequency of numbers (RFN) and the Relative frequency of occurrence method (RFO 2) used by Yoxon and Yoxon (2000), but even these methods only had a similarity of 80.2% (Table 4.3). The method which was most consistent in its similarity to other techniques was the Relative frequency of occurrence method (RFO 1) used by Watson (1978), which produced dietary data that was 61-63% similar to the four methods that it could be directly compared to. The highest level of disparity between techniques was between RFO 2 and RWP, which had a similarity of only 43.5%. All of the methods were significantly associated with a confidence level over 95%. The strongest correlations were between RFO 1 and frequency of occurrence (FO) ($r_s = 0.82$, $p < 0.001$) and between RFO 1 and RFO 2 ($r_s = 0.87$, $p < 0.001$). The weakest correlations were between RWP and RFO 2 ($r_s = 0.63$ $p < 0.001$) and between RWP and FO ($r_s = 0.69$ $p < 0.001$).

Table 4.1 Comparison of spraint analysis methods for fish prey present in more than 1% of spraints collected on Gower between July 2005 and June 2007. FO % = Frequency of occurrence, RFO 1 % = Relative frequency of occurrence (Watson, 1978), RFO 2 % = Relative frequency of occurrence (Yoxon and Yoxon, 2000), RWP % = relative dry weight of prey remains in spraints, RFN = relative frequency of numbers.

Common name	**Taxonomic name**	**FO %**	**RFO 1 %**	**RFO 2 %**	**RWP %**	**RFN**
Blenny	Blenniidae sp	5.4	2.2	1.2	0.8	0.8
Brown trout	*Salmo trutta*	20.9	8.0	2.3	2.1	0.5
Bullhead	*Cottis gobio*	70.8	27.3	56.6	18.4	51.5
European eel	*Anguilla anguilla*	33.8	13.0	7.7	4.9	0.7
Fifteen-spined stickleback	*Spinachia spinachia*	14.4	5.5	2.6	0.4	2.0
Flounder	*Platichthys flesus*	1.3	0.5	1.1	0.3	2.7
Four-bearded rockling	*Enchelyopus cimbrius*	1.3	0.5	0.1	0.4	0.1
Goby	Gobiidae sp	21.8	8.4	19.2	2.3	15.4
Three-spined stickleback	*Gasterosteus aculeatus*	15.8	6.1	2.6	0.4	2.1
Unspecified Cyprinidae	Cyprinidae sp	8.2	3.2	0.7	0.4	0.1
Unspecified flatfish	Hetrosomata sp	18.6	7.2	5.0	1.8	8.0
Unspecified fish		1.1	0.6	0.0	0.6	0.5

Table 4.2 Comparison of spraint analysis methods for non- fish prey, present in more than 1% of spraints collected on Gower between July 2005 and June 2007. FO % = Frequency of occurrence, RFO 1 % = Relative frequency of occurrence (Watson, 1978), RFO 2 % = Relative frequency of occurrence (Yoxon and Yoxon, 2000), RWP % = relative dry weight of prey remains in spraints, RFN = relative frequency of numbers.

Prey type	**FO %**	**RFO 1 %**	**RFO 2 %**	**RWP %**	**RFN**
Amphibian	14.2	5.5	0.2	10.5	4.4
Avian	9.5	4.0	>0.1	12.5	3.3
Crustacean	5.4	2.1	>0.1	15.4	1.8
Insect	9.2	3.6	0.1	7.4	3.6
Mammalian	2.7	1.1	>0.1	2.3	1.0

Table 4.3 Renkonen's index of similarity between the dietary data produced by different spraint analysis techniques applied to otter spraints from Gower. RFO 1 % = Relative frequency of occurrence (Watson, 1978), RFO 2 % = Relative frequency of occurrence (Yoxon and Yoxon, 2000), RWP % = Relative dry weight of prey remains in spraints, RFN = relative frequency of numbers.

Renkonen's Similarity %	RFO 1 %	RFO 2 %	RWP %
RFO 1 %	-	-	-
RFO 2 %	61.8	-	-
RWP %	63.1	43.5	-
RFN	63.5	80.2	47.4

4.5 Discussion

4.5.1 Comparability of different spraint analysis techniques

Numerous feeding studies have been undertaken on captive animals in attempts to quantify errors associated with different analysis methods (see sections 1.10.3 and 1.12.5). The comparability of different faecal analysis methods has received considerably less attention, but this is an important source of error when comparing dietary studies that may have used different methods. The ability to directly compare studies is important for investigating geographical and long-term trends in diet. The current study found that the dietary data, produced by different spraint analysis methods, had a relatively low level of similarity; ranging from 43.5% to 80.2%. The disparity between frequency of occurrence and volumetric methods agrees with previous studies (Hansson, 1970; Jacobsen and Hanson, 1996; Zabala and Zuberogoitia, 2003). These studies analysed diets containing a small number of prey types, which is not a realistic situation in a wild generalist carnivore population (e.g. Hall *et al.* 1998; Leopold *et al.* 1998; Zielinski *et al.* 1999; Clavero *et al.* 200). The current study determined the comparability between different analysis methods in a highly diverse diet, revealing a higher level of disparity than previously recorded. The discrepancies between values for fish and non-fish prey suggest that prey structure has a large influence on the values obtained by different dietary analysis methods. This is probably because different prey types have different proportions of hard remains and varying resistance to digestion (Reynolds and Aebischer, 1991). For example, amphibian remains are more susceptible to digestion than mammalian and avian remains (Rosalino *et al.* 2003). Fish remains are generally excreted by otters within 24 hours, but the remains of birds and mammals can occur in spraints up to three days after ingestion (Carss and Parkinson, 1996). Feeding trials, evaluating different faecal analysis methods usually investigate the differential recover of a small number of prey types with similar structures, such as fish (Dellinger and Trillmich, 1988; Staniland, 2002) or mammals (Floyd *et al.* 1978; Rühe *et al.* 2008). Previous feeding trials, carried out on captive otters, included very few non-fish prey types (Carss and Parkinson, 1996; Jacobsen and Hansen, 1996; Kloskowski *et al.* 2000b). Dietary diversity appears to influence the level of comparability between different analysis methods. In a diverse diet there is likely to be greater variation in the size, structure, proportion and digestibility of remains associated with different prey types, thereby increasing the potential for dissimilarity between analysis methods. Therefore, future feeding trials should provide diets that reflect the true spectrum of prey diversity available to wild populations of the species under investigation.

The ranking of prey types was significantly correlated between all of the methods used in this study. However, Spearman's rank correlation does not assess differences among prey types which may be biologically meaningful (Zabala and Zuberogoitia, 2003), so Renkonen's index of similarity was used to indicate differences among prey types. The highest level of similarity, and strongest correlations, were between methods based on frequency of occurrence. The lowest levels of similarity, and weakest correlations, were between the volumetric relative RWP method and the frequency of occurrence methods. These results are to be expected, as frequency of occurrence methods measure diet in a similar way, so there is autocorrelation between them. The volumetric RWP method tended to produce higher values for non-fish prey and lower values for fish prey, than the frequency of occurrence methods. Crustacean occurred in 5.4% (143/2627) of otter spraints on Gower, and four of the methods used in this study (FO %, RFO 1 %, RFO 2 %, and RFN) ranked it as a minor prey type. However, the RWP of crustacean was 15.4%, which ranked it as the second most important prey type. Conversely, gobies and sticklebacks were ranked as important prey by all of the frequency of occurrence methods but were of minor importance based on the RWP. This demonstrates that the interpretation of dietary data derived from wild populations is strongly influenced by the choice of analysis method.

4.5.2 Implications of the disparity between frequency and volumetric data

This study demonstrates a low level of similarity between dietary data produced by volumetric and frequency of occurrence methods in a carnivore with a highly diverse diet. Volumetric analysis methods are thought to produce a more accurate reflection of actual diet and biomass intake, than frequency of occurrence methods (Bekker and Nolet, 1990; Jacobsen and Hansen, 1996). Non-fish prey formed 48.1 % of otter diet, based on the volumetric RWP method, compared to 0.3% - 41% with the different frequency of occurrence methods. If volumetric analysis methods are more accurate, these figures imply that the importance of non-fish prey in otter diet is underestimated by frequency of occurrence methods (see section 4.1). This raises concerns on the accuracy of current views regarding the trophic ecology of otters and other fish-eating generalist carnivores, whose diets are traditionally assessed using frequency of occurrence methods e.g. Smooth-coated otters *Lutra perspicillata* (Anoop and Hussain, 2005), Neotropical river otter *Lontra longicaudis* (Helder-José and Ker de Andrade, 1997), American mink (Lodé, 1993), Grizzly Bear *Ursus arctos horribilis* (Mattson and Reinhart, 1995). It is, however, unclear whether volumetric methods actually produce a more accurate interpretation of diet than frequency of occurrence methods. The relationship between the weight of ingested material and the volume of remains recovered in spraints varies between fish species (Ferrario *et al.* 1995) and carnivores often pluck fur and feathers before feeding (Van Dijk *et al.* 2007), which may result in a large volume of remains when only a small amount of flesh is ingested. Research may be necessary to determine how feeding behaviour and the structure of different prey types affects the accuracy of different dietary analysis methods, in order to create correction factors, such as those for Eurasian badgers (Rodriguez and Delibes, 1992) and American mink (Akande,1972).

4.5.3 Study limitations

Several spraints analysis methods were not included in this comparison (see appendix table 7), and some of these may prove to be more comparable. However, nearly all analysis methods are based either on the frequency of occurrence, volume of prey remains or minimum prey numbers, and an example of each was used in this comparison. The captive feeding trial carried out by Jacobsen and Hansen (1996) concluded that scoring the bulk of prey remains on a scale of 1-10 was the most accurate method of analysing otter spraints. This method could not be used in this study as it requires spraints to contain less than 10 different prey types, which was often not the case on Gower. This study was undertaken on a wild population, so the number of prey items ingested was not known, and could not be related to the dietary data produced by the different analysis methods. However, the aim of this study was to investigate the comparability of different analysis methods, not the accuracy of spraint analysis. This has value, as in a range of carnivore species, comparisons are often made between dietary studies that used different methods of analysis (e.g. Carss, 1995; Pauly *et al.* 1998; Schley and Roper, 2003). Studies on wild populations are beneficial as it is difficult to replicate realistic feeding conditions in captivity, due to the large number of factors that influence digestion (see section 4.5.2).

4.5.4 Recommendations for standardisation

A standardised protocol has been proposed for sea bird dietary studies (Barrett *et al.* 2007); a similar protocol is proposed here for dietary studies of otters and other mammalian carnivores, based on the results of this study. The most frequent objectives of otter dietary studies are (i) to describe the diet of a population (e.g. Webb, 1975; Kruuk *et al.* 1987; Brzeziński *et al.* 1993), (ii) to compare dietary composition between different times, habitats and populations (e.g. Beja, 1991; Clavero *et al.* 2003; Preston *et al.* 2007), (iii) to determine dietary overlap with sympatric carnivore species (e.g. Cloade and MacDonald, 1995; Bonesi *et al.* 2004), (iv) to measure the impact of predation on human economic activities (e.g. Kloskowski,2000a; 2005; Freitas *et al.* 2007). A standard minimum requirement for otter dietary studies would provide a baseline for comparison between studies, but this does not prevent a more complex analysis from being undertaken. Recommendations for the standardisation of otter dietary studies are provided in table 4.4.

Table 4.4 Recommendations for the standardisation of spraint collection and analysis protocol in otter dietary studies.

Spraint collection protocol	**Spraint analysis protocol**
• Provide a grid reference for all study sites and report the frequency of collections. • Minimum study duration of one year with data collected during all seasons. • Spraints collected in their entirety, as is it not known if prey remains are evenly distributed within the matrix. • Spraints should be individually stored and analysed. • The minimum sample size required to detect differences between two geographically separate carnivore populations, should be treated as 94 (Trites and Joy, 2005), until a comparable analysis has been undertaken in otters.	• Prey should be identified to the lowest taxonomic level possible and described using scientific nomenclature. • Unidentified prey occurrence data should be reported. • To maximise comparability with previous studies, dietary data should ideally be expressed using **both** Relative frequency of occurrence and a volumetric method. • Trophic niche parameters such as breadth, richness, and where applicable overlap, should be calculated (Krebs, 1989). • Diet similarity between areas should be expressed suing an index of percentage similarity (Krebs, 1989)

4.5.5 Conclusions

In a wild carnivore population, with a highly diverse diet, there were high levels of discrepancy between the dietary data produced by different faecal analysis methods, particularly between volumetric and frequency of occurrence methods (see section 4.5.3). The level of comparability between different analysis methods appears to be lower in more diverse diets. When making comparisons between studies or investigating geographical and longitudinal trends in diet, data should be converted to a single method. Where this is not possible, non-parametric statistical analysis may be used, as the prey ranks produced by different analysis methods were significantly correlated. Using hard part analysis methods to study diet will clearly underestimate the occurrence of soft-bodied prey, regardless of the specific method used or the source of the sample material. It is therefore, important to test the application of novel techniques for studying diet, which are potentially more accurate (see section 8.6) and provide useful information concerning the sample population (see section 8.4). Fundamentally, the limitations of current techniques have to be remembered and we should not be content with our sparse knowledge of carnivore trophic ecology.

Chapter 5

Temporal and spatial variation in otter *Lutra lutra* diet on the Gower peninsular

"How many things by season, seasoned are. To their right praise and true perfection"

William Shakespeare (The Merchant of Venice, 1598)

Summary

1. In many carnivore species diet varies temporally and spatially. In heterogeneous landscapes dietary variation may be facilitated by variation in habitat use. Otters are able to forage in marine, freshwater and terrestrial habitats, but there have been few comprehensive studies of otter populations living at the interface of these habitats. Small lowland rivers are an important habitat for otters throughout their range, but relatively few studies have been undertaken in this habit. There is also a lack of information concerning the ecology of UK otter populations outside of Scotland.
2. The trophic niche of otters inhabiting four small lowland coastal rivers on the Gower Peninsular was investigated over a two year period. Dietary data was obtained through the analysis of spraints collected at fortnightly intervals. Spatial and temporal trends in dietary composition and trophic niche breadth were investigated, and used to elucidate patterns in foraging strategy and habitat use.
3. Otter diet on Gower contained freshwater fish (RFO 58.7%), marine fish (RFO 24.5%) and non-fish prey (RFO 16.2%), indicating that the population was occupying a broad trophic and habitat niche throughout the year.
4. Otter diet varied spatially more than it did temporally. Dietary variation was primarily due to differences in the consumption of alternate prey items and trophic niche width increased during winter
5. *Synthesis and Applications.* This study confirmed that microhabitat structure can have a strong influence on carnivore diet, causing significant dietary variation between similar habitats. It can be inferred that the trophic structure of riparian communities may differ in time and space. The results demonstrate the importance of a diverse prey base to carnivore populations inhabiting environments with denuded populations of preferred prey. Declines in freshwater prey populations may reduce the viability of small lowland rivers as otter habitat. However, prey declines in coastal rivers may be compensated by an increased reliance on marine prey.

5.1 Introduction

Otters predate a range of prey types with diverse life histories, (see section 1.12.8). It has been shown that fish, which form the major component of otter diet, are patchily distributed in rivers and that both the size and density of these patches varies longitudinally (Duncan and Kubecka, 1996). Differences in landscape structure and environmental complexity have a strong influence on prey availability, and therefore on spatial patterns in otter diet (Kruuk *et al.* 1990; Clavero *et al.* 2004). Prey activity and behaviour in aquatic systems is also strongly regulated by water temperature (Adams *et al.* 1982), which drives seasonal trends in prey availability that otters are also obliged to adapt to. This means that otter prey is rarely uniformly distributed either temporally or spatially. When prey is not uniformly distributed, and occupies different habitats, predators often show prey switching to maximise foraging efficiency (Begon *et al.* 1996; also referred to extensively in chapter 1). Otters are thought to adjust their spatial use of habitats in order to optimise their foraging efficiency (Roche, 2001; Chalupa, 2006). Variation in prey availability means a temporal and spatial analysis of diet is necessary to study otter trophic ecology. This approach is frequently used in dietary studies of carnivores, including Red fox (Molsher *et al.* 2000) and Polar bears (Iverson *et al.* 2006), as it allows investigation of how trophic niche varies in time and space on a variety of scales.

Wales is one of the few regions within the otter's global range with confirmed marine activity (Liles, 2003a). Therefore, investigating otter trophic ecology in Wales is of particular scientific and conservation interest. There is a lack of current data on the diet of otters in Wales, especially in regards to temporal and spatial variation in trophic niche at the population level. This is the first long-term study of otter ecology in Wales, aiming to investigate temporal and spatial variations in diet, through the analysis of spraints collected from four river systems on the Gower peninsula. The ability to forage in marine, freshwater and terrestrial environments is an unusual trait in carnivore species. Only two previous studies have provided information regarding marine foraging by otters living in rivers (Beja, 1991; Clavero *et al.* 2004). Both of these studies sampled in specific areas and habitats that were not fully indicative of otter foraging in coastal rivers. The current study provides an important longitudinal investigation of otters foraging at the marine/freshwater interface, using a sampling regime that covers the entire length of coastal rivers. It is also the first comprehensive study of otters living at the marine/freshwater interface in the UK.

In recent years there has been a large decline in eels (Dekker, 2003), a core prey of otters in the UK (see section 7.4.2). Meanwhile, other important prey items, such as amphibians (Weber, 1990; Clavero *et al.* 2005), are also threatened (Stuart *et al.* 2004). In response to this, a study of otter diet in a UK freshwater system is appropriate to identify prey species currently of importance to otters. The data generated will provide an evidence base for applied conservation, both in Wales and in lowland river systems elsewhere in the UK, an important otter habitat in which very few studies have been undertaken (Lanszki *et al.* 2009). In a broader context, this study provides longitudinal data on variation in the trophic niche of a density dependent carnivore population inhabiting a heterogeneous landscape. Understanding how trophic niche varies in time and space at the population level is useful, both for hypothesis testing and modelling of carnivore trophic ecology.

5.2 Aims and hypotheses

1. What is the trophic niche of the otter population on the Gower peninsular?

2. To determine if there is spatial and temporal variation in the total trophic niche width (TNW) of the otter population on the Gower peninsular?
   Null Hypothesis: There is no significant spatial or temporal variation in trophic niche breadth.

3. To determine if otters on the Gower peninsular are foraging in the marine environment, and to identify seasonal patterns in the consumption of marine prey.

4. To determine if there is spatial and temporal variation in the composition of diet in the otter population on the Gower peninsular?
   Null Hypothesis: There is no significant spatial and temporal variation in the consumption of frequent prey items by otters on the Gower peninsular.

5. To investigate the influence of meteorological factors on the observed temporal and spatial variation in otter diet on the Gower peninsular?

5.3 Materials and Methods

Otter spraints were collected fortnightly between July 2005 and June 2007 following the protocol described in section 2.3.1. Dietary analysis was undertaken following the protocol described in section 2.7. The drawbacks of determining otter diet through spraint analysis are well documented elsewhere (Carss and Elston, 1996; Carss and Parkinson, 1996). Relative frequency of occurrence (see section 2.7.2, equation 2) was used to describe otter diet in this study, as this method produces a relatively accurate interpretation of diet (Erlinge, 1968; Carss and Parkinson, 1996; Jacobsen and Hansen, 1996) and has been frequently used by previous otter dietary studies. The distribution of the data was tested for normality using a Kolmogorov-Smirnov (KS) test. The homogeneity of the variance was assessed using a Levene's test. A two-way Analysis of Variance (ANOVA) was used to investigate seasonal and between site variations in Shannon-Weiner TNW, and the consumption of marine prey, using season and study site as the fixed factors. Renkonen's index (see section 2.9.7 equation 9) was used to assess the similarity in dietary composition between seasons and study sites.

To explore variation in the composition of otter diet Multiple Analysis of Variance (MANOVA) was undertaken on prey RFO % values, with study site and season as the fixed factors. Only the top ten ranked prey types were included in the temporal and spatial analyses of otter diet, as including rare prey occurrences can have a strongly distorting effect (Field, 2007), leading to unimportant trends biasing the analysis. Determining the top ten prey types, using the overall median rank from all four sites, could bias the ranking towards prey that were frequent components of diet at one site, but absent from others. To account for this the overall population rank was assigned using a population rank index. The population rank index takes into account the number of study sites each prey type was recorded at. This provides a more useful indication of the overall importance of each prey type to the otter population. Population rank index values closest to zero indicate the most important prey types.

$$\text{Population Rank Index} = \frac{\text{Mean overall rank at all sites}}{\text{Number of sites where the prey type was consumed.}}$$

Where significant differences were detected, a Least Significant Difference (LSD) *post hoc* test was applied. Pearson's correlation tests were used to investigate if the occurrence of the top ten ranked prey types were associated with rainfall, wind speed or air temperature. The Bonferroni method was used to reduce the critical value, to account for the increased likelihood of detecting significant trends when making multiple comparisons (Dytham, 2003). No formal assessment of prey populations was carried out for reasons discussed in section 5.5.4. However, electrofishing was carried out on the Pennard and Burry Pills by the Environment Agency in August 2005. The data generated was kindly provided and is presented in the results. Information regarding the timing of amphibian breeding in South

Wales was provided by Peter Hill (South Wales Amphibian and Reptile Group Conservation Officer) and is also presented in the results.

5.4 Results

5.4.1 The diet and trophic niche of otters on Gower

In total, 2651 spraints were collected between July 2005 and June 2007. Dietary analysis recorded a total of 223,814 identifiable remains representing 6,818 prey occurrences comprising of 52 prey types. Fish accounted for the 83.8% of otter diet and 15 families of fish were recorded including both marine and freshwater species (Table 5.1). Bullhead was the most frequent prey item with a RFO of 27.3% and RWP of 24.5%. Spraints were analysed using several different methods in order to investigate the comparability of different techniques (see chapter 4). The different methods had a relatively low level of comparability (see section 4.4.1, page 102) and in many cases the ranking of prey categories varied between methods. However, all of the methods ranked bullhead as the most important prey item on Gower (Table 4.1, page 103). Other frequently occurring prey items were eels, sticklebacks, gobies, brown trout and flatfish. The proportion of fish remains that could not be identified, either through the published keys or the reference collection, was very low (Table 5.1). There were marked differences in the estimated importance of fish and non-fish prey between the RFO and RWP data. Non-fish prey included amphibians, mammals, birds, crustaceans and insects. Amphibians were the most frequently occurring non-fish prey, although insect and bird remains were recorded at moderate frequencies. Crustaceans occurred at relatively low frequencies whilst mammals were rarely consumed.

Table 5.1 RFO % and RWP % of fish prey in otter diet on the Gower peninsula between July 2005 and June 2007 (Spraints = 2651).

Common Name	Taxonomic	RFO %	RWP %
Fish total		**83.78**	**51.86**
Blennies	*Blennidae sp*	2.08	5.83
Brill	*Scophthalmus*	0.03	0.02
Brown trout	*Salmo trutta*	8.04	3.39
Bullhead	*Cottis gobio*	27.27	24.47
Chub	*Leuciscus cephalus*	0.19	0.05
Common bream	*Abramis brama*	0.26	0.02
Common carp	*Cyprinus carpio*	0.01	0.01
Unidentified Cyprinidae	Cyprinidae sp	3.17	0.53
Dab	*Limanda limanda*	0.12	0.04
Eelpout	*Zoarcidae*	0.03	0.00
European eel	*Anguilla anguilla*	13.01	7.40
Fifteen-spined stickleback	*Spinachia spinachia*	5.53	0.89
Flounder	*Platichthys flesus*	0.48	0.26
Four-bearded rockling	*Enchelyopus*	0.51	0.84
Gobies	*Gobiidae sp*	8.39	2.36
Minnow	*Phoxinus phoxinus*	0.04	0.00
Pike	*Esox lucius*	0.09	<0.01
Pipefish	*Sygnathidae*	0.04	0.01
Plaice	*Pleuronectes platessa*	0.01	0.01
Roach	*Rutilus rutilus*	0.1	0.05
Rudd	*Scardinius*	0.12	0.02
Saithe	*Pollachius virens*	0.01	0.01
Three-bearded rockling	*Gaidropsarus*	0.04	0.58
Three-spined stickleback	*Gasterosteus*	6.09	0.62
Wrasse	Labridae sp	0.07	1.14
Unidentified flatfish	Hetrosomata sp	7.17	2.62
Unidentified Percidae	Percidae sp	0.29	0.09
Unidentified Fish		0.59	0.61

Table 5.2 RFO % and RWP % of non-fish prey in otter diet on the Gower peninsula between July 2005 and June 2007 (Spraints = 2651).

Common Name	Taxonomic name	RFO %	RWP %
Non-fish prey total		**16.2**	**48.15**
Insect		**3.55**	**7.43**
Coleoptera	*Dysticus sp*	0.16	0.02
Golden-ringed dragonfly larvae	*Cordulegaster boltonii*	0.12	0.13
Other Odonata larvae	*Ashena sp*	0.22	0.20
Unidentified insects		3.05	7.07
Crustacean	Crustacean	**2.10**	**15.42**
Amphibian		**5.46**	**10.50**
Anuran sp	*Bufo bufo, Rana temporaria*	4.15	7.84
Newts	*Triturus sp*	1.31	2.66
Mammalian		**1.11**	**2.31**
Bank vole	*Myodes glareolus*	0.15	0.07
Brown rat	*Rattus norvegicus*	0.01	0.13
Common shrew	*Sorex araneus*	0.03	0.03
Rabbit	*Oryctolagus cunniculus*	0.06	0.08
Water shrew	*Neomys fodiens*	0.09	0.15
Weasel	*Mustela nivalis*	0.03	0.02
Wood mouse	*Apodemus sylvaticus*	0.15	0.34
Unidentified mammalian		0.68	1.48
Avian		**3.97**	**12.49**
	Anseriforme	1.16	6.73
	Charadiiformes	1.20	2.36
	Ciconiiformes	0.03	0.03
	Galliforme	0.70	1.03
	Gruiformes	0.01	0.14
	Passerine	0.21	0.78
	Rallidae	0.25	0.44
	Unidentified Avian	0.41	0.99

Otter diet on Gower was quite diverse with an overall TNW value of 0.69 (Table 5.3). The niche width data was normally distributed (Kolmogorov-Smirnov: $z = 1.08$, $p = .019$), but an arcsine transformation was required to make the variance equal. The arcsine transformed niche width data was analysed using a two-way ANOVA with replication, which indicated that the trophic niche breadth of the otter population on Gower varied significantly between seasons, but not between study rivers (Table 5.4). LSD *post hoc* tests revealed that otter TNW was significantly broader in winter than in summer (MD = 6.28 ± 2.7, $p = 0.03$) and autumn (MD = 8.17 ± 2.7, $p = 0.006$).

Table 5.3 Seasonal variation in Shannon-Wiener TNW (*H'*) values for otter diet on Gower (summer 2005 $n = 281$, autumn 2005 $n = 289$, winter 2005-2006 $n = 269$, spring 2006 $n = 283$, summer 2006 $n = 329$, autumn 2006 $n = 215$, winter 2006-2007 $n = 247$, spring 2007 $n = 641$, summer 2007 $n = 97$).

	River Clyne	Burry Pill	Pennard Pill	Bishopston Pill	Overall Gower
Summer 2005	0.74	0.72	0.81	0.7	0.71
Autumn 2005	0.82	0.65	0.66	0.7	0.67
Winter 2005-2006	0.81	0.75	0.87	0.89	0.78
Spring 2006	0.84	0.78	0.82	0.79	0.79
Summer 2006	0.83	0.69	0.77	0.84	0.7
Autumn 2006	0.85	0.75	0.88	0.52	0.74
Winter 2006-2007	0.79	0.78	0.88	0.97	0.78
Spring 2007	0.76	0.77	0.79	0.85	0.71
Summer 2007	0.82	0.82	0.88	n/a	0.76
Overall	0.72	0.65	0.78	0.79	0.69

Table 5.4 Output from a two-way ANOVA (with replication) carried out on arcsine transformed otter niche width data collected from four river systems on the Gower peninsula between July 2005 and June 2007. Niche breadth was the dependent variable; study river and season were the fixed factors.

Factor	*d.f.*	SS	MS	*F*-ratio	*P*-value	Power	Partial Eta
River	3	139.44	46.48	1.56	0.22	0.36	0.16
Season	3	299.06	99.69	3.34	0.04	0.69	0.29
Error	25	745.78	29.83				

d.f = degrees of freedom, SS = sum of squares, MS = mean square, *p* = significance, Partial Eta = effect size.

5.4.2 Temporal and spatial variation in the proportion of marine prey in otter diet on the Gower Peninsular

Freshwater fish formed 58.7% of the prey occurrences in otter diet on the Gower Peninsula, whilst marine fish made up 24.5% of prey occurrences and non-fish contributed 16.2%. The proportions of marine fish, freshwater fish and non-fish prey showed several small spatial (Table 5.5) and seasonal variations (Figure 5.1).

Table 5.5 Spatial variation in the proportion of marine fish, freshwater fish, unidentified fish and non-fish prey in otter diet on Gower between July 2005 and June 2007. The number of spraints analysed from each site are presented in parentheses.

Study Site	**Freshwater fish** RFO %	**Marine fish** RFO %	**Non-fish** RFO %	**Unidentified fish** RFO %
River Clyne (*n* = 481)	58.3	19.5	20.8	1.4
Burry Pill (n = 1542)	61.1	24.7	13.8	0.4
Pennard Pill (*n* = 612)	53.0	27.8	18.6	0.6
Bishopston Pill (*n* = 75)	52.1	27.0	20.9	0
Overall Gower (*n* = 2651)	58.7	24.5	16.2	0.6

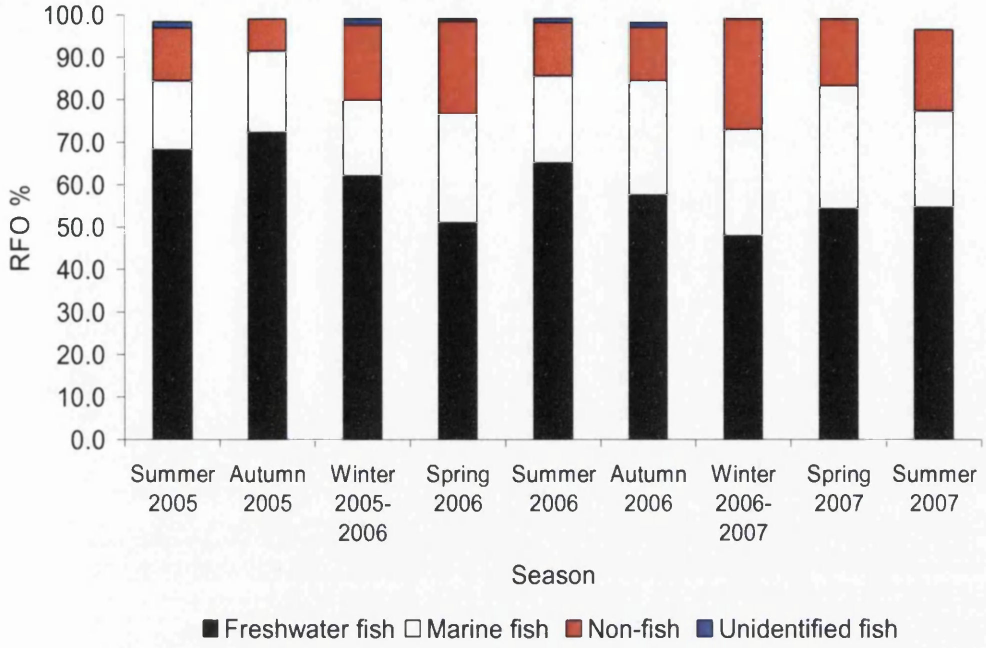


Figure 5.1 Seasonal variation in Relative frequency of occurrence (RFO %) of marine fish, freshwater fish, non-fish and unidentified prey groups in otter diet on Gower (summer 2005 n = 281, autumn 2005 n = 289, winter 2005-2006 n = 269, spring 2006 n = 283, summer 2006 n = 329, autumn 2006 n = 215, winter 2006-2007 n = 247, spring 2007 n = 641, summer 2007 n = 97).

A two-way ANOVA with replication was performed on arcsine transformed proportional data with the RFO % of marine species in otter diet as the dependent variable. This indicated that there were no significant differences in the proportion of marine prey consumed by otters on the Gower peninsula between the four study sites, or between the four seasons (Table 5.6).

Table 5.6 Output from a two-way ANOVA with replication carried out on arcsine transformed proportional otter diet data collected from four river systems on the Gower peninsula between July 2005 and June 2007. The Relative frequency of occurrence (RFO %) of marine prey was the dependent variable; study river and season were the fixed factors.

Factor	*d.f.*	SS	MS	*F*-ratio	*P*-value	Power	Partial Eta
River	3	250.96	83.66	0.64	0.60	0.16	0.07
Season	3	656.89	218.96	1.66	0.20	0.38	0.17
Error	25	3291.07	131.64				

d.f = degrees of freedom, SS = sum of squares, MS = mean square, p = significance, Partial Eta = effect size.

5.4.3 Spatial and temporal variation in the composition of otter diet on the Gower Peninsular

The Renkonen's index percentage similarity values indicated that the composition of otter diet varied with season and between the study rivers (Tables 5.7 and 5.8). The mean similarity in diet between seasons was 74.0% (± 6.4 SD) and the mean similarity between sites was 70.6% (± 5.7 SD). This indicates that the composition of otter diet varied by a mean of 26% (± 6.4 SD) between seasons and 29.4% (± 5.7 SD) between the study rivers. The high similarity values, recorded between the same season from year one and two, indicated that the seasonal composition of otter diet was relatively synonymous between the two years. There was a trend for high levels of similarity between adjacent seasons, with summer 2006 at least 80% in resemblance with both spring and autumn 2006. Likewise summer 2005 had a high degree of similarity with autumn 2005. The lowest levels of concordance were between summer diet and winter diet, with a mean similarity of 65.4 % (± 3.9 SD). There was also a trend for lower levels of analogy between seasons that were separated by the largest time periods. For example, otter diet during summer 2005 had a higher similarity to that of summer 2006 than summer 2007. The diet of autumn 2005 also had a low degree of similarity with the diet of spring and summer 2007. The composition of otter diet had a high level of similarity between the River Clyne, Pennard and Burry Pills (Table 5.7), whereas otter diet on the Bishopston Pill had marginally lower similarity to the other study sites.

Table 5.7 Renkonen's percentage similarity in otter diet between study sites on Gower.

Study site	River Clyne (%)	Burry Pill (%)	Pennard Pill (%)
River Clyne	-	-	-
Burry Pill	71.2	-	-
Pennard Pill	77.8	75.5	-
Bishopston Pill	63.1	65.3	70.7

Table 5.8 Percentage similarity between seasons in otter diet on the Gower peninsula calculated using Renkonen's percentage similarity (section 2.9.7, equation 9).

Study site	Summer 2005 (%)	Autumn 2005 (%)	Winter 2005-2006 (%)	Spring 2006 (%)	Summer 2006 (%)	Autumn 2006 (%)	Winter 2006-2007 (%)	Spring 2007 (%)
Summer 2005	-	-	-	-	-	-	-	-
Autumn 2005	83.3	-	-	-	-	-	-	-
Winter 2005-2006	67.8	76	-	-	-	-	-	-
Spring 2006	70.3	68.9	76.6	-	-	-	-	-
Summer 2006	87.1	71.2	70.8	75.1	-	-	-	-
Autumn 2006	77.3	77.8	80.1	80.2	81.3	-	-	-
Winter 2006-2007	63.6	67.9	77.8	75	67.1	78.1	-	-
Spring 2007	72.9	68.5	75.8	86.5	75.6	82.7	78.4	-
Summer 2007	72.9	68.5	62.9	69.9	74.1	72.1	60.2	70.3

Some prey types showed few temporal or spatial variations in their occurrence in otter diet (Tables 5.9 and 5.10). Bullhead was by far the most frequent prey item recorded on each river over the entire study period. Eel was the second most frequent prey item, at all sites except for Bishopston. Brown trout was a frequent component of otter diet at all sites, except for Burry, where it was consumed at moderate levels. Birds were consumed at a moderate level, consistent between seasons and study sites. Seasonal and between site variations in occurrence were recorded in several prey types (Tables 5.9 and 5.10). The observed temporal and spatial variations were not due to discrepancies in sample size, between study sites or seasons, as the RFO % values obtained for Gower significantly correlated with the adjusted values (see section 2.9.7) for season ($r_s = 0.417$, $p = 0.008$, $n = 8$) and study site ($r_s = 0.273$, $p = 0.023$, $n = 4$).

To investigate which dietary components varied temporally and spatially, the 10 most frequently occurring prey types recorded in the pooled spraint data were identified. To reduce discrepancies caused by using many different levels of taxonomic classification, fish were grouped to family level, with the exception of flatfish which is routinely grouped as an order in otter dietary studies (e.g. Watson, 1978; Kruuk and Moorhouse, 1990; Watt, 1995; Kingston *et al.* 1999). Non-fish prey were organised to class level, as is normal practice in otter dietary studies. This excluded 17 minor prey types, with a RFO % value <1, which may have generated unimportant temporal and spatial trends in the analysis. At each study site, prey types were ranked according to their RFO% (Table 5.9). These ranks were used to calculate the population rank index (see section 5.3), which was used to determine the 10 most important prey types for otters on Gower. At each site, the two years of seasonal data was combined, as there was no significant difference in the occurrence of any of the top 10 prey categories, between the first and second year of the study. To make the sample sizes equal, between seasons and study sites, the data from summer 2007 was excluded from the analysis, as it only represented one month, and no data was obtained from Bishopston Pill during this period.

Table 5.9 Spatial variation in the Relative frequency of occurrence (RFO %) and rank of the 10 most frequently occurring prey in otter diet, at each study site on Gower, between July 2005 and June 2007. Core prey types, with high RFO % on all of the study rivers are shown in bold. The population rank index indicates the overall importance of each prey type to otters on Gower and is used to determine the overall population rank.

Prey type	**River Clyne (*n* = 481)**		**Burry Pill (*n* = 1542)**		**Pennard Pill (*n* = 612)**		**Bishopston Pill (*n* = 75)**		**Population rank index**	**Overall population rank**
	RFO %	**Rank**	**RFO %**	**Rank**	**RFO %**	**Rank**	**RFO %**	**Rank**		
Amphibian	10.7	5	4.1	8	5.1	8	6.8	6	1.69	7
Anguillidae	**14.1**	2	**12.7**	3	**13.2**	2	**10.9**	3	0.63	2
Avian	5.4	6	3.7	10	4.5	=9	5.4	7	2	8
Blennidae	1.6		0.3		6.4	6	10.2	=4	2.5	9
Cottidae	**24.6**	1	**29.4**	1	**23.1**	1	**21.3**	1	0.25	1
Crustacean	0.0		1.5		5.7	7	0.0		7	12
Cyprinidae	4.3	9	4.3	7	2.8		1.4		4	10
Gasterosteidae	3.6	10	16.5	2	4.5	=9	10.2	=4	1.56	=5
Gobiidae	5.3	7	9.4	4	8.5	5	2.0	=9	1.56	=5
Insect	4.4	8	3.9	9	1.2		1.4		4.25	11
Labridae	0.0		0.0		0.1		2.7	8	8	13
Pleuronectiformes	10.8	4	6.7	5	9.3	4	2.0	=9	1.08	4
Salmonidae	12.0	3	5.9	6	10.7	3	11.6	2	0.88	3

Table 5.10 Variation in the Relative frequency of occurrence (RFO %) and rank, of the top 10 prey types in otter diet, for each season on Gower between July 2005 and June 2007. Core prey types, with high RFO % during all seasons, are shown in bold. (Summer 2005 and 2006 *n* = 610, autum 2005 and 2006 *n* = 504, winter 2005-2006 and 2006-2007 *n* = 516, spring 2006 and 2007 *n* = 924).

	Spring (*n* = 2)		Summer (*n* = 2)		Autumn (*n* = 2)		Winter (*n* = 2)	
	RFO %	Rank	RFO %	Rank	RFO %	Rank	RFO %	Rank
Amphibian	4.8	8	4.1	7	2.6	9	7.6	4
Anguillidae	**12.9**	3	**19.9**	2	**8.9**	3	**5.8**	**5**
Avian	3.2		5.4	6	2.8	8	2.7	=9
Cottidae	**26.3**	1	**29.7**	1	**22.2**	1	**19.0**	1
Cyprinidae	5.0	6	1.6	10	5.3	7	4.5	7
Gasterosteidae	**13.3**	2	**12.4**	3	**7.6**	**5**	**9.2**	3
Gobiidae	10.6	4	2.5	=8	8.4	4	9.4	2
Insect	4.9	7	2.5	=8	1.8	10	2.7	=9
Pleuronectiformes	8.5	5	9.4	5	5.8	6	4.2	8
Salmonidae	4.7	9	10.2	4	9.2	2	5.1	6

The two-way MANOVA indicated that there was no significant variation in the occurrence of major prey items between study sites or seasons (Table 5.11).

Table 5.11 Output from two-way MANOVA carried out on otter diet data collected from four river systems on the Gower peninsula between July 2005 and June 2007. The RFO % values for the top 10 ranked prey types for otters on the Gower peninsula were the dependent variables. Study river and season were the fixed factors.

Factor	Wilks λ	*d.f.*	*F*-ratio	*P*-value	Power	Partial Eta
Season	<0.001	3	3.0	0.17	0.33	0.95
Study site	<0.001	3	2.9	0.17	0.32	0.95

d.f = degrees of freedom, *p* = significance, Partial Eta = effect size.

5.4.4 Influence of meteorological factors on seasonal variation in otter diet on Gower

A Pearson's correlation test, including a Bonferroni correction, indicated that there was no significant relationship between mean temperature, rainfall and wind speed and the proportion of marine fish, freshwater fish or non-fish prey in otter diet on Gower. There was also no relationship between the measured meteorological variables and the occurrence of any individual prey type, in otter diet.

5.4.5 Prey availability

Electrofishing, carried out by the Environment Agency, showed that under the national fisheries classification scheme the Pennard Pill was classed as a grade B trout river and the Burry Pill as a grade D. The mean density of trout par was 20.4 per 100 m^2 on Pennard and 5.8 per 100 m^2 on Burry. The mean density of trout fry was 15.9 per 100 m^2 on Pennard and 10.2 per 100 m^2 on Burry. Eels were caught on both rivers and the data indicated that Pennard Pill had higher densities than Burry Pill. Bullhead were caught on Pennard at similar densities to eel, but were not detected on the Burry Pill. The electrofishing protocol also included Salmon *Salmo salar*, Brook lamprey *Lampetra planeri*, Sea lamprey *Petromyzon marinus* minnows, sticklebacks and Stone loach *Noemacheilus barbatulus* but none of these species were found on either river. No electrofishing was carried out on the River Clyne or Bishopston Pill.

In South Wales, common toads were observed moving towards breeding ponds at the end of February 2008, but this is believed to be earlier than usual due to the changeable weather conditions. This also indicates that toad breeding aggregations are less dense in times of unusual weather, although the period of their availability to otters was probably extended under such conditions. Metamorphosed toads were observed leaving the water between May and June 2008, which was also earlier than usual. Common frogs were recorded in breeding ponds during the middle of January 2008. All three of the UK newt species, Smooth *Triturus vulgaris*, Palmate *Triturus helveticus* and Great crested *Triturus cristatus*, are present on Gower (Russell, 2002). In South Wales, newts were observed entering the ponds in February 2008 and remained there until June, with the females staying in the water longer than males.

5.5 Discussion

5.5.1 Habitat niche of otters on small coastal lowland rivers

Until recently, marine activity of otter populations in the UK was believed to be restricted to Scotland (Carss, 1995). This is the first long-term detailed study of coastal otter populations in Wales, significantly adding to knowledge regarding use of the marine environment by this species. Otters on the Gower Peninsular were using freshwater, marine and terrestrial habitats throughout the year. Marine prey was recorded in spraints collected several km upstream from the coast, indicating that otters moved inland following bouts of coastal foraging. Inland freshwater habitats were a particularly important source of prey and provided access to freshwater, which is essential for washing and drinking (Kruuk and Balharry, 1990). Inland areas may contain more suitable breeding habitat than coastal areas (Beja, 1996). Therefore, access to inland freshwater habitat is likely to be important to the fitness of coastal otter populations. Concurrent use of marine and freshwater habitats has been observed in coastal populations of other Mustelid species (Dunstone and Birks, 1987; Medina-Vogel *et al.* 2004). Maintaining access for individuals to move to both habitats may have broad importance to coastal populations of species from this family.

Carnivore home ranges are often larger than expected, according to their energetic requirements (Kelt and Van Vuren, 2001). Large ranges, incorporating different habitats, are likely to contain a higher diversity of potential prey, and therefore, provide greater facility for prey switching in response to temporal and spatial variation in prey availability. This increases the reliability of locating prey resources and consequently has a fitness benefit for populations. The current study describes a carnivore population consistently utilising different foraging habitats (e.g. rivers, lakes, ephemeral ponds, woodland and coastline) within a landscape. The use of different foraging habitats may be driven by the low abundance of freshwater fish on the study rivers (see sections 2.1.2 and 5.4.5). Otters may be able to inhabit small lowland rivers, with denuded fish populations, due to their ability to exploit different prey communities in adjacent habitats. Therefore, a decline in prey diversity across a landscape or the loss of adjacent wetland habitat, could potentially lead to declines in otter populations on small lowland rivers. This study also demonstrates that otters transcend food webs, influencing prey communities in distinct and spatially separate habitats.

On Gower, it was clear that individual otters were using both marine and freshwater habitats, as individual spraints regularly contained prey from marine and freshwater origin. This confirms that the pattern of habitat use observed at the population level is, to some extent, retained at the individual level. However, it could not be determined if all individuals in the population behaved similarly in their respective use of marine, freshwater and terrestrial habitats. Recent studies have recorded evidence of niche partitioning within animal populations, suggesting that it is primarily driven by competition (Svanbäck and Bolnick, 2007; Tinker *et al.* 2008; Araújo *et al.* 2009). Otters are territorial, and dominant individuals are likely to control access to the best quality habitat (Kruuk and Moorhouse, 1991). Niche partitioning could facilitate co-habitation of a landscape by reducing interactions with other otters, and allow continued population growth (Van Valen, 1965). On Gower, the opportunity for otters to consume unique prey is high, due to the close association of freshwater, marine and terrestrial habitats. This requires further investigation in otter populations, as it has potential implications for conservation management and our understanding of the spatial organisation of animal populations (see sections 8.10 and 8.12).

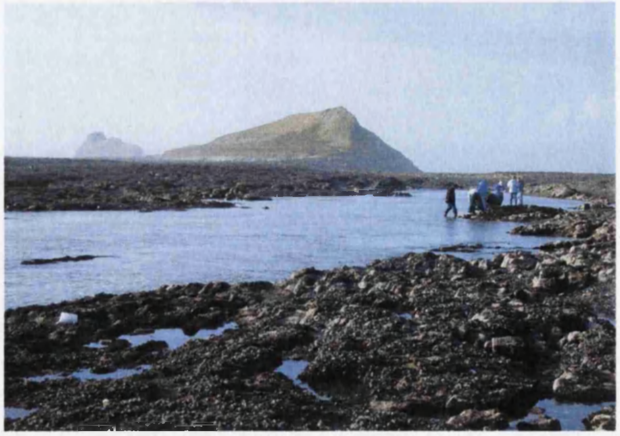


Photo 5.1 Coastal foraging areas around Gower can be a rich source of food. Photo shows the diverse rocky shore habitat by worms head, West Gower (Chris Hill).

5.5.2 Trophic niche of otters on small coastal lowland rivers

Otters on Gower had a broad trophic niche indicative of a generalist foraging strategy (see section 1.3). The population TNW value of 0.69 recorded in this study was similar those recorded in other locations across Europe (see chapter 7, table 7.1). Fish were the major prey of otters on Gower and freshwater fish constituted just over half of all prey occurrences. Although, fish formed the largest component of diet there was no evidence that otters were fish specialists, as non-fish prey types frequently occurred (see also section 7.5.2). Many prey items shared similar traits and behaviours (e.g. slow-swimming, solitary), despite inhabiting distinct habitats. In particular, the majority of fish taken in both freshwater and marine environments were demersal; suggesting that otter foraging behaviour on Gower is effective at capturing bottom dwelling prey. Focusing on this 'type' of prey may be a reinforced behavioural adaptation to foraging in a heterogeneous landscape. The demersal zone is an edge, a habitat feature that predators are known to exploit (Andren and Angelstam, 1988).If this trait is present in other carnivore populations, using functional prey groups in dietary studies would help to identify trophic networks (Araújo *et al.* 2008). Demersal hiding behaviour in fish appears to be an ineffectual defence against otter predation. Anti-predation behaviour develops in response to the type threat posed (Ferrari *et al.* 2007); therefore, otters are unlikely to pose the most important predation threat to fish populations on Gower.

In recent years, otters have frequently been sighted in the sea around Gower and other areas of Wales (Parry and Forman, *unpub. data*). This study confirms that otters in this location spend a significant amount of time foraging in the marine environment (see also section 6.5.1). Marine fish formed approximately one quarter of all prey consumed on Gower. This is in contrast to other studies of coastal foraging otters around Europe, where marine fish dominates diet (Heggberget, 1993; Watt, 1995; Kingston *et al.* 1999). A similar trend, of marine prey consumption, has been recorded in other carnivores which forage both in freshwater and marine habitats e.g. North American river otter (Larsen, 1984), Common cormorant (Leopold *et al.* 1998) and the American mink (Delibes *et al.* 2004). Freshwater prey was expected to dominate diet in the current study, as spraints were collected along coastal rivers rather than sampling specifically from coastal sites. This approach should be adopted in other coastal areas, to help determine the relative importance of marine and freshwater habitats. Otters are capable of covering distances well in excess of the length of the study rivers (Kruuk, 2006), and presence of both marine and freshwater prey in spraints on Gower implies that otters can chose which habitat to forage in. Beja (1991) suggested that otters preferentially forage at inland locations, due to the higher availability of prey in freshwater habitats (cf. marine habitats). Inland habitats do provide resources other than prey (see section 5.5.1), and it is presumably easier to defend these resources due to the linear structure of rivers, but the fitness value of marine and freshwater habitats remains unclear.

On Gower, bullhead was consistently the most important dietary component at every site and in every season, occurring at more than twice the frequency of the second ranked prey type, which was eel (Table 5.1). A number of behavioural and physiological traits make bullhead susceptible to otter predation. Bullhead show crepuscular feeding activity and shelter under channel substrate (Tomlinson and Perrow, 2003), which coincides with the activity patterns of otters on Gower (Parry *pers. obs.*), and makes them highly vulnerable to the stone turning foraging behaviour of otters (Erlinge, 1968; Chanin, 1985). They are also slow swimming and have virtually no scales (Tomlinson and Perrow, 2003), making them relatively easy to catch and (in theory) digest. Bullhead is a frequent prey item in several freshwater systems in Wales (Forman and Parry *unpub. data*) and in other areas of the UK and Europe (Davies, 1994; Copp and Roche, 2003; Britton *et al.* 2006; Brzeziński *et al.* 2006; Lanski *et al.* 2009). The current study indicates that bullhead may be a particularly important prey in small lowland rivers, a habitat that can support high densities of bullhead (Tomlinson and Perrow, 2003).

Non-fish prey were an important component of otter diet, throughout the year, accounting for 16.2% of prey occurrences. Although, many studies refer to otters as fish specialists (see section 1.12.10), as an opportunistic predator inhabiting a landscape where there is a diverse prey base, it is unsurprising that non-fish prey were frequently consumed. The relatively low abundance of freshwater fish on Gower (see sections 2.1.2 and 5.4.5) may have lead to amphibians, birds and insects being consumed more frequently than recorded elsewhere in the UK (Watt, 1995; Yoxon, 1999; Copp and Roche, 2003). It is difficult to gauge the importance of non-fish prey to otters. Volumetric analysis indicated that the importance of non-fish prey on Gower was equivalent to that of fish. However, it is unclear whether this method produces an accurate interpretation of otter diet (see section 4.5.2). Previous studies have estimated the energetic contribution of prey, without considering the costs associated with the entire predation sequence (see section 1.5), which is (admittedly) difficult to measure. Insects are often considered to be of negligible dietary importance to otters due to their infrequent occurrence (Carss and Parkinson, 1996) and low contribution to biomass (Roche, 2001). Insects frequently occurred in spraints from Gower and the majority of occurrences were in spraints that consisted wholly of insect exoskeletons, but also contained otter hair, thus confirming direct predation. The cost of handling insects is low and they have a calorific value (per gram) at least equivalent to that of many fish species (Harris *et al.* 2007), so they are a profitable prey resource.

Photo 5.2 Odonata remains in otter spraint (Gareth Parry).

Amphibians are likely to be associated with lower capture and subjugation costs than fish, and therefore, are a potentially valuable source of food. The occurrence of newt in spraints on Gower is only the third record of predation on *Triturus sp* in over 100 published studies of otter diet (see section 7.4.1). The low number of newt occurrences in otter dietary studies could be because they are rarely predated, but this seems unlikely. Chanin (1985) suggested that dietary studies may be misidentifying newt remains, which is likely as they are very different to those of other amphibians. Newt vertebrae have a distinctive structure, which can easily be distinguished from those of anurans. Their maxillae are also shorter, more curved, and less tapered, than maxillae (Parry *per.obs.*). The ability to identify newt remains is important, as some species (e.g. Great crested newt) are of considerable conservation concern. Otters may be an important predator of newts and spraint analysis could help to detect newt populations during their terrestrial stage.

Small lowland rivers provide good foraging opportunities, as they have narrow channels and contain a large number of small pools, so prey is more easily cornered than in larger rivers. Nevertheless, Bullhead are a small bony fish and the size of eels consumed by otters on Gower was also relatively small (Mean length = 10.6 cm ± 4.8 SD, see appendix table 3). This implies that fish prey in small lowland rivers may be small, and subsequently of poor quality. To compensate for this, otters may need to consume greater quantities, spend more time foraging and increase their consumption of alternate prey. Otters on Gower supplemented their diet with both marine and terrestrial prey, however, in equivalent habitats in inland areas otters may rely heavily on non-fish prey items (Lanszki *et al.* 2009). These findings indicate that although small lowland rivers contain easily obtainable prey, otters may have a broad TNW to compensate for the low quality of prey. Access to alternate prey is likely to be very important to maintaining otter populations in small lowland rivers, and this may be facilitated by being able to forage in different habitats.

It has been suggested that otter populations on small lowland rivers occupy a broad TNW due to temporal variation in fish availability driven by environmental factors, reflecting foraging adaptation to short-term sub-optimal conditions (Lanszki *et al.* 2009). Hydrological stability is thought to have an important influence on the trophic diversity of otter populations (Clavero *et al.* 2008; Ruiz-Olmo and Jiménez, 2009). Across much of Europe, the frequency and duration of dry periods is likely to increase in the future (Briffa *et al.* 2009; Vautard *et al.* 2007). This could increase the duration of sub-optimal foraging conditions for otters inhabiting small watercourses in some areas. If otters are only able to tolerate such conditions for short period of time, the size, viability and persistence of populations on small watercourses may be reduced and these habitats could become unviable for otters. Importantly, this study demonstrates that otter populations on small coastal rivers readily forage in the marine environment, which could provide an important source of food during periods of decreased prey availability in freshwater habitats. If predictions of future global climatic change are correct, small coastal rivers could become an increasingly important otter habitat, as other habitats become untenable. In the UK, the potential impact of the predicted rise in sea levels (Gregory and Oerlemans, 1998) on coastal river habitats also needs consideration. This study demonstrates that otter populations can persist under conditions that necessitate the regular consumption of non-fish prey. Follow-up surveys undertaken in 2008 and 2010 detected an increase in sprainting activity on Gower (Parry *unpub. data*), so a partial reliance on non-fish prey does not appear to restrict the distribution of the population.

5.5.3 Temporal and spatial variation in niche width and dietary composition

The TNW of the otter population on Gower increased during winter. A similar trend was recorded in recent studies on otter populations in other European locations (Ottino and Giller, 2004; Brzeziński *et al.* 2006; Prigioni *et al.* 2006). Seasonal variation in TNW has also been recorded in other carnivores, such as the European Pine Marten *Martes martes* (Zalewski, 2004) and the Stella Sea Lion *Eumetopias jubatus* (Sinclair and Zeppelin, 2002). Such temporal trends are usually attributed to seasonal reductions in the availability of preferred prey, as foraging theory predicts dietary diversification when preferred prey types are scare (MacArthur and Pianka, 1966). On Gower, there was no seasonal variation in the proportions of prey obtained from different habitats. Thus, the winter increase in trophic niche was facilitated by accepting alternate prey items, rather than markedly altering their foraging habitat. Although, alternate prey can be obtained by foraging in different micro zones within a habitat (Matthews *et al.* 2010).

Renkonen's percentage similarity values (Tables 5.7 and 5.8), indicated that there was both spatial and temporal variation in the composition of otter diet on Gower (Tables 5.7 and 5.8). The overall mean level of seasonal dietary difference was 26% ± 6.4 SD (see section, 5.4.3). Seasonal variation in otter diet on Gower is likely to be driven by seasonal trends in prey availability, which are common in aquatic systems. For example, fish availability varies temporally (Duncan and Kubecka, 1996; see also section 5.5.5) and amphibians show seasonal fluctuations in their abundance (Duellman and Trueb, 1986). The mean distance separating the study sites was 6.8 km ± 1.2 SD, but despite this relatively close proximity the mean level of spatial dietary difference was 29.4% ± 5.7 SD (see section 5.4.3). Considering the similar habitats of the study rivers (see section 2.1.2), it is surprising that dietary composition varied more spatially than seasonally. Carnivore diet can vary on a small spatial scale if the landscape is sufficiently complex (Clavero *et al.* 2004; Farías and Kittlein, 2007; Lemmons *et al.* 2010). Gower certainly falls into this category as it has a diverse landscape, providing suitable habitat for a large range of marine, freshwater and terrestrial prey species (Mullard, 2006). The relatively high consumption of flatfish in this study (cf. Beja, 1991; Heggberget, 1993; Kruuk and Moorhouse, 1990) is consistent with broad differences in coastal habitat structure. Habitat structure appears to be the dominant factor driving spatial variation in otter diet in many populations (*op. cit.*). This study demonstrates that even subtle differences in habitat structure can lead to considerable spatial variation in otter diet.

Optimising foraging efficiency requires adaptation to spatial and temporal changes in the profitability of a patch or prey type (Roche, 2001). Behavioural dietary shifts enable a quick response to changes in environmental or social conditions (Araújo *et al.* 2008), Carnivores usually adapt to seasonal or spatial differences in the abundance of common prey by varying trophic niche width (see section 1.3) or utilising switching behaviour (see section 1.5). There was however, no significant spatial or seasonal variation in the occurrence of major prey types in otter diet on Gower. Therefore, this study demonstrates a carnivore population adapting to variation in season and habitat structure by changing the composition of alternate prey items, which occur at lower levels in diet. Such patterns could be driven by interspecific competition for prey resources (Burskirk *et al.* 2000), but it is more likely that otters were foraging opportunistically and dietary composition reflected variation in prey communities, driven by environmental factors and habitat structure. Opportunistic patch based foragers (see section 1.12.7), may have a diet that strongly reflects variation in the micro-distribution of prey in time and space, although, some selection of prey by individuals is possible.

Amphibians have a pronounced seasonal cycle in their habitat use, moving to water between late winter and early summer and entering a terrestrial stage from late summer onwards (Duellman and Trueb, 1986). The occurrence of amphibians throughout the year in otter diet on Gower indicates that otters are successful at locating amphibians during their terrestrial stage. This demonstrates that otters forage in terrestrial habitats during autumn and winter, adding to the small body of information concerning the terrestrial activity of otters (see section 8.3). On Gower, amphibians were an important component of otter diet throughout the year, which is analogous to otter populations inhabiting freshwater habitats in central Europe (Brzeziński *et al.* 1993; Lanszki *et al.* 2001; Baltrūnaitė, 2006). Therefore, the predicted declines of amphibians could have significant implications for otter populations in some areas of their European range (see section 8.13).

Photo 5.3 Amphibian breeding pond on the River Clyne.

Otters are clearly highly adaptable foragers, and there is emerging evidence that environmental factors influence prey selection (Prigioni *et al.* 2006). Foraging in the sea is more energetically demanding at lower temperatures (Kruuk and Balharry, 1990), but there was no relationship between temperature and the occurrence of marine prey in otter diet on Gower. Therefore, there is no evidence that variation in ambient temperature rendered marine foraging areas completely unprofitable. On small rivers, intense rainfall can quickly increase turbidity and discharge rate, leading to a decrease in the consumption of freshwater fish (Remonti *et al.* 2008). Under these conditions, diversifying diet may be an efficient foraging strategy, as an increase in the discharge rate increases the energy expenditure and risk associated with foraging in small rivers. The rivers in the current study were small and prone to spate (see sections 2.1.3-2.1.6), but surprisingly there was no relationship between rainfall and dietary composition, despite several prolonged periods of heavy rain during the study. Increased rainfall may only have a short-term impact on the turbidity and discharge rate of small rivers, due to quick drainage rates. Investigating short term responses in otter foraging behaviour requires the relationship between meteorological variables and diet to be measured on a finer temporal scale than was possible in this study. Remote logging devices (see section 1.10.5) are a potential method of achieving this level of resolution.

5.5.4 Study limitations

This study investigated the factors underlying variation in otter diet, but did not statistically assess the influence of prey abundance. Otters are thought to take prey roughly according to its availability (Heggberget, 1993; Watt, 1995; Taastrøm and Jacobsen, 1999; Lanszki *et al.* 2001); however, factors other than population size and density can infuence the availability of a prey type (see sections 1.5 and 1.8). Attempting to determine prey selection by otters is fraught with potential error, the most significant, but often overlooked source of bias stems from the methods used to sample prey populations. Sampling method has an important impact on the perceived structure of prey communities, and there are errors associated with every available sampling method (see section 1.12.6). Electrofishing has been cited as an efficient method of sampling fish communities (Mazzoni *et al.* 2000), and studies investigating otter prey selection commonly use electrofishing to estimate fish populations (e.g. Roche, 2001; Copp and Roche, 2003; Jacobsen, 2004). The effectiveness of electrofishing varies with both conductivity, bottom substrate and habitat structure at the sample point (Taastrøm and Jacobsen, 1999; McInerny and Cross, 2000). Furthermore, the results do not always show a linear relationship with the density of fish populations (Hansen *et al.* 2004), tending to underestimate populations of small fish (Heggberget and Moseid, 1994; Jacobsen, 2004). Electrofishing did not detect bullhead on the Burry Pill, or stickleback on the Burry and Pennard Pills, despite both being highly abundant (Parry *pers. obs.*) and frequent otter prey. This poses a statistical problem as underestimating the abundance of one prey type, leads to overestimations for the preference of another (Jacobsen, 2004).

Otters have a very diverse diet, but studies of prey selection rarely obtain population data for non-fish prey (see section 1.12.6), as it is difficult and destructive to obtain. This however, could affect any statistical preferences calculated for fish prey. Data generated from sampling fish populations alone, cannot be used to investigate otter dietary preferences. This study statistically investigated the effect of temporal, spatial and meteorological variation on otter diet. Differences in prey availability were assumed to be a key factor driving temporal and spatial variation in otter diet. The results were qualitatively discussed, in context of known trends in prey populations. It is acknowledged that changes in prey abundance, have an influence on otter diet, but as the actual availability of a prey type is difficult to quantify, this was not possible to investigate statistically.

5.5.5 Conclusions and implications for conservation management and research

The trophic niche of otters on Gower was considerably different to what was expected, based on the limited findings of short-term studies carried out in Wales (Stephens, 1957; Henshilwood, 1981; Slater and Rayner, 1993; Davies, 1994) and studies undertaken in freshwater habitats elsewhere in the UK (e.g. Carss *et al.* 1990; Copp and Roche, 2003). This highlights the adaptability of otters, whilst underlining the importance of undertaking long-term studies and basing conservation management on ecological information collected from local populations. Habitat management, aimed at otter conservation in Wales should promote a diverse prey base, protect bullhead populations and maintain marine access for otters living on coastal rivers.

This study confirms that small lowland rivers, in close proximity to the coast, are regularly occupied by otters in Wales. Where the coast is within the feasible home range of otters, conservation programs should consider that access to coastline may provide a source of food and a potential route of dispersal. There is a need to determine the current and historical importance of coastal areas to otter populations, particularly in the UK (see section 8.12). In the face of global climate change, coastal rivers could become increasingly important otter habitat, due to the diversity of available prey. Otter populations on small lowland rivers utilise a diverse prey base, which is achieved by foraging in marine or terrestrial habitats. Therefore, access to different foraging habitats is probably important to otter conservation on small lowland rivers. Access to alternate prey items may be of general importance to carnivore populations inhabiting low quality habitats.

Carnivores, dependent on declining or threatened prey species, are themselves at risk of extinction (Fuller and Sievert, 2001). Otter populations appear to be highly susceptible to prey declines (Delibes, 1990), which may cause an area to suddenly become untenable (Kruuk and Carss, 1998). The diversity of otter diet on Gower may reflect impoverished freshwater fish populations, suggesting that the otter population is vulnerable to further declines in prey communities. This requires conformation and careful evaluation. This study identifies several important otter prey items currently threatened by population declines, notably eels and amphibians. The loss or depletion of bullhead populations could severely reduce the quality of small lowland rivers as otter habitat. Changes in environmental factors that affect bullhead populations, such as Biochemical Oxygen Demand (BOD) substrate and sediment dynamics

(Tomlinson and Perrow, 2003) could also be detrimental to otter populations. Current fish sampling techniques are clearly inadequate at monitoring bullhead populations (see section 5.4.5), and as such, we are ill-equipped to detect population declines in this core prey item. The implications of declines in these prey items are discussed further in section 8.14.

Dietary studies, such as this one, assess the realised trophic niche, which is also influenced by competition, foraging ability and environment (Sargeant, 2007). This study demonstrates that, on a fine scale, carnivore diet may be more strongly influenced by habitat variation than seasonality. At small spatial scales, variation in habitat structure exerts a larger influence on prey assemblages than climate, which would be more uniform. As otter populations in the UK recover they will increasingly be affected by frequency dependent regulation. Intraspecific resource competition can influence trophic diversity at the population level (see section 1.7). The otter population on Gower had a broad trophic niche width and the consumption of alternate prey items varied in time and space, characteristics which are associated with populations that have undergone competitive release (Van Valen, 1965; Svänback and Bolnick, 2007). Such populations are composed of relatively specialised individuals, only using a subset of the population niche (Bolnick *et al.* 2003; Tinker *et al.* 2007; Araújo *et al.* 2009). This area requires further investigation, as competitive release enables larger population sizes than would otherwise be possible (Van Valen, 1965) and conservation models currently assume that all individuals have similar patterns of resource use (Bolnick *et al.* 2002; Durrell, 2000). Population viability, and reproductive output, may be affected if conservation programs can't identify niche partitioning within populations (see section 8.9).

Chapter 6

Diet of the Eurasian otter (*Lutra lutra*) within the Pembrokeshire marine SAC region

"The weed, so placid before, was kicked and entangled by the searching otter"

Henry Williamson (Tarka the Otter, 1927, Putman, London)

Summary

1. The prevalence of otter marine activity and the importance of the marine environment to this species is poorly understood. Studying temporal variation in the trophic niche of coastal otter populations furthers understanding of life-history traits related to foraging strategy and habitat use. Wales is one of the few countries where coastal activity has been recorded and a recent increase in marine otter sightings could indicate remarkable developments within Welsh populations.
2. The trophic niche of coastal otter populations in Pembrokeshire was investigated over a 12 month period through the analysis of spraints collected from 21 coastal sites. Temporal trends in dietary composition and trophic niche breadth were investigated, and used to elucidate seasonal patterns in foraging strategy and habitat use.
3. Marine activity was more widespread than previously thought, and otters were frequently using marine, freshwater and terrestrial habitats throughout the year.
4. Marine prey formed the largest component of otter diet, although, freshwater fish and non-fish prey were also frequently consumed. Diet was very diverse compared to other European coastal populations and a spring contraction in trophic niche width coincided with the estimated timing of breeding activity.
5. *Synthesis and Applications.* This study suggests that the importance of marine habitats to coastal otter populations may be overlooked, due to a deficit of studies and the lack of a validated coastal survey technique. The findings further understanding of the niche occupied by coastal otter populations. Potential explanations and implications are proposed for an increase in the occurrence of otter marine activity. Seasonal variation in niche breadth indicates a spring shift in foraging strategy coinciding with breeding activity, which may have significant implications for otter conservation.

6.1 Introduction

The otter is one of only a few Eurasian carnivores that has evolved the ability to actively forage both in water and on land (Oliveira *et al.* 2008), and this species is highly capable of hunting in both freshwater (Carss *et al.* 1990; Copp and Roche, 2003) and marine (Kruuk and Moorhouse, 1990; Heggberget, 1993) environments. A considerable amount of research has been undertaken on otter diet in freshwater habitats across Europe. In contrast, only a few studies have examined otter diet and behaviour in coastal regions. Research carried out in Scotland since the 1970s elucidated a number of fascinating aspects of the otter's ability to forage in marine waters (e.g. Watson, 1978; Kruuk *et al.* 1987; Kruuk and Moorhouse, 1990; Watt 1995), whilst researchers in Norway (Heggberget, 1993), Portugal (Beja, 1991) Eire (Kingston *et al.* 1999) and Spain (Clavero *et al.* 2004) have described various aspects of otter trophic ecology in coastal areas. Very little information is available from coastal otter populations in other areas; consequently, the prevalence of marine activity within this species' European range is currently poorly defined.

The largest and most stable otter populations in the United Kingdom are considered to be in Scotland, (Harris *et al.* 1995; Strachan, 2007). Scotland has a significant length of coastal habitat that supports high otter population densities (Kruuk, 2006). There are considerable differences in otter activity patterns between Scotland and other areas of the species European range, notably that otters are predominately diurnal in Scotland but nocturnal in most other regions (Carss, 1995). Such profound differences in activity patterns are likely to influence foraging behaviour and the type of prey encountered. Further investigation is required to determine the significance of coastal habitats to the ecology and conservation of otter populations, in areas where the species is considerably more nocturnal. In the UK there is a lack of published information on otter populations outside of Scotland, despite declines being more severe in Wales (Jones and Jones, 2004) and England (Crawford, 2003). The coastline of South Wales provides a wealth of opportunities for otters, with large sections of remote or inaccessible coastline that provide potential foraging, resting and breeding sites (Liles, 2003a; 2003b; 2009).

It is known that otters are widely distributed in Pembrokeshire (Jones and Jones, 2004) and preliminary surveys have indicated that otters are utilising coastal areas for foraging and breeding at some locations (Liles, 2003a). Accordingly, Pembrokeshire may represent one of the most important areas for otters in Wales, but very little is known about the ecology of the otter population in this region. The Pembrokeshire coast is subject to concurrent conservation and human economic interest. The presence of oil refineries in Milford Haven means that there is also a risk of crude oil spillage, whilst the Pembrokeshire coast has also been identified as a potential site for tidal renewable energy development (Project Management Support Services, 2006). Thus, the extent to which otters use marine habitats in Pembrokeshire needs to be determined, so that potential conflict with human industrial and recreational activities can be assessed and incorporated into conservation management plans.

Trophic niche describes the way an organism utilises food resources within its environment (Begon *et al.* 1996) and is an integral component of the total niche. It is important to study carnivore trophic niches as this determines the fitness of populations and their role in the trophic interactions of food webs (Miller *et al.* 2001). Field studies record the realised niche, which is a manifestation of interactions with other organisms and environmental factors (Hutchinson, 1957). Dietary data is typically reported using parameters such as niche width, which describes the diversity of prey taken (Sergeant, 2007).

6.2 Study aims

This study describes the trophic niche of otters inhabiting coastal areas of Pembrokeshire over a 12 month period, addressing five specific aims

1. To determine the extent to which coastal otter populations in Pembrokeshire are using marine, freshwater and terrestrial habitats.

2. To define the trophic niche of the otter population, inhabiting coastal areas of Pembrokeshire?

3. To investigate seasonal variations in the population total trophic niche width (TNW) of otters inhabiting Pembrokeshire coastal sites.
   Null Hypothesis: There is no seasonal variation in TNW.

4. To investigate seasonal variation in the prey composition of diet, in otter populations at Pembrokeshire coastal sites.
   Null hypothesis: There are no seasonal patterns in the composition of diet.

5. Calculate TNW using data from previous studies conducted in coastal areas of Europe to provide an overview of the degree of dietary generalisation or specialisation in coastal foraging otter populations.

6.3 Materials and Methods

6.3.1 Spraint collection and dietary analysis

Spraints were collected and stored as described in section 2.3.2 and dietary analysis carried out as described in section 2.7. Volunteers were given training, by the Pembrokeshire Marine SAC group, to help them identify and collect otter spraints. All spraint bags returned were checked, by the author, to confirm that they contained otter spraint. Many of the volunteers had taken part in spraint collections for a previous study, carried out between 2004 and 2005, and spraints were collected from known sprainting sites. The combination of this experience and training provided by the Pembrokeshire marine SAC group meant that spraints were successfully collected at all study sites and the misidentification of otter spraints was relatively low. The other criterion required for samples to be included in the dietary analysis was that each bag must contain only one otter spraint. The results of the dietary analysis were expressed using the relative frequency of occurrence (RFO %) described by Watson (1978) (see section 2.7.2, equation 2). The proportions of marine fish, freshwater fish and non-fish prey in otter diet were assessed, in order to determine the extent of marine foraging. Fish prey was classified as marine or freshwater using the classifications of Wheeler (1969) (Table 6.1). A full year of spraints was only available from one site, severely reducing the power of statistical analysis of spatial trends in diet, so this was not undertaken.

Table 6.1 Classification of marine and freshwater fish prey for the purpose of investigating the marine component of otter diet on the Pembrokeshire coast.

Common name	Taxonomic name
Marine Fish	
Blenny	Blennidae
Brill	*Scophthalmus rhombus*
Dab	*Limanda limanda*
Eelpout	*Zoarces viviparus*
Fifteen-spined stickleback	*Spinachia spinachia*
Five-bearded rockling	*Ciliata mustela*
Flounder	*Platichthys flesus*
Four-bearded rockling	*Enchelyopus cimbrius*
Goby	Gobiidae
Great Pipefish	*Syngnathus acus*
Plaice	*Pleuronectes platessa*
Unidentified Flatfish	Heterosomata
Unidentified Sculpins	Cottidae
Wrasse	Labridae
Freshwater fish	
Salmonids	Salmonidae
Bullhead	*Cottis gobio*
Chub	*Leuciscus cephalus*
Unidentified Cyprinids	Cyprinidae
European eel	*Anguilla anguilla*
Three-spined stickleback	*Gasterosteus aculeatus*
Minnow	*Phoxinus phoxinus*

6.3.2 Statistical analysis

Otter trophic niche was measured as described in sections 2.9.5 and 2.9.9. Variation in proportion of marine prey and seasonal variation in TNW was investigated using one-way Analysis Of Variance (ANOVA). Renkonen's index of percentage similarity (see section 2.9.7, equation 9) was used to determine if dietary composition varied significantly between seasons. The top ten prey types were determined using the overall RFO % values. These were then used to investigate seasonal variation in diet composition through one-way ANOVA. Where significant results were detected, a least significant difference (LSD) *post hoc* test was applied to investigate which pairings differed significantly.

6.4 Results

6.4.1 Distribution and habitat use of coastal otters in Pembrokeshire

Otter spraints were successfully collected at all study sites and there was evidence that use of marine, freshwater and terrestrial habitats was widespread. Non-fish prey was recorded at 66.7 % (14/21) of sites, whilst both marine and freshwater prey was recorded in spraints at 76.2% (16/21) of sites, including sites situated well within the estuary. Interestingly, spraints containing only prey originating from marine habitats were recorded at just 14.3% (3/21) of sites. Two sites returned no samples that passed the inclusion criteria.

6.4.2 Trophic niche and temporal variation in diet

In total, 232 spraints were collected of which 180 passed the criteria to be included in the dietary analysis. The most frequent reason for rejection was the presence of multiple spraints in one bag. There were 578 prey occurrences and 30 different prey types were identified. Fish constituted 85.3% of the overall RFO % (Table 6.2). Sticklebacks (12.8%), gobies (12.5%), eels (10.9%) and blennies (10.4%) were the most frequent prey items overall. Crustaceans (6.6%), amphibians (3.5%) and birds (3.3%) and were the most frequent non-fish prey items with insects and mammals occurring at relatively low frequencies. Crustacean remains were mostly *Carcinus sp*, the majority of bird remains were from the Rallidae family and the mammalian remains were predominantly rabbit. A very small number of fish remains were not identifiable through either the reference collection or the published keys, which suggests they are potentially previously unrecorded otter prey items.

Table 6.2 Otter diet on the Pembrokeshire coast July 2007- June 2008 expressed as relative frequency of occurrence (RFO %). Number of spraints = 180.

Prey type	Taxonomic name	RFO %
Fish		85.3
Blennies	*Blennidae sp*	10.4
Brill	*Scophthalmus rhombus*	0.3
Bullhead	*Cottis gobio*	2.4
Chub	*Leuciscus cephalus*	0.5
Dab	*Limanda limanda*	1
Eelpout	*Zoarcidae*	0.9
European eel	*Anguilla anguilla*	10.9
Fifteen spined stickleback	*Spinachia spinachia*	6.2
Five-bearded rockling	*Gaidropsarus vulgaris*	1.9
Flounder	*Platichthys flesus*	1.4
Four-bearded rockling	*Enchelyopus cimbrius*	6.6
Gobies	*Gobiidae sp*	12.5
Minnow	*Phoxinus phoxinus*	0.2
Pike	*Esox lucius*	0.2
Pipefish	*Sygnathidae*	1.9
Plaice	*Pleuronectes platessa*	0.5
Salmonidae	Salmonidae sp	2.8
Three-spined stickleback	*Gasterosteus aculeatus*	6.6
Wrasse	*Labridae sp*	4.3
Unidentified Cottidae	Cottidae sp	2.8
Unidentified Cyprinidae	Cyprinidae sp	5.7
Unidentified flatfish	Hetrosomata sp	5
Unidentified Fish		0.3
Insects		**0.9**
Coleoptera	*Dysticus sp*	0.7
Odonata	*Ashena sp*	0.2
Crustacean	*Crustacean*	**6.3**
Amphibian		**3.5**
Anuran sp	*Rana temporaria, Bufo bufo*	1.9
Newts	*Triturus sp*	1.6
Mammalian		**0.7**
Avian		**3.3**
Total		**100**

Marine fish constituted the largest component of otter diet throughout the year (Figure 6.1). A one-way ANOVA indicated that there was no significant seasonal variation in the proportion of marine fish in otter diet ($F_{3,10} = 0.3$, $p = 0.8$).

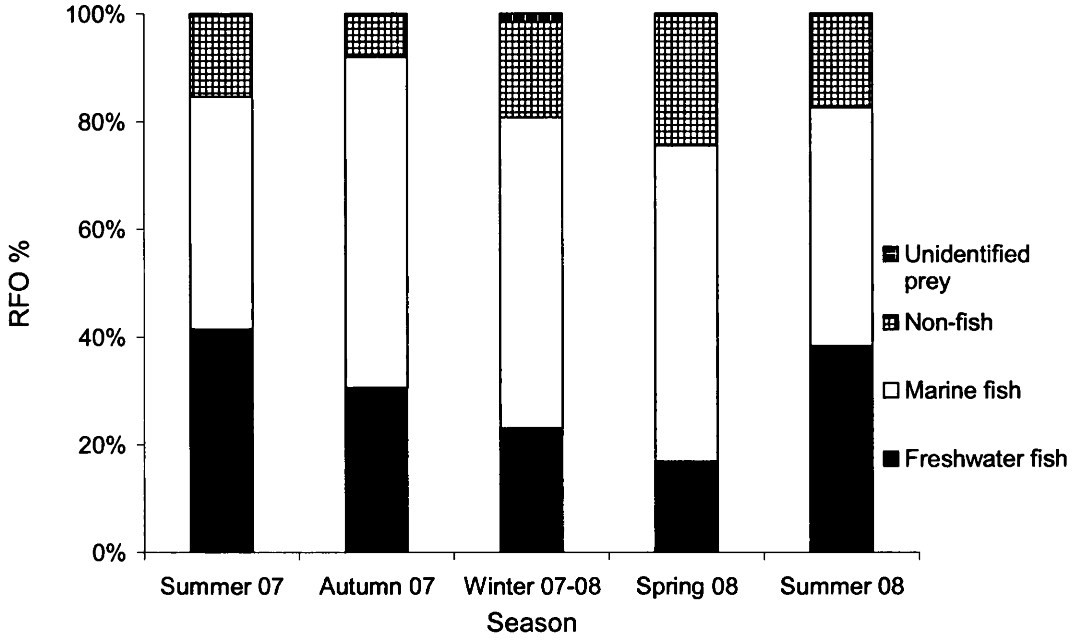


Fig 6.1 Seasonal variation in the relative frequency of occurrence (RFO %) of freshwater fish marine fish non-fish and unidentified prey in otter spraints analysed from Pembrokeshire between July 2007- June 2008 (summer 2007 *n* = 23 autumn 2007 *n* = 35 winter 2007-2008 *n* = 53 spring 2008 *n* = 40 summer 2008 *n* = 7).

There was seasonal variation in the composition of otter diet over the study period (Table 6.3). Dietary composition in spring was relatively similar to all other seasons, with a mean similarity of 88% (± 6 SE). The mean level of similarity between all seasons was 72% (± 5 SE). Dietary composition in summer 2008 had a lower similarity with all other seasons. There was also a low level of similarity in the composition of diet between winter and summer. The highest similarity in diet was between winter 2007-2008 and spring 2008, when diet was dominated by gobies (winter RFO = 13.1%, spring RFO = 18.9%) and amphibians (winter RFO = 6.93%, spring RFO = 9.43%). There was also a high degree of similarity between autumn 2007 and spring 2008. The 10 most important prey types were determined using the overall RFO % values (Table 6.4). This excluded 20 prey types, with overall RFO values <3%. One-way ANOVA showed that the occurrence of eels varied significantly between seasons ($F_{3,10} = 9.08$, $p = 0.006$) and *post hoc* tests indicated that eel RFO% was significantly lower in winter and spring than in summer ($p<0.05$). No other major prey type displayed significant seasonal variation in occurrence.

Table 6.3 Renkonen's Percentage similarity index values, between seasons, in otter diet on Pembrokeshire 2007-2008.

Renkonen's Similarity %	Summer 2007	Autumn 2007	Winter 2007-2008	Spring 2008
Summer 2007	-	-	-	-
Autumn 2007	72.0	-	-	-
Winter 2007-2008	54.6	73.0	-	-
Spring 2008	81.8	82.4	100	-
Summer 2008	50.9	64.7	62.3	80.3

Table 6.4 Rank importance and seasonal variation in the relative frequency of occurrence (RFO %), of the top ten prey types in otter spraints analysed from Pembrokeshire between July 2007- June 2008. (Summer 2007 *n* = 23, autumn 2007 *n* = 35, winter 2007-2008 *n* = 53, spring 2008 *n* = 40, summer 2008 *n* = 7).

Prey Category	Summer 2007	Autumn 2007	Winter 2007-2008	Spring 2008	Summer 2008	Overall rank
Angullidae	22.8	11.7	3.1	5.7	14.3	3
Blennidae	14.0	9.5	7.7	13.2	4.8	4
Crustacean	8.8	2.9	6.2	11.3	14.3	= 7
Cottidae	5.3	6.6	5.4	3.8	0	9
Cyprinidae	7.1	7.3	8.5	5.7	0	= 7
Gadidae	5.3	13.1	6.9	7.6	9.5	5
Gasterosteidae	7.0	12.4	14.6	5.7	14.3	1
Gobiidae	14.0	12.4	13.1	18.9	9.5	2
Labridae	3.5	1.5	4.6	5.7	4.8	10
Pleuronectiformes	5.3	11.00	9.2	15.7	9.5	6

6.4.3 Population total niche width

The population TNW calculated for otter diet at Pembrokeshire coastal sites was 0.88 (± 0.2 SE) and trophic niche richness was 20.2 (±2.3 SE) (Table 6.5). One-way ANOVA demonstrated significant seasonal variation in trophic niche width ($F_{3,10} = 7.1$, $p = 0.01$) and *post hoc* tests indicated that niche width was narrower in spring than in all other seasons ($p<0.05$). Comparing the TNW value obtained by this study to those from other locations across the otter's range it can be seen that diet on the Pembrokeshire coast is particularly diverse (Table 6.6).

Table 6.5 Seasonal variation in trophic niche richness and total niche width values of the coastal otter population in Pembrokeshire 2007-2008.

Season	Number of spraints	Niche richness	Total niche width Shannon-Wiener (*H'*)
Summer 2007	23	22	0.95
Autumn 2007	35	26	0.90
Winter 2007-2008	54	23	0.91
Spring 2008	40	17	0.68
Summer 2008	7	13	0.96
Mean (± SE)	31.8 ± 10.2	20.2 ± 2.3	0.88 ± 0.2

Table 6.6 Total niche width values for otter diet, calculated using data provided in selected coastal studies across their range.

Study Location	Total niche width Shannon-Wiener (*H'*)
Eire (Murphy and Fairley, 1985)	0.84
Eire (Kingston *et al.* 1999)	0.73
Norway (Heggberget, 1993)	0.78
Norway (Heggberget and Moseid, 1994)	0.79
Pembrokeshire Wales	**0.92**
Portugal (Beja, 1991)*	0.70
Portugal (Beja, 1997)	0.69
Scotland (Watson, 1978)	0.81
Scotland (Watt, 1995)*	0.80
Scotland (Yoxon, 1999)	0.76
Spain (Clavero *et al.* 2004)	0.76
Gower Wales (Parry *unpub.data*)	0.69
Mean (± SE)	0.77 ± 0.2

*Mean niche width value across all sites

Discussion

6.5.1 Use of the coastal habitats by otter populations

This study confirms that use of the marine environment is widespread in coastal otter populations across Pembrokeshire, with diet containing a larger proportion of marine prey than in the preliminary study of Liles (2003a). Marine activity has recently been recorded in otters inhabiting other coastal areas of Wales (Parry and Forman *unpub. data*) and England (Jaggs, 2009). Whether this represents a current trend for increased use of the marine environment by otters inhabiting coastal areas of the UK is unclear. The current and historical prevalence of marine activity in coastal otter populations may be underestimated, as population monitoring surveys usually target freshwater systems and there is a dearth of longitudinal data from coastal areas.

Two possible explanations are proposed, for the widespread marine activity of otters in Pembrokeshire and the increasing number of records of marine activity in Wales. Firstly, there is historical evidence that prior to the declines of the 20th century otters were regularly sighted foraging in the sea off the coastline of Wales (Dillwyn, 1848). However, a survey of the Welsh coastal sites undertaken in the 1980s found no evidence of coastal otter activity (Andrew Crawford *pers. com.*). Therefore, as otter populations in Wales recover (Jones and Jones, 2004); use of the marine environment may be increasing due to density-dependent effects. Otters are territorial (Kruuk and Moorhouse, 1991) and individuals may be pushed into coastal areas when there are high population densities in inland freshwater systems. The last National Otter Survey of Wales returned 97% (64/66) of sites in Pembrokeshire as positive (Jones and Jones, 2004), which suggests that there is potential for intraspecific competition for inland territories. However, this study demonstrates that otters in Pembrokeshire are using marine, freshwater and terrestrial habitats, indicating that otters at coastal sites do not appear to be restricted from accessing inland habitats.

An alternative explanation is that the marine environment has always been a component of the habitat niche of coastal otter populations in the UK, but marine activity has been under-recorded in the past due to difficulties in surveying such terrain. The standardised UK otter survey technique is more appropriately designed for linear riparian systems (Mason and MacDonald, 1986), and unfortunately no validated method for detecting otters in coastal areas exists. Detection probabilities are likely to be lower in coastal areas than those in riparian systems, due to the influence of tides that frequently wash away otter signs (Kruuk, 1992). Given the increased awareness of otter activity in many coastal areas in Europe (Beja, 1991;

Heggberget, 1993; Kingston *et al.* 1999; Clavero *et al.* 2006), the development of a robust otter coastal survey monitoring tool would be timely and of significant utility.

6.5.2 The diet and trophic niche of otters inhabiting coastal areas

Marine fish formed the largest proportion of otter diet throughout the year, clearly indicating that marine prey are an important resource for otters inhabiting coastal areas of Pembrokeshire. In contrast to the study of Clavero *et al.* (2006), freshwater and terrestrial prey was frequently consumed throughout the year on both rocky and sandy shores. Climatic differences may cause greater seasonal variation in prey availability in Mediterranean freshwater habitats compared to those at more northerly latitudes. Slow swimming, demersal fish were the most frequent marine and freshwater prey items. This indicates that otter foraging behaviour on the Pembrokeshire coast is effective at catching prey with similar life-histories in both freshwater and marine environments. This could be a behavioural trait that has evolved to facilitate the use of different foraging habitats. The demersal zone represents an edge, which is a habitat feature commonly associated with foraging carnivores (Andren and Angelstam, 1988), and Sea otters also frequently consume demersal prey (Tinker *et al.* 2008).

Although the coastal otter population of Pembrokeshire relied heavily on marine prey resources, they were not obligate marine foragers and inland freshwater habitats provided a frequently used source of food. Otters in the Pembrokeshire coast had a broad TNW (0.92), a feature of all the coastal otter populations included in the analysis (Table 6.6), indicating a broad trend for high trophic diversity in coastal otter populations (see also Jędrzejewska *et al.* 2001). It is interesting to note that the TNW of the Pembrokeshire population was the greatest of all the studies sampled. This can be explained by two factors. Firstly, in contrast to many previous studies of coastal otter populations (Watson, 1978; Kruuk and Moorhouse, 1990; Heggberget and Moseid, 1994; Kingston *et al.* 1999), otters on the Pembrokeshire coast regularly foraged inland. Secondly, otter diet is thought to reflect the complexity of the surrounding environment (Clavero *et al.* 2004) and the Pembrokeshire coastline is heterogeneous and bordered by extensive riparian systems, providing a complex and diverse network of habitats and prey, thus facilitating a diverse diet. Trends in otter trophic diversity may differ between coastal and freshwater habitats due to differences in prey assemblages, particularly in the diversity of fish communities. As opportunistic foragers (Kruuk and Moorhouse, 1990; Watt, 1995), otters would be expected to have a broad trophic niche where there is a diverse prey base. This study demonstrates that otters living in coastal areas can potentially forage in marine, freshwater and terrestrial habitats, and as such have access to a higher diversity of prey than inland populations (Jędrzejewska *et al.* 2001). Trophic niche width is also very broad in another coastal foraging otter, the Sea Cat *Lutra feline* (Medina-Vogel *et al.* 2004), and this could be a common feature of semi-aquatic carnivores foraging at the freshwater/marine interface

The broad overall TNW trophic niche width indicates a generalist foraging strategy on the Pembrokeshire coast. However, there was a significant contraction of niche width in spring, which suggests that otters are facultative foragers (Glasser, 1984) adapting their strategy according to changes in their environment. The observed seasonal trend in TNW contrasts previous dietary studies of otters (Brzeziński *et al.* 2006; Prigioni *et al.* 2006) and other carnivore species (Sinclair and Zeppelin, 2002; Zalewski, 2004; Rosalino *et al.* 2005), in which TNW undergoes a significant increase during winter. Trends in niche width are usually attributed to seasonal reductions in the availability of preferred prey, as foraging theory predicts dietary diversification when preferred prey types are scare (MacArthur and Pianka, 1966). The spring contraction of TNW coincided with a reduction in eel consumption, but it is counterintuitive that this should lead to a decrease in niche width. It is likely that either certain prey items increased in abundance, thereby increasing the profitability of a more specialised strategy, or that a reduction in the abundance and diversity prey during spring increased the utilisation of the remaining prey resources by the entire population.

The apparent contraction of TNW during spring may have implications for otter conservation, as coastal populations are thought to breed during this period (Kruuk *et al.* 1987). Gobies, flatfish, blennies, crabs and amphibians, were all frequent prey taken during this most trophically challenging period. In particular, amphibians are relatively plentiful during winter and spring due to this group's tendency to aggregate in large numbers to spawn (Duellman and Trueb, 1986); consequently, they often form an important component of otter diet during this period (Weber 1990; Clavero *et al.* 2005). It is worthy of note that coastal foraging otters also follow this widespread trend in otter ecology. It is now common knowledge that there are significant pressures affecting amphibian populations throughout the world (IUCN 2008). This prey group clearly forms an important component of otter diet at a critical time of year in many areas (the commencement of breeding). The impact of possible widespread amphibian declines on otter reproductive success and wider trophic cascade effects (Dunne *et al.* 2002) clearly warrants further urgent investigation.

Otters are believed to be vulnerable during winter, largely due to decreased prey availability and the increased metabolic cost of foraging at lower ambient temperatures (Kruuk *et al.* 1987; Kruuk and Balharry, 1990). This could lead to otters increasing their range, foraging in different habitats or taking alternative prey (Beja, 1997; Roche, 2001). It is possible that otters switched prey in freshwater areas during winter, in response to the reduced availability of eels. The Renkonen's index values indicated considerable seasonal variation in dietary composition. The low sample size collected in summer 2008 probably contributed to the low level of dietary similarity between this period and other seasons in the study. However, there was a large amount of variation in dietary composition between other seasons as well, notably between summer 2007 and winter 2007-2008. Despites this, only one major prey type showed significant seasonal variation in occurrence in otter diet. Seasonal variations in carnivore diet are likely to reflect seasonal trends in prey availability. A winter decrease in eel predation has been recorded previously (Jenkins and Harper, 1980) and is thought to be due to the over-wintering behaviour of eels (see section 1.8.2). The disparity in dietary composition between winter and summer demonstrates that the composition of otter diet on the Pembrokeshire coast varies seasonally, but the lack of variation in the most frequent prey types indicates that it is the composition of alternative prey that is subject to the most variation.

This study was only able to detect trends in prey consumption that occurred at the population level. In many species populations are composed of relatively specialised individuals, only using a subset of the population niche (see section 1.6). Inter-individual differences driven by intraspecific competition can cause dietary variation (Svänback and Bolnick, 2007). Consequently, trends in diet recorded at the population level may not accurately reflect the diet of each individual. On the Pembrokeshire coast, otter diet was highly diverse and variation in dietary composition appeared to be due to changes in the consumption of alternate prey items, both common features of populations composed of individual specialists (Bolnick *et al.* 2007). The high diversity of marine, freshwater and terrestrial prey, available to otters, would facilitate trophic diversification within the population. Therefore, some of the seasonal variation in dietary composition detected in this study may have been generated by sampling different individuals with highly diverged specialist diets. Recent research on sea otters has revealed that populations of this obligate marine forager are comprised of individual otters whose individual niches differ from the population level TNW (Estes *et al.* 2003; Tinker *et al.* 2008). Individual niche variation may also occur in Eurasian otter populations inhabiting the marine/freshwater interface, and potentially throughout this species' range.

6.5.3 Conclusions and conservation management implications

This study demonstrates that use of the marine environment by otters in Pembrokeshire is more frequent and widespread than previously thought. Currently, the importance of coastal habitats may be underestimated because population monitoring programs across Europe have focused on riparian systems, and survey techniques have not been developed for coastal areas. Marine environments would not have escaped the impacts of chemical bioaccumulation, which are considered to be the principal factor behind otter population declines in the UK (Chanin and Jefferies, 1978), but the impact is unlikely to have been as severe as in landlocked freshwater habitats. Coastlines could also function as corridors or routes of dispersal, aiding emigration to new freshwater or coastal systems. Determining the current and historical importance of marine habitats is important to elucidate the function of coastal otter populations as sources or sinks of recruitment at the metapopulation scale. The marine environment provided the most important prey resources for coastal otter populations in this study, but the consumption of freshwater and terrestrial prey indicates that access to inland habitats by coastal otters is also required. Marine habitats may provide important prey resources, but inland areas provide access to freshwater crucial for drinking and washing (Kruuk, 2006), and may contain more suitable breeding habitat (Beja, 1996; Liles, 2003b). Consequently, the conservation management of otters in coastal areas should ensure the protection of both marine and freshwater habitat. In particular, an emphasis on maintaining access between marine and freshwater habitats should be incorporated into management plans.

The impact of human disturbance on biodiversity is currently a priority area of research in ecology (Sutherland, 2007). In areas, such as Pembrokeshire, there is potential for human leisure and industrial activities to unknowingly cause detrimental disturbance to coastal otter populations. Fishing, jet skis, boat trips and coasteering are increasingly popular in many coastal areas of the United Kingdom. This study illustrates that otter populations utilise coastal habitats in Pembrokeshire more frequently than previously thought. As coastal sites provide important foraging areas and possible breeding sites (Heggberget and Christensen, 1994; Liles, 2003b; 2009) the potential for disturbance by increased human access to remote coastal sites may be much greater than previously considered. There has certainly been an increase in the number of otter sightings over recent years throughout the study area, suggesting human - otter contact is more frequent. It may also be that otters are beginning to habituate to certain low level disturbance at some sites, as a trade-off for utilising a profitable resource (Tüzün and Albayrak, 2005). The reality is likely to be a combination of the two factors, but research is required to quantify the impact, and if necessary to provide mitigation advice and solutions to conservation managers and statutory conservation bodies.

The trophic diversity of otters on the Pembrokeshire coast demonstrates a broad influence on prey communities. The otter's ability to forage on land and in water enables them to effectively exploit coastlines and estuaries. Many of the marine fish consumed in this study use estuaries and shallow coastal waters as nursery areas (Beck *et al.* 2001), and as such, otters are potentially a key predator influencing their populations. Eels were an important prey resource in this study and widespread declines in eel populations (Feunteun, 2002) may pose a significant evolutionary challenge to otters in the UK and Ireland, where they have historically been an important prey item (Webb, 1975; Carss, 1995; Kingston *et al.* 1999). Amphibians are clearly an important food resource; this is of concern given amphibian population declines (IUCN, 2008) and the fact that reliance on this vulnerable prey group commonly coincides with periods of otter breeding activity (Kruuk, 2006). Loss of amphibians could lead to declines in otter population fitness and force switching to alternative prey items, resulting in trophic cascade effects in coastal and wetland ecosystems. Therefore, the relationship between amphibian prey and otter reproduction needs to be assessed.

It is possible to identify both the gender and identity of individual otters using a number of molecular approaches (see sections 8.4 and 8.6). It is therefore, possible to examine the structure of trophic niche partitioning at the population and individual level using field derived faecal samples. This would prove a useful comparative picture of how other carnivore populations partition their prey resources at the individual level to that provided in Sea otters (Estes *et al.* 2003; Tinker *et al.* 2008). Moreover, novel analysis tools such as network analysis (Araújo *et al.* 2008), can provide a powerful new opportunity to categorise how individual otters partition food resources within populations. This and similar approaches that incorporate prey distribution within foraging habitats, as well as prey taxonomic identity, into analyses can facilitate greater understanding of how populations are structurally, trophically and spatially organised.

Chapter 7

The influence of temporal and spatial scales in otter feeding ecology: A systematic meta-analytical review of Eurasian otter *Lutra lutra* diet.

"The trick to forgetting the big picture is to look at everything close up."
Chuck Palahniuk (Lullaby, 2002, Doubleday, New York)

Summary

1. Identifying the scale at which trophic variation is best explained helps identify the most important factors influencing carnivore diet. Systematically collating dietary data from across a species global range provides a better indication of fundamental trophic niche and foraging strategy. Analysing spatiotemporal patterns in collated data sets produces results with a higher power and enables the influence of scale to be investigated. The output has considerable conservation and ecological value, as it indicates a species capacity to respond to changes in environmental conditions.
2. Otter dietary data was systematically collected from across its geographical range. Pooled data was analysed, to identify patterns in trophic diversity and dietary composition at three spatial scales; biogeographic region, country and habitat, and on a temporal scale.
3. Otters have a broad fundamental trophic niche, but the realised TNW varies considerably between studies, demonstrating a facultative foraging strategy. Across Europe, fish are the core prey of otters but non-fish are an important dietary component.
4. Habitat level environmental variation has a strong influence on otter trophic diversity and dietary composition. Broad spatial trends in otter diet are often the result of differences occurring at the habitat level, rather than geographical gradients in biodiversity.
5. *Synthesis and Applications.* The low concordance of otter diet across Europe underlines the importance of basing conservation management on local information. Marine activity may be more widespread in otters than currently recorded. The adaptability of otter foraging behaviour suggests resiliance to environmental change, so it is unclear why there is a history of population declines in this species. This study demonstrates that the trophic niche of generalist carnivores can strongly reflect habitat level variation. Therefore, appropriate habitat management is very important for the conservation of generalist carnivores and ecosystems dominated by them.

7.1 Introduction

Ecological patterns vary significantly with scale, and each species interacts with its environment on multiple scales (Wiens, 1989a; Bowyer and Kie, 2006). As patterns occurring at different scales often have unique causes and biological consequences it is important to understand local and broad scale patterns (Levin, 1992). Local studies provide essential information on key ecological traits, such as behaviour, competition and social organisation. In contrast, large scale studies provide information on the evolutionary significance of life-history traits and ecological variation. For example, local level patterns in carnivore diet are caused by the microdistribution of prey, and are subject to density dependent (e.g. competition) and density independent (e.g. foraging ability) factors. One potential consequence of local level patterns is trophic niche partitioning (see section 1.6). Large scale trends in carnivore diet are influenced by a species ability to adapt to different environmental gradients. This provides a better estimation of fundamental niche (see section 1.1), and therefore, reflects evolutionary adaptations that determine a species global distribution and extinction risk (Krebs, 2001). Understanding dietary patterns at different scales is necessary to conserve species and provide comparative data on diet and range. Predicting a species' response to changes in global environment, climate and biodiversity, requires knowledge of large scale patterns (Levin, 1992). This is particularly important in keystone carnivores (see section 1.2), which exert a strong influence on other species in their ecosystems (Leibold *et al.* 1997). Examination of a species ecological niche (see section 1.1) is therefore an extremely useful approach when investigating such patterns occurring at difference scales.

Systematic review is an important mechanism for objectively synthesising and reanalysing large bodies of data to obtain findings of a significantly higher power (Pullin and Knight, 2001; Stewart *et al.* 2005). When followed by meta-analysis, this is an effective approach to summarising broad ecological topics, assessing large scale geographical trends and identifying the mechanisms underlying them. This information can then be fed back into conservation policy.

Large scale dietary reviews identify the habitats and prey resources used by carnivores, and potential competitive and predatory interactions. Despite the utility of this information, there have been few systematic reviews of carnivore diet. Such approaches can help determine if widespread views regarding carnivore diets are supported by empirical data, and test ecological hypotheses regarding large scale trends in diet. There are many global trends in biodiversity, such as the recognised latitudinal gradients in species richness (Pianka, 1966; Roy *et al.* 1998; Hawkins, 2001; Willig *et al.* 2003), which determine the availability of prey species and consequently influence carnivore trophic ecology (Lozano *et al.* 2006). A review of wild cat dietary studies found that dietary diversity increases at lower latitudes, reflecting the main latitudinal trends in biodiversity (Virgós *et al.* 1999). In genets however, an increased trophic diversity in Mediterranean habitats did not reflect a latitudinal trend (Lozano *et al.* 2006). This was attributed to variability in prey resources driven by fragmented and highly heterogeneous habitats, a phenomenon known *as "Mediterraneity"* (Virgós, 2002). In raptors, broad geographical trends in trophic diversity may be longitudinal or latitudinal depending on the type of prey consumed (Korpimäki and Marti, 1995).

Otters have a complex niche as they forage in aquatic and terrestrial environments (Oliveira *et al.* 2008). Therefore, geographical trends in the distribution and diversity of otter prey may differ from those carnivores previously studied. Two recent studies (Jędrzejewska *et al.* 2001; Clavero *et al.* 2003) investigated broad spatial trends in otter diet (see section 1.12.9). These studies produced conflicting results; Clavero *et al.* (2003) found that otter diet varied along a latitudinal gradient, which primarily represented the differences between temperate and Mediterranean ecosystems. In contrast, Jędrzejewska *et al.* (2001) found no evidence of a latitudinal gradient and suggested that habitat-related differences in prey assemblages had a greater affect on dietary variation. Although, these studies provided a valuable insight into otter dietary trends the process of literature selection used in these reviews was somewhat subjective. The otter has one of the largest geographical distributions of any carnivore species (Figure 1.1, page 43), and as such there are substantial differences in prey assemblages across its range. The large body of available literature makes the otter a highly suitable model for testing the application of the systematic review to carnivore feeding ecology. The influence of factors such as latitude, longitude, and habitat are all useful to re-examine using a larger, systematically acquired data set.

7.2 Study aims

The aim of this study is to comprehensively summarise a large proportion of the literature on otter diet through a systematic review. Factors influencing variation in otter feeding ecology will be investigated through a meta-analysis of the collated data. The implications for life history traits, predator-prey relationships and conservation management will be discussed. Stewart *et al.* (2005) suggest setting a core over-arching question for the systematic review to address. As this study was not evaluating an intervention, the question consisted of the topic and the desired knowledge outcome (*op. cit.*). The core question addressed by the review was:

"How does the composition and diversity of otter diet vary temporally and spatially across its European range?" This was addressed using five specific aims.

1. Does otter total niche width (TNW) differ between Mediterranean regions, the UK/Ireland and Central Europe?
   Null Hypothesis: There is no difference in otter TNW and dietary composition between the Iberian Peninsula, the UK/Ireland and Central Europe.

2. To determine the relationship between latitude/longitude and otter TNW and diet composition.
   Null Hypotheses: Otter TNW and dietary composition does not vary with latitude or longitude.

3. To evaluate how broad habitat types (riparian, lake/pond, estuarine, coastal) affect otter TNW and diet composition.
   Null Hypothesis: Otter TNW and dietary composition does not vary with broad habitat type.

4. To determine if there are core prey types that frequently occur in otter diet across its European range.

5. How might future changes in prey assemblages affect otter populations?

7.3 Materials and methods

The systematic review was undertaken following the protocol described in section 2.8. Relevant studies were identified using the method described in section 2.8.1. Strict inclusion criteria were used to ensure the quality and comparability of the data included in the meta-analysis (see section 2.8.2). Shannon Wiener niche breadth (see section 2.9.9, equation 10) was used to investigate spatial and temporal trends in trophic diversity. Studies were assigned to one of four broad habitat types; riparian, lake/pond, estuarine and coastal, based on information provided within the materials and methods of each study. Study sites were assigned a value of longitude and latitude to an accuracy of 0.5° using information provided within the studies. Where co-ordinate data was not provided, it was obtained using maps from a detailed atlas (Philips, 2008). Variation in the diversity and composition of otter diet, between large biogeographic regions, was investigated using studies undertaken within the Iberian Peninsular, the UK/Ireland and Central Europe. The rationale used to define broad habitat types, access to the marine environment and Mediterranean regions are described in section 2.8.2. All statistical analyses were carried out as described in section 2.9.10.

7.4 Results

7.4.1 Review statistics

The literature search identified 187 relevant articles of which 119 contained otter dietary data. Only 64.7% (77/119) of these studies met the criteria for inclusion in the meta-analysis. The most common reasons for rejection were either that the data did not represent a full year or was expressed so that conversion to RFO % was not possible. Excluded studies often failed to meet more than one of the inclusion criteria (see section 2.8.2). Peer-reviewed journal articles accounted for 87.2% (68/78) of the studies included in the analysis. Two studies were from unpublished data sets provided by an academic (Dan Forman *pers. com.*), whilst four data sets were obtained from PhD theses (Yoxon, 1999, Roche, 2001). One data set was a report published by the Nature Conservancy Council (Henshilwood, 1981) and one from a report published by the Vincent Wildlife Trust (Watson, 1978). Dietary data from this study (see chapters 5 and 6) were also included in the analysis. Data included in the meta-analysis represented 39,131 spraints, collected from 17 countries between 1969 and 2008. Countries from Central Europe, the UK/Ireland and the Iberian Peninsula were the best represented (Table 7.1). Very little data was available on otter diet outside of Europe and none of it met the inclusion criteria. Data obtained from the methodology of the studies included in the review revealed that 13 different methods have been used to express the results of spraint analysis (see appendix table 7). There was also substantial variation in spraint collection protocol, the duration of studies and the sample size collected (see appendix tables 8 and 9).

Table 7.1 Country origin of European dietary studies included in the meta-analysis, and respective median, minimum and maximum TNW (Shannon-Wiener *H'*) of otter diet.

Country	**Number of study sites**	**TNW (Shannon-Wiener *H'*)**
Bulgaria	1	0.60
Czech Republic	11	0.67 (min = 0.31, max = 0.96)
England	4	0.80 (min = 0.75, max = 0.82)
Finland	1	0.76
Germany	3	0.51 (min = 0.40, max = 0.51)
Hungary	5	0.66 (min = 0.35, max = 0.68)
Italy	2	0.53 (min = 0.38, max = 0.67)
Netherlands	1	0.94
Northern Ireland	1	0.81
Norway	2	0.77 (min = 0.77, max = 0.78)
Poland	2	0.69 (min = 0.61, max = 0.76)
Portugal	10	0.70 (min = 0.63, max = 0.86)
Republic of Ireland	7	0.73 (min = 0.62, max = 0.84)
Scotland	10	0.76 (min = 0.20, max = 0.84)
Spain	11	0.56 (min = 0.13, max = 0.76)
Sweden	1	0.73
Wales	6	0.75 (min = 0.46, max = 0.88)

7.4.2 Differences in otter trophic niche between biogeographic regions

The median TNW of otters varied significantly (Kruskal-Wallis: $h = 9.0$, $p = 0.01$, $n = 71$) between studies in the Iberian Peninsula, the UK/Ireland and Central Europe (Figure 7.1). Dunn's multiple comparison tests indicated that the median TNW of otters was significantly higher in the UK/Ireland than in Iberia (MD = 15.15, $p<0.05$) and Central Europe (MD = 15.15, $p<0.05$). There was also considerable variation in TNW evident within all three regions (Figure 7.1). The RFO % of fish it did not differ between the three regions (Kruskal-Wallis: $h = 0.8$, $p = 0.96$, $n = 71$), but there were significant differences in the number of fish families in otter diet (Kruskal-Wallis: $h = 22.9$, $p < 0.01$, $n = 71$). The median RFO % of the top three marine and freshwater fish, and the top five non-fish prey, differed significantly between the three regions (see appendix table 4). Dunn's tests were carried out to determine the nature of this variation (see appendix table 5). Otter diet in the UK and Ireland was associated with a significantly higher diversity of fish prey than Central Europe, with eels of particular importance. Otter diet in Central Europe was associated with a significantly higher proportion of cyprinids, and an obvious absence of marine fish. Amphibians and reptiles were more frequent dietary components in continental Europe than in the UK and Ireland. The predation of large aquatic insects resulted in a higher occurrence of invertebrates in Central Europe than in the UK/Ireland. Most non-fish prey types tended to occur more frequently in continental Europe. Interestingly, birds were a more frequent component of diet in the UK than in the Iberian Peninsula (see appendix, table 5).

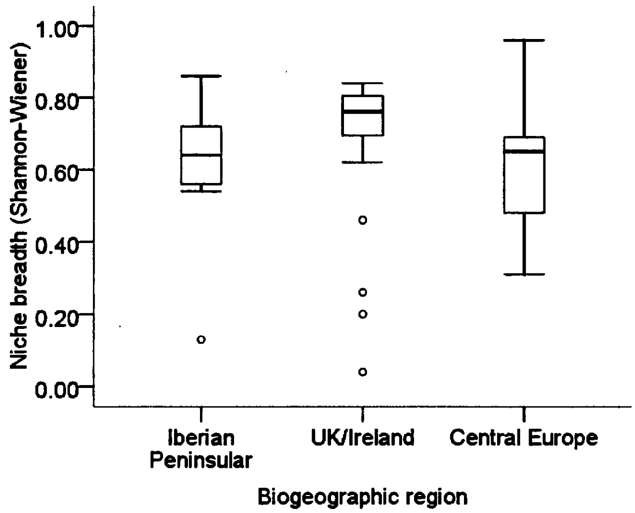


Figure 7.1 Box plot illustrating median TNW recorded in otter dietary studies carried out in the Iberian Peninsula ($n = 21$), UK/Ireland ($n = 27$) and Central Europe ($n = 23$). Horizontal line marks the median niche breadth, box and whiskers indicate the inter-quartile range and full range respectively, outliers are marked with circles.

7.4.3 Longitudinal and latitudinal variation in otter trophic niche

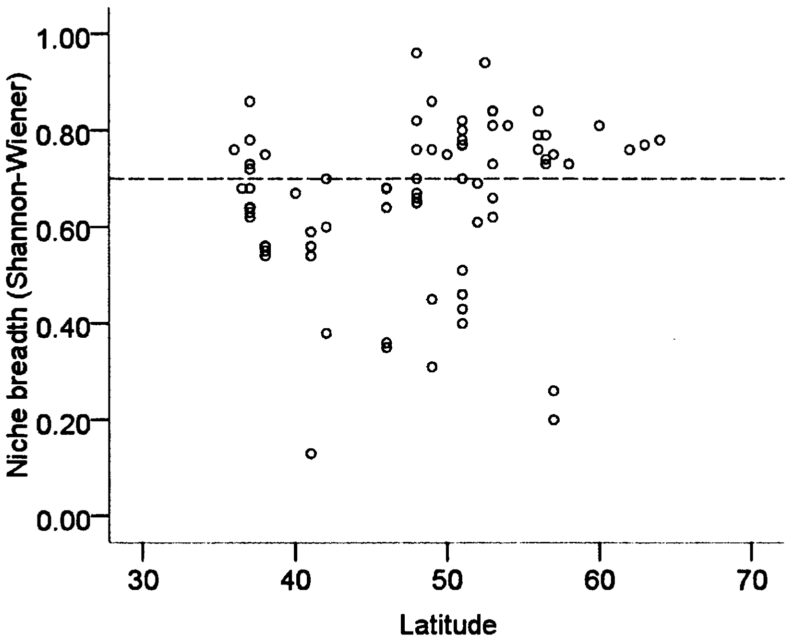
One obvious fact that is evident is that otter diet is very diverse, with 44 families of fish prey and 10 categories of non-fish prey recorded in studies across Europe. The median TNW of otters in Europe was 0.70, but it is interesting to note the overall range of TNW values (0.13 to 0.96). Considerable variation between countries in TNW is also clearly evident (Table 7.1). A Kolmogorov-Smirnov (KS) test indicated that the niche breadth data was normally distributed, but a Levene's test indicated inequality in the variance between samples. This could not be corrected satisfactorily by transforming the data, so non-parametric tests were used to investigate differences in TNW between countries. There were significant differences in the median TNW of otter between countries (Kruskal-Wallis: $h = 26.6$, $p = 0.05$, $n = 77$), but there were no significant latitudinal or longitudinal trends in TNW ($r = 0.2$, $p = 0.1$, $n = 77$), and studies undertaken at similar co-ordinates recorded considerably different TNW values (Figure 7.2). Over the last four decades there was no significant variation in mean TNW across Europe (Kruskal-Wallis: $h = 5.7$, $p = 0.2$, $n = 77$) (Table 7.2), or in the occurrence of the top prey types (see section 7.4.3) (Kruskal-Wallis: $h = 3.2$, $p = 0.3$, $n = 77$).

Table 7.2 Temporal variation in median TNW (Shannon-Wiener *H'*) of otters across their European range (all studies pooled).

Decade	Median TNW (Shannon-Wiener *H'*)	Number of studies
1960s	0.73	1*
1970s	0.79 (min = 0.79, max = 0.81)	3
1980s	0.66 (min = 0.20, max = 0.94)	29
1990s	0.69 (min = 0.13, max = 0.96)	18
2000s	0.69 (min = 0.31, max = 0.86)	16
Overall	0.70 (min = 0.13, max = 0.96)	77

* Please note low sample size

(a)



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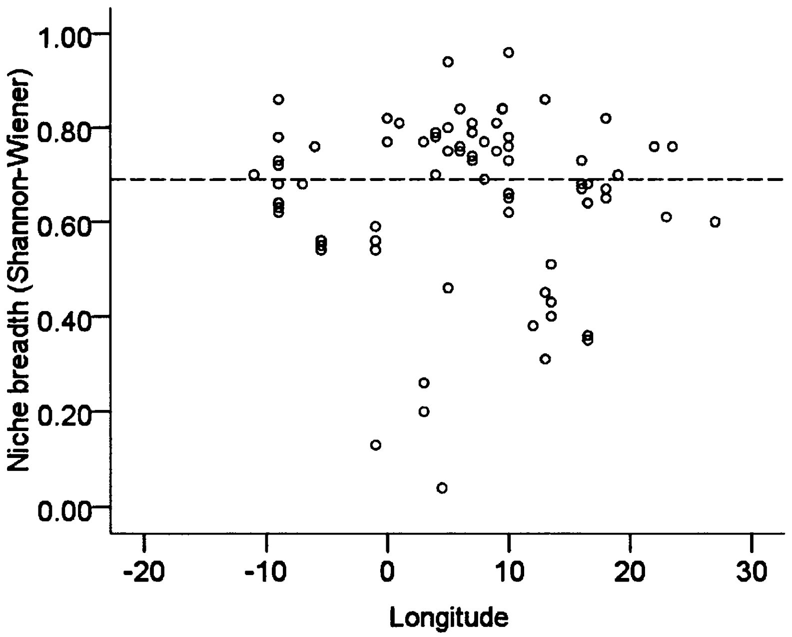

Figure 7.2 TNW (Shannon Wiener *H*') of otters plotted against latitude (a) and longitude (b) of study site. Longitude -10 = 10°W, 10 = 10°E. Dashed line indicates the median TNW. Study sites = 77.

The median RFO % of fish prey in otter diet across Europe was 78% (minimum 2%, maximum = 98.8%) and this was not correlated with latitude or longitude. A Principal Component Analysis (PCA) was undertaken on a matrix of RFO % values for the top three marine and freshwater fish families, and the top five non-fish prey types, recorded in otter diet across their European range (for rationale see section 2.9.10). Prior to analysis, data were tested for normality and homogeneity of variances. The data was shown to be normally distributed, but the variances were not homogeneous so the data was arcsine transformed to square root, after which the variance was homogenous. All of the variables were shown to have positive kurtosis, which allows for the assumption of low type I error rates (Underwood, 1996). The Bartlett test indicated that the factor model was appropriate ($p = 0.001$) and the Kaiser-Meyer-Olkin test showed that the sample size was adequate (KMO = 0.6). The first and second components explained 31.7% (eigenvalue = 3.5) and 16.9% (eigenvalue = 1.9) of the variation respectively, and the first five components explained 79.2% of variation. The first component was generated by contrasting the occurrence of cyprinids, amphibians, mammals and invertebrates against the absence of marine fish, such as blennies, gobies and gadids (Figure 7.3 and Table 7.3). The second component was mainly generated by contrasting the occurrence of birds and mammals against the absence of cyprinids and reptiles.

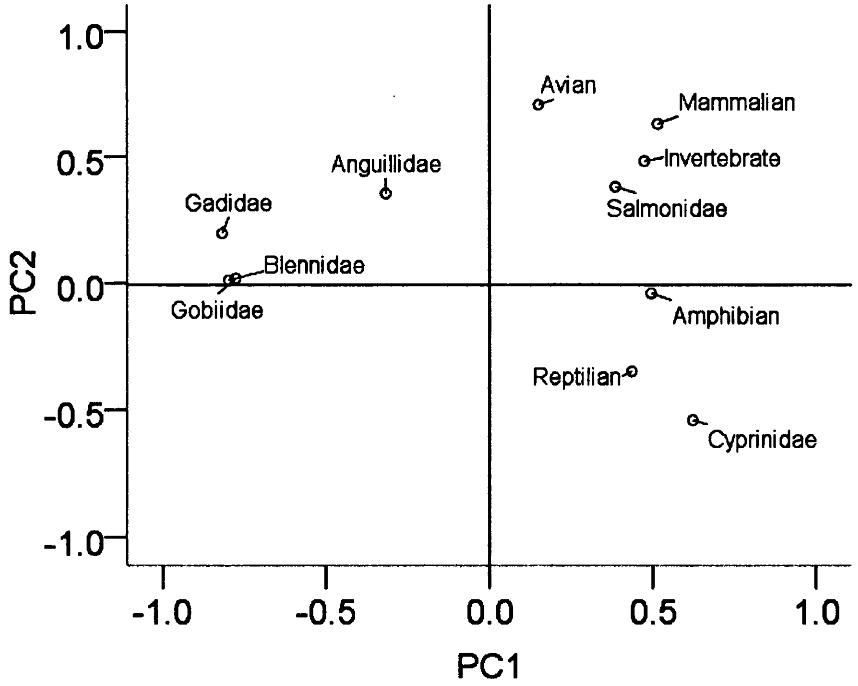

Figure 7.3 Weighting to each prey type for the first two components extracted from a PCA, using a matrix of RFO % data for the top three marine and freshwater fish families, and the top five non-fish prey types taken from 77 studies of otter diet across its European range.

Table 7.3 Spearman's rank correlations between prey types and the first two PCA components extracted. Variance explained by each component in parentheses.

Prey type	PC 1 (31.7%)	PC 2 (16.9%)
Amphibian	0.54*	-0.05
Anguillidae	-0.52*	0.46*
Avian	0.15	0.53*
Blennidae	-0.77*	0.05
Cyprinidae	0.66*	-0.48*
Gadidae	-0.81*	0.21
Gobiidae	-0.73*	0.02
Invertebrate	0.46*	0.41*
Mammalian	0.63*	0.47*
Reptilian	0.33*	-0.31*
Salmonidae	0.40*	0.43*

Critical level after Bonferroni correction $*p = 0.005$

The scores for PCA components one and two were not normally distributed, so a Spearman's rank correlations were used to investigate relationships with latitude and longitude. Component one was positively correlated with longitude and component two was positively correlated with latitude (Table 7.4). This indicates that the composition of otter diet primarily varies with longitude. The occurrence of cyprinids, amphibians, mammals and invertebrates increased with longitude, whilst occurrence of marine fish decreased with longitude. There is also a latitudinal gradient in the composition of otter diet, defined by an increased occurrence of birds and decreased occurrence of cyprinids and reptiles, at higher latitudes (Table 7.3).

Table 7.4 Spearman's rank correlation between latitude and longitude, and the first and second components extracted from a PCA analysis of the RFO % of the top three marine and freshwater fish families, and the top five non-fish prey types, in otter diet across its European range (Studies = 77).

Variable	Latitude	Longitude
Principal component 1	$r_s = -0.20$	$r_s = 0.40*$
Principal component 2	$r_s = 0.42*$	$r_s = 0.10$

Critical level of significance after Bonferroni correction $*p = 0.0125$

7.4.4 Differences in otter trophic niche between broad habitat types

The median TNW of otters differed significantly between habitat types (Kruskal Wallis: $h = 11.9$, $p = 0.003$, $n = 77$) (Table 7.5). The median TNW of otters was significantly lower in lakes/ponds than in coastal and estuarine habitats (Table 7.6). Otters had access to the marine environment in 36.4% (28/77) of the studies included in the analysis. TNW varied significantly depending on access to the marine environment (Kruskal Wallis: $h = 10.3$, $p < 0.001$, $n = 77$).

Table 7.5 Variation in the median TNW (Shannon-Wiener *H'*) of otters between broad habitat types, in studies undertaken across its European range ($n = 77$).

Broad habitat type*	Median TNW (Shannon-Wiener *H'*)	Number of studies
Coastal	0.75 (min = 0.63, max = 0.84)	19
Estuarine	0.76 (min = 0.62, max = 0.86)	7
Lake/pond	0.45 (min = 0.31, max = 0.94)	11
Riparian	0.67 (min = 0.13, max = 0.96)	40

*For designation rationale see methods section 2.8.2.

Table 7.6 Results of Dunn's multiple comparisons test, showing variation in otter TNW (Shannon-Wiener *H*') between broad habitat types. Coastal (*n* = 19), estuarine (*n*= 7), lake/pond (*n* = 11), riparian (*n* = 40).

Significant differences in median otter trophic niche breadth between broad habitat types
Coastal > Lake/pond (MD = 34.33, $p<0.01$)
Estuarine > Lake/pond (MD = 34.89, $p<0.01$)

MD = Difference in mean rank sum

A Scheirer-Ray-Hare (SRH) test indicated that the first PCA component (Figure 7.3) varied significantly with broad habitat type (Table 7.7). This suggests that variation in the composition of otter diet across Europe is strongly influenced by differences in habitat type. The SRH tests provided a poor explanation of the affect of habitat on PCA component two, as the effect size was low.

Table 7.7 Output from a SRH test carried out on the first and second PCA components. The weighting scores for components one and two were the dependent variables and broad habitat type was the fixed factor.

Factor	*d.f.*	SS	SS/MS_{Total}	*P*-value	Power	Partial Eta
Component 1						
Broad habitat type	3	26995.02	13.41	**<0.01**	1.00	0.71
Component 2						
Broad habitat type	3	3305.02	1.64	0.65	0.56	0.09

d.f = degrees of freedom, SS = sum of squares, MS = mean square, *P* = significance, Partial Eta = effect size.

7.4.5 Separation of otter diet across Europe

A dendrogram generated through TWINSPAN, using the dietary data extracted from studies included in the review, showed that there is considerable variation in the composition of otter diet across Europe (Figure 7.4). Diet was separated according to broad habitat type, regardless of the study location. There was a clear separation of the dietary data between studies with and without marine access, and studies undertaken on lakes/ponds appear to be clustered. A number of riparian dietary studies, particularly those from Eire and Wales fell at intermediate positions between coastal and freshwater diets. These represent studies undertaken on rivers, where some brackish and marine prey is recorded due to the large range otters. The first division (eigenvalue = 0.48, Figure 7.4) separated dietary studies carried out in habitats with access to marine foraging areas (e.g. Watson, 1978; Beja, 1991; Heggberget, 1993; Watt, 1995; Yoxon, 1999) from those carried out in inland freshwater habitats (e.g. López-Nieves and Hernando, 1984; Jurajda *et al.* 1996; Lanszki and Molnar, 2003; Georgiev, 2006). The second division (eigenvalue = 0.23, Figure 7.4) clustered studies in freshwater habitats where salmonidae, cyprinidae, cottidae and amphibians were the main prey items (e.g. Ruiz-Olmo and Palazon, 1997; Copp and Roche, 2003; Ottino and Giller, 2004). The third division (eigenvalue = 0.35, Figure 7.4) separated coastal diets dominated by gobies, blennies and rockling, (e.g. Heggberget, 1993; Yoxon, 1999), from those dominated by mullet (Clavero *et al.* 2004; Beja, 1991 Odeceixe study area). The small eigenvalues obtained show that each division explains a small proportion of the variation in otter diet across Europe, which reinforces the diversity and flexibility of otter diet and provides an evolutionary context, across its range.

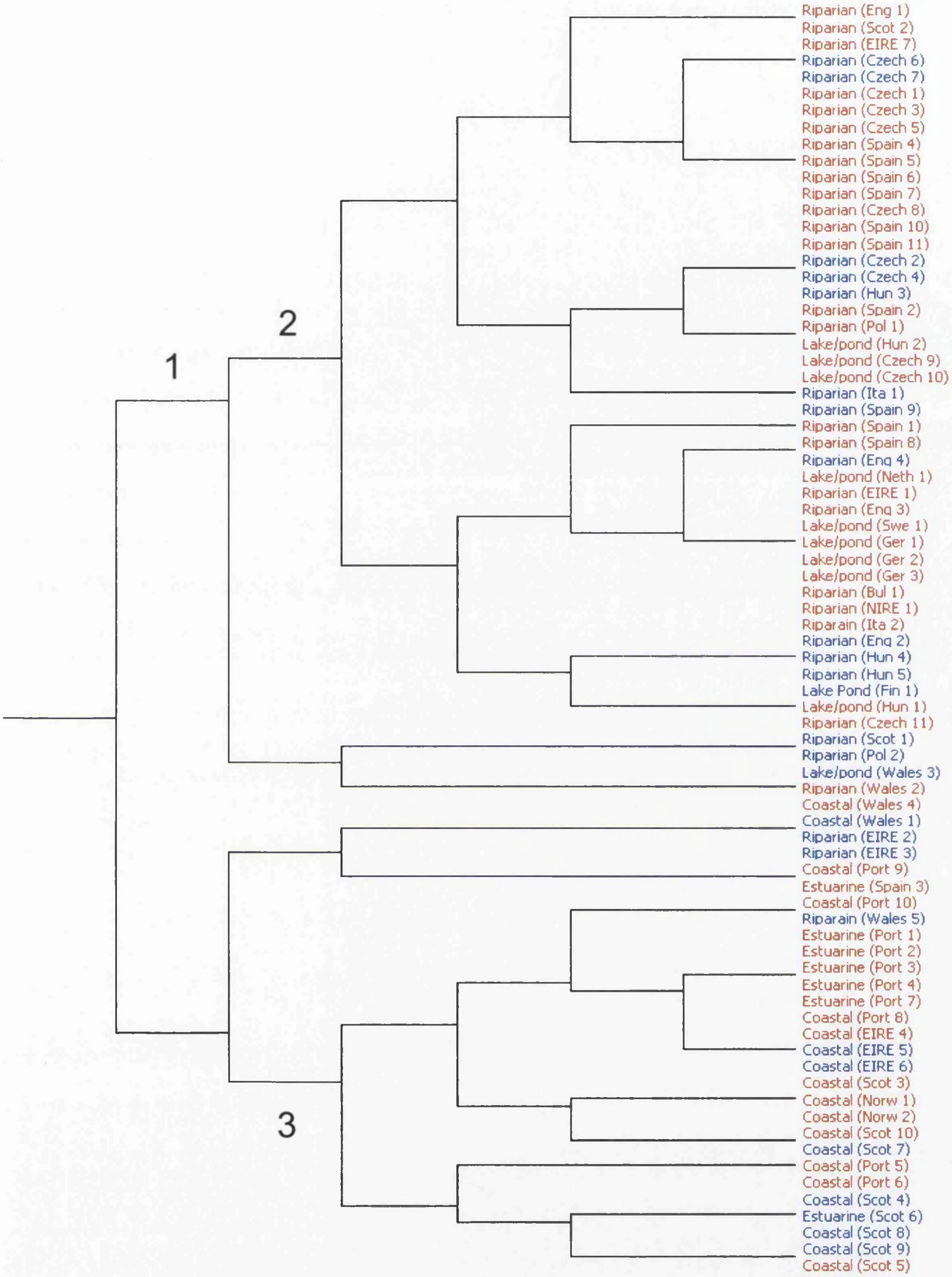

Figure 7.4 Dendrogram showing the separation of otter diet recorded in studies carried out in different habitat types across Europe, showing first three divisions. Generated using TWINSPAN, from Community Analysis Package (CAP) 4. Bul = Bulgaria, Czech = Czech Republic, Eng = England, Fin = Finland, Ger = Germany, Hun = Hungary, Ita = Italy, Neth = Netherlands, NIRE = Northern Ireland, Norw = Norway, Pol = Poland, Por = Portugal, Scot = Scotland, Swe = Sweden.

7.4.6 Otter dietary specialisation

The Kendall concordance correlation coefficient (K) produced from the dietary data provided by the 77 study sites was 0.3 ($p = 0.001$). This value indicates that the concordance of prey RFO% in otter diet throughout Europe is relatively low. Non-fish prey was recorded in 96.1% (74/77) of otter dietary studies. The RFO% of cyprinidae was negatively associated with TNW ($r = -0.4$, $p < 0.01$, $n = 77$). No other prey types had a significant negative association with TNW. A SRH test demonstrated that trophic niche richness was not affected by the presence of cyprinidae ($SS/MS_{Total} = 2.13$, $p = 0.1$, $n = 77$), indicating that other prey types were not ignored where cyprinids are consumed. A Kruskal-Wallis test indicated that the RFO% of several prey types varied between habitat types (See appendix, table 6). Dunn's tests demonstrated that salmonids, cyprinids and non-fish prey occurred more frequently in dietary studies undertaken in riparian habitats, whereas studies in lake/pond habitats were dominated by cyprinids (Tables 7.9 and 7.10). Marine fish and eels occurred frequently in otter diet in all estuarine and coastal habitats.

Table 7.8 Results of Dunn's multiple comparisons test, showing fish prey types with significant variation in their RFO% in otter diet between habitat types. Coastal ($n = 19$), estuarine ($n = 7$), lake/pond ($n = 11$), riparian ($n = 40$).

Prey type	Median, minimum and maximum RFO %	Habitats with significant differences in the RFO % in otter diet
Anguillidae	riparian = 0 (min = 0, max = 43.2)	estuarine > lake (MD = 31.31, $p < 0.05$)
	lake/pond = 0.2 (min = 0, max = 88.8)	coastal > riparian (MD = 16.54, $p < 0.05$)
	estuarine = 11.8 (min = 1.0, max = 29.4)	coastal > lake (MD = 25.10, $p < 0.05$)
	coastal = 6.6 (min = 0, max = 42.0)	
Blennidae	riparian = 0 (min = 0, max = 2.2)	estuarine > riparian (MD = 38.64, $p < 0.001$)
	lake/pond = 0 (min = 0, max = 0)	estuarine > lake (MD = 39.36, $p < 0.001$)
	estuarine = 10.7 (min = 2.3, max = 27.6)	coastal > riparian (MD = 28.16, $p < 0.001$)
	coastal = 5.2 (min = 0, max = 35.0)	coastal > lake (MD = 30.55, $p < 0.001$)
Cyprinidae	riparian = 17.1 (min = 0, max = 79.2)	riparian > estuarine (MD = 30.53, $p < 0.01$)
	lake/pond = 63.8 (min = 14.3, max = 88.5)	riparian > coastal (MD = 29.28, $p < 0.001$)
	estuarine = 0 (min = 0, max = 1.1)	lake > estuarine (MD = 50.64, $p < 0.001$)
	coastal = 0 (min = 0, max = 6.6)	lake > coastal (MD = 49.39, $p < 0.001$)
Gadidae	riparian = 0 (min = 0, max = 8.5)	estuarine > riparian (MD = 31.24, $p < 0.001$)
	lake/pond = 0 (min = 0, max = 0)	estuarine > lake (MD = 34.79, $p < 0.01$)
	estuarine = 4.8 (min = 0.8, max = 21.4)	coastal > riparian (MD = 34.74, $p < 0.001$)
	coastal = 8.6 (min = 0, max = 28.3)	coastal > lake (MD = 38.29, $p < 0.001$)
Gobiidae	riparian = 0 (min = 0, max = 12.5)	estuarine > riparian (MD = 36.64, $p < 0.001$)
	lake/pond = 0 (min = 0, max = 0)	estuarine > lake (MD = 39.36, $p < 0.001$)
	estuarine = 6.2 (min = 2.1, max = 23.6)	coastal > riparian (MD = 28.16, $p < 0.001$)
	coastal = 4.9 (min = 0, max = 19.1)	coastal > lake (MD = 30.89, $p < 0.001$)
Salmonidae	riparian = 8.2 (min = 0, max = 93.2)	riparian > lake (MD = 21.74, $p < 0.05$)
	lake/pond = 0 (min = 0, max = 5.4)	riparian > estuarine (MD = 25.82, $p < 0.05$)
	estuarine = 0 (min = 0, max = 2.1)	riparian > coastal (MD = 21.15, $p < 0.001$)
	coastal = 0 (min = 0, max = 11.4)	

MD = Difference in mean rank sum

Table 7.9 Results of Dunn's multiple comparisons test, showing non-fish prey types with significant variation in their RFO% in otter diet between habitat types. Coastal (*n* = 19), estuarine (*n*= 7), lake/pond (*n* = 11), riparian (*n* = 40).

Prey type	Median, minimum and maximum RFO %	Habitats with significant differences in the RFO % in otter diet
Amphibian	riparian = 9.3 (min = 0, max = 38.0) lake/pond = 0.2 (min = 0, max = 14.0) estuarine = 7.3 (min = 0, max = 23.0) coastal = 0 (min = 0, max = 2.0)	riparian > lake/pond (MD = 25.22, $p<0.01$) riparian > coastal (MD = 30.91, $p<0.001$) estuarine > coastal (MD = 28.50, $p<0.05$)
Invertebrate	riparian = 4.2 (min = 0, max = 25.0) lake/pond = 0.2 (min = 0, max = 3.4) estuarine = 2.4 (min = 0, max = 9.2) coastal = 0.04 (min = 0, max = 25.0)	riparian > coastal (MD = 22.72, $p<0.001$)
Mammalian	riparian = 0.05 (min = 0, max = 44.0) lake/pond = 0.01 (min = 0, max = 7.4) estuarine = 0 (min = 0, max = 0) coastal = 0 (min = 0, max = 5.7)	riparian > estuarine (MD = 29.98, $p<0.01$) riparian > coastal (MD = 20.77, $p<0.01$)
Reptilian	riparian = 0 (min = 0, max = 13.6) lake/pond = 0 (min = 0, max = 0.01) estuarine = 0 (min = 0, max = 1.8) coastal = 0 (min = 0, max = 0.07)	riparian > coastal (MD = 16.87, $p<0.01$)

MD = Difference in mean rank sum

7.5 Discussion

7.5.1 Biogeographical trends in TNW

The richness and diversity of otter diet is comparable to many "generalist" carnivore species, such the American mink (Jędrzejewski *et al.* 2001), Eurasian badger (Goszczyński *et al.* 2000), coyote *Canis latrans* (Ranft *et al.* 2005) and red fox (Cavallini and Volpi, 1996). The current study also revealed a very large range in otter TNW values across Europe. In some cases, markedly different TNW values were recorded by different studies undertaken within the same country, (Table 7.1). This demonstrates considerable spatial variation in otter foraging strategy, suggesting that they are highly facultative strategists. If prey resources are subject to temporal and spatial variation it is advantageous to have a flexible foraging strategy (see section 1.5). Facultative strategists become more or less specialised depending on the abundance of food resources and competition (Glasser, 1984; Mitchell, 1990). Otter diet is less diverse in more stable and complex habitats (Clavero *et al.* 2008; Ruiz-Olmo and Jiménez, 2009), which also supports the theoretical basis of a facultative foraging strategy (Glasser, 1982).

There was significant variation in otter TNW between the three biogeographic regions and individual countries (see section 7.4.2 and 7.4.3), but there were no significant latitudinal or longitudinal trends in TNW (Figure 7.2). This is in contrast to previous studies undertaken on otters (Clavero *et al.* 2003), other Palearctic carnivores (Korpimäki and Marti, 1995; Goszczyński *et al.* 2000; Lozano *et al.* 2006) and Nearctic carnivores (Iriarte *et al.* 1990). Most known latitudinal trends in carnivore trophic diversity have been identified in exclusively terrestrial species, which consume prey from a relatively low number of taxonomic classes. As such, these trends are usually consistent with known spatial trends in prey diversity (e.g. Iriarte *et al.* 1990; Korpimäki and Marti, 1995; Lozano *et al.* 2006).Otters, in comparison, are highly adaptable, as they are able to forage in freshwater, marine, and terrestrial environments. Consequently, otters consume a broad range of prey types with different geographical patterns in diversity (see section 1.12.8). For example, latitudinal gradients are the main diversity pattern in marine fish (Roy *et al.* 1998) and birds (Järvinen, 1979), but variation in habitat structure has a stronger influence on richness patterns in freshwater fish (Oberdorff *et al.* 1995) and amphibians (IUCN, 2008). A geographical gradient in the diversity of one prey type may be counterbalanced by a contrasting gradient in a different prey type. This study demonstrates that broad geographical gradients in prey diversity may not have a strong affect on TNW in highly adaptable carnivores, and that TNW may vary on a finer spatial scale in these species (see section 7.5.4).

Surprisingly, studies of otter populations in the UK and Ireland had a higher median TNW than studies undertaken on Mediterranean populations. This is in stark contrast to previous studies in otters (Clavero *et al.* 2003) and other Palearctic carnivores, which found a trend for increased trophic diversity in Mediterranean regions (Virgós *et al.* 1999; Lozano *et al.* 2006). The current study analysed a larger sample than Clavero *et al.* (2003), including more studies from Central Europe and describing diet to a more detailed level. Therefore, the current study represents a more robust analysis of geographical trends in otter diet across Europe. This study demonstrates that mediterranei*ty* does not lead to an increase in otter trophic diversity. As otters are semi-aquatic, trophic diversity may be higher in areas where there is unrestricted access to water throughout the year (e.g. UK/Ireland). Mediterraneity does not affect the trophic diversity of polecats, as interspecific competition causes polecats to specialise on lagomorphs in Mediterranean areas (Santos *et al.* 2009). One shared trait between otters and polecats is their flexible ability to predate a broad range of prey from different habitats (Carss, 1995; Lodé, 1996). This enables them to respond to changes in competition or environmental conditions by altering their foraging strategy or switching prey items. This adaptable behaviour is observed in many Mustelids (Goszczyński *et al.* 2000; Sidorovich, 2000) and could explain the absence of a Mediterranean trend for increased trophic diversity. Research is required to determine adaptability in other carnivores, as this could a key factor affecting species resilience to global environmental change.

7.5.2 Biogeographical trends in otter dietary composition

Fish are clearly the core prey of otters across their European range, but non-fish prey consistently formed an important component of diet. This study found no evidence to suggest that otters are fish specialists, as an increase in fish RFO% was not paralleled by a decrease in trophic niche breadth, and other prey types were not ignored when fish are abundant, a prerequisite for specialisation (Zach and Smith, 1981; Stephens and Krebs, 1986). Fish are usually the most abundant prey in otter habitats; hence, otter diet is usually dominated by fish. Nevertheless, non fish prey are recorded in most dietary studies (see section 7.4.6), forming a major component of diet in some areas (e.g. Brezeziński *et al.* 1993; Jurajda *et al.* 1996; De la Hay, 2008). Non fish prey is often consumed more frequently during periods of reduced fish availability or unfavourable environmental conditions. For example, in many areas amphibian consumption peaks during winter and spring (Weber, 1990; Clavero *et al.* 2005), whilst in Mediterranean areas reptile consumption usually peaks during the dry season. The ability to predate non-fish prey appears to be a useful strategy to coping with seasonal environmental change.

The *K* coefficient value indicated a low level of concordance in the RFO % of prey items in otter diet across Europe (see section 7.4.6). This value obtained is similar to the values obtained for martens, badgers and red fox by Virgós *et al.* (1999) and indicates a highly variable diet. The composition of otter diet had a complex relationship with longitude, and to a lesser extent with latitude (Tables 7.3 and 7.4). Longitudinal trends in carnivore diet have been recorded previously, but they are rare and usually of secondary importance to latitudinal trends (Korpimäki and Marti, 1995). The longitudinal trend in otter dietary composition can be linked to the semi-aquatic foraging behaviour of otters, as longitude is more indicative of access to the marine environment than latitude (see section 7.5.4). This is supported by the strong negative correlation between PCA component one and the occurrence of marine fish in otter diet. Otter marine activity has been recorded in several areas of Europe (e.g. Watson, 1978; Heggberget, 1993; Beja, 1991; Clavero *et al.* 2004), and this ability does not appear to be restricted to a specific latitude or region. Marine fish were always consumed in studies undertaken in coastal and estuarine areas, demonstrating that otters are extremely capable of exploiting the marine environment (see sections also 5.5.1 and 6.5.1). The conservation management of otter populations within reasonable proximity to the coast should considered the potential use of marine habitats. For some prey types (e.g. reptiles), observed trends in consumption by otters agreed with known trends in its diversity and abundance (Schall and Pianka, 1978). However, the high occurrence of birds in otter diet in the UK/Ireland, is in contrast to known latitudinal trends in avian diversity (Järvinen, 1979). Importantly, many of the significant geographical trends in prey consumption can be attributed to environmental variation that occurred on finer scale than latitudinal gradients (see section 7.5.4)

7.5.3 Long-term trends in trophic niche breadth and dietary composition

This study found no evidence that the diversity or composition of otter diet has changed significantly since the 1970s. Recent studies have suggested that the consumption of eels by otters in the UK is declining (Bonesi *et al.* 2004; Britton *et al.* 2006), which has been linked to the massive declines in European eel populations that have occurred over the last few decades (Moriarty and Dekker, 1997; Feunteun, 2002). Although, there was no evidence of an overall long-term decline in eel consumption across Europe, the sample size and distribution of studies differed between the decades, which could conceal any changes in prey occurrence. Further work is needed to assess the impact of prey declines as they could pose a threat to otter populations and ecosystem stability (see section 8.13).

7.5.4 Habitat level variation in trophic niche breadth and dietary composition

Otter TNW varied within countries (Table 7.1), indicating that it is influenced by factors that vary on a finer scale than longitudinal and latitudinal trends in biodiversity. The large range in TNW values recorded within some countries e.g. Czech Republic and Portugal (Table 7.1) appeared to reflect differences between studies undertaken in different habitats. The analysis confirmed that otter trophic diversity varied significantly between broad habitat types, with higher TNW values recorded in habitats that incorporated the marine environment. Many broad geographical trends in TNW could be linked to variation occurring at the habitat level. For example, the difference in median TNW between Scotland and Spain was due to the greater number of coastal studies undertaken in Scotland. Likewise, the significant variation in otter TNW between biogeographical regions is probably due to the larger number of coastal studies undertaken in the UK/Ireland (c.f. Iberia and Central Europe). There is evidence that otter trophic diversity can vary at a finer habitat scale, as there were considerable differences in otter TNW between the Italian studies, despite both being undertaken in riparian habitats

(Table 7.1). This is plausible as variation in microhabitat structure can have a strong influence on communities (Price, 1978; Grossman and Freeman, 1987). This study demonstrates that habitat structure has a significant influence on otter trophic diversity. Habitat variation has also been found to influence trophic diversity patterns in European polecats (Lodé, 1997) and Eurasian badgers (Goszczyński *et al.* 2000). Habitat level variation may be the principal force driving geographical trends in Mustelid diet. As this has evolutionary and fitness implications (see section 8.9) it requires further investigation in other Mustelid species.

TWINSPAN analysis is very effective method of classifying complex multivarient data (Hill, 1979). This ordination technique demonstrated that habitat level variation is the main factor affecting the composition of otter diet (Figure 7.4). For example, studies from the same country were not always grouped in the same cluster e.g. coastal (Watson, 1978) and riparian (Carss *et al.* 1990) areas of Scotland. The first division was clearly based on access to the marine environment (see section 7.4.5). The PCA indicates that otters inhabiting coastal areas are more reliant on fish, whereas terrestrial foraging habitats are more important at inland locations. Subsequent divisions appeared to reflect finer scale differences between habitats, due to factors such as coastal structure, surrounding riparian habitat, and climate. Variation in dietary composition was probably influenced by other environmental factors, previously identified as influencing otter diet, such as hydrological stability (Clavero *et al.* 2008), altitude (Remonti *et al.* 2009); and habitat complexity (Ruiz-Olmo and Jiménez, 2009). Habitat structure is known to have a strong influence on community diversity (Gaston, 2000; Jeanneret *et al.* 2003). The current study demonstrates that this pattern can be reflected in the trophic niche of an opportunistic carnivore.

Otters appear to show a strong functional response towards prey, taking what is available. Consequently, otter dietary composition can reflect fine scale variation in prey communities and is poorly defined at broad geographical scales. For example, amphibians were consumed more frequently in Central Europe compared to the UK, due to the presence of wetland forests which hold large amphibian populations (Brzeziński *et al.* 1993; Lanszki and Molnar, 2003). Eels were a frequent prey item in the UK/Ireland, but occurred less frequently in otter diet in continental Europe (see appendix table 5), as the inland location of most studies means summer upstream eel migrations have a lower influence on abundance (Naismith and Knights, 1988). The importance of eels, as an otter prey item, has probably been overstated due to the high volume of studies conducted in the UK and Ireland in the 1980s and 1990s. Otters can clearly adapt their foraging behaviour in order to obtain different prey types in different habitats. This represents an interesting dietary trend, which may be an innate or learnt response to variation in prey behaviour or environmental conditions, and could reflect differences in life-history strategies across their global range. This trait would help facilitate the large global distribution of otters (Figure 1.1), as it enables them to adapt to different habitats and prey communities. In theory, it should also provide some resiliance to environmental change.

Otter diet was found to be unique to the time and place of the study, demonstrating that diet at the species level does not reflect that at the population level, suggesting that otters may occupy different trophic niches in different habitats (Figure 7.4 and Table 7.7). Otter populations may be subject to different selection pressures, depending on their habitat. Therefore, it is important that otter conservation management is based on data obtained from local populations, rather than generic species level data. The predation pressure exerted on prey communities, and competitive interactions with other carnivores, may vary across the European range of otters. The important influence of habitat structure on carnivore diet and foraging behaviour requires further investigation in a range of species. This could provide useful information for habitat management and restoration, or the conservation of endangered prey species, which would ultimately be of benefit to carnivores

Photo 7.1 Otter habitats can be unpredictable. During dry periods the water level in small rivers, such as this one on Gower, falls quickly (Gareth Parry).

7.5.5 The importance of scale in carnivore dietary studies

Studying ecological patterns at a single spatial scale (e.g. local levels) may conceal the most important factors influencing variation, as variables occurring at one spatial scale can interact to produce a response at another (Bowyer *et al.* 2002). This is evident in the current study, as some broad patterns in TNW and prey consumption reflected the geographical distribution of studies undertaken in different habitats (see section 7.5.4). The influence of spatial scale is manifested in the contrasting findings of Jędrzejewska *et al.* (2001) and Clavero *et al.* (2003), with the former primarily detecting variation on a smaller habitat scale and the latter on a larger geographical level. That otter diet varies on both scales cannot be disputed, but the challenge is to identify the scale which is most informative about decisions related to foraging strategies and other life-history traits. This requires consideration of the scale at which an organism makes decisions concerning the life-history trait being studied (Kie *et al.* 2002; Bowyer and Kie, 2006). Most of the variation in otter diet can be explained at the habitat level. Important resources tend to affect species on a landscape level (Dussault *et al.* 2005) and prey is an essential resource for carnivores (Fuller and Sievert, 2001). Therefore, factors affecting prey availability at the habitat level are likely to have a significant influence on a species' ecology and resulting trophic patterns may be maintained to macrogeographic scales, as is the case with hydrological stability and otter diet (Clavero *et al.* 2008).

7.5.6 Influence of prey classification on broad geographical trends in otter diet

This study distinguished fish prey into families, whereas previous studies have grouped fish prey into one single category (Jędrzejewska *et al.* 2001; Clavero *et al.* 2003). Describing fish to family level produces higher niche breadth values in areas where a higher diversity of fish is consumed. Consequently, geographical patterns in TNW will be influenced by the distribution of coastal studies, as marine foraging otters have access to a higher diversity of fish (see section 7.5.4), and therefore, tend to have broader trophic niches (see section 7.4.4). This approach is appropriate, as otters consume a huge diversity of marine and freshwater fish with considerably different distributions (Maitland, 2000), life histories (Wheeler, 1969) and defensive mechanisms (Keenleyside, 1979; Chivers and Mirza, 2001). Assigning all fish to a single category would represent a huge number of species, with large variations in their ecology and behaviour. Broad geographical trends in distribution and abundance vary between species due to ecological differences (Schall and Pianka, 1978), so describing prey to a higher taxonomic level provides a more intuitive depiction of geographical trends. Furthermore, studies of geographical dietary variation in other carnivore species generally describe important prey items to order or species level (Lodé, 1997; Virgós *et al.* 1999; Goszczyński *et al.* 2000; Lozano *et al.* 2006; Manfredi *et al.* 2004) and there is no logical reason why otters should be an exception.

Classifying fish prey to family level is a conservative approach, as it understates the richness within each family. Describing diet to species level would produce a more accurate depiction of patterns in otter diet (see section 8.6), and may uncover latitudinal and

Mediterranean trends for increased diversity. However, a species level approach is difficult, as many otter dietary studies have a low resolution of identification. Fish cannot always be identified to species level and non-fish prey is rarely described beyond class level. The most useful method of classifying prey items, when studying foraging strategy, is not necessarily taxonomic (Levin, 1992). Identifying prey species is clearly important for carnivore conservation, but functional divisions, based on features such as size, profitability or life-history traits (e.g. demersal prey) may be more useful in future studies of foraging strategy, habitat use and life-history traits. This approach has recently be adopted by a network analysis of anuran diet by Araújo *et al.* (2008) who detected within population trophic partitioning, according to functional prey divisions. A similar approach could be used to investigate carnivore populations (see section 8.9).

7.5.7 Evaluation of the systematic review methodology

It is inevitable that some relevant data was not located by the search strategy as ecological data from unpublished sources and non-government organisations is not always easily accessible. A small number of studies identified during the search as containing information relevant to otter diet could not be obtained, despite contacting the authors and organisations involved in producing them. It is concerning that no data collected from outside of Europe was included in the analysis. Several studies of otter diet have been undertaken in Asian regions of Russia, but access to them is difficult. The otter inhabits a vast proportion of Asia (see section 1.12.1) where prey assemblages are likely to differ considerably from those in Europe. One study was obtained from Asia, but it did not pass the inclusion criteria. This knowledge gap may conceal important features and trends in otter ecology (see section 8.13). It is also detrimental to otter conservation, as there is a need to understand the ecology and status of populations in Asia.

A frequent objective of carnivore dietary studies is to describe the diet of a population within a given area and make comparisons with other populations. The lack of standardisation in the methodology of otter dietary studies suggests that many studies do not measure population diet at the same scale, which limits the capacity for comparisons between studies. Therefore, is it is important to set strict inclusion criteria in reviews such as this. Due to the inclusion criteria, some dietary studies could not be included in this review (see section 7.4.1). Adherence to the inclusion criteria increases the reliability of conclusions drawn by reducing the effect of methodological variation, inadequate sample size and seasonally biased data. The large body of work carried out on otter diet meant that, even after excluding studies, a large data set was available for statistical analysis. Despite the strict inclusion criteria, it is likely that the sex ratio, demography and number of individuals sampled varied between studies. Ideally the "grain size" (proportion of total population sampled) should remain constant (Wiens, 1989a), but dietary studies of elusive carnivores rarely define parameters such as population size or demography. This is a limitation to using systematic review and meta-analyses to investigate large-scale geographical trends in trophic ecology, as the method assumes that each study accurately describes the diet of the population within the study area. Unless each constituent study is representative of diet at the population level, real geographical tends may be concealed or specious trends identified. This issue could be addressed by standardising the methodology of dietary studies (see section 8.6) and using molecular tools to determining grain size (see section 8.9).

7.5.8 Conclusions and future direction

Systematic review followed by meta-analysis effectively summarised otter trophic niche across Europe. This approach has many benefits over standard subjective reviews (see section 7.1) and could extract useful information concerning a range of niche parameters (see section 8.7). This study highlights the lack of accessible high-quality data from otter populations outside of Europe (see section 7.4.1) and the bias towards data collected from one habitat type in some regions (see section 7.5.4). More information is required from outside of Europe, coastal areas of continental Europe and inland habitats in the UK, in order to bridge knowledge gaps. To determine the significance of dietary patterns and habitat to life-history strategies, evolutionary processes and conservation management requires more detailed information, which cannot be obtained through traditional faecal analysis techniques (see section 8.6).

As an apex carnivore, with a broad fundamental trophic niche, otters are potentially an important element of biodiversity, linking distinct trophic webs. Carnivores with highly diverse diets may exert selective pressure on a broad range of species (Leibold *et al.* 1997). Otters are highly adaptable facultative foragers, able to predate a wide range of prey types in a range of different habitats. Adaptations to aquatic foraging do not appear to hinder their ability to catch terrestrial prey (see section 8.3). Such traits would help facilitate the wide global distribution of this species, and explains why otters can inhabit locations with ephemeral water sources (see section 8.11) and low fish abundance (see section 5.5.3). This study suggests that global otter distribution is unlikely to be limited by prey populations and otters should be more resilient to future biodiversity loss (Sala *et al.* 2000) than specialist carnivores. In Europe, however, there have been several major historical declines in otter populations, the earliest of which pre-dates any significant human alteration or degradation of habitat (Randi *et* *al.* 2003). It is unclear why this highly adaptable carnivore remains susceptible to severe population declines. Future research should address this question, as it could provide important knowledge for carnivore conservation.

This study demonstrates the important influence of habitat structure and dynamics on carnivore foraging behaviour and diet. Factors such as habitat structure and hydrological stability appear to exert a stronger influence on otter trophic niche than latitude or longitude. Carnivore diet affects breeding success (Harrington *et al.* 1983; Croxall *et al.* 1999), and otters breed more regularly in stable and complex habitats (Ruiz-Olmo and Jiménez, 2009). The considerable influence of habitat on otter diet implies that population fitness may be partly determined by habitat structure (see section 8.10). Therefore, appropriate habitat management is crucial to the conservation of this species. Non-fish prey may be an important resource, enabling otters to surviving periods of sub-optimal conditions. Future work should investigate how carnivore diet affects reproductive productivity at various spatial scales, to determine if differential productivity relates to trophic niche or habitat. This could ascertain if some populations are more susceptible to declines in prey populations, habitat loss or climate change.

Chapter 8

General discussion

"Real knowledge is to know the extent of one's ignorance"

Confucius (c. 551-479 BC)

8.1 Monitoring and studying populations using faecal sign surveys

The difficult, but essential, task of monitoring elusive carnivore populations frequently relies on the identification of field signs particularly faeces (see section 1.11). Scat surveys have become an invaluable census technique for many rare and elusive carnivores e.g. Iberian lynx *Lynx pardinus* (Palomares *et al.* 2002), snow leopard (Janecka *et al.* 2008), pine marten (Birks *et al.* 2005) and wildcat (Lozano *et al.* 2007). Data in chapter 3 clearly demonstrates that field sign surveys designed for broad scale population monitoring programs may not provide meaningful or reliable data at a smaller spatial scales. Unreliable monitoring techniques can have damaging consequences for conservation, as they may produce conflicting or spurious reports of a population's status (Birks *et al.* 2005), or fail to detect population declines (Maxwell and Jennings, 2005). Population surveys are also used to obtain data for studies of ecological topics such as competition (Bonesi *et al.* 2004; McDonald *et al.* 2007) and habitat use (Clevenger, 1994; Prigioni *et al.* 2008). Therefore, unreliable survey techniques can lead to specious conclusions regarding species ecology, interactions between species, and community structure

It has been suggested that monitoring programs for threatened species should achieve a power of at least 0.8 (Kendall *et al.* 1992). This power is the probability of correctly rejecting false null hypotheses (Gravetter and Wallnau, 2006); in this study it was the probability of detecting otters in areas where they were present. The power of the standard 600 m transect survey technique used by the National Otter Surveys (see section 1.13), was substantially lower than 0.8 (Figure 3.3 page 83), indicating that it could not reliably detect otter presence on small lowland rivers. The standard survey technique may be a useful method for monitoring crude distribution changes at a national scale (Mason and Macdonald, 1987), but it was not designed to determine presence or absence at single isolated sites. It is, however, frequently used to determine otter presence and distribution in small areas subject to development proposals or conservation plans (see section 3.1).This has implications for local level otter conservation, which often relies on distribution data obtained using the standard survey method. Ecological studies that require population distribution or density data must consider the detection probability of the survey method. This study indicated that detection probabilities can vary seasonally and with study scale (see section 3.5.5), which could result in important habitats being overlooked and misconceptions regarding interspecific competition. It is more important to standardise field surveys by their detection power, than by survey design (Gu and Swihart, 2003; Tyre *et al.* 2003; Mackenzie *et al.* 2004). Therefore, surveys may need to be designed according to spatial scale and season, in order to achieve equal detection power.Variation in the detection probabilities of field sign surveys may have wider significance due to the large number of species which are monitored in this way.

8.2 Improving the accuracy small scale otter surveys

The National Survey data should be used as no more than an initial indicator of otter distribution at local levels (see section 3.5.4). The River Clyne returned a negative result when surveyed by the 2002 National Survey (Jones and Jones, 2004), despite otter presence being confirmed by Liles (2000) and throughout this study. Robust techniques need to be developed to detect and monitor carnivore populations at small scales, as this is the level at which many conservation decisions are made (see section 3.1) and ecological studies undertaken (see section 3.5.4). Scat surveys are currently the most efficient method of detecting small and medium-sized carnivores (see section 1.11.2). However, survey design should be tailored to the scale, habitat, season and objectives of the study. It could be argued that this will reduce the comparability of studies, but this will not be the case if detection powers are equal between studies (see section 8.1). The reliability of the survey technique should be assessed by estimating the detection probabilities for all target species, using methods such as the one outlined by Mackenzie *et al.* (2002). Investigating the relationship between landscape level processes and the detection power of field surveys may aid population monitoring programs in elusive carnivores.

When the objective is to detect or monitor populations of conservation concern on a small scale, it may be necessary to modify the methods used in broad scale monitoring programs, such as the National Otter Surveys. This study demonstrates that increasing transect size improves the probability of detecting otters, but this action alone was insufficient to achieve a detection power of 0.8. Previous studies have found that increasing the number of visits per site will improve both the detection probability and the precision of occupancy rate estimates (Mackenzie *et al.* 2002; Tyre *et al.* 2003). This study found that it was necessary to increase the number of study sites and undertake repeat surveys, in order to detect otters with a power of 0.8. There was convergence in a 0.8 power of detection between different survey designs, therefore, the optimal approach depends on the study objectives and resources available (see section 3.5.5). Expending unnecessary survey effort wastes resources and may cause unwarranted disturbance to species. Optimising survey design prevents this and provides more reliable data. Improving population monitoring on a small scale will also increase the resolution of population data collected on broader scales, thus providing more accurate data for conservation at local, national and global scales.

8.3 Terrestrial activity of otters

Practically all surveys of otter populations, and studies of otter ecology, are focussed around water bodies, but activity has been recorded some distance from water bodies (Reuther and Dolev, 2000). On Gower, spraints were frequently found on dry river beds and occasionally on woodland paths (see sections 2.1.5 and 2.1.6). The perceived ecology of otters may be skewed by a scarcity of information regarding the terrestrial activity and behaviour of otters. Overland movements and the use of dry river beds as corridors could be important for dispersal, thus, increasing gene flow between populations. It is naïve to assume that all important otter activity is linked to water bodies. The dietary review demonstrates the adaptability of otter foraging behaviour (see section 7.5.1). This enables otters to inhabit areas with very low freshwater availability, by adopting a diet more typical of fully terrestrial carnivore species or foraging in the marine environment (see section 5.5.2). Information regarding terrestrial movements of otters may provide information that can be used to reduced mortality on roads, currently a frequently cited cause of unnatural death in otters (Philcox *et al.* 1999). It is important that this gap in our knowledge is addressed; a useful starting point would be to target areas that may serve as corridors between water bodies. This could be investigated by adapting the current transect survey technique (see section 3.5.7), but the utilisation of bio-logging devices, such as the Daily Diary (see section 1.10.5) would generate more useful data.

8.4 Using molecular tools to increase the benefits of faecal sign surveys

It is important to maximise the benefit of population surveys as a considerable amount of resources are invested in undertaking them. A fundamental limitation of spraint surveys is that they provide very little information about the size, density, demography or fecundity of a population (see section 1.11). Previous studies have resampled within survey data to determine the transect size required to detect a decline in field signs (Kendall *et al.* 1992). The ability of otter surveys to detect a change in the number of spraints is not important, due to the role of spraints as a scent mark (see section 1.12.4). When faeces have a role in intraspecific communication the abundance of faecal signs provides a poor reflection of abundance and density of the species (Gallant *et al.* 2007). Fundamentally, a change in sprainting activity does not necessarily indicate a decline in the number or density of otters within an area (see section 1.13). This matter should be addressed by using molecular tools to obtain estimates of population size from spraint surveys, providing validation for the standard survey method e.g. do more spraints mean more otters.

The use of molecular tools to extract DNA from faeces, removes the apparently high risk of species misidentification (Birks *et al.* 2005; Harrington *et al.* 2010), and can provide estimates of population abundance and density (Harrison *et al.* 2002). Molecular techniques can also obtain useful information such as sex ratio (Reed *et al.* 1997; Dallas *et al.* 2003), relatedness and genetic diversity (Zedrosser *et al.* 2007). This information enables important ecological topics such as competition (see section 1.7), social organisation (Frantz *et al.* 2006) and reproductive fitness (Hauer *et al.* 2002) to be studied in greater detail. Pertinent questions could be addressed, such as whether different genders have different habitat preferences, whether habitat structure is related to individual reproductive fitness, and is population fitness higher in heterogenous or homogenous habitats. A molecular approach could also investigate if kin selection (Krebs and Davies, 1993) occurs in solitary carnivores, through increased tolerance of niche overlap between related individuals. This could change perceptions of the inclusive fitness of individuals and populations, and therefore, has important evolutionary consequences. This next step has been initiated via a British Ecological Society grant to Forman *et al.* to investigate differential gender marking in a riparian system using a molecular approach.

8.5 Standardisation of carnivore dietary studies

The factors contributing to a lack of standardisation in carnivore dietary studies are typified in otters (see sections 4.5.4 and 7.5.5). The lack of standardisation, reliability and comparability of otter dietary studies means that relatively little is known about otter diet other than a list of prey items (Carss, 1995). Faecal hard part analysis is frequently used to study the diet of mammalian carnivores, but it has fundamental flaws (see section 1.10.3), which have been investigated through feeding studies on captive animals (e.g. Dellinger and Trillmich, 1988; Carss and Parkinson, 1996; Jacobsen and Hansen, 1996; Tollit *et al.* 2003). Attempts to improve reliability have resulted in the development of several different analysis methods (see section 4.1). The study undertaken in chapter four demonstrates that different analysis methods produce dietary data with a low level of comparability. Therefore, it is difficult to compare otter dietary studies that use different methods of spraint analysis, which significantly hinders investigations of broad dietary trends and ecological concepts (see section 8.5). This has implications for dietary studies in a range of carnivores, as similar methods of hart-part analysis are used in many species (see section 4.1).

Spraint analysis is the method most frequently used to obtain otter dietary data (see section 1.12.5). Spraint collection protocol defines the scale at which diet is being investigated (see section 7.5.5). It is important to collect ecological data at a scale that matches the objectives of the study (Bowyer and Kie, 2006). However, this is seldom considered in carnivore dietary studies, largely due to difficulties in determining the number of individuals being sampled (see section 8.6). Data from the systematic review (see appendix tables 7-9) demonstrates a lack of standardisation in collection protocol and sample size between otter dietary studies. This is likely to affect the scale of studies, and as such, has consequences for the interpretation of the dietary data obtained. Ultimately, dietary studies undertaken at different scales can not be compared as they are not addressing the same question (Wiens, 1989a).

Whilst a considerable amount of work has been undertaken to assess the reliability of different spraint analysis techniques (e.g. Carss and Parkinson, 1996; Carss and Elston, 1996; Jacobsen and Hansen, 1996), little progress has been made regarding the comparatively simple task of standardising studies. This is a situation reflected in many mammalian carnivores where, perhaps rightly so, work has focused on the accuracy of dietary analysis (e.g. Dellinger and Trillmich, 1988; Zabala and Zuberogoitia, 2003; Van Dijk *et al.* 2007). Studying concepts such as the evolution of life-history traits, fundamental trophic niche (see section 1.1) and foraging strategy (see section 1.5) requires the comparison of data collected from different locations. Standardisation improves the comparability, and therefore, the value of studies investigating the trophic ecology of a species. This study provided guidelines to help standardise the spraint collection and analysis protocol for otter dietary studies (Table 4.4, page 107). This protocol could be easily adapted to studies in other mammalian carnivores where diet is also investigated using faecal analysis.

8.6 Advancing dietary studies in elusive carnivores

Assessing diet through faecal hard-part analysis is a reasonable method of identifying vertebrate prey consumed by carnivores, but determining the full realised trophic niche (see section 1.1) requires the ability to detect invertebrate prey. Invertebrates have been recorded in the diet of several carnivores e.g. Red fox (Cavallini and Volpi, 1996), Eurasian badger (Rosalino *et al.* 2005) coyote (Ranft *et al.* 2005) and gennet (Virgós *et al.* 1999). Invertebrates with exoskeletons are often detectable in faeces e.g. odonata nymphs and crustaceans (Table 5.2, page 114), but prey with few or no hard remains is poorly detected (Carss and Parkinson, 1996). Otters may consume slugs (Andrew King *pers. com.*), which would not be recorded through spraint analysis. Such prey may represent a profitable meal, as it is easy to catch and requires little handling. The consumption of soft-bodied prey by carnivores needs to be addressed and there are numerous molecular techniques that enable this information to be extracted from faeces (Freeman and Smith, 1998; Symondson, 2002; Iversson *et al.* 2004; Codron *et al.* 2005). Molecular tools also enable all vertebrate prey to be identified to species level (Deagle *et al.* 2005), thereby, improving the resolution of dietary studies and providing a more complete depiction of trophic niche. It is important to test the application of novel techniques for studying diet, which are potentially more accurate, but to retain comparability with historical data they should be presented alongside current methods. Molecular tools can also be used to obtain information about the individuals and populations being studied (see section 8.4). Combing this information with dietary analysis would ensure the independence of the data and indicate the scale of a study, thus, providing evolutionary context (Levin, 1992). This also enables study of trophic partitioning (see section 8.9), which is an important concept for competition and evolutionary theories (see section 1.6).

It is important to determine the relationship between the volume of prey remains in faeces and the energetic contribution of prey items. This would generate more meaningful data that could be used to study the fitness consequences of foraging strategies (see section 1.5) and relate diet to life history strategies. Characteristic key bones have been used to estimate the number, size and biomass of prey items (Zijlstra and van Eerden, 1995; Prenda *et al.* 2002 Lanszki and Molnar, 2003), but the accuracy of this technique has been questioned (Cottrell and Trites, 2002; Tollit *et al.* 2003; Tollit *et al.* 2007). Theoretically, it is possible to determine the quantity of prey consumed by analysing DNA extracted from faeces (Bowles, 2009), which could greatly improve estimates of prey consumption leading to a better understanding of energetic requirements and forging strategy. Studying foraging strategies and behaviour requires information on the full sequence of predation (see section 1.5) and failed predatory events, which can not be obtained by faecal analysis. Prey selection studies should consider variation in prey encounter and capture rates, caused prey anti-predation mechanisms and individual foraging ability. It is essential that prey availability is not defined solely by abundance data.

Molecular dietary analysis is clarely a promising area of research, but many techniques require verification, and widespread application is currently inhibited by the high cost of materials. There are other technologies which hold potential for studying predation in elusive species. Remote data loggers can provide information on the timing and amount of food ingested (see section 1.10.5). Recent advances in bio-logger technology (see section 1.10.5) have enabled capture attempts to be measured in marine carnivores (Viviant *et al.* 2010). This holds great potential for advancing core areas of foraging theory, particularly if combined with values of prey availability that incorporate all of the factors affecting availability (see section 1.8.2). Furrther development to enable the reliable identification of prey, would make this a very useful tool for studying carnivore trophic ecology. .

8.7 Using systematic review and meta-analysis to summarise ecological topics

A systematic review is considerably less biased than a standard subjective review as it follows a strict methological protocol, which gives an objective approach to data acquisition (Pullin and Knight, 2001). In some ecological topics there may be insufficient high quality evidence to enable robust conclusions to be drawn, but the application of meta-analysis has proven effective at handling sparse data of variable quality (Stewert *et al.* 2005). Systematic reviews combined with meta-analysis can be used to identify statistically significant ecological patterns and rigorously test broadly accepted paradigms (Stewert *et al.* 2005). This is a useful method of investigating ecological variation, providing it with evolutionary context and producing a better estimation of fundamental niche (see section 1.1). Broad geographical trends in niche indicate the factors limiting the distribution of a species, and provide an insight into its capacity to adapt to environmental change. Such information is very useful for conservation biologists. In chapter seven this approach was used identify significant trends in otter diet and investigate if they were related to a number of factors believed to influence dietary variation in carnivores (see sections 7.4.2-7.4.6). This study highlighted a considerable level of unfounded concepts surrounding otter diet, which could be alternately described as "trophic naivety" (see section 8.8).

8.8 Trophic diversity of otters in Europe

Large scale dietary reviews are important as they describe the trophic niche of a species more completely (Lozano *et al.* 2006). Chapter 7 revealed that otter diet is extremely diverse across its European range (see section 7.4.2). This indicates that the fundamental trophic niche of otters includes prey from a diverse range of taxa. The review identified a considerable amount of variation in otter diet across Europe and a previously unknown longitudinal trend in diet composition. There was no evidence of a latitudinal or Mediterranean trend in trophic diversity (Figure 7.1), which is in contrast to previous work undertaken in otters (Clavero *et al.* 2003) and other medium-sized Palaearctic carnivores (Virgós *et al.* 1999; Lozano *et al.* 2006). The reasons for these conflicting conclusions are discussed in section 7.5.1, but a key observation is that variation in the diversity and composition of otter diet primarily occurs at the habitat level and, as a semi-aquatic carnivore, access to marine foraging areas has an obvious influence on diet (see sections 5.5.2, 6.5.2, 7.5.2 and 7.5.4).

Factors that vary on a small scale, such as competition, prey assemblages and habitat structure, appear to have the strongest influence on otter diet (see section 7.5.4). This is supported by the prevalence of spatial variation over temporal variation in otter diet on Gower (see section 5.5.3), and differences in the consumption of marine prey between Gower and other coastal otter populations (see section 5.5.2), both of which were linked fine scale variation in habitat structure. Variation in habitat structure is likely to be particularly important to carnivores as it influences the diversity and structure of prey communities (see section 7.5.4). Consequently different habitats may be associated with different levels of foraging success and have different fitness values (see section 8.10). A number of the patterns observed in otter trophic diversity are homologous with other Mustelids (see sections 7.5.2 and 7.5.4) possibly reflecting evolutionary adaptations within this family (see section 8.9). This is an interesting observation that requires further investigation and contrasting with other carnivore families.

8.9 The evolutionary significance of carnivore dietary variation

Large scale geographical patterns in carnivore diet provide information on the evolutionary importance of dietary variation. The wide distribution of otters is no doubt linked to its remarkable foraging abilities, which enable this species to obtain food in a range of environments (see section 8.11). A number of otter life-history traits are thought to have evolved in response to variations in food availability, such as polyestrous cycle of females (Kruuk *et al.* 1987) or the flexibility in social organisation when food resources become limited (see section 1.12.4). There are large differences in climate, habitat structure and prey communities across the geographic range of otters. It is doubtful whether otters would be so widely distributed and persist in such a range of challenging environments if they were an obligate specialist. In many areas otter populations are recovering from severe population declines (Crawford, 2003; Jones and Jones, 2004; McDonald *et al.* 2007; Prigioni *et al.* 2007). Variability within a species is key to withstanding multiple extinction threats (Gittleman *et al.* 2001) and the resilience of otter populations is undoubtedly due in part to the considerable behavioural and ecological plasticity of this species.

Otters have evolved foraging behaviours that are highly adaptable, enabling them to live in a wide range of habitats and adapt to abiotic and biotic changes that occur on a range temporal and spatial scales (see section 8.11). This could explain the absence of geographical trends in trophic diversity which are present in other carnivore species (see section 8.8). Evolving foraging behaviours that are effective at locating and capturing a broad range of prey types would be beneficial if prey availability, environmental conditions and competition are variable (see section 1.3). The ability to utilise a broad range of food resources has evolutionary significance as it is associated with higher fitness values (Burnell and Hamilton, 1983), which is reflected in the lower extinction risk associated with generalist carnivores (McKinney, 1997). Trophic plasticity may be widespread in the Mustelidae and could be linked to the evolution of behavioural, morphological and physiological adaptations, which enable them to inhabit unpredictable and variable environments. Furthermore, it may facilitate the co-existence of species with similar niches, due to fine-scale habitat heterogeneity (Wiens, 1989b) and character convergence (McDonald, 2002). Specialist species are considered to be more prone to population declines, due to environmental change and landscape degradation, than generalist species (Devictor *et al.* 2008). The trophic plasticity of otters suggests that they should be relatively resilient to environmental change (see section 7.5.8); however, historically this has not been the case (Randi *et al.* 2008). The most important factor affecting the distribution and viability of otter populations may not be prey availability. The semi-aquatic behaviour of this species means that water quality and availability has a strong influence on diet (Clavero *et al.* 2008), social organisation (Sulkava *et al.*2007), reproduction (Ruiz-Olmo *et al.* 2002; 2009), marking behaviour (Kruuk, 1992) and mortality (Chanin and Jefferies, 1978). Research is required to determine if the availability and quality of freshwater is the main environmental factor limiting otter populations.

Conservation programs and important ecological concepts, models and tools are based on the assumption that all individuals within a population use the same resources (Bolnick *et al.* 2002; Durrell, 2000). Several studies have recently provided compelling evidence that this assumption is frequently violated (Svänback and Bolnick, 2007; Tinker *et al.* 2008; Araújo *et al.* 2009). Temporal and spatial differences only explained half of the variation observed in otter diet throughout Europe (see section 7.4.3). Interspecific competition can have a significant influence on carnivore diet (Creel and Creel, 1996; Fedriani *et al.* 2000; Gerstell and Bednarz, 1999). However, very little is known about the influence of intraspecific competition on individual trophic niche. Intraspecific competition can drive population trophic niche expansion (Bolnick, 2001), individual trophic partitioning (Svänback and Bolnick, 2007), and allow growth in density dependent populations (Van Valen, 1965). Some patterns in otter dietary variation on Gower were characteristic of a population that has undergone trophic niche expansion (see section 5.5.5). To understand trophic partitioning (see section 1.6) and the evolutionary significance it holds at the population level, carnivore dietary data needs to be linked to individuals using molecular tools (see section 8.6) and studies carried out on temporal scales that are representative of species life spans (see section 8.13).

Linking dietary data to individuals can provide a more accurate depiction of trophic ecology and allow investigation into intraspecific competition and trophic partitioning. A small number of studies have linked diet to individuals, producing remarkable results and far reaching ecological implications (Fedriani and Kohn, 2001; Svänback and Bolnick, 2007; Tinker *et al.* 2007). Individual specialisation has broad consequences as it enables growth in density dependent populations, maintains polymorphisms and drives disruptive selection (see section 1.7). Otters are a territorial density dependent carnivore (see section 1.12.4) with a broad fundamental trophic niche (see section 8.8) and extremely adaptable foraging behaviour (see section 8.11). This makes the otter an ideal model organism for studying individual trophic partitioning in-carnivore populations using non-invasive sampling techniques.

8.10 Influence of habitat on carnivore fitness

This study demonstrates that habitat level variation has a strong influence on carnivore diet (see section 8.8) and suggests that generalist carnivores have evolved a range of foraging behaviours, perhaps suiting different habitats (see sections 8.9 and 8.11). For example, the home range of carnivores is often larger than predicted by energetic requirements (Kelt and Van Vuren, 2001) and home ranges tend to be larger in homogenous habitats, where prey resources are depauperate or unpredictable (White and Ralls, 1993; Goszczyński *et al.* 2000) This may reflect the need to include a range of different habitats, to enable switching behaviour in response to temporal variation in the foraging value of different habitats (see section 8.11). Different habitats are associated with differences in population niche breadth (Table 7.5, page 163) and potentially foraging success (see section 8.12). If habitat level variation has the strongest influence on carnivore diet (see section 8.8) then different habitats could have different fitness values, due to the association between diet and reproductive success (Pierotti and Annett, 1991).

Otters are territorial (see section 1.12.4) and habitat selection theory predicts that territorial behaviour should be driven by fitness differences between different areas (Morris, 1989). Dominant individuals may control access to habitats with important seasonal prey resources, such as ponds (Weber 1990; Ruiz-Olmo *et al.* 2002). However, foraging success is also affected by individual ability (see section 1.8.4); therefore, the optimal habitat may vary depending on ability and experience. A habitat which is highly profitable for a skilled forager may be less profitable for less experienced individuals. Spatial organisation within carnivore populations may be driven by habitat partitioning according to fitness value, which is reinforced by foraging ability and social status. This concept has considerable importance for models attempting to predict the impact of habitat loss on carnivore populations (Durrell, 2000).

8.11 Otter foraging strategy and behaviour

It has long been argued that otters are trophic specialists due to their reliance on fish (see section 1.12.10). The systematic review produced a low K-coefficient (see section 7.4.6) and many studies have recorded broad trophic niche values (table 7.1, page 157), suggesting that otters diet varies considerably across Europe and they have a broad fundamental trophic niche (see section 7.5.1). Several typical generalist carnivores predominantly predate prey from one or two taxonomic classes e.g. coyotes (Ranft *et al.* 2005) and Red fox (Cavallini and Volpi, 1996). Most otter dietary studies have recorded prey from multiple classes (see section 7.4.2), but trophic diversity is overlooked by pooling all fish prey into one category. The assumption that all fish are relatively equally obtainable is unlikely to be the true (see section 7.5.6). The variability of otter diet may be due to opportunistic predation of the most abundant and easily obtainable prey (see section 1.12.10), which in aquatic systems is usually fish. If otter foraging abilities restricted them to fish they would be poorly adapted to living in habitats where water is a limited resource. However, otters are widespread in many areas of Europe where the availability of water is severely limited during summer (Barbosa *et al.* 2003; Pedroso *et al.* 2006; Prigioni *et al.* 2006a), or winter (Sulkava, 1996), so they are clearly able to survive in habitats with a low availability of fish.

It is too crude to classify otters as generalist or specialist foragers when there is considerable variation between populations, and a wide range in niche breadth across Europe (table 7.1, page 157). This suggests that otters are facultative foragers (Glasser, 1984), enabling them to adapt to changes in prey assemblages and environmental conditions. Dietary specialisation is a behavioural adaptation, rather than true specialisation which is genetically fixed (Futuyma and Moreno, 1988). Like several other Mustelids e.g. European polecat (Lode, 1993) Eurasian badger (Goszczyński *et al.* 2000) and American mink (Sidorovich, 2000), otters can predate a range of prey types and may optimise diet according to prey availability (see section 1.8.2), environmental conditions (see section 1.8.3), experience and ability (see section 1.8.4). The broad trophic niche of otters on Gower suggests that a generalist foraging strategy is advantageous where regular prey resources are limited.

Otter foraging has been described by several authors (Chanin, 1985; Watt, 1993; Kruuk, 2006) and includes a range of different behaviours, which are all highly explorative, making them efficient at flushing out and capturing a range of prey types. This is demonstrated by the similar life-history and behavioural traits of several prey types predated on Gower (see section 5.5.2) and Pembrokeshire (see section 6.5.2). Otters may have evolved a range of different search behaviours as an adaptation to foraging in unpredictable environments, where prey is often distributed in patches (see section 5.1). Behavioural plasticity enables switching between prey and foraging habitat, facilitating the variability in otter diet observed on a range of scales by this study (see sections 5.5.3, 6.5.2, 7.5.2 and 7.5.4), which provides further evidence that prey switching (Begon *et al.* 1996) is a more appropriate foraging strategy for otters, than Optimal Foraging Theory (MacArthur and Pianka, 1966). This theory assumes homogenous encounter and capture rates for all prey types (Sih and Christensen, 2001), and therefore, provides a poor explanation of diets containing mobile prey. A switching strategy permits a response to changes in prey behaviour, capture rates or environmental factors, therefore, allowing individuals to maintain fitness in an unpredictable environment. Otter populations require a broad prey base, to facilitate switching behaviour and the loss of prey species may destabilise populations (see section 8.13).

Obtaining information on the energetic contribution of prey items and individual reproductive success would enable foraging strategy to be directly linked to fitness (see section 8.6). The success of different foraging behaviours is not known, but it may be integral to prey and habitat switching decisions made by carnivores. Certain foraging behaviours may be maternally learnt (see section 1.8.4) and determine the life-history strategies and fitness of a population. Further research should attempt to measure the success associated with different foraging behaviours in a range of carnivores, perhaps by using remote bio-logging devices (see section 1.10.5), and determine how this influences foraging strategy.

8.12 Otter trophic ecology and coastal foraging in Wales

This study indicates that otters in Wales have a broad trophic niche (see sections 5.5.2 and 6.5.2), containing a larger proportion of non-fish prey than Scottish populations (Watson, 1978, Carss *et al.* 1990; Watt, 1995; Yoxon, 1999). Otter dietary studies in England (Webb, 1975; Britton *et al.* 2006; De la Hay, 2008), and Northern Ireland (Preston *et al.* 2006) also recorded a higher occurrence of non-fish prey than the Scottish studies, indicating that otter trophic niche in Scotland is different to the rest of the UK. This has conservation value as Scottish otter populations were less affected by the declines of the 20th century (Strachan, 2007) (see section 1.12.1).This could be due to the large coastal populations in Scotland (Harris *et al.* 1995) that were not affected by the pollution of inland water systems. Otter breeding has been recorded on the Welsh coastline (Liles, 2003a), and marine prey form an important component of otter diet at coastal sites and on coastal riparian systems in Wales (see sections 5.5.2 and 6.5.2). Therefore, coastal populations may have been important to the survival, and subsequent re-colonisation of otters in some parts of Wales. Alternatively, as the UK otter population recovers (Strachan and Jefferies, 1996), density dependent regulation may drive dispersal to coastal sites.

Coastal otter populations have been studied in several areas of Europe (Watson, 1978; Beja, 1991; Heggberget, 1993), but very little is known about the importance of marine foraging areas to otters inhabiting coastal rivers. On Gower, and in other areas of South Wales (Parry *unpub. data*), spraints containing marine prey have been collected several km inland. This suggests that otters are moving inland following marine foraging bouts, which could be due to the need for freshwater (Kruuk and Balharry, 1990) or the higher availability of resting sites inland (Liles, 2003a). Research is needed to investigate why inland otters used coastal foraging areas. Foraging success may be higher in the marine environment (Kruuk, 2006) or coastlines may link riparian systems, avoiding the need for overland journeys. It is possible that only a small proportion of the population foraged in marine habitats on Gower (see section 5.5.1) and Pembrokeshire (see section 6.5.2). Foraging success associated with different habitats, may determine the fitness value of them, which could be a key factor regulating social organisation (see section 8.10). Studying foraging success in different habitats, the historical use of coastal habitats and the social status of individuals inhabiting coastal areas, will help determine if coastal habitats are high or low quality territory. This will provide context for the importance of coastal areas to otter populations.

8.13 Implications for otter ecology and prognosis for conservation

This study identifies important limitations in two key techniques used to monitor and study otter populations (see section 3.5.4 and 4.5.1). Several other shortcomings of these techniques have been identified in previous studies (e.g. Kruuk *et al.* 1986; Carss and Parkinson, 1996; Carss and Elston, 1996; Ruiz-Olmo *et al.* 2001). Scientific knowledge is only as reliable as the methods used to obtain it. This means that our knowledge of carnivores such as the otter is very limited, and it is naïve to assume that we have anything more than a very basic understanding of their ecology. Diet must be linked to linked to different individuals and different sexes (see section 8.6) to provide it with ecological, evolutionary and conservation context (see section 8.9). There is an absence of studies carried out on temporal scales which are representative of life spans. The IUCN state that at least three generatiuons of continuous data are needed to formulate sound ecologically based conservation programs (IUCN, 2001). Otters have the potential to live for more than 10 years (Kruuk, 2006; Sulkava *et al.* 2007), but few dietary studies have produced more than three years of consecutive data (see appendix table 9). Long-term studies are important to investigate the capacity of individuals and populations to respond to changes in, environmental conditions, population demography and prey populations. A lack of quality data from outside Europe, and a habitat bias in some regions (see sections 7.5.7 and 7.5.8), represents a major gap in our understanding of the life-history traits of otters in these regions.

Sharp declines in eel populations have been recorded in Europe (Feunteun, 2002; Dekker, 2003). Eels are an important prey of otters in the UK (see section 8.8), but were taken less frequently in this study than in previous studies carried out in Wales. A similar longitudinal trend has been recorded at sites in England (Bonesi *et al.* 2004). Eels are highly profitable prey, due to their high lipid content (Kruuk and Carss, 1996), so a decline in their abundance could implicate a source of trophic pressure on otters in the UK. Bullhead populations are not secure either, due to a lack of knowledge regarding their distribution and biology (Tomlinson and Perrow, 2003).Global declines in amphibian populations (Stuart *et al.* 2004; IUCN, 2008) may affect an important prey resource for otters (see sections 5.5.3 and 7.5.2), and other Mustelids (Lodé, 1996; Sidorovich *et al.* 1998; Goszczyński *et al.* 2000). Amphibian prey is potentially crucial to sustain a breeding otter population, as the peak consumption of amphibians is often during spring and winter, when the risk of starvation is highest (Kruuk *et al.* 1987; Sulkava *et al.* 2007) and females often have cubs (Liles, 2003b). Amphibians are an important prey resource for many carnivore species (Lodé, 1996; Lanszki *et al.* 1999; Sidorovich, 2000), and as there is no obvious substitute for amphibian prey, the decline in amphibians poses a serious problem for ecosystems. The trophic importance of different amphibian species is poorly understood, as there is no published reference key for amphibian remains. The ability to identify amphibian remains in carnivore faeces to species level could aid monitoring of amphibian distribution and habitat use, particularly during their terrestrial stage. It would also improve understanding of the position of amphibians in food webs and their importance to carnivore populations. As a result of this study a key is now being prepared in conjunction with the Amphibian Reptile Conservation Trust (ARC).

Modelling the impact of prey declines on carnivore populations would provide an important tool for conservation. Predicting the response to changing prey resources is particularly important for carnivores living in habitats subject to anthropogenic interference (Beckmann and Berger, 2003). Otter conservation needs to adopt a holistic habitat approach, maintaining prey diversity so there is opportunity to adapt to changing environmental conditions and declines in important prey species. Maintaining prey diversity may also reduce conflict with human economic activities, such as fish farming (Kemenes and Nechay, 1990; Polednik *et al*. 2004). It is imperative to recognise that, despite the large body of published work, we actually know very little about otter ecology due to the limitations of the study techniques. New technologies could significantly advance our understanding of these remarkable and highly complex carnivores, which fill an integral ecological role. With a willingness to embrace and fund new techniques comes the potential for ground-breaking advances in ecological theory.

Photo 8.1 Otter eating a crab in Scotland (Charis White).

Appendix

Spraint site Number	SS	BNG	Substrate	Height from Water	Length from water	Side of Channel	Extra notes

Figure 1 Field sheet used for spraint collection on Gower

Table 1 Number of otter spraints collected per month on each of the Gower study rivers between July 2005 and June 2007.

month	River Clyne	Burry Pill	Pennard Pill	Bishopston Pill	Total
Jul-05	46	38	16	3	103
Aug-05	39	125	11	3	178
Sep-05	18	98	34	4	154
Oct-05	11	17	0	0	28
Nov-05	32	75	0	0	107
Dec-05	18	37	0	0	55
Jan-06	8	38	34	2	82
Feb-06	17	91	22	2	132
Mar-06	0	32	25	3	60
Apr-06	29	66	42	8	145
May-06	15	52	5	6	78
Jun-06	20	47	10	0	77
Jul-06	39	106	24	5	174
Aug-06	8	32	28	10	78
Sep-06	29	41	2	0	72
Oct-06	7	32	33	1	73
Nov-06	3	57	10	0	70
Dec-06	3	22	18	0	43
Jan-07	25	79	36	0	140
Feb-07	12	33	16	3	64
Mar-07	22	111	81	0	214
Apr-07	44	142	114	25	325
May-07	6	65	31	0	102
Jun-07	19	68	10	0	97
Totals	470	1504	602	75	2561

Table 2 The probability of detecting otters on the Gower study rivers by repeatedly surveying two sites, separated by 500 m of river bank, using transects of varying length (m)The solid horizontal line marks the 0.8 level of power and the vertical dashed line marks the seasonal detection probabilities associated with a standard 600 m transect survey.

Transect size (m)	Probability of detecting otters				
	Summer	Autumn	Winter	Spring	overall
50	0.16	0.13	0.16	0.18	0.16
100	0.24	0.21	0.26	0.28	0.25
150	0.32	0.26	0.34	0.36	0.32
200	0.35	0.31	0.41	0.42	0.38
250	0.42	0.35	0.46	0.47	0.42
300	0.46	0.38	0.5	0.51	0.46
350	0.49	0.41	0.53	0.55	0.49
400	0.52	0.44	0.56	0.58	0.52
450	0.55	0.47	0.59	0.6	0.55
500	0.57	0.49	0.61	0.63	0.58
550	0.59	0.52	0.64	0.65	0.6
600	0.61	0.54	0.66	0.67	0.62
650	0.63	0.57	0.69	0.69	0.64
700	0.65	0.6	0.71	0.7	0.66
750	0.67	0.62	0.73	0.72	0.69
800	0.69	0.64	0.75	0.74	0.71
850	0.71	0.66	0.77	0.76	0.73
900	0.73	0.68	0.79	0.77	0.74
950	0.74	0.7	0.81	0.79	0.76
1000	0.75	0.72	0.82	0.8	0.77
1050	0.77	0.74	0.84	0.81	0.79
1100	0.78	0.76	0.85	0.82	0.8
1150	0.79	0.78	0.87	0.83	0.82
1200	0.8	0.78	0.88	0.85	0.83
1250	0.81	0.81	0.9	0.85	0.84

Table 3 Mean length and weight of eels consumed by otters on the Gower peninsular between July 2005 and June 2007. Calculated using the equation of Britton and Shepherd (2005).

	Mean length year 1 (mm)	Mean weight year 1 (g)	Mean length year 2 (mm)	Mean weight year 2 (g)	Overal mean length (mm)	Overal mean weight (g)
Clyne	165.33	23.83	163.34	22.99	164.49	23.47
Burry	167.36	24.64	166.58	24.32	167.06	24.52
Pennard	166.98	24.46	166.22	24.15	166.35	24.2
Bishopston	167.29	24.59	164.15	23.26	164.71	23.5
Gower	167	24.5	165.66	23.93	166.4	24.24

Table 4 Output from a KW test, indicating differences in the median RFO% of the top three marine and freshwater fish, the top five non-fish prey and the number of fish families between otter diet in the Iberian Peninsular ($n = 21$), UK ($n = 27$) and central Europe ($n = 23$).

Prey type	Kruskal-Wallis *h*	P-value
Avian	9.87	<0.01
Amphibian	7.56	0.02
Invertebrate	9.18	0.01
Mammalian	10.12	<0.01
Reptilian	17.80	<0.01
Anguillidae	40.75	<0.01
Cyprinidae	23.47	<0.01
Salmonidae	7.64	0.02
Gadidae	18.46	<0.01
Gobiidae	8.75	0.01
Blennidae	16.14	<0.01

$P = 0.05$

Table 5 Results of Dunn's multiple comparison tests showing dietary components with significant variation in their occurrence in otter diet between biogeographic regions. Prey categories are measured in RFO % and fish families as frequencies Central Europe studies = 23, UK/Ireland studies = 28, Iberian Peninsula studies = 21, MD = Difference in mean rank sum.

Prey type	Median, minimum and maximum RFO %	Habitats with significant differences in the RFO % in otter diet
Amphibian	Iberian Peninsula = 6.5 (min = 0, max = 23.0) UK/Ireland = 1.1 (min = 0, max = 17.1 Central Europe = 10.0 (min = 0, max = 38.0)	Central Europe > UK/Ireland (MD = 14.39, $p<0.05$)
Anguillidae	Iberian Peninsula = 0.3 (min = 0, max = 35.2) UK/Ireland = 10.9 (min = 0, max = 88.9) Central Europe = 0 (min = 0, max = 3.0)	UK/Ireland > Iberian Peninsula (MD = 17.80, $p<0.01$) UK/Ireland > Central Europe (MD = 35.76, $p<0.001$) Iberian Peninsula > Central Europe (MD = 17.96, $p<0.01$)
Avian	Iberian Peninsula = 0 (min = 0, max =0.9) UK/Ireland = 1.0 (min = 0, max = 20.0) Central Europe = 0.0 (min = 0, max = 20.0)	UK/Ireland > Iberian Peninsula (MD = 17.79, $p<0.01$)
Blennidae	Iberian Peninsula = 2.3 (min = 0, max = 35.0) UK/Ireland = 0.0 (min = 0, max = 30.3) Central Europe = 0 (min = 0, max = 0)	Iberian Peninsula > Central Europe (MD = 19.93, $p<0.001$) UK/Ireland > Central Europe (MD = 13.43, $p<0.05$)
Cyprinidae	Iberian Peninsula = 1.8 (min = 0, max = 93.2) UK/Ireland = 0.0 (min = 0, max = 66.6) Central Europe = 39.1 (min = 0, max = 88.5)	Central Europe > Iberian Peninsula (MD = 20.82, $p<0.01$) Central Europe > UK/Ireland (MD = 26.97,$p<0.001$)
Gadidae	Iberian Peninsula = 0 (min = 0, max = 6.6) UK/Ireland = 0.4 (min = 0, max = 28.3) Central Europe = 0 (min = 0, max = 0)	Iberian Peninsula > Central Europe (MD = 16.24, $p<0.05$)
Gobiidae	Iberian Peninsula = 2.6 (min = 0, max = 23.6) UK/Ireland = 0 (min = 0, max = 12.5) Central Europe = 0 (min = 0, max = 0)	Iberian Peninsula > Central Europe (MD = 14.14, $p<0.05$) UK/Ireland > Central Europe (MD = 21.81, $p<0.001$)
Invertebrate	Iberian Peninsula = 0.4 (min = 0, max = 14.6) UK/Ireland = 0.0 (min = 0, max = 23.0) Central Europe = 5.6 (min = 0, max = 25.0)	Central Europe > UK/Ireland (MD = -16.93, $p<0.01$)
Mammalian	Iberian Peninsula = 0 (min = 0, max = 1.3) UK/Ireland = 0 (min = 0, max = 23.0) Central Europe = 0.6 (min = 0, max = 44.0)	Central Europe > Iberian Peninsula (MD = 18.75, $p<0.01$)
Number of fish families	Iberian Peninsula = 6 (min = 2, max = 14) UK/Ireland = 9 (min = 3, max = 16) Central Europe = 4 (min = 2, max = 12)	UK/Ireland > Central Europe (MD = 26.86, $p<0.001$)
Reptilian	Iberian Peninsula = 0.2 (min = 0, max = 8.1) UK/Ireland = 0 (min = 0, max = 1.4) Central Europe = 0 (min = 0, max = 4.6)	Iberian Peninsula > UK/Ireland (MD = 20.40, $p<0.001$)
Salmonidae	Iberian Peninsula = 0 (min = 0, max = 93.2) UK/Ireland = 2.1 (min = 0, max = 89.7) Central Europe = 0 (min = 0, max = 48.0)	UK/Ireland > Iberian Peninsula (MD = 15.38, $p<0.05$)

Table 6 Output from a KW test, indicating differences in the median RFO% of the top three marine and freshwater fish, the top five non-fish prey and the number of fish families in otter diet between broad habitat types. Riparian (n = 40), Lake/pond (n = 11), Estuarine (n= 7), coastal (n = 19).

Prey type	Kruskal-Wallis *h*	P-value
Amphibian	30.66	<0.01
Avian	3.94	0.26
Invertebrate	16.90	<0.01
Mammalian	20.34	<0.01
Reptilian	15.11	<0.01
Anguillidae	16.36	<0.01
Cyprinidae	47.06	<0.01
Salmonidae	21.76	<0.01
Gadidae	50.56	<0.01
Gobiidae	43.05	<0.01
Blennidae	56.17	<0.01
Fish families	38.36	<0.01

Table 7 Summary of different spraint analysis methods employed in the literature.

Name of technique	Description
Area counting	(Jacobsen and Hansen, 1996)
Bulk estimation 1	(Jenkins *et al.* 1979)
Bulk estimation 2	(Wise, 1980)
Frequency of numbers	(Lanszki and Körmendi, 1996)
Frequency of occurrence	See section 2.7.1, equation 1
Relative frequency of numbers	See section 2.7.5, equation 5
Relative frequency of occurrence 1	See section 2.7.2, equation 2
Relative frequency of occurrence 2	See section 2.7.3, equation 3
Relative percentage weight	See section 2.7.4, equation 4
Occurrence	(Gormally and Fairley, 1982)
Percentage biomass	(Harna, 1993)
Percentage weight	(Kingston *et al.* 1999)
Score-bulk analysis	(Jacobsen and Hansen, 1996)

Table 8 Variation in collection protocol between studies included in a systematic review of otter diet. Studies = 77.

Spraint collection method	**Percentage use in studies from systematic review (%)**
Spot checks	24.7 (19/77)
Standard route or transect 50-600 m	6.5 (5/77)
Standard route or transect 601-1000 m	5.2 (4/77)
Standard route or transect over 1 km	39.0 (30/77)
Full surveys	6.5 (5/77)
Not specified	18.1 (14/77)

Table 9 Variation in the duration and sample size of otter dietary studies included in a systematic review of 77 studies.

Methodological variable	**Proportion of studies from systematic review (%)**
Study Length	
1 year	49.9 (38/77)
1-2 years	24.7 (19/77)
2 -3 years	19.5 (15/77)
3 years +	6.5 (5/77)
Spraint sample size	
59-100	16.9 (13/77)
101-500	48.1 (37/77)
501-1000	19.5 (15/77)
1001+	15.6 (12/77)

Glossary

Anthropogenic = Effects, processes, objects, or materials are those that are derived from human activities.

Behavioural plasticity = Physiological and morphological adaptive change.

Biodiversity = Biological diversity.

Benthic = Living on or in the seabed.

Boolean = Method of searching for information in databases that combines search terms with the operators AND, OR, NOT, and parentheses.

Coasteering = Physical activity that encompasses movement along the intertidal zone of a rocky coastline on foot or by swimming.

Community = Group of interacting organisms sharing an environment.

Confluence = Meeting of two or more bodies of water.

Core area = Area where an individual spends more than 50% of its time.

Crepuscular = Active at dawn or dusk.

Demersal = Dwelling at or near the bottom of a body of water.

Diurnal = Active during the day.

Disruptive selection = Advantageous selection of rare phenotypes due to high population density in a density dependent population.

Ecological niche = The role an organism occupies and the function it performs in an ecosystem.

Ecological paradigm = A set of assumptions, concepts, values, and practices constituting a view of reality of an ecological topic.

Ecosystem = A dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit.

Ecotype = Largest scale biogeographic division of the earth's surface based on the historic and evolutionary.

Electrofishing = Fish sampling technique using electric currents and electric fields.

European Habitat Directive = European Union directive adopted in 1992 as an EU response to the Berne Convention. It aims to protect some 220 habitats and approximately 1000 species considered to be of European interest, which are listed in the directive's Annexes.

False negative = Type II error, recording a negative result when an effect is actually present.

Flow regime = The pattern of flow in a river that can be described in terms of quantity and variability of water flows.

Foraging patch = Limited area that contains food resources.

Fragmentation = The breaking up of a habitat, ecosystem, or land-use type into smaller parcels.

Generalist = A species that can live in many different habitats and can feed on a number of different organisms.

Genetic diversity = The variety of different types of genes in a species or population.

Genetic drift = Random change in gene frequencies in populations.

Gene flow = The movement of genes from one population to the other through movement of individuals between those populations.

Heterogeneous = Non-uniform in structure or composition.

Holistic = View of the natural environment that encompasses an understanding of the functioning of the complete array of organisms and chemical-physical factors acting in concert rather than the properties of the individual parts.

Homogeneous = Uniform in structure or composition throughout.

Hydrometric area = Region defined by water systems.

Hypertrophication = The extreme over-enrichment of a water body with nutrients, resulting in excessive growth of organisms and depletion of oxygen concentration.

Idiosyncratic = Structural or behavioural characteristic peculiar to an individual.

Intertidal = The zone between high and low tide.

Interspecific competiton = Competition for resources between individuals of different species.

Intraspecific competion = Competition for resources between individuals of the same species.

Keystone species = Species that have a key role in an ecosystem, affecting many other species, and whose removal may lead to a series of extinctions within the system.

Kin selection = Selection favouring individuals who maximise their gene contributions to future generations by aiding related individuals.

K-Selected species = Species that invest more heavily in fewer offspring.

Levee = Embankment that is built in order to prevent a river from overflowing.

Lutrinae = Subfamily which covers otters.

Maternal Learning = Information passed from mother to offspring during the period of parental care.

Maxillae = Bones that form the upper jaw.

Mediterraneity = Variability in prey resources driven by fragmented and highly heterogeneous habitats.

Mustelidae = Taxonomic group often know as the weasel family, of which the otter is a member.

Niche = The environmental parameters within which individuals and populations survive, grow and reproduce.

Niche partitioning = Degree of differential resource use by coexisting species.

Nocturnal = Active during the night.

Non-Invasive = Method of study that does not directly interfere with the animal.

Obligate = "by necessity" Organism restricted to a particular set of environmental conditions.

Olfactory communication = Communication that takes place using scent.

Optimal foraging model = The strategies employed by an organism to optimise its energy intake from its environment.

Organochlorine pesticides = A class of pesticides containing chlorine e.g. delidrin and Aldrin.

Otolith = Bone-like structure found in the inner ear of many species of fish.

Pharyngeal = Skeletal structure in the back of the mouth.

Piscivore = Carnivorous animal which lives on eating fish.

Poaching = Breakdown in soil structure caused by trampling.

Population abundance = Relative representation of a species in a particular ecosystem, usually measured as the mean number of individuals found per sample.

Population demographic = The structure of age and sex classes within a population of organisms and changes that occur within this population over time.

Qualitative = Observations that do not involve measurements and numbers.

Quantitative = Can be expressed as a number or quantity.

Prey availability = The availability of a prey type to a carnivore, which is affected by abundance as well as many factors related to behaviour and habitat structure.

Radio-telemetry = Automatic measurement and transmission of data from remote sources via radio.

RAMSAR = site of international importance under the RAMSAR convention.

Secondary ingestion = The occurrence of prey remains in a spraint contained in the stomach contents of a prey item.

Sediment Dynamics = Changes in the structure and composition of sediment at the bottom of water bodies.

Source-sink populations = Theoretical model used to describe how organisms in a high quality habitat act as a source that allows the population to increase, maintaining the populations in a low quality habitat 'sink' that, on its own, would not be able to support a population.

Specialist = A species with a very narrow range in habitat or food requirements.

Spraint = Faecal deposits produced by otters.

Subcutaneous = Beneath the skin.

Super predation = When one individual kills and eats a competing individual.

Systematic = Set of orderly, structurally inter-related steps based on a network of concepts, principles and rules.

Territory = Area that an animal consistently defends.

Topographical = Features of the physical landscape.

Torpid = Dormant or hibernating.

Trophic diversity = The diversity of prey consumed by a carnivore.

Trophic niche = Position within community food web, showing sources of energy utilisation.

Trophic partitioning = Differential use of energy resources by individuals within a population.

Type I error = The null hypothesis is falsely rejected.

Type II error = The null hypothesis is falsely accepted.

Vibrissae = Specialized hairs, usually employed for tactile sensation.

Wildlife and Countryside Act 1981 = Act passed to consolidate and amend existing national legislation and to implement the Convention on the Conservation of European Wildlife and Natural Habitats and the Conservation of Wild Birds.

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