ECOLOGICAL EFFECTS OF THE FEEDING AND CONSTRUCTION ACTIVITIES OF THE EURASIAN BEAVER (*CASTOR FIBER*) IN SCOTLAND: IMPLICATIONS FOR REINTRODUCTION

By

Kevin Christopher Jones

Submitted to

The Faculty of Natural Sciences, University of Stirling, September 2006

for the degree of

Doctor of Philosophy

Volume I

This research was undertaken at the School of Biological and Environmental Sciences,
University of Stirling, UK

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Abstract

Beavers have been described as a "keystone species" and "ecosystem engineers", and in this dual role have great potential to physically modify their environment through tree-felling, foraging and construction activities. The resultant change in habitat heterogeneity can affect the flora and fauna that share the habitat with them. There has been recent interest in reintroducing the Eurasian beaver to the United Kingdom after an absence of over 400 years. To date, no research (aside from this thesis) has focussed on beaver ecology and behaviour in Scotland. This study has investigated the ecological effects of a small number of beavers in two enclosed but semi-natural Scottish sites at Bamff in Perthshire. The research conducted over a three-year period, with particular emphasis on the effects of tree-felling, foraging and construction activities.

Trees were felled for both dietary and construction purposes, with felling rates being influenced by habitat availability, quality and the degree of habitat modification required. Highest rates were evident during the initial colonisation period of marginal sites (*c.* >300 trees / beaver / calendar year), and lowest rates in later years of occupation of more optimal sites (*c.* 55 – 70 trees / beaver / calendar year). Preferences were generally for willow and aspen trees, with conifers almost entirely avoided, and smaller trees preferred over larger ones. Proximity of trees to waterbodies was also an important factor, with nearer trees favoured, and generally most felling occurred within 50 m of water. Such behaviour followed the principles of optimal central place foraging. These preferences were less predictable however when intense construction activity was undertaken, with larger trees preferred and generic preferences for deciduous trees apparently invalid. In such cases, close proximity to the construction site was of prime importance. Increased cover of herbaceous plant species was observed in beaver-created canopy gaps in riparian woodland, whilst macrophyte diversity within waterbodies increased slightly in areas of herbaceous grazing. The diversity of terrestrial ground invertebrates was highest in areas of heavy tree-felling, and invertebrate richness and abundance was greatest in areas of herbaceous grazing under an intact tree-canopy. Furthermore, the abundance, diversity and richness of macroinvertebrate communities were increased by beaver-generated woody debris in ponds and streams. Overall, 30% of all macroinvertebrate species collected were found only in beaver-affected areas, due to the refugia and food supply provided by beaver dams, caches and lodges, as well as hydrological effects of these structures.

These results are discussed with reference to future plans to return the beaver to Scotland. The habitat usage and modification of riparian ecosystems in northern Britain is likely to be similar to that found in this study, and the results are believed to be relevant, applicable and transferable to many areas of Scotland.

Statement of originality

I hereby confirm that this is an original study written by the undersigned, and that all research material has been duly referenced and cited.

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1 Introduction

1.1 Introduction

In the last century, factors such as climate change, habitat destruction, hunting, environmental pollution and the rapidly increasing human population, have led to species extinction rates accelerating dramatically. It is now estimated that extinction rates are 10,000 times greater than the natural rate, and that between 50 and 150 species of animal and plant become extinct every day (UNDP, 2006). In the United Kingdom alone approximately 170 species have been lost in the last 100 years (Environment Agency, 2006). In order to halt and reverse this global threat to species and habitat diversity, several international agreements were made during the 1970s and 1980s, such as the Bern, Bonn, Ramsar and CITES (Convention for the International Trade in Endangered Species) Conventions. These were followed in June 1992 by the United Nations Conference on Environment and Development, the so-called Earth Summit, in Rio de Janeiro, Brazil, which was attended by the governments of 157 countries. There, the UK and other attendant states signed the Convention on Biological Diversity (CBD), making commitments to address the global decline in biodiversity. Upon ratification of the CBD into UK national legislation in 1994, the UK Biodiversity Action Plan (BAP) was established, which details 391 species and 45 habitats as priorities for local and national action (Environment Agency, 2006).

Against this background of globally threatened biodiversity, amongst mammals only the auroch (*Bos taurus primigenius* L.) and European wild horse (*Equus caballus* L.) have become extinct in Europe within the last 500 years. This compares favourably to other parts of the world. For example, since 1800 Australia has lost 9 mammals, whilst the West Indies have lost at least 10 mammalian species (Mallinson, 1978). Species extinctions should be considered to be the ultimate endpoint of the threats to wildlife however, and many mammals within Europe are exhibiting shrinking geographical distributions and population sizes. For example, of the UK BAP-listed species, 31 are mammals with 11 of these being terrestrial species (UK Biodiversity Action Plan, 2006). This represents 17% of the 63 terrestrial mammal species present in the UK, including the numerous naturalised alien species often regarded as pests, such as grey squirrel (*Sciurus carolinensis* Gmelin), rabbit (*Oryctolagus cuniculus* L.) and fallow and roe deer (*Dama dama* L. and *Capreolus capreolus* L.). Furthermore, of 68 wild species of rodents extant across Europe, 9 are classed as endangered, 13 are vulnerable, and a further 12 are deemed to be rare (Amori & Zima, 1994).

One "vulnerable" species listed by Amori & Zima (1994) is the Eurasian beaver (*Castor fiber* L.), whereas the IUCN classify the beaver as "Low risk: near threatened" (IUCN, 2004). Such differences in terminology reflect the difficulty in classifying the status of a species over a very large geographical range, covering numerous countries. For example, populations of beavers in one country may be very small and in danger of local extinction, but the species population over the whole geographical range is considered to be robust enough to currently avoid being afforded the maximum levels of protection. Indeed, populations of the Eurasian beaver are generally increasing over much of their range (Amori & Zima, 1994) thanks largely to timely conservation efforts that have enabled the species to recover from the brink of extinction.

1.2 Thesis rationale and objectives

Widespread reintroduction and translocation schemes, together with legal protection of the beaver in many countries, have been instrumental in the recovery of the Eurasian beaver across Europe. As a member of the European Union, Britain has a legal obligation to investigate the desirability of reintroducing the beaver, and this process is currently most advanced in Scotland. Such a reintroduction could have both beneficial and potentially harmful ecological and socio-economic effects, which would require assessment and consideration based on the results of the numerous similar schemes undertaken around Europe. This project will assess the ecological effects of beavers within Scotland, and will add to the abundant research conducted within many other European countries. At the conception of this project, it was anticipated that the Scottish Executive would grant permission for a formal trial reintroduction of beavers to the Knapdale area of Scotland, and that these animals would form the study population for this project. After this decision was delayed, it was decided to shift the focus of the thesis on to a smaller population of captive beavers held in large enclosures in a private Scottish estate. The ecological effects of the feeding and construction behaviour of *C. fiber* have been investigated within the context of the Scottish environment. Some predictions of the potential effects of a future reintroduction of beavers to Scotland have been made based upon these findings of enclosed beavers within Scotland.

1.3 Thesis structure and hypotheses

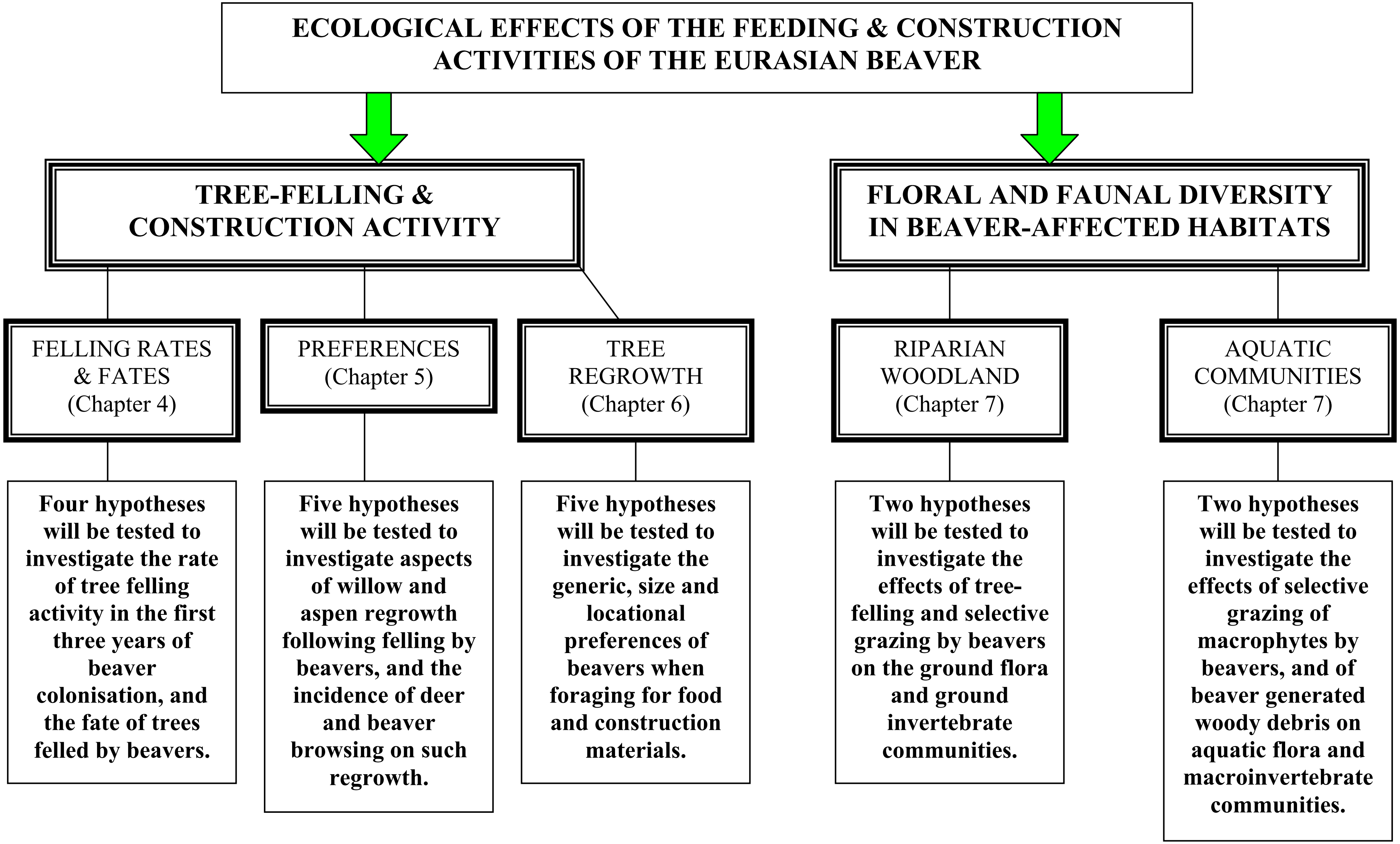
The following chapter will examine the changing fortunes of *Castor fiber*. Firstly, aspects of the species origins, biology, ecology and geographical distribution, are covered. Reasons for the patterns of population change are then examined, particularly the reintroduction and translocation schemes that have been undertaken throughout Europe, and finally the current situation in the UK is considered with particular emphasis on Scotland. This is by no means an attempted comprehensive study of the

Eurasian beaver, as excellent general texts already exist (*e.g*. Wilsson, 1971; Kitchener, 2001) and very detailed coverage of the history, general biology, socio-economic and political aspects of the species exist in numerous other publications (*e.g*. Conroy & Kitchener, 1994; Macdonald *et al*., 1995; Nolet, 1997; Kitchener & Conroy, 1997; Nolet & Rosell, 1998; Rushton *et al*., 2000; Collen & Gibson, 2001; Gaywood, 2001; Halley & Rosell, 2002). It is an attempt to provide background to this thesis and the context of the research undertaken.

In Chapter 2, the available literature concerning the feeding and construction activities of the Eurasian beaver (and when applicable, the North American beaver), have been reviewed. Chapter 3 describes the habitats present at both the enclosed study sites used in this project, and the site of the proposed formal trial reintroduction at Knapdale. Chapters 4 and 5 will investigate the effects of tree-felling activity by beavers, against a background of dietary preferences and construction activities. Tree-felling rates and the fates of felled trees will first be examined in Chapter 4, with felling patterns and preferences considered in Chapter 5. This approach will address gaps in the available literature, by investigating beaver felling and foraging activity in a more holistic manner. Whilst many published studies have considered the felling activity and foraging preferences of beavers, most have been based on data obtained from a single year, and even fewer have included a parallel investigation into tree-felling for construction purposes. Furthermore, almost all studies have been conducted on established beaver colonies outside of the UK. Through examination of the foraging preferences and tree-felling rates of beavers in two contrasting Scottish sites over the first three years of colonisation (which is arguably the most important period following a reintroduction), in parallel with observations on caching, construction and degree of wastage of felled trees, these chapters will add to the available literature. Chapter 6 will further investigate the relationship between beavers and trees, by focusing on the regrowth rates of willow and aspen trees following felling by beavers. Despite the acknowledged preference of beavers for these species, few other studies have investigated the growth response of felled willow and aspen, especially in the light of deer grazing of regrowth. Chapter 6 will address these gaps in the literature. Chapter 7 will consider the effects of beaver activity on herbaceous vegetation and invertebrate communities, in both aquatic and terrestrial habitats. Finally, Chapter 8 will discuss the findings of Chapters 4 - 7 in the context of the potential effects of a beaver reintroduction to Scotland, with particular focus on Knapdale – the site of the proposed trial reintroduction scheme.

The overarching hypotheses of this thesis, as outlined in Figure 1.1, are that the tree-felling activities of beavers are controlled by interactions between tree species and size preferences, and tree location. Furthermore, the felling activity will vary not only seasonally, but also between years, and can be linked to the amount of construction activity undertaken by the beavers. These felling and construction activities will serve to create a mosaic of aquatic and terrestrial habitats, which will lead to increased plant and invertebrate diversity. Specific hypotheses will be described and tested during the course of the experimental chapters of this thesis (Chapters 4-7), in order to expand upon these general hypotheses.

Figure 1.1 Overview of hypotheses that will be tested in this thesis.



Four hypotheses will be tested to investigate the rate of tree felling activity in the first three years of beaver colonisation, and the fate of trees felled by beavers.

Five hypotheses will be tested to investigate aspects of willow and aspen regrowth following felling by beavers, and the incidence of deer and beaver browsing on such regrowth.

Five hypotheses will be tested to investigate the generic, size and locational preferences of beavers when foraging for food and construction materials.

Two hypotheses will be tested to investigate the effects of tree-felling and selective grazing by beavers on the ground flora and ground invertebrate communities.

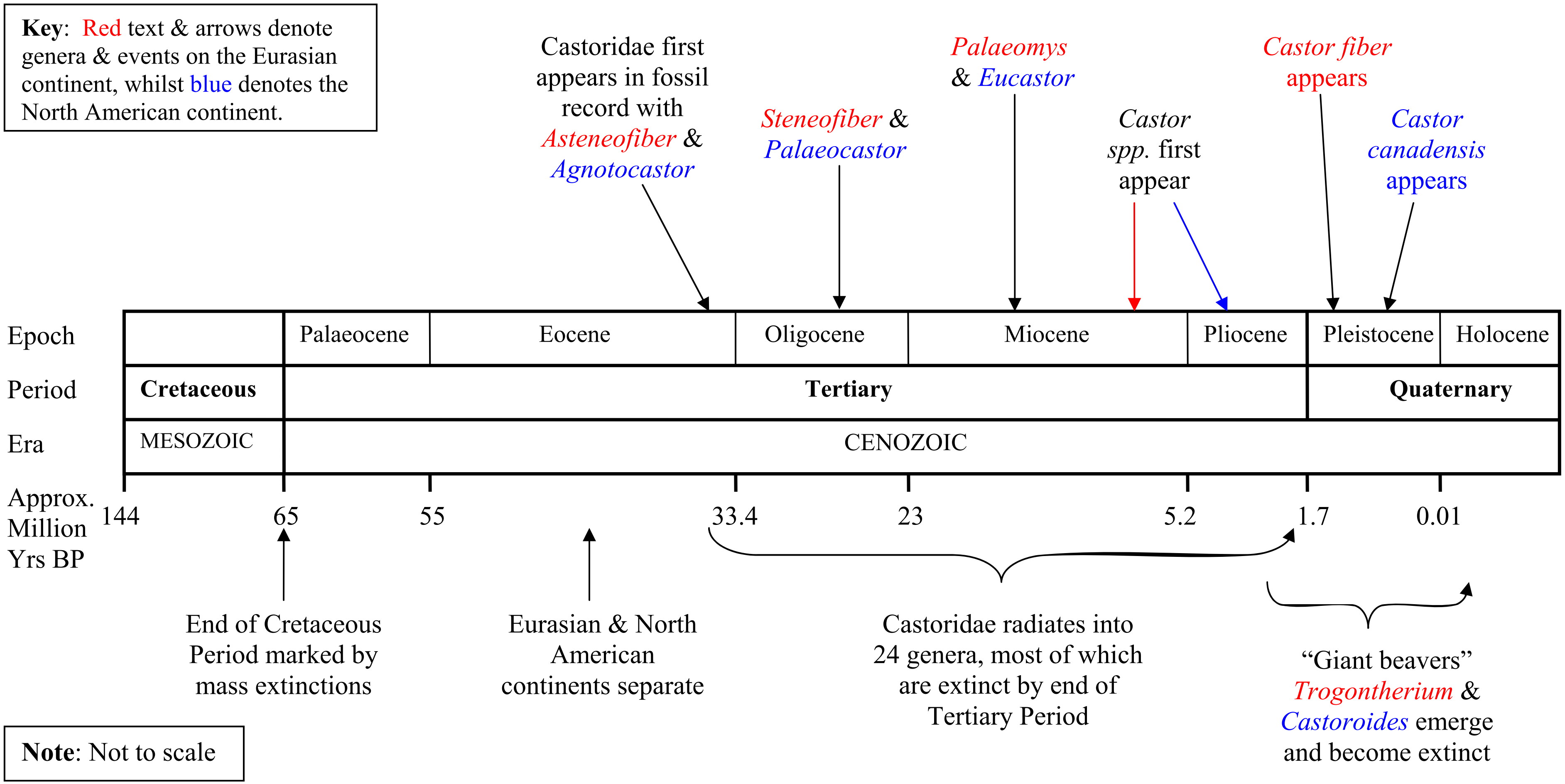
Two hypotheses will be tested to investigate the effects of selective grazing of macrophytes by beavers, and of beaver generated woody debris on aquatic flora and macroinvertebrate communities.

1.4 Beavers and the fossil record

It is not until the latter stages of the Eocene epoch (approximately 35 million years before present) that the beaver family (Castoridae) appears in the fossil record, with remains of *Agnotocastor galushai* being discovered in North America (Novak, 1987 *op. cit.* Emry, 1972; Kitchener, 2001) and almost simultaneously in Belgium with the genus *Asteneofiber* (Hugueney & Escuillié, 1995). Between this time and the beginning of the Pleistocene Period (approximately 2 million years BP), the Castoridae had radiated into 24 separate genera, most of which were extinct by end of the Tertiary, and had colonised Eurasia with the genus *Propalaeocastor* (Hugueney & Escuillié, 1995; Wu *et al.*, 2004). Some of these diverse genera were notable for their large body sizes, with *Castoroides* and *Trogontherium* representing giant beavers from the New World and Old World respectively. It was long believed that the largest of these extinct beavers – *Castoroides ohioensis* – reached sizes similar to modern black bears (*Ursus americanus* Pallas), but recently a more accurate estimate of 60 - 100 kg body mass (Reynolds, 2002) has become widely accepted (*cf. Castor fiber* which generally weighs 11 - 27 kg). Figure 1.2 shows a simplified evolutionary history of the beavers.

Perhaps most significantly however, the genus *Castor* emerged in the late Miocene (approximately 10 million years BP) in Germany, and is the sole surviving beaver genus today. This genus later appeared in North America (*c.* 4 million years BP), possibly after crossing the North Pacific land bridge (Müller-Schwarze & Sun, 2003). Modern representatives of the beaver family fall into two distinct species – the North American beaver (*Castor canadensis* Kuhl) and the Eurasian beaver (*C. fiber*). Both species are relatively young with *C. fiber* first appearing in Europe between 1 and 2 million years ago, and *C. canadensis* appearing even more recently in North America around 1

Figure 1.2 Simplified evolutionary history of the beaver.



million years ago (Novak, 1987 *op. cit.* Stirton, 1935). Although the majority of findings concerning both the ancestry and distribution of the Castoridae are palaeontological, other evidence also exists. For example, the remains of a beaver dam in sediment deposits in Finland provided information on the chronology and presence of *C. fiber* (Hirvas & Niemelä, 1995). Further details of the ancestry and fossil record of the beaver can be found in several reviews (*e.g.* Pilleri, 1983; Novak, 1987; Kitchener, 2001; Korth, 2001; Müller-Schwarze & Sun, 2003).

In terms of geographical range the two modern beaver species cover most of the Northern hemisphere. *C. canadensis* ranges from northern Canada, through the USA and into northern Mexico, whilst the Eurasian beaver has a similarly large range, extending throughout Europe into Mongolia and China, and from within the Arctic Circle to as far south as Bulgaria and northern Spain. Whilst *C. fiber* has never colonised Ireland, it was already resident in mainland Britain before the landmass separation from continental Europe.

Whilst it is generally accepted that the only surviving members of the Castoridae today are *C. fiber* and *C. canadensis*, there are believed to be many subspecies in existence throughout the extensive geographical ranges of these two species. Kitchener (2001) suggests there are eight subspecies of the Eurasian beaver, whilst Hall & Kelson (1959) list 24 subspecies of the North American beaver. Differences in these subspecies are often small, manifesting themselves as subtle variations in fur colour for example, and the existence of some subspecies is apparently uncertain (Kitchener, 2001). The morphological differences between the Eurasian and American beavers are better documented however, with differences in the numbers of chromosomes, as well as differing structures of the skull, hair, and anal glands.

1.5 Population crash: a history of persecution

At around the same time as the Eurasian beaver was expanding its geographical range over Europe and north-east Asia (*c.* 1-2 million years BP), early Hominids were emerging from Africa and colonising the Old World (Pough *et al.*, 2002). As modern man spread across the continent, and later followed the beaver into North America, the close relationship between human populations and beaver numbers began to develop, with devastating effects on both extant species of beaver. It was not until comparatively recently in the Middle Ages, however, that the persecution of the Eurasian beaver became widespread and systematic. From an estimated 60 million Eurasian beavers that once occupied their natural range (Czech & Schwab, 2001), populations had fallen to only *c.* 1,200 animals by the end of the 19th Century (Halley & Rosell, 2001).

The main reason for the population crash of the Eurasian beaver was hunting. Although beaver fur has been used for hats and clothing for thousands of years, it was the demands of fashion-conscious Europeans in the Middle Ages that led to the accelerated demand for beaver pelts. The thick, warm fur, and the waterproof felt that was manufactured from it, led to the huge popularity of beaver hats throughout Europe, with this fashion persisting for over 400 years (Kitchener, 2001). The widespread hunting of beavers inevitably led to localised extinctions, and by the end of the 16th Century *C. fiber* had been extirpated from Britain and much of Belgium and Denmark, with the populations in Iberia, Italy, western France and most of Finland following suit over the next hundred years. This steady decline continued until the beginning of the 20th Century when the species was at the brink of extinction. At this point only *c.* 1,200 animals survived in 8 scattered populations in Germany, France, southern Norway, Russia, Belarus, Ukraine, Mongolia and China, with approximately 350 beavers living in Western Europe (Halley & Rosell, 2003).

As *C. fiber* became increasingly scarce and the pelts became more difficult and expensive to obtain, the focus shifted to the New World. The largest and most successful exporter of pelts to Europe – the Hudson's Bay Company – traded in beaver fur for over 200 years, selling 3 million pelts in just 24 years from 1853 (Newman, 1987). Indeed the pursuit of beavers by trappers, led to the rapid exploration and settlement of the hostile northern wilderness of North America. The role of the beaver fur trade in the human colonisation of Canada cannot be underestimated. As one author states "the hunt for beaver became the quest for a nation" (Newman, 1987), and today the beaver is honoured as Canada's national animal. However, this once abundant animal had been completely eradicated from many parts of the United States and Canada by the early 1900s. For example, it was estimated that several million beavers lived within the Adirondack wilderness of New York State prior to the settlement of Europeans (*c.* AD 1500) (Müller-Schwarze & Sun, 2003 *op. cit.* Radford, 1907), but by 1900 this figure had fallen to just 15 individuals (Müller-Schwarze & Sun, 2003). A similar decline was in evidence throughout North America, with an estimated population of 10 million animals in Canada alone in 1670, having been reduced so dramatically as to threaten the survival of the species by the beginning of the 20th Century (Johnson & Chance, 1974; Newman, 1987; Novak, 1987 *op. cit.* Taylor, 1985).

Although the fur trade was the primary reason for the persecution of both beaver species, other factors contributed to the population crashes observed on both sides of the Atlantic Ocean. As well as being prized for their pelt, beavers were also hunted for food. This pressure was further exacerbated by the scaly tail of a beaver being designated as fish rather than meat, and hence a food permitted for consumption by Roman Catholics and Orthodox Christians on Fridays and during Lent (Mukerjee, 1994).

Another reason for the hunting of beavers was to obtain a substance known as castoreum. Plant secondary compounds ingested by beavers are concentrated and secreted by the castor sacs to produce castoreum, which together with a substance produced by the anal glands is used as a form of communication and territoriality by scent marking (Rosell & Nolet, 1997). However, many human civilisations have used castoreum throughout history for a wide variety of reasons, and indeed still continue to do so. Mertin (2003) describes castoreum as having been used as a base for perfumes, as an aphrodisiac and as an ingredient of cigarettes and fumigating candles, whilst Medieval beekeepers used it to increase honey production and Lapplanders added it to snuff (Pilleri, 1984). The most common usage of castoreum however, has been for its perceived medical properties. One of the constituents of castoreum is salicylic acid, which is present in the beaver's diet in willow bark, and is the active ingredient of aspirin. This could explain the use of castoreum as a panacea for a range of maladies up to the 17th Century, whilst in the Roman Empire it was used to induce abortions (Müller-Schwarze & Sun, 2003). Historically, it was wrongly believed that the testicles of beavers secreted castoreum (Kitchener, 2001), which may explain why they were imported at great expense between the 10th and 19th Centuries into the Middle East for traditional healing of many medical complaints (Lev, 2003). Even today in Israel and Jordan, the testicles of the Eurasian beaver are used in an effort to enhance sexual libido (Lev, 2003).

A secondary factor that surely influenced the population decline of both *C. fiber* and *C. canadensis* is that of habitat destruction. As human populations increased both in Europe and North America, and as these civilisations became more technologically advanced, the encroachment of mankind into habitat occupied by beavers became increasingly important. During the Neolithic (*c.* 4,000 years B.C.), woodland clearance became common as humans sought land for settlement and cultivation in northern Europe (*e.g.* Schmidtchen & Bork, 2003), and more recently since the 19th Century the practice of draining wetlands to improve agricultural land also destroyed beaver habitat. However, as both the Eurasian and North American beavers easily adapt to changing environmental conditions, habitat destruction was of secondary importance to hunting in the near-extinction of the beavers (Kitchener, 2001).

1.6 The return of the beaver

1.6.1 The return of the Eurasian beaver

In the 19th and 20th Centuries the Eurasian beaver had begun to recover from the brink of extinction, in terms of both population size and distribution. Norway was first to protect the beaver in 1845, and by 1922 the remaining five European countries with remnant beaver populations had also introduced hunting bans. Only the remnant far-eastern population in Mongolia / China has failed to ever be granted legal protection. The introduction of these hunting bans eased the pressure on the small number of surviving animals, and by the late 20th Century all the protected remnant populations had increased considerably. For example, the Rhône population in France had increased from an estimated 30 individuals (Nolet & Rosell, 1998 *op. cit.* Richard, 1985) to around 5,000 in 1995 (Macdonald *et al.*, 1995), whilst the German Elbe population had increased from 200 (Nolet & Rosell, 1998 *op. cit.* Heidecke, 1986) to an estimated 2,800 in 1991 (Nolet & Rosell, 1998 *op. cit.* Heidecke & Klenner-Fringes, 1992). Legal protection of beavers was also adopted in four other European countries – Sweden, Finland, Poland and Spain – but unfortunately these hunting bans occurred after the extirpation of beavers from these countries.

As hunting pressure was relaxed across Europe, the beaver slowly began to naturally recolonise areas it had been extirpated from, but it was the advent of active conservation schemes that had profound effects on the status of the Eurasian beaver. Since the 1920s the reintroduction of *C. fiber* from these relict populations into other countries within the species natural range, as well as the translocation of animals from populations within different areas of the same country, have been instrumental in the resurgence of the Eurasian beaver. An estimated 157 reintroduction schemes have occurred in western Europe in the last 90 years, together with countless unrecorded schemes in the former Soviet Union (Halley & Rosell, 2003), accelerating the natural spread of the species over its range. Such has been the success of these schemes that some countries to which the beaver has returned have never actively reintroduced the species (*e.g.* Luxembourg, Bosnia-Herzegovina and Slovenia), instead relying on natural recolonisation from reintroduced or translocated populations in neighbouring countries. In Belgium the estimated population of 200-250 animals (Van den Bergh & Manet, 2003) is largely derived from 101 Bavarian beavers unofficially released in numerous "clandestine" reintroductions between 1998 and 2001 (Verbeylen, 2003). From the surviving 8 small remnant populations, the Eurasian beaver has now recolonised 28 countries across its natural range, and increased its population from *c.* 1,200 to an estimated figure of 639,000 – 742,000 in 2003 (Halley & Rosell, 2003). To date, the only countries in which the beaver was once resident but has yet to recolonise are Bulgaria, Italy, England, Scotland and Wales. Indeed in Bavaria, southern Germany, the beavers that were translocated to the area in the 1960s and 1970s have recolonised so successfully, that the population now acts as source of animals for reintroduction schemes, zoos and private collections via so-called "re-extroductions" (Schwab & Schmidbauer, 2001; 2003).

Table 1.1 summarises the resurgence of *Castor fiber* across its geographical range, using data from excellent review papers by Halley & Rosell (2001; 2002; 2003). Further details of the reintroduction schemes undertaken on a country-by-country basis are provided by Macdonald *et al.* (1995) and Halley & Rosell (2002), as well as by numerous authors in the conference proceedings of the 2nd European Beaver

Symposium (Czech & Schwab, 2001) and the 3rd International Beaver Symposium (2003).

Table 1.1 The Resurgence of *Castor fiber* across Eurasia.

Country	**Date of**			**Estimated population (2003)**
	Extinction	**Legal protection**	**Reintroduction / Translocation**	
Austria	1869	-	1970 - 1990	>1,300
Belarus	Remnant	1922	-	24,000
Belgium	1848	-	1998 - 2000	200 - 250
Bosnia-Herzogovina	Unknown	-	-	0[1]
Bulgaria	Unknown	-	Planned	0
Croatia	1857	-	1996 – 1998	180
Czech Republic	17th Century	-	1991 – 1992 1996	500
Denmark	500 B.C.	-	1999	60 - 70
England	11th Century	-	-	0
Estonia	1841	-	1957	11,000
Finland	1868	1868	1935 – 1937 1995	2,000[2]
France	Remnant	1909	1959 – 1995	7,000 – 10,000
Germany	Remnant	1910	1936 – 1940 1966 – 1989 1999 – 2000	8,000 – 10,000
Hungary	1865	-	1991 – 1993 1996 – 2003	>400
Italy	1541	-	Proposed	0
Kazakhstan	Unknown	-	-	1,000
Latvia	1830s	-	1927 – 1952 1975 – 1984	>100,000

Table 1.1 (continued) The resurgence of *Castor fiber* across Eurasia.

Country	**Date of**			**Estimated population (2003)**
	Extinction	**Legal protection**	**Reintroduction / Translocation**	
Lithuania	1938	-	1947 – 1959	50,000 – 70,000
Luxembourg	18th Century	-	2000	1[3]
Mongolia / China	Remnant	-	1959 – 1985	800
Netherlands	1826	-	1988 – 2000	177 – 227
Poland	1844	1923	1943 – 1949 1975 – 1986	18,000 – 23,000
Romania	1824	-	1998 – 1999	>170
Russia	Remnant	1922	1927 – 1933 1934 – 1941 1946 – 1964	232,000 – 300,000
Scotland	16th Century	-	Proposed[4]	0
Serbia	1903	-	2004	30
Slovenia	Unknown	Unknown	1999	<6[5]
Slovakia	1851	-	1995	>500
Spain	17th Century	1981	2003	18
Sweden	1871	1873	1922 – 1939	>100,000
Switzerland	1820	-	1956 – 1977	>350
Ukraine	Remnant	1922	-	6,000
Wales	12th Century	-	-	0

[1] Suspected to have naturally recolonised from Croatia but no data available.

[2] Finland also has an estimated population of 14,000 *Castor canadensis*.

[3] Naturally recolonised from Belgium.

[4] Proposal for a trial reintroduction was rejected in September 2005.

[5] Naturally recolonised from Croatia.

1.6.2 The return of the North American beaver

Prior to European settlement of North America, the population of *Castor canadensis* was estimated at *c.* 60 – 400 million (Baker, 2003 *op. cit.* Seton, 1929), but widespread hunting throughout the 17th, 18th and 19th Centuries led to extinction of the species in some parts of the United States and Canada, with the remaining population greatly reduced in the surviving areas by the start of the 20th Century (*e.g.* Johnson & Chance, 1974; Novak, 1987 *op. cit.* Taylor, 1985). However, as concern grew over the falling populations of the North American beaver and the market for beaver pelts declined (Warren, 1927), beaver numbers began to increase through the 1900s. This recovery occurred through the introduction of regulations limiting the beaver hunting season and the permitted catch methods, operating in conjunction with active conservation schemes similar to those employed in Europe (Baker, 2003). Such translocations of beavers together with hunting restrictions have led to increasing populations throughout North America, except in Mexico where numbers are decreasing (Novak, 1987 *op. cit.* Landin, 1981). Recent estimates of the population of *C. canadensis* are *c.* 6-12 million (Naiman *et al*., 1986; Hadidian, 2003 *op. cit.* Kwon, 1997). A more detailed review of the North American beaver and its changing fortunes through recent centuries is supplied by Novak (1987).

Several projects have translocated the North American beaver outside its natural range into countries in which it is often subsequently classed as an alien species in conflict with the human population. Between 1940 and 1950 for example, 50 beavers were introduced into Tierra del Fuego, Argentina from Canada, but by the 1990s this population had expanded to *c.* 25,000 and hunting had been authorised to control the increasing numbers (Lizzaralde, 1993). *C. canadenis* was also introduced into Europe, with now-extinct wild colonies having once been present in Austria (Sieber, 2001), France (Halley & Rosell, 2002 *op. cit.* Moutou, 1997) and Poland (Halley & Rosell, 2002), and escapes into the wild from private collections in England and Scotland (Kitchener, 2001). Extant introduced populations of the North American beaver exist in Finland (Lahti & Helminen, 1974), northwest Russia (Curry-Lindahl, 1967) and Siberia (Saveljev & Safonov, 1999). Whilst the Russian colonies of *C. canadensis* are generally very small (Saveljev & Safonov, 1999), the species is extremely common in Finland and is predominant over the Eurasian beaver. A recent Finnish survey estimated *C. fiber* populations to be *c.* 2,000 compared to an estimated 14,000 North American beavers, with very small numbers having recently crossed over the border into Sweden (Halley & Rosell, 2003).

1.6.3 The road to recovery

Whilst current populations of both species of beaver are considerably lower than the estimated peak numbers prior to human exploitation in North America and Eurasia, the last century has seen a dramatic shift in the beavers fortunes. From near-extinction in Europe *Castor fiber* has recolonised much of its natural range, and this geographical spread and population increase are still continuing today. A similar recovery has been witnessed in the United States and Canada with the North American beaver. This resurgence of the beaver can be attributed to the collapse of the fur trade and legislative protection, operating in conjunction with widespread reintroduction and translocation schemes and the adaptability and resilience of the animal itself.

1.7 The beaver in Britain

The evidence for the presence of beavers in Britain has been extensively analysed and falls into a number of categories including palaeontological and archaeological remains, and historical documentary evidence. Palaeontological evidence for the former presence of the Eurasian beaver in Britain is provided by 55 sites in which skeletal remains have been found, predominantly in England (Aybes & Yalden, 1995) with findings of beaver gnawed wood and felled tree stumps also having been recorded (Wells *et al.*, 2000). Furthermore, several archaeological sites in England and south Wales have produced the remains of human structures that have employed such beaver-cut wood, such as the Star Carr platform in Yorkshire (Coles & Orme, 1983). Coles (1992) also describes archaeological evidence of possible beaver canals, lodges, food caches and dams. The vast majority of the palaeonotological and archaeological evidence have been discovered in England, however, with few sites yet discovered in either Wales or Scotland.

Beaver bones have been discovered in only three sites in Scotland since the 18th Century, in Perthshire, Berwickshire and Roxburghshire (Kitchener & Conroy, 1996), as well as beaver-cut wood in Berwickshire (Conroy & Kitchener, 1994). All of this fossil evidence survives today in various museum collections. Further palaeontological evidence that survives only as written records have been discovered in other Scottish areas (Dumfriesshire, Caithness, Sutherland and Rossshire), as reviewed by Conroy & Kitchener (1994). Archaeological remains of beavers have been discovered at five Scottish sites, either in caves or middens (rubbish tips), in Ayrshire, Morayshire and Edinburgh (Kitchener & Conroy, 1997). The relative scarcity of fossil and archaeological remains of beavers in Scotland compared to England however, should not be regarded as indicative of the population sizes of beavers when they were extant in Britain. Whilst the limestone areas which provide ideal conditions for the preservation of bone are common in England, such geology is rare in Scotland where widespread acidic soils lead to rapid demineralisation of bone remains. The majority of the palaeontological evidence found in Scotland has been at the interface of acidic bogs and calcium-rich marl deposits, which allow the most robust bone structures (usually skulls) to survive (Kitchener & Conroy, 1996). It is also true that far fewer excavations have been undertaken in suitable areas of Scotland when compared to England (Conroy & Kitchener, 1994).

Less convincing archaeological evidence are the so-called "otter and beaver traps" excavated in many European countries, including Wales and Ireland (Munro, 1891; Munro & Gillespie, 1919). The exact purpose of these devices was not known by the authors, and as well as being thought to be traps for beavers, otters and fish, other suggested uses included a cheese-press, a peat mould, a pump and even a musical instrument! Given the uncertainty surrounding these devices, together with the fact that Ireland has never been colonised by beavers, such remains have been discounted as evidence of the presence of beavers in Britain.

Palaeontological and archaeological remains therefore provide positive evidence that *C. fiber* once inhabited England, Wales and Scotland and was a natural part of the UK fauna, with radiocarbon dating indicating the approximate age of the Scottish specimens as between 1,500 – 7,700 years old (Kitchener & Bonsall, 1997). However examination of historical archives allows estimation of when the beaver became extinct in Britain, such as in the excellent review by Conroy & Kitchener (1994). Through examination of written records dating back to the 1100s, these authors outline several references to the presence of beavers in Scotland, which are summarised in Table 1.2.

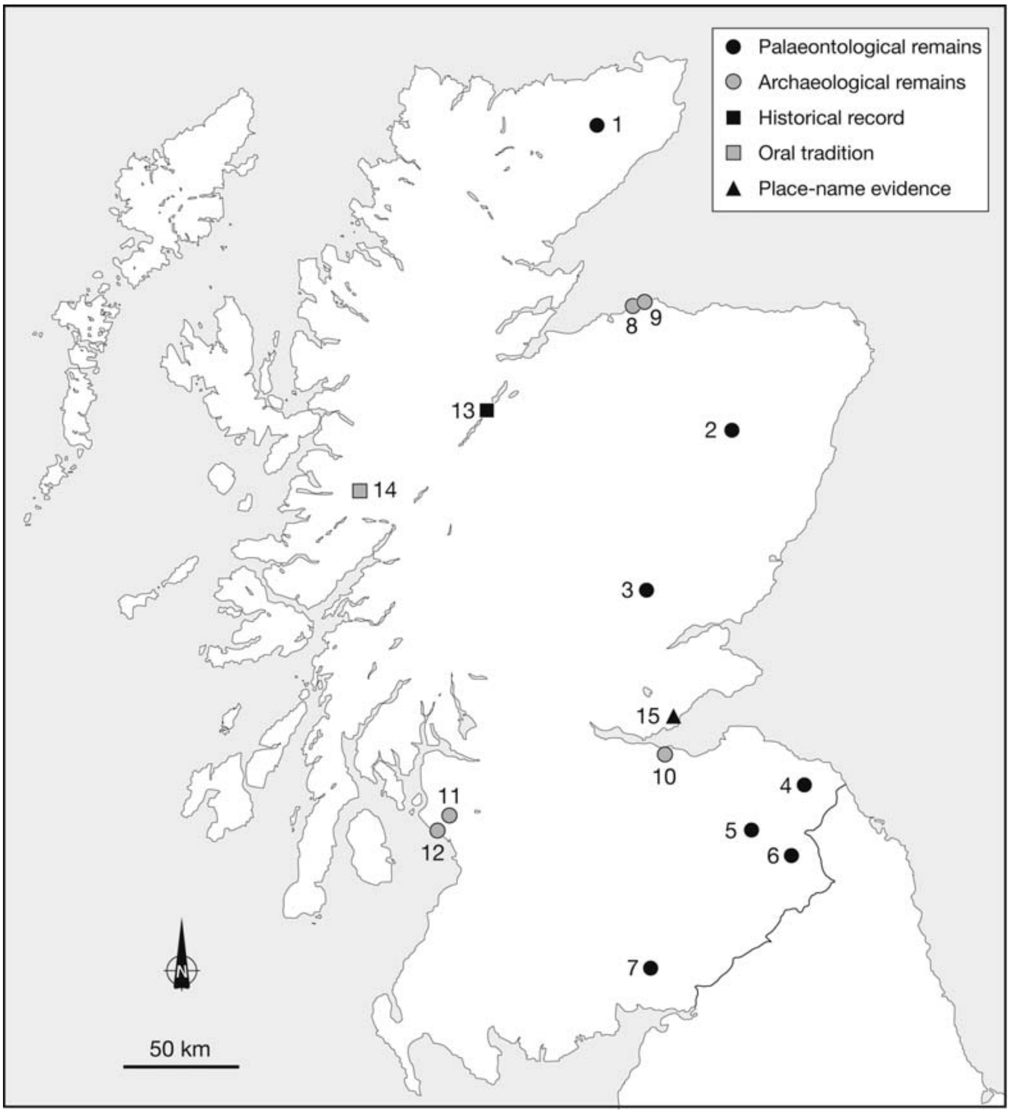
Table 1.2 Documenting the beaver in Scotland.

Date	Source	Author	Details
1124 – 1153	Assisa Regis David de Tolloneis	-	Beaver pelts present in documents listing export duties on furs and pelts.
1188	Itinerarium Cambriae	Sylvester Giraldus de Barri	Travel accounts including reference to the presence of beaver in both Scotland and Wales.
1306 - 1329	The Ayr Manuscript	-	Mention is made of beaver and many other types of pelt, although it is uncertain whether the beaver pelts were imported to Scotland.
1424	-	-	List of tolls on fur-bearing animals was produced during the first parliament of King James I. The beaver is absent from the list.
1482	-	-	List of export duties on fur-bearing animals shipped from Leith, which does not include the beaver.
1527	Scotorum Historiae	Bishop Hector Boece	Describes the existence of beavers on Loch Ness, and also lists the beaver as a source of fur export from Scotland.
1684	Scotia Illustrata	Sir Robert Sibbald	States that it was unknown whether beavers were still indigenous to Scotland at the time of writing.

Analysis of place-names in Britain also discovered 20 places named after beavers, predominantly in low-lying areas of England, with one Scottish exception – Beverkae in Fife (Aybes & Yalden, 1995) which is probably of 19th Century origin and hence not indicative of the presence of beavers (Yalden, 1999). It should be noted however, that the apparent bias in favour of place-names in England is possibly due to the major source being the county-volumes compiled by the English Place-Name Society, and as the authors themselves state "the relative unfamiliarity to us of Celtic or Gaelic place-name elements and animal names also hinders our interpretation of the evidence". Kitchener and Conroy (1996) also describe an "oral tradition" of the beaver in Lochaber surviving until the 19th Century. Figure 1.3 shows the locations of all of the Scottish sites at which physical and documentary evidence of the presence of beavers have been found, as detailed in Conroy & Kitchener (1994), Kitchener & Conroy (1996; 1997) and Aybes & Yalden (1995).

From all of the combined palaeontological, archaeological and documentary evidence, the historical presence of beavers throughout mainland Britain seems certain, but the timing of the species extinction from England, Wales and Scotland is, however, the subject of some uncertainty. It is generally accepted that the beaver was first extirpated from England in the 11th Century, followed by Wales (12th Century), and surviving in Scotland until the 16th Century (*e.g.* Harting, 1880; Halley & Rosell, 2001; 2003).

Figure 1.3 Locations of all Scottish sites at which physical or documentary evidence of the presence of beavers have been found. Data from Conroy & Kitchener (1994), Kitchener & Conroy (1996; 1997) and Aybes & Yalden (1995)



Key

1 Caithness, Sutherland & Rossshire
2 West Aberdeenshire
3 Loch of Marlee, Kinloch, Perthshire (NO141445)
4 Middlestot's Bog, Edrom, Berwickshire (NT815515)
5 West Morrison Bog, Berwickshire (NT604404)
6 Linton Loch, Roxburghshire (NT776263)
7 Lockerbie, Dumfriesshire (NT135815)
8 Hopeman, Drummuir, Morayshire (NJ145699)
9 Sculptor's Cave, Covesea, Morayshire (NJ176709)
10 Edinburgh Castle, Edinburgh (NT251736)
11 Cleaves Cove, Dalry, Ayrshire (NS290495)
12 Ardrossan, Ayrshire (NS239422)
13 Loch Ness area
14 Lochaber area
15 Beverkae, Fife (NT2790)

1.8 The reintroduction of the beaver to Britain

The natural range of the Eurasian beaver has therefore been shown to include mainland Britain. Although the Eurasian beaver has staged a dramatic recovery from the threat of extinction throughout much of mainland Europe in the last century, Britain currently remains one of few areas yet to be recolonised, together with Bulgaria and Italy. Whilst these latter two could potentially rely on natural recolonisation from neighbouring countries, consideration of reintroduction schemes is underway in both countries (Halley & Rosell, 2003). The British Isles, however, can only be recolonised by beavers if the animal is actively reintroduced.

Since the Victorian era, Britain has had a long tradition of introducing alien or exotic species to these shores, often with such success that the animals or plants soon reach pest status, having detrimental effects on native species and the landscape. Lever (1979; 1980) details some 19 naturalised alien mammal species present in the UK, of which at least 11 have reached pest status to some degree, such as the American mink (*Mustela vison* Schreber), grey squirrel, rabbit and roe deer. Indeed, in recent history the coypu (*Myocastor coypus* Molina) became naturalised in the British countryside after escaping from fur farms in East Anglia and southern England, causing such ecological problems that its systematic eradication from the wild had to be conducted over many years (Norris, 1967; Lever, 1979).

Within the last 140 years however, beavers have been released into the British countryside. In Scotland, for example, the Marquis of Bute released four beavers into a large enclosure on the island of Bute in 1874, followed by a further seven in 1875 (Black, 1880 reprinted in Gibson, 1980; Harting, 1880). All of the Bute beavers are believed to have died by 1890, but some doubts exist as to which species of beaver these animals were. One source claims that a pair of both *C. fiber* and *C. canadensis* were originally released (Lever, 1985), but recent sources suggest that all animals released were North American beavers (Conroy & Kitchener, 1994; Kitchener & Conroy, 1996), whilst one claims to have documentary evidence that the animals were Scandinavian *C. fiber* (Kitchener & Conroy, 1996 *op. cit.* J. Gibson *pers. comm.*). Other sources make no mention at all of the species type released (Black, 1880 reprinted in Gibson, 1980; Harting, 1880). As the animals were confined to an enclosure, and never established a wild population, the arguments are largely moot, and the incident cannot be truly described as either an alien introduction or a native reintroduction. Other incidents are clearly failed attempted introductions of the North American beaver, including releases to Inveraray (Gibson, 1976), Suffolk (Harting, 1880) and Sussex (Conroy & Kitchener, 1994). Kitchener & Conroy (1996) also reported unconfirmed anecdotal evidence of beavers being present on at least two sites in Morayshire in the early 1900s.

Following the lessons that have been learnt from the somewhat carefree introduction of alien species by the Victorians, Britain now adopts very rigorous planning and consideration procedures before allowing species translocations to take place. Generally speaking, the introduction of alien species is avoided nowadays, and reintroduction of once-native species is very carefully regulated. Yalden (1986) considered the potential for reintroducing extinct British mammals – a list that includes the brown bear (*Ursus arctos* L.), wolf (*Canis lupus* L.), wild boar (*Sus scrofa* L.), moose (*Alces alces* L.) and lynx (*Lynx lynx* L.) as well as the Eurasian beaver – and to date, only the boar is present in the wild in the UK through escapes from specialist farms, which is testament to the cautious approach adopted today. The reintroduction of bird species has been more successful however, with the osprey (*Pandion haliaetus* L.), white-tailed eagle (*Haliaeetus albicilla* L.) and great bustard (*Otis tarda* L.) all returning to Britain in recent years through reintroduction schemes, and the status of the red kite (*Milvus milvus* L.) having been greatly improved by the importation of continental birds (Cocker & Mabey, 2005).

Despite the cautious approach adopted by the UK, there are legal requirements that Britain must adhere to in relation to species reintroductions. Article 22 of the European Commission's "Habitats Directive" (Council Directive 92/43/EEC on the conservation of natural habitats and wild fauna and flora) states that Member States shall "study the desirability of reintroducing species in Annex IV that are native to their territory where this might contribute to their conservation". As a signatory of the Habitats Directive, Britain must therefore consider the reintroduction of the Eurasian beaver and other extinct, formerly-native animals listed on Annex IV, such as those listed by Yalden (1986). Article 22 stipulates that any reintroduction must include an investigation that "(takes) into account experience in other Member States or elsewhere……that such reintroduction contributes effectively to re-establishing these species at a favourable conservation status and that it takes place only after proper consultation of the public concerned". This legislation does not commit the Member States to actually reintroducing species however, and only requires an investigation of the desirability of doing so.

As well as these legal requirements that must be satisfied, Britain has adopted and adheres to the "good-practice" guidelines published by the World Conservation Union (*e.g.* IUCN, 1987; 1998). Stanley-Price (1991) provides a thorough review of the IUCN criteria that should be satisfied in relation to mammal reintroduction schemes. These criteria include the assessment of the suitability and desirability of reintroducing the species, consideration of the potential socio-economic and ecological impacts of the reintroduction, public consultation during the planning phase, and extensive post-project appraisal measures should the reintroduction occur. The following sections will briefly describe the pertinent stages and processes necessary for the potential reintroduction of the beaver to the UK, with particular focus on the recent proposed trial reintroduction scheme to Scotland. Several excellent reviews exist in which these stages are considered in full detail (*e.g*. Macdonald *et al.*, 1995; Scottish Natural Heritage, 1998; Macdonald & Tattersall, 1999; Gaywood, 2001; 2005). Figure 1.4 is a simplification of the stages and processes involved in such a reintroduction.

1.8.1 The feasibility of reintroducing the beaver to Scotland

After establishing that the Eurasian beaver was once a native species in Scotland, and identifying that the causes of its extinction are no longer a threat to its survival in the UK, the next stage is to investigate the feasibility of reintroducing the animal into the modern Scottish landscape. An evaluation of the following issues is required:

- **What relict population is genetically most similar to the animals extirpated from the UK?**

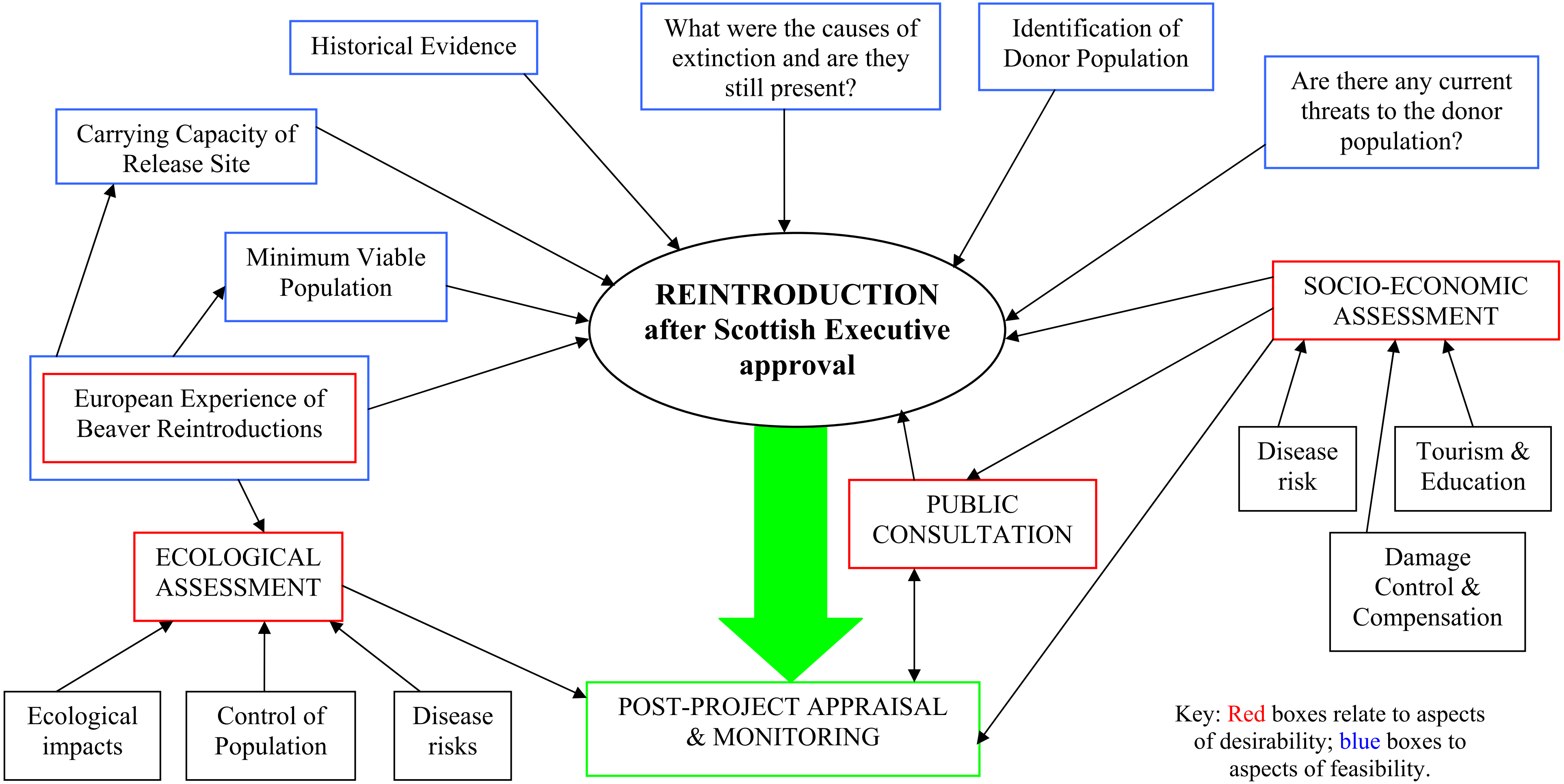
The eight relict populations of the Eurasian beaver were traditionally thought to represent eight genetically different subspecies of *C. fiber*, although the existence of some of these has been thought to be suspect (*e.g*. Kitchener, 2001) and the number of actual subspecies has attracted considerable debate.

Table 1.3 The remnant subspecies of *C. fiber* and their geographical strongholds.

Location of remnant population	**"Traditional" subspecies**	**"Modern" subspecies following genetic analyses**
Southern Norway	*C. fiber fiber*	*C. fiber fiber*
River Elbe, Germany	*C. fiber albicus*	
River Rhône, France	*C. fiber galliae*	
Belarus	*C. fiber belarusicus*	*C. fiber vistulanus*
Ukraine	*C. fiber osteuropaeus*	
Northwest Russia	*C. fiber pohlei*	
Southern Central Russia	*C. fiber tuvinicus*	
Mongolia	*C. fiber biruli*	

Table 1.3 lists these eight "traditional" remnant subspecies of *C. fiber* with their geographical strongholds, together with those suggested by recent genetic analyses of these metapopulations. For example, Macdonald *et al.* (1995) suggest four, differing from the theories of Heidecke (1986; reported in Macdonald *et al.*, 1995), whilst Lavrov (1983) postulated that the populations in eastern and western Europe were completely distinct species. As the subspecies of the extirpated British beaver is unknown, some authors have argued that any subspecies could be justified for reintroduction (Macdonald *et al.*, 1995). In an attempt to rectify this confusion and comply with IUCN guidelines, Macdonald *et al.* (1995) suggested that a reintroduction to Scotland would best employ beavers of Norwegian stock (*C. fiber fiber*), whilst a similar proposal in southern England should use French (subspecies *galliae*) or German (subspecies *albicus*) beavers. Similarly, the proposed trial reintroduction of beavers to Scotland in

Figure 1.4 A simplification of the key stages and processes involved in a potential Scottish reintroduction of beavers.



Key: Red boxes relate to aspects of desirability; blue boxes to aspects of feasibility.

2001, favoured the Norwegian beaver as donor animal following morphometric skull analysis (Gaywood, 2005 *op. cit.* Kitchener & Lynch, 2000). However, recent analysis of genetic material from these populations indicates that only two subspecies are justifiable – *Castor fiber fiber* and *Castor fiber vistulanus* (Halley & Rosell, 2003 *op. cit.* J.-F. DuCroz *pers. comm.*), suggesting that the extant beavers in Norway, Germany and France are all the same subspecies (*C. fiber fiber*), and presumably equally suitable for release into Scotland.

- **Would removal of animals from this donor population in any way jeopardise the survival of the donor population?**

Current estimates of beaver population sizes in France, Germany and Norway are *c.* 85,000 animals in total, with the vast majority being in Norway (Halley & Rosell, 2003). Whilst the population in each of these countries is healthy and generally increasing, the high numbers in Norway justify the decision of SNH to select this donor population in preference to those in France and Germany. The effects on such large donor populations of removing the small number of beavers necessary for a reintroduction to Britain, is likely to negligible, and these populations have successfully supplied animals for numerous other European reintroductions.

- **Do suitable habitats for the beaver currently exist in Scotland, and if so what are the locations, sizes and connectivity of these habitats?**

It is first necessary to briefly consider what exactly is "beaver suitable habitat". Beavers are both extremely adaptable animals and capable of physically modifying a habitat to create conditions suited to their needs. The particular ways in which beavers modify habitats in their roles of keystone species and ecosystem engineer will be explored in more detail in Chapter 2. However, despite such plasticity and adaptability, certain general habitat requirements can be identified from observations within Europe; these are discussed in detail in many publications (*e.g.* Macdonald *et al.*, 1995; 1997; Macdonald & Tattersall, 1999; Scottish Natural Heritage, 1998; Parker *et al.*, 2000; Kitchener, 2001). Optimal beaver habitat is generally low-gradient, slow-flowing river systems lined with predominantly broadleaved riparian woodland, with a soft sediment and bank structure. Although the Scottish landscape has undoubtedly changed since the last beavers roamed the countryside, potentially suitable habitat for beavers does still exist. Indeed within Britain, Scotland is viewed by some authors as having the greatest amount of suitable, available land for a beaver reintroduction, due to the comparative abundance of remote, isolated areas which have been comparatively little affected by humans (Macdonald *et al.*, 1995).

Several studies have attempted to identify those areas within Scotland that would provide the best habitat for a potential beaver reintroduction. The surveying of all of the rivers and stream networks within Scotland – over 50,000 km in total length (SEPA, 2005) – would be extremely time-consuming and costly. Consequently, the potential of Geographical Information Systems (GIS) using existing cartographic and habitat data in conjunction with aerial photography, was highlighted by Macdonald *et al.* (1995) as a relatively rapid and cost-effective method of identifying sites meeting the habitat requirements of beavers. Using habitat-suitability criteria supplied by SNH and the Institute of Terrestrial Ecology (ITE), Webb *et al.* (1997) analysed all suitable river networks in mainland Scotland outside the industrialised and heavily populated central belt. Of the 13 river systems analysed, five contained good amounts of suitable habitat, and lie predominantly within the north and central areas of Scotland (Ness, Tay, Spey, Dee / Don and Lomond river systems). Furthermore, the authors suggested that the clumped distribution of these systems would not hinder dispersal of beavers from one system to another. Conversely, the northern and western Highlands, the Tweed, and the Buchan area in the northeast of Scotland offered little suitable habitat for beavers.

A different approach to assessing the habitat potential present in Scotland has also been adopted, involving both qualitative (Parker *et al.*, 2000) and semi-quantitative (Macdonald *et al.*, 1997; 2000) site surveys that specifically targeted "good" beaver habitat, as selected by SNH. At each site, assessments of the vegetation, topographical and hydrological conditions were made, as well as gathering the opinions of local experts on these matters. Whilst Macdonald *et al.* (1997; 2000) did not reveal the locations of the assessed sites, Loch Coillie-Bharr in the Knapdale area of Argyll (see Figure 1.3 on page 25) was identified as the best of the sites assessed by Parker *et al.* (2000).

- **Assuming suitable habitat exists, is a reintroduction of beavers to Scotland likely to succeed?**

As well as the identification of suitable sites, and assessment of their connectivity, the carrying capacity also needs to be considered together with the estimated minimum viable population (MVP) sizes necessary for any potential reintroduction to succeed. No consensus on the MVP for a beaver reintroduction exists, although in general terms larger populations of a species are more capable of surviving adverse environmental conditions, disease and genetic drift than small populations (Caughley, 1994). The carrying capacity of any habitat will also depend upon the size and quality of the habitat, not simply upon an assessment of whether it is suitable or unsuitable for colonisation. For example, Macdonald & Tattersall (1999) cite estimates of river length from 6 - 50 km as being required for a viable population of beavers.

Whilst accepting the inherent uncertainty involved in the assessment of both MVP and carrying capacity of suitable habitat, simulation modelling approaches based on Population Viability Analysis (PVA) have been used to predict the success of a reintroduction under different conditions (Boyce, 1992). For example, in the Netherlands the viability of a reintroduced population was simulated using a generic computer software package (VORTEX) in a single area of beaver habitat with an estimated carrying capacity of 190 beavers (Nolet & Baveco, 1996). The natality rates of the reintroduced beavers were lower than in the parent population in Germany, and the model predicted that if the low birth rates were a function of poor habitat quality and hence a permanent feature of the reintroduction, the probability of success was low. However, if the low birth rates were merely an artefact of the initial population, and not of their offspring, the viability of the reintroduced animals was good. Subsequent analysis of the established reintroduced beaver population indicated greatly increased natality, which suggested that the long-term viability of the population had improved (Nolet *et al.*, 2005). On average, the life span of a Eurasian beaver is 7 – 8 years (Kitchener, 2001).

An application of VORTEX to produce a PVA for beavers in Scotland was based on a single habitat with a carrying capacity of 400 animals, using a reintroduced population of 5 – 50 beavers (Macdonald *et al.*, 1995). From these simulations it was concluded that whilst a population derived from an initial 5 pairs had a 40% chance of survival over 100 years, this figure increased to 80% with an initial population of 20 - 50 pairs. It was also found that supplementing even small initial populations regularly over the first 20 years of colonisation led to greatly increased survival rates. Similar simulations using VORTEX were produced by other studies (Rushton *et al.*, 2000; South *et al.*, 2000), based on the nine unspecified sites in Macdonald *et al.* (1997). These simulations, involving an initial population of 20 beavers, concluded that a reintroduction to Scotland would be likely to succeed only if the natality rates were higher than those initially observed in the Netherlands.

These modelling approaches and qualitative habitat assessments concluded that there was a good chance that a viable population of beavers could survive in the long-term in Scotland. The qualitative assessment of a small number of sites by Parker *et al.* (2000) suggested that viable populations of beavers could be supported in Scotland, but that the colonies might be fragmented. Based on the simulation models, estimates of the total population of beavers that Scotland could potentially support range from 200 – 1,000 individuals (Webb *et al.*, 1997) to 180 – 390 families (*c.* 900 - 1,950 animals) (Macdonald *et al.*, 2000; Rushton *et al.*, 2002). Each of the nine potential release sites analysed by Macdonald *et al.* (1997) were considered likely to support less than 11 beaver families each (*c.* 40 – 60 animals). Furthermore, 94 suitable sites for beaver colonisation were identified within Scotland, and connectivity between them was determined to be sufficient so as not to impede species dispersal (Macdonald *et al.*, 1997; Webb *et al.*, 1997).

- **Where should a reintroduced Scottish population of beavers be released?**

After deciding on a suitable donor population, and considering the habitat assessments and population modelling that had been commissioned to investigate the feasibility and potential success of reintroducing beavers to Scotland, a specific site had to be selected for any proposed reintroduction. Subsequently, the Knapdale site (as qualitatively surveyed by Parker *et al.* (2000)) was selected as the release area for the proposed trial reintroduction of 2002 (M. Gaywood *pers. comm.*). Once the site had been selected, a more constrained simulation model of population dynamics could be developed, specifically focussing on the habitat conditions present at Knapdale. Previous models contained assumptions that whilst being valid for a reintroduction of beavers to the whole Scottish landscape, were not valid for the temporally and spatially constrained reintroduction scheme that was planned at Knapdale. For example, the model of Rushton *et al.* (2000) underestimated available habitat if it was fragmented, whilst South *et al.* (2000) employed a large spatial scale in the habitat analysis, making the predictions inaccurate when applied to the small, fragmented Knapdale site (Rushton *et al.*, 2002). Both of these models were designed to investigate the dispersal of beavers from a release site, whereas in Knapdale dispersal is assumed to be irrelevant as the beavers are likely to be restricted to the Knapdale area by habitat and landscape features. In response to this, a VORTEX model specific to the Knapdale habitat and using assumptions valid for the potential reintroduction to Knapdale, was commissioned by SNH (Rushton *et al.*, 2002).

The Knapdale model predicted that the possibility of the extinction of 12 reintroduced beavers over a 5 year scheme, was very low. Using published data on pertinent aspects of beaver biology (*e.g.* reproductive rate, mortality, litter size) three scenarios were envisioned – high, medium and low. The "high" scenario, for example, assumed high natality, high litter size and low mortality, whilst the "low" scenario assumed the opposite to be true. The results were that under optimum conditions (high scenario) the initial population of 12 beavers would increase to 50 beavers, compared to populations of 26 and 14 in the medium and low scenarios respectively (Rushton *et al.*, 2002). A second approach by the same authors using a “home-range formation model” instead of VORTEX, predicted that the population would increase to as high as 64 beavers over 5 years in optimum conditions, with a mean value over all the simulations of 28 beavers. Both types of model used by Rushton *et al.* (2002) concluded that the reintroduction of beavers to Knapdale should increase in population size in all but a few, worst-case scenarios.

With the feasibility of a reintroduction to Knapdale being supported by ecological modelling data, attention shifted to the *desirability* of such a scheme. As well as considering ecological factors, many socio-economic issues that would impact upon the desirability of a reintroduction were also considered when assessing the merits of a potential reintroduction of beavers to Knapdale. These issues are summarised in Figure 1.4 and detailed in the following section.

1.8.2 The desirability of reintroducing the beaver to Scotland

- **What are the likely ecological effects of a release of beavers to Knapdale?**

Due to the ability of beavers to modify their habitat by through feeding behaviour, they have been termed “keystone species” (*e.g.* Kitchener, 2001). Furthermore, the physical habitat modifications caused by other aspects of beaver behaviour, such as dam building, have led to the term “ecosystem engineer” also being applied to beavers (*e.g.* Jones *et al.*, 1994). Acting in these roles of keystone species and ecosystem engineer, beavers therefore have a great capacity to modify the riparian and stream environment that they occupy, with concommitant effects on the flora and fauna that are also present. As part of the planning work prior to submitting an application for reintroduction of beavers to Knapdale, SNH commissioned several highly detailed reports, exploring and reviewing many aspects of the ecological effects of beavers. Based on both a wide range of published literature and the expertise of many international beaver researchers, these reviews collated the abundant evidence from numerous reintroduction and translocation schemes that had taken place in both Europe and North America (Scottish Natural Heritage, 1998). These reports included reviews of potential impacts on fish populations and ecology (Collen, 1997), woodland habitats (Reynolds, 2000) and the effects of beaver dams on local hydrology (Gurnell, 1997). These reviews have a broad scope and should be consulted for more detailed examination of the issues, both of the perceived positive and negative effects, than can be covered in this chapter.

The ability of beavers to fell mature trees provides scope for significant habitat modification. As obligate herbivores, trees are felled for food, with the beaver stripping and eating the bark, cambium and leaves, but trees are also felled as a source of materials for constructing lodges and dams. Despite being generalist feeders, beavers do have distinct preferences for certain tree species and sizes, preferentially selecting these trees when available (*e.g.* Simonsen, 1973; Łapiński & Staliński, 2001). For example, aspen (*Populus tremula* L.) is a highly preferred species (Simonsen, 1973; Lahti & Helminen, 1974), whilst conifers are generally avoided (Reynolds, 2000). By selectively felling trees in riparian zones, beavers can alter the species and structural diversity within these areas, creating canopy gaps which allow a diverse ground flora to develop (Reynolds, 2000). After felling, the terrestrial woody remains of beaver feeding provide valuable habitat for invertebrates and small mammals, as well as a substrate for fungi and lichen (Humphrey *et al.*, 2002), whilst the increased woody debris in watercourses produced by beavers acts a refuge and food source for macroinvertebrates and fish (Godfrey, 2003). Unsuccessfully felled or snagged trees provide a standing dead wood resource that provides nesting sites and food for many bird species, and roosting sites for bats (Balodis, 1994; Danilov, 1995). In some cases however, beavers fell valuable fruit trees or those of high heritage value (Rouland, 1991), although generally trees can be easily protected from beavers, and only those within short distances of watercourses are likely to be under any threat (*e.g.* Hill, 1982; Novak, 1987).

One of the most obvious ways a beaver can modify the stream environment is by building a dam across the river channel. Such structures and the ponds produced by them have many perceived positive impacts on stream flow and water quality. For example, dams regulate stream flow and reduce the detrimental effects of irregular flows, by storing water during periods of high flow and releasing it slowly during low-flow conditions (Bergstrom, 1985). The ponds also act as sediment sinks reducing the deposition of silt in downstream river reaches, store organic matter and plant nutrients, and reduce the acidity of stream water (Naiman & Melillo, 1984; Smith *et al.*, 1991; Cirmo & Driscoll, 1993). Many heavy metals that are toxic to fish and other wildlife, such as aluminium, are deposited behind beaver dams and converted to less toxic forms (Smith *et al.*, 1991). This water quality improvement is reflected in the capacity of rivers to self-purify, which is reported as being up to ten times greater in the presence of beaver dams and ponds (Scottish Natural Heritage, 1998). However, whilst reduced silt loads in stream channels are generally beneficial to fish, where a dam is built immediately downstream of spawning areas siltation of gravels may be detrimental to fish spawning. The presence of a dam can also present a physical barrier to upstream migration of spawning fish, and downstream migration of young fish (*e.g.* Schlosser, 1995). However, ponds can act as refugia and resting areas for migrating fish, although in some cases the increased decomposition of organic matter in ponds can lead to a decrease in dissolved oxygen levels, which can have negative impacts on fish (Smith *et al*., 1991).

The water impounded by beaver dams and the resultant ponds and raised watertable, leads to the creation of wetlands. The diversity of physical conditions produced by dams creates a mosaic of habitats, which leads to increased diversity of plants, fungi, invertebrates, fish, amphibians, mammals and birds. Furthermore, as well as creating a spatial habitat mosaic, the abandonment of ponds by beavers leads to a temporal succession of wetlands through to "beaver meadows" and eventually scrub and woodland, each with an associated flora and fauna (*e.g*. Wright *et al*., 2002). Standing dead wood can be created by the raised watertable, providing "biodiversity hotspots", although in areas of commercial forestry damage to, and loss of conifers can occur (Danilov, 1995). Localised flooding can also lead to damage to agricultural land, property and roads, causing conflicts with human interests (Lisle, 2003). It is also worth considering, however, that the Eurasian beaver does not always build dams, and such damage could be considered minor in comparison to that caused, for example, by deer, squirrels and rabbits.

The extent to which any of these perceived negative impacts of beaver activity actually occur, and to some extent the perceived benefits too, will depend on the location and extent of the habitat modification. Despite the increasing beaver populations in mainland Europe, the species is not considered to be a pest in any country (Scottish Natural Heritage, 1998). A more detailed review of the effects of feeding and construction activities of beavers reported from many studies in both Europe and North America is presented in Chapter 2.

- **What are the potential socio-economic effects of a beaver reintroduction?**

As well as measurable changes in ecological and physico-chemical parameters following beaver activity, a reintroduction of any animal to an area will have some socio-economic impacts on the local human population. In situations where beaver activity has negatively affected human interests in riparian zones, the consequences can be financially costly as well as of some nuisance value. In many European countries that have reintroduced beavers, frameworks and support mechanisms have been developed to assess any damage caused by "nuisance beavers", and if appropriate financially compensate the affected parties. In the most extreme cases, beavers can be trapped and relocated to more remote areas. For example, in France the beaver population is *c.* 7,000 – 10,000, a large proportion of which are located within the Rhône catchment (Halley & Rosell, 2003). In a seven year period between 1982 and 1989, only 110 incidents of beaver damage were reported to the authorities. The majority of these cases were of damage to fruit trees, although damage to crops, ornamental trees and river banks were also reported, with only 6% of all cases relating to damage occurring over 30 m from the riverbank (Macdonald *et al.*, 1995). The same authors also document around £3,200 of compensation having been paid out in response to beaver damage in the Netherlands over a six-year period from 1988. In Switzerland compensation for beaver damage is small when compared to that paid out for damage by wild boar (*c.* £3,600 annually for beavers compared to £572,000 for boar damage in 1992 alone) (Macdonald *et al.*, 1995). It is also usual for the most conflict between beavers and man to occur during the latter stages of colonisation, when increased populations force beavers to occupy sub-optimal habitat more frequently, rather than during the initial period following reintroduction (Halley & Rosell, 2003).

One economic benefit of beaver reintroductions has been the development of “beaver tourism” and “beaver safaris” (*e.g.* Mertin, 2003). France, Poland, the Netherlands and Austria have found that the influx of people to view beavers produce tangible financial rewards, often into rural economies (Macdonald *et al.*, 1995). In Poland, for example, the revenue generated by “beaver tourism” was greater than the costs associated with beaver damage compensation (Scottish Natural Heritage, 1998). Beaver colonies also offer the opportunity for school-children to study biology and natural history during organised tours and events (Mertin, 2003). Furthermore in some European countries with high populations of beavers such as Lithuania and in Scandinavia, limited hunting quotas provide further revenue for rural hunters and trappers. Indeed, in Lithuania beavers comprise 75% of the annual catch of fur-bearing animals (Macdonald *et al.*, 1995). The potential for increased angling opportunities and associated revenue has been suggested as a further economic benefit of a beaver reintroduction, due to the beneficial effects beaver ponds have to fish stocks (Collen, 1997).

A final socio-economic factor to consider is that of any potential health risks to either humans or livestock as a result of a beaver reintroduction. As wild animals, beavers can carry and transmit a range of diseases including rabies, tularemia and pneumonia (Scottish Natural Heritage, 1998), as well as acting as a vector of waterborne pathogens such as *Giardia, Campylobacter, Cryptosporidium and Salmonella* (Rosell *et al.*, 2001). It is important to note that any animals imported to Britain for release as part of a reintroduction would undergo a period of quarantine, and only healthy disease-free animals would be released. Furthermore *Giardia*, for example, is already present in some Scottish watercourses and is carried by a wide range of native mammal hosts (Halley, 2005; Stewart, 2005). In Norway (the source of any donated animals for a Scottish reintroduction) the examination of between 130 and 250 beavers for these four pathogens yielded no evidence of infection (Rosell *et al.*, 2001). This study suggests that although *Giardia* is present in Norwegian watercourses and that giardiasis is apparently increasing in the human population, beavers are not responsible for transmission of the pathogens into drinking water supplies, and that the alternative name "beaver fever" (*e.g.* Müller-Schwarze & Sun, 2003) is perhaps unwarranted.

- **What are the views of the general public on a proposed beaver reintroduction?**

One of the requirements of the Habitats Directive legislation is that the planning of any potential reintroduction scheme includes "proper consultation of the public concerned", as do the IUCN guidelines. A consultation process was commissioned by SNH, and conducted nationally by Scott Porter Research and Marketing Ltd. (1998). Across Scotland, three sectors of the population were targeted – the "passive public", the "pro-active public" and "key consultees". These groups were asked two questions:

1. Do you support a proposal to restore the European beaver to the wild in Scotland?
2. If so, do you support such a reintroduction beginning during the next three years?

A detailed assessment of responses from the various consultees can be found in the original report (Scott Porter Research and Marketing Ltd., 1998), although Gaywood (2001; 2005) summarises the major findings of the consultation exercise. Firstly the "passive public", representing members of the general public who it was thought would probably not voice their opinions on the subject, provided broad support for the proposal. Of 2,141 responses 63% were positive, with only 12% of the passive public against the proposal.

Secondly, the “pro-active public” (*i.e.* members of the public who would actively voice their opinions if given a means to do so) was overwhelmingly in favour of a reintroduction, with 86% of 1,944 responses being positive, mostly favouring rapid action on the subject. It is interesting however, that support was much lower (13 - 43% of 195 responses) in the pro-active consultees with a declared interest in angling, commercial fishing and agriculture.

A similar pattern was observed in the responses of the “key consultees”, which included organisations and individuals that could have specific interests in the outcome of the proposed reintroduction. Of the 281 key consultees – including academic, agricultural, conservation, fieldsports, angling / fishing, forestry and water management sectors – only 144 responses were received. Again many of those opposed to an introduction were generally in the angling / fishing sector, due to the perceived adverse effects of beavers on fish stocks, whilst conservation, academic, forestry, water management and agricultural sectors were generally pro-reintroduction. It is important to note that of those in favour of the proposal however, some concerns were raised over potential adverse impacts of a beaver reintroduction, which evidently were not allayed by the consultation document that accompanied the questionnaire (Scottish Natural Heritage, 1998).

1.8.3 The proposed trial reintroduction of beavers to Knapdale

Having determined that a beaver reintroduction was feasible, and following public consultation, was generally viewed as desirable, the process moved on to site selection. However, some concerns were raised by the key consultees regarding the potential impacts of a reintroduction, and recommendations for further investigation of the potential impacts were made. For example, one concern was over the potential for the population of released beavers to increase uncontrollably, and how such an occurrence would be managed. The financial cost of a reintroduction and the research and management that would be necessary post-release, was also a source of concern amongst the key consultees. In order to address these perceived areas of uncertainty, a trial reintroduction was planned in which a small population of beavers would be closely monitored for a set time period within a Scottish site.

Specifically, the study would investigate the ecology of the Eurasian beaver in the Scottish environment, and assess the effects on existing land use practices such as forestry and agriculture. After an initial year of preparation in which three to four beaver families would be trapped in Norway and quarantined in the UK, the animals would be released on to a single Scottish site for a monitoring period of five years. After this period, during which the ecological effects of the radio-tracked animals would be closely observed, a further year would follow in which the trial would be assessed, and if deemed successful a full-scale reintroduction to Scotland would be considered. If for any reason the project needed to be terminated during the monitoring phase, an exit strategy was present within the framework of the proposed trial.

As a result of the numerous GIS-based analyses of the Scottish landscape and simulation models of population dynamics (see section 1.8.1) the Knapdale Forest in mid-Argyll was selected as the trial reintroduction site. The Forest Enterprise (FE) site has a number of advantages (Gaywood, 2005):

- The loch and stream network and surrounding broadleaf woodland is ecologically suitable for beavers.
- It offers relatively good natural containment of the beavers.
- Access for field workers is good and visitor facilities already exist.
- The site is a working forest with ongoing woodland management and restoration, providing an insight into the interaction between beavers and forestry practices.
- Local SNH and FE offices are located near to the site.
- There is only one main landowner to liaise with.

Consultation of the local public by SNH in 2000 found wide support and enthusiasm for the project, although concerns about potential adverse effects of the trial were raised by some respondents. Since the selection of the Knapdale site, numerous surveys to provide baseline ecological data have been commissioned by SNH, such as on the hydrology and channel geomorphology (D. Gilvear *pers. comm.*), and terrestrial and aquatic vegetation (Murphy *et al.*, 2002; Armstrong *et al.*, 2004; Brandon-Jones, 2004).

1.8.4 The Scottish Executive and current status of the trial reintroduction

In January 2002, following the development of a framework for the trial reintroduction of beavers to Knapdale – a scheme that had been determined to be both feasible and desirable – a formal application for the trial was made to the Scottish Executive under the requirements of the "Wildlife and Countryside Act 1981". In late 2002, further information was requested for consideration by the Minister for the Environment and Rural Development which was supplied by SNH in early 2005, in their role of proposers of the scheme (Scottish Natural Heritage, 2005). The project remained on hold until a decision was made in September 2005, when the proposal was rejected. The decision was partly based upon the fear that the reintroduction would have adverse effects on the Knapdale forest, part of which is a Special Area of Conservation (JNCC, 2002). As such, any damage caused could be considered a contravention of the EC Habitats Directive – the very law which implemented the requirement for an investigation into reintroducing the beaver to Scotland. The exit strategy included in the proposal which potentially involved the killing of beavers, also caused concern as beavers are a species protected under European law. The full decision statements by the Deputy Minister and a Senior Government Official are available on the website of the Scottish Executive (2005), and are available in Appendices A1 and A2 of this thesis respectively. Since the decision, work has continued on meeting the requirements specified in the Minister's decision (M. Gaywood *pers. comm.*).

1.9 The future for beavers in Britain

Absent from Britain for over 400 years, the reintroduction of the Eurasian beaver has been discussed for over 30 years. In compliance with European law, a trial reintroduction of beavers to Scotland was proposed by SNH in 2002, but rejected by the Scottish Executive in 2005. This decision was made despite numerous successful similar reintroductions that had been implemented across Europe, and was contrary to the widespread support the project had received from a range of public sectors.

Currently Scotland, England and Wales remain as some of the very few European countries not to have reintroduced the beaver to its natural range. Interest in potential beaver reintroductions in England and Wales have been raised, but to date no firm proposals have been made, and Scotland remains at the forefront of the beaver's proposed return to Britain.

Although no wild beavers are currently present in the UK, several small populations exist in fully-enclosed private collections in both England and Scotland. For example, in 2002 several Eurasian beavers were released for study into the Ham Fen Wildlife Reserve, owned by the Kent Wildlife Trust (Campbell & Tattersall, 2003), and in the same year, four beavers were released into a private estate in Bamff, Perthshire (see Figure 1.3 on page 25) (Ramsay, 2002). More recently, in 2005 a small number of beavers were released into the Cotswold Water Park near Gloucester, receiving widespread national media coverage (*e.g.* Pierce, 2005; Mackay, 2005).

The original purpose of this thesis was to monitor the ecological effects of the Knapdale beavers for three years from late-2002. In the absence of these beavers, focus shifted to those beavers captive in large semi-natural enclosures within the aforementioned Perthshire private estate. The ecological effects of the tree-felling and construction activities of these beavers have been investigated, and are discussed in this thesis. It is hoped that the evidence presented by, and the conclusions drawn from, this study of beavers living in the Scottish landscape, will assist in any future decision-making process that may arise in Scotland.

2 Feeding and construction activities of the Eurasian beaver (*Castor fiber* L.)

2.1 Introduction

The aim of this chapter is to review the available literature on the feeding and construction activities of the Eurasian beaver (*Castor fiber* L.). It must also be noted that in some cases research relating to the North American beaver (*Castor canadensis* Kuhl) is covered. This is justified by the very similar behavioural, biological and ecological characteristics that the two species share, as well as there being a large body of information available on the American species, which in some cases is apparently under-reported in the Eurasian beaver. This is especially so in terms of environmental impacts of the beaver (Macdonald *et al*., 1995; Nolet, 1997). The aim of the review is to provide background to the thesis, to provide a summary of our current understanding and to identify gaps in the literature. This thesis will focus on such gaps that are identified in the available literature.

2.2 Biology and ecology of the Eurasian beaver

The beaver is a semi-aquatic mammal, showing numerous physiological and behavioural adaptations to their amphibious lifestyle, and is the most specialised swimmer of all the rodents (Wilsson, 1971). The powerful hind limbs with large webbed feet and characteristic broad, flattened paddle-like tail allow the beaver to swim very efficiently. The nostrils, eyes and ears are situated high on the head, with the eyes being covered by a transparent protective membrane (the nictitating membrane) to facilitate swimming underwater (Novak, 1987 *op. cit.* Lancia & Hodgdon, 1984). The nostrils and ears automatically close when the nose touches water (Warren, 1927), and the tongue and epiglottis effectively block the trachea and allow the mouth to be opened to safely gnaw submerged roots, although swallowing solid food is not possible underwater (Kitchener, 2001). The thick fur present traps a layer of insulating air close to the skin keeping the beaver warm in icy waters (Novak, 1987 *op. cit.* Scholander *et al.*, 1950), whilst the stiff outer guard hairs help to repel water.

Beavers show many physiological responses that are common to diving mammals, allowing them to remain submerged for periods of up to 15 minutes (Hill, 1982 *op. cit.* Irving & Orr, 1935). For example, the very efficient lungs permit huge amounts of air to be exchanged with the bloodstream (Rue, 1964), and whilst diving the blood supply to the brain is increased (Hill, 1982 *op. cit.* Irving, 1937). The beaver is also able to tolerate very high concentrations of carbon dioxide (Rue, 1964), and dramatically reduce its heart rate by as much as 79% (Novak, 1987 *op. cit.* McKean, 1982).

Beavers are social animals living in family groups, usually comprising a monogamous pair of adults, between two to four young of the year (called kits) and often two or three yearlings. Although the maximum number recorded in a single colony is 18 North American beavers (Kitchener, 2001), the averages for both species of beaver are much lower, with 3.8 and 5.2 being documented for *C. fiber* and *C. canadensis* respectively (Rosell & Parker, 1995). It is thought, however, that habitat quality, especially preferred food availability, will determine the size of a colony (Hill, 1982 *op. cit.* Gunson, 1970), with each colony defending its territory against neighbouring beavers.

Both species of beaver act as “keystone” species (*e.g.* Kitchener, 2001). Their activities affect the physical landscape, which in turn affects the flora and fauna that share the habitat with them. Furthermore, they have also been described as ecosystem engineers (*e.g.* Jones *et al.*, 1994) due to the direct physical mechanisms used by beavers to modify the ecosystem, rather than just the trophic effects implied by the term "keystone species" (Begon *et al.*, 1996). These physical effects on the environment include damming of streams, wetland creation and tree-felling, and can sometimes interfere with human uses of the landscape. More detailed accounts of the effects of beavers on the landscape and the associated fauna and flora can be found in many excellent reviews (*e.g.* Naiman *et al.*, 1986; Novak, 1987; Naiman *et al.*, 1988; Nolet, 1997; Collen & Gibson, 2001; Kitchener, 2001).

2.3 Foraging and feeding behaviour of the Eurasian beaver

This review will now focus on the foraging and feeding behaviour of the Eurasian beaver, as these aspects are integral to the roles of keystone species and ecosystem engineer, and are central to the subject of this thesis. Indeed, due to the ability of beavers to fell mature trees and because foraging is confined to a zone surrounding a central place, beavers have great potential to alter forest ecosystems through herbivory (Johnston & Naiman, 1990). Furthermore, browsing by the Eurasian beaver in France has been shown to include economically important species, including many types of fruit trees and vines (Rouland, 1991), whilst feeding on commercial arable and vegetable crops in Norway has also been observed (F. Rosell *pers. comm.*).

2.3.1 Adaptations to herbivory

Both the Eurasian and North American beavers are entirely herbivorous and have been described as being "choosy generalists" (Novak, 1987 *op. cit.* Harper, 1969) with a diet that consists of many species of trees, shrubs, herbs, grasses, forbs and aquatic macrophytes. Indeed, the beavers' diet has been documented as including 80 tree species and 149 other herbaceous and aquatic plants (Kitchener, 2001).

Although it is one of the very few mammals that eats large quantities of tree bark, the digestive system is largely the same as in many other rodents (Currier *et al*., 1960) and the digestive secretions do not contain cellulase enzymes (Nasset, 1953, Kitts *et al*., 1957). There is however evidence to suggest that a commensal microflora exists in the lower gut which shows cellulytic activity (Kitts *et al*., 1957; Currier *et al*., 1960). The lower gut has a very poor ability to absorb nutrients however, and only around 30% of cellulose, the primary nutrient available in vegetation, is absorbed into the bloodstream (Currier *et al*., 1960). In order to extract further energy from woody material the beaver practices coecotrophy, in which the primary faeces produced is reingested and passes through the gut a second time allowing further digestion to occur. It has been noted that the otherwise precocious young (called "kits") do not properly practice coecotrophy until they are a month old and are feeding on a predominantly solid diet (Lancia & Hodgdon, 1983). As kits have not been observed eating other adult beavers faeces however, exactly how young beavers develop the gut microflora necessary to digest cellulose is unknown (Kitchener, 2001).

2.3.2 Woody species selectivity and foraging strategies

Much research has been conducted on the selectivity of woody species of both *C. fiber* and *C. canadensis,* but less so in terms of non-woody species and aquatic macrophytes. The following sections will detail examples of the apparent inherent preferences of beavers for certain woody species, and the ways in which selectivity is shown based on prey size, distance and season, as well as considering interactions between these factors.

2.3.2.1 Prey species preferences

As mentioned earlier, beavers have a very broad diet with a great deal of plant species eaten, including 80 tree species (Kitchener, 2001). Furthermore, Simonsen (1973) has documented some 26 woody species eaten by the Eurasian beaver over a three-year period in southern Norway alone. However although beavers will eat a wide variety of woody material, they do show apparently marked preferences for certain genera and species. For example, it was noted that, although *C. canadensis* in Ohio ate all of nearly twenty woody species available in the study area, preference was for just four tree species - yellow poplar (*Liriodendron tulipifera*), American hornbeam (*Carpinus caroliniana*), and red and sugar maples (*Acer rubrum* and *A. saccharinum*) (Svendsen 1980). Similar results were shown for the same area in an earlier study (Nixon & Ely, 1969).

Similarly the Eurasian beaver also shows apparent feeding preferences. In Poland for example, *C. fiber* fed largely on willow (*Salix spp.*), with common alder (*Alnus glutinosa*) and birch (*Betula spp.*) also well harvested. Other species show only occasional usage, such as Norway maple (*Acer platanoides*), dogwood (*Cornus sanguinea*), lime (*Tilia cordata*) and bird cherry (*Prunus padus*) (Łapiński & Staliński, 2001). Many other European studies have shown preferences for certain woody species too, although the exact species lists do often vary between study areas (*e.g.* Semyonoff, 1957a; 1957b; Simonsen, 1973).

In a review of the literature regarding the feeding habits of the North American beaver, Northcott (1971 *op. cit.* Denny, 1952) stated that “investigators concurred on the general list of plants taken for food by beaver, namely in order of choice – aspen (*viz.*

American aspen *Populus tremuloides* Michx.), willow, cottonwood, alder, maple and ash". Indeed, in Minnesota aspen was the most important browsed species (Aldous, 1938), comprising 99% of the browsed woody material at one pond studied (Johnston & Naiman, 1990). Six years of beaver browsing of a stand previously dominated by aspen, resulted in the proportions of less preferred species such as alder and ash becoming of increasing local importance (Johnston & Naiman, 1990).

In the diet of *C. fiber*, a different species of aspen – the European aspen (*P. tremula*) – is also generally accepted as being preferred over other available tree species (*e.g.* Simonsen, 1973; Lahti & Helminen, 1974; Kitchener, 2001; Batty, 2002). In some cases although more individual trees of other species are cut, the overall volume of aspen eaten is so high that it forms the largest component of all the woody species present in the diet (Gorshkov *et al.*, 1999).

True measures of species preference must take into account availability however, not solely the crude amounts of each species eaten. Jenkins (1979) found that 90% of the trees cut by the North American beaver in Massachusetts were of just six genera – oak (*Quercus alba*, *Q. rubra* and *Q. velutina*), birch (*Betula populifolia* and *B. lutea*), pine (*Pinus strobus* and *P. resinosa*), maple (*Acer rubrum* and *A. saccharum*), witch hazel (*Hamamelis virginiana*) and ironwood (*Carpinus caroliniana*). Electivity indices (Jacobs, 1974) were then applied to these data in order to determine whether the amounts of each species eaten was independent of abundance, and therefore a true measure of preference. Such analysis showed that the beavers were indeed selecting tree species by preference rather than availability, and that some species that only formed a very small part of the diet were highly preferred but scarce. For example, six black cherry trees (*Prunus serotina*) were felled from an available total of just nine trees in the study area. Similarly work on the Eurasian beaver in the Netherlands used electivity indices and demonstrated preference for a number of willow species (Nolet *et al.*, 1994).

Caution must still be exercised when interpreting the preference results from such electivity indices. For example in this Dutch study, common alder (*Alnus glutinosa*) had a positive electivity index, indicating that the species was positively selected, albeit to a considerably lesser degree than some other species. It has been shown in other studies however (*e.g.* Simonsen, 1973) that although the leaves of alder are eaten, the bark is strongly avoided possibly due to the high levels of resin that it contains (Nolet *et al.*, 1994 *op. cit.* Hegnauer & Hegnauer, 1962-1992).

Beavers clearly show preferences for certain tree species therefore, but what criteria and methods do they use in selecting these favoured species? It has been observed that beavers in Louisiana (Chabreck, 1958), Massachusetts (Jenkins, 1975 *op. cit.* Jenkins 1974; Jenkins 1978; 1979) and Minnesota (Johnston & Naiman, 1990) remove small patches of bark from trees that were then left standing and otherwise untouched. In this way, it is believed that the beavers are sampling the tree bark and thereby assessing the nutritional quality of the different tree species at that time (Jenkins, 1979; 1980). Indeed, Jenkins (1980) considered six possible reasons why the beavers may be sampling trees in this manner, with the collected data supporting the hypothesis that the nutritional value of the tree is being tested by the animal. Also, although conifers are generally regarded as being avoided by beavers, in some cases it has been noted that *C. canadensis* removes the bark of pines (*Pinus strobus* and *P. resinosa*) leaving the tree standing, and licks the sap from the tree instead (Svendsen, 1980). The same author did document very occasional felling of the *Pinus spp.* with bark being stripped and eaten, whilst common juniper (*Juniperus communis*), Scots pine (*Pinus sylvestris*) and possibly Norway spruce (*Picea abies*), were eaten in small quantities by *C. fiber* in southern Norway (Simonsen, 1973). Hartman (1992) on the other hand concluded that whilst beaver damage to conifers was only a minor problem in Swedish forests, no straightforward reasons exist for such beaver attacks on conifers.

2.3.2.2 Prey size and selectivity

As well as selecting woody species based on dietary preference, tree size also plays a role in the selectivity shown by beavers, with smaller diameter trees generally being selected before larger stems (*e.g.* Simonsen, 1973; Jenkins, 1979). As with the species data however, the tree sizes felled need to be put into the context of tree sizes available to the beavers, although under certain circumstances exceptionally large trees are felled. For example, one felled willow (*Salix spp.*) in Belarus had a diameter of 106 cm (Kitchener, 2001).

In Norway, it was estimated that each beaver felled between 12 and 47 trees or shrubs every month, showing a preference for smaller diameter stems, with mostly trees in the diameter range 3-8 cm being felled (Simonsen, 1973). However in the case of European aspen (*Populus tremula*) bigger trees appeared to be selected, with around 18% of available trees over 8cm in diameter being felled, compared to 0.6% below 2 cm and 15% between 3 and 8 cm diameter (Simonsen, 1973). A similar trend was observed in Minnesota, USA where approximately 65% of all stems browsed in this study were less than 5 cm in diameter (Johnston & Naiman, 1990), whilst Aldous (1938) noted that the large aspen were only felled after the smaller aspen had been utilised. Indeed only 22 of 456 felled trees were of 22.5 cm diameter or greater, although as no size-availability data are included in this study it is unclear whether this is an artefact or a genuine trend (Aldous, 1938).

In good quality habitat characterised by an abundance of favoured species such as shrubby willows (*Salix spp.*), the majority of trees felled are often in the smaller size range (*e.g.* Łapiński & Staliński, 2001). Furthermore, in the Netherlands it was found that *C. fiber* favoured shrub willows over other willows showing a tree-like growth form, and that this preference was apparently due to size rather than species selectivity (Nolet *et al.*, 1994). In terms of classical optimal foraging theory (*e.g.* Begon *et al.*, 1986) the choice of shrubby species over trees would be beneficial due to the reduced handling time required, all other things being equal (Nolet *et al.*, 1994 *op. cit.* Saether, 1990). A shrub provides numerous shoots at a height that are immediately accessible to the beaver, whereas a tree has to be felled before the thinner branches become available.

The response of red willow (*Salix lasiandra*) to actual and simulated beaver browsing was studied in Oregon, USA (Kindschy, 1985; 1989), where it formed the major winter food item. These willow stands were inaccessible to livestock and only grazed upon by beavers. On average over four years, 82% of stems available to *C. canadensis* were removed, commonly of 1.3 - 2.5 cm diameter, with stems of less than 0.3 cm diameter seldom browsed. The beavers were shown to select primary trunks of around 24 cm diameter and remove the numerous secondary stems growing from this trunk. On average the beavers left 18 cm of secondary stems each year, which then produced several tertiary stems the following year. Although the browsed willow showed approximately 50% reduction in height and canopy width after 4 years (Kindschy, 1985), it began spring growth up to 50 days earlier than unbrowsed willow, and showed around six times more stem growth annually. In this way the beavers coppicing of the tree induces a shrubby growth form, which provides an abundant supply of favoured small stems.

Although these studies demonstrate that in general small stems are favoured over large stems, and that a shrubby growth form offers more readily harvestable food than an otherwise equally favoured tree species, beavers still show great flexibility in their exploitation of a woody resource. For example, if only large size classes are available in an area, they will be readily browsed. Łapiński & Staliński (2001) observed many large Scots Pine (*Pinus sylvestris*) and oak (*Quercus spp.*) being felled in poor quality habitat. Furthermore this flexibility is manifested to a greater degree with more preferred species such as aspen, willow and birch (*e.g.* Jenkins, 1979), which when available – even if only present in large diameter classes – are readily selected. In poorer quality habitat where larger and often less favoured tree species are dominant, foraging areas also tend to be very transient (Łapiński & Staliński, 2001).

In these ways, beavers can be thought of as managing the tree resources surrounding their home area in a generally sustainable manner, although in some cases complete wastage or non-use of felled trees has been observed. Simonsen (1973) noted that such wastage was highest in the larger diameter classes, with around 30 - 40% of trees felled in the 12 - 26 cm diameter classes being wasted compared to less than 4% wastage in those trees smaller than 5 cm in diameter. In some cases (around 2% of total felling) *C. fiber* started to gnaw through trees but then stopped and apparently discarded the tree. This behaviour was most common in larger diameter trees, especially the oaks (Simonsen, 1973). Similar wasteful behaviour has been observed in *C. canadensis* with high degrees of aspen wastage (up to 64%), especially in the larger size classes being recorded (Stegeman, 1954; Northcott, 1971 *op. cit.* Swank, 1949; Northcott, 1971 *op.*

cit. Gibson, 1957; Northcott, 1971). When small stems are selected non-use of only 1% of cut stems was observed in Ohio, which was suggested in part to be due to the lower likelihood of small branches becoming lodged or snagged on neighbouring branches and being unavailable to the beaver (Nixon & Ely, 1969). Aldous (1938) gives figures of 29% and 22% of cut aspen and birch respectively being completely wasted, mainly due to such lodging. Conversely however, lodging was of greatest importance towards the smaller end of the felled size-range (10 - 15 cm diameter), with the larger, heavier size classes are more likely to crash through the surrounding canopy.

Further wastefulness was documented by Aldous (1938), who estimated that the beavers utilised only 36% by weight of the felled aspen, with the remaining 64% wasted. In the larger diameter aspen it was common for only the palatable upper parts of the felled tree to be utilised, with considerable portions of less-favoured lower trunk left untouched. The benefit of such apparently wasteful feeding is explained by the fact that larger trees have the highest ratios of top to trunk material, and therefore offer the greatest amount of preferred small stems and leaves, although the actual amount of wasted material can be considerable.

2.3.2.3 Prey distance and selectivity

It is widely acknowledged that beaver foraging takes place preferentially within riparian zones surrounding the lodge or pond (*e.g.* Hill, 1982; Novak, 1987; Kitchener, 2001) although the exact distances travelled to acquire food will vary according to habitat quality. In Minnesota, Johnston & Naiman (1990) noted that all beaver browsing was confined to just 55 m from the water, whilst in Norway it was observed that *C. fiber* seldom travelled more than 100 m from water in order to gather food (Simonsen, 1973).

However, when highly preferred tree species are present in an otherwise poor habitat, beavers have been recorded as travelling much greater distance over land. For example, Northcott (1971) investigated the feeding habits of beavers in the predominantly coniferous forests of Newfoundland. It was found that in the relative absence of preferred tree species, beavers would travel longer distances (up to 188 m) through difficult terrain to feed on aspen (*Populus tremuloides*). Another study on Newfoundland discovered that a beaver had travelled 238 m from water to fell a single aspen (Northcott, 1971 *op. cit.* Miller, 1960).

So pronounced is the effect of distance on species selection that it has been used to infer ranked preferences of beaver for woody species. For example, Nixon & Ely (1969) observed that although foods selected by beavers in Ohio were partly based on availability, the mean distance travelled to cut alder (*Alnus serrulata*) and maple (*Acer rubrum* and *A. saccharinum*) was approximately four times greater than that for ironwood (*Carpinus caroliniana*). Therefore it was concluded that beavers show a preference for these three species over ironwood. Obviously the abundance of felling in a heterogeneous woodland environment will follow a distance decay function, based upon preference and distance from the waters edge.

2.3.2.4 Beavers as central place foragers

It seems evident that the likelihood of any particular tree being felled by a beaver is dependent upon species, size and distance from water. Beavers adopt a strategy known as central place foraging (Orians & Pearson, 1979; Schoener, 1971; 1979), in which foraging occurs over an area surrounding a central lodge or pond, to which food items are returned to be eaten. According to this theory an animal should maximise its net rate of energy intake per unit feeding time, and Schoener (1979) predicts that prey selectivity should increase with increasing distance foraged over.

Jenkins (1980) investigated the feeding behaviour of *C. canadensis* in Massachusetts, USA, with particular reference to this foraging strategy. In this study, it was found that significant negative correlations existed between felled tree size and distance from the water for oak, maple, birch, and cherry at at least some of the sites investigated. Some of these correlations were partially dependent on differences in the densities and sizes of trees available at different distances from the water, though not all of the correlations can be disregarded in this way. For example, at one site there was a lower mean size of felled birch further away from the pond than nearer to it, even though birch was predominantly of greater diameter at increasing distance from the water. Of the tree species that did not show a negative relationship between size and distance, either low densities at certain distances or limited size ranges were thought to have removed the opportunity for choice by the beaver. When the author introduced a temporal element to the investigation, it was found that a general preference for small trees was evident for some species (Jenkins, 1980). For example, at a given distance and location small oak and maple were removed first, followed later by larger trees of these species. These results support Schoener's (1979) model for animals feeding on prey items larger than themselves, such as beavers feeding on trees, in which the increased handling time for large items outweighs the nutritional advantages of selecting such items. A study of the North American beaver in North Dakota showed that as distance from the water increased, the diameter of cut trees decreased, whilst the opposite was true of uncut trees (Pinkowski, 1983). This suggests that as beavers forage further from water, smaller trees are actively selected, presumably validating a minimal energy expenditure model.

If beavers are feeding on items smaller than themselves, and handling time is therefore less significant, it might be expected that larger prey sizes would be selected at greater distances due to the greater energetic rewards (Schoener, 1979). When North American beavers in Utah were observed (McGinley & Whitham, 1985) feeding on cottonwood (*Populus fremontii*) branches, all food items were sufficiently small (ranging from 1.5 to 30 mm in diameter) for differences in handling time between the smallest and largest to be considered negligible. In this study, possible complications to the beaver foraging such as age-related plant defences (McGinley & Whitham, 1985 *op. cit.* Whitham *et al.*, 1984), were eliminated by selecting an even-age stand of trees. It was found that larger twigs were selected than were left on the tree at all distances from the pond, which supports this model of central place foraging. Furthermore, it was predicted that as the value of selecting small branches would decrease with distance, the smaller diameters should be excluded from the diet at greater distances. This was shown to be the case, and the mean size of the smallest twigs removed from a tree increasing from 1.6 mm at 3.5 m from the pond, to a value of 12.3 mm at a distance of 20.7 m. These data are in stark contrast to the findings in several other studies (Jenkins, 1980; Pinkowski, 1983; Belovsky, 1984) in which beavers feeding on larger trees generally ignored any bigger trees that were available further from the lodge.

2.3.2.5 Dietary seasonality and the interactions between prey species, size and distance

It has already been shown that selectivity of foraging becomes more pronounced as distances from water increase. For example in Argentina, the introduced *C. canadensis* in Tierra del Fuego selected larger trees near to the pond, and smaller trees further from the water (Lizarralde, 1993). In addition, the distances that beavers are prepared to travel in order to cut certain species varies with species preference, often with great distances travelled to obtain highly favoured aspen (Northcott, 1971; Simonsen, 1973). Size, species and distance travelled all therefore exert an influence on foraging behaviour of beavers, but there is also a temporal aspect involved too.

The beaver diet shows great seasonality in terms of which types of vegetation are selected throughout the year. Woody material forms the bulk of the diet during the late-autumn, winter and early-spring periods, whilst herbaceous and aquatic species dominate the diet during late-spring, summer and early-autumn months (*e.g.* Svendsen, 1980; Roberts & Arner, 1984). However, more subtle effects of time on the diet of beavers have also been observed.

Jenkins' (1979) studies of *C. canadensis* in Massachusetts found that 90% of the trees cut were of just six genera, with each showing significant variation in contribution to the diet over time. The use of electivity indices (Jacobs, 1974) showed that the beavers tree species preference changed with season. For example, oak (*Quercus spp.*) and witch hazel (*Hamamelis virginiana*) were preferred in autumn 1973 but not earlier, birch was favoured in autumn 1972 but not the following spring or autumn, and pine (*Pinus spp.*) was selected against in the autumn of 1972 but not in the following autumn. Other trees were clearly continuously disliked by the beavers, such as spruce (*Picea spp.*). Such apparent shifts in seasonal species preference from year to year is suggested as being due to differences in levels of nutrients, and that by sampling patches of bark the beaver is able to select a balanced diet (Jenkins, 1979).

The seasonal nature of the beavers diet has implications for the vegetation structure of the beavers' foraging area, as well as to the diet of the animal itself. Timing of the cutting seems to be of great importance, with trees browsed in midsummer, especially in August, showing inhibited growth persisting for the following two years. If the cutting occurred in late-autumn or early-spring whilst the tree was dormant, growth was rapid, and trees browsed in June and July even showed extended growing seasons with delayed leaf fall (Kindschy, 1989). As beaver browsing of willow mainly occurs during late spring and autumn, the dormant trees respond by exhibiting very rapid growth, and the browsing can be thought of as occurring during the period when the trees are least susceptible to grazing pressure. The beavers were effectively coppicing the willow, and the author suggested that beaver grazing was not the cause of the decline of the red willow that had been observed in other livestock-grazed riparian areas of Oregon (Kindschy, 1985). Similarly in Europe, Fustec *et al.* (2001) showed that the cutting of trees by *C. fiber* stimulates shoot development and can "rejuvenate riparian forests", and it has been suggested that the practice of coppicing employed by foresters and woodland managers, actually developed after humans historically observed the activities of the beaver (Green, 2000).

2.3.2.6 Caches

Throughout much of the geographical range of both the Eurasian and North American beavers, winter ice-cover of ponds is a common occurrence. During this time, which can last from a few days in warmer latitudes to extremely long periods of 6 - 8 months in higher latitudes (Novakowski, 1967; Aleksiuk, 1970), the beavers are generally confined in their lodges and burrows with no access to the surrounding land. Although in extreme cases there are reports of beavers having gnawed through the ice to escape the pond and forage on land (Beer, 1942), a winter food source often consists of a cache of woody material located near to the entrance of the lodge or burrow. As well as being essential to icebound beavers, such caches have important uses for researchers of beaver behaviour. Aerial surveys of cache presence have been used as a means of accurately censusing beaver populations (*e.g.* Hay, 1958), although some authors have found this method to be unsatisfactory (Swenson *et al.*, 1983). Another use is to help identify the woody species eaten by beavers by examination of the constituents of the cache (*e.g.* Slough, 1978), although it is important that aspects of beaver behaviour are taken into account before the results of any cache analyses are interpreted in dietary studies.

Whilst caching behaviour appears to be an innate response to a number of environmental factors such as declining food quality and falling temperature (Semyonoff, 1957a; Wilsson, 1971), the extent of cache building varies with latitude and altitude (*e.g.* Hill, 1982). Whilst beavers in northern areas of their range produce large, well-organised and often numerous food stores (Aleksiuk, 1970; Slough, 1978; Hartman & Axelsson, 2004 *op. cit.* Vasin, 2001), animals in warmer climates tend to produce small, disorganised caches (Aleksiuk, 1970; Hartman & Axelsson, 2004 *op. cit.* Djoshkin & Safonov, 1972). Indeed, beavers in warm climates may not produce any winter cache at all. Hartman & Axelsson (2004) describe Blanchet's (1959) observation that Eurasian beavers in the mild climate of the Rhône Valley, France did not build caches, but that when a pair were translocated to a much colder region of Switzerland cache building quickly commenced. This, and other aforementioned studies, suggests that whilst cache building by beavers is driven by requirement, it is an inherent instinct for all beavers.

Construction of a cache is apparently more complicated than simply collecting a supply of woody material and placing them near to the lodge however. Slough (1978 *op. cit.* Roberts, 1937) described the winter caching behaviour of captive *C. canadensis* as a two-stage process. Firstly a "raft" or "cap" of woody material is formed, followed by the placement of other materials underneath. The raft then sinks as it waterlogs and is often trapped in the ice, ensuring the food component of the cache rests well below the water surface. Slough (1978) studying the North American beaver in Canada, noted that different woody species occupied different parts of the cache, although the overall cache composition reflected the riparian relative abundance. Highly preferred species such as willow (*Salix spp.*) and trembling aspen (*Populus tremuloides*) (Novak, 1987) were placed unpeeled throughout the cache, whilst the less preferred alder (*Alnus spp.*) was generally confined to the raft. Similarly, other species that were commonly found in the raft portion were also of low preference – white birch (*Betula papyrifera*), subalpine fir (*Abies lasiocarpa*) and white spruce (*Picea glauca*). When preferred species such as aspen were present in the raft, they had generally first been peeled of bark. In cases where lodges were situated near to floating marsh vegetation, the food items were secured underneath the vegetation mat with peeled sticks and mud placed on top to weigh the marsh down. It was also noted that in many cases the cache was incompletely browsed over the winter, with alder usually remaining untouched, and that the remaining material was used for lodge or dam repairs, or left to form the raft for the following winter. Other authors have documented similar findings. Slough (1978 *op. cit.* Dennington & Johnson, 1974) reported incomplete cache usage, with conifers being used as the raft materials. Northcott (1971) also noted incomplete usage, with alder and conifers commonly left unbrowsed, whilst Townsend (1953 cited in Slough, 1978) observed the use of unbrowsed cache remains to form the raft the following year.

2.3.3 Non-woody terrestrial vegetation and aquatic macrophytes

Feeding studies have shown that neither *C. fiber* nor *C. canadensis* can survive on a diet of woody materials alone (*e.g.* Schneider, 2001 *op. cit.* O'Brien, 1938; Schneider, 2001 *op. cit.* Schulte, 1985). The metabolic and energy requirements are best served by a mixed diet of woody species and herbaceous material, with woody plants supplying mineral elements (Schneider, 2001 *op. cit.* Nolet, 1994) and herbaceous species supplying salts (Schneider, 2001). Almost 150 species of herbaceous and aquatic plants have been shown to be eaten by *C. fiber* and *C. canadensis* throughout their geographic range (Kitchener, 2001), with 16 species fed upon by the Eurasian beaver in southern Norway alone (Simonsen, 1973). Nevertheless the use of non-woody vegetation was largely ignored, unquantified or its importance unappreciated, with many early studies of beaver feeding focussing only on woody species by counting fallen tree stumps, looking at cache composition, and investigating woody plant remains at feeding sites (*e.g.* Shadle & Austin, 1939; Novakowski, 1967).

Svendsen (1980) directly observed six *C. canadensis* colonies in Ohio and determined that at certain times of the year, a beavers diet contains a large non-woody component, and for some periods almost exclusively non-woody vegetation. In late-spring and through the summer, grasses and forbs with no apparent species preferences became very important in the beavers diet, and woody material made up less than 20% of the food consumed. In Norway it was observed that in the summer months beavers spent much more time eating non-woody vegetation than trees, with one year showing a figure as low as 1% of the total daily consumption comprising bark (Simonsen, 1973). The length of time that beavers spend continuously feeding between late afternoon and sunset each day has also been shown to vary throughout the year. Svendsen (1980) showed that this feeding period doubled from 2 hours to 4 hours in the summer as the *C. canadensis* took advantage of the summer herbaceous growth.

Many species of aquatic plants are known to be favoured in the summer diet of *C. fiber*, such as horsetail (*Equisetum fluviatile*), water lilies (*Nuphar lutea* and *Nymphaea alba*), quillwort (*Isoetes lacustris)*, pondweed (*Potamogeton natans)*, common reed (*Phragmites communis)* and bogbean (*Menyanthes trifoliata*) (Simonsen, 1973). Northcott (1971) showed that the most important component of summer food in *C. canadensis* in Newfoundland was aquatic vegetation, particularly the roots of water lilies (*Nuphar variegatum* and *N. microphyllum*), although other species were also eaten such as rushes (*Juncus spp.*) and bottle sedge (*Carex rostrata*). It should be noted however, that the potentially rich summer food supply of water lilies that may be present in a pond is not always accessible to the beaver. Water lily roots in ponds with rocky beds for example, may be completely inaccessible to beavers as a food source as the beavers cannot extract the roots from amongst the rocks (Northcott, 1972). Furthermore, Svendsen (1980) observed that beaver kits in Ohio fed mostly on aquatic vegetation during the summer months, from the safety of the pond, whilst the adults were feeding on terrestrial grasses and forbs.

At other times of the year, beavers opportunistically take advantage of herbaceous material becoming accessible. For instance in winter after the ice had melted beavers moved up to 50 metres from the water to forage extensively for Christmas Fern (*Polystichum acrostichoides*) fronds and rhizomes. Horsetail (*Equisetum spp.*) stalks were apparently favoured too, with approximately 60% of the available total being removed and fed upon throughout the year. Svendsen (1980) noted that aquatic vegetation not only formed a large part of the diet of *C. canadensis* during the summer, but also well into the autumn and winter until the *Potamogeton* and *Elodea* beds died off. Evidence exists that aquatic macrophytes can also be cached through the winter in the same manner as woody material, with Slough (1978 *op. cit.* Dennington & Johnson, 1974) observing pond lilies (*Nuphar variegatum*) stored underneath black spruce (*Picea mariana*).

Often the effects of browsing on grasses and forbs can be dramatic as the beavers take advantage of the herbaceous vegetation during spring and summer. For example, one study noted that the average height of vegetation in a meadow browsed by *C. canadensis* was 6.3 cm compared to 57 cm in an unbrowsed exclosure, although the vegetation recovered when the beavers moved to new territories (Svendsen, 1980). However the flexibility of the beavers diet is again apparent, and in the absence or scarcity of aquatic vegetation it has been shown that woody shrubs such as buttonbush (*Cephalanthus occidentalis*) are fed on through the summer, especially if terrestrial non-woody species such as grasses and forbs are not plentiful (Nixon & Ely, 1969).

2.4 Construction activities of the Eurasian beaver

It is important to note that many of the aforementioned studies of the dietary preferences of beavers have been based on counting cut trees. As trees are felled for both feeding and construction purposes however, the results can sometimes be misleading. For example, Northcott (1971) observed that of the small quantities of trees cut in the summer, alder was most important and was used mainly for dam repair, whilst terrestrial non-woody species and aquatic vegetation formed the main component of the diet. The use of alder as a construction material rather than for food has also been documented by other authors (*e.g.* Pinkowski, 1983), and similarly, beavers in Ontario used large amounts of unpalatable coniferous species in the construction of dams, but almost none in their caches (Doucet *et al.*, 1994a). Many researchers therefore also try to assess any wood utilisation in dams and lodges simultaneously in order to better interpret the actual preferences for feeding alone (*e.g.* Jenkins, 1979).

2.4.1 Dams

Dams are perhaps the iconic image of a beaver colony, and are built for a number of reasons, but primarily as a means of protection. On land beavers are slow moving and vulnerable to predation, and within lodges and dens they are also at risk. To counter this threat, a water depth sufficient for the entrance of the lodge to be submerged is necessary to provide a refuge from predators, as well as being deep enough to provide a submerged winter food cache that is large enough to sustain the colony through periods of winter ice cover. Furthermore, the increased area of impounded water upstream of a dam allows the beaver to forage further into riparian woodland than would otherwise be safe, whilst floating felled trees over a large pond permits easier transportation of woody material back to the lodge. Dams therefore offer a degree of protection to a beaver colony, as well as being of considerable benefit to the animal's lifestyle.

Dams represent a considerable investment of time and energy by beavers however, during both the initial construction phase and subsequent maintenance of the structure, and are only built when the water level is too shallow to fulfil the requirements of the beavers. For example, in a 25-year study of reintroduced *Castor fiber* to the Loire valley in France, 82 sites were colonised along 702 km of watercourse, but only a single dam was built (Fustec *et al*., 2001). In water of greater than one metre depth dam building activity of *C. fiber* is generally rare, with 80 - 90% of dams being built in water shallower than 0.6 meters (Collen & Gibson, 2001). Also dam building in the Eurasian beaver is often more pronounced in upland streams with steep gradients, than in shallower sloping lowland areas, and a cascade system of a series of dams is often evident in these uplands (Collen & Gibson, 2001 *op. cit.* Zurowski, 1989; Zurowski, 1992). Eurasian beaver dams range from a few centimetres high and less than a metre in length (Curry-Lindahl, 1967; Balodis, 1994) to 200 metres long and up to 3 m high (Collen & Gibson, 2001 *op. cit.* F. Rosell *pers. comm*). The building activity of the North American beaver is considered to be even greater, with dam building more common than in *C. fiber* (Danilov & Kan'shiev, 1983), and dams of up to 700 metres long (Collen & Gibson, 2001 *op. cit.* Ives, 1942) and over 5 m high (Collen & Gibson, 2001 *op. cit.* Grasse & Putnam, 1955) being recorded. In northwestern Russia, colonies of both species of beaver co-exist in similar ecological conditions, allowing direct comparisons of dam-building activity to be made. It was observed that approximately 18 - 54% of Eurasian beaver colonies created dams, compared to 75 - 100% of North American beaver colonies (Danilov & Kan'shiev, 1983), suggesting less prolific dam building activity by *C. fiber* than *C. canadensis*.

Beavers in North Dakota also showed an interesting phenomenon when the structure of a dam was investigated. It was found that the composition of species used in the dam reflected the availability of tree species, although almost half of all the aspen present in the dam had been peeled of bark, compared to only 13% of green ash (*Fraxinus pennsylvanica*) (Pinkowski, 1983). This would suggest that the proximity of woody material is of paramount importance when building a dam, rather than the species of tree selected, but that highly palatable branches are used as both a food source and a building material. Extensive details of the dam building behaviour of both the Eurasian and North American beavers can be found in the excellent reviews by Gurnell (1997) and Morgan (1868) respectively.

As beavers modify the stream environment to produce conditions beneficial to themselves, the riparian habitat undergoes considerable change. Behind dams, water is impounded and land inundated, leading to a change in vegetation structure over a number of years. Flood intolerant trees die back to be replaced by moisture-loving species and emergent macrophytes, and as sediment accumulation increases the pond ultimately becomes organically-rich "beaver meadow" with grasses, sedges and woodland edge species dominating (Collen & Gibson, 2001 *op. cit.* Welch, 1935). This progression of vegetative succession in an ecosystem subjected to beaver activity has also been simulated in a recent model (Sturtevant, 1998). The building activity of the beaver therefore produces a much more heterogeneous landscape than previously existed, and subsequently floral and faunal biodiversity increases within these habitat mosaics. Furthermore, the felling of trees in the riparian zone for food or dam and lodge construction opens the forest canopy, creating light areas that allow a shade-intolerant herb layer to develop, whilst the dam structure itself provides refuge for a wide variety of macroinvertebrates (Clifford *et al.*, 1993).

2.4.2 Lodges

A beaver colony is centred around a lodge, den or burrow, in which the whole colony resides protected from predators and adverse weather conditions. Like dams, lodges are structures inextricably linked to the presence of beavers on a watercourse. However, lodges are not always constructed by a beaver colony, and often a network of burrows or dens are sufficient to provide shelter and protection to the beavers. For example, in the Rhône valley in France, burrows are the predominant form of shelter with lodges only being constructed when conditions are unsuitable for tunnelling into the banks (Erome, 1984). Furthermore, the construction activities of the Eurasian beaver again appear to be less common than in the case of the North American beaver. When the two species were compared coexisting in similar conditions in northwestern Russia, it was observed that approximately only 12 - 47% of Eurasian beaver colonies created lodges, compared to 54 - 67% of North American beaver colonies (Danilov & Kan’shiev, 1983).

The construction of a lodge represents a considerable investment of time and energy – as do the construction of dams – and consequently are built only when riparian conditions are unsuitable for burrow development. If stream banks are of a suitable height, incline and material to facilitate digging, burrows will be built by the beavers in preference to lodges. An excellent study of beaver burrows and lodges built by *C. fiber* on the Rhône River, and the conditions in which each type of residence is built, can be found in Erome (1984). Only when stream banks are unsuitable for burrowing due to being very low, rocky or of a shallow slope, will lodges be built taking one of two forms – the Brook Lodge and the Bank Lodge.

In low-lying or marshy areas where little shelter is available for colonising beavers, immediate construction of a brook lodge will occur. Observations of reintroduced *Castor fiber* to the low-lying lakelands of northern Poland indicated that brook lodges were the predominant beaver dwelling, with 76% of occupied sites having at least one brook lodge present (Zurowski, 1992). These conical structures are created using felled woody material, rocks, mud and soil, providing a large multi-chambered dwelling with a submerged entrance for a colony of beavers. Indeed, brook lodges reaching over 2 m high and 14 m in diameter have been described in Norway (Kitchener, 2001) with similar sizes recorded in North America (Müller-Schwarze & Sun, 2003).

In areas with higher and steeper banks however (though not so steep or high as to favour burrowing), bank lodges are constructed (*e.g.* Wilsson, 1971). These structures are intermediate to burrows and brook lodges, consisting of chambers or hollows dug into a bank covered with woody material sealed with earth and mud, often being created by enlarging existing bank dens. More detailed descriptions of the types of lodges built by both species of beaver, and the methods and materials used in their construction can be found in several published studies (*e.g.* Aeschbacher & Pilleri, 1983; Erome, 1984; Zurowski, 1992).

The building of a lodge therefore is by no means prerequisite to the survival of a colony of beavers, and the type of dwelling constructed will be influenced by the riparian landscape being colonised. Even when conditions favour the energy expending construction of a brook or bank lodge, the lodge will not necessarily be occupied permanently by any or all of the colony. It is not uncommon for several large lodges to be built within a single territory (*e.g.* Hay, 1958; Zurowski, 1992; F. Rosell *pers.comm.*; Jones & Gilvear *pers. obs.*), with the colony periodically moving between different lodges and foraging areas. Both occupied and unoccupied lodges will be regularly maintained and improved, and re-used for many decades. For example, Kitchener (2001) cites the example of a lodge in Russia that was used by beavers for 40 years. Furthermore the occupancy of lodges shows some seasonality, with adult males leaving the lodge during the breeding season whilst the female is pregnant, for example.

As mentioned earlier (section 2.4.1) in the roles of keystone species and ecosystem engineer, beavers modify their habitat to create conditions that are favourable to themselves. These modifications create a range of physical conditions, habitat heterogeneity and increased biodiversity, predominantly through the impoundment of watercourses with dams. The creation of lodges not only provides shelter for the beavers however, with muskrat (Patenaude, 1983), voles, mice and moths (Müller-Schwarze & Sun, 2003 *op. cit.* Griffin, 1999) also having been observed inside lodges. Furthermore, studies in Belarus have shown that the presence of Eurasian beavers is not only beneficial to otters (*Lutra lutra*) and European mink (*Mustela lutreola*) by providing impoundments in which fish and amphibian prey species thrive (Anon., 2002 *op. cit.* Sidorovich, 1990; 1997), but that female otters also use beaver lodges and burrows to give birth and raise young (Sidorovich, 1991). Yet another example of the increased habitat complexity and biodiversity that can be created by the construction of beaver lodges can be found in a study of the rocky-shored, macrophyte-impoverished lakes of northwestern Ontario, Canada. In these lakes, abandoned lodges of North American beaver provide accumulations of coarse woody debris and entrapped sediment, leading to increased species richness and abundance of macroinvertebrates and amphibians (France, 1997a).

2.5 Summary

The Eurasian beaver (*Castor fiber*), like its North American cousin (*C. canadensis*), is a strict herbivore and is thought of as a choosy generalist. Their broad diet has been documented as including over 220 species of trees, herbaceous and aquatic plants (Kitchener, 2001), although it varies throughout the species' geographical range. As well as spatial dietary variation, there is a temporal change with a distinct seasonality demonstrated in beaver feeding preferences. The degree and nature of this seasonality also seems to vary throughout the geographical range of the two species. Much work has previously been conducted on the feeding preferences and foraging behaviour of both species of beaver (*e.g.* Aldous, 1938; Semyonoff, 1957a; 1957b; Curry-Lindahl, 1967; Simonsen, 1973; Jenkins, 1978; 1979; 1980; Svendsen, 1980; Belovsky, 1984). These studies demonstrate that apparently simple and predictable inherent preferences are strongly influenced by season, distance travelled and size of food item, and that foraging strategies will differ with food type being employed.

Although a considerable body of research exists on the Eurasian and North American beavers, due to the absence of *C. fiber* in the British Isles since its extirpation in the 16th Century, the feeding ecology of this species in Britain and the concomitant effects on the landscape have yet to be fully investigated. There is a comparative paucity of information on the contribution of herbaceous and aquatic vegetation to the diet throughout the range of the two species. This is due to difficulties in determining the amounts of these plant types consumed, as any feeding remains are often more difficult to find and quantify than the remnants of woody material and tree stumps. Direct observation is the most reliable way of quantifying the proportion of non-woody vegetation in the diet, but observing beavers feeding when they are largely crepuscular and nocturnal in habit is inherently difficult. This difficulty is further confounded by the potentially large areas that beavers forage over. When studies of feeding activity and preferences are based solely on the evidence of felled trees and the remaining stumps, further inaccuracies can arise. Much of the felled wood may only be used for the construction of lodges and dams, so the extent and composition of these structures should also be considered when assessing the source and fate of felled woody material. This study will address this matter by considering the use of felled trees for construction purposes in parallel with felling for food, as well as wastage of felled woody material by beavers.

This thesis will investigate the feeding and construction activities of captive beavers in Scotland, and the effects of these ecosystem engineers on the riparian zone, through the hypotheses outlined in Figure 1.1 (Chapter 1, page 7). The implications of these activities and likely effects of a potential future reintroduction of the Eurasian beaver to Scotland will be explored in detail in Chapter 8 and elsewhere in this thesis.

3 Study site descriptions and habitat mapping

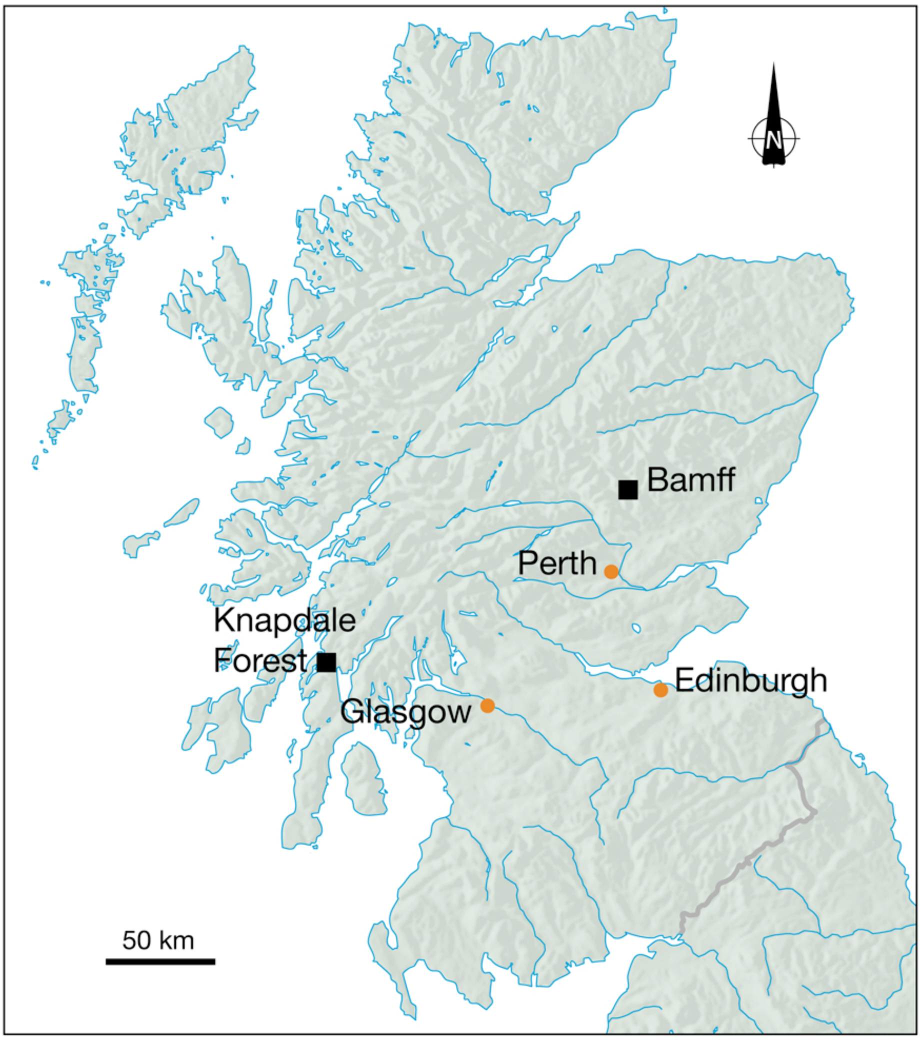
3.1 Introduction

The following chapter will describe the location and habitat types present at the primary study site used throughout this thesis - the privately-owned Bamff estate in Perthshire. As stated earlier (see section 1.7), the delayed and ultimately rejected proposal for a trial reintroduction of beavers to Knapdale, led to the focus of this thesis shifting to the captive beavers at Bamff. The observations and experiments conducted at Bamff that are discussed in subsequent chapters of this thesis, will often be considered in the context of Knapdale Forest. This is believed justified as any future reversal of the Scottish Executive's decision that may occur, would seem likely to be focussed on the Knapdale area, as originally proposed. Descriptions of the habitats present within Knapdale Forest are therefore also described in this chapter, derived from surveys commissioned by Scottish Natural Heritage as part of the original proposal documents submitted to the Scottish Executive. Throughout this chapter (and indeed the wider thesis) all botanical sources for British species were obtained from Stace (2001), with various unreferenced online floras being consulted for non-British species. Figure 3.1 shows the locations of the Bamff estate and Knapdale Forest.

3.2 The Bamff estate

The Bamff estate is located in eastern Scotland near Blairgowrie, approximately 40 km north-northeast of Perth (Figure 3.2). Situated in the foothills of the Grampian Mountains, the estate comprises 525 ha of hills, forest and farmland rising to 425 m above mean sea level. Roe deer numbers are believed to be low to moderate on the estate (P. Ramsay *pers. comm.*). The area receives approximately 1,250 mm of rain annually, with a mean maximum temperature of 11.6°C and mean minimum temperature of 4.7°C (British Atmospheric Data Centre, 2003). Snow and short-term ice cover occasionally occur in winter.

Figure 3.1 Location map showing the Bamff estate study area and the Knapdale Forest proposed trial reintroduction site.



The beavers (the population fluctuated between 3 and 5 individuals) are located in two large enclosures each bounded by beaver-proof fencing, located approximately 0.9 km apart and situated at an elevation of 200m above mean sea level. The two sites are of contrasting habitat, one (the "Stream Site") being an area of young willow plantation and meadow, and the other (the "Lake Site") consisting of two small artificial lakes linked to each other by a short channel, surrounded by mature conifer plantation. The sites cover approximately 13 ha and 9 ha respectively, and space is presumed to be non-limiting. Both sites are enclosed by Rylock®-type stock fencing (*c.* 1m high) with rabbit netting reinforcement at the base, which has been dug into the ground to prevent burrowing. An electric wire placed at beaver nose height (*c.* 0.3 m high) also encircles the sites, just inside the stock fencing. Full details of the history and character of the two sites can be found in an article written by the landowner of the Bamff estate (Ramsay, 2002). The estate boundary and the locations and boundaries of the Stream and Lake Sites are shown in Figure 3.3.

Figure 3.2 Location map of the Bamff estate. (The inset shows the approximate area covered by Figure 3.3).

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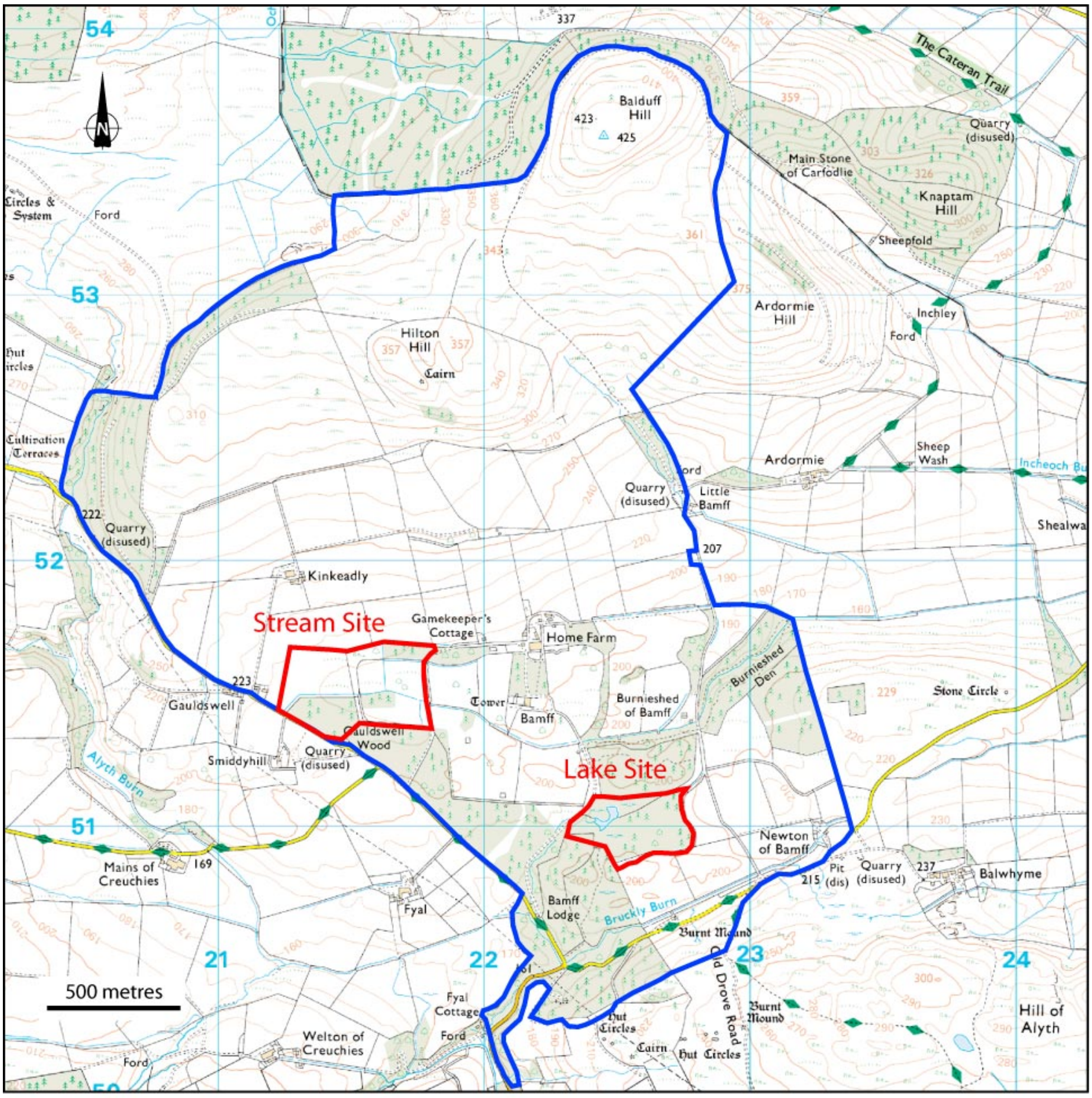
Beaver territories vary greatly in size, typically reflecting the habitat suitability and quality (Fustec *et al*., 2001), and are expressed either linearally (*e.g.* a length of river occupied by a colony) or areally (*e.g.* an area of pond and surrounding woodland). Further variation is caused by differences in colony size, which will affect territory size, and is again linked to habitat quality. For these reasons, published data on territory sizes of both the Eurasian and North American beavers often show great variability.

Figure 3.3 Map showing the boundaries of the Bamff estate (shown in blue) and the Stream and Lake study areas (shown in red).



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For example, Müller-Schwarze & Sun (2003) collated data from numerous studies on the North American beaver and found territory sizes to vary between 2.3 – 42.8 ha in area, and 84 – 1,863 m of riverbank. Investigations on radio-tagged beavers in Canada suggested that the home-range (*i.e.* the entire area foraged over) used by individuals varies seasonally (Wheatley, 1994). This study showed that summer home ranges were on average approximately 10 ha in area, falling to *c.* 3 ha in autumn and 0.25 ha in winter. Finally, following monitoring of Eurasian beavers in France over 25 years, it was concluded that long-term maintenance of a beaver population requires 1.79 km of willow-lined banks per colony (Fustec *et al.*, 2001). Given these published figures, and the fact that the average colony size is in the range 4 – 8 beavers (Müller-Schwarze & Sun, 2003) - at any time during the period of study in this project, the maximum number of beavers within either of the Bamff sites never exceeded three animals - it seems likely that the assumption that the Bamff beavers are not significantly limited by space is justified.

3.2.1 The Stream Site

The Stream Site covers approximately 13 ha of land near to the south-western boundary of the estate (Figure 3.3), and is characterised by young mixed plantation and tall herb meadow. A drainage ditch bisects the site from west to east, with tributary drains entering it from the north and south dividing the site into four approximately equal quarters. These ditches are generally 0.5 – 2 m wide, with a typical unimpounded water depth of 0.1 – 0.3 m. The western half of the site was planted with deciduous species in 1993 by the landowner, in order to improve the nature conservation value of the site, and two small ponds were later created in 2001 (Ramsay, 2002). These planted trees together with some that have seeded from adjacent semi-natural woodland, were typically 2 - 5 m tall at the time of this project. The eastern half of the site is meadow, which to the north of the main ditch is being restored to wetland and contains another pond, and to the south of the ditch the higher and drier meadow area is managed and grazed to promote herb-rich pasture. The two halves of the site are divided by an 18th Century causeway-like feature, and are separated by stock-proof but not beaver-proof fencing. Figure 3.4 shows the site boundary and location of waterbodies, and Figure 3.5 shows the typical habitat present in the western half of the Stream Site.

Figure 3.4 Aerial photograph of the Stream Site showing site boundary and waterbodies, taken prior to the introduction of beavers to the site.

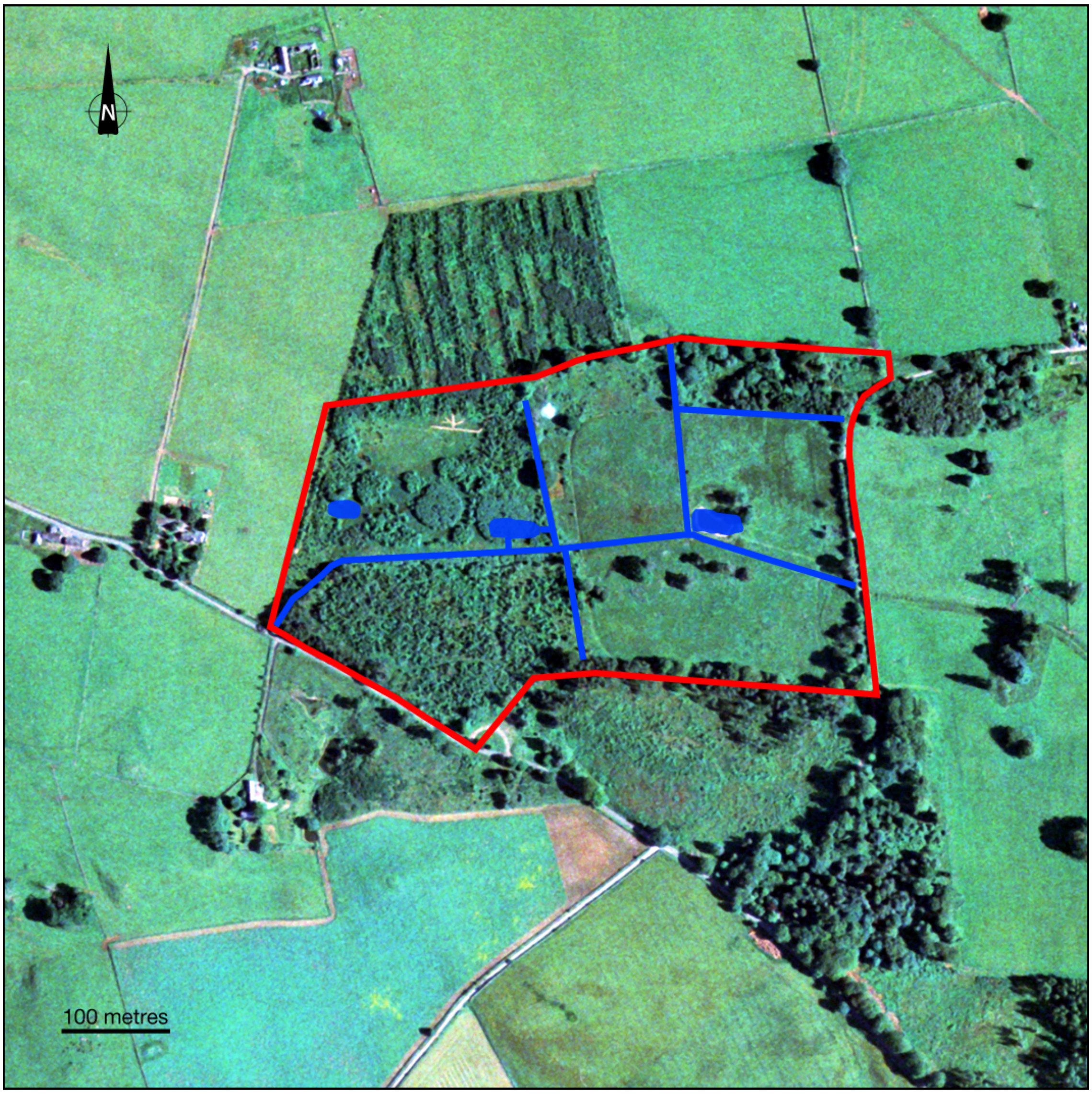
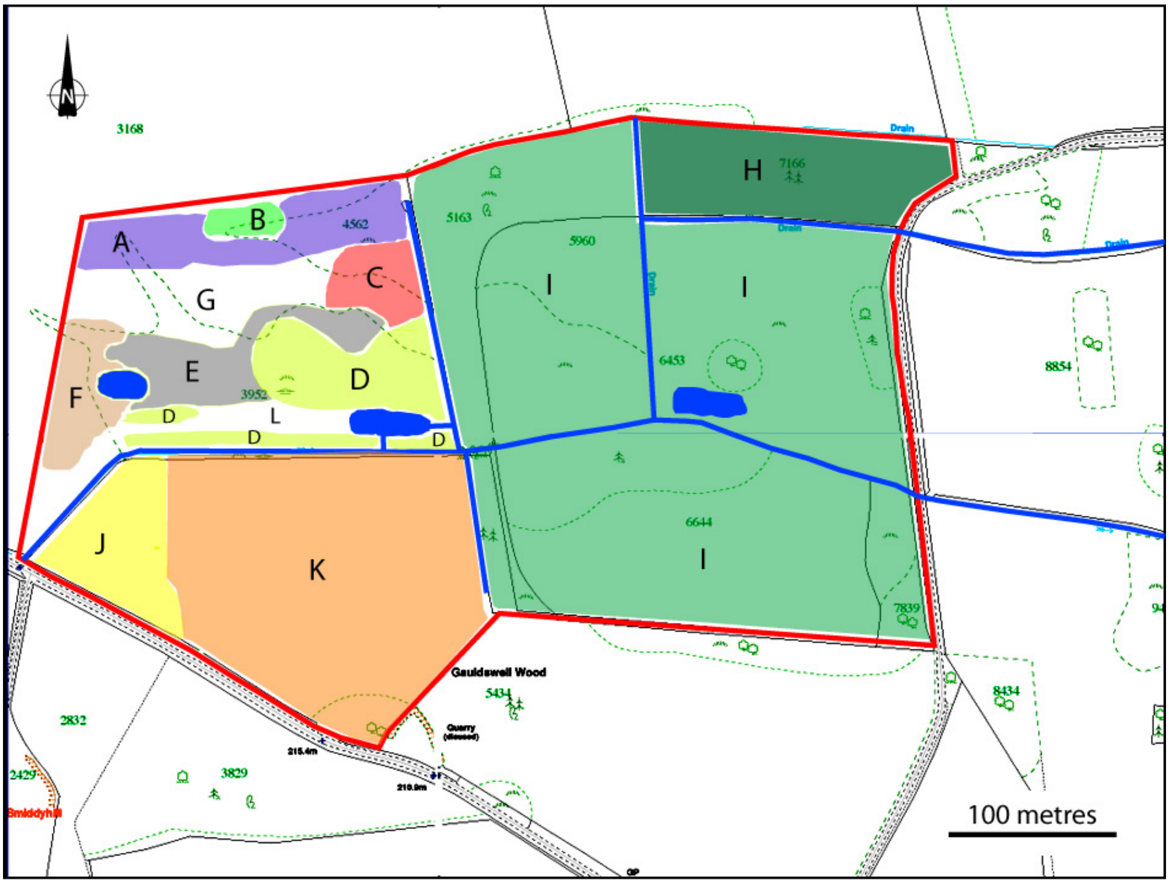


Figure 3.5 Photograph of a pond at the Stream Site.

During the early phase of this project, baseline surveys of tree availability were undertaken in the western half of the Stream Site. In early spring 2003, twenty quadrats (10 m x 10 m) were used to assess tree species composition, with a further twenty quadrats assessed in autumn 2003. Where possible, deciduous trees were recorded to species although in some cases some deciduous trees were only recorded to genus, and the genera of conifers were not recorded (based on the general avoidance of felling conifers by beavers). Within each quadrat the girths of all trees were measured with a measuring tape at "beaver height" (approximately 0.3 m up the trunk) or in the case of felled trees immediately below the cut, and the approximate distance of the quadrat location from the nearest pond estimated. It should be noted, however, that tree stems with an approximate diameter $\leq$ 1 cm were not recorded in these surveys. In the case of stools with multiple stems arising from below "beaver height" (predominantly willow stools), each stem was measured and recorded as a separate tree available to the beavers. Later in the project (winter 2004), a further ten quadrats were sited in specific areas which had been missed by the random quadrat approach, and which had proven to be especially important to foraging beavers or which represented an hitherto unrepresented habitat type. These ten targeted quadrats were of the same dimensions as the random quadrats, except where habitat features (*e.g.* drainage ditches, ponds) made specifically tailored quadrat sizes more practicable. Within all of the targeted quadrats, however, the tree parameters measured and the procedures followed were identical to those conducted within the random quadrats. No surveys were conducted in the meadow (eastern) area of the site as the only trees present were scattered mature deciduous individuals of very large diameter, and therefore thought to be of low desirability to foraging beavers. The results of these surveys and a walk-over assessment of the whole site identified eleven different terrestrial habitat types, as shown in Figure 3.6. Descriptions of each of these habitats are detailed in Table 3.1.

As shown in Figure 3.6, the northern half of the plantation area is characterised by deciduous species, predominantly willow (*Salix cinerea* L., *Salix aurita* L. and *Salix caprea* L.), birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) and alder (*Alnus glutinosa* L. and *Alnus incana* L.). Aspen (*Populus tremula* L.) comprises only a very small component of the canopy, with only 11 trees present at the time of introducing beavers to the site, all located towards the north of Habitat F. In the southern half of the plantation, the tree canopy is mixed with Douglas fir (*Pseudotsuga menziesii* Mirb.), Norway spruce (*Picea abies* L.) and birch, with willow and aspen generally present in the riparian zones. Other woody species present in smaller quantities throughout the plantation include cherries (*Prunus avium* L. and *Prunus padus* L.), ash (*Fraxinus* *excelsior* L.) and sessile oak (*Quercus petraea* Matt.), with hawthorn (*Crataegus monogyna* Jacq.) and elder (*Sambucus nigra* L.) in the shrub layer.

Figure 3.6 Habitat map of the Stream Site. (Ponds and ditches are shown in royal blue). See Table 3.1 for description of habitat patches.



Based on the Ordnance Survey map © Crown copyright

Table 3.1 Terrestrial habitat types present at the Stream Site.

Habitat (as shown on Figure 3.6)	**Habitat description**
A	Young deciduous plantation of birch, alder, ash and oak canopy. Hawthorn common in shrub layer.
B	Young mixed plantation of coniferous, oak and ash canopy.
C	Young deciduous plantation of birch-dominated canopy.
D	Young deciduous plantation of willow-dominated canopy.
E	Young deciduous plantation of alder-dominated canopy.
F	Young deciduous plantation of birch-dominated canopy, with alder, ash and willow also common canopy species. Aspen present but uncommon.
G	Open area dominated by herb layer and rank species. No canopy.
H	Mature broadleaf woodland.
I	Open area dominated by rank species. No canopy. Periodic livestock grazing.
J	Young mixed plantation of coniferous, willow and ash canopy. Elder common in shrub layer.
K	Young mixed plantation of coniferous and birch canopy. Important riparian patches of willow- and alder-dominated canopy.
L	Open area dominated by rank species, especially nettles. No canopy.

The herbaceous communities were assessed by a walk-over survey and consist of predominantly tall herb and rank species, with common nettle (*Urtica dioica* L.), hogweed (*Heracleum sphondylium* L.) and creeping soft-grass (*Holcus mollis* L.) particularly common amongst the wooded areas of the plantation. In the meadow area in the eastern half of the site, and in one open area of meadow within the plantation, the community is more herb-rich, and tall species such as nettle and hogweed are uncommon.

3.2.2 The Lake Site

The Lake Site covers approximately 9 ha of land near to the southern boundary of the Bamff estate (Figure 3.3), and incorporates two mature artificial ponds covering *c.* 2 ha. These ponds were created around a century ago for recreational purposes, the eastern pond originally being a curling pond, and are linked to each other by a short channel. A number of small shallow drains flow into the two ponds, and a single shallow stream flows out of the western pond (the “lochan”) and ultimately out of the site. Figure 3.7 shows the site boundary and pond and outflow locations, and Figure 3.8 shows the typical habitat present in the lochan.

The tree composition of the Lake Site was assessed in spring 2003 by using ten 10 m wide belt transects stretching 50 m from the lake bank into the surrounding woodland. The first transect was located at a random position around the pond margin, with subsequent transects being spaced at approximately regular intervals around the lake margin, separated by around 100 m of shoreline. Trees within the transects were measured and recorded in a similar manner to those at the Stream Site, with deciduous trees being recorded to species (except in the cases of willow and birch which were recorded to genus), and the genera of conifers were unrecorded. Furthermore, as well as trunk girth, the approximate distance from the shore of all trees within the transects was also measured. Where trees were located within the water of the ponds, transects were extended into the water to include them, with trunk girth measurements made in the same manner as for those on the shore. Following initial walk-over surveys of the site, the woodland surrounding the ponds was determined to be almost entirely mature coniferous plantation beyond the riparian zone, dominated by Norway spruce (*Picea abies* L.), Scots pine (*Pinus sylvestris* L.) and European larch (*Larix decidua* Miller).

As coniferous species are of low desirability to beavers and most beaver activity occurs within riparian areas (see sections 2.3.2.1 and 2.3.2.3), the decision to extend the belt transects for only 50 m from the shoreline was believed to be justified. No aspen trees are found within the Lake Site.

Figure 3.7 Aerial photograph of the Lake Site showing site boundary, ponds and outflow stream, taken prior to the introduction of beavers to the site.

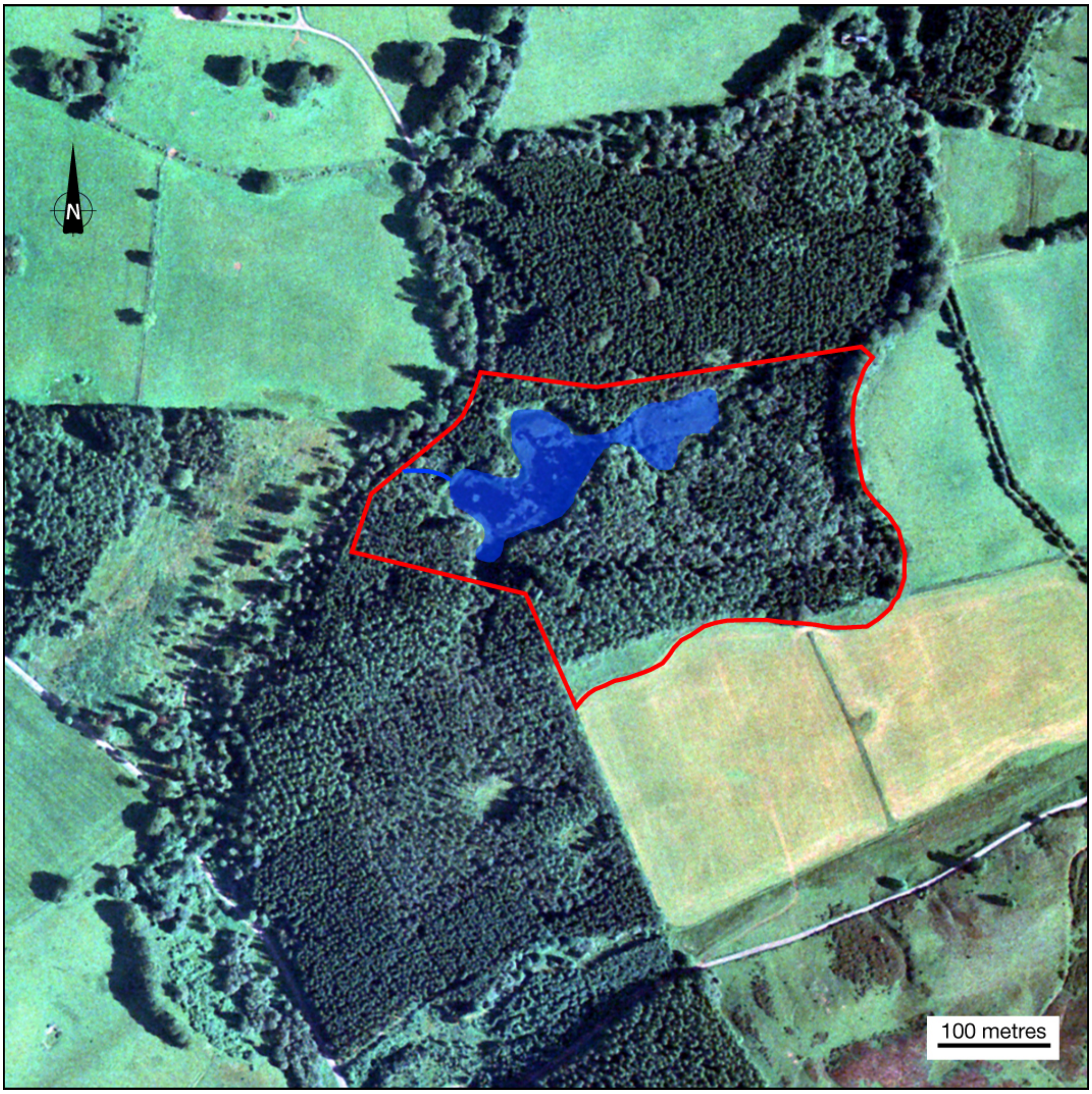


Figure 3.8 Photograph of the Lake Site.

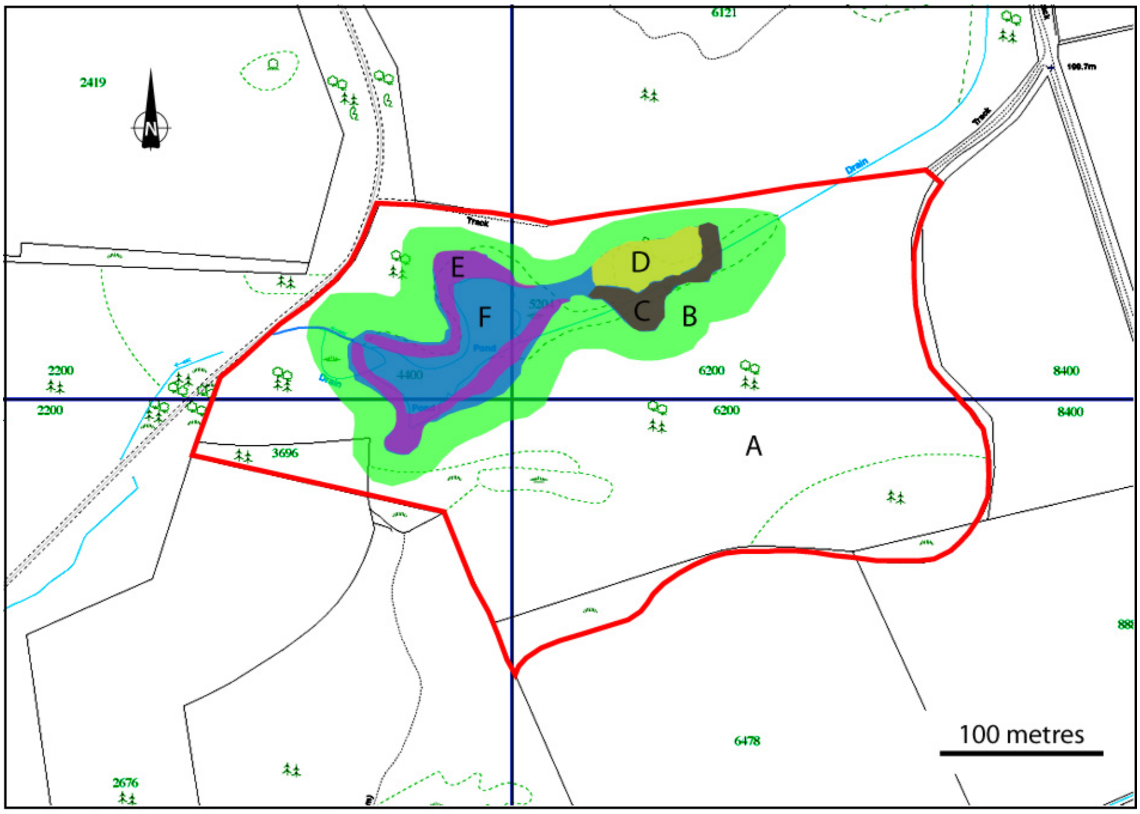
The results of the transects and observations made during the walk-over survey identified two major tree canopy habitats. The canopy near to the lake shore is composed of mature conifers and mixed-age deciduous species, whilst further from the lakes deciduous species become increasingly rare and the canopy is dominated by mature conifers. The herbaceous communities under the dense conifer canopy are dominated by small herb species, whilst the more open mixed areas near to the shoreline are characterised by longer grasses and rushes, with greater woodrush (*Luzula sylvatica* Huds.) especially abundant.

The aquatic communities within the two lakes fall into four main habitat types. The lochan (western pond) is characterised by fringing emergent macrophytes, particularly yellow flag (*Iris pseudacorus* L.), bottle sedge (*Carex rostrata* Stokes) and water horsetail (*Equisetum fluviatile* L.), and large areas of open water dominated by floating-leaved species including broad-leaved (*Potamogeton natans* L.) and bog (*Potamogeton polygonifolius* Pourr.) pondweeds. The curling pond (eastern pond) is dominated by wet willow carr and floating mixed sedge swamp, with abundant bogbean (*Menyanthes trifoliata* L.) and bottle sedge. Table 3.2 details the aquatic and terrestrial habitat types present within the lakes and the surrounding woodland at the Lake Site, and Figure 3.9 shows the locations of these habitats.

Table 3.2 Terrestrial and aquatic habitat types present at the Lake Site.

Habitat (as shown on Figure 3.9)	**Habitat description**
A	Mature coniferous plantation.
B	Mixed riparian woodland, comprising mature conifers and mixed-age deciduous species.
C	Wet willow carr, including a small component of birch carr, with sparse macrophyte community.
D	Floating sedge swamp with isolated shrub willows.
E	Emergent macrophytes, including floating rafts of vegetation.
F	Open water dominated by floating–leaved macrophytes.

Figure 3.9 Terrestrial and aquatic habitat map of the Lake Site.



Based on the Ordnance Survey map © Crown copyright

3.2.3 The Bamff beavers

In March 2002, a male and female adult beaver from Norway were introduced to the Stream Site, into an artificial lodge located in the eastern pond of the plantation area. In May 2002, however, the female was found dead pinned under a felled tree (P. Ramsay *pers. comm.*). This kind of incident has been reported previously in both species of beaver, and while it does not occur frequently, it should not be viewed as a freak event (Kile & Rosell, 1996). Following this death, in June 2002 a second adult female of Norwegian stock was introduced to the Stream Site. Soon afterwards in January 2003, the male beaver died of natural causes (liver disease and high parasite burden), and the surviving female was left alone until the addition of a new male from Bavaria, Germany in November 2004. Finally, in May 2005, the female died of natural causes (liver disease and old age) and has yet to be replaced (May 2006) leaving the male on his own. On average, the life span of a Eurasian beaver in the wild is 7 – 8 years (Kitchener, 2001).

In July 2002, two young adult Bavarian female beavers of approximate age 14 months, were introduced into the Lake Site. Again an artificial lodge had been constructed to house the new beavers, this time located on the northern bank of the channel linking the two lochans. These animals lived in the Lake Site alone until November 2004, when an adult male from Bavaria was released into the enclosure.

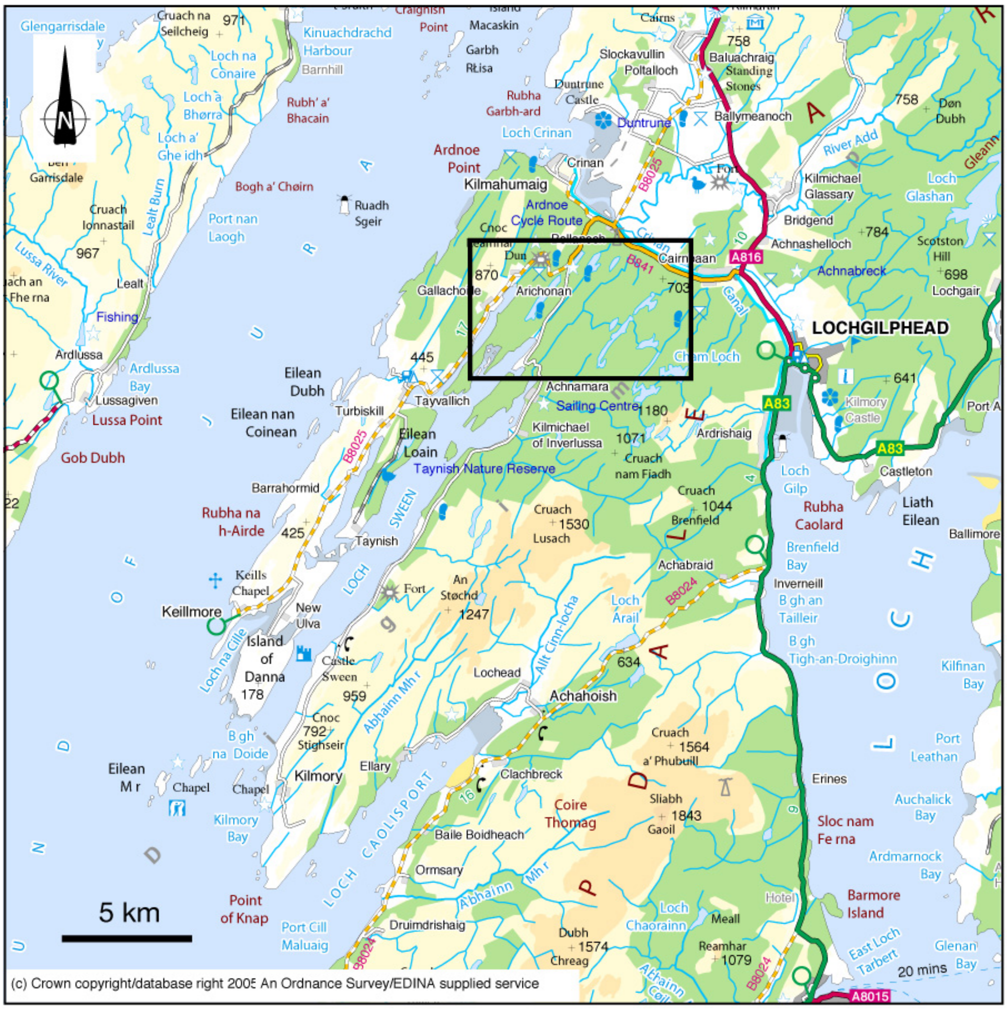
Six of the seven Bamff beavers had been captured in, and translocated from large and expanding populations in either southern Norway or Bavaria, Germany, and one was sourced from a zoo. In all cases, the released beavers were subjected to lengthy periods of quarantine prior to release into the Bamff sites. At the time of writing (May 2006), three beavers are present in the Lake Site (two females and a male) and only one in the Stream Site (a single male). Further details of the Bamff sites and beavers can be found in an article written by the landowner shortly after the release of the Lake Site beavers (Ramsay, 2002).

3.3 Knapdale Forest

Knapdale Forest is located in Argyllshire, southwest Scotland, approximately 80 km west of Glasgow (Figure 3.1), and its name derives from the Gaelic description of the predominant topographical features of the area – *Cnapps*, or hills, and *Dalls*, or fields (Forestry Commission, 2005). The Forest Enterprise owned site lies within the wider Taynish and Knapdale Woods Special Area of Conservation (SAC) (NGR NR785887), which covers approximately 970 ha, of which around 44% is deciduous broadleaved woodland and 20% coniferous woodland (JNCC, 2002). The SAC has been designated based on two qualifying habitat types, listed in Annex I of the European Commission "Habitats Directive", which together comprise over 25% of the total area of the site. The larger of these habitats are the old sessile Atlantic oak woods, which cover approximately 170 ha and are considered to form one of the best examples of its type within the UK. These oak woods are notable for the outstanding lichen and bryophyte communities that they support, as well as a rich ground flora (JNCC, 2005a). The second habitat type of special interest are the oligotrophic to mesotrophic standing waters (*c*. 90 ha), which are characterised by a distinctive macrophyte flora including nationally scarce plant species such as pillwort (*Pilularia globulifera* L.) (JNCC, 2005b). Furthermore, the SAC also supports nationally important populations of two animal species listed in Annex II of the Habitats Directive – the marsh fritillary butterfly (*Euphydryas aurinia* Rottemburg) (JNCC, 2005c) and the otter (*Lutra lutra* L.) (JNCC, 2005d). The SAC incorporates the Taynish National Nature Reserve (NNR) – largely owned by Scottish Natural Heritage (SNH) - as well as several Sites of Special Scientific Interest (SSSI), and lies within the Knapdale National Scenic Area (NSA).

As mentioned in section 1.6.3, Knapdale Forest was selected as the release site for the proposed trial reintroduction of beavers to Scotland for a number of reasons, such as the natural containment that the area offers. It was anticipated that dispersal of beavers released in the favoured area centred around Loch Linne (NGR NR798910), would be restricted by the Crinan Canal to the north and the sea loch of Loch Sween to the south (Figure 3.10). Further obstacles are posed by the steep slopes separating catchments which hinder the movement of beavers, and the widespread coniferous plantations in the area (M. Gaywood *pers. comm.*). After the selection of the Loch Linne area of Knapdale Forest as the trial reintroduction site, several habitat surveys were commissioned by SNH (Murphy *et al.*, 2002; Armstrong *et al.*, 2004; Brandon-Jones, 2004), from which the following data have been collated.

Figure 3.10 Location map of the Knapdale Forest area. (The inset shows the approximate area covered by Figure 3.11).



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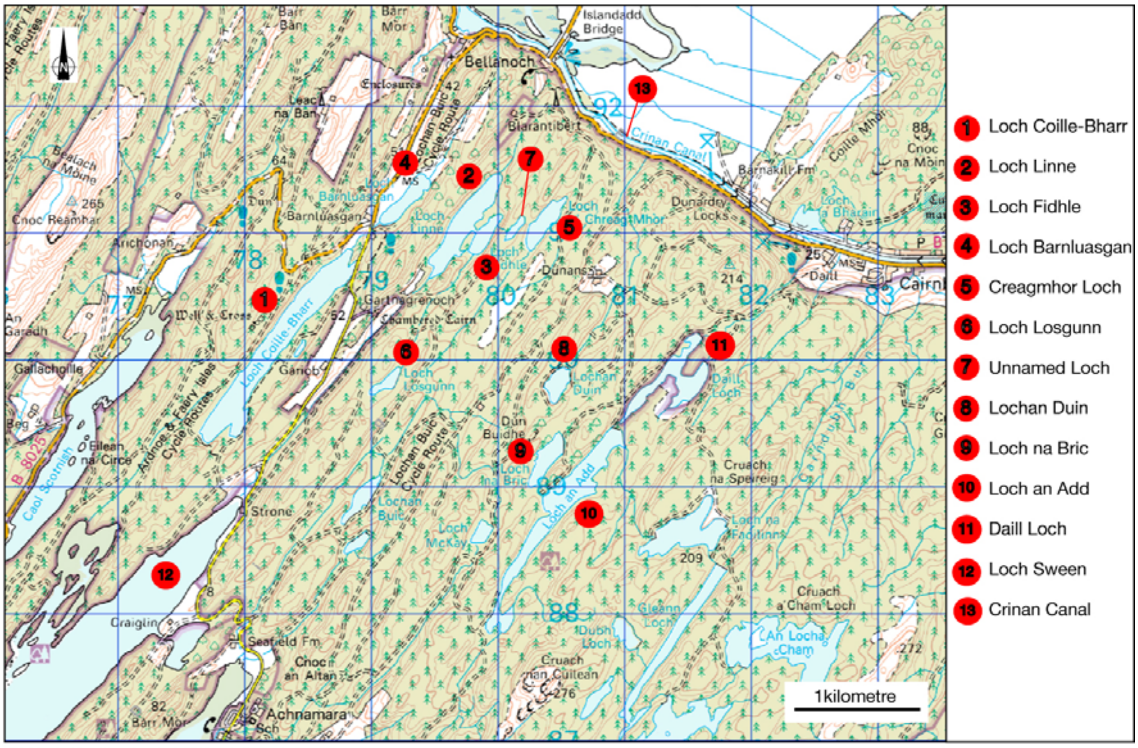
3.3.1 Aquatic habitats

During the summer of 2002, the aquatic macrophyte communities and riparian vegetation of eleven lochs in the Loch Linne area were surveyed (Murphy *et al.*, 2002). Seven “primary” lochs were selected for detailed survey, as they were viewed as the most likely candidates for the release of beavers in the proposed trial reintroduction. These lochs (Coille-Bharr, Linne, Fidhle, Barnluasgan, Creagmhor, Losgunn and

"Unnamed") are natural lochs with little or no water-level regulation, and were sampled along 2 - 4 transects around the loch perimeters. Each transect was selected as representative of the different vegetation habitat zones present around the perimeter of each loch, and extended from *c*. 2 m from the water's edge on the bankside into the loch as far as the littoral macrophyte zone. Along each transect the riparian, emergent and littoral plant communities were assessed for percentage cover by three 2 m x 2 m quadrats, and supplementary data on species composition over the whole loch were collected by visual assessments from the bankside. Wherever possible, the survey also included sampling of the inflow and outflow streams of each of these primary lochs. The four remaining "secondary" lochs (Duin, na Bric, an Add and Daill) were selected based on their close proximity to the primary lochs, and were thought to be potentially suitable for colonisation by an expanding beaver population following reintroduction. These secondary lochs were all regulated water-supply reservoirs, and were surveyed for species percentage cover by visual assessment from the loch banks. The locations of all of the eleven surveyed lochs are shown in 3.11.

The major findings of the study (Murphy *et al*., 2002) were that all of the primary lochs support abundant species-rich macrophyte and riparian communities, with the exception of Loch Collie-Bharr. The especially rich vegetation of Lochs Linne and Fidhle were deemed to be most suitable for beavers dietary requirements, providing abundant emergent and floating-leaved macrophytes, as well as predominantly deciduous riparian woodlands (see Figure 3.12). Characteristic macrophyte species include bottle sedge, common club-rush (*Schoenoplectus lacustris* L.), white water-lily (*Nymphaea alba* L.), yellow water-lily (*Nuphar lutea* L.), bogbean, water horsetail, great fen-sedge (*Cladium mariscus* L.) and broad-leaved pondweed.

Figure 3.11 Location map of the proposed Knapdale trial reintroduction area, showing the locations of the surveyed lochs.



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The secondary loch surveys generally indicated rather poor macrophyte communities, ascribed principally to the water-level fluctuations that these reservoirs experience. For example, Loch an Add appeared to support no macrophytes of any kind in the 2002 survey, although Lochan Duin provided more likely beaver habitat with diverse floating-leaved vegetation and pondweeds (*Potamogeton spp.*). The steep rocky shores of these reservoirs, with the exception of Lochan Duin, would also present a significant obstacle for any colonising beavers to overcome.

Figure 3.12 Photograph of typical macrophyte communities found in Loch Linne (from Murphy *et al*., 2002).

The authors concluded that reintroduced beavers should be released into Lochs Linne and Fidhle, although the other surveyed primary lochs in the area should also be able to support beaver colonies. The secondary lochs were deemed to be of too low habitat quality for beavers to thrive in, with the possible exception of the well vegetated Lochan Duin. Furthermore, the authors concluded that a beaver reintroduction was "unlikely to cause major degradation of the aquatic or bankside flora of the target Knapdale lochs", with the vegetation being unlikely to show significant alteration in the presence of beavers (Murphy *et al*., 2002)

3.3.2 Terrestrial habitats

Armstrong *et al*. (2004) identified 17 distinct areas surrounding Loch Linne and the connecting loch to the east, Loch Fidhle, based on the tree canopy and field layer vegetation (Figure 3.13). From this field assessment, eight habitat types were identified as shown in Table 3.3, of which only the first six were considered particularly suitable for use by beavers. Five of these six habitat types were sampled in detail by setting up a transect running through each habitat for a distance of 50 m perpendicular to the loch edge when possible. Habitat type 2 was not sampled by this method due to the close similarity of it and the sampled habitat type 4. Each transect was divided into five contiguous 10 m x 4 m plots, with a 2 m x 2 m quadrat sited in the centre of each plot. Within each quadrat, the percentage cover of herbaceous field and ground layer species, the vegetation height, and the presence of any deer browsing on saplings and herbaceous plants were recorded. The percentage tree canopy cover, the diameter of any deadwood present (both standing and fallen), the diameter (at breast height) of all trees and shrubs greater than 1.5 m high, and the number of deer pellet groups present were also measured. Each quadrat was sampled once between late-April and early-June 2003 by two surveyors.

Figure 3.13 Aerial photograph of Lochs Linne and Fidhle, showing the surveyed transects and habitats identified by Armstrong *et al*. (2004).

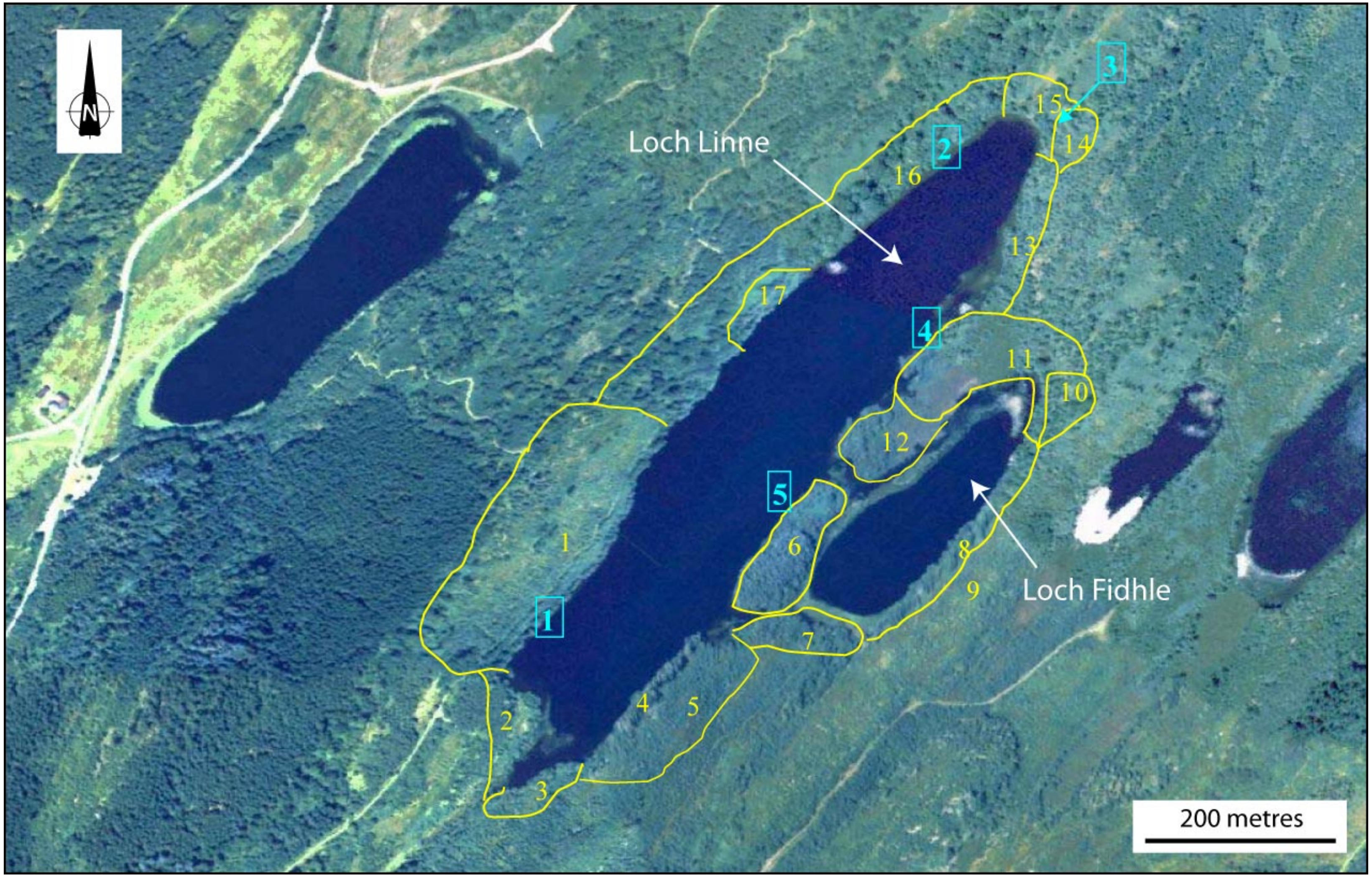


Table 3.3 Habitat types present in the area surrounding Lochs Linne and Fidhle (after Armstrong *et al.*, 2004).

Habitat type	Area (as shown in yellow in Figure 3.13)	Transect (as shown in blue in Figure 3.13)
1 Birch at sapling stage with dwarf shrub / herb field layer	1	1
2 Mature birch / alder with *M. caerulea* / *Sphagnum* field layer	2, 3, 7	N/A
3 Mature birch / alder with grass / herb field layer	10, 14	3
4 Mature birch / alder with heather / *M. caerulea* / bog myrtle field layer	11, 12	4
5 Mature oak / hazel / with *M. caerulea* / heather / blaeberry field layer	16	2
6 Mature Scots pine plantation with heather / blaeberry field layer	6	5
7 Sitka spruce plantation (*c*. 15 years old) with heather / blaeberry field layer	5, 9	N/A
8 Open, with some mature birch /oak and *M. caerulea* / bracken field layer	15	N/A
9 Steep slopes - unsurveyed.	4, 8, 13, 17	N/A

As well as the surveys conducted by Armstrong *et al*. (2004) focussing specifically on the area within Knapdale Forest chosen as the release site for the proposed trial reintroduction, a second study (Brandon-Jones, 2004) surveyed the wider Knapdale Forest area. Within this study, all semi-natural woodland lying within a 100 m buffer zone around all freshwater bodies inside the Forest Enterprise Knapdale Forest landholding, was surveyed. Using pre-existing National Vegetation Survey (NVC) Phase 1 survey polygons identifying the different woodland vegetation communities present in the survey area, a representative quadrat within each polygon was surveyed between May and June 2003. In each quadrat the percentage cover of canopy, shrub and field layer vegetation were recorded by two surveyors.

Whilst the detailed results of these sampling programmes can be found within the original documents, they are beyond the scope of this thesis. The following key points are worthy of note, however, having particular relevance to beaver ecology. Perhaps the most interesting result is that the favoured food item of beavers – aspen – was not found to be present in either of the two surveys. It should be noted however, that the survey of Armstrong *et al*. (2004) was confined to a relatively small area around Loch Linne, whilst that of Brandon-Jones (2004), although covering a much greater area of forest, was restricted to surveying within 100 m of waterbodies. It seems possible that small patches of aspen may exist within the wider area of Knapdale Forest, that have gone undetected by the two survey methodologies. Both these surveys chose to focus on the immediate riparian woodlands as the majority of beaver activity occurs near to the shoreline, but beavers are known to actively seek out aspen stands often travelling great distances to obtain these trees (see section 2.3.2.3).

Brandon-Jones (2004) also notes that deciduous woodland forms only a small part of Knapdale Forest, with coniferous plantations covering large areas, and where deciduous woodland does exist it is often in small fragmented patches. In the Loch Linne area, however, large areas of predominantly birch woodland are present, with alder and hazel also important species, and abundant small diameter trees available (Armstrong *et al*., 2004). Such small diameter trees are often favoured by beavers (see section 2.3.2.2). In some areas around Loch Linne, the presence of willow – another preferred species of beavers – was important in riparian zones. Eared willow (*Salix aurita*), goat willow (*Salix caprea*) and grey sallow (*Salix cinerea*) were found to be important components of the woodland, particularly within 10 metres of the water's edge with trees extending into permanent standing water, often in the form of coppiced stools (Armstrong *et al.*, 2004). Elsewhere in the forest, however, the wider study of Brandon-Jones (2004) found willow to be relatively uncommon. Finally, deer numbers around Loch Linne were low, although in certain areas damage to saplings was sufficiently high as to potentially limit tree regeneration (*e.g.* habitat types 3 and 5 – see Table 3.3) with little impact on ground flora being observed (Armstrong *et al.*, 2004). This study also noted that deer apparently preferred rowan saplings to birch, with most damage done in winter or early-spring.

The surveys conducted at Bamff and Knapdale have shown that the types of habitat occupied by the Bamff beavers also form important areas within the proposed Knapdale release area. Other important similarities exist between the Bamff sites and Knapdale Forest. For example, aspen – the favoured woody food item of beavers – is scarce or absent in both areas - and deer grazing pressures are likely to be comparable between the sites. Deer numbers at the Bamff estate were adjudged to be low to moderate, and recent measures to reduce the browsing pressure by controlling deer populations at Knapdale have been successfully implemented by Forest Enterprise and Deer Management Groups (M. Gaywood *pers. comm.*). It is anticipated that such similarities between the areas will allow the data gathered from the Bamff estate to be more confidently applied to the proposed Knapdale release area.

3.4 Summary

The two Bamff study sites are of contrasting habitat type – one being a young deciduous plantation with two small purpose-built ponds, and the other a mature conifer plantation surrounding two shallow mesotrophic lochans with abundant macrophytes and willow carr. As such they include a wide range of broad habitat types typical of the areas that beavers would be likely to inhabit if reintroduced to Scotland. Any future trial reintroduction of beavers to Scotland is likely to focus on the Knapdale Forest area of Argyllshire, particularly Lochs Linne and Fidhle, which have been extensively surveyed in preparation for such a scheme. There is enough similarity between the sites to justify the assertion that the habitat usage and exploitation observed at Bamff is likely to follow a similar pattern at Knapdale if beavers are reintroduced. The sites surveyed at Knapdale and Bamff contain abundant habitat that is suitable for the survival of beavers, supporting the assertion (Chapter 1.8.1, page 32) that sufficient habitat exists in Scotland for a beaver reintroduction to be both feasible and successful.

Furthermore, the suitability of many other Scottish sites for a beaver reintroduction have been considered during the initial phases of the proposed trial reintroduction scheme, as outlined in Chapter 1.8.1. Although detailed habitat descriptions of these potential release sites is beyond the scope of this thesis, should the focus of a proposed reintroduction shift away from Knapdale in the future, the data presented in the following chapters could usefully be applied to other sites.

4 Effects of beaver activity on riparian tree communities: i) Tree-felling rates and fates

4.1 Abstract

In the event of a trial reintroduction of beavers to Scotland, it is likely that short-term public scrutiny of the effects of tree-felling activities of beavers will be intense. Although considerable work has been conducted on tree-felling activities by beavers throughout Europe and North America, there is an apparent paucity of information on the rate of tree-felling that occurs immediately following the arrival of beavers to a site, and whether this rate varies through time. **It is proposed in this chapter, that felling rate varies through time following colonisation of a site, decreasing after initially high levels of felling, and increasing as the territory expands or new territories are developed.** The reason for this proposed cycle is related to the degree of construction work undertaken at a site, and is therefore likely to be site specific, with optimal habitat requiring less physical modification than marginal sites. An understanding of how felling rates are influenced by habitat factors, and how they vary through time, will be useful in predicting the likely effects of a release of beavers to a reintroduction site.

Felling rates were found to vary between years with maximum rates observed in the first year of colonisation, corresponding to the period of most intensive construction activity. The site that required most modification, and was therefore perceived as marginal habitat, showed higher rates than those observed at a less modified, more optimal site. As well as being influenced by construction activity, there is also evidence that the caching intensity and degree of wastage of felled trees also influences the felling rate. It was found that the provision of caches acts in conjunction with construction activities to raise the felling rate, and that caching behaviour varied between sites, with most caches built at the marginal site. Wastage of felled trees also varied between sites, with most wastage occurring at the marginal site, whilst tree

species, size and location also influence the degree of usage of felled trees by beavers. Most wastage was observed in large specimens of tree species which beavers have an apparent low preference for, especially when located some distance from a pond or lake. It was also evident that felling rate varies within years as well as between years, with higher rates generally occurring in the autumn and early winter months, and lower rates in late-winter. This variation was shown to be influenced by caching activity, which is most intense during autumn.

It was also found that caching activity did not occur at the optimal site, where there is evidence of winter feeding on submerged herbaceous material, which removed the requirement for a woody cache. This absence of caching at the optimal site, coupled with a lack of construction work undertaken during the second and third years of occupation of the optimal site, allowed estimates of minimum felling activity for dietary needs to be made. At such an optimal site, it was estimated that 55 - 70 trees would be felled by each beaver per calendar year during the consolidation phase of colonisation of the site, when felling is predominantly for dietary needs. This compares to estimates of over 300 trees felled by a beaver per calendar year during the initial phase of colonisation at marginal sites.

4.2 Introduction

Whilst the following three chapters investigate the effects of beavers on the trees present at the Bamff estate, this chapter specifically considers the tree-felling rates and fates within the two study sites. Much of the background information, timeline, and survey methodologies referred to throughout this chapter are also relevant to Chapters 5 and 6. In order to avoid any repetition, however, the pertinent details and surveys will be described fully in this chapter only. Firstly the timeline of the major events that occurred at Bamff during the three years of study, together with the timing of certain surveys of the tree canopy are outlined. This section is followed by a detailed explanation of the methodologies employed during the tree availability and felling surveys of the two Bamff sites. The remainder of the chapter focuses specifically on the tree-felling rates observed and the fates (or degree of wastage) of these felled trees, following three years of study at the two contrasting Bamff sites.

Many previous studies have investigated the tree-felling activities of beavers, with the aim of identifying preferred species and / or sizes of trees (*e.g.* Aldous, 1938; Beer, 1942; Svendsen, 1980; Roberts & Arner, 1984; Belovsky, 1984). These studies have all been based upon a single year of investigation, or when conducted over several years, have not considered any annual variations in felling activity that may have occurred. Other studies have incorporated data on foraging distances in order to assess the validity of optimal foraging theories when applied to beavers (*e.g.* Pinkowski, 1983; Jenkins, 1979; 1980; Nolet *et al*., 1994; Gallant *et al*., 2004), often over several years of investigation. However, to this author's knowledge, very few studies have investigated the rates of tree-felling activity (*i.e.* the number of trees felled per beaver per unit of time) that occurs in sites of differing habitat quality, and how these rates vary with the time elapsed since colonisation of a site. Simonsen (1973) calculated the annual tree-felling rate per beaver for three (presumably well-established) beaver colonies in Norway over a three-year period, but the data are pooled over the complete study period, and the author did not relate this to any observed construction activity. The majority of other pertinent studies have quantified annual felling requirements of beavers by weight (*e.g.* Aldous, 1938; Stegeman, 1954; Hall, 1960) or volume (Beer, 1942), again with little or no consideration of the role of construction activity.

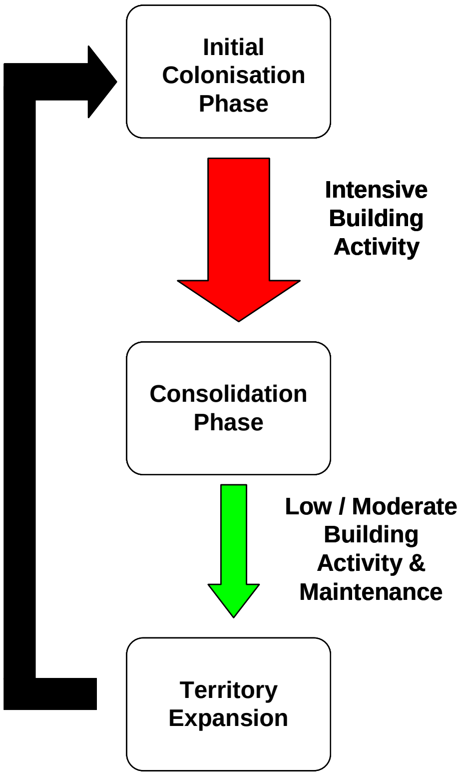
The vast majority of studies of tree-felling by beavers are based on evidence of feeding remains (*i.e.* cut tree stumps), rather than other more direct methods. Two notable exceptions have used analysis of stomach contents (Roberts & Arner, 1984) or some direct observations of beaver activity (Belovsky, 1984) to investigate dietary preferences. However, beavers fell trees for two reasons – as a food source, and as a construction material – so many of the aforementioned studies are likely to incorporate some degree of error by failing to distinguish the dual uses of felled trees. In order to eliminate such errors, some studies state that most material used in dams and lodges had been stripped of bark, and so dietary preferences based on cut stumps were valid. Other studies simply state that no construction activity occurred during the study period, and therefore felling was solely for food. These latter studies do appear to ignore the role of cache development, however. Furthermore, relatively few studies (*e.g.* Aldous, 1938; Stegeman, 1954; Brenner, 1962; Simonsen, 1973) have examined the degree of utilisation of woody material by beavers, with most studies apparently assuming that all felled stumps are indicative of complete usage.

In the event of a reintroduction of beavers to Scotland, the focus of public scrutiny is likely to be on the short-term effects of the animals on riparian habitat. There is a danger that this may lead to the decision to reintroduce the beaver being quickly and harshly prejudged, based on the immediate effects of the released animals. Such "first impressions" may even be used by those opposed to the reintroduction to sway public (and governmental) opinion, and could possibly overshadow the formal assessment of the long-term success of the reintroduction, which would be conducted five years after the scheme had began. In an attempt to avoid such prejudice, this chapter will investigate the rate of tree-felling activity of beavers in two contrasting Scottish sites over the first three years of colonisation. Whilst the evidence has been based on the number of cut tree stumps present at each site, observations on caching and construction activity and degree of wastage of felled trees have also been incorporated into the interpretation of the data.

Assuming that the amount of trees that need to be felled for dietary reasons by an adult beaver is constant from one year to another, the only variable is the amount of trees felled each year for building purposes. It seems reasonable to hypothesise that building activity will be greatest when a beaver first colonises an area, as a lodge or den will be built to provide shelter and dams erected to impound water and provide a ponded area around the lodge that is safe from predators. This intense construction period should be reflected by a high tree-felling rate in the first year of colonisation, especially in marginal habitats that will require a greater degree of initial habitat modification.

Subsequent years should be considered as a consolidation period, when the beaver will concentrate efforts on maintaining and improving existing dams and lodges rather than building new structures. The felling rate should fall from the initial high value throughout this consolidation period. The duration of the consolidation phase when felling activity is decreased is likely to depend on the habitat quality, with optimal habitat being exploited for longer periods than poorer, more marginal habitat. As the territory begins to become resource-depleted over subsequent years of foraging, this consolidation phase will in time be followed by a period of exploration and territorial expansion. New lodges and dams will be built as the beaver relocates to a new feeding area, and the felling rate should once again increase. Figure 4.1 shows the proposed cyclical pattern of tree-felling by beavers.

Figure 4.1 Proposed cyclical pattern of tree-felling by beavers.



One of the assumptions that was made as part of this proposed cyclical tree-felling pattern is that the woody material required for the dietary requirements of beavers is constant through time, and between different beavers. Studies have shown that whilst an urge to cache material in autumn and winter is inherent in beavers (*e.g.* Hartman & Axelsson, 2004), the degree to which caching occurs is apparently variable. Beavers in southern latitudes tend to store small amounts of material in disorganised heaps, whilst those in colder northern areas create numerous large well-organised caches of woody material (*e.g.* Aleksiuk, 1970). As environmental effects and individual variability affect caching behaviour, it should not immediately be discounted from contributing to variations in felling rate therefore, and there is no reason to assume that caching behaviour is constant.

During this study, observations were made at the Bamff sites on the extent of construction and caching activities, and of wastage of felled trees (*i.e.* the degree of non-usage of felled trees by beavers), and felling rates will be considered using these data. The following hypotheses will be tested:

4.1 Tree-felling rates are cyclical, being initially high during the early phases of colonisation, decreasing through subsequent years, and finally increasing again as territories are expanded.

4.2 Tree-felling rates are a direct product of the degree of construction work and caching behaviour exhibited by beavers.

4.3 Marginal habitats (*e.g.* the Stream Site) will require the greatest degree of habitat modification, and hence exhibit higher felling rates, than more optimal habitats (*e.g.* the Lake Site).

4.4 The degree of wastage of felled trees will be low overall, but increase as distance from a beaver pond increases. As the ponds are smaller at the Stream Site than at the Lake Site, and hence the amount of woodland in close proximity to the ponds is smaller, it is proposed that wastage will be greatest here.

4.3 "Beaver years" and timeline of events

The dietary seasonality of beavers has been discussed in detail in section 2.3.2.5. Generally woody material forms the bulk of the diet during the late-autumn, through winter into the early spring, with terrestrial and aquatic herbaceous material dominating at all other times. The beavers diet therefore consists of an herbaceous period and a woody period, which do not correspond directly to the months of a calendar year. It is useful, for the purposes of this study, to consider the occupation of the two Bamff sites by beavers in terms of "beaver years". This is further justified by the fact that the beavers were introduced to the different sites some months apart within the calendar year (March 2002 at the stream site; June 2002 at the lake site). The start of the beaver year was taken to be the point at which the beaver diet shifts from woody to herbaceous material for the first time in the calendar year (*i.e.* late-spring), running through the year until the end of the woody period (*i.e.* the start of the herbaceous period of the subsequent year). Figure 4.2 shows the timeline of the study period, indicating the major events and surveys conducted throughout this time, and descriptions of these events and surveys can be found in Table 4.1.

Throughout the following chapters of this thesis, unless otherwise stated, references to year of activity (*e.g.* tree-felling, construction *etc.*) represent the "beaver year" as shown in Figure 4.2, not the calendar year. For example, in the following sections of this chapter on tree-felling activity, reference to Year 2 felling indicates the period of wood dependence (and hence tree-felling activity) that occurred during the second year of beaver occupation or "beaver year", *i.e.* start of October 2003 – end of April 2004.

Figure 4.2 Timeline of the study period showing the major events and tree surveys conducted at both Bamff sites.

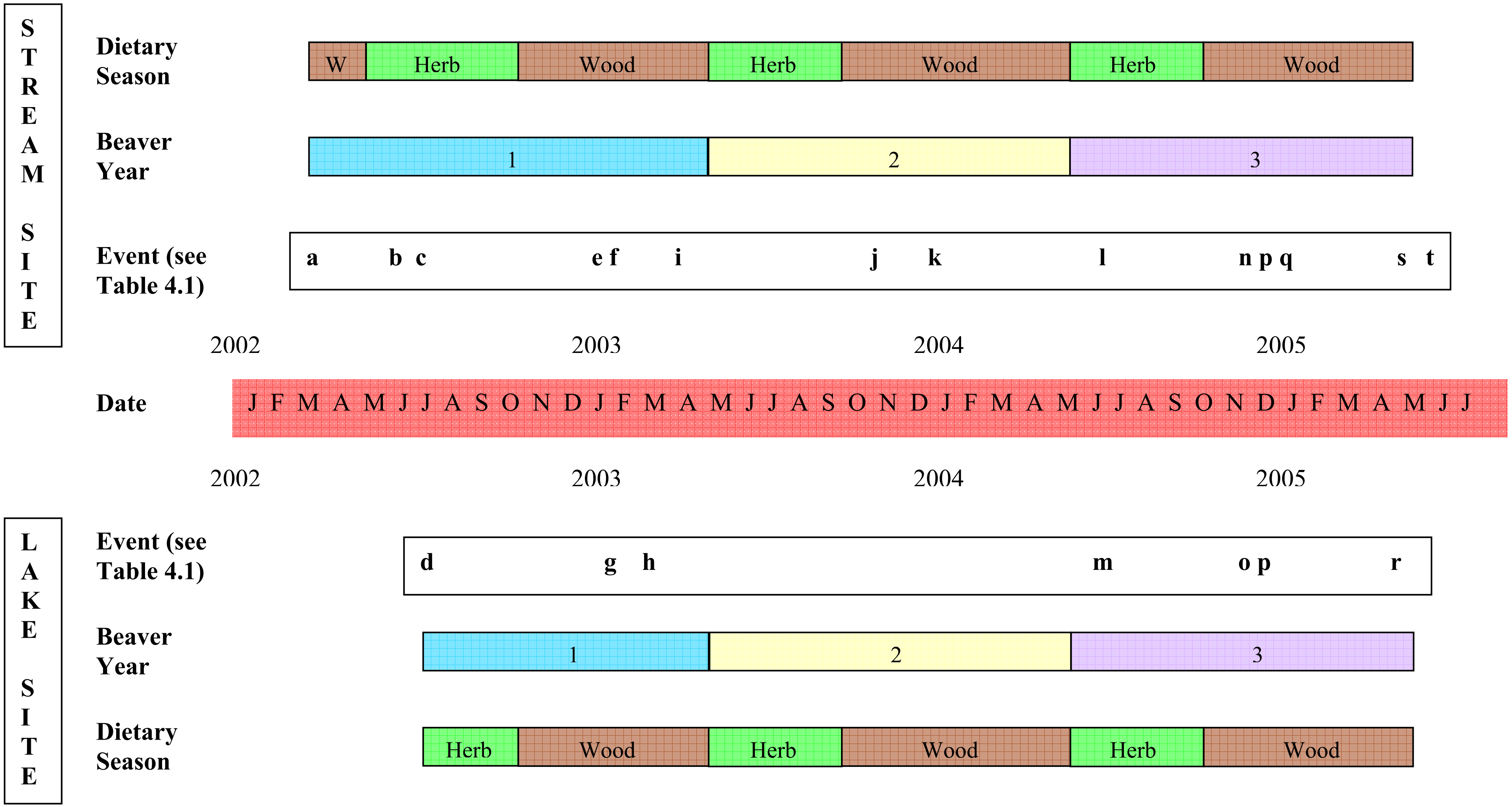


Table 4.1 Major events and tree surveys conducted at Bamff.

Event (see Figure 4.2)	Date	Description
a	*c*. 01/03/02	Two beavers (1 male and 1 female) introduced to Stream Site.
b	21/05/02	Female beaver dies at Stream Site.
c	11/06/02	Female beaver introduced to Stream Site.
d	*c*. 01/06/02	Two female beavers introduced to Lake Site.
e	18/01/03	Male beaver dies at Stream Site.
f	21/01/03	Tree-felling survey 1 at Stream Site.
g	21/01/03	Tree-felling survey 1 at Lake Site.
h	28/02/03	Tree availability survey 1 at Lake Site.
i	18/03/03	Tree availability survey 1 at Stream Site.
j	27/10/03	Tree availability survey 2 at Stream Site.
k	15-23/12/03	Tree-felling survey 2 at Stream Site.
l	02/06/04	Tree-felling survey 3 at Stream Site.
m	03/06/04	Tree-felling survey 2 at Lake Site.
n	18/11/04	Tree-felling survey 4 at Stream Site.
o	19/11/04	Tree-felling survey 3 at Lake Site.
p	19/11/04	One male beaver introduced to Lake Site. One male beaver introduced to Stream Site.
q	16/12/04	Tree availability survey at Stream Site.
r	22/04/05	Tree-felling survey 4 at Lake Site.
s	30/04/05	Tree-felling survey 5 at Stream Site.
t	16/05/05	Female beaver dies at Stream Site.

4.4 Explanation of terminology

To avoid possible confusion, the following terms frequently used throughout this and subsequent chapters are defined below.

Felled	a tree that has been successfully felled by a beaver, the trunk (usually) having been chewed through completely.
Stump	the rooted remains of a successfully felled tree, the trunk of which has been completely cut through.
Log	the unrooted remains of a successfully felled tree, the trunk of which has been completely cut through.
Incompletely-Felled	a tree that has been successfully felled, apart from a narrow section of bark and cambium tissues that are still intact.
Base	the rooted remains of an Incompletely-Felled tree below the cut.
Trunk	the bole of an Incompletely-Felled tree above the cut. These trunks lie horizontally and are attached to the base by a thin strip of bark and cambium.
Nibbled	a tree that has been partially cut through before felling was abandoned by the beaver, and remains standing vertically. Trees that have been subjected to small areas of bark stripping are also included in this category.

The term Incompletely-Felled is used only in conjunction with the willow regrowth measurements discussed in Chapter 6, in order to distinguish the regrowth of stumps and logs of completely severed trees from that arising from those felled trees in which a only small section of cambium is intact. In all other aspects, Incompletely-Felled trees are analogous to felled trees, as the trunk has been almost entirely severed and the tree does not stand vertically. The tree availability surveys (section 3.2), felling surveys (section 4.4.2) and fate of felling surveys (section 4.7.2) make no differentiation between Felled and Incompletely-Felled trees, simply recording any tree trunk entirely cut through or laying horizontally due to beaver gnawing as felled. Quantification of the numbers of Incompletely-Felled trees was conducted by specific surveys at both sites (section 6.3.3.1).

4.5 Methods and materials

4.5.1 Tree availability surveys

Tree availability surveys were conducted at both Bamff sites to assess the size and composition of the woody resource available to the beavers, and these surveys have been fully described in Chapter 3 of this thesis. The survey methodology at the Stream and Lake Sites can be found in sections 3.2.1 and 3.2.2 respectively.

4.5.2 Tree-felling surveys

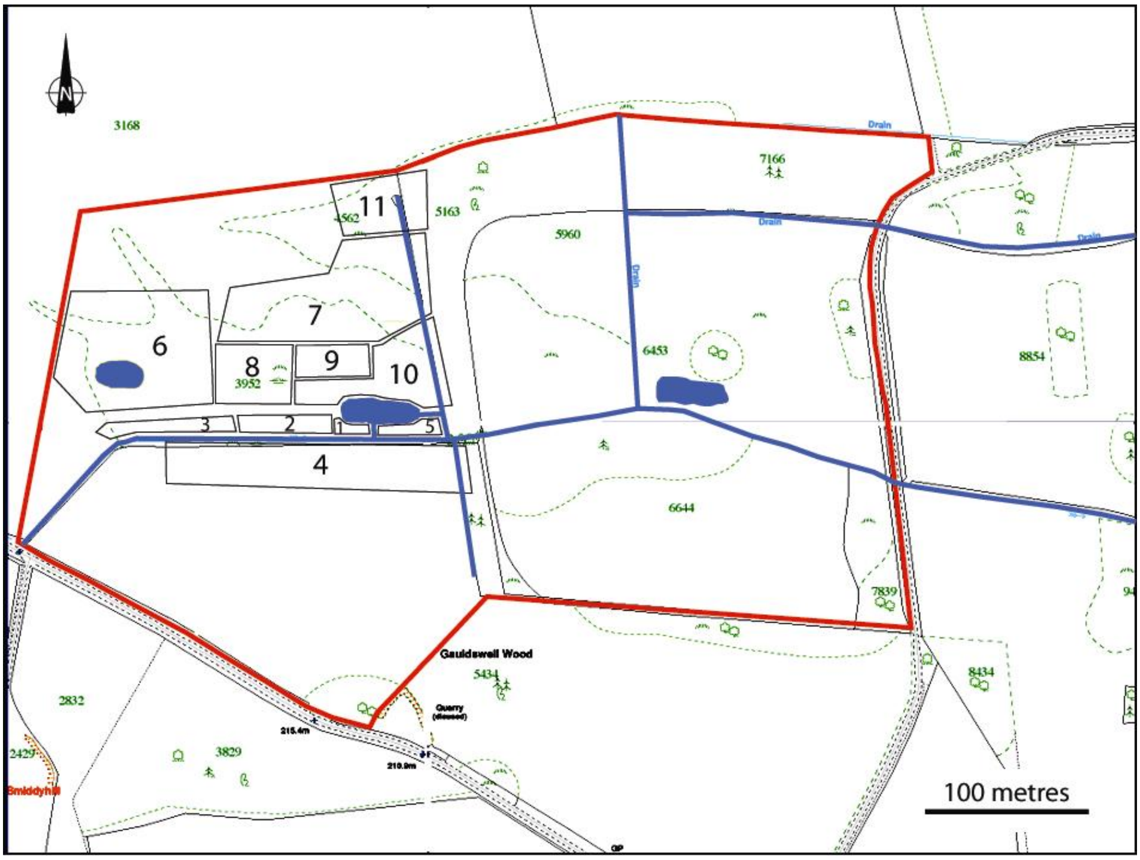
During the three year study period, numerous surveys were conducted of all successfully felled trees (hereafter referred to as “felled”) present at both the Stream and Lake Sites at the Bamff estate. Five surveys were conducted at the Stream Site and four at the Lake Site, on the dates shown in Figure 4.2 and Table 4.1. During each survey, a pair of surveyors walked through the whole of each site, identifying the genera (and where possible species) and year of felling of each beaver-cut stump, and measuring the girth of each stump immediately below the cut. As in the availability surveys, only trees of diameter greater than approximately 1 cm were recorded, and the genera of coniferous trees were generally unrecorded.

Supplementary data were also collected during the course of the latter two felling surveys at each site (surveys 4 and 5 at the Stream Site, and surveys 3 and 4 at the Lake Site) incorporating only those trees felled in year 3. In addition to the parameters measured in previous felling surveys, these surveys included the presence / absence of stump and log regrowth, presence / absence of deer browsing of this regrowth, degree of bark stripping of the felled log (when present) and fate category. Distinguishing between beaver and deer grazing of woody material is generally straightforward due to differences in the dentition of the animals. Deer only have lower incisors, with the upper incisors replaced by a horny plate, and consequently shoots bitten off have a frayed or ragged appearance (Bang & Dahlstrom, 1972). Beavers however, have both sharp upper and lower incisors so cut stems and branches generally have smooth edges (Jones *pers. obs*).

In order to distinguish those stumps already recorded in previous surveys, each stump was marked with a small amount of forestry paint of differing colour depending on the felling year. For example, all trees felled in year 1 were marked with red paint and all year 2 stumps marked green. Occasionally a tree would be missed during the course of one survey, but identified in the next survey. In such cases, it was generally a simple task to determine in which year the stump had been created due to the appearance of the stump (*e.g.* the colour, degree of weathering, covering of algae / moss, and length of any regrowth present). Again, as in the availability surveys, any multiple cut stems arising from the same stool (predominantly willow stools), were measured and recorded as separate felled trees.

Throughout the course of the initial surveys, it became apparent that at the Stream Site a number of felling blocks or zones could be identified. The boundaries of these felling zones were marked by natural and artificial landmarks (*e.g.* drainage ditches, glades, rides, fences), as well as some of the changes in canopy structure and composition that marked the boundaries of the habitat types identified in Figure 3.6. The zones often (although not exclusively) correspond to these different habitat types, although they were determined in order to assist the surveying process, and as newly beaver-exploited areas became apparent in later surveys, new felling zones were established. As well as facilitating the process of surveying the heterogeneous habitat of the Stream Site, the allocation of stumps to a particular felling zone provides a means of determining the approximate distance of the felled trees from the nearest pond. The location of each felling zone is shown in Figure 4.3.

Figure 4.3 Map showing the locations of the felling zones at the Stream Site.



Based on the Ordnance Survey map © Crown copyright

The habitat structure at the Lake Site did not easily lend itself to the allocation of stumps into specific felling zones, with the majority of deciduous trees being confined to the visually-uniform structure of Habitat C (see Figure 3.9) – the wet willow carr. At the Lake Site therefore, information concerning the location of all felled trees recorded in each felling survey, was restricted to either "On Land" or "In Water". In all other respects, the survey methodologies employed at both sites were identical.

The results discussed in this chapter regarding tree-felling rates were calculated from the data gathered during the five felling surveys undertaken at the Stream Site, and four felling surveys at the Lake Site, as described above. Observations of any construction projects undertaken by the beavers that were made during numerous visits to the Bamff sites during the course of this study, together with anecdotal evidence of the dates of beaver mortality / introduction from the landowner of the estate, have been incorporated into the calculations of annual felling rate in the manner described in section 4.5.3.

4.5.3 Tree fate surveys

The fate of felled trees was assessed by one survey at each of the two Bamff sites, conducted in June 2004, incorporating trees felled in both years 1 and 2. At the Stream Site, 50 randomly selected felled trees in close proximity (<20 m) to the beaver lodge were assessed, together with 50 trees further from the main pond (>20 m) located along the banks of the east-west drainage ditch. The former 50 trees ("Near") were located within felling zones 1, 5 and 10, whilst the latter 50 trees ("Distant") were predominantly found in felling zones 2 and 3. The genus, girth and year felled of each of the stumps were recorded, together with the following categorical variables: fate;

degree of bark stripping present on log (*i.e.* the felled trunk); presence of stump regrowth; presence of log regrowth; presence of deer grazing on regrowth.

The "Fate" category was assessed on a five point scale as shown in Table 4.2, whilst the degree of bark stripping on the felled log (if the log was still present) was assessed as None, Minor (*c.* ≤ 25%) or Extensive (*c.* 26 - 100%). The presence / absence of any stump or log regrowth was recorded, as was the presence / absence of any deer grazing damage to any such new shoots.

Table 4.2 Fate categories used for the Fate of Felling surveys.

Fate category	**Description**	**Degree of wastage**
1	Stem completely removed (*i.e.* not within 5 m of stump).	Low ↓ High
2	Stem largely chopped and removed (*c.* >50% removal).	
3	Stem partially chopped and removed (*c.* 20 - 50% removal).	
4	Stem largely intact except minor branches (*c.* <20% removal).	
5	Felled but otherwise intact.	

An almost identical survey was conducted at the Lake Site, with the only difference being in the selection of the felled stumps. In this case, 86 felled trees were selected that were located within permanently inundated areas of the loch margins (IW "In Water"), as well as 14 felled trees situated on the dry banks of the loch (OL "On Land"). The reason for this uneven split of the surveyed trees is the scarcity of felled trees on the dry banks of the loch throughout the site.

Supplementary data were also collected during the course of the latter two felling surveys at each site (surveys 4 and 5 at the Stream Site, and surveys 3 and 4 at the Lake Site, as described in section 4.5.2) incorporating only trees felled in year 3. These data included recording the genus, girth, fate category and degree of bark stripping of 315 trees at the Stream Site and 141 trees at the Lake Site. The presence / absence of stump and log regrowth and deer grazing, however, were only recorded at some of these supplementary trees (130 of the 315 supplementary Stream Site trees, and 117 of the 141 supplementary Lake Site trees).

4.5.4 Data analysis

In all cases throughout this thesis, the measured girth of any trees or stumps was transformed into a diameter by simple calculation (Diameter = Girth / 3.142). The diameter of a tree trunk is a common parameter measured by foresters, being routinely measured at a height up the trunk of 1.3 m, known as diameter at breast height (DBH) (*e.g*. Hamilton, 1975; Philip, 1994). In this study, DBH is impractical for many of the measured trees as beavers cut trees much closer to the ground, so all girth measurements (and derived diameters) were measured at "beaver height" – approximately 0.3 m above the ground. In the case of felled trees, measurements were made immediately below the cut.

Annual tree-felling rates at both the Stream and Lake Sites were derived from the tree-felling surveys conducted at both sites during the course of the study. Although beaver numbers present at the Lake Site remained constant (2) throughout the study period, the number present at the Stream Site fluctuated between 1 and 2 beaver as occasional deaths occurred. In order to standardise the felling rates between the two sites it is necessary to account for these population changes by calculating the number of trees felled per beaver per day, which have been expressed as “beaver days” (see Tables 4.3a and 4.3b). For example, on 21/05/02 the male beaver at the Stream Site died leaving just the female beaver present. The number of “beaver days” present in May 2002 therefore is calculated as 52 - *i.e.* (21 days x 2 beavers) + (10 days x 1 beaver). As well as allowing comparisons to be made between the felling rates observed at the two Bamff sites, such an approach will permit predictions for potential reintroduction schemes, which are likely to involve larger colonies of beavers than at Bamff, to be made more confidently.

The annual felling rates have been calculated assuming the beavers fell trees predominantly during the period of dietary dependence on woody matter (*i.e.* October – end of April as detailed in Figure 4.2). The exceptions to this are the Year 1 rates for both sites, due to the extended “woody season” imposed on the newly colonising beavers. In both cases, the rates have been calculated to include an extra fortnight of tree-felling activity to account for the extra construction-related felling that occurred during colonisation of the new sites. The beavers apparently began lodge construction almost immediately after being released to the Lake Site, whilst at the Stream Site the artificial lodge was used and dam building only commenced approximately 18 weeks after introduction to the site (P. Ramsay *pers. comm.*; Ramsay, 2002). The extension of the Year 1 woody season by only two weeks is believed justified, therefore.

Furthermore, the felling season at the Stream Site in Year 3 has been extended by 11 days, as construction of a large dam is known to have commenced on September 20th 2004.

As well as the annual felling rates that have been calculated for the whole of each of the three years of felling, where possible, each felling year has been divided into two parts. These two parts approximately represent the felling rates observed in the early part of the felling year (*i.e.* October, November and December) and the latter part (January, February, March and April). The exact split for each year's data into these categories varies slightly between year and site, due to each survey being conducted on a different date of the year. Tables 4.3a and b summarise the duration of the entire three felling years, and each of the derived early and late felling seasons for each year at the Stream and Lake Sites respectively.

The number of trees present in each fate category was tested for statistical significance by comparing the data to a uniform spread of trees between the five categories. Therefore, the null hypothesis is that the distribution of felled trees between the fate categories is uniform, and this was tested by *G*-test (Dytham, 2003). A limitation to this test, however, is that it does not provide a *P*-value when zero trees are observed in any fate category. The Kruskal-Wallis test was used to detect any differences between the diameters of trees present within each fate category, with significant effects being further analysed by *post-hoc* pairwise Mann-Whitney *U* tests (Dytham, 2003). All tests were performed using Minitab® Release 14, except the *G*-test which was calculated in Microsoft Excel 2003. In all cases, the statistical significance of results are reported using the standard convention (* $P<0.05$; ** $P<0.01$; *** $P<0.001$), and unless denoted as such they should be interpreted as not being significant (*i.e.* $P>0.05$).

Table 4.3a Durations and source data for each of the three entire felling years (bold font), and early ("a") and late ("b") felling seasons within each year (normal font), at the Stream Site.

Year	Start date	End date	Felling surveys	Calendar days	"Beaver days"
1	**14/07/02**[1]	**27/07/02**[1]	**1 & 2**	**226**	**349**
	1/10/02	**30/04/03**			
1a	14/07/02[1]	27/07/02[1]	1	127	250
	1/10/02	21/01/03			
1b	22/01/03	30/04/03	2	99	99
2	**1/10/03**	**30/04/04**	**2 & 3**	**213**	**213**
2a	1/10/03	23/12/03	2	84	84
2b	24/12/03	30/04/04	3	129	129
3	**20/09/04**[2]	**30/04/05**	**4 & 5**	**223**	**386**
3a	20/09/04[2]	18/11/04	4	60	60
3b	19/11/04	30/04/05	5	163	326

[1] Felling season extended in Year 1 and Year 1a due to early commencement of construction work for 14 days in July, prior to the main felling season.

[2] Felling season extended in Year 3 and Year 3a due to early commencement of construction work for 11 days in September, prior to the main felling season.

Table 4.3b Durations and source data for each of the three entire felling years (bold font), and early ("a") and late ("b") felling seasons within each year (normal font), at the Lake Site.

Year	Start date	End date	Felling survey	Calendar days	"Beaver days"
1	**14/07/02[3]** **1/10/02**	**27/07/02[3]** **30/04/03**	**1 & 2**	**226**	**452**
1a	14/07/02[1] 1/10/02	27/07/02[1] 21/01/03	1	127	254
1b	22/01/03	30/04/03	2	99	198
2	**1/10/03**	**30/04/04**	**2**	**213**	**426**
2a[4]	N/A	N/A	N/A	N/A	N/A
2b[4]	N/A	N/A	N/A	N/A	N/A
3	**1/10/04**	**22/04/05**	**3 & 4**	**204**	**563**
3a	1/10/04	11/11/04	3	49	98
3b	12/11/04	22/04/05	4	155	465

[3] Felling season extended in Year 1 and Year 1a due to early commencement of lodge construction work for 14 days in July, prior to the main felling season.

[4] The data for Year 2 at the Lake Site are unable to be split into early and late felling season rates due to the quantity and timing of the surveys conducted there.

4.6 Results

4.6.1 Annual felling rates

The number of trees felled by beavers at the two Bamff sites showed considerable annual variation over the three years of study, with a maximum number of trees felled of 631 and a minimum of 109 trees per year. Table 4.4 shows the numbers of trees felled by beavers in each of the first three years of occupation of the Stream and Lake Sites at Bamff. It is noticeable that in each year, more trees were felled at the Stream Site than at the Lake Site, and at each site the number of trees felled is high in the first year, falling in the second year and rising slightly in the third year.

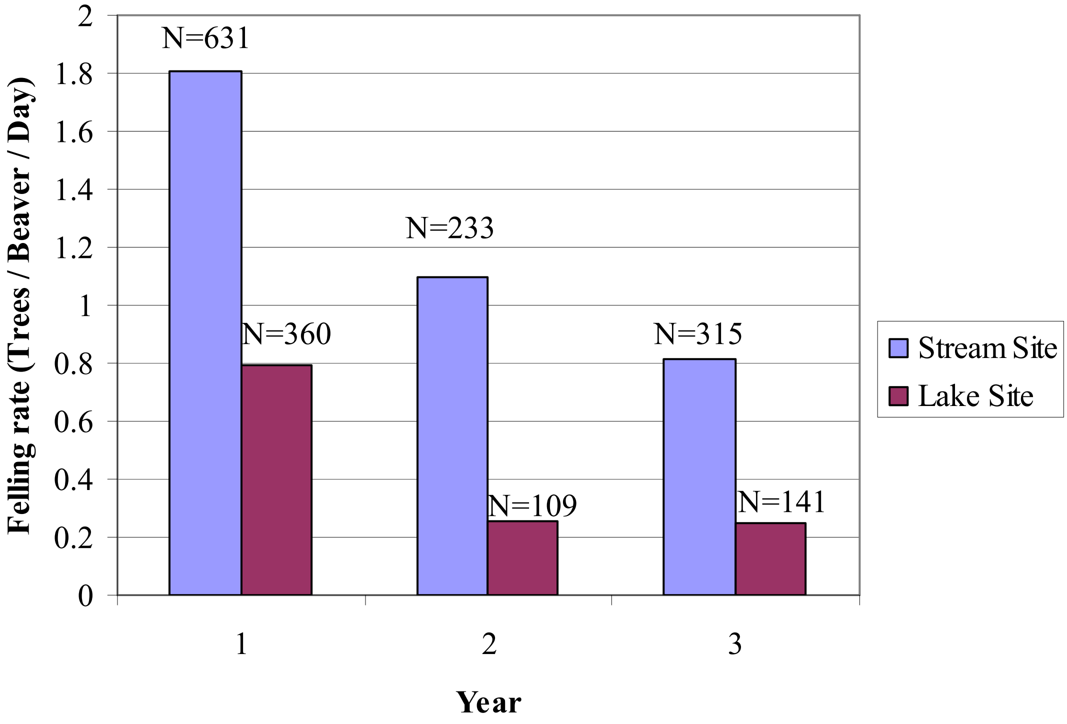
When differences in the number of beavers present at each site during each year, and the duration of the felling season at each site in each year, are accounted for by calculating the felling rate in number of trees / beaver / day, a different pattern is evident to that shown by the absolute felling data. Figure 4.4 shows the annual felling rates at both sites. In this case, the felling rate decreased from an initial high value, and continued to decrease over the two subsequent years, with this pattern most evident at the Stream Site. It is also noticeable that the initial felling rate at the Stream Site (1.81 trees / beaver / day) is approximately double that observed at the Lake Site (0.80 trees / beaver / day).

Table 4.4 Number of trees felled annually (bold font), and in early (“a”) and late (“b”) felling seasons within each year (normal font), at the Stream and Lake Sites.

Year	Number of trees felled	
	Stream Site	**Lake Site**
1	**631**	**360**
1a	316	242
1b	315	118
2	**233**	**109**
2a	203	Unknown[1]
2b	30	Unknown[1]
3	**315**	**141**
3a	185	24
3b	130	117

[1] The data for Year 2 at the Lake Site are unable to be split into early and late felling season rates due to the quantity and timing of the surveys conducted there.

Figure 4.4 Annual felling rates at the Stream and Lake Sites. The N values on each bar represent the number of trees felled.



When felling rates are calculated for the early and late sectors of each felling season, in three of the five instances that data are available for, the felling rate is higher in the early sector than in the late sector of the year. Only the first year of felling at the Stream Site shows the opposite trend with a lower felling rate in the early sector (1.28 trees / beaver / day) than the late sector (3.18 trees / beaver / day). The data for the third year of felling at the Lake Site show broadly similar felling rates in both sectors, at 0.25 trees / beaver / day in both the early and late sectors. These data for the Stream and Lake Sites are illustrated in Figures 4.5a and b respectively.

Figure 4.5a Early- ("a") and late-sector ("b") felling rates for each felling year at the Stream Site. The N values on each bar represent the number of trees felled.

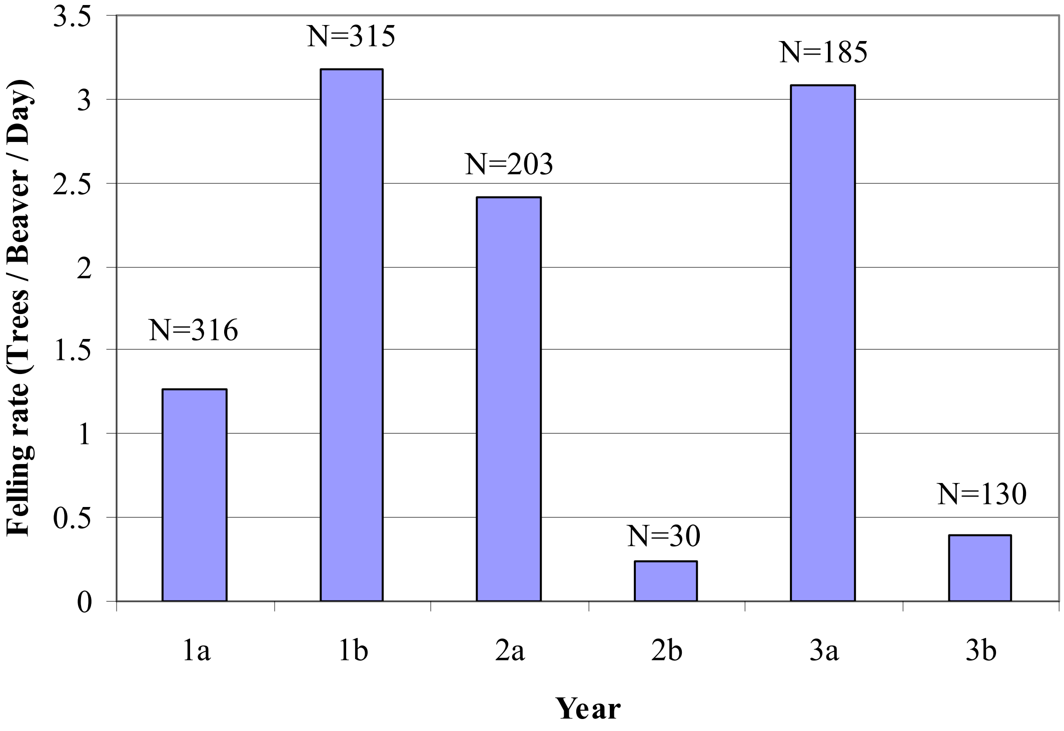
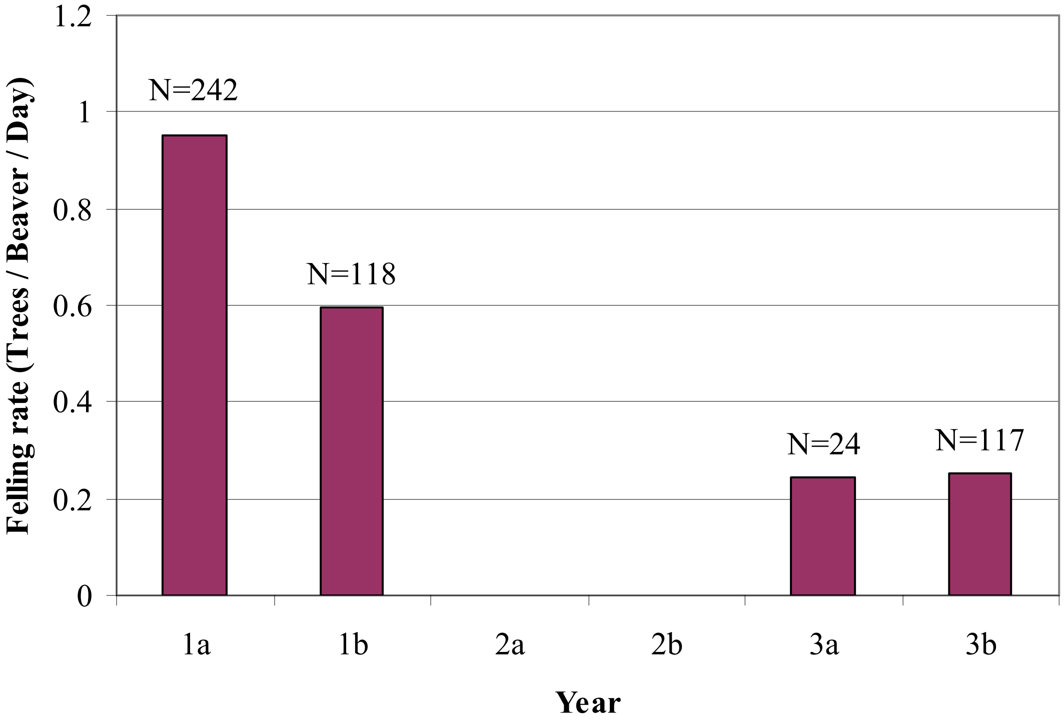


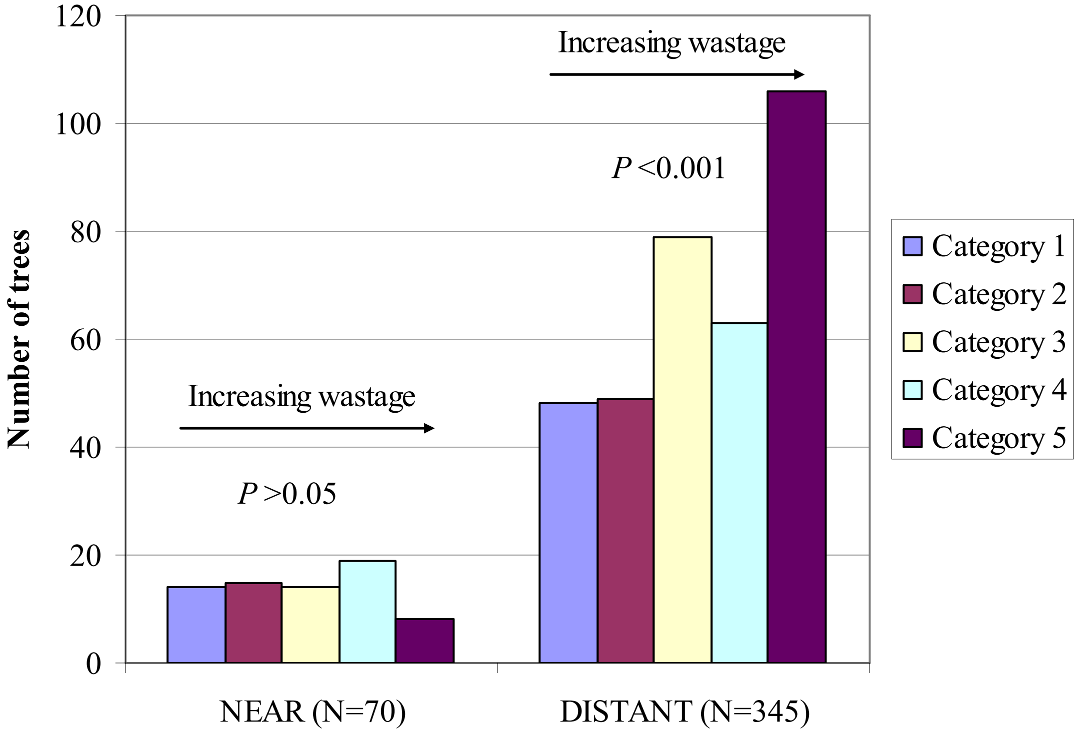
Figure 4.5b Early- ("a") and late-sector ("b") felling rates for each felling year at the Lake Site. The N values on each bar represent the number of trees felled.



4.6.2 Fate of felled trees

The general trend at the Stream Site was for felled trees to be approximately uniformly distributed between the five fate categories when near to a pond (NEAR $P>0.05$). As distance increased from a pond, however, more felled trees were associated with fate categories 4 and 5 than would have been expected by a purely uniform distribution (DISTANT $P<0.001$). Figure 4.6 shows these two distribution trends for each distance category.

Figure 4.6 Fate of felled trees in close proximity to (NEAR), and further from ponds (DISTANT) at the Stream Site. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.



Separating the data into the three tree genera felled in the greatest quantities (*Alnus spp.*, *Betula spp*. and *Salix spp*.) showed that only the distribution of *Betula spp*. in the DISTANT category was significantly different to a uniform distribution (P<0.001). The data for *Alnus spp*. near to a pond could not be tested by G-test, as felled trees were only distributed through three of the five fate categories. Figures 4.7a, b and c show the distributions of felled trees into fate categories for these three main genera.

Figure 4.7a Fate of felled alder trees (*Alnus spp.*) in close proximity to (NEAR), and further from ponds (DISTANT) at the Stream Site. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.

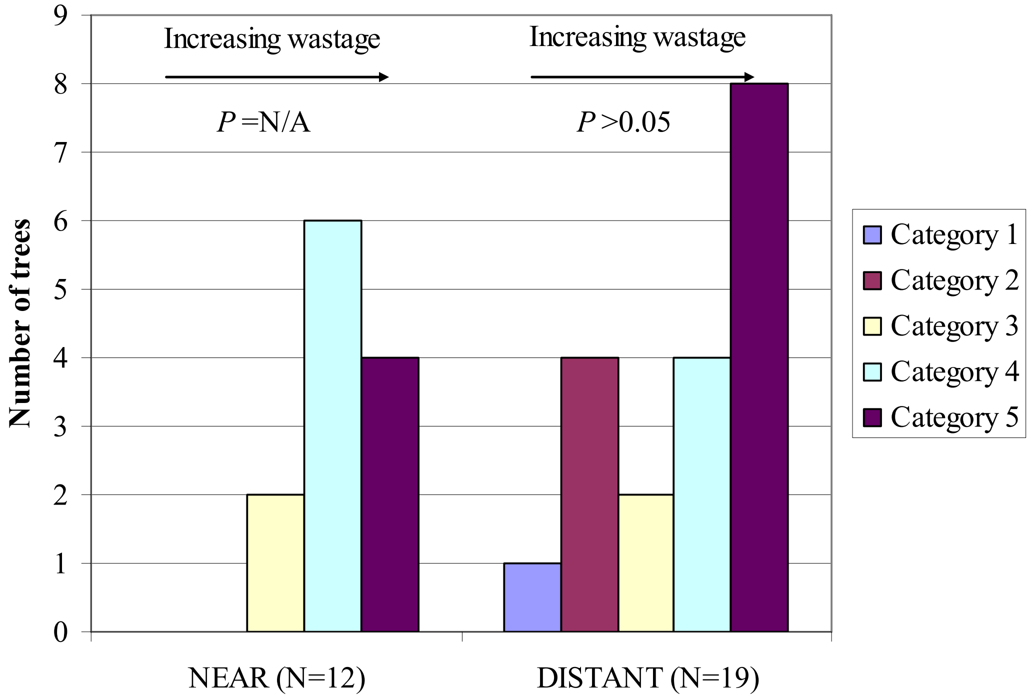


Figure 4.7b Fate of felled birch trees (*Betula spp.*) in close proximity to (NEAR), and further from ponds (DISTANT) at the Stream Site. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.

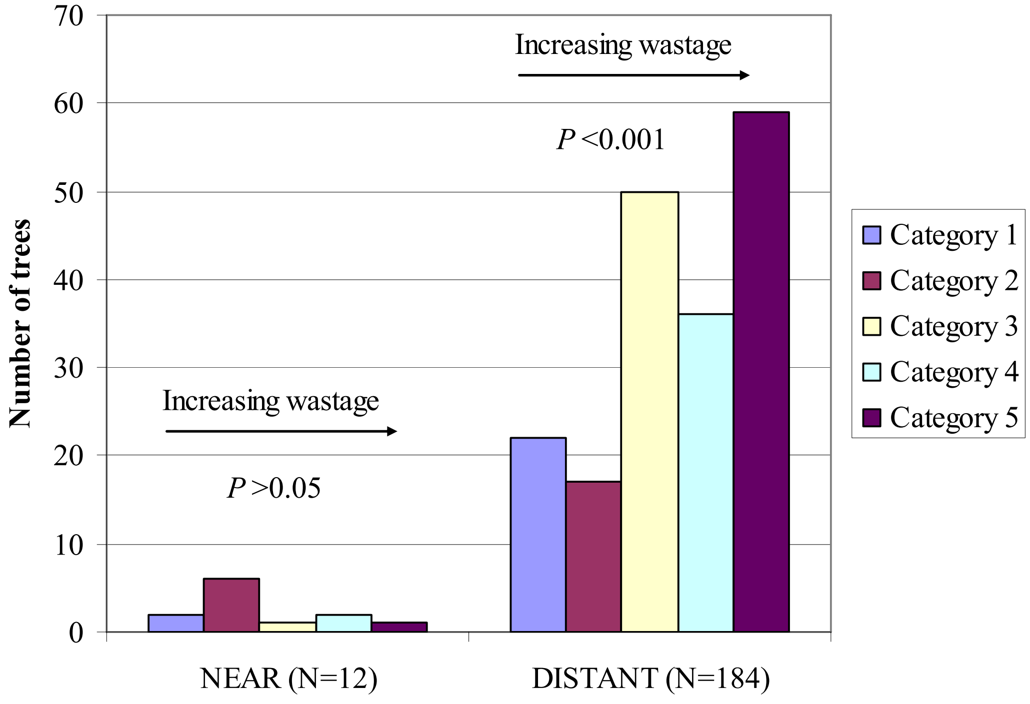
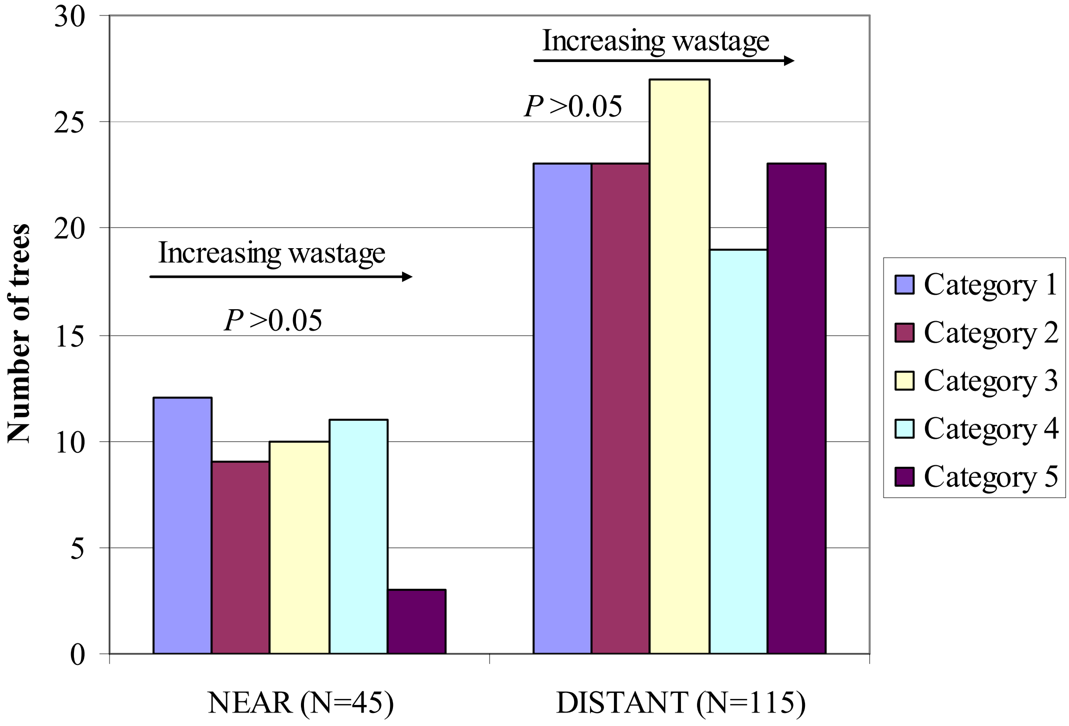
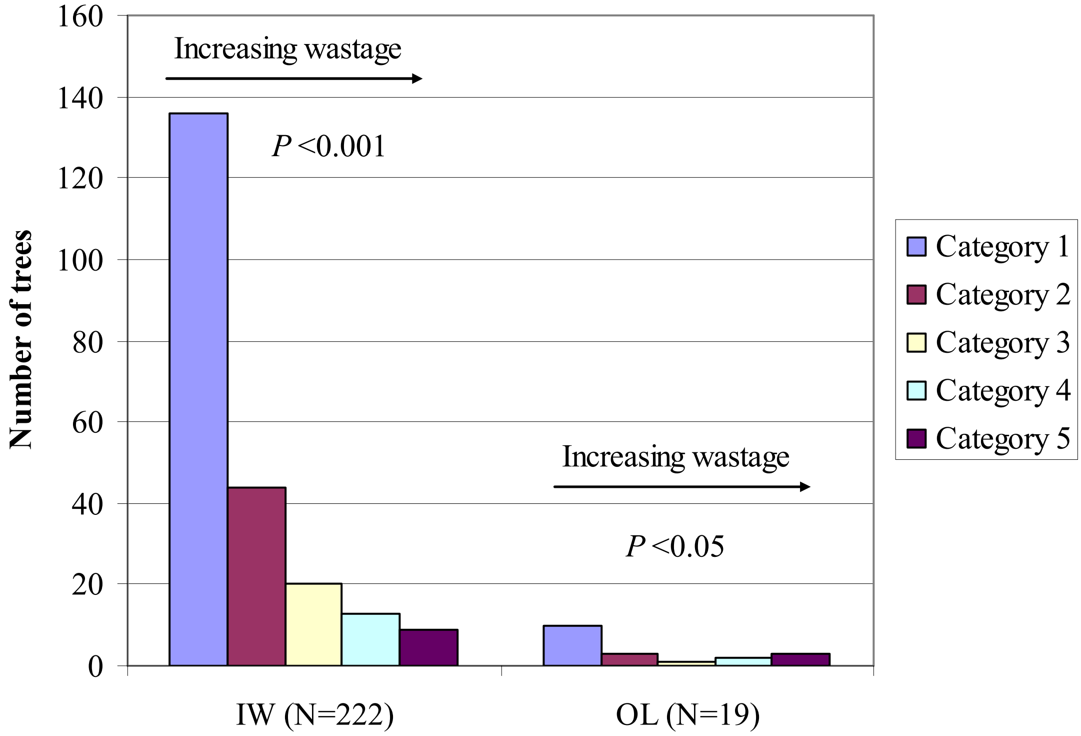


Figure 4.7c Fate of felled willow trees (*Salix spp.*) in close proximity to (NEAR), and further from ponds (DISTANT) at the Stream Site. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.



At the Lake Site, when considering trees located within the water of the lakes (IW) and on the shores of the lake (OL), the general trend was for more felled trees (both *Betula spp*. and *Salix spp*.) to be associated with fate categories 1 and 2 than would have been expected by a purely uniform distribution ($P<0.001$ and $P<0.05$ respectively). Figure 4.8 shows these two distribution trends.

Figure 4.8 Fate of felled trees within the water of the lake (IW), and on the shores of the lake (OL) at the Lake Site. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.



Separating the data into the only two tree genera recorded as felled in these surveys (*Betula spp*. and *Salix spp*.), showed that only the distribution of *Salix spp*. in the IW category was significantly different to a uniform distribution (*P*<0.001) (Figures 4.9a and b). The data for both *Betula spp*. and *Salix spp*. in the OL category could not be tested by G-test, as felled trees were not distributed in all of the five fate categories.

Figure 4.9a Fate of felled birch trees (*Betula spp.*) within the water of the lake (IW), and on the shores of the lake (OL) at the Lake Site. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.

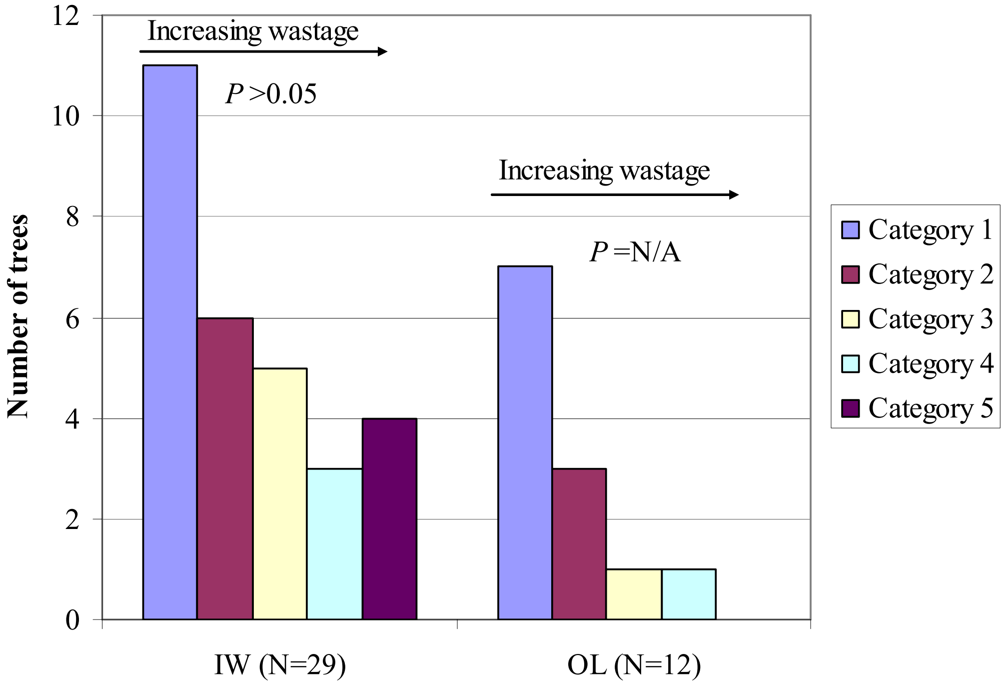
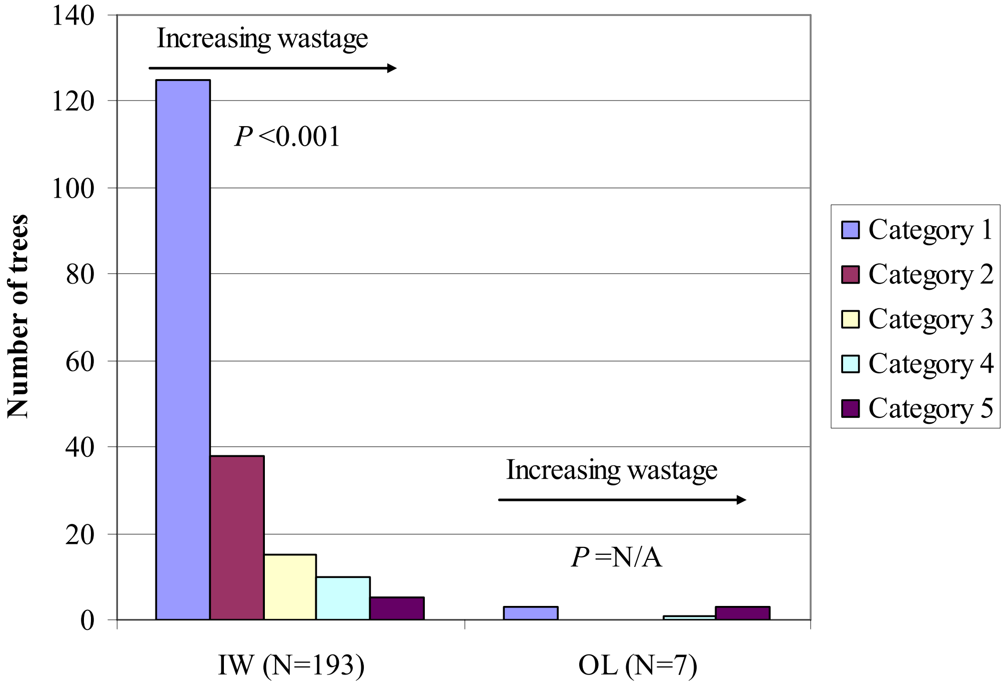
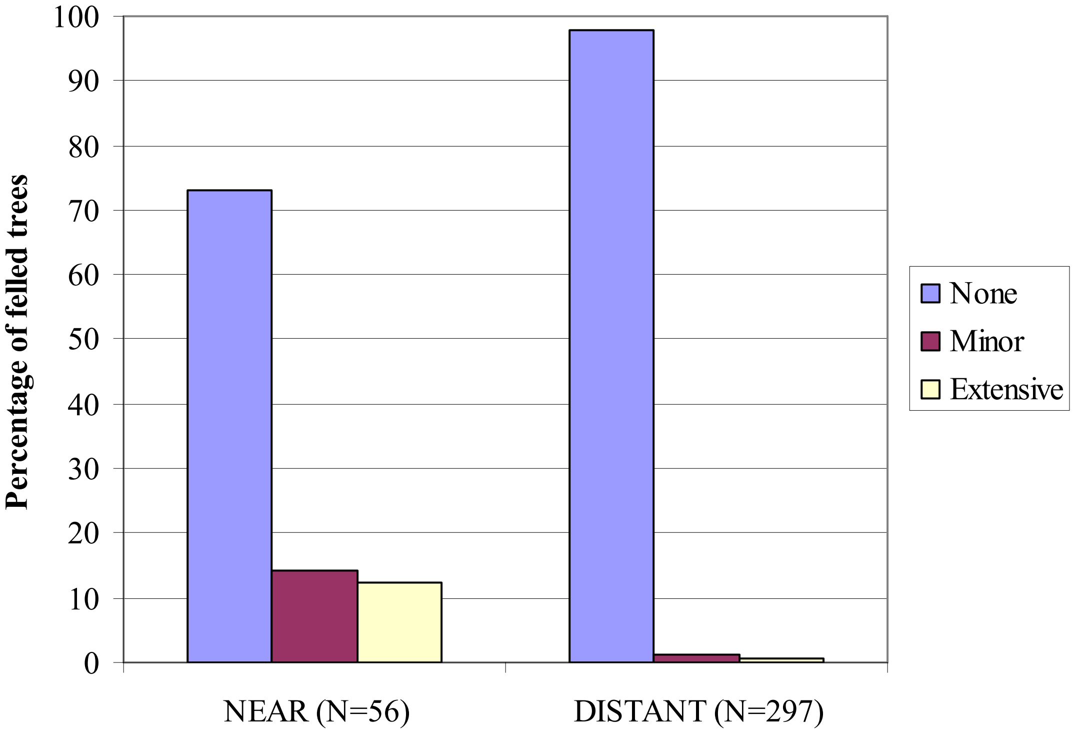


Figure 4.9b Fate of felled willow trees (*Salix spp.*) within the water of the lake (IW), and on the shores of the lake (OL) at the Lake Site. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.



When the degree of bark stripping of those felled trees not completely removed from the felling site by the beavers (*i.e*. those in fate categories 2-5) is examined, it is evident that the majority of trees are not stripped of bark *in situ*. At the Stream Site, a higher percentage of trees (*c*. 27%) are stripped of bark (either to a minor or extensive degree) when felled near to a pond than those felled a greater distance from the ponds (c. 2%) (Figure 4.10).

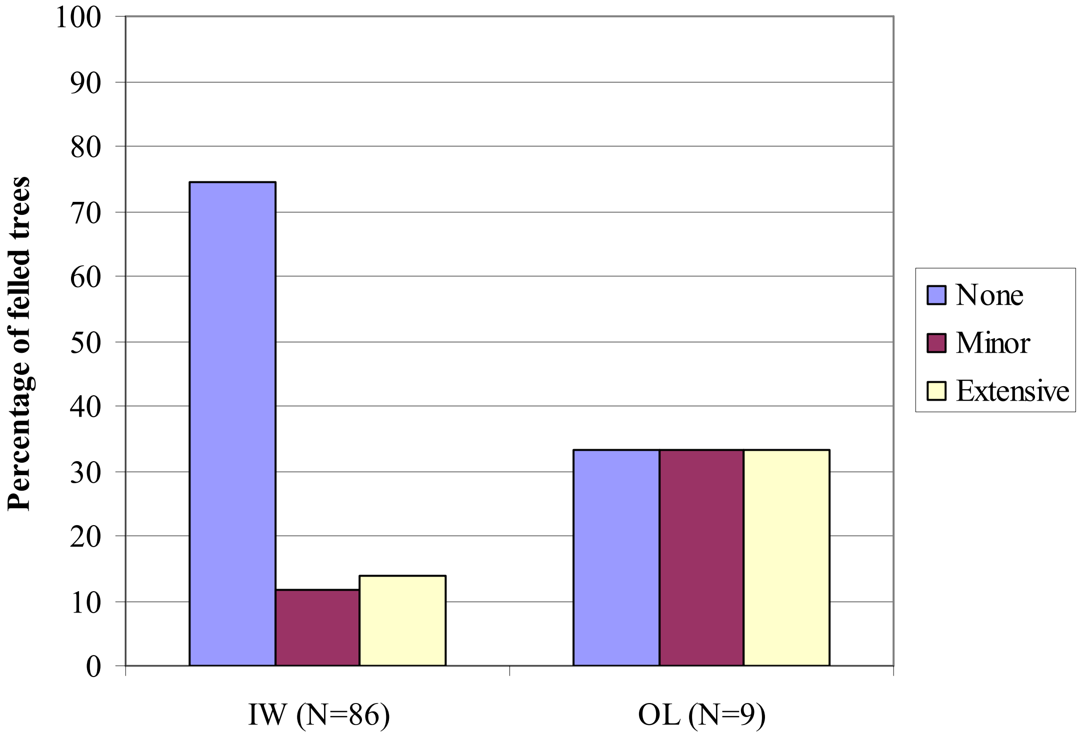
Figure 4.10 Percentage of felled trees in close proximity to (NEAR), and further from ponds (DISTANT) at the Stream Site, that show bark stripping. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.



At the Lake Site, a similar level of bark stripping (*c*. 26%) is evident in those trees felled within the water of the lake (IW) to those near to the ponds at the Stream Site.

The trend observed in those trees felled on the banks of the loch (OL) is different, with approximately 67% of felled trees showing some degree of bark stripping, although the sample size is very small in this case (Figure 4.11).

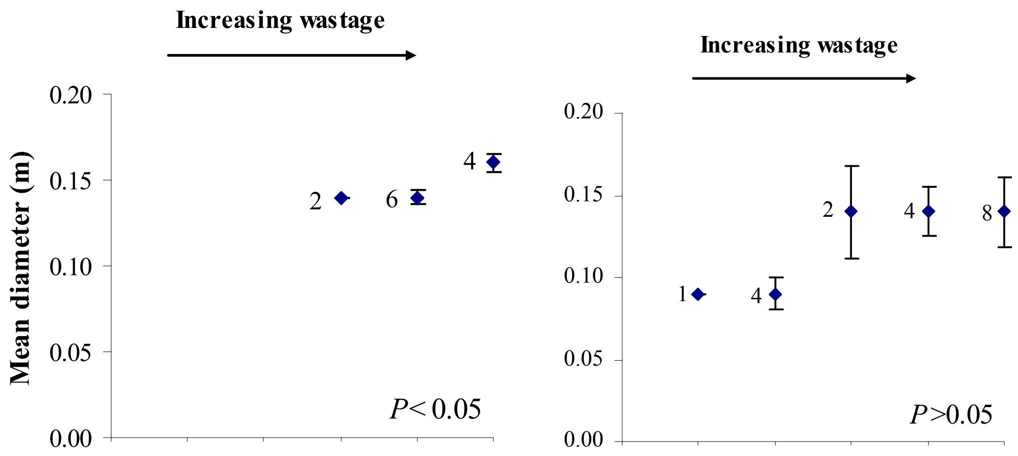
Figure 4.11 Percentage of felled trees within the water of the lake (IW), and on the shores of the lake (OL) at the Lake Site, that show bark stripping. N values represent the number of felled trees in each distance category. See page 124 for descriptions of categories.



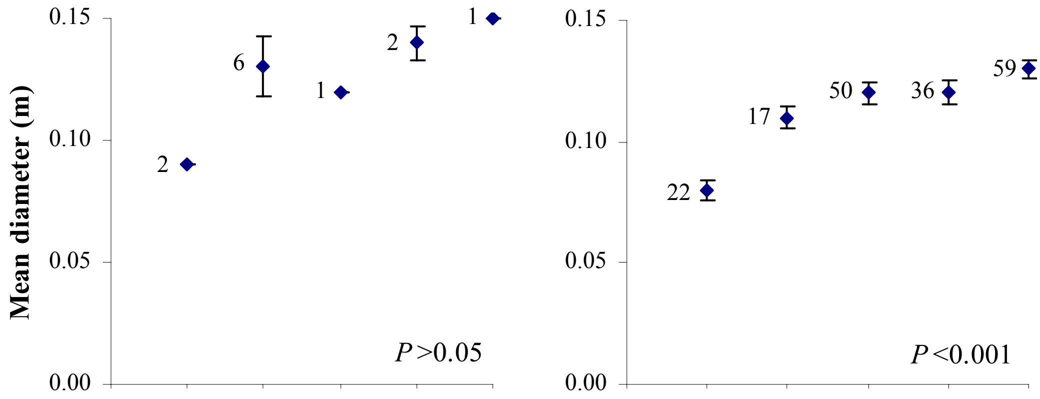
Examination of the mean diameters of trees present in each fate category shows that generally the diameter of completely utilised trees (fate category 1) are of smaller diameters than those trees that show higher degrees of wastage. At the Stream Site, however, these trends are not significant in either birches near to the ponds (Figure 4.12b, left graph) or alders further from the ponds (Figure 4.12a, right graph). Similarly, the trend for willow on the loch banks of the Lake Site is also not significant (Figure 4.13b, right graph). Significant results of *post-hoc* testing of pairwise comparisons are shown in Table 4.5, with all other possible comparisons being not significant (P>0.05).

Figure 4.12 Mean diameter (± 1 SE) of felled trees (a) *Alnus spp.* b) *Betula spp.* and c) *Salix spp.*) present in each fate category at the Stream Site. In each graph, wastage increases from left to right, and the left hand graphs show trees felled near to the ponds, with distant trees in the right hand graphs. Sample size is shown next to each data point. *P*-values show significance of the Kruskal-Wallis test. See page 124 for descriptions of categories.

a) *Alnus spp.*



b) *Betula spp.*



c) *Salix spp.*

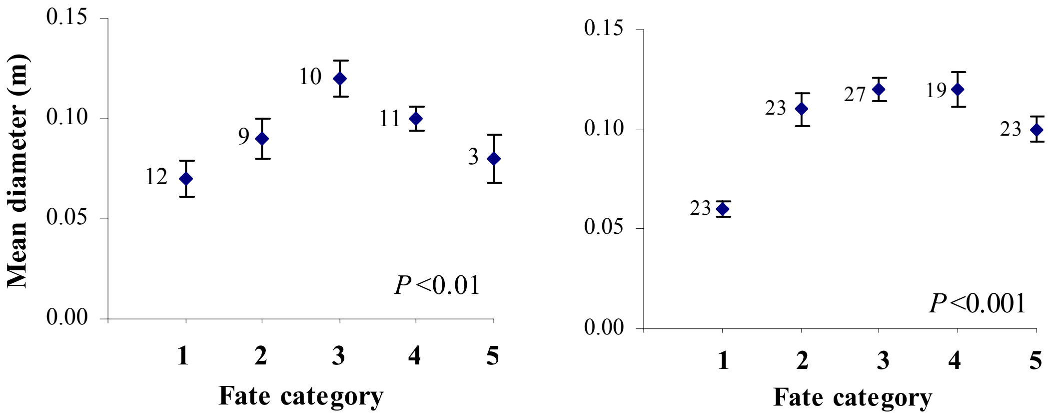
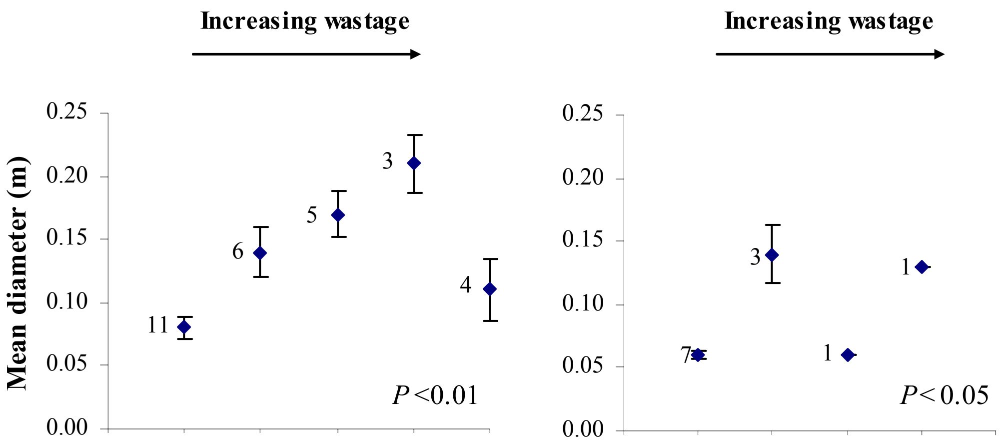


Figure 4.13 Mean diameter (± 1 SE) of felled trees (a) *Betula spp.* and b) *Salix spp.*) present in each fate category at the Lake Site. In each graph, wastage increases from left to right, and the left hand graphs show trees felled within the water of the loch, with trees on the wooded banks shown in the right hand graphs. Sample size is shown next to each data point. *P*-values show significance of the Kruskal-Wallis test. See page 124 for descriptions of categories.

a) *Betula spp.*



b) *Salix spp.*

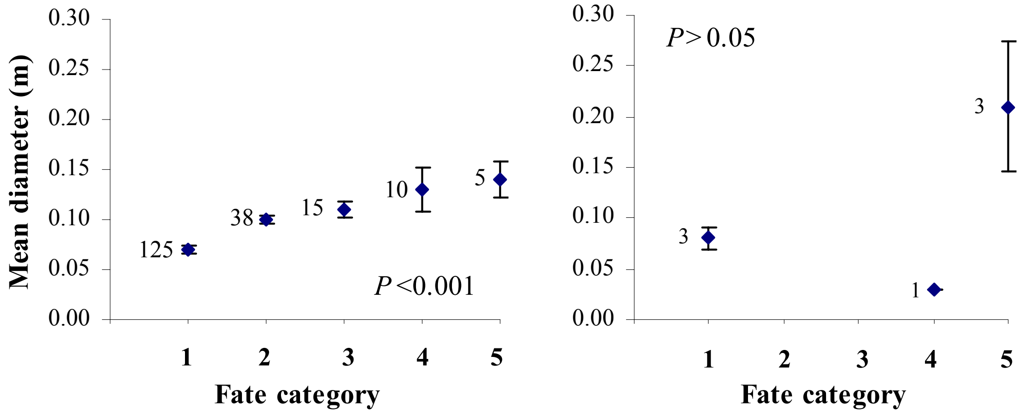


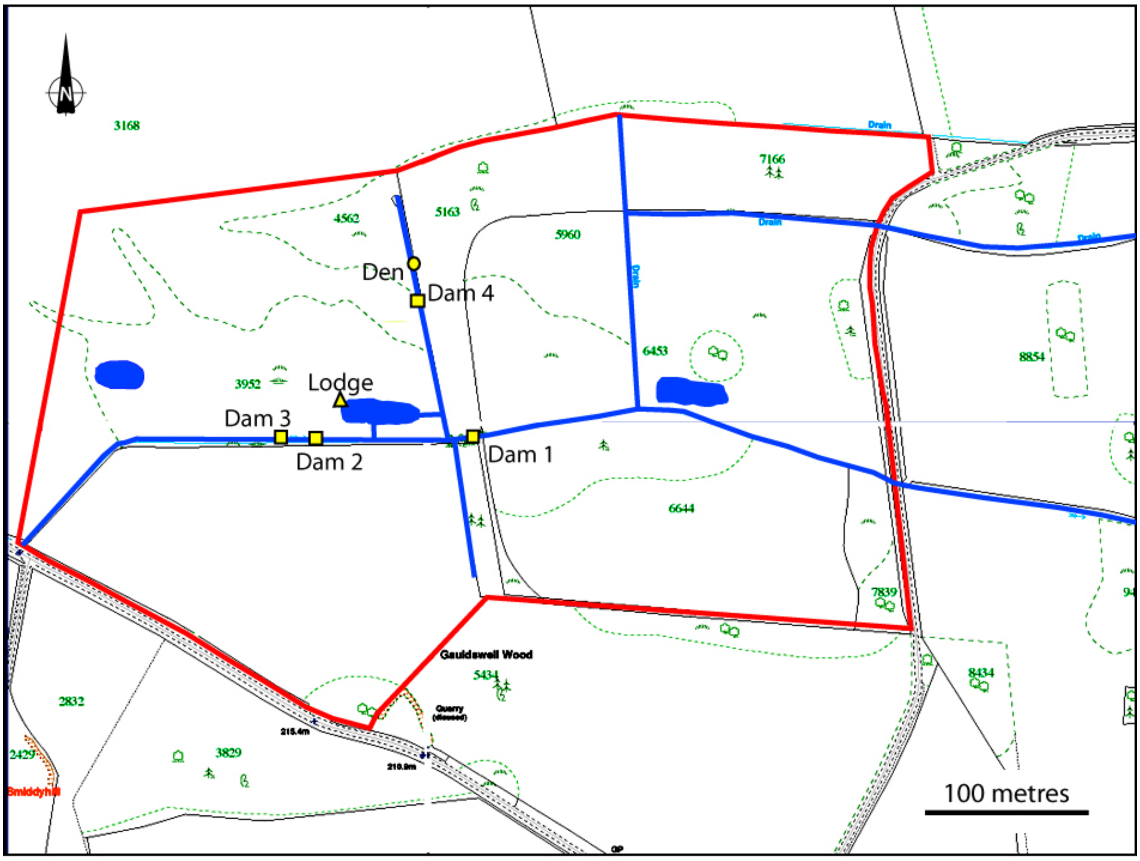
Table 4.5 Summary of significant *post-hoc* pairwise comparisons of the diameter of trees in each fate category. See page 124 for descriptions of categories.

Fate category comparison	**Stream Site**				**Lake Site**		
	***Salix spp.* Near Pond**	***Alnus spp.* Near Pond**	***Salix spp.* Distant**	***Betula spp.* Distant**	***Salix spp.* In Water**	***Betula spp.* In Water**	***Betula spp.* On Land**
1 v 2			$P<0.001$	$P<0.001$	$P<0.001$	$P<0.05$	$P<0.05$
1 v 3	$P<0.01$		$P<0.001$	$P<0.001$	$P<0.001$	$P<0.01$	
1 v 4	$P<0.05$		$P<0.001$	$P<0.001$	$P<0.01$	$P<0.05$	
1 v 5			$P<0.001$	$P<0.001$	$P<0.01$		
2 v 5				$P<0.01$	$P<0.05$		
3 v 5	$P<0.05$		$P<0.05$	$P<0.05$			
4 v 5		$P<0.05$					

4.6.3 Observations on construction and caching

At the Stream Site, the beavers have undertaken five separate construction projects during the three years of study – four dams and a single bank den. The locations of these structures are shown in Figure 4.14.

Figure 4.14 Map showing the locations of dams (■), lodges (▲)and den (●)at the Stream Site.



Based on the Ordnance Survey map © Crown copyright

In mid-July 2002 (*i.e.* Year 1) Dam 1 was constructed on the site of a pre-existing but broken weir-like structure, of approximate dimensions 3.0 m (W) x 0.7 m (H) x 0.7 m (D)[*] as shown in Figure 4.15. Two smaller dams (Dams 2 and 3 – see Figure 4.16) were constructed upstream of this dam later in 2002, each of approximately 0.7 m (W) x 0.4 m (H) x 0.5 m (D). A large structure (Dam 4) was built in September 2004 (*i.e.* Year 3), of dimensions 4.4 m (W) x 1.0 m (H) x 0.9 m (D) as shown in Figure 4.17. No lodge was constructed at the Stream Site as the beavers immediately occupied the artificial lodge after their introduction to the site, although a bank den (Den 1) was constructed a short distance upstream of Dam 4 following the construction of this dam (Figure 4.18).

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[*] Dam dimensions measured are height above the stream bed of the centre of the dam (H), width of the dam across the channel (W) and crest breadth at the centre of the dam (D).

Figure 4.15 Photograph of Dam 1 at the Stream Site, taken in April 2004.

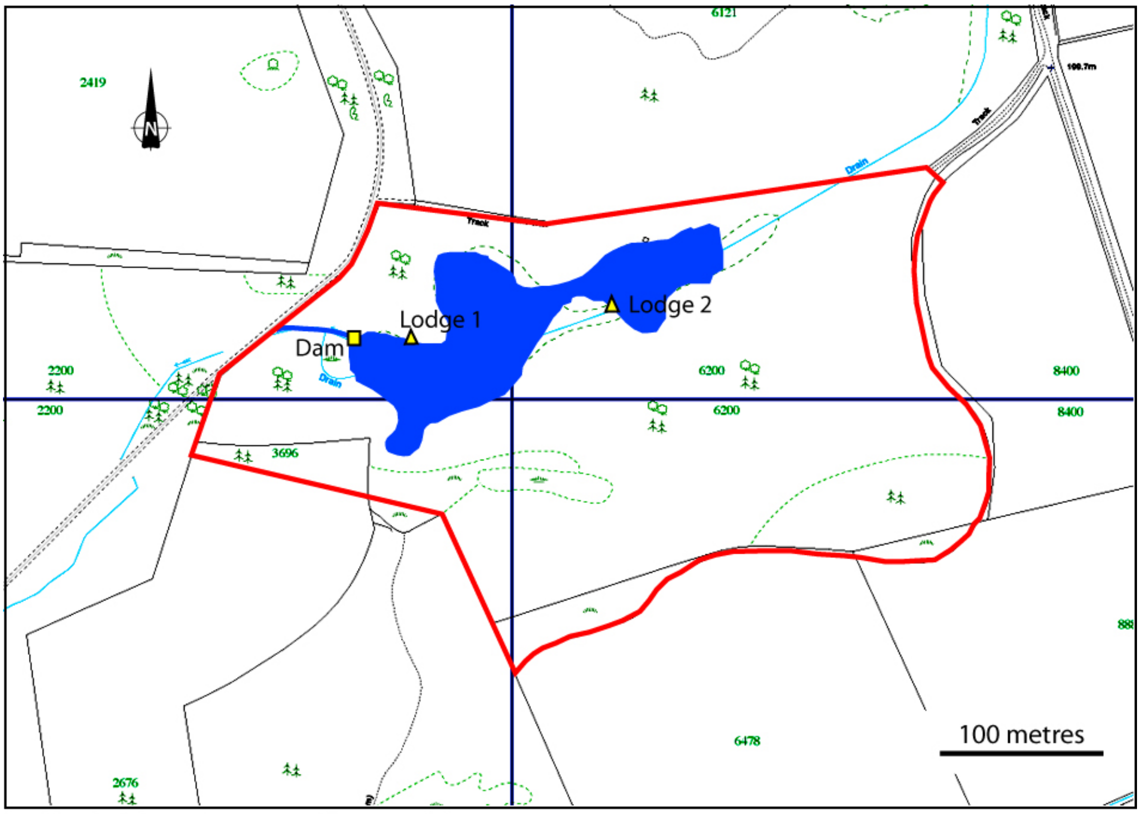
Figure 4.16 Photograph of Dam 2 at the Stream Site, taken in April 2004.

Figure 4.17 Photograph of Dam 4 at the Stream Site, taken in April 2005.

Figure 4.18 Photograph of bank Den 1 at the Stream Site, taken in November 2004.

In comparison to the Stream Site, the Lake Site beavers have undertaken far fewer construction projects, the locations of which are shown in Figure 4.19. Only one dam (Lake Dam) was constructed, located on the site of an existing broken sluice on the outlet of the loch (Figure 4.20).

Figure 4.19 Map showing the locations of dam (■) and lodges (▲) at the Lake Site.



Based on the Ordnance Survey map © Crown copyright

In stark contrast to the Stream Site beavers, the artificial lodge at the Lake Site was quickly rejected and a large bank lodge (Lodge 1) constructed in the first few weeks following release into the site which was occupied for the period of study (Figure 4.21). In April 2004 (*i.e.* the end of Year 2), construction of a second bank lodge (Lodge 2) was begun, but work was abandoned after approximately two weeks and the lodge was never completed (Figure 4.22).

Figure 4.20 Photograph of Lake Dam at the Lake Site, taken in April 2005.

Figure 4.21 Photograph of Lodge 1 at the Lake Site, taken in April 2005.

Figure 4.22 Photograph of Lodge 2 at the Lake Site, taken in April 2005.

Caching activity was observed to occur to greatly different degrees at the two sites. During December 2002 (Year 1) a single cache was observed in each of the two ponds in the western half of the Stream Site, with five more having been built outside the lodge by the time of survey in August 2004. As caching of woody material generally begins in the autumn, the caches recorded in this survey are attributed to the previous autumn of 2003 (*i.e.* Year 2). In contrast, no caches were discovered at all at the Lake Site during the three year study period. Table 4.6 summarises the caching and construction activity observed at the two Bamff sites, with an indication of the amount of work conducted by the beavers.

Table 4.6 Construction and caching activity at the Bamff sites.

Year	Stream Site	Lake Site
1a	Dam 1 (Large) 2 Caches (Moderate) Dam 2 (Small) Dam 3 (Small)	Lodge 1 (Large) Lake Dam (Moderate)
1b		
2a	5 Caches (Large)	
2b		Lodge 2 (Small)
3a	Dam 4 (Large) Den 1 (Large)	
3b		

4.7 Discussion

The data for both sites partially support the hypothesis that tree-felling rates by beavers are cyclical (Hypothesis 4.1, page 115). At both sites, the initial felling rate was high and fell dramatically in Year 2, as hypothesised. At the Lake Site, the felling rates in Years 2 and 3 were approximately equal, suggesting that the felling activity has stabilised and the site is in the consolidation phase of colonisation (as defined on page 114). At the Stream Site, however, the felling rate continued to fall in Year 3, suggesting that stability had not yet been attained at the site, and the consolidation phase is yet to begin (or is only just beginning). However, for cyclicity to be truly judged as having occurred, increased felling activity must be evident as the consolidation phase ends and territory expansion (and increased felling and construction activity) occurs.

Observations of the beavers suggested that this stage had not been reached at either site by the end of this research project. It is therefore apparent that three years is too short a time period for a full cycle to occur in either marginal habitat (*e.g.* the Stream Site) or an optimal habitat (*e.g.* the Lake Site), so Hypothesis 4.1 cannot be accepted at either of the Bamff sites. Further years of study at both sites would be required to fully test the validity of this hypothesis, as will be discussed in Chapter 8 of this thesis.

It is evident that the initial felling rate at the Stream Site is considerably greater than that observed at the Lake Site. Furthermore, although the trend at the Stream Site is of decreasing felling rates during the three years of study, the final rate (Year 3) is approximately equal to the initial felling rate observed at the Lake Site. Earlier (section 4.5.1) it was assumed that any changes in felling rate would be explained by changes in construction activity, as feeding behaviour would be constant between years (and beavers). Hypothesis 4.2 therefore proposed that felling rates would be directly influenced by the degree of construction and caching undertaken by the beavers, and the intensity of such activities should correspond to the felling rates observed at each site. It was observed that construction activity was most intense during Year 1 at both sites, with three dams built at the Stream Site, and a large bank lodge and small dam built at the Lake Site. Little activity occurred at the Lake Site in Years 2 and 3, corresponding to the low and stable felling rates in these years. In Years 2 and 3 at the Stream Site, construction activities were less intense than in Year 1, but more intense than the second and third years at the Lake Site. If Hypothesis 4.2 is to be accepted, according to the felling rate data we would expect to observe decreasing construction / caching intensity in Years 2 and 3 at the Stream Site than in Year 1, though still higher than the intensities at the Lake Site during these years. Indeed, the construction and caching patterns do correspond to the annual trends in felling rate observed at the two Bamff sites, and

Hypothesis 4.2, that felling rates are a direct product of construction and caching activity is therefore accepted.

Furthermore, the approximately constant felling rate during Years 2 and 3 at the Lake Site, during a period in which no caching and very little construction activity occurred, suggests that this felling rate results almost entirely from the feeding activities of the beavers. It might be inferred from these data therefore, that the minimum felling rate required to satisfy the dietary requirements of an adult beaver is approximately 0.25 trees / beaver / day of the felling season, or approximately 55 – 70 trees per calendar year, in a similar habitat to the Lake Site (*i.e.* a large lake with abundant macrophyte beds and a plentiful supply of riparian willow coppice). However, these rates do not take into consideration "invisible" construction work, such as maintenance of existing structures, so the accuracy of this figure is likely to depend upon the number of dams and lodges present in the territory. For example, the more dams and lodges present, the more trees will be needed to be felled for maintenance, and the approximate number of trees felled per beaver per calendar year during the consolidation phase will be at the higher end of this range.

It was initially suggested that the Stream Site represented habitat that would require considerably greater modification than the Lake Site. This is largely due to the lack of large areas of open water present at the Stream Site, which beavers require for safe habitation and exploration of nearby woodland. As a greater degree of modification would be required, more trees would be felled and felling rates would be higher than at the Lake Site. The observations of construction behaviour at the two sites over the study period, together with the annual felling rate data, confirm the suggestion that the Stream Site is of more marginal habitat value than the Lake Site. Hypothesis 4.3 is therefore accepted, as the observed construction intensity (and hence felling rate) was greater at the Stream Site than within the more optimal conditions of the Lake Site.

Whilst this study has shown that a cycle of annual felling rates exists at the Bamff sites, driven largely by different construction intensities between years, there is also a degree of variation in felling rate within each year. In three out of five felling years for which data are available for the early and late sectors of each year (two at the Lake Site and three at the Stream Site), there is a high felling rate in the early sector, which decreases in the later sector. Broadly, these sectors correspond to the periods before and after December 31st each year, and it is assumed that the majority of caching and construction work will occur in the earlier sector. This assumption is supported by the observations made on the construction activity at Bamff (Table 4.6), in which almost all of the building works were conducted during the early part of each felling year.

These observations also support the assumption that caching activity plays an important role in producing the high felling rates observed during the early-sectors, as well as construction activity. Rapidly falling autumn temperatures is one factor that triggers cache initiation (*e.g.* Semyonoff, 1957a; Wilsson, 1971), as beavers begin to form an underwater store of food in order to survive periods of winter ice-cover. In each of the three study years, minimum air temperatures began to fall rapidly towards 0°C during October with temperatures below freezing point observed from December through to March (Met Office, 2006). Further support for the significant influence of caching on the early sector felling rates is provided by Year 2 at the Stream Site, which shows a significantly higher early-sector felling rate than observed in the late-sector, despite the fact that no construction activity had occurred that year. This high level of early-season felling in Year 2 is likely to be predominantly due to the high caching intensity that was observed at the Stream Site during this period.

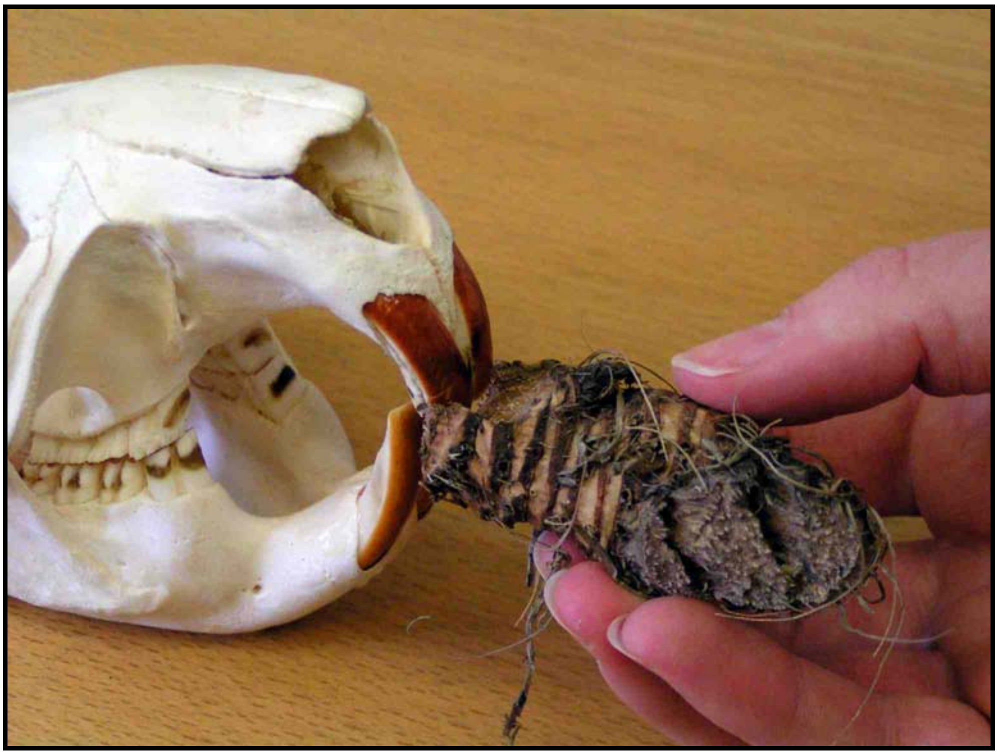
With regard to caching activity, the most striking trend evident from the Bamff data is that whilst caching occurred both regularly and intensely at the marginal habitat of the Stream Site, no evidence of any caches were discovered at the more optimal conditions of the Lake Site. This could be due to the relative ease of surveying the small ponds of the Stream Site when compared to the larger, deeper waters of the Lake Site. However, as caches are usually placed within the immediate vicinity of the lodge – an area which was repeatedly carefully surveyed at the Lake Site – it is unlikely that this is the sole explanation for this lack of caches. Given the extremely close proximity of the two Bamff study areas, any climatic variation between the two sites is also assumed to be negligible and not responsible for the observed difference in caching activity. The resident beavers do originate from different latitudes, and presumably climates, however. Generally, those in the Lake Site have been imported from southern Germany, whilst the Stream Site beavers originated approximately 800 miles further north in Norway. Other studies of beavers that have been translocated from one climate to another (*e.g.* Hartman & Axelsson, 2004), suggest that existing caching behaviour is quickly modified to suit the new environmental conditions. Whilst it seems plausible that the Bamff beavers initially had inherently different caching urges, it seems unlikely that after three years in Scotland similar behavioural patterns would not have emerged between the Norwegian and German animals.

If sampling error, climate and inherent behaviour are therefore eliminated as potential reasons for the different caching trends observed at the Bamff sites, some other site-specific factor must be exerting an influence on the behaviour of the beavers. It is proposed that this factor is the abundance of macrophytes present within the waterbodies of the two sites. At the Stream Site, the small ponds and ditches support only small amounts of macrophytes and marsh vegetation such as spearwort (*Ranunculus lingua* L.), water cress (*Rorippa nasturtium-aquaticum* L.), yellow iris (*Iris pseudacorus* L.) and angelica (*Angelica sylvestris* L.). Due to the relatively low supply of macrophytes, this winter store of rhizomes is small and the main food item is likely to be the cached woody material. At the Lake Site, however, there are large beds of emergent, amphibious, submerged and floating macrophytes, including large areas of yellow iris and bogbean (*Menyanthes trifoliata* L.). Both of these species have large rhizome systems which act as nutrient stores during the autumn and winter. It is possible that the Lake beavers have a ready-made cache of nutritious winter material already, and therefore do not need to create large stores of woody material. Large areas of iris grazing have been observed in the spring and summer at the Lake Site, with evidence from feeding platforms that the rhizomes and fleshy lower leaves are preferred. Such herbaceous grazing by the Bamff beavers during the warmer months will be further considered in Chapter 7 of this thesis, but abundant iris rhizomes that had been gnawed by beavers during the winter months (Figure 4.23) were also discovered at the Lake Site. This evidence suggests that the lack of caching activity at the Lake Site is indeed due to the beavers feeding on submerged herbaceous material during winter, and therefore the building of a woody cache to support them through periods of ice-cover is unnecessary.

It is also interesting to note that the division of the felling year into early- and late-sectors, provides further support for the conclusion that there is a minimum felling rate required to satisfy the dietary requirements of an adult beaver. From the Lake Site data, it was calculated that this corresponds to a felling rate of approximately 0.25 trees /

beaver / day of the felling season. The late-sectors of Years 2 and 3 at the Stream Site – periods when no construction or caching activity occurred - show very similar felling rates to this "minimum" value, at 0.23 and 0.39 trees / beaver / day respectively.

Figure 4.23 Photograph of yellow iris (*Iris pseudacorus*) rhizome showing evidence of beaver gnawing.



The interpretation of felling rates thus far, have not attempted to account for the "invisible" construction work conducted during the maintenance and improvement of existing structures. Whilst it is logical to assume that the impact of this maintenance will depend upon the degree of construction activity undertaken, and therefore play an increasingly important role in marginal habitats such as the Stream Site, verification of this is very difficult. Direct evidence would need to be gathered by time-consuming direct observations of the beavers' activity, and indirect evidence would often remain unobserved if maintenance occurred gradually, or indeed if it occurred during a short time period that was between site visits. It has therefore been assumed that maintenance of lodges and dams during this study, is likely to occur throughout the year at both sites, and to a lesser degree at the optimal conditions of the Lake Site. It also seems likely that the importance of maintenance will increase through time at marginal sites, such as the Stream Site, as more structures are built. The aforementioned difficulties in collecting data on lodge and dam maintenance, however, preclude validation of these assumptions.

By manipulation of data on felling rates both in this study and that previously published, estimated daily amounts of felling per beaver (as calculated over a calendar year, not a "felling year") can be derived, with the Bamff data expressed as 0.60 - 0.87 and 0.16 - 0.59 trees / beaver / day at the Stream and Lake Sites respectively. These values correspond well to the derived values from the available literature, *e.g.* Bradt (1938; 0.59 trees / beaver /day), Shadle *et al.* (1943; 0.10 - 0.32 trees / beaver / day), Nixon & Ely (1969; 0.80 - 0.96 trees / beaver / day) and Simonsen (1973; 0.39 - 1.52 trees / beaver / day).

Another factor exerting an influence on tree-felling rates that has been assessed at the Bamff sites is the degree of wastage of felled trees by beavers. Regardless of the ultimate use of felled trees, a high degree of wastage by beavers will inevitably lead to more felling, and hence higher felling rates, in order to meet the dietary demands of the animals and the construction requirements of the site. It was hypothesised (Hypothesis 4.4) that whilst wastage levels would be low at both Bamff sites, wastage would increase with distance from waterbodies, and therefore would be greatest at the Stream Site. After felling a tree, a beaver needs to spend time removing sections of trunk and branches that are small enough to transport back to the safety of the pond. With increasing distance from the pond, the degree of risk of predation increases, so it is possible that beavers become more vigilant and thus more likely to leave felled trees before utilisation is complete. Also, for the same reasons, the degree of *in situ* feeding on felled material – manifested as bark-stripping – should decrease with increasing distance from a waterbody.

In areas distant to the ponds at the Stream Site, significantly more trees were present in the fate categories that were indicative of high wastage than would be expected by a uniform distribution of trees between the categories. However, this relationship was not present when trees were felled near to ponds. Furthermore, this tendency to waste trees as distance increases from safety, is only evident in felled alders and birches, and there is no effect on willow trees. This suggests that the increased risk of spending time handling a felled willow is compensated for by a benefit to the beaver that birch and alder do not provide. In other words, it seems likely that willow trees are preferred above alder and birch, and therefore beavers are less likely to waste a felled tree despite the increased risk of spending time away from the pond. At the Lake Site, too few trees were felled distant to the lakes to show any significant trends. However, within the safety of the shallow waters of the lakes, the trend was for significantly less wastage (greater utilisation) than would be expected by a uniform distribution.

These trends are further supported by the rarity of *in situ* bark-stripping of felled trees at a distance from water compared to that observed near to the ponds at the Stream Site, or indeed within the water at the Lake Site. Even at close proximity to safety, however, the overwhelming trend is for felled trees to show no *in situ* bark-stripping, suggesting that cut sections of trunk are carried elsewhere to a safer location such as a feeding platform away from the pond margins, or even the lodge, before feeding commences.

In summary, the degree of wastage did increase with distance from ponds at both sites, as predicted, so Hypothesis 4.4 is accepted. However, at the Stream Site there was a surprisingly high tendency of trees near to the pond to be utilised inefficiently by beavers, with almost 60% of felled trees showing less than 50% utilisation. This high rate of wastage amongst “safe” trees at the Stream Site was unexpected, and perhaps shows the high levels of vigilance adopted by beavers even when foraging very near to safety.

In a study of wastage of felled trees by North American beavers (*Castor canadensis*) in habitat believed to be similar to the Stream Site at Bamff (Aldous, 1938), 27% of highly-preferred aspen (*Populus tremuloides*) were completely utilised, with 29% completely wasted. This corresponds quite well to the results observed at the Stream Site for the preferred willow trees (22% complete usage and 16% complete wastage). It is noticeable that greater wastage of preferred species occurred in the study of Aldous than at the Stream Site, which was attributed to a high degree of lodging of felled aspen on other unfelled trees, which occurred rarely in willows at Bamff. The less preferred species of white birch (assumed to be *Betula papyrifera* Marsh) showed only 16% complete usage by beavers, and 22% complete wastage (Aldous, 1938). Again there is a similar trend observed in the less preferred birches at the Stream Site at Bamff (12% complete usage and 31% complete wastage). Furthermore, at Bamff, alders are assumed to be less preferred than birch or willow (see Chapter 5), and show very low levels of complete usage (3%) and high levels of complete wastage (39%).

The figures for the Lake Site showed very high levels of complete usage (64% in willow and 44% in birch) and low levels of complete wastage (4% in willow and 10% in birch), largely due to the high component of trees present in the water of the loch, and the extremely close proximity of bankside trees to the water. Similar figures of complete wastage, in the range 1 - 6% of all felling, have been documented in studies conducted in broadly similar habitat to the Lake Site (Brenner, 1962; Nixon & Ely, 1969; Simonsen, 1973).

At Bamff larger trees were more likely to be completely wasted than smaller felled trees, a finding supported by other studies (Aldous, 1938; Stegeman, 1954; Simonsen, 1973). For example, Stegeman (1954) reports complete wastage of 2% of small (*c.* 0.05m diameter) and 35% of large (*c.* 0.20 m) felled trees, which are consistent with those of Simonsen (1973) in which 1.2% of small (diameter ≤ 0.02 m) and 36% of large (>0.24 m diameter) trees are completely wasted. Aldous (1938) noted that although greater wastage occurs in large trees, which when partially used tend only to have the upper branches removed, the bark of upper branches is preferred by beavers to that of the main trunk. The greater ratio of branches to trunk in large trees means that more preferred material is available to beavers than in smaller trees, although more material is also wasted. For example, Aldous (1938) suggests that 50% usage of a single 7 inch diameter tree (*c.* 0.18 m) provides the same amount of food to a beaver as four completely used 3 inch trees (*c.* 0.08 m).

These published works and the results presented in this chapter, clearly show that beavers often fell more trees than they require for food and construction purposes, although the extent of wastage will depend upon stand factors, such as tree species and sizes available, as well as habitat factors, such as the proximity of trees to water and the density of the canopy. The influence of these wastage trends further support the observed differences in felling rate between the two Bamff sites. The consistently higher felling rates at the Stream Site are therefore not only a product of the greater degree of construction and caching evident at the site, and of the inferred higher requirement for regular maintenance of these structures, but also of the higher wastage of felled trees here. This effect of wastage is likely to be constant throughout the felling year, and therefore have no effect on the early- and late-sector trends observed at the Stream Site.

5 Effects of beaver activity on riparian tree communities: ii) Tree-felling patterns and preferences

5.1 Abstract

The previous chapter provided data on the number of trees felled by beavers at Bamff, and how the felling rates varied with time since colonisation of a site, and habitat suitability of the site. In order to predict the potential effects of a beaver reintroduction to Scotland, the preferences of beavers for certain trees, sizes of tree and foraging area need to be considered in conjunction with felling rates. Some authors have produced computer models that predict the possible impacts of a reintroduction scheme to the UK, based upon the preferences of beavers in other European countries or North America. However, no published data exist on such aspects of beaver ecology within the UK itself not withstanding that already published using data from the Bamff sites. This chapter presents the foraging preferences of beavers within the Scottish landscape over three years after initial colonisation of two sites. The sites represent contrasting habitat quality, with the data allowing comparisons of beaver behaviour to be made between a marginal and more optimal environment in Scotland.

Preferences for different tree species were found to vary, with willow and aspen being consistently favoured, and elder and conifers generally avoided. However, when a variety of palatable broad-leaved species were available, the beavers diet was apparently wide, despite the abundance of the most preferred species remaining high. It was also evident that the beavers were preferentially foraging as near to the safety of water as possible, with most felling activity being confined to woodland immediately surrounding a pond, or within the shallow waters of the lochs. Comparatively few trees were felled at distances greater than 50 metres from a pond at the Stream Site, or anywhere on land at the Lake Site. As time progressed through the study, the riparian resource at the Stream Site began to become depleted, and consequently the beavers

were forced to forage at greater distances from the ponds more often. This temporal variation did not occur at the Lake Site, as the larger resource of trees situated within the water of the lochs were not sufficiently depleted over the three-year study to necessitate the beavers foraging on land more frequently.

As well as these generic and locational preferences exhibited at Bamff, there was also evidence of size-selectivity occurring. The nature of this selectivity varied between the two sites, however. At the Lake Site, the beavers foraged as hypothesised, by consistently selecting for the smallest trees, and selecting against the largest trees. At the Stream Site, the smallest trees were consistently selected against, with larger trees being preferred. The reasons for this difference in behaviour were unclear, although the role of felling to supply construction materials was proposed as a possible answer. It was shown that when felling in areas of high construction activity, the beavers were less selective in terms of the genera and size of trees felled, with proximity apparently the most important factor in determining tree selection.

Finally, the felling behaviour of beavers was investigated for compliance with optimal foraging theories. It was hypothesised that the felling patterns would be those expected of a central place forager feeding on large, single prey items. This hypothesis was accepted at the Lake Site, but the unexpected size-selectivity patterns exhibited by the Stream Site beavers meant that the hypothesis was rejected at this site. It is proposed that the central place foraging theory was applicable to beavers foraging in optimal or well-developed habitats, but was not valid for beavers in marginal habitats requiring considerable modification.

5.2 Introduction

Amongst the herbivores of Europe and North America, beavers have the unique ability to fell mature trees, providing both a food source and a construction material with which the beaver physically modifies its environment. Such modifications rely upon a plentiful supply of wood and are integral to the beaver's dual-role of "keystone species" and "ecosystem engineer" (*e.g.* Jones *et al.*, 1994; Kitchener, 2001). Due to their ability to fell mature trees and because foraging is confined to a zone surrounding a central place, beavers have great potential to alter forest ecosystems through herbivory (Johnston & Naiman, 1990). Indeed, it is this felling of trees and the subsequent creation of dams, that are likely to cause most concern to the public when considering a trial reintroduction of beavers to Scotland (*e.g.* Scott Porter Research & Marketing Ltd. 1998). Further conflicts can occur when beaver foraging threatens biodiversity interests and habitats with special protection designations. For example, European aspen is a tree species of high conservation value in the UK, supporting a variety of threatened invertebrates and fungi (Cosgrove *et al.*, 2005). It is also widely believed to be the preferred food item of beavers (e.g. Simonsen, 1973, Gorshkov *et al.*, 1999).

Much interest has been focussed on the foraging strategies adopted by both the North American and Eurasian beaver, with field studies being used to test optimal foraging theories, such as those of Schoener (1971), Orians & Pearson (1979) and Pyke (1984). Such studies have generally investigated the preferences of beavers for different food items of varying sizes at a range of distances from a pond, and then compared the results to the foraging patterns predicted by the published theories. Although many studies have investigated the tree-felling activity and woody species food preferences of the beaver in Europe, most have been conducted on well-established beaver colonies (*e.g*. Simonsen, 1973; Lahti & Helminen, 1974; Haarberg & Rosell, 2006). The studies of the reintroduced beavers in the Biesbosch area of the Netherlands offer a notable exception (Nolet *et al*., 1994), as does the research presented in these thesis conducted at Bamff.

Whilst of considerable value to theoretical ecologists, these studies and those conducted in North America (*e.g*. Jenkins, 1980; McGinley & Whitham, 1985; Basey *et al*., 1988; Fryxell & Doucet, 1993; Gallant *et al*., 2004) also have important practical implications. Given the great capacity of beavers to physically modify their habitat, and the potential conflicts with human interests that such modifications can lead to, a full understanding of such a vital aspect of beaver ecology is very valuable to conservationists and ecologists. Furthermore, reintroduction schemes and natural range expansion has seen the return of beavers to many areas of Europe and North America after lengthy absences. In these areas, the possibility of conflict is likely to be high as the public are unaccustomed to the felling of trees by beavers.

Knowledge of foraging patterns and preferences of beavers would therefore be useful in predicting the likely effects of a beaver reintroduction to a particular area of Scotland. Particularly vulnerable trees of high conservation or economic interest, for example, could be targeted for protection from beavers by fencing. Indeed one of the criteria for the recent rejection of the proposed Knapdale trial reintroduction scheme was the perceived threat to the qualifying interests of the Atlantic oakwoods SAC within the release area. The foraging data gathered in this study could be used in conjunction with published studies from elsewhere in Europe and North America, to better assess the likelihood of beavers having detrimental impacts on this protected area.

The aim of this chapter is to investigate the foraging patterns of Eurasian beavers during the first three years of release to two enclosed Scottish sites, focussing particularly on the preferences shown for certain woody species, the tree size-selectivity exhibited, and the distances foraged over. Comparisons will be made with similar studies and optimal foraging theories, with the following hypotheses tested:

5.1 Generic preferences will be exhibited by the beavers, with aspen and willow preferrred and elder and coniferous species avoided.

5.2 When constructing dams, proximity of trees should override species or size preferences, with trees nearest the construction site being preferred.

5.3 Size preferences will be exhibited by the beavers, with small trees generally preferred over larger ones.

5.4. Beavers will exploit areas near to the pond in preference to areas a greater distance away.

5.5 The beavers will act as optimal central place foragers and felling patterns will reflect those predicted by this strategy for single-prey loaders feeding on large items.

5.3 Methods and materials

5.3.1 Tree availability surveys

Tree availability surveys were conducted at both Bamff sites to assess the size and composition of the woody resource available to the beavers, and these surveys have been fully described in Chapter 3 of this thesis. The survey methodology at the Stream and Lake Sites can be found in sections 3.2.1 (page 85) and 3.2.2 (page 91) respectively.

5.3.2 Tree-felling surveys

During the three year study period, numerous surveys were conducted of all successfully felled trees (hereafter referred to as “felled”) present at both the Stream and Lake Sites at the Bamff estate. Full details of all surveys undertaken have previously been described in section 4.5.2 (page 120).

It is important to note that the locations of available and felled trees were surveyed according to the methods described in sections 3.2.1, 3.2.2 and 4.5.2. The use of handheld global positioning systems (GPS) were trialled at both Bamff sites, but only sporadic satellite signals were obtained under the tree canopy and readings were deemed to be inaccurate and inconsistent.

5.3.3 Cafeteria experiments

Cafeteria experiments were trialled at both Bamff sites in order to gain first-hand data on the tree species preferences of beavers, rather than preferences inferred from felling trends which are affected by felling for non-dietary purposes. The first trial (Cafe S1) was conducted in early August 2004, by fixing small branches of various tree species to a line of string (*c*. 0.5 m long) attached at either end to a small stake fixed into the ground. In order to maximise the chance of the beavers encountering the cafeteria, the line stretched across a well-used beaver trail leading from the pond into the surrounding woodland, that showed signs of recent use in the form of stripped woody remains. The number of leaves initially present on each branch were counted and recorded, and recounted after 24 hours, at which point the methodology was assessed. It was discovered that the leaves of the branches had rapidly dried out during the short period of the trial and had been left untouched by the beavers. However, the experimental set-up had been flattened suggesting that the beavers had used the trail and simply chosen to avoid the offered food items, possibly because of the decreased palatability due to partial desiccation of the leafy branches.

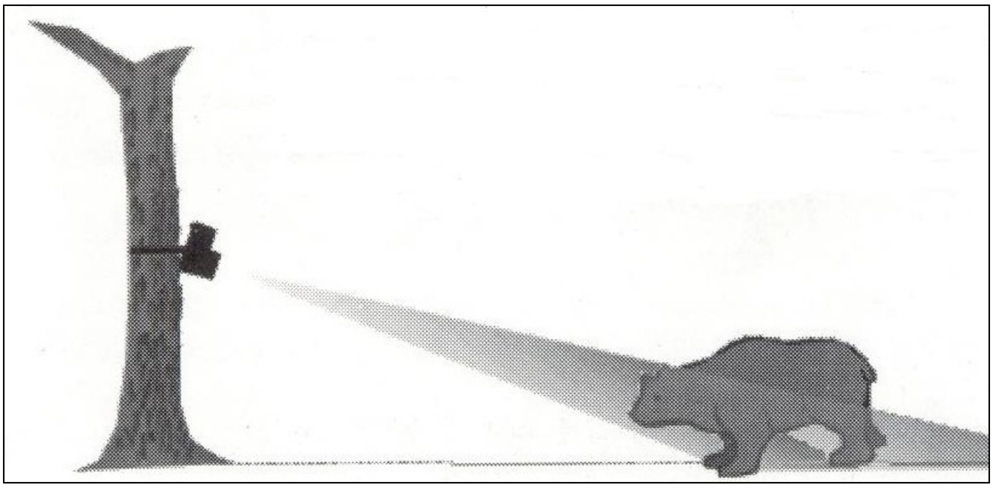
The second trial (Cafe S2) was conducted in mid-September 2004 using a modified version of the first trial, in an attempt to reduce the effects of the deterioration of the food items. Small branches were loosely secured to one of three stakes driven into the ground in the area surrounding the beaver lodge, which showed signs of recent beaver activity. The cut end of each branch was driven into the ground to further secure the material and to allow some water uptake to occur from the soil. The material was collected after 48 hours and showed no evidence of beaver feeding, despite the presence of other beaver activity having occurred nearby. Again, the leafy branches were badly dried out and were probably of low palatability, and it is hypothesised that this is why they were ignored by the beavers.

During the summer of 2005 (July – August), a revised cafeteria methodology (Cafe S3) was implemented at the Stream Site. Leafy branches of different species were loosely tied to a single stake, located on a well-used beaver trail running from the pond into the surrounding woods. To avoid the problems of the material drying out and deteriorating, small plastic beakers of water were dug into the ground at the base of the stake and their tops covered with waterproof duct tape to prevent evaporation. The cut end of each branch was then pushed through the tape into the water reservoir, which also contained a small amount of proprietary house-plant food. The number of leaves present on each branch were counted at the start of the cafeteria and recounted after leaving the material *in situ* for 48 hours. The cafeteria was re-set seven times giving eight separate cafeteria results (Cafe S3.1 – S3.8), and the immediate area was occasionally baited with apples and carrots in order to attract the beavers to the area. Figure 5.1 shows the typical arrangement of the food items in Cafe S3. One branch each of willow (*Salix spp*.), grey alder (*Alnus incana*), birch (*Betula spp*.), sessile oak (*Quercus petraea*), white poplar (*Populus alba*) and beech (*Fagus sylvatica*) were present in each of the eight cafeterias.

Figure 5.1 Typical arrangement of food items in Cafe S3.

However, this methodology would only demonstrate the preferences of the beavers for the food items if some material (assumed to be the least preferred species) was left by the beavers. If all of the material, or indeed all of two or more species offered, was removed, there would be no way of knowing which species had been eaten first, and hence which was the preferred food item. In an attempt to eliminate this limitation, this third set of cafeterias had the addition of a TrailMaster TM550® passive infrared trail monitor connected to a specially modified Canon Sureshot A1® waterproof film camera with flash. These were secured to ranging poles approximately 3 m from the cafeteria, facing the offered food items, and being a "heat and motion" sensor any movement of warm bodies within the field of sensitivity would trigger an "event" to be recorded (time and date) and a photograph taken. The equipment was configured in a manner so that animals smaller than beavers could pass the monitor without triggering a "event", by experimenting with the monitor's settings (*e.g.* infrared pulse interval) as described in the operating manual supplied with the equipment. To prevent the film and camera batteries being entirely used during non-beaver events, such as passing deer, the camera was only activated between dawn and dusk. Furthermore, as the monitor "sees" movement over *c*. 20 m away in a detection zone covering an angle of 150°, the equipment was configured facing downwards towards the cafeteria (as shown in Figure 5.2), with much of the angle reduced by covering all but a thin section of the centre of the sensor with masking tape. It was anticipated that this set-up would detect the movement and presence of the beaver at the cafeteria, and the sequence of triggered photographs would allow the order of feeding to be determined, and hence preferences inferred.

Figure 5.2 Limiting the detection range of the trail monitor by angling the sensor down towards the cafeteria.



During August 2005 this same experimental methodology was used at the Lake Site on five occasions (Cafe L3.1 – L3.5) at a well-used feeding station on the floating rafts of vegetation. The only difference in the procedure was the absence of the pots of water, with the cut stems being driven into the saturated soil of the mat instead. This amendment proved satisfactory, with no apparent desiccation of the leafy branches occurring during each cafeteria. For a short period prior to the first cafeteria, and occasionally during the course of the experiment, the feeding platform was baited with carrots and apples. One branch each of birch, sessile oak, beech and sycamore (*Acer pseudoplatanus* L.) were present in all five cafeterias, willow and rowan (*Sorbus aucuparia* L.) present on four occasions, and white poplar used in only one cafeteria.

5.3.4 Cache assessment

In August 2004 (Year 2) the numbers of discrete caches present in the two ponds of the Stream Site were recorded and assessed. The physical dimensions (length, height and width) of each pile were measured and an approximate volume of stored material was calculated from these figures, together with an estimate of the total number of branches stored in each cache. In over half the number of caches found, detailed assessment of the size (branch length and mid-point girth) and species composition of a representative sample (*c*. 20-40% of all branches present in the cache) of the stored branches was made, together with the presence / absence of adventitious roots. Supplementary data on the approximate size distribution of branches in the remaining caches was provided by visual assessment. No caches were discovered at any time during the three-year study at the Lake Site.

5.3.5 Data analysis

Much of the data gathered during the availability, felling and fate surveys (as described in sections 3.2, 4.4.2 and 4.7.2 respectively) have been used during the analysis and discussion of the results of the tree-felling patterns and preferences. All measured girth values were transformed into diameters in the manner described in section 4.4.3, and tree / branch diameters reported as per the following size-class scheme:

Class 1 – diameter ≤ 4 cm
Class 2 – diameter 5 - 10 cm
Class 3 – diameter 11 - 16 cm
Class 4 – diameter ≥ 17 cm

Throughout the results section, tree locations are referred to as three categories at the Stream Site, and two categories at the Lake Site. Stream Site locations are determined by the proximity of trees to the nearest pond or lodge. The nearest zone to a pond or lodge is the “Riparian” zone (RP) - within 20 m of a pond or lodge – whilst the most distant zone is “Distant Woodland” (DW) which is further than 50 m away.

Intermediate to these zones is “Near Woodland” (NW) which covers the area 20 – 50 m from a pond or lodge. In terms of the felling zones described in section 4.5.2 and illustrated in Figure 4.3, each of the three locations at the Stream Site contained the following felling zones:

RP	Felling zones 1, 5, 6 and 10
NW	Felling zones 2, 3, 4 and 9
DW	Felling Zones 7, 8 and 11

In Year 3, however, the construction of Dam 4 and the subsequent pond and den development immediately upstream of it, meant that the NW zone incorporated felling zone 7 in addition to those listed above, whilst the DW zone only contained felling zones 8 and 11. No adjustment to the RP zone in Year 3 due to this dam was required. The locations of trees at the Lake Site were simply classified as either “On Land” (OL) or “In Water” (IW).

Where appropriate, results were tested using the Kruskal-Wallis test, with significant effects being further analysed by *post-hoc* pairwise Mann-Whitney *U* tests (Dytham, 2003). All tests were performed using Minitab® Release 14. In all cases, the statistical significance of results are reported using the standard convention (* $P<0.05$; ** $P<0.01$; *** $P<0.001$), and unless denoted as such they should be interpreted as not being significant (*i.e.* $P>0.05$).

5.3.5.1 Electivity indices

The preference of beavers for a particular genus of tree was examined by calculating an electivity index (*ln Q*) (after Jacobs, 1974) which relates the relative abundance (*ra*) of a genus to the relative use (*ru*) of that genus. The index was calculated using the data collected in the availability surveys (section 3.2) and the felling surveys (section 4.5.2) conducted at both Bamff sites. The index used was:

$$ln\ Q = \ln[(ru(1-ra)) / (ra(1-ru))]$$

with a value greater than zero indicating preference for a genus, and a value less than zero indicating selection against the genus (Jacobs, 1974). The significance of the *ln Q* of a genus *i* was calculated by the equation:

$$X^2 = (ln\ Q)^2 / [1/x_i + 1/(m - x_i) + 1/y_i + 1/(n - y_i)]$$

where x_i is the number of trees of genus *i* felled and y_i is the number of all trees of genus *i* present (*i.e.* felled and standing). The total number of all felled trees irrespective of species is represented by *m*, whilst *n* is the total number of all trees (felled and standing) present in the sampled area. The X^2 statistic was then compared to a χ^2–distribution with one degree of freedom (Jenkins, 1979; Nolet *et al.*, 1994). The data used to calculate the electivity indices (*ln Q*) were collected during the numerous tree-felling and availability surveys conducted at both sites throughout the study, using relative felling and availability values. However, in order to test the statistical significance of the index by converting it to X^2, absolute felling and availability figures had to be derived. This was performed by relatively straightforward calculations and extrapolations.

For example, at the Stream Site, as the size, composition (tree species and diameters) and location of each of the availability quadrats were known, the composition of a particular felling zone (see Figure 4.3) could be extrapolated from its component availability quadrats. Firstly the area of each felling zone was estimated from site maps of known scale, and divided by the total known area of the availability quadrats present in the zone, to give a multiplication factor specific to that felling zone. The total number of available trees present in the availability quadrats was then multiplied by the multiplication factor for the felling zone, to give an estimated total number of trees available in the whole zone. Using the tree species and size compositions from the availability quadrats, it was then a simple matter of factoring up the numbers by the multiplication factor to give an estimate of total numbers of each tree species / sizes available within each felling zone. The worked example below shows this process for Felling Zone 2 at the Stream Site.

A	Approximate area of Zone 2 (m^2)	793
B	Number of availability quadrats present in Zone 2	2
C	Total surveyed area (*i.e.* **C** x quadrat area) (m^2)	200
D	Zone 2 multiplication factor (*i.e.* **A** / **C**)	3.965
E	Multiply species-size composition data from the two availability quadrats in Zone 2 by **D** to give estimated species-size composition for whole of Zone 2, as shown in Table 5.1 using data for willow trees.	

This process was repeated for each tree species found in every availability quadrat throughout all 11 felling zones, so that an estimate of tree species-size composition of each felling zone was developed. These compositions are applicable to the period immediately prior to introduction of the beavers to the Stream Site (Time = 0), as the availability surveys (although obviously conducted after beavers were present) included all felled trees present in each quadrat in the availability calculations. At the end of each felling year, the species-size data of trees felled by beavers in each felling zone (as recorded in the felling surveys) could simply be subtracted from the estimated compositions for the zone at the start of the year, i.e. at the start of year 2, the estimated composition was derived from the Time = 0 composition minus the trees felled in year 1.

Table 5.1 Example of calculation of overall tree species-size composition for *Salix spp.* at Felling Zone 2 of the Stream Site.

Trunk diameter (m)	Number of trees present in availability quadrats	Multiplication factor (D)	Estimated total number of trees in Felling Zone
0.00 – 0.02	0	3.965	0
0.02 – 0.04	16	3.965	63
0.04 – 0.06	3	3.965	12
0.06 – 0.08	1	3.965	4
0.08 – 0.10	0	3.965	0
0.10 – 0.12	3	3.965	12
0.12 – 0.14	2	3.965	8
0.14 – 0.16	5	3.965	20
0.16 – 0.18	5	3.965	20
0.18 – 0.20	2	3.965	8
0.20 – 0.22	0	3.965	0
0.22 – 0.24	0	3.965	0
0.24 +	0	3.965	0
Total	**37**	**3.965**	**147**

The accuracy of this approach for estimating the availability of trees initially present in each felling zone from data collected in a relatively small number of quadrats, is inevitably affected by the percentage of the zone area covered by the quadrats. Generally 10 - 20% of each zone area was covered by the quadrats, although in some of the smaller zones the figure was larger (*e.g.* 36% in Zone 5). As the Stream Site was largely planted by the landowner (P. Ramsay *pers. comm.*), and the felling zones determined (amongst other things) by canopy features, the uniformity of the composition of each zone is perhaps greater than would be evident in an area of entirely self-seeded natural woodland. The estimates are therefore believed to be accurate reflections of the species-size composition within each felling zone.

5.3.6 Explanation of terminology

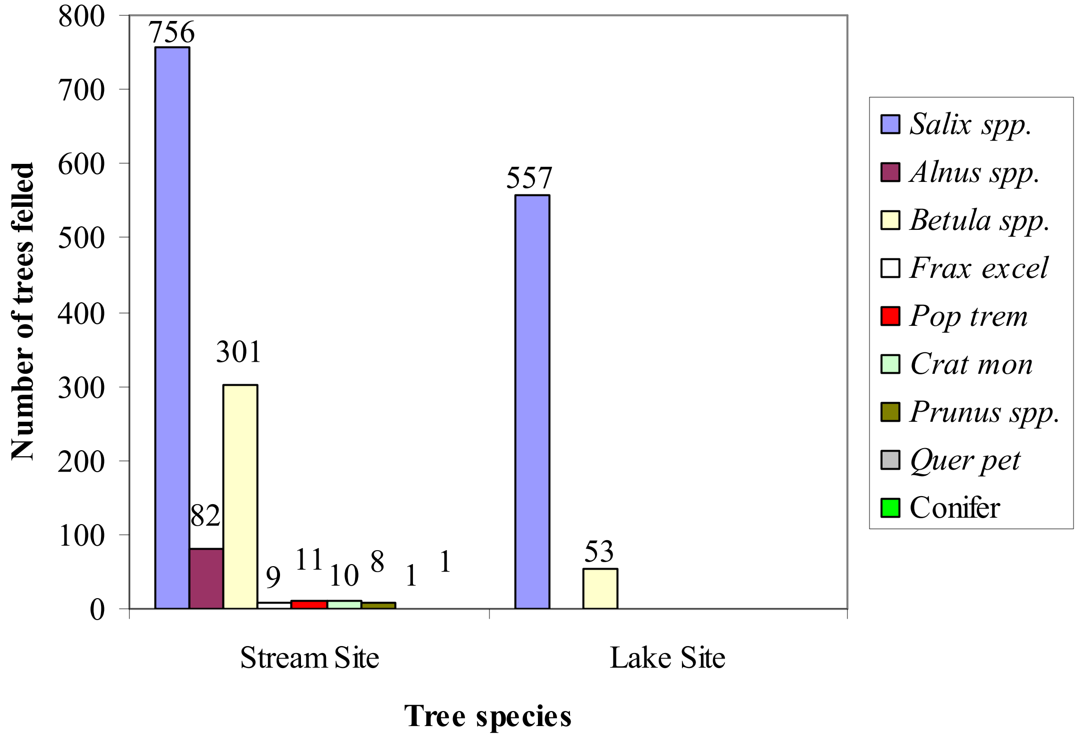
Definitions of the terminology used in this chapter can be found earlier in this thesis, in section 4.4. In addition, throughout this chapter, references will be made to tree species / sizes / locations being “selected for” or “selected against”. The term “selected for” indicates that a tree species for example, is felled disproportionately more than its relative availability. Such a situation is indicated by a positive electivity index (lnQ), and the tree species can be described as preferred by beavers. “Selected against” indicates the opposite situation in which trees are felled in lower proportions than their availability, as shown by a negative electivity index value, with such trees being described as unpreferred by beavers.

5.4 Results

5.4.1 Absolute felling trends

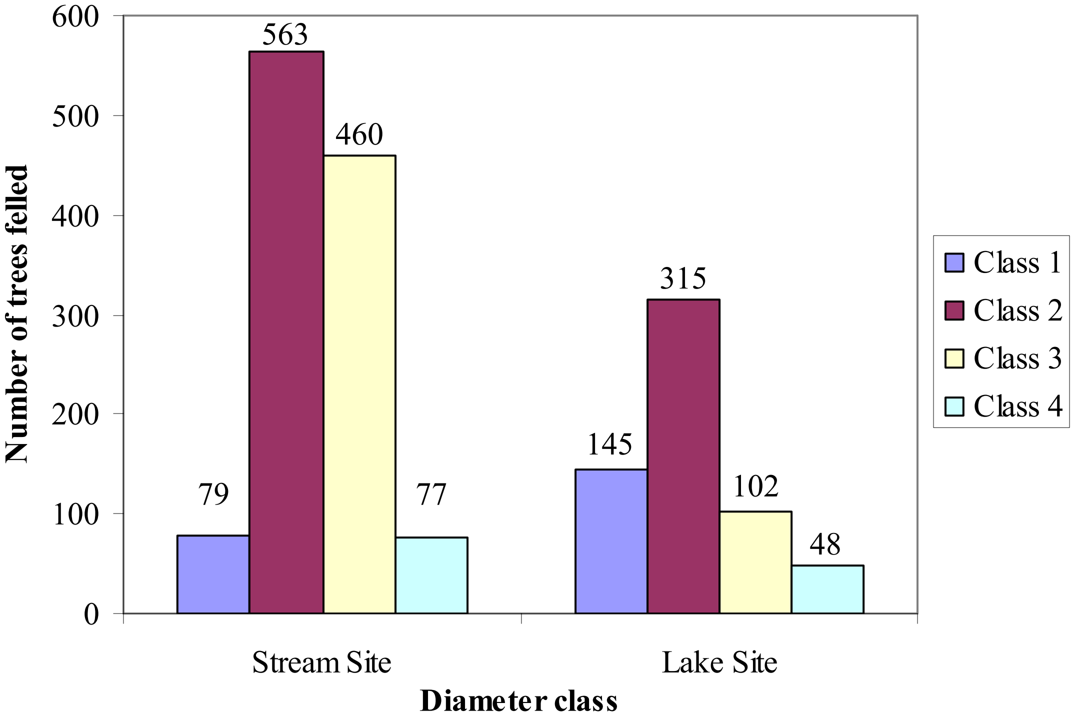
In total, 1,179 trees of nine different species were felled at the Stream Site over the study period, compared to 610 trees of just two species at the Lake Site. Of all the trees felled, only one case of conifer felling was observed, that of a small (diameter ≤ 4 cm) Douglas fir (*Pseudotsuga menziesii* Mirb.) at the Stream Site, despite the high availability of conifers at both sites. Figure 5.3 shows the numbers of each species felled at the Stream and Lake Sites using data pooled over the three years of study. The data clearly show that willow trees are felled in greatest numbers at both sites, followed by birch, with relatively small numbers (if any) of other deciduous species felled.

Figure 5.3 Numbers of trees of each species felled by beavers at the Stream and Lake Sites, using data pooled over three years of study.



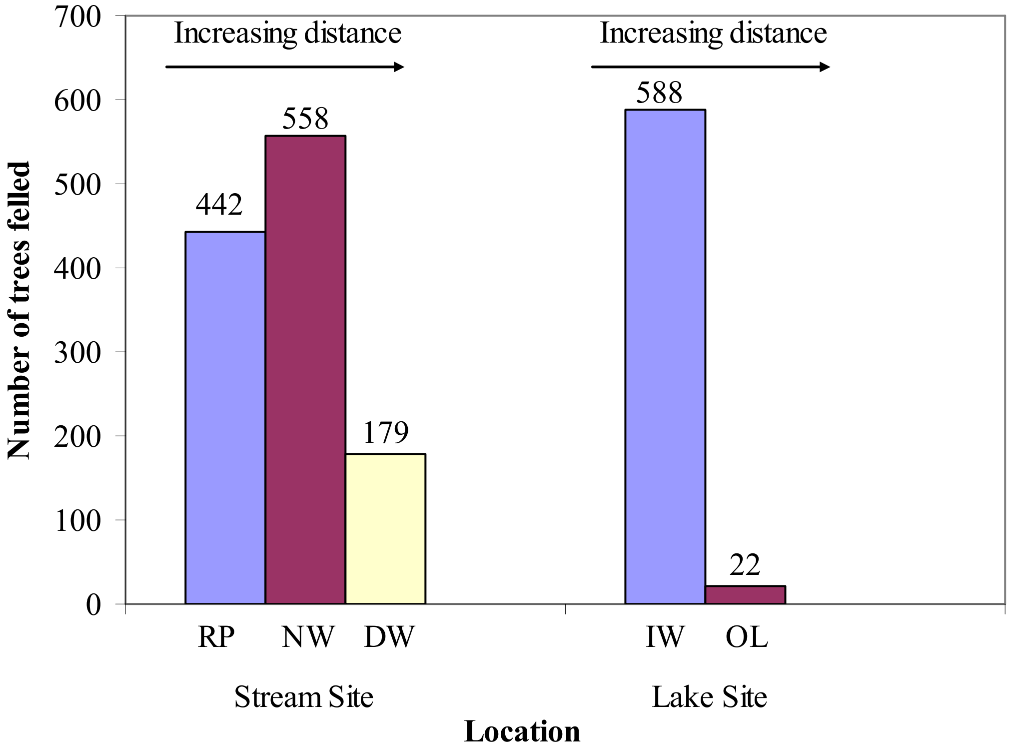
In terms of sizes of trees felled, the majority of felling at both sites was in the Class 2 range (diameter 5 - 10 cm) at both sites, with a major contribution also played by Class 3 (diameter 11 - 16 cm) trees. The largest trees (Class 4, diameter ≥ 17 cm) were generally felled in small numbers at both sites, as were the very smallest trees (Class 1, diameter ≤ 4 cm), although the Class 1 trees were of greater importance to the beavers at the Lake Site than those at the Stream Site (Figure 5.4).

Figure 5.4 Numbers of trees of each diameter class felled by beavers at the Stream and Lake Sites, using data pooled over three years of study.



The number of felled trees at different distances from waterbodies at each site are shown in Figure 5.5, with generally declining felling activity evident at both sites as distance increases. Using data pooled from all three years of study, *c*. 37% of felling occurred within 20 m of a beaver pond (RP zone) and *c*. 85% within 50 m of a pond (RP + NW zone). At the Lake Site, *c*. 96% of all felling in three years of study occurred within the shallow water of the lochs (IW), with only a very small number of trees felled in the riparian woodland (OL).

Figure 5.5 Numbers of trees felled by beavers at different distances from a pond at the Stream Site, or from the loch banks at the Lake Site. The data are pooled over three years of study at each site.



Felling preferences, however, need to be judged in the context of availability, be it of different tree genera, sizes, locations of trees, or indeed combinations of these factors. The following sections will address this issue by reporting the calculated electivity indices for each factor and interaction.

5.4.2 Effect of tree species on tree-felling by beavers

Figures 5.6a and 5.6b show the percentage abundance of available and felled trees at each site, in each of the three years of study. It is noticeable that the diversity of trees available to the beavers was greater at the Stream Site, which was reflected by the greater number of tree species felled there. The species of trees felled by the beavers generally showed little variation at the Stream Site for the first two years, but during Year 3, willow and alders became less important as birch dominated the felling activity. It is also evident that approximately 50% of available trees within 50 m of the loch banks at the Lake Site were apparently unpalatable coniferous species, and that there was little variation in species felling patterns over the three years.

Figure 5.6a Percentage abundance of available (left hand bars A) and felled (right hand bars F) tree species at the Stream Site, in each of the three years of study.

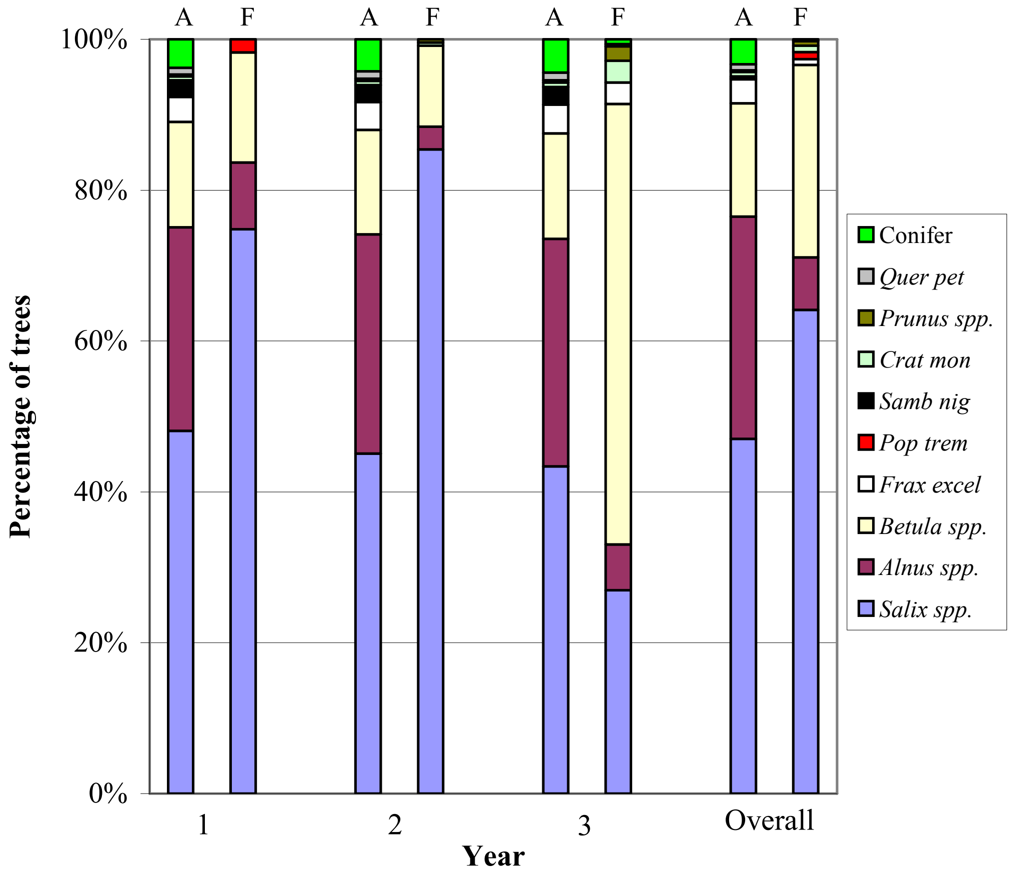
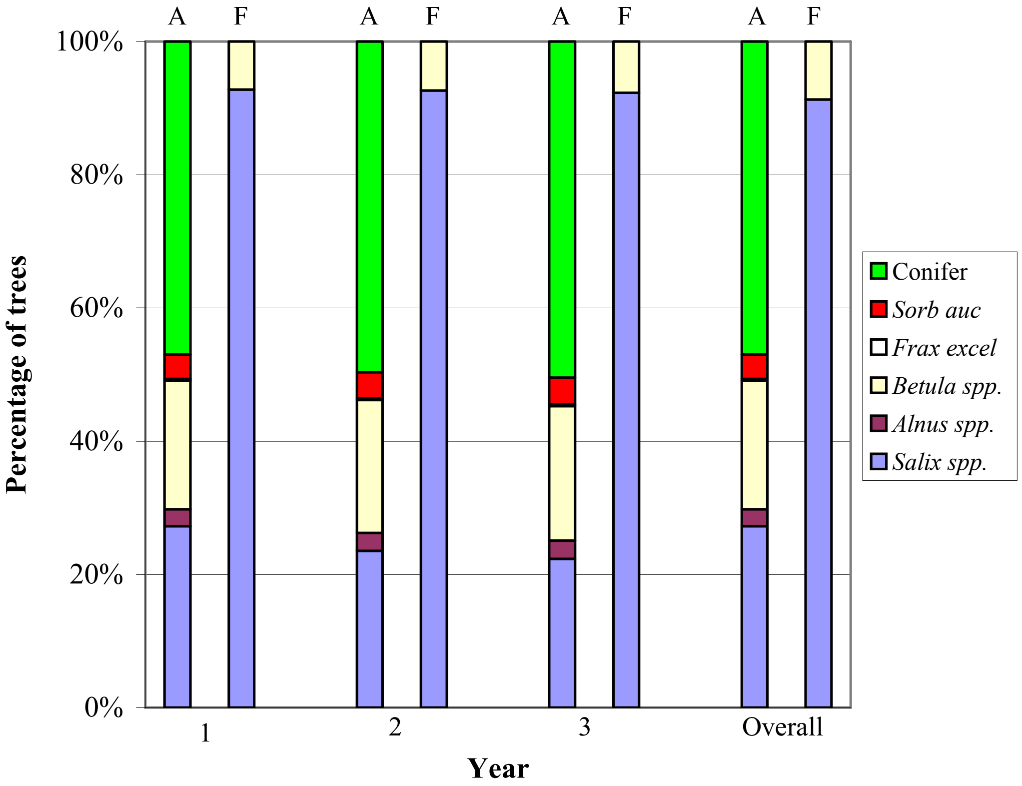


Figure 5.6b Percentage abundance of available (left hand bars A) and felled (right hand bars F) tree species at the Lake Site, in each of the three years of study.



From these felling and availability data, true measures of species preference in the form of electivity indices were calculated for each study year, as shown in Figures 5.7a and 5.7b. The most commonly felled species at the Stream Site were willows, but willows were also the most abundant trees there. Figure 5.7a shows that these trees were significantly selected for by the beavers (P<0.001) except in Year 3 when it was significantly selected against (P<0.001), and that alder (the third most commonly felled species there) was consistently significantly selected against (P<0.001 in all three years). No significant selection for or against birches (the second most commonly felled species at the Stream Site) was evident in the first two years, although significant selection for birch was evident in Year 3. All aspen trees were felled in Year 1, showing significant preference for the species (P<0.001), and in Year 3 hawthorn and cherry trees were significantly selected for by beavers (P<0.001 for both species), whilst conifers (P<0.01) and oaks (P<0.001) were significantly selected against.

Figure 5.7a Species electivity indices for the Stream Site.

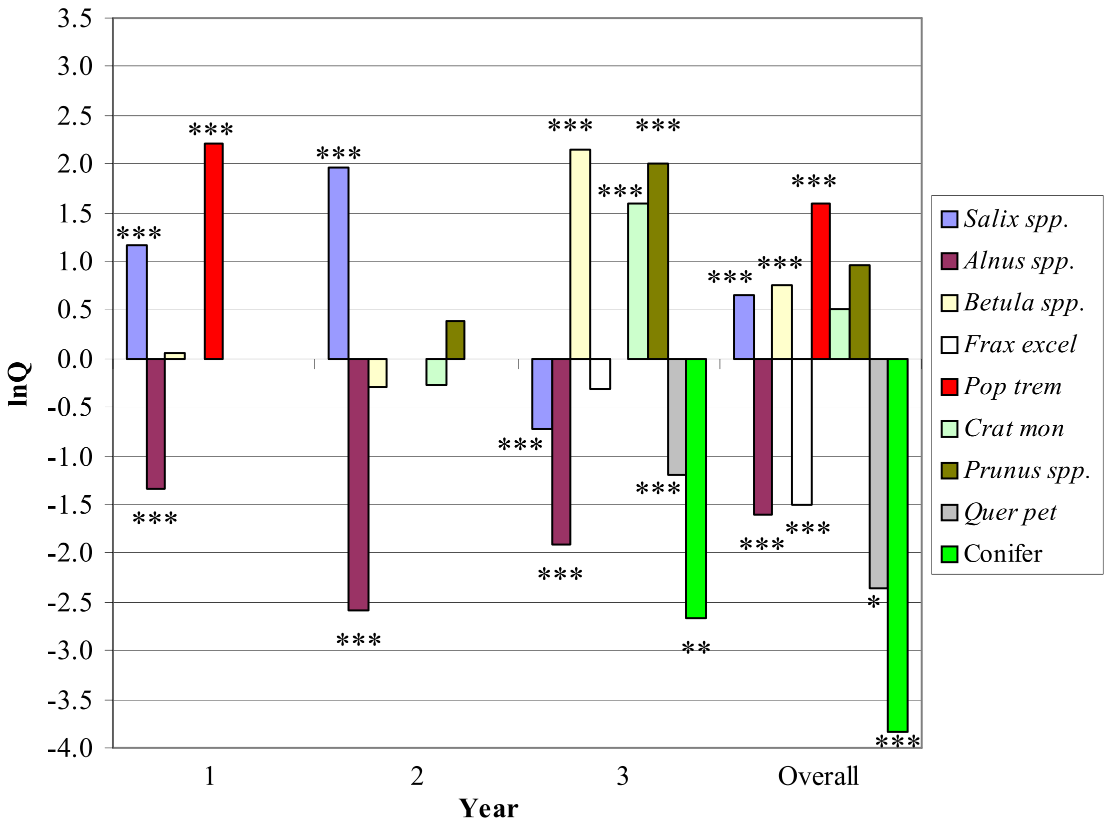
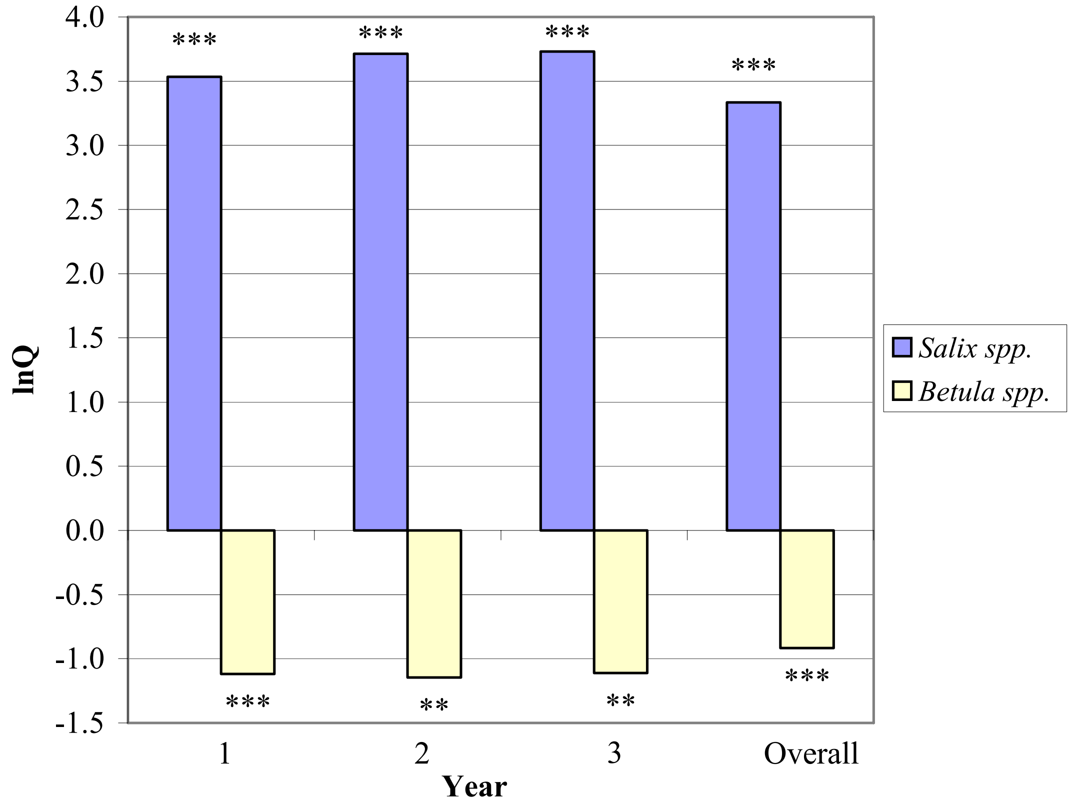


Figure 5.7b Species electivity indices for the Lake Site.



At the Lake Site, little variation in species electivity indices was evident, with birch being significantly selected against in all three years (*P*<0.001) and willow being consistently significantly selected for (*P*<0.001) (Figure 5.7b).

For all the following analyses of the tree-felling trends, only three genera of trees (willow, birch and alder) at the Stream Site and two (willow and birch) have been considered. All other species were felled in such low numbers, each contributing to less than 1% of the total number of felled trees, that they have been excluded from further investigation.

5.4.3 Effect of tree size on tree-felling by beavers

When the available and felled trees are categorized by size, different patterns of availability and use are evident at the Stream and Lake Sites, as shown in Figures 5.8a and 5.8b respectively. The major difference between the two sites is in the availability of small trees sizes to the beavers. At the Stream Site, *c*. 5% of available willows, birches and alders were in the Class 1 diameter class ($\leq$ 4 cm diameter) compared to approximately 19% of trees (willow and birch only) at the Lake Site, whereas very large trees (Class 4 = $\geq$ 17 cm diameter) were more common at the Lake Site (*c*. 15%) than at the Stream Site (*c*. 8%). In terms of felling, the most noticeable difference is that small trees (Class 1) comprised a much smaller proportion of all the felled trees at the Stream Site (<10% of all felling in each year) than was observed at the Lake Site where they contributed to *c*. 10 - 30% of felling, and this trend was most noticeable in Year 1.

Figure 5.8a Percentage abundance of available (left hand bars A) and felled (right hand bars F) tree sizes at the Stream Site, in each of the three years of study.

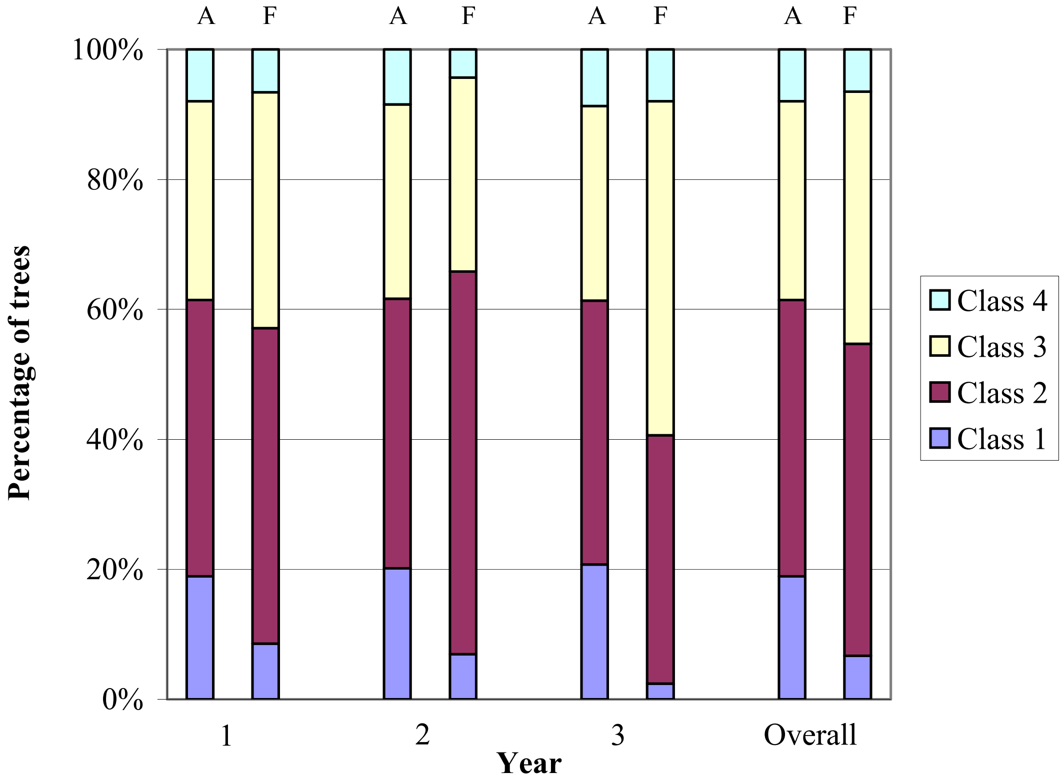
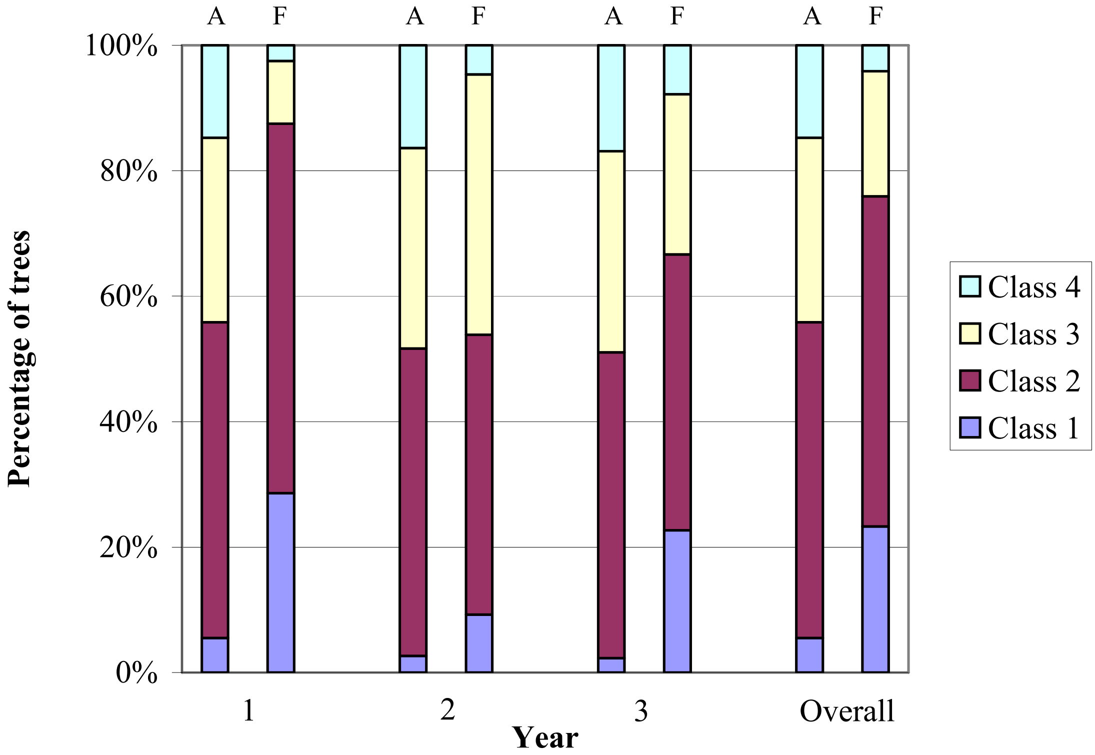


Figure 5.8b Percentage abundance of available (left hand bars A) and felled (right hand bars F) tree sizes at the Lake Site, in each of the three years of study.



Calculation of electivity indices shows that the smallest trees (Class 1) were selected against by beavers in each of the three years of study at the Stream Site (*P*<0.001 in all cases). However, the opposite trend was evident at the Lake Site, where Class 1 trees were significantly selected for in all years (*P*<0.001 in all cases). At both sites the largest trees were selected against in each year, although the trend was most significant at the Lake Site. Selection of the two intermediate classes (Class 2 = 5 - 10 cm diameter; Class 3 = 11 - 16 cm diameter) showed great variation, between sites and years. Generally speaking, Class 2 trees were preferentially selected for by the Stream Site beavers in each year, with the results often being highly significant. This diameter class was generally neither selected for, nor against at the Lake Site, however. Finally, the Class 3 trees were largely selected for at the Stream Site but against at the Lake Site, although the electivity indices varied considerably between years. Figures 5.9a and 5.9b show the electivity indices for each diameter class of tree over the three years of study at the Stream and Lake Sites respectively.

Figure 5.9a Electivity indices for felled trees of different diameter classes in each of the three years of study at the Stream Site.

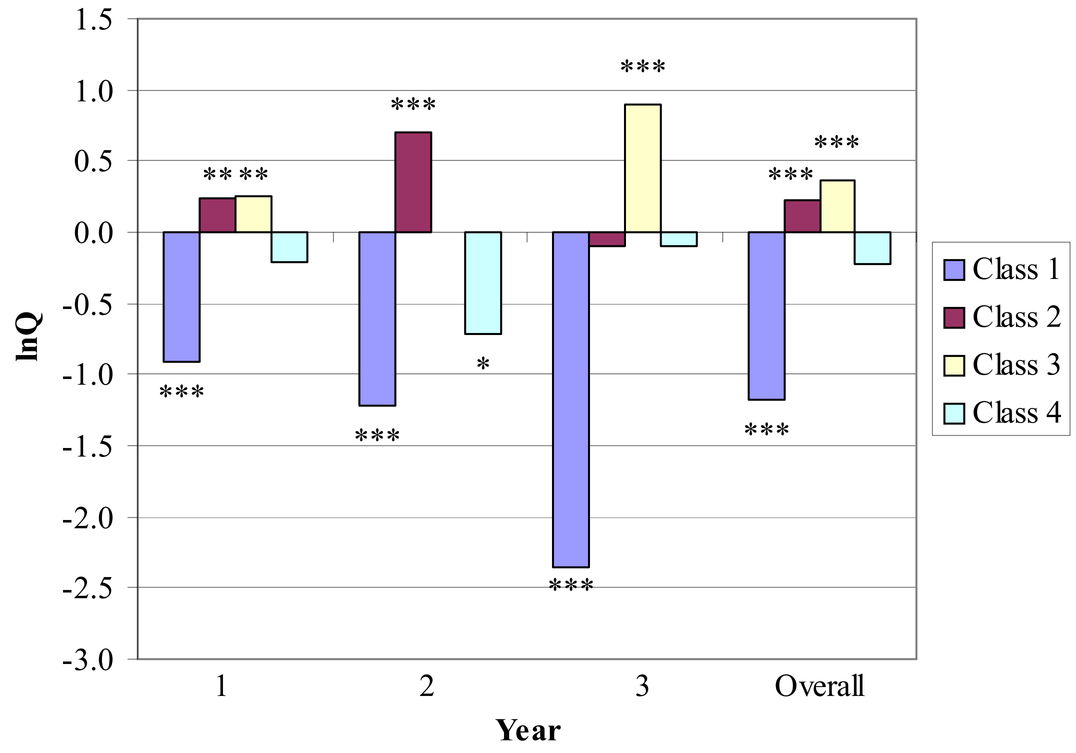
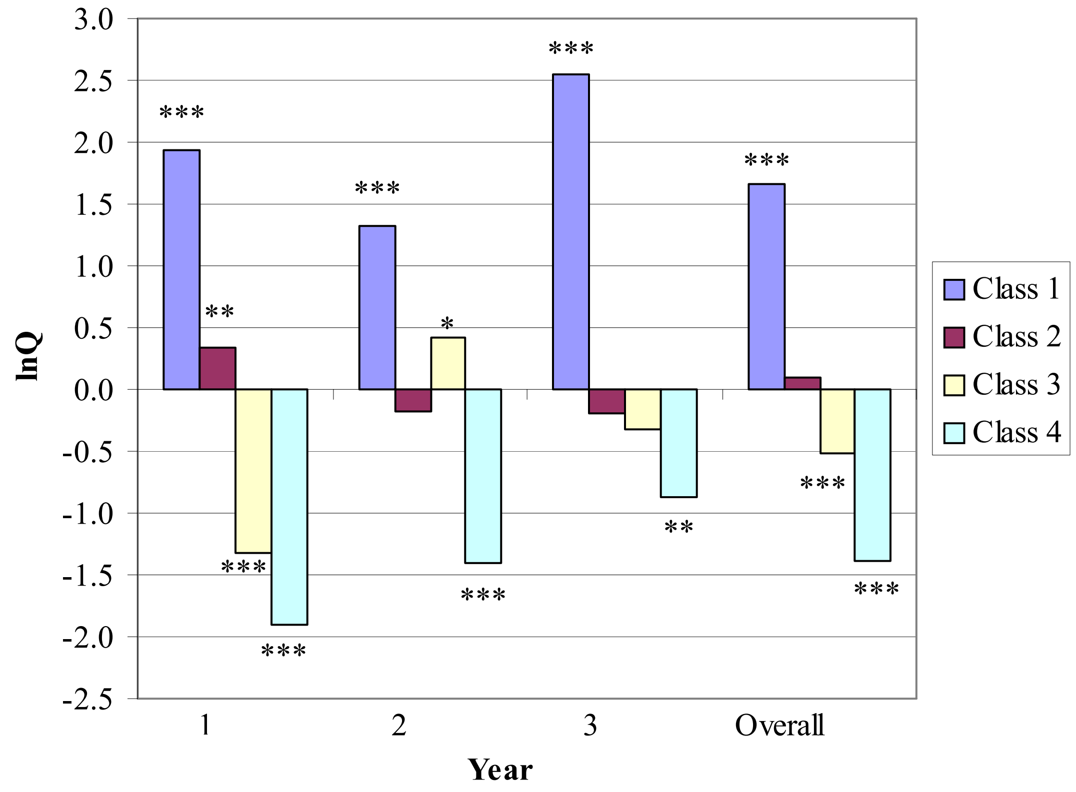


Figure 5.9b Electivity indices for felled trees of different diameter classes in each of the three years of study at the Lake Site.



5.4.4 Effect of proximity to water on tree-felling by beavers

The proportions of all available and felled willow, birch and alder at varying distances to a beaver pond at the Stream Site are shown in Figure 5.10a. Generally, the availability of these trees was approximately the same for each distance category (*c.* 30 - 35%), although the annual felling patterns show some locational variation. For example, in Year 1 the vast majority of felling was conducted in the RP zone (≤ 20 m from a pond) with very little felling in the most distant DW zone (≥ 50 m from a pond). In Years 2 and 3 however, the majority of felling occurred in the intermediate NW zone (20 - 50 m from a pond), with very little felling nearer to the ponds, despite the RP resource not having been fully utilised.

Figure 5.10a Percentage abundance of available and felled trees at varying distances from a beaver pond at the Stream Site, in each of the three years of study.

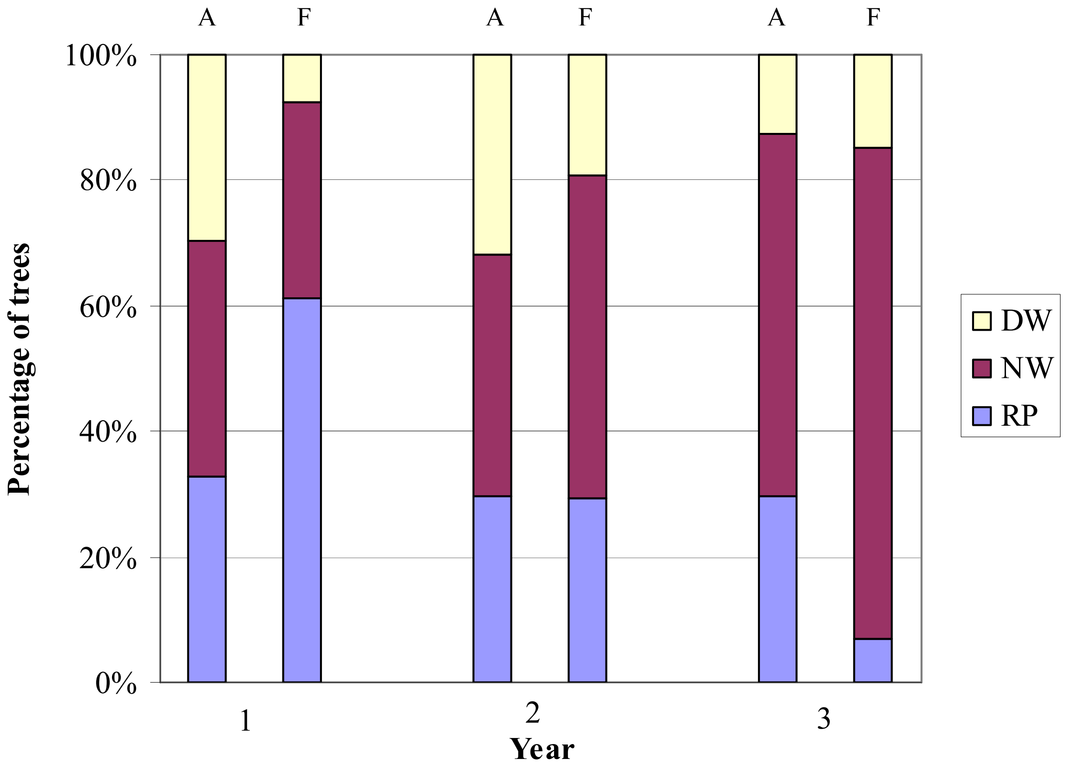
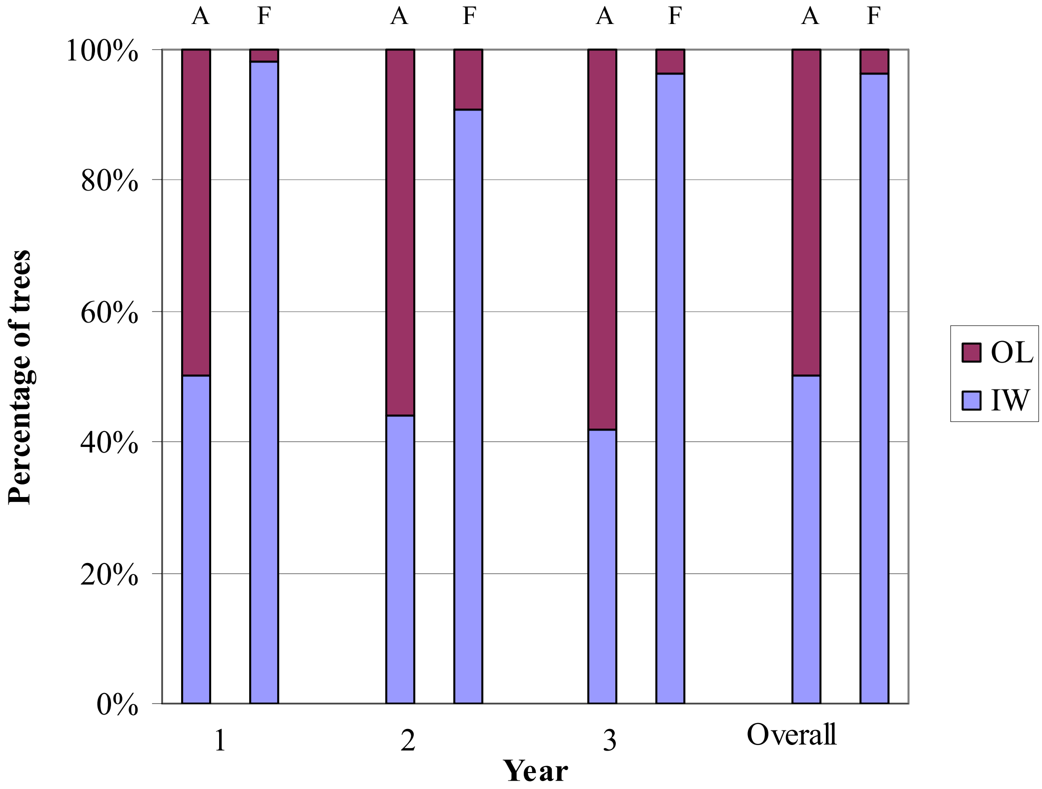


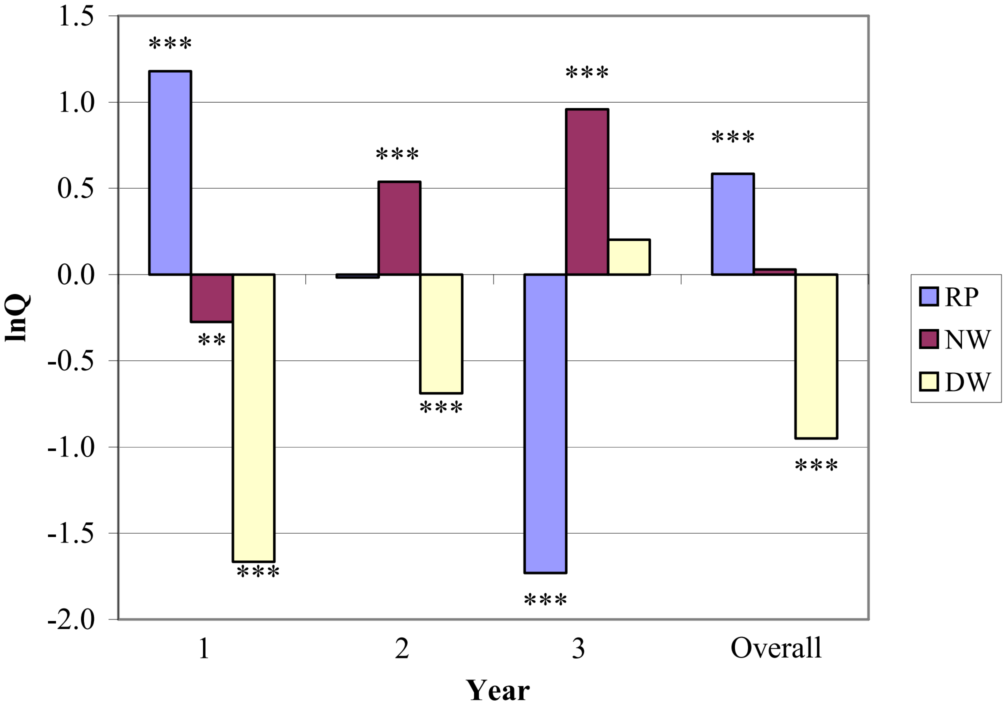
Figure 5.10b Percentage abundance of available and felled trees at varying distances from a beaver pond at the Lake Site, in each of the three years of study.



At the Lake Site the abundance of birch and willow was approximately equal in both the IW category (within the water of the loch) and the OL (on land) category, but the felling was almost entirely concentrated within the IW zone in all three years of study. Indeed, in each of the study years, less than 10 trees were felled on the land surrounding the lochs. The proportions of all available and felled willow and birch within the loch and on the banks of the Lake Site are shown in Figure 5.10b.

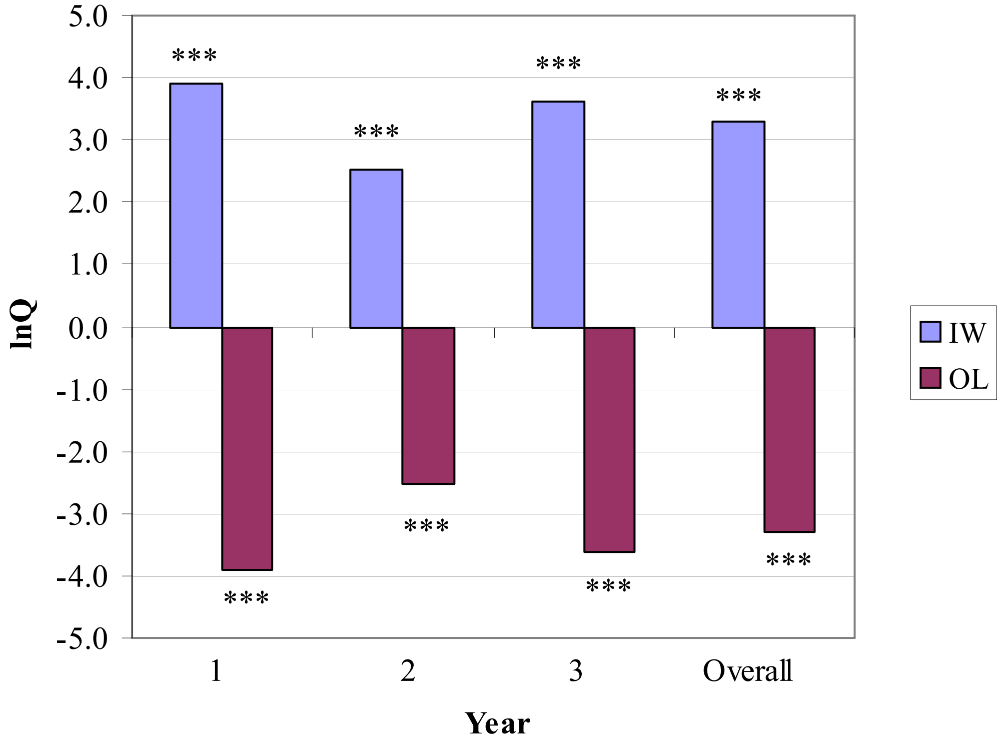
The electivity indices for the Stream Site show that trees within 20 m of a lodge were significantly selected for in Year 1, but by Year 3 they were significantly selected against ($P<0.001$ in both cases). Trees further than 50 m from a lodge were significantly selected against in the first two years ($P<0.001$ in both cases) and selected for in Year 3, though not significantly so ($P>0.05$). In Year 1, trees in the intermediate zone were significantly selected against ($P<0.01$), but by Years 2 and 3 they were significantly selected for ($P<0.001$ in both cases). Figure 5.11a shows the electivity indices for felled trees at different proximities to a beaver lodge at the Stream Site.

Figure 5.11a Electivity indices for felled trees at different proximities to a beaver pond in each of the three years of study at the Stream Site.



At the Lake Site, willows and birches within the water of the loch were consistently significantly selected for by the beavers, whilst those trees on land were significantly selected against ($P<0.001$ in all cases). These electivity indices are shown in Figure 5.11b.

Figure 5.11b Electivity indices for felled trees within the loch and on the banks in each of the three years of study at the Lake Site.



5.4.5 Effect of the interaction between tree species and size on felling preferences of beavers

Categorisation of the available and felled trees of each of the three predominant genera at the Stream Site into size classes showed some interesting trends, as shown in Table 5.2. In the case of willow and birch, large trees (Class 4, ≥ 17 cm diameter) formed a small percentage of all felled trees in all three years, however, the availability of these trees was also low. Large alders formed a much greater component (*c*. 25 - 30%) of all the felled alder trees however, although the availability of Class 4 trees of this genus was also proportionately greater than in willows or birches. At the opposite end of the size scale, Class 1 trees (diameter ≤ 4 cm) generally formed considerably less than 10% of all felling in each of the three genera, with birches showing this trend to the greatest degree and alders to a lesser degree. In all cases, the intermediate size trees of

Classes 2 and 3 (diameters 5 - 10 cm and 11 - 16 cm respectively) formed the highest proportion of available and felled trees, although subtle differences occurred between different genera and years.

Table 5.2 Percentage abundance of available (extrapolated) and felled trees of different sizes of each of the three most heavily felled tree genera at the Stream Site, in each of the three years of study. N values indicate the number of trees present in each category.

Genus	**Diam. class**	**Year 1**		**Year 2**		**Year 3**	
		Available	**Felled**	**Available**	**Felled**	**Available**	**Felled**
Salix spp.		**N=2745**	**N=472**	**N=2306**	**N=199**	**N=2134**	**N=85**
	1	26.0	10.6	28.8	7.5	30.4	5.9
	2	42.7	51.9	40.6	60.3	39.0	57.6
	3	26.4	32.0	25.4	28.7	25.3	33.0
	4	4.9	5.5	5.2	3.5	5.3	3.5
Alnus spp.		**N=1541**	**N=56**	**N=1487**	**N=7**	**N=1481**	**N=19**
	1	11.2	1.8	11.6	14.3	11.5	6.3
	2	27.4	12.5	27.9	14.3	28.0	25.0
	3	44.6	60.7	44.0	42.8	44.0	37.4
	4	16.8	25.0	16.5	28.6	16.5	31.2
Betula spp.		**N=798**	**N=92**	**N=710**	**N=25**	**N=688**	**N=184**
	1	9.5	2.2	10.4	0.0	11.0	0.5
	2	70.8	53.3	72.5	51.7	73.7	31.0
	3	17.8	43.5	15.0	44.8	13.1	60.3
	4	1.9	1.0	2.1	3.5	2.2	8.2

At the Lake Site, small willows formed a large proportion of all felled trees of this genus (*c.* 10 - 30%) in all three years despite low availability, but this trend was not reflected in the birch trees. As at the Stream Site, very large willows formed only a small proportion of all felled willows, however, the felling of Class 4 birches generally reflected the availability of these large trees at the Lake Site. Again, the majority of felled and available trees of both genera were of the intermediate size classes, as shown in Table 5.3.

Table 5.3 Percentage abundance of available (extrapolated) and felled trees of different sizes of each of the two most heavily felled tree genera at the Lake Site, in each of the three years of study. N values indicate the number of trees present in each category.

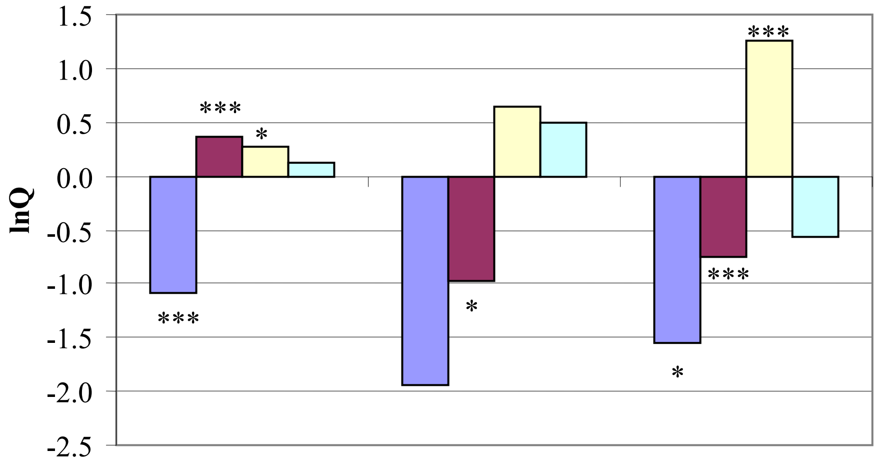
Genus	**Diam. class**	**Year 1**		**Year 2**		**Year 3**	
		Available	**Felled**	**Available**	**Felled**	**Available**	**Felled**
Salix spp.		**N=1800**	**N=334**	**N=1472**	**N=101**	**N=1373**	**N=122**
	1	6.8	30.2	1.8	11.9	2.3	26.2
	2	57.0	58.1	56.6	54.4	55.9	46.7
	3	28.2	9.6	32.2	29.7	32.0	23.0
	4	8.0	2.1	9.4	4.0	9.8	4.1
Betula spp.		**N=1271**	**N=26**	**N=1248**	**N=8**	**N=1242**	**N=19**
	1	3.7	7.7	3.7	0.0	3.7	0.0
	2	40.9	69.2	40.2	37.5	40.1	26.3
	3	31.3	15.4	31.6	37.5	31.7	42.1
	4	24.1	7.7	24.5	25.0	24.5	31.6

Calculation of electivity indices indicated which of these trends were statistically significant. At the Stream Site, it is evident that the smallest trees of all three species are generally selected against by beavers, with the exception of alder in Year 2. This selection against Class 1 willows was significant in all three years, as it was for birches in the two years that small birch were felled (Years 1 and 3). Felling of the largest size-class of trees showed considerable variation between species and years, although the only significant trend was the selection for Class 4 birches in Year 3. The Class 2 willow trees were consistently selected for, whilst in alder and birch these trees were consistently selected against. Class 3 trees were also consistently preferred in both birch and willow, whilst alder showed more variation. In general the trends for all size-classes of alder throughout the study were not significant. All of the electivity indices for the varying size classes of the three major felled genera at the Stream Site are shown in Figure 5.12.

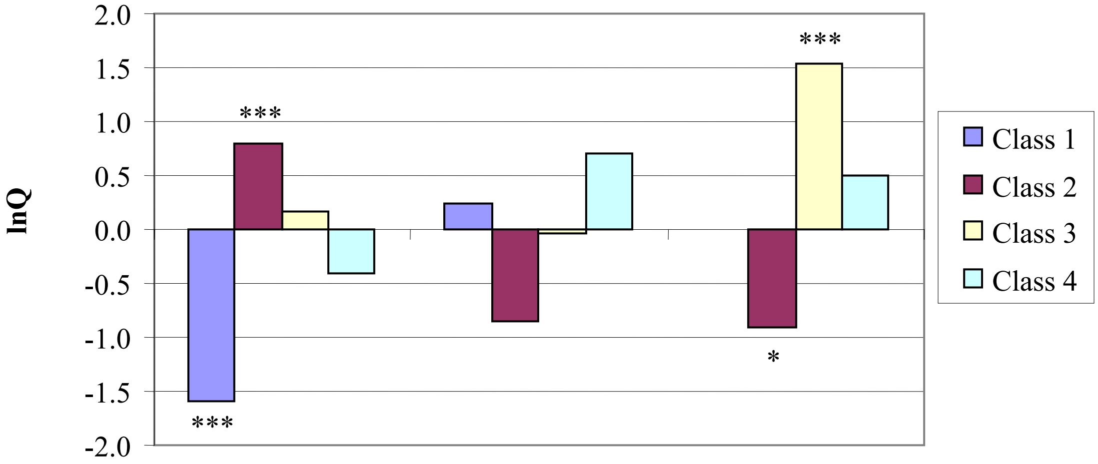
At the Lake Site, the trend for small willows is the exact reverse as observed at the Stream Site, with Class 1 trees being consistently and significantly selected for. The intermediate and large diameter class willows were generally selected against by the beavers in all years of the study, although not all results were significant. No trends can be identified in the felling of birch trees of different sizes, with the only significant result being the selection for Class 2 trees in Year 1. Figure 5.13 shows all of the electivity indices for the varying size classes of the two major felled genera at the Lake Site.

Figure 5.12 Electivity indices of different diameter classes of felled trees of three genera in all three study years at the Stream Site.

a) Year 1



b) Year 2



c) Year 3

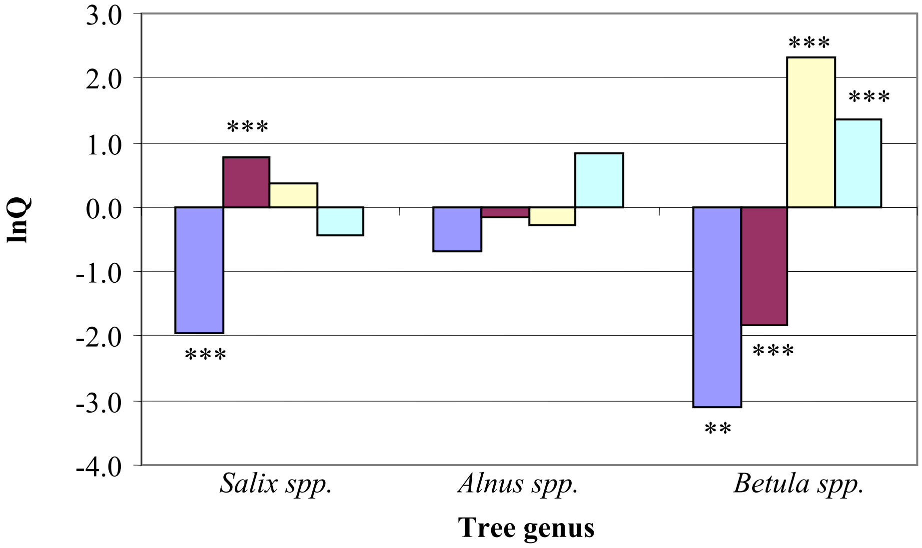
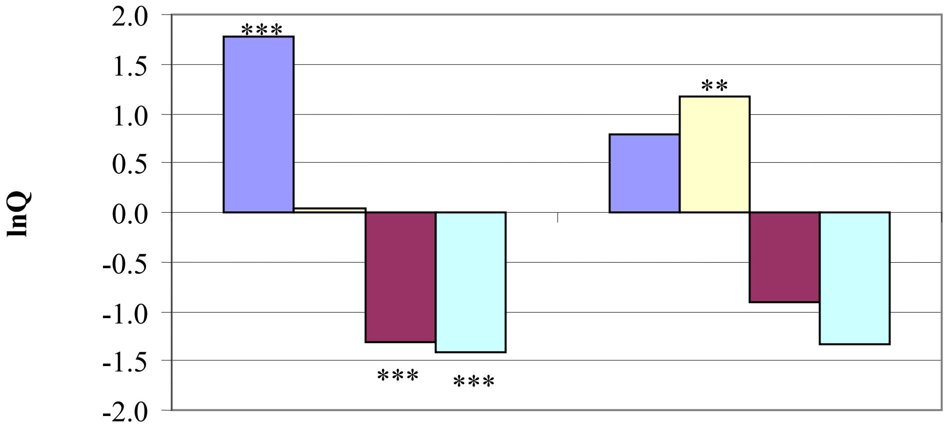
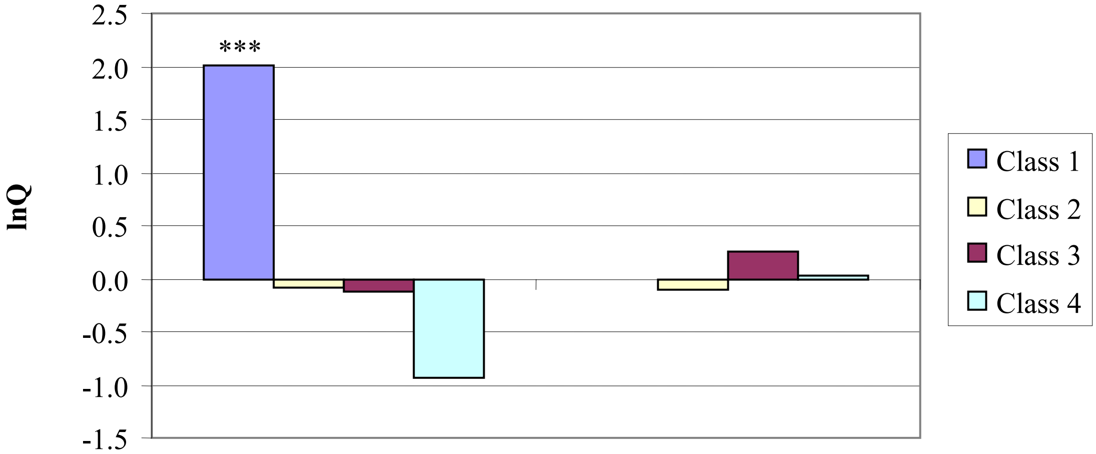


Figure 5.13 Electivity indices of different diameter classes of felled trees of two genera in all three study years at the Lake Site.

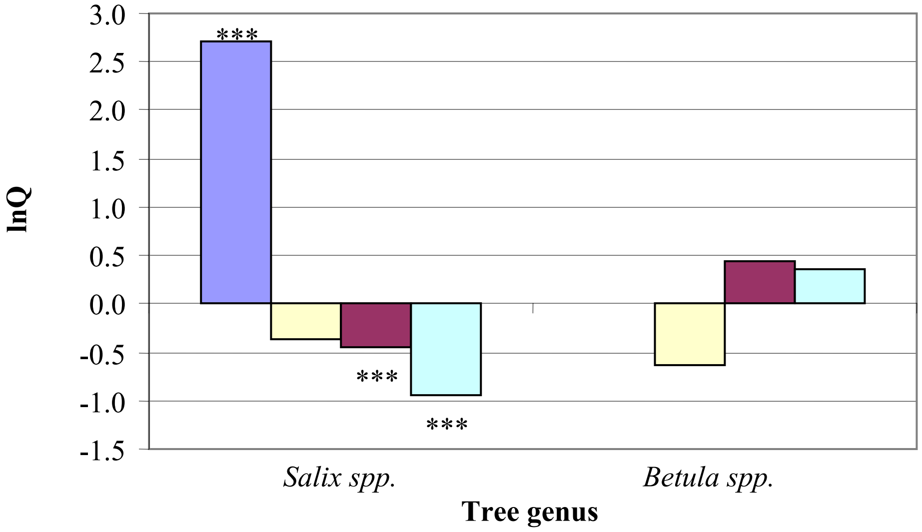
a) Year 1



b) Year 2



c) Year 3



5.4.6 Effect of the interaction between tree species and location on felling preferences of beavers

It is clear from the results at the Stream Site (Table 5.4) that in Year 1 felling was concentrated within 20 m of the ponds (see section 5.4.1), but closer examination of the data showed that this trend was valid for all three of the predominantly felled genera. Generally little felling of any of these three genera occurred over 50 m from a pond (*i.e.* in the DW zone) in Year 1. The degree of utilisation of trees in the RP zone generally decreased in Years 2 and 3 across all three genera, except for alders in Year 3. In this case, the alders nearest the pond were the most heavily felled of all the alders felled that year. However, for both willows and alders, the resource near to the ponds still formed an important source of felling in Years 2 and 3, although the main focus of the beavers' felling activity had often shifted to areas further from the ponds. It is interesting to note that this was not true of the birch trees in the RP zone, however, which were only exploited at a very low level in Year 2, and not at all in Year 3, despite the resource remaining abundant in these years.

Table 5.4 Percentage abundance of available (extrapolated) and felled trees of the three most heavily felled tree genera at three different locations at the Stream Site, in each of the three years of study. N values indicate the number of trees present in each category.

Genus	Location	Year 1		Year 2		Year 3	
		Available	**Felled**	**Available**	**Felled**	**Available**	**Felled**
Salix spp.		**N=2745**	**N=472**	**N=2306**	**N=199**	**N=2134**	**N=85**
	RP	39.9	58.9	36.5	33.7	36.3	23.5
	NW	36.1	33.1	36.7	53.3	50.4	76.5
	DW	24.0	8.0	26.8	13.0	13.3	0.0
Alnus spp.		**N=1541**	**N=56**	**N=1487**	**N=7**	**N=1481**	**N=19**
	RP	19.6	75.0	18.9	0.0	39.3	51.3
	NW	40.4	10.7	41.6	14.3	50.1	18.0
	DW	40.0	14.3	39.5	85.7	10.6	30.7
Betula spp.		**N=798**	**N=92**	**N=710**	**N=25**	**N=688**	**N=184**
	RP	33.3	65.2	31.0	4.0	31.8	0.0
	NW	36.5	34.8	36.5	48.0	61.5	83.2
	DW	30.2	0.0	32.5	48.0	6.7	16.8

At the Lake Site, it is clear that the abundance of the two main genera varies considerably between the two locations, with willows being predominantly found within the water, and birches mainly on the banks. Despite this difference, the majority of felling of both birch and willow trees was located within the water, with the beavers venturing on to the shore to fell either genus only very rarely in any of the three years of study, as shown in Table 5.5.

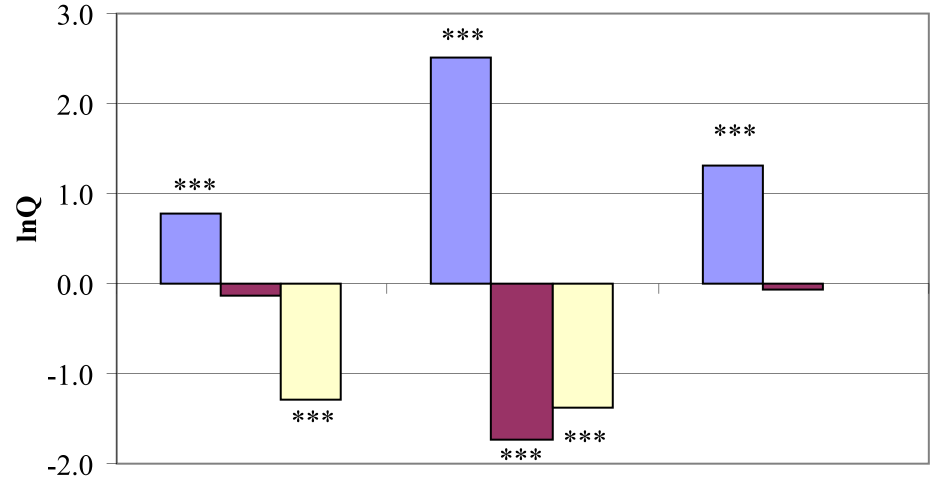
Table 5.5 Percentage abundance of available (extrapolated) and felled trees of the two most heavily felled tree genera at two different locations at the Lake Site, in each of the three years of study. N values indicate the number of trees present in each category.

Genus	Location	Year 1		Year 2		Year 3	
		Available	**Felled**	**Available**	**Felled**	**Available**	**Felled**
Salix spp.		**N=1800**	**N=334**	**N=1472**	**N=101**	**N=1373**	**N=122**
	IW	79.4	99.1	75.1	94.1	73.6	99.2
	OL	20.6	0.9	24.9	5.9	26.4	0.8
Betula spp.		**N=1271**	**N=26**	**N=1248**	**N=8**	**N=1242**	**N=19**
	IW	8.5	84.6	7.1	50.0	7.0	78.9
	OL	91.5	15.4	92.9	50.0	93.0	21.1

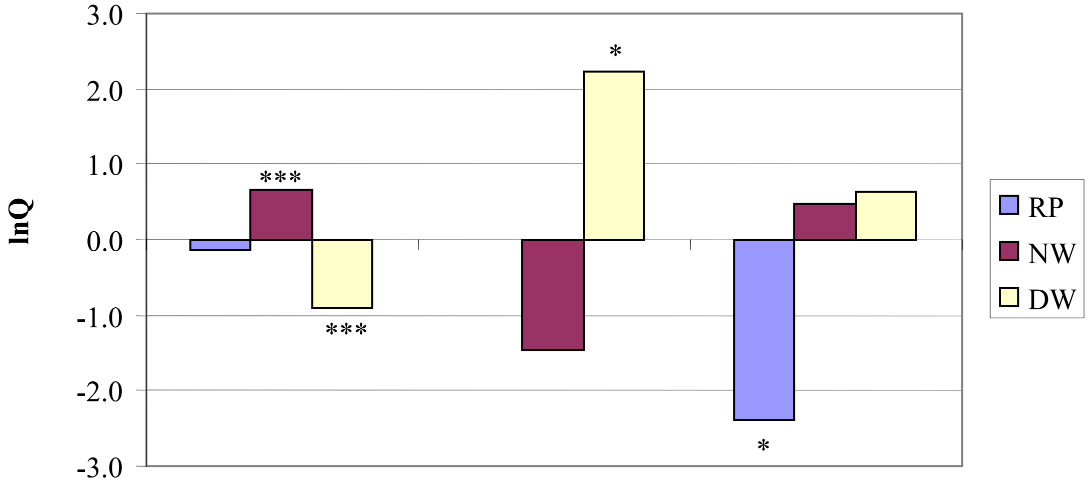
The electivity indices for the Stream Site (Figure 5.14) show that in Year 1, the area immediately surrounding the ponds was significantly favoured by the beavers for felling of all three tree genera, with trees of all genera in areas further than 20 m from the ponds being selected against – often significantly - or avoided completely. In Year 2, the willow and birch trees in the RP zone were selected against, whilst alders in this zone were avoided completely. Furthermore, in Year 2 the beavers significantly avoided the most distant willows, whilst significantly preferring the most distant alders, and most distant birch trees (although not significantly). These patterns were generally reinforced in Year 3, with the only anomaly being the apparent preference for the alders nearest to the pond, although this preference was not significant. At the Lake Site (Figure 5.15) the willows and birches located within the water of the loch were consistently highly significantly selected for by the beavers throughout the study, whilst those on land were consistently selected against (*P*<0.001 in all cases).

Figure 5.14 Electivity indices of felled trees of three genera in three locations in all three study years at the Stream Site.

a) Year 1



b) Year 2



c) Year 3

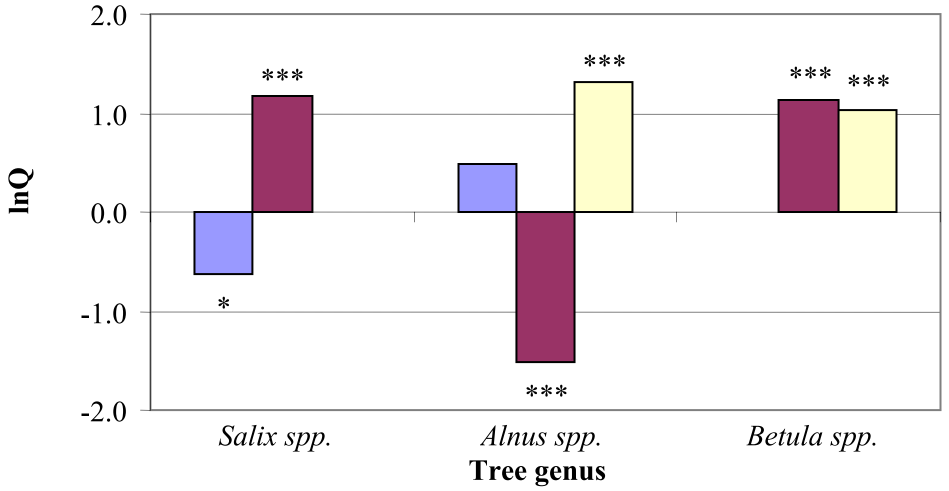
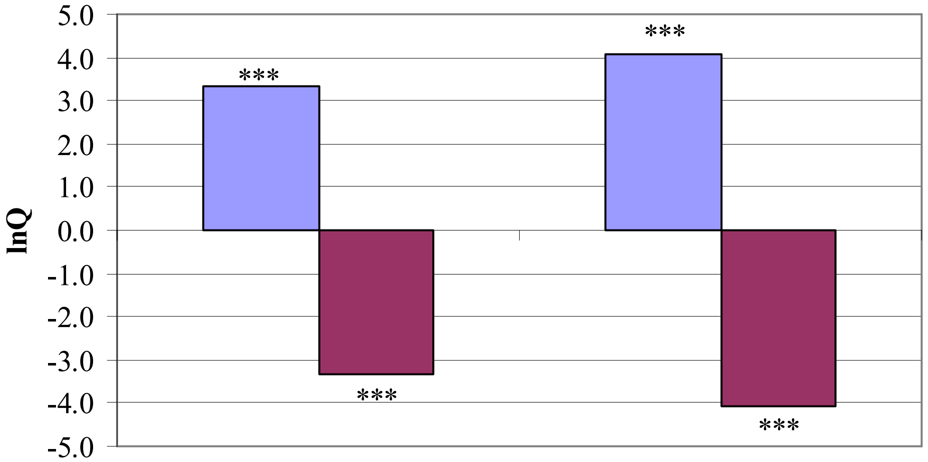
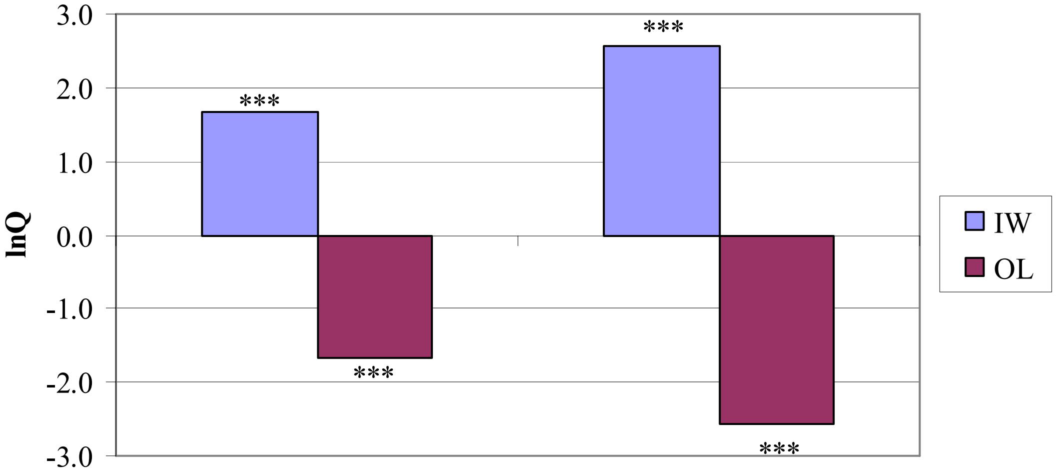


Figure 5.15 Electivity indices of felled trees of two genera in two locations in all three study years at the Lake Site.

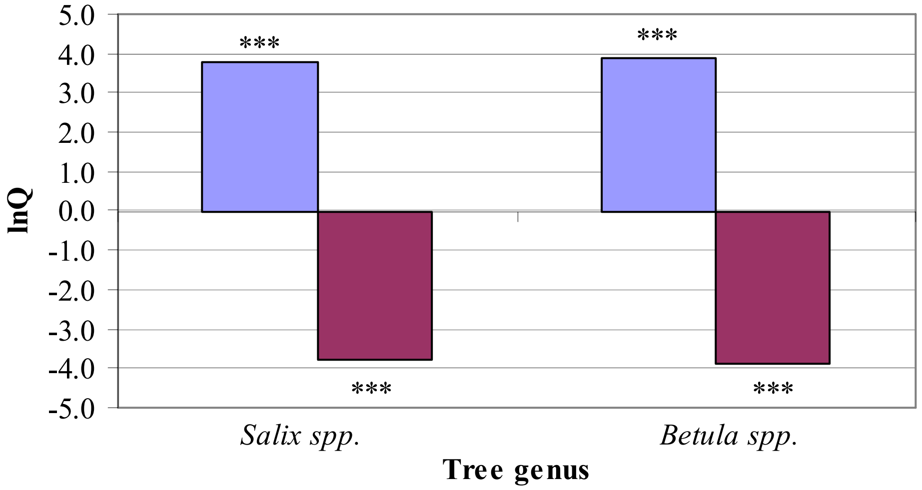
a) Year 1



b) Year 2



c) Year 3



5.4.7 Effect of the interaction between location and tree size on felling preferences of beavers

Generally, the availability of the smallest three diameter classes (trees <17 cm diameter) were approximately equal in those areas nearest to the ponds (RP) and of intermediate distance (NW) throughout the study. The exception to this was the low abundance of the smallest trees (Class 1) furthest from the ponds in the DW zone. The largest trees (diameter ≥ 17 cm) were consistently scarce at all locations. In general, the felling of trees at all distances from the ponds broadly reflected the abundance of each size class within each zone, with the most noticeable exceptions being the apparent favouring of the very largest trees located furthest from the ponds, and rejection of the largest trees nearest the ponds (Table 5.6).

Table 5.6 Percentage abundance of available (extrapolated) and felled trees of different sizes at three different locations at the Stream Site, in each of the three years of study. N values indicate the number of trees present in each category.

Location	Diam. class	Year 1		Year 2		Year 3	
		Available	Felled	Available	Felled	Available	Felled
RP		N=1665	N=343	N=1342	N=68	N=1275	N=20
	Class 1	17.3	9.6	19.0	8.8	19.5	5.0
	Class 2	47.1	55.1	44.4	70.6	43.0	75.0
	Class 3	26.7	29.2	26.5	19.1	26.9	15.0
	Class 4	8.9	6.1	10.1	1.5	10.6	5.0
NW		N=1904	N=194	N=1725	N=119	N=2488	N=225
	Class 1	29.9	10.3	31.9	7.6	24.2	1.8
	Class 2	33.6	42.8	32.8	57.1	36.7	39.1
	Class 3	27.2	40.2	25.8	31.1	30.7	52.0
	Class 4	9.3	6.7	9.5	4.2	8.4	7.1
DW		N=1514	N=77	N=1436	N=44	N=540	N=43
	Class 1	6.9	0.0	7.3	2.3	8.0	4.7
	Class 2	48.5	29.9	49.1	45.4	52.6	16.3
	Class 3	39.0	61.0	38.0	43.2	33.7	65.1
	Class 4	5.6	9.1	5.6	9.1	5.7	13.9

The smallest trees were generally of low abundance throughout the Lake Site (Table 5.7), as were the very largest trees within the water of the lochs, although the abundance of these very large trees was higher on the loch shores. Again, the felling patterns broadly reflected the availability of each size class at both locations, with some notable exceptions. Within the water of the loch, the smallest trees were apparently favoured with the largest trees being avoided, but this relationship appeared to break down when considering trees on the land surrounding the lochs. It should be noted, however, that felling of trees of any size was extremely rare on the land throughout the whole study, comprising less than 4% of all the trees felled at the Lake Site in the three-year study.

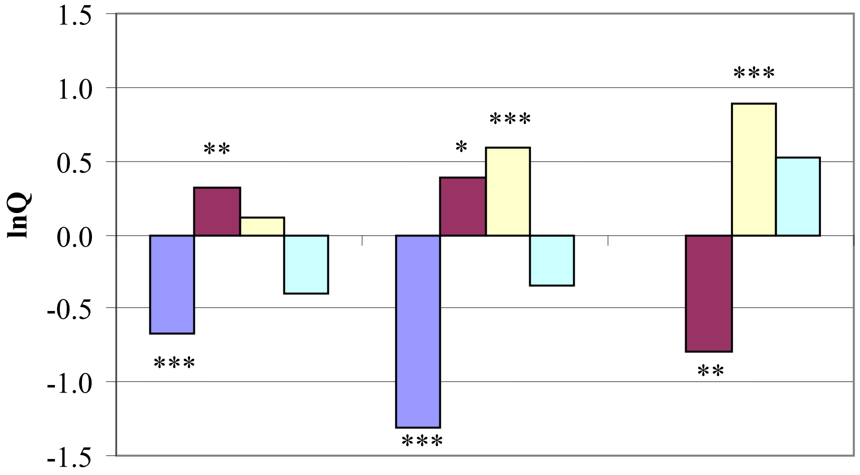
Table 5.7 Percentage abundance of available (extrapolated) and felled trees of different sizes at three different locations at the Lake Site, in each of the three years of study. N values indicate the number of trees present in each category.

Location	Diam. class	Year 1		Year 2		Year 3	
		Available	Felled	Available	Felled	Available	Felled
IW		**N=1540**	**N=353**	**N=1196**	**N=99**	**N=1118**	**N=135**
	Class 1	7.9	28.9	2.2	12.1	2.9	23.7
	Class 2	57.3	58.9	56.3	53.5	55.5	43.7
	Class 3	25.6	9.6	30.2	30.3	29.8	25.9
	Class 4	9.2	2.6	11.3	4.1	11.8	6.7
OL		**N=1536**	**N=7**	**N=1529**	**N=10**	**N=1520**	**N=5**
	Class 1	3.1	14.3	3.0	0.0	3.0	0.0
	Class 2	43.4	57.1	43.3	50.0	43.2	60.0
	Class 3	33.3	28.6	33.4	30.0	33.4	20.0
	Class 4	20.2	0.0	20.3	20.0	20.4	20.0

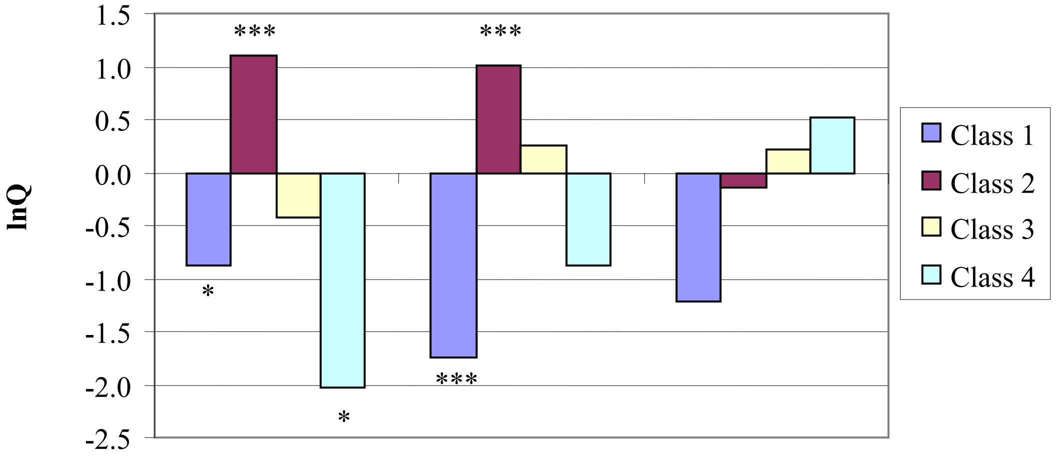
Examination of the electivity indices for these data at the Stream Site (Figure 5.16) showed that the smallest trees (diameter ≤ 4 cm) were consistently and significantly selected against within 50 m of a pond, and were similarly unpreferred by beavers at distances over 50 m from a pond, although not significantly so. Class 2 trees were generally consistently and significantly selected for within 50 m of a pond, although they were selected against at distances greater than this. Class 3 trees (diameter 11 - 16 cm) were only significantly selected for by beavers at distances greater than 20 m from a pond. The largest trees (Class 4) were generally consistently selected against within 50 m of a pond, and selected for further from the safety of water, although most of these trends were not significant.

Figure 5.16 Electivity indices of felled trees of different sizes in three locations in all three study years at the Stream Site.

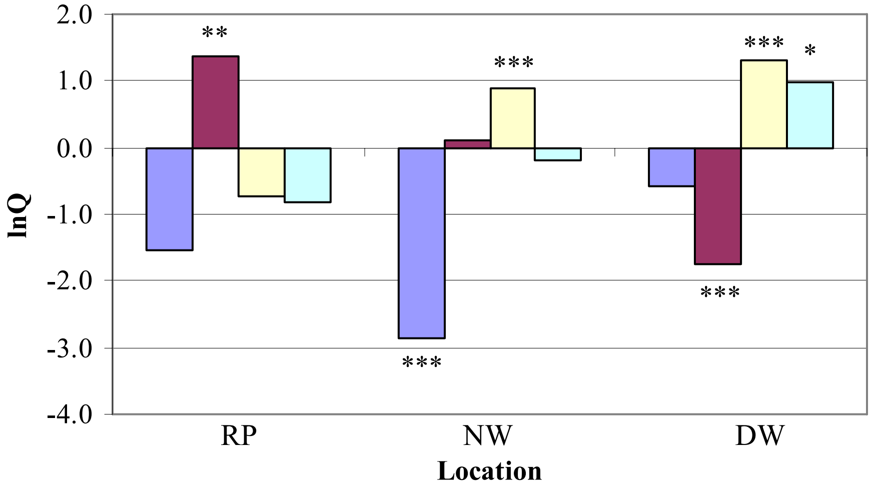
a) Year 1



b) Year 2



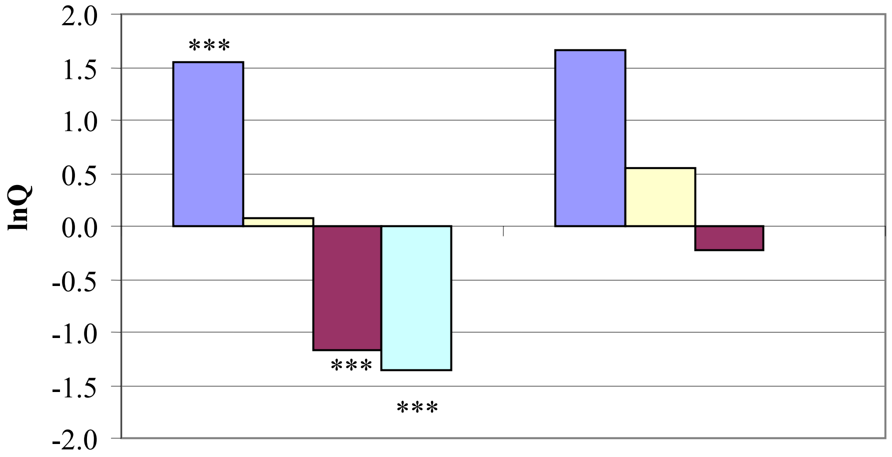
c) Year 3



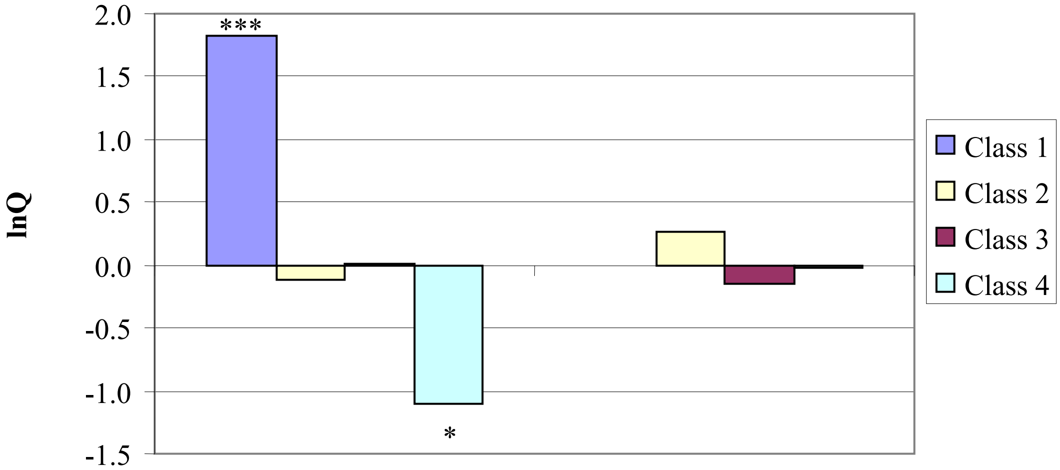
At the Lake Site (Figure 5.17) electivity indices for the trees within the water of the lochs (which comprise *c*. 96% of all felling), generally show the preferences of the beavers to be for the smallest trees throughout the study, with increasingly larger trees being less preferred. On the land surrounding the lochs, the general trend is the same as within the water, with the smaller trees being favoured over larger ones. However, due to the very small number of trees felled in this area throughout the study, this pattern is not significant.

Figure 5.17 Electivity indices of felled trees of different sizes in two locations in all three study years at the Lake Site.

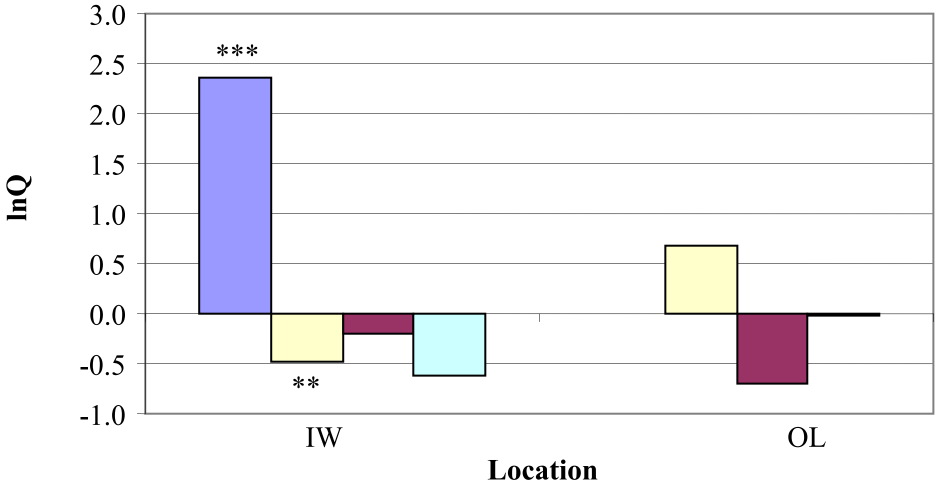
a) Year 1



b) Year 2



c) Year 3



5.4.8 The combined effect of the interaction between tree genera, location and tree size on the felling preferences of beavers

Further categorizing the felling and availability data for the Stream Site into size classes within each location for each tree genus shows the patterns illustrated in Table 5.8. In the area immediately surrounding the ponds (RP zone) the felling patterns of willows generally appeared to reflect the availability patterns in each year of the study, with the majority of felled trees being of Class 2 size (diameter 5 - 10 cm). It is also evident that very little alder of any size were felled near to the ponds despite an adequate supply of available trees, and all of those were in felled Year 1 and were larger than 10 cm diameter. A similar trend was observed in birches, with the vast majority of trees felled in Year 1 and broadly followed the availability of each size class. Further from the ponds in the NW zone (20 - 50 m), willow was again the most felled genus numerically in each year except Year 3, when birch was felled in large amounts despite the great abundance of available willow remaining in this area. Alder was very abundant throughout the NW zone but was felled in very small numbers in each year of the study. It is interesting to note that small willows (Class 1) were the most abundant size-class of available willow in the NW zone, but consistently were felled in very small numbers, with Class 2 and 3 trees being apparently preferred. Small birches were also felled in low numbers, with beavers apparently favouring Class 3 and 4 trees of this genus when available. In general, very few trees were felled at distances greater than 50 m from a pond (DW zone), with highest amounts of felling being of willow and lowest amounts of alder, although the availabilities of these two genera were approximately equal. In general, the felling patterns for each size-class of the three genera reflected the availabilities, although large proportions of the very largest willow and birches (Class 4, diameter $\geq$ 17 cm) were felled. It is also noticeable that the beavers felled very few of the smallest trees when they were available in the DW zone.

The Lake Site data (Table 5.9) clearly show that trees within the water of the loch are predominantly willows, and that trees favoured by beavers surrounding the loch are predominantly birches. Medium-sized willows (Classes 2 and 3) within the loch are most abundant, although considerable felling of the smallest (Class 1) trees was evident, and very little felling of the largest trees occurred throughout the study. Birches located in the IW zone were predominantly in size Class 2, although proportionately greater amounts of felling of the larger (Classes 3 and 4) trees were observed. Generally, so few trees of any size of either genus were felled on the loch shores (OL zone) throughout the study (*c*. 4% of all felling) that any trends are difficult to identify.

Table 5.8 Numbers of available (extrapolated) (red) and felled (black) trees of four different size-classes of three genera at three different locations, in each of three years of study at the Stream Site.

Genus	Location	Diam. class	Year 1		Year 2	Year 3*
			Available	Felled	Felled	Felled
Salix spp.	RP	1	216	32	6	1
		2	520	166	48	15
		3	333	34	12	3
		4	27	12	1	1
Alnus spp.	RP	1	40	0	0	0
		2	70	0	0	0
		3	72	13	0	0
		4	121	9	0	0
Betula spp.	RP	1	32	1	0	0
		2	194	23	0	0
		3	40	23	1	0
		4	0	0	0	0
Salix spp.	NW*	1	419	18	9	(427) 4
		2	257	57	58	(343) 34
		3	206	69	34	(214) 13
		4	108	12	5	(91) 2
Alnus spp.	NW*	1	107	1	0	(131) 0
		2	187	3	0	(257) 3
		3	262	1	1	(485) 3
		4	68	1	0	(117) 1
Betula spp.	NW*	1	44	1	0	(43) 0
		2	196	23	10	(314) 51
		3	50	8	2	(89) 89
		4	0	0	0	(13) 13
Salix spp.	DW*	1	78	0	0	(43) 0
		2	395	22	14	(182) 0
		3	185	18	11	(59) 0
		4	2	2	1	(0) 0
Alnus spp.	DW*	1	26	0	1	(1) 1
		2	165	4	1	(87) 1
		3	354	20	2	(107) 6
		4	70	4	2	(16) 4
Betula spp.	DW*	1	0	0	0	(1) 1
		2	174	3	5	(15) 6
		3	52	9	6	(22) 22
		4	15	1	1	(15) 2

* The availability figures for each genus in the NW and DW zones are shown in brackets in Year 3, with felled numbers shown outside the brackets. This is because the beavers occupied a new pond behind Dam 4 in Year 3, which extended the NW area and diminished the DW zone, so availabilities were altered accordingly.

Table 5.9 Numbers of available (extrapolated) (red) and felled (black) trees of four different size-classes of two genera at two different locations, in each of three years of study at the Lake Site.

Genus	Location	Diam. class	Year 1		Year 2	Year 3
			Available	Felled	Felled	Felled
Salix spp.	IW	1	122	101	12	32
		2	793	192	52	57
		3	380	31	28	28
		4	135	7	3	4
Betula spp.	IW	1	1	1	0	0
		2	89	16	1	2
		3	14	3	2	7
		4	7	2	1	6
Salix spp.	OL	1	0	0	0	0
		2	234	2	3	0
		3	127	1	2	0
		4	10	0	1	1
Betula spp.	OL	1	47	1	0	0
		2	431	2	2	3
		3	385	1	1	1
		4	301	0	1	0

Examination of the electivity indices for trees at the Stream Site (Table 5.10) indicated that the smallest willow trees (Class 1) were generally consistently selected against by the beavers within 50 m of the ponds (RP and NW zones). No Class 1 willows were felled at all over the three year study at distances greater than 50 m from a pond, despite moderate availability. Conversely, Class 2 willows (diameter 5 - 10 cm) were consistently selected for by the beavers within 50 m of the ponds. Larger willows (Class 3) were generally selected against within the immediate surroundings of the pond (RP zone), but preferred by beavers at greater distances from the ponds. Finally, the largest willow trees were generally avoided by beavers, except at distances of greater than 50 m from the ponds.

Table 5.10 Electivity indices for trees of four different size-classes of three genera at three locations at the Stream Site, over three years of study. Red figures indicate significantly positive index values and blue represents significant negative index values.

Genus	Location	Diam. class	Year 1	Year 2	Year 3
Salix spp.	RP	1	-0.169 **	-1.095*	-1.734
		2	0.532***	1.175***	1.520**
		3	-0.359*	-0.699*	-1.091
		4	0.595	-0.701	0.543
Alnus spp.	RP	1			
		2			
		3	1.533***		
		4	0.040		
Betula spp.	RP	1	-1.839		
		2	-1.034**		
		3	1.689***		
		4			
Salix spp.	NW	1	-1.727***	-2.271***	-2.088***
		2	0.496**	1.312***	1.340***
		3	1.105***	0.852***	0.268
		4	-0.385	-0.949*	-0.858
Alnus spp.	NW	1	-0.034		
		2	0.849	0.760	
		3	-1.286	-0.247	
		4	0.492	0.218	
Betula spp.	NW	1	-1.713		
		2	0.203	0.910	-1.466***
		3	0.470	0.005	1.755***
		4			1.159**
Salix spp.	DW	1			
		2	-0.304	-0.262	
		3	0.655*	0.686	
		4	2.800**	3.208*	
Alnus spp.	DW	1		1.462	2.949*
		2	-0.788	-0.636	-2.044
		3	0.612	-0.971	-0.028
		4	0.261	1.373	1.807**
Betula spp.	DW	1	-2.158**		0.550
		2	2.101***	-1.384*	-0.498
		3	0.228	1.419*	1.237*
		4		0.269	-1.745*

Generally too few alders were felled to indicate any significant preference or locational aspects, although smaller size-classes are broadly avoided near to the ponds and larger trees preferred further from water. Small birches are generally selected against and larger trees are generally preferred regardless of distance from a pond, although very large trees are avoided the furthest distances from water.

At the Lake Site, the smallest willows were consistently and significantly selected for by the beavers when foraging within the shallow water of the lochs (IW zone), whilst the larger willows were generally significantly selected against. This trend was reversed for birch trees, however. Although the very smallest birches were very rare within the IW zone, Class 2 trees were selected against and larger trees (Classes 3 and 4) were preferred by beavers. Too few trees regardless of size or genus were felled on the loch shores to provide any significant trends. All electivity indices for the three-factor interaction of species-location-size are shown in Table 5.11.

Table 5.11 Electivity indices for trees of four different size-classes of two genera at two locations at the Lake Site, over three years of study. Red figures indicate significantly positive index values and blue represents significant negative index values.

Genus	Location	Diam. class	Year 1	Year 2	Year 3
***Salix* spp.**	**IW**	**1**	1.549***	1.792***	2.413***
		2	0.104	0.014	-0.256
		3	-1.253***	-0.100	-0.414
		4	-1.574***	-1.400*	-1.392**
***Betula* spp.**	**IW**	**1**	1.656		
		2	-0.417	-2.499*	-3.258***
		3	0.090	1.885	1.738**
		4	0.396	1.552	2.234***
***Salix* spp.**	**OL**	**1**			
		2	0.158	-0.534	
		3	-0.040	-0.040	
		4		1.969	
***Betula* spp.**	**OL**	**1**	2.070		
		2	0.531	0.531	1.631
		3	-0.394	-0.394	-0.395
		4		-0.049	

5.4.9 Cafeteria experiments

The first two experimental procedures (Cafes S1 and S2) showed no signs of beaver feeding, which was attributed to the rapid drying out of the food items offered. The third methodology (Cafes S3 and L3) were improvements on the first two procedures as the offered material was still apparently fresh at the end of each cafeteria period. However, of the thirteen experimental runs conducted over the two Bamff sites using this methodology, only one cafeteria (Cafe S3.4) showed any removal of the offered material. Unfortunately, the cafeteria was visited prior to the camera becoming active (*i.e.* before dusk), and from the remains it was unable to be determined whether the food had been browsed by beavers or deer. In this instance, all of the offered food items were heavily browsed showing over 75% removal of material in all cases. Given the time of day that the cafeteria was visited, however, it seems likely that the browser was a deer or rabbit, rather than a beaver, and the results have been disregarded. Further work needs to be undertaken to determine an effective cafeteria methodology, in order to better assess the dietary preferences of beavers for different woody species.

5.4.10 Cache assessment

Seven discrete caches were present in the two Stream Site ponds in August 2004, comprising an estimated 225 branches of mean length 1.2 m. Only two species of tree were present in the caches, with willow predominant (92%) and some infrequent birch (8%), with no apparent vertical stratification of branches by species within the caches. In terms of size distribution of branches, there was a negative relationship between branch diameter class and abundance in the caches. Branches of less than 11 cm diameter formed the majority of the cached material (Class 1 = 43%, Class 2 = 36%) with larger branches relatively scarce (Class 3 = 14%, Class4 = 7%). It was also estimated that *c*. 91% of all willow branches showed development of adventitious roots, whilst no birch branches showed this development.

5.5 Discussion

5.5.1 Food species preferences

The Eurasian beaver is known to have a very broad diet and Kitchener (2001) documented 80 woody species in its diet, although marked preferences for certain genera and species have been recorded (*e.g*. Bryant & Kuropat, 1980). It was hypothesised that generic preferences would be exhibited by the Bamff beavers, with aspen and willow preferred, and conifers and elder avoided (Hypothesis 5.1).

European aspen (*Populus tremula*) is widely regarded as the food item favoured above all others when available (Simonsen, 1973; Lahti & Helminen, 1974; Kitchener, 2001). Only a very small number of aspen were present at the Stream Site at Bamff, but it was observed that all of these trees were felled soon after the beavers were introduced to the site, suggesting high species preference despite the low availability. This is supported by the highly significant positive electivity index for aspen in Year 1 ($P<0.001$). No aspen were present at the Lake Site.

Throughout the study, nine genera / species of trees were felled, although only willow, birch and alder were felled in large quantities, and some species despite their often high abundance were almost entirely avoided by beavers. Principal amongst these were all coniferous species and the deciduous elder (*Sambucus nigra*) and sessile oak (*Quercus petraea*). The general resistance of elder to herbivory is well-known due to the high concentration of toxic secondary compounds, such as sambunigrin, present in its tissues (Atkinson & Atkinson, 2002), and complete avoidance of elder species by beavers has been observed in other European studies despite high availability (Nolet *et al*., 1994; Haarberg & Rosell, 2006). The general avoidance of conifers by beavers is supported by numerous studies in Europe and North America (*e.g*. Simonsen, 1973; Hartman, 1992; Müller-Schwarze *et al*., 1994), with the only conifer felled at Bamff being a very small specimen which was subsequently left intact by the beavers. Studies noting higher levels of coniferous felling than were observed at Bamff, often found large quantities of otherwise untouched coniferous material in the structure of dams (Doucet *et al*., 1994a) or the uneaten "raft" material of caches (Slough, 1978 *op. cit.* Dennington & Johnson, 1974). Beavers are known to sample the palatability of trees before felling (*e.g*. Jenkins, 1979; 1980), and it seems likely that an "over-enthusiastic" example of this behaviour led to the felling of this particular small conifer. It should also be noted that several instances of small (<0.25 m^2) patches of bark being stripped from large, mature conifers were observed at the Lake Site. Such behaviour has been documented in the Eurasian beaver (Simonsen, 1973) and the North American beaver (Svendsen, 1980), and has been proposed as a mechanism of ingesting small amounts of coniferous sap and bark in order to provide a balanced diet (Jenkins, 1979).

Willow species are also highly preferred by beavers (*e.g*. Nolet *et al*., 1994; Lapinski & Stalinski, 2001; Haarberg & Rosell, 2006) and data from the Stream and Lake Sites strongly support this preference. Willow made up 64% and 91% of all felled trees but only 47% and 27% of available trees at the Stream and Lake Sites respectively. The positive selection of willow by beavers was highly significant in all three years of study at the Lake Site and in Years 1 and 2 at the Stream Site. The wider range of palatable deciduous species available at the Stream Site (eight species) compared to the Lake Site (four species) possibly contributed to the apparent lower reliance of beavers on willow in general. Indeed, it may be that the Stream Site beavers are attempting to balance their diet by occasionally substituting preferred willow with other less preferred but abundant deciduous species, which the Lake Site beavers have fewer opportunities to do due to the low availability of other species. For example, beavers reintroduced to the willow-dominated Biesbosch area of the Netherlands, showed significant positive selection for a wide range of rare deciduous species such as alder, ash, cherry, and hazel, which was attributed to the beavers attempting to select a balanced diet (Nolet *et al.*, 1994). It has been documented that captive beavers reared entirely on restricted diets show weight-loss and even death after several weeks, even when the diet consists solely of highly preferred species such as aspen (Müller-Schwarze & Sun, 2003 *op. cit.* O'Brien, 1938). **The data at both Bamff sites support the predictions made by Hypothesis 5.1, that generic preferences for trees would be exhibited by the beavers, with willow and aspen preferred and conifers and elder avoided. Hypothesis 5.1 is therefore accepted.**

Birch trees were the second most commonly felled trees at both Bamff sites, although the apparent preferences for this genus differ between sites. At the Stream Site, the beavers had a neutral preference for birch, generally felling in proportion to availability, except in Year 3 when it was significantly selected for. At the Lake Site, however, birch was consistently significantly selected against, which was probably related to distance factors rather than pure species preferences of the beavers. The vast majority of felling at the Lake Site was of the highly preferred willows, which were predominantly situated within the shallow water (< 0.5 m deep) of the loch. The general lower preference of beavers for birch was probably exacerbated by the fact that birch was only abundant on the loch shores. The influence of distance on foraging preferences of the Bamff beavers will be discussed in section 5.5.3.

It is also interesting to note the relatively large amount of alder felled at the Stream Site (the third most abundantly felled species), although in terms of availability, however, alder is consistently selected against by beavers. This low preference for alder supports other European studies (*e.g.* Nolet *et a*l., 1994), although recent observations in Norway suggest a neutral attitude of beavers towards to grey alder (*Alnus incana*) (Haarberg & Rosell, 2006). It has been proposed that alder is felled for construction purposes rather than as a food item (Pinkowski, 1983). In our study, the species composition of dams and lodges was not quantified, but a good correlation exists between the numbers of alder felled annually at the Stream Site and the degree of construction activity undertaken there (see Table 4.6). The first year showed the highest number of felled alders followed by Year 3, which corresponds well to the observed intensities of construction activity. Furthermore, in Year 2 when no construction occurred, only 7 alders were felled despite alder representing the second most abundant genus at the site.

It is not suggested, however, that alder is the sole material used in beaver constructions, as regrowth from cut willow incorporated into dams and lodges has been observed at the Stream Site (see section 6.5.1), whilst branches of birch and other deciduous species have also been observed in the structures. It seems likely that when building dams and lodges the most influential factor controlling selection of suitable trees is distance, with the nearest trees always being chosen regardless of palatability, species or size (Hypothesis 5.2). A beaver should not waste energy by bypassing trees of low preference near to a dam / lodge site in order to access any other trees to be used for building further away. The pattern of felling around a structure should therefore reflect the species availability in that area. If this hypothesis is valid, tree species that are selected against or completely ignored by beavers in areas during periods of no construction activity, should become more important in the same area during periods of high construction activity. Examination of the data for felling Zone 7 at the Stream Site allows this hypothesis to be tested, as it is an area of relatively high tree species richness (6 species) and experienced no construction in Years 1 and 2, but high activity in Year 3. During the first two years, in addition to the three most abundant species in the zone (willow, birch and alder) only one other tree species was felled (hawthorn) which was selected for by beavers, but not significantly so. In Year 3, however, during intense construction activity ash, cherry and hawthorn were preferred by the beavers, with two of these species showing highly significant positive electivity indices (hawthorn $P<0.001$ and cherry $P<0.01$). **These results support Hypothesis 5.2 that during periods of intense construction, beavers positively select otherwise unpreferred tree species which presumably are used for building rather than food.**

As much of the published data on generic preferences of beavers report felled quantities without availabilities, or cover only a small number of all the tree species known to be felled by beavers, comparisons between studies are difficult. However, in general, the generic preferences of the Bamff beavers reflect those observed in numerous published studies in both Europe and North America. Aspen is highly preferred when available (*e.g.* Aldous, 1938; Shadle & Austin, 1939; Beer, 1942; Shadle *et al.*, 1943; Hall, 1960; Simonsen, 1973; Pinkowski, 1983; Fryxell & Doucet, 1991; 1993; Doucet & Fryxell, 1993; Müller-Schwarze *et al.*, 1994), with willow also a preferred food item of beavers (Shadle & Austin, 1939; Shadle *et al.*, 1943; Beer, 1942; Hall, 1960; Roberts & Arner, 1984; Müller-Schwarze *et al.*, 1994; Nolet *et al.*, 1994; Haarberg & Rosell, 2006). Many of these studies also note the important role of birches in the diet of beavers, with alders often felled in moderate quantities, and conifers and elder usually of low preference or avoided completely. The occasional importance of other woody species to beavers, such as oak, ash, rowan, cherry and hawthorn, serves to indicate the wide dietary flexibility of beavers in the absence of preferred species (*e.g.* Nixon & Ely, 1969). Furthermore, as well as the derived electivity indices, the analysis of cache contents at the Stream Site support the conclusion that willow is a highly preferred species, followed by birch.

5.5.2 Food size preferences

Beavers are known to select trees by size as well as species, with smaller trees being felled in preference to larger ones (*e.g.* Simonsen 1973, Jenkins 1979), and it was hypothesised that the beavers at Bamff would behave in this manner throughout this study (Hypothesis 5.3). The general trend at the Lake Site supports this hypothesis, with the smallest trees consistently and significantly preferred, and the very largest trees selected against. However, at the Stream Site Hypothesis 5.3 is rejected, as the smallest trees are consistently and significantly selected against by the beavers, although the avoidance of the largest trees is as predicted. The reasons for this unexpected selection pattern are unknown.

The high intensity of building by the beavers at the Stream Site may play a role in influencing the sizes of trees felled. It may be that the smallest trees simply do not provide enough useful material for dam and lodge building, and the proportion of intermediate-sized trees felled is therefore increased, but this seems unlikely for the following reasons. Firstly, although the construction activity at the Stream Site was often very intensive, it seems unlikely that it was of unprecedented levels, and one would expect at least some colonies in the published literature to have experienced similar levels of activity. Secondly, in Year 2 no construction took place yet the smallest trees were still significantly selected against.

Some studies have demonstrated that individual beavers, or beavers from different neighbouring colonies, can show different generic felling preferences despite similar availabilities (*e.g*. Jenkins, 1975; Müller-Schwarze & Sun 2003 *op. cit* Shelton 1966). It seems possible therefore that different beavers also have different tree-size preferences. It is also thought that beavers can apparently detect the nutritional content and chemical composition of individual trees by sampling a small amount of bark without felling the tree (Jenkins, 1978). As chemical analyses of different size classes of tree were not conducted in this study, this possibility cannot be verified. However, if this was the reason for the unusual size-selection exhibited at the Stream Site, then abundant sampled / nibbled trees in the smallest size-class should have been present there. Although this aspect was not specifically recorded during the study, it was not an obvious feature of the site (*pers. obs.*), so it seems unlikely to be a reasonable explanation of the observed trends. Further consideration of the interactions between tree-size, species and location that follow (section 5.5.4) may shed light on this apparently unusual aspect of tree selection at the Stream Site.

5.5.3 Locational preferences

Studies have demonstrated that beaver felling largely takes place in the riparian zone, although exact distances travelled to acquire food will vary according to habitat quality (Simonsen, 1973; Johnston & Naiman, 1990), so it was hypothesised that felling activity at the Bamff sites would decrease with increasing distance from the ponds

(Hypothesis 5.4). At the Stream Site trees within 20 m of a pond are significantly preferred whilst those further than 50 m away are selected against (*P*<0.001 in both cases), whilst at the Lake Site the same trends exist with trees within the water of the lochs being significantly preferred over those on the shore. **Hypothesis 5.4, which proposed that felling activity would decrease with increasing distance from the ponds, is therefore accepted.**

It is noticeable, however, that the Stream Site shows temporal variation, with the riparian areas becoming less preferred as time progresses, and the woodlands of intermediate distance becoming increasingly preferred. This is likely to be indicative of resource depletion around the ponds of the Stream Site, which is not yet apparent within the aquatic resource of the Lake Site. The ponds at the Stream Site are considerably smaller than the lochs at the Lake Site, so the wooded riparian areas are correspondingly smaller and more rapidly depleted. As these riparian areas are dominated by willow, the high stem regrowth rates detailed in Chapter 6 are likely to replenish this resource within a relatively short period, and it is predicted that riparian areas will again be preferred by foraging beavers at the Stream Site. The data for the Lake Site also suggest that beavers are likely to preferentially forage within aquatic carr areas rather than felling the same tree species just a few metres away on land.

5.5.4 Interactions between tree genera, size and location, and their influence on felling patterns

Many studies have demonstrated that beaver foraging behaviour complies with that predicted by specific optimal foraging models, that assume that beavers select prey in order to maximise the net rate of energy or nutrient intake per unit of time, *i.e.* that beavers are energy maximisers. (*e.g.* Pinkowski, 1983; McGinley & Whitham, 1985). As an animal that travels away from a central-place in it's territory (*i.e.* a lodge or pond) to gather food items, which it then transports back to the central place for consumption, the beaver is known as a central place forager (*e.g.* Jenkins, 1980). The reviews of Schoener (1971) and Orians & Pearson (1979) provide excellent overviews of the ecological theory of central place foraging and should be consulted for a full appraisal of the subject. Only the aspects pertinent to foraging by beavers will now be discussed, with reference to the results obtained in this study.

General assumptions of the central place foraging theory include the sequential encountering of trees by foraging beavers, that trees are randomly distributed in terms of size, species and location, and that searching for prey cannot occur simultaneously with food handling and provisioning (*i.e.* chopping up large trees into manageable portions) (*e.g.* Fryxell & Doucet, 1993). Crucial to the theory is the idea of the "round trip", including an outbound trip, a foraging period and a return trip (Orians & Pearson, 1979). Although energy is used in all three phases, it is only gathered in the second phase, and the costs of a return trip will be greater than an outward trip due to the costs of hauling prey back to the central place. By felling trees much larger than themselves, beavers are known as single-prey loaders, "capturing" a single tree per round trip and returning it to the central place for consumption. For each round trip, two alternative strategies can apply by making different assumptions about the handling or provisioning time *i.e.* the time taken for a beaver to fell a tree and process it into transportable sections.

The first strategy involves the assumption that handling time is independent of food size, and is applicable when beavers feed on very small twigs of trees and shrubs. In this case, provisioning time is not related to prey size, with cutting and transporting the smallest twigs costing the same amount of time and energy as for the largest twigs. Other provisioning costs will increase with increasing distance from the central place in the usual manner, so the profitability of all twigs should decrease. In this situation, the greatest profitability at all distances should be from the largest twigs, because these offer higher energy returns per unit cost than smaller items, so large twigs should be preferred at all distances and small items deleted from the diet further from the pond. In a study of beavers foraging for small food items (twig diameter *c*. <0.01 m) in the USA, handling time was assumed to be independent of food size (McGinley & Whitham, 1985). Under these conditions it was predicted that larger items would be preferred at all distances, fewer branches would be cut with increasing distance from the beavers' pond, and that the smallest branches would be deleted from the diet at the greatest distances. The observed behaviour supported these predictions.

An alternative, and arguably more realistic, scenario involves beavers feeding on larger items than those measured by McGinley & Whitham (1985). When large items are selected, the provisioning time increases with increasing prey size (Schoener, 1979). In order to maximise energy intake, prey selectivity will increase as distance from the central place increases, and this should be manifested by preference for smaller over large trees further from a beaver's pond. In other words, as distance increases, the higher energy content of large trees is outweighed by the increased time and effort involved in felling, handling and transporting the items back to the pond. Studies of beavers foraging on large branches or trees have shown this increase in size-selectivity and decrease in number of trees felled with distance in North America (*e.g.* Jenkins, 1980; Pinkowski, 1983; Belovsky, 1984; Basey *et al.*, 1988) and Europe (Haarberg & Rosell, 2006). At Bamff the beavers were feeding on large items, so the observed behaviour should be the same as that reported in these studies, if they were foraging optimally.

At Bamff there was good evidence to support the prediction that numbers of felled trees would decrease with increasing distance from a pond, a key tenet of central place foraging theory. At both sites, the overall trend through the three-year study was for significant preference for trees within 20 m of the ponds at the Stream Site, or within the water of the lochs at the Lake Site. Annual trends at the Stream Site suggest that resource depletion was occurring around the ponds, with the beavers forced to forage in patches increasingly further away as time progressed, which was supported by field observations. This trend was not replicated at the Lake Site however, where the preference for the aquatic woody resource was as strong in Year 3 as it was at the start of the study.

In terms of selectivity of different species at different distances, the Stream Site produced some interesting results. According to the theory, as selectivity increases with greater distances from the central place, the most profitable items should be increasingly selected and less profitable foods deleted from the diet. This should mean that the most preferred species (willow) should be of even greater preference as distance from the ponds increases, and the selection against the unpreferred species (*e.g.* alder) should increase. In Year 1, beavers showed significant positive selection for the three most commonly felled species (willow, alder and birch) near to the ponds supporting the predicted low selectivity at close proximity to the ponds. However, by Year 3, highly preferred willow trees had been deleted from the diet at distances greater than 50 m from a pond, whilst the unpreferred alder was significantly selected for, as was birch.

This is contrary to the predictions of central place foraging theory, which could be due to three reasons.

Firstly, the value of a food item is likely to be related to the danger of predation that the beavers are exposed to, or perceive, not just the energetic cost / benefit relationship of that item. It is possible that at great distances from the safety of a pond, a beaver is less inclined to spend time searching for the most preferred food items, and is more likely to accept species of lower preference more readily. Despite the absence of any predators of beavers in Scotland, it is likely that the study animals exhibit an innate response to the threat of predation by adopting a more vigilant approach to foraging at greater distances from safety. Studies in Norway using predator scents suggest that beavers show an innate fear of wolves and lynx, despite having been allopatric with wolves for the last century, and the lynx reaching near-extinction in the 1930s (Rosell & Sanda, 2006). The effects of such an innate response could be responsible for the unpredicted foraging activity observed at the Stream Site. The Lake Site beavers did not show this response, with preferred willows remaining the chosen food item in both distances categories used in this study. Given that almost all of the terrestrial willow resource present at the site was still located ≤ 5 m from the water's edge, it is little surprise that these "distant" trees are treated as relatively low-risk food items by the beavers. In this case, selection of willows within the water of the lochs is likely to be predominantly due to the decreased time and effort required to haul these items to a feeding platform or the lodge.

Secondly, the availability of preferred willow trees is very low at distances greater than 50 m from a pond, and is progressively depleted rather than replenished naturally over the timescale of the study (*e.g. c*. 13% of all trees available at this distance in Year 3).

This very low availability may lead to such a small chance of encountering the tree when foraging, perhaps exacerbated by the perceived increase risk of spending time searching at great distances from safety, that very low numbers of the tree are likely to be felled. Finally there is also the possibility that the beavers are using an agenda other than foraging for food, and so behave in a manner contrary to that expected. For example, the criteria for selection of construction materials may be significantly different to those for food items, when palatability, concentration of plant defences and size (see section 5.5.2) are of lesser importance. The majority of studies of foraging beavers referred to throughout this chapter have been of animals confined to a relatively small experimental area, or of mature colonies which presumably do not exhibit great levels of construction activity. It is also common for researchers to attribute all felling to feeding because the majority of material used in dams and lodges is of stripped woody material (*e.g.* Gallant *et al*., 2004). This was not the case at the Stream Site at Bamff, where abundant use was made of branches with intact bark in the construction of dams, dens and lodges (see Figures 4.16 and 4.17 for example).

Further support for the influence of construction on the foraging patterns observed around the ponds of the Stream Site could be derived from the size selection patterns observed. Generally, smaller items should be preferred even in close proximity to the ponds, but it was evident that the Class 2 willow trees (5 - 10 cm diameter) were consistently of high preference and the smallest trees (diameter $\leq$ 4 cm) were of low preference in these areas. It seems unlikely that this is due to decreased palatability of the youngest trees, as several studies have shown that young *Salix* are of high palatability with low concentrations of secondary compounds (*e.g.* Veraart *et al.* unpublished data cited in Haarberg & Rosell, 2006). Similar size-selection patterns were evident in both alder and birch trees. It is possible that smaller trees simply do not offer suitable construction materials in the way that larger trees do, and so are selected solely for food. The role of construction could be masking the usual preferences observed in riparian zones of mature colonies that conform to the central place foraging theory, as published in much of the available literature. Conversely, at the Lake Site in the relative absence of construction work, the trend amongst the nearest willows (*i.e.* those within the water) was as would be predicted under optimal foraging scenarios, with preference shown for smallest trees.

These deviations at the Stream Site from the predicted optimal behaviour, have to this author's knowledge only been replicated in one other study. In a study of the foraging activity of beavers in Canada, Gallant *et al.* (2004) categorised 25 study areas of well-established beaver colonies, into "superior", "intermediate" or "inferior" habitat quality. The deciding factor for allocation of sites into these classes was the proportion of deciduous trees in the habitat, with the highest proportions signifying superior habitat quality. The results indicated that in the superior habitat, beavers selected larger trees of all four species measured at increasing distances from the central place, contrary to that predicted for an optimal central place forager feeding on large items. In inferior and intermediate quality habitats, no significant relationship between distance and size-selectivity was evident, which the authors attributed to the general reluctance of beavers in poorer habitats to forage at great distances from the ponds. They also noted that beavers could be apportioning more energy into foraging for the abundant macrophytes present in these habitats than for woody material.

There are some interesting parallels between this study and that undertaken at Bamff. For example, the Stream Site would clearly be "superior" habitat according to the classification of Gallant *et al.* (2004), with *c.* 96% of available trees being deciduous species. Beavers foraged over large areas of the Stream Site and the superior sites in Canada, and showed similar size-selectivity patterns at different distances from the ponds. Conversely, the Lake Site would be classed as inferior or intermediate with only 53% of all trees being deciduous. The very low numbers of trees felled in the most distant areas (the OL category) at the Lake Site prevent significant trends being identified, so direct comparisons to the inferior sites in the study of Gallant *et al*. (2004) are not possible. However, the role of macrophytes in the diet of the Lake Site beavers has already been noted earlier in this thesis (section 4.7).

Finally, in a study of the beavers reintroduced to the Biesbosch area of the Netherlands (Nolet *et al*., 1994), it was suggested that beavers may sample trees more frequently to assess the nutrient concentrations of different species when they first enter an area. It seems possible that this idea could equally be extended to size-selectivity, as well as species-selectivity. However, can the unpredicted (non-optimal) foraging patterns observed at the most distant areas of the Stream Site at Bamff, be explained effectively by the unfamiliarity of the beavers to the area? If so, one might expect the size-selectivity to return to predicted patterns with increasing time since initial colonisation. There is no evidence that this occurred within the three-year study, however, with highly significant selection for the largest trees at distances greater than 50 m from the central place in Years 1 and 3. Due to the comparatively high turn-over of beavers at the Stream Site this possible "learning curve" approach of the beavers cannot be completely eliminated.

In summary, the beavers at both sites show at least some compliance with the behaviour that would be predicted of a single prey-loading central place forager, feeding on large food items. Species selection generally reflects that reported in many other studies, with suitable resources exploited nearer to the ponds before distant resources. Whilst the Lake Site shows size-distance selectivity as predicted by ecological theory (and indeed observed in many studies), the Stream Sites beavers exhibit a different foraging trend. Hypothesis 5.5 is therefore accepted at the Lake Site, but rejected at the Stream Site. This difference has been attributed to the high intensity of construction work conducted at the site, which was absent from the Lake Site and the well-developed colonies referred to in the majority of the available literature. It is apparent that beavers are extremely flexible in terms of foraging, adopting an optimal approach for dietary needs, and a different strategy when construction work is a priority. This apparent flexibility is further supported by the relationship between foraging patterns and habitat quality (Gallant *et al*., 2004) which was evident at Bamff. It is interesting to note that earlier in this study (Chapter 4) the Stream Site was classed as a marginal site, and the Lake Site as optimal, which is the direct opposite of that assumed above, due to different assessment criteria being applied. If one considers that a marginal habitat is one that requires large amounts of physical modification of the environment, and *vice versa*, the conclusions reached in Chapter 4 are valid. The classification also remains valid if the criteria involve the provision of a good mix of woody species and macrophytes available to the beavers, or the provision of a readily available source of preferred woody species at close proximity to the safety and convenience of a pond. However, if the assessment involves the particular proportions of deciduous to coniferous trees available, the opposite conclusions on habitat quality would be reached at Bamff. This serves to illustrate the complexity of issues involved in assessing the suitability of different habitats for a flexible, adaptable ecosystem engineer, such as the beaver.

5.5.5 Summary

Although a wide range of tree species have been documented as forming part of the diet of beavers, and at Bamff nine genera / species were felled, preferences for certain species were evident. Hypothesis 5.1 predicted that of these preferences, aspen and willow trees would be selected for by beavers, and this was supported by the data at Bamff. Furthermore, it was predicted that other species would be avoided, particularly elder and coniferous trees, and again this was found to be the case at Bamff. Hypothesis 5.1 was therefore accepted. There was also evidence to suggest that when a range of palatable deciduous species is available, a number of different species are felled even when highly preferred willow trees are abundant. This was attributed to the beavers attempting to avoid mineral deficiencies caused by a single-prey diet, and instead select a more balanced food intake. During periods of intense construction activity, it was hypothesised that tree proximity would be the overriding factor in determining felling patterns, with other preferences (tree species and size) becoming of secondary importance (Hypothesis 5.2). This was indeed supported by the data, with otherwise unpreferred species being felled in relatively large amounts in close proximity to newly-built dams, and Hypothesis 5.2 was accepted.

It was proposed that beavers would show selectivity in terms of size of trees felled, with smaller trees being preferred over larger ones (Hypothesis 5.3). At the Lake Site the data supported this hypothesis and it was accepted. However, at the Stream Site the smallest trees were consistently selected against, and the hypothesis was rejected. Some possible explanations for this unexpected result at the Stream Site were considered, such as the effects of felling to supply the numerous construction projects undertaken at this site, or the possibility of inherent differences in behaviour and preferences between individual beavers. However, no satisfactory answer for this deviation from the hypothesised trend was found, and further investigation is required.

Hypothesis 5.4 stated that beavers would preferentially forage near to water, with felling activity decreasing with increasing distance from a pond. At the Stream Site, trees within 20 m of the ponds were highly significantly preferred, whilst those located over 50 m from water were highly significantly selected against. Similarly, at the Lake Site, trees located within the shallow water at the margins of the lochs were highly significantly selected for, whilst those on land were highly significantly selected against. Hypothesis 5.4 was therefore supported by the data at both sites, and was accepted. The data did suggest, however, that the tree resource immediately surrounding the ponds at the Stream Site were becoming depleted, and trees further from the ponds were being selected for by the beavers as time progressed through the study. Reasons for this resource-depletion at the Stream Site, which did not occur at the Lake Site, were briefly discussed.

Finally, the felling activity was examined in the context of optimal foraging theory, specifically assuming that the beavers were central place foragers feeding on single, large prey items (Hypothesis 5.5). This involved a synthesis of the generic, size and locational preferences shown by the beavers, and discussed earlier. At the Lake Site, the behaviour of the beavers did comply with the central place foraging theory and Hypothesis 5.5 was accepted. However, at the Stream Site, the unexpected preference for large trees over smaller ones led to Hypothesis 5.5 being rejected. This deviation from the expected behaviour at the Stream Site was attributed to the high degree of construction activity undertaken at the site, which required considerable amounts of felling. It was proposed that beavers do not follow conventional ecological theory when felling trees for building purposes, and dietary preferences and behavioural patterns do not apply during periods of intense habitat modification. It was proposed that such "aberrant" behaviour is most likely to be evident during the initial stages of colonisation of marginal habitats.

6 Effects of beaver activity on riparian tree communities: iii) Tree regrowth rates

6.1 Abstract

Knowledge of the factors affecting the number of trees felled by beavers each year, together with the preferences of the animals for certain tree species, sizes and locations, allow predictions to be made as to the effects a beaver colony may have on an area of riparian woodland. However, until now in this thesis, the available tree resource has been considered non-renewable, which will clearly limit the accuracy of any predictions made regarding beaver activity. Such a limitation is also likely to lead to pessimistic, as well as unrealistic, conclusions being drawn regarding the short-term effects on trees of a potential beaver reintroduction to Scotland. Given the perceived conflict between a beaver reintroduction and the desire to restore riparian broadleaf tree communities, especially of highly preferred willow and aspen trees, knowledge of how these trees respond to felling by beavers is essential. This chapter presents data on willow and aspen regrowth following tree-felling by the beavers at the two Bamff study sites, by quantifying the regrowth of willow stems from cut stumps, felled logs and partially severed ("Incompletely-Felled") trees, and comparing it to growth of stems in the canopies of untouched willows. Aspen regrowth from the root suckers arising from all of the completely felled parent trees was quantified at the Stream Site.

Maximum annual regrowth was observed in incompletely-felled trees, followed by cut stumps and then unfelled control trees. Mean regrowth rates were *c.* 18 m regrowth per m of measured tree section per year in incompletely-felled trees. This was approximately 12 times more annual regrowth than that observed in unfelled trees, despite apparently selective browsing of the regrowth of incompletely-felled trees by roe deer. Although incompletely-felled willows represent a relatively small component of felling activity (*c.* 9% of all felled willow), they contribute disproportionately to the

biomass of beaver-engineered riparian woodlands, creating a more complex multi-layered habitat structure. Generally, all willow regrowth in inundated areas was avoided by deer, and harvesting of regrowth by beavers was rare during the study period. The data also suggested that sexual, as well as vegetative, reproduction is promoted by beaver felling of willows, with earliest catkin production observed on the regrowth of incompletely-felled trees, followed by stumps, and finally control willows. Significant regrowth from 11 stumps of aspen in 2 years post-felling occurred by suckering, with 85 suckers of mean height 2.1 m being recorded, all of which were subsequently avoided by browsing deer and beavers.

These data suggest that rapid regeneration of willow and aspen will occur in riparian woodlands in the event of major felling activity by Eurasian beaver, even in the presence of low to moderate levels of roe deer browsing, and that the conservation status of both these trees or the wider habitats that they form would not be threatened by a reintroduction of beavers to Scotland.

6.2 Introduction

Riparian tree-felling is often cited as a source of concern amongst groups opposed to a reintroduction of the beaver to Scotland (Scott Porter Research & Marketing Ltd., 1998; Scottish Executive, 2005 – in Appendices A1 and A2 of this thesis), particularly over the potential conflict between beaver felling activity and the desire to restore broadleaf riparian communities (Broadmeadow & Nisbet, 2002; Forestry Commission, 2003). Willow species (*Salix spp.*) have great importance in riparian areas of conservation interest, due to the stabilisation of stream banks that they provide, reducing the effects of bank erosion (Lewis & Williams, 1984). The conservation of aspen (*Populus tremula*) woodland is especially important in Scotland, since aspen supports specialist invertebrates, bryophytes, lichens and fungi, several of which are listed as 'Priority' species in the UK Biodiversity Action Plan (Cosgrove *et al.*, 2005).

Such potential conflicts to the status of riparian tree communities could be exacerbated by certain aspects of beaver behaviour and felling activity, which have been highlighted in earlier chapters of this thesis and other published sources. The majority of beaver felling activity is located in the riparian zone, generally within 50 metres of the waters edge (Hall, 1960; Simonsen, 1973; Novak, 1987; Johnston & Naiman, 1990). Aspen is often the favoured prey species when available (Simonsen, 1973; Lahti & Helminen, 1974; Gorshkov *et al.*, 1999), and beavers will travel further away from the safety of water in order to reach this species, with foraging distances up to 238 m being recorded (Northcott, 1971 *op. cit.* Miller, 1960). Furthermore, willow species also rank highly on the beavers list of preferred food items (Nolet *et al.*, 1994; Łapiński & Staliński, 2001; Jones *et al.*, 2003).

Willow forms an important component of the overall tree canopy at the Bamff study site, making up approximately 47% and 27% of all the trees present at the Stream and Lake Site respectively (see section 5.4.2). Even allowing for the abundance of willow at these sites, the beavers have shown a preference for willow over other tree species available over a three-year period, with 73% of all felled trees being willow (see section 5.4.1). By contrast, aspen represents a very small resource, and all 11 trees present were felled within six months of introducing beavers to the site. These observations indicate that both species of tree are heavily consumed thus supporting the existing literature on the beaver's diet from other countries, as discussed in section 2.3.2.1. It was estimated that the Stream Site initially contained *c*. 2,700 willow trees, which, if the rates of felling observed over the three years of study were to continue unabated would be fully exploited in approximately 10-12 years. Critically however, these estimates assume that both the rate of felling and numbers of beavers remain constant through time (contrary to what has been shown in Chapter 4), and that prey switching will not occur. Perhaps more significantly they also assume that the willow resource is non-renewable. This highlights the need to consider the willow regrowth that occurs post-felling, especially against a background of deer browsing that is virtually endemic in Scotland.

Vegetative reproduction is very successful in both willow and aspen. Willows readily coppice from cut stumps (Fuller & Warren, 1993) and severed branches (Edlin, 1958), and drift of vegetative fragments is the principal method by which new sites are colonised. Unrooted willow stems are commonly employed when rapid revegetation of newly engineered riverbanks is required (Lewis & Williams, 1984; Schaff *et al.*, 2002). Aspen sends up suckering shoots from the root system (Borset, 1960; Worrell, 1995a) as can be readily observed in managed hedgerows. Few studies however, have been conducted on the response of either willow or aspen to cutting by beavers. Notable exceptions include the measurement of Red willow (*Salix lasiandra* Benth.) regrowth following felling by the North American beaver (*Castor canadensis*) (Kindschy, 1985) or simulated beaver cutting (Kindschy, 1989). In both of these studies, geographical features isolated the felled trees from other browsers.

In the UK, such "other browsers" include six species of deer living in the wild, which are increasing in both numbers and range (Gill, 1992a; Putman & Moore, 1998; Mayle, 1999). Scotland is home to four of these species – the native roe (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) and the introduced sika (*Cervus nippon* Temminck) and fallow deer (*Dama dama* L.) (Mayle, 1999). Of these, roe are the most numerous and most likely to overlap with habitats potentially used by beaver, whether historically or as part of any future reintroduction. Browsing by deer has many well-documented adverse effects on commercial forestry and important natural habitats including damage to both developing and mature trees, and poor regeneration (Gill, 1992a; Putman, 1996). In the event of a trial reintroduction of beavers to Scotland, any effects of coppicing by beavers are likely to be influenced to some degree by deer.

At the Stream Site, the amount of stem regrowth occurring in cut willow was measured by selecting 10 trees in each of three categories representing the range of outcomes of beaver felling activity – "Incompletely-Felled", "Stump" and "Control". The incompletely-felled category comprised willow that had been felled by the beavers, with the trunk (above the cut) lying horizontally but still attached to the base (below the cut) by a strip of bark and cambium tissues, often as narrow as 2 cm in width (Figure 6.1). As the cambium had not been entirely severed, these trees were still alive and apparently healthy. The stump category consisted only of the stumps remaining after complete felling, whilst the control trees were untouched by beavers. Full definitions of the stump and incompletely-felled categories can be found in section 4.4.

Figure 6.1 Example of an “incompletely-felled” willow at the Stream Site, showing stem regrowth from the trunk and base.

This study will investigate the regrowth of willow and aspen trees following felling by beavers within the two enclosed sites at the Bamff estate. The impact of browsing by roe deer on any regrowth will also be considered, and the following hypotheses will be tested:

6.1 Following felling by beavers, willow trees will show a high incidence of shoot regrowth from cut stumps and the trunks of incompletely-felled trees.

6.2 The amount of annual stem regrowth from a measured section of the trunk of incompletely-felled willows will be greater than the annual growth of stems on a similar length branch of an untouched tree.

6.3 Deer browsing will have a greater impact on the regrowth arising from the cut stump of willow trees than that arising from the incompletely-felled willows.

6.4 Aspen trees will respond to felling by beavers by readily and rapidly suckering from the roots.

6.5 The incidence of beaver and deer browsing of aspen suckers will be low.

6.3 Methods and materials

6.3.1 Tree availability surveys

Tree availability surveys were conducted at both Bamff sites to assess the size and composition of the woody resource available to the beavers, and these surveys have been fully described in Chapter 3 of this thesis. The survey methodology at the Stream and Lake Sites can be found in sections 3.2.1 and 3.2.2 respectively.

6.3.2 Tree-felling surveys

During the three year study period, numerous surveys were conducted of all successfully felled trees (hereafter referred to as “felled”) present at both the Stream and Lake Sites at the Bamff estate. Full details of all surveys undertaken have previously been described in section 4.5.2.

6.3.3 Tree regrowth surveys

6.3.3.1 Willow regrowth surveys

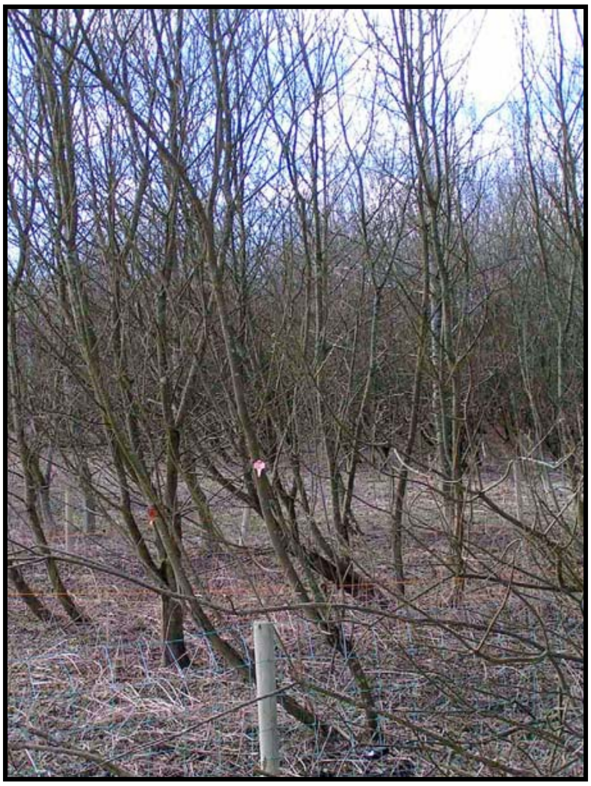
During numerous site visits to and surveys of the Bamff sites, it was observed that incompletely-felled willow trees were a relatively scarce resource. Due to this perceived scarcity, the first 10 such trees found during a walk-over survey of the areas of major beaver activity were selected for inclusion in the regrowth surveys. Candidate trees for the more common stump category were randomly selected by choosing the nearest willow stump exhibiting some stem regrowth to each incompletely-felled tree. Control trees were required to be tall enough to be considered mature, whilst being slender and flexible enough to allow branches to be bent giving access to the crown. Trees over 8 cm diameter were generally too thick and inflexible to be suitable for assessment. Where suitable control trees occurred within pre-existing beaver-proof exclosures (see section 7.3.1 for full details) they were selected, and any remaining control trees outside the exclosures were selected randomly. The beaver-proof exclosures were bounded by fencing approximately 0.9 m high that allowed access by deer.

Once suitable incompletely-felled and control trees had been selected, a short section of trunk of 0.5 – 1 m length, exhibiting growing shoots or buds was chosen on each tree. The lengths of all growing shoots present in this section were measured, the extremities of the section marked, and the tree identified by a tag detailing the tree number and category. For the stumps, the lengths of all growing shoots present were measured and the tree tagged. Other variables that were measured and recorded were tree girth (measured at “beaver height” or immediately below the cut, as appropriate), girth and length of measured section on incompletely-felled and control trees, number of growing shoots above and below the cut on incompletely-felled trees, and number of catkins present on all three tree categories. When data on the number of growing shoots on a tree were collected, the presence or absence of browsing on these shoots, whether by deer or beavers, was also recorded. Initial measurements were made during late March to early April 2004 (Regrowth Survey 1), and repeat measurements made in early April 2005 (Regrowth Survey 2), so that all growth increments represent one year of tree growth. Typical examples of the trees used in each category are shown in Figures 6.1, 6.2 and 6.3.

In addition to the surveys of the annual regrowth exhibited by the 30 experimental trees at the Stream Site, surveys were also conducted in late-June 2005 to specifically quantify all the incompletely-felled trees present after three years of felling at both the Stream and Lake Sites. These surveys recorded the girth below the cut, the species / genus of tree, the year of felling, the presence / absence of any stem regrowth from the base and trunk, and the presence / absence of deer browsing on this regrowth.

Figure 6.2 Example of a willow "stump" at the Stream Site, showing stem regrowth.

Figure 6.3 Example of a willow "control" at the Stream Site.



6.3.3.2 Aspen regrowth surveys

Only 11 aspen trees were present within the Stream Site when the beavers were introduced to the site (March 2002), and these had all been felled by October 2002. Within the stand of numerous suckering saplings that have grown since felling of the original 11 trees occurred, ten saplings typical of the size range of the whole stand were randomly selected for study. The approximate stem diameter at "beaver height", height of the sapling and total length of woody material present in these saplings was measured on one occasion only in November 2004, so all growth measurements therefore represent two years of tree growth. The total number of suckering saplings present was also noted at this time. Figures 6.4a and 6.4b show an area of the measured stand of aspen suckers in both spring and summer of 2005 respectively, following felling of the parent trees in October 2002.

Figure 6.4a Aspen suckers at Stream Site, taken in April 2005.

Figure 6.4b Aspen suckers at Stream Site, taken in June 2005.

6.3.4 Data analysis

Much of the data gathered during the availability, felling and fate surveys (as described in sections 3.2, 4.4.2 and 4.7.2 respectively) have been used during the analysis and discussion of the results of the willow and aspen regrowth experiments. All measured girth values were transformed into diameters in the manner described in section 4.4.3. The length and number of the growing stems in each measured section of the control and incompletely-felled trees were standardised by expressing them on a per metre section basis. No such standardisation was possible for the data collected from stumps. Where appropriate, results were tested using the Kruskal-Wallis test, with significant effects being further analysed by *post-hoc* pairwise Mann-Whitney *U* tests (Dytham, 2003) and correlations were tested using the Spearman rank-order correlation. All tests were performed using Minitab® Release 14. In all cases, the statistical significance of results are reported using the standard convention (* $P<0.05$; ** $P<0.01$; *** $P<0.001$), and unless denoted as such they should be interpreted as not being significant (*i.e.* $P>0.05$).

6.3.5 Explanation of terminology

Definitions of the terminology used in this chapter can be found earlier in this thesis, in section 4.4.

6.4 Results

6.4.1 Willow regrowth

Following complete felling by beavers, 86% and 77% of willows showed evidence of regrowth from stumps at the Stream Site and Lake Site respectively (Figure 6.5a). Regrowth from the felled trunks ("logs") occurred less frequently, in 39% and 34% of cases at the Stream and Lake Sites respectively (Figure 6.5b). It was estimated that 8.7% of all beaver cut willow at the Stream Site and 0.7% at the Lake Site were incompletely-felled. Of these trees, the numbers showing regrowth from the base (Figure 6.6a) and fallen trunk (Figure 6.6b) were high at both sites. At the Stream Site, 86% of these incompletely-felled trees showed regrowth from the base and 96% from the trunk, compared to 100% showing regrowth at the Lake Site from both base and trunk.

Figure 6.5a Percentage of felled willow showing stem regrowth from cut stumps.

The N values on each bar represent the number of trees present in each category.

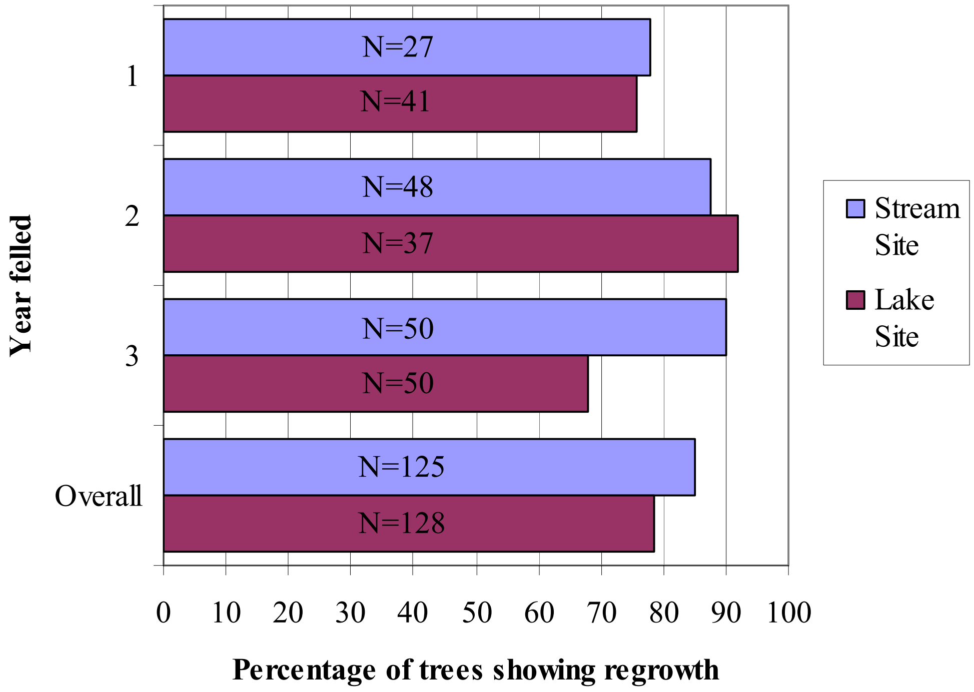


Figure 6.5b Percentage of felled willow showing stem regrowth from felled logs.

The N values on each bar represent the number of trees present in each category.

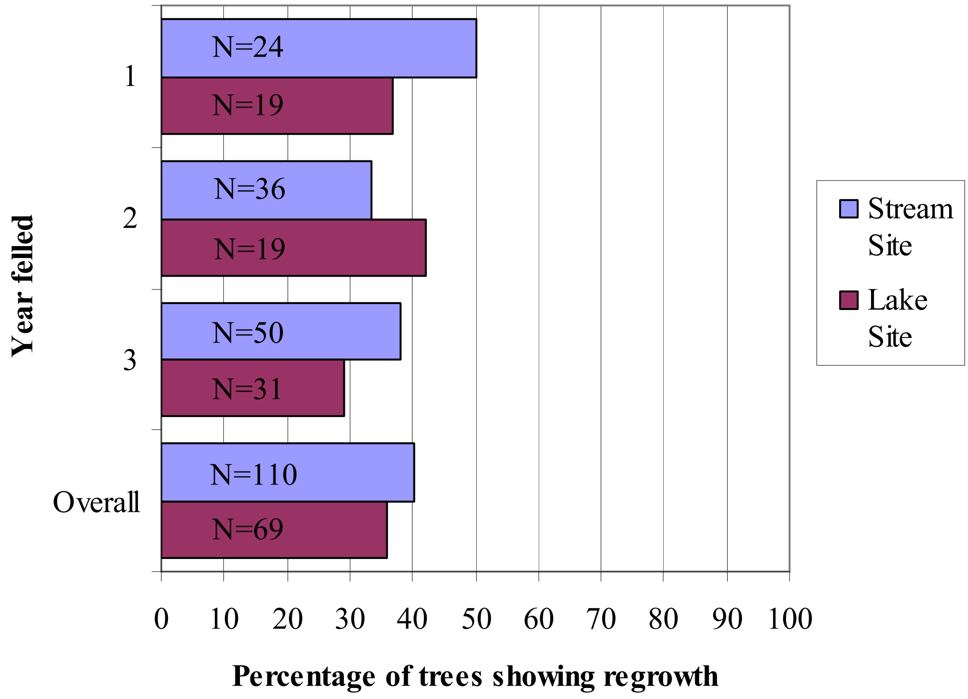


Figure 6.6a Percentage of incompletely-felled willow showing stem regrowth from the base. The N values on each bar represent the number of trees present in each category.

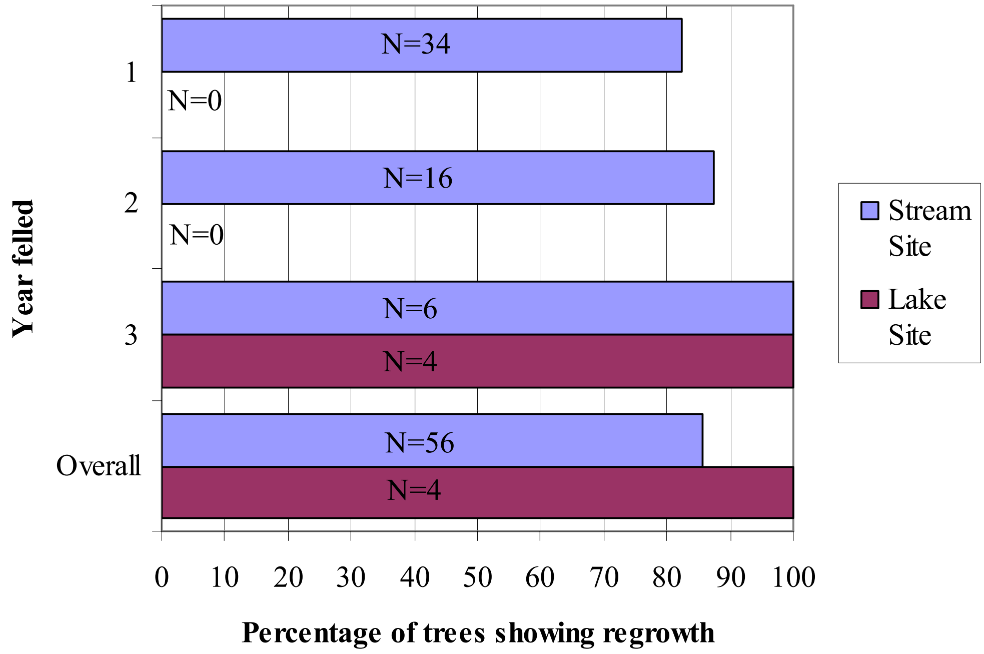
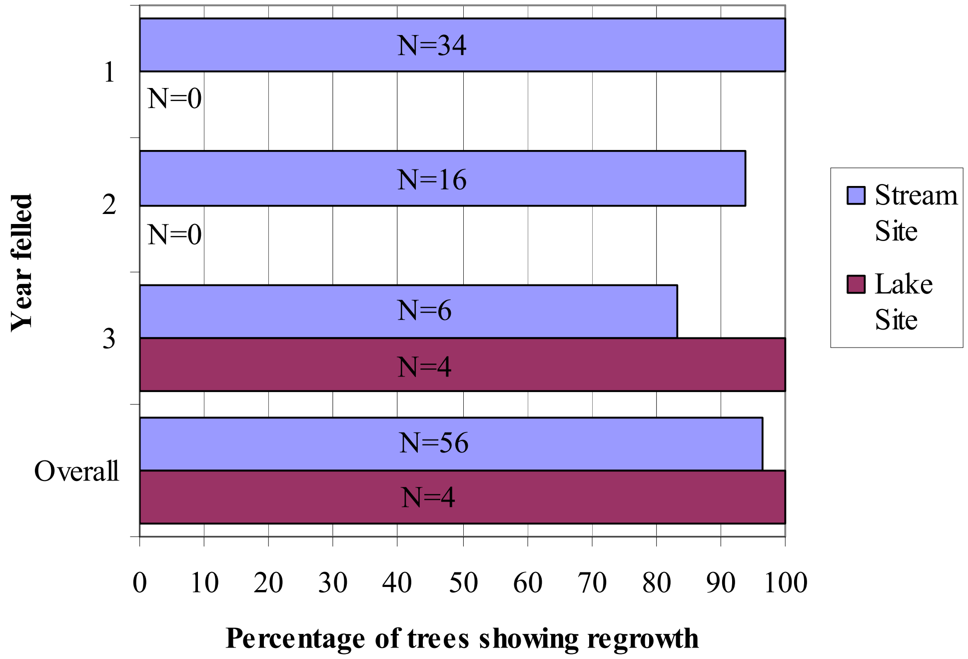
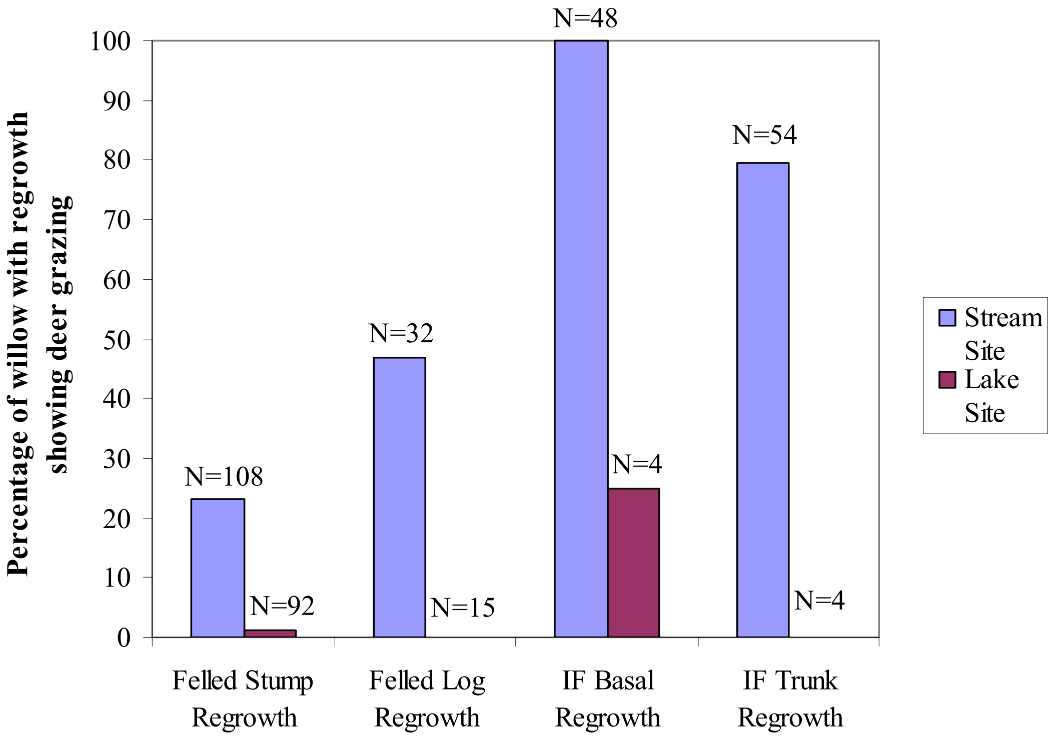


Figure 6.6b Percentage of incompletely-felled willow showing stem regrowth from the trunk. The N values on each bar represent the number of trees present in each category.



The frequency of browsing by deer on the regrowth of felled and incompletely-felled willow at both sites is shown in Figure 6.7. This was considerably greater at the Stream Site than at the Lake Site. The most vulnerable regrowth was from the base and trunks of incompletely-felled trees at the Stream Site, where between 79% and 100% of all sprouting trees showed at least some evidence of deer browsing. Regrowth at the Lake Site was largely avoided by deer, the least susceptible to browsing being that from the logs of felled trees and the trunks of incompletely-felled trees. At both sites, the incidence of browsing on shoots of unfelled trees was rare and not quantified further.

Figure 6.7 Percentage of felled and incompletely-felled willow with stem regrowth showing evidence of deer browsing. The N values on each bar represent the number of trees present in each category.



When comparing standardised annual willow stem regrowth, large variability was evident both within and between felling categories. Of the assessed trees, 14% of incompletely-felled trees and 40% of stumps exhibited negative amounts of regrowth due to heavy and repeated browsing of shoots, predominantly by deer but occasionally by beavers. These trees are relatively uncommon at the study site, but at sites with larger deer populations the numbers of heavily browsed trees may be more significant. The data suggest that regrowth from the trunk of an incompletely-felled tree was greater than that observed for a similar length of control tree, and from the whole stump of a felled willow. However, the significance of these differences is marginal (*P*=0.059). The mean growth increments observed in all three categories are shown in Table 6.1. The sample size of the control trees was seven, rather than the 10 trees initially measured, because three of the trees outside the beaver-proof exclosures were subsequently felled by beavers. One of the controls had exhibited considerable apparent negative growth values, possibly due to disease or damage by small rodents or strong winds, but was not excluded from data analysis. Similarly the sample size of the incompletely-felled trees was only seven due to three trees having been completely felled by the beavers in a second visit sometime after the initial measurements had been made. A similar pattern was observed when considering the mean increase in number of growing shoots present on the three categories of trees, with the greatest number on incompletely-felled trees (Table 6.1), but this trend was not significant (*P*=0.193).

Table 6.1 Mean annual increase (± SE) in stem growth (m) and number of growing shoots on standardised[*] lengths of willow trees. The N values represent the number of trees present in each category.

	Control (N=7)	**Incompletely-Felled (N=7)**	**Stump (N=10)**
Stem Growth (m)	1.54 ± 3.00	17.77 ± 9.40	2.69 ± 3.89
Number of Growing Shoots	6.90 ± 11.49	46.10 ± 16.93	9.60 ± 8.44

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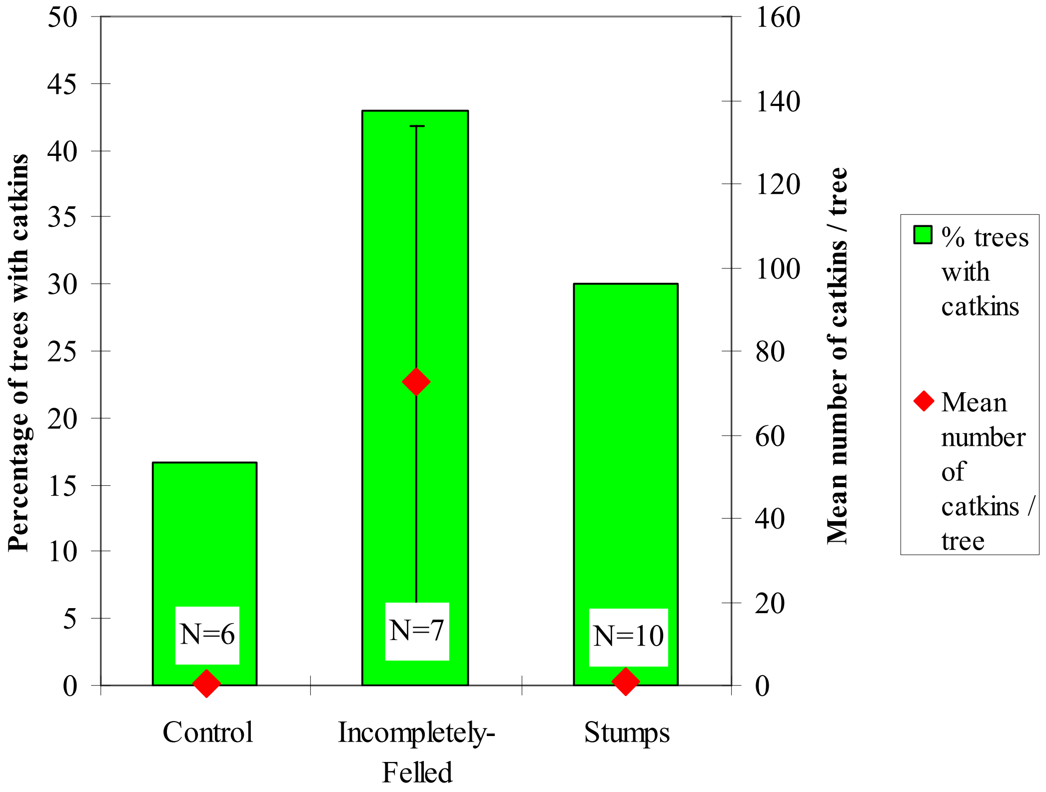
[*] Stump data have not been standardised to 1 m length of tree.

The timing of flowering in the second year of the survey (Regrowth Survey 2) also varied between the three categories of willow trees (Figure 6.8), with incompletely-felled trees flowering earliest, followed by stumps, with control trees flowering latest of all. The mean number of catkins per tree was also far greater in the incompletely-felled trees than in the other two categories, although this trend was not significant (*P*=0.413). Data from the initial survey (Regrowth Survey 1) supported these trends although the datasets are smaller due to the data being collected over a 3 week period.

Figure 6.8 Percentage of trees with catkins, and mean number of catkins per tree (± SE) in Survey 2. The N values on each bar represent the number of trees present in each category.



The trees of each category were of found to be of different sizes (*P*=0.001, *post-hoc* P<0.05 for all three pairwise comparisons). Due to the methodological artefacts of tree selection, control trees had the smallest diameters whilst the Incompletely Felled category consisted of the largest trees. The controls had to be sufficiently slender to bend and allow access to the canopy, whilst the incompletely-felled trees were generally larger, as small diameter trees are usually completely felled by the beavers leaving a distinct stump and log. However, there were no correlations between tree diameter and annual growth increment, or between diameter and mean number of catkins present per tree, in any of the three categories (Tables 6.2a and 6.2b).

Table 6.2a Results of Spearman Rank-Order Correlations (r_s) between tree diameter and standardised growth increment. Sample size is represented by N, and level of statistical significance by *P*. [1]

Category	**N**	**r_s**	***P***
Control	6	0.164	0.726
Incompletely-Felled	7	-0.309	0.500
Stump	10	0.292	0.413
All Categories	23	0.078	0.717

Table 6.2b Results of Spearman Rank-Order Correlations (r_s) between tree diameter and number of catkins per tree. Sample size is represented by N, and level of statistical significance by *P*. [2]

Category	**N**	**r_s**	***P***
Control	6	0.323	0.532
Incompletely-Felled	7	-0.585	0.168
Stump	10	0.224	0.534
All Categories	23	0.128	0.561

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[1] Growth increment cannot be normalised for stump data.

[2] Number of catkins per tree is calculated as the mean number of catkins present on each tree in both of the Regrowth Surveys.

Examination of the data also suggests that the non-random selection procedure of trees chosen for the stump and incompletely-felled categories were unlikely to have introduced valid sampling biases. For example, the decision to specifically select stumps that showed some regrowth, rather than purely randomly sampling all the stumps available, is believed to be justified by the very high incidence of regrowth from willow stumps observed at the Stream Site (as shown in Figure 6.5a). Similarly, the scarcity of incompletely-felled willows, which make up approximately only 9% of all the felled willow trees present at the Stream Site, is also believed to justify the non-random selection procedure adopted for these trees. The trees selected for the incompletely-felled and stump categories are therefore believed to be a representative sample of the whole willow resource. However, due to the practical constraints involved in the selection of the control category trees, possible effects of sampling bias in favour of small diameter trees cannot be eliminated, as only 46% of all willows were slender enough to be considered as candidate trees.

6.4.2 Aspen regrowth

A total of 85 suckers of aspen were counted, and summary data for the 10 measured suckers of aspen are shown in Table 6.3. The mean amount of woody tissue produced per sucker is 7.16 m, equivalent to an estimated total length of woody tissue over all 85 suckers of 609 m (± SE 92 m). No signs of browsing by either beavers or deer were found on any of the 85 suckers present, except for one incident of “bark fraying” by roe deer.

Table 6.3 Regrowth of aspen suckers in 2 years post-felling of parent tree. Sample size (N)=10.

	Tree Height (m)	Trunk Diameter (m)	Total Regrowth (m) / Sucker	Number of Stems / Sucker
Mean ± SE	2.08 ± 0.08	0.016 ± 0.001	7.16 ± 1.08	17.1 ± 2.4
Minimum	1.71	0.010	3.58	9.0
Maximum	2.40	0.020	13.01	28.0

6.5 Discussion

6.5.1 Willow regrowth following felling by beavers

Given the well-documented ability of willow to coppice from stumps (*e.g.* Fuller & Warren, 1993), regrowth of felled willow over a period of years should represent a considerable replenishment of the overall resource. Indeed, 86% of the felled willow at the Stream Site and 77% at the Lake Site, exhibited at least some regrowth from the cut stumps. Furthermore, in cases where the felled trunks remain in the immediate vicinity of the stump, 39% and 34% of these logs show evidence of regrowth at the Stream and Lake Sites respectively. An excellent example of the regrowth ability of cut willow branches and logs, can be found at the beaver lodge at the Stream Site which shows abundant new willow growth in each growing season (Figure 6.9a and 6.9b).

Figure 6.9a Willow regrowth from cut branches and logs that make up the structure of the beaver lodge at the Stream Site, taken in April 2004.

The occurrence of regrowth from both stumps and felled logs was lower at the Lake Site, where almost all willows were located within the shallow water around the margins of the loch, than at the Stream Site where no trees were inundated. Although the growth of control and felled willow trees was not measured at the Lake Site, it seems likely that whilst they are capable of net-growth under such waterlogged conditions, the rate of growth is retarded due to root submersion, which causes anaerobic conditions in the root zone (Naiman *et al.*, 1986; Jackson & Attwood, 1996). The roots of the Salicaceae, which includes willows and poplars, are known to be tolerant of anaerobic conditions for long periods, although inter-specific differences in this tolerance are great (Karrenberg *et al.*, 2002). Whilst some studies have observed willows thriving in beaver ponds after five years of inundation (Amlin & Rood, 2001), others have documented reduced biomass in continuously inundated willow (Pezeshki *et al.*, 1998) and decreased shoot extension rates after lengthy periods of root submersion (Jackson & Atwood, 1996). Indeed, some authors have suggested that growth of flooded willow stops after two growing seasons and mortality increases (Knighton, 1981; Ohmann *et al.*, 1990). At the Lake Site willows have been present in inundated areas for over three years, and probably considerably longer, and show no evidence of increased mortality, although water levels have increased by approximately 0.2 m due to a beaver dam constructed at the lake outflow.

Figure 6.9b Willow regrowth from cut branches and logs that make up the structure of the beaver lodge at the Stream Site, taken in August 2004.

Willow also produces copious adventitious roots after flooding, which enable the plant to survive and grow in saturated soils (Krasny *et al.*, 1988), and we frequently observed such root development on cut branches in dams (Figures 6.10a and 6.10b) and underwater food caches (Figures 6.11 and 6.12). This ability of willow fragments to root under inundated conditions, as well as the frequent occurrence of stem regrowth from felled stumps and submerged trunks at the Lake Site (albeit less frequently than at the Stream Site) suggests that the willow resource will continue to regenerate after beaver activity. It remains to be seen whether the lower frequency of vegetative reproduction from stumps and trunks, and any growth from smaller willow fragments that remain after feeding by the beavers, will be sufficient to compensate for felling of mature willow. No perceptible change in the overall extent of willow has been observed over three years of beaver presence however. Figure 6.13 illustrates this point, showing the abundance of willow regrowth that has occurred in an area of very heavy felling activity (Felling Zone 10 – see section 4.5.2.) in three years following the release of beavers into the Stream Site. Regeneration from seed is also likely to become increasingly important at the Lake Site. Some local dieback (*c.* <1% of whole resource) of conifers (*Picea abies* and *Pinus sylvestris*) around the pond has begun due to soil waterlogging associated with a rise in water levels caused by a beaver dam on the lake outflow, which will create gaps in the otherwise complete coniferous canopy. Willow seeds show high germination rates in saturated soils (Krasny *et al.*, 1988) and it seems likely that these gaps will be exploited by willow seedlings. For a time, this standing dead wood also provides invertebrate habitat, and therefore a food source and nesting site for birds and bats (*e.g.* Humphrey *et al.*, 2002).

Figure 6.10a Dam 1 at the Stream Site in January 2004.

Figure 6.10b Dam 1 at the Stream Site in September 2004, showing vegetation cover including abundant willow regrowth from branches incorporated into the structure.

Figure 6.11 Emergent willow regrowth from submerged cached willow branches at the Stream Site.

Figure 6.12 Submerged willow branch found in a beaver food cache at the Stream Site, showing adventitious root development and extent of shoot regrowth.

Figure 6.13 Abundant willow regrowth in an area of very heavy felling activity (Felling Zone 10), taken in July 2005.

Intermediate to the stumps and felled trunks that occur when beaver felling was successful, are "incompletely-felled" willows. Larger diameter trees were more prone to incomplete felling, with 92% being ≥ 11 cm in diameter. Such trees accounted for almost 1 in 10 felled willows at the Stream Site, but were much rarer at the Lake Site (<1% of all felled willow). Although larger willows were of approximately equal availability at the two sites (around 35% of all willows present), the pattern of felling was different at the two sites, with trees of ≥ 11 cm diameter comprising 36% of all felled willow at the Stream Site, and only 19% at the Lake Site. Incompletely-felled trees would therefore be expected to be more common at the Stream Site. However, of those trees most likely to be incompletely-felled (≥ 11 cm diameter), 21% were incompletely-felled at the Stream Site, compared to only 4% at the Lake Site. The exact reason for this site-specific difference is unclear.

One explanation is that beavers behave differently between the two study sites. Beavers often dam waterbodies to enable foraging further into the surrounding woodland without the need to leave the water, thus minimising the time spent on land where they are vulnerable to predators (Kitchener, 2001). The willows at the Lake Site are located almost entirely within shallow water, thus a lower perceived threat may allow beavers to fell more trees completely, resulting in a lower incidence of incompletely-felled trees. In contrast, the higher incidence of incompletely-felled trees at the Stream Site could be due to beavers adopting a more vigilant (and occasionally inefficient) approach to felling whilst on land.

The incompletely-felled trees, though comparatively scarce, have strong potential to regenerate from both the base and the attached trunk. At the Lake Site, all of the bases and trunks of the incompletely-felled trees exhibited stem regrowth, whereas in the completely felled trees, stump and log regrowth were much rarer. The high occurrence of basal regrowth when compared to the stumps remaining after complete felling is probably due to the connection to existing photosynthesising tissue. Thus photosynthesis from the surviving crown of the incompletely-felled willow may "kick-start" stem regrowth at the base of the tree, perhaps also reducing the effects of waterlogging stress compared to stumps.

At the Stream Site, approximately the same high frequency of regrowth from stumps was observed regardless of whether trees were incompletely or completely felled. As inundation stress at the Stream Site was not a factor, this "kick-start" was less obvious and sprouting from both types of stump was very common. However, the occurrence of regrowth from the trunk of the incompletely-felled trees was much greater than from logs left after complete felling. Incompletely-felled trunks are likely to benefit from an intact connection to the root system, whereas the completely felled logs lack this connection. The consequence of this from a habitat perspective is that incompletely-felled trees contribute disproportionately to woodland regeneration, thereby creating a different canopy architecture in which there is a proliferation of near-ground growth that presumably offers superior cover for beavers when foraging out of water.

At both sites, with greater than 75% of cut willow stumps showing stem regrowth, and more than 85% and 95% of incompletely-felled willow displaying regrowth from the base and trunk respectively, the data clearly support the original hypothesis that beaver-felled willows would show a high incidence of stem regrowth from stumps and trunks. Hypothesis 6.1 is therefore accepted. It should be noted, however, that the sample size for the incompletely-felled trees at the Lake Site is very small, so should be viewed with some caution.

Browsing by other mammals, especially deer, will influence the extent of regrowth of trees felled by beavers. As deer populations in Britain are known to be increasing in both numbers and geographical distribution (Putman & Moore, 1998), the likelihood of a reintroduced beaver population interacting with deer is high. Widespread damage to coppice regrowth in Britain is caused by deer, especially roe deer (Joys *et al.*, 2004), through bark stripping, removal of twigs, stems, leaves, needles, and buds, and uprooting of seedlings (Gill, 1992a). Furthermore, willow and aspen are widely acknowledged as being highly preferred by both roe and red deer, in winter and summer (reviewed by Gill, 1992a; Kay, 1993).

At Bamff, roe deer numbers are low to moderate (Ramsay *pers. comm.*) and browsing of regrowth reveals a number of trends. Firstly, whilst browsing of willow regrowth by deer is common at the Stream Site, it is extremely rare at the Lake Site. The presence of deer tracks and dung, as well as (infrequent) browsing of regrowth, show that deer are present at the Lake Site. No estimates of population sizes have been attempted, and it is possible that this site simply supports fewer deer compared to the Stream Site. The two sites are, however, only 1 km apart with no deer fencing between them, so it is likely that they lie within the same territory. Red deer (*Cervus elaphus*), for example, have been documented as travelling within 3 - 9 km of tag sites (Daniels & McClean, 2004). Some other factor is therefore needed to explain why browsing of willow regrowth is so rare at the Lake Site.

The most obvious possibility is that trees at the Lake Site are located predominantly within shallow water (0.2 – 0.5 m), and it is possible that roe deer do not choose to browse in such areas when terrestrial food sources of comparable quality are readily available locally. Gill (2000) suggests that deer readily browse in wet woodlands, feeding on vegetation in pond and river margins, although this is not supported by our data. It was also evident that regrowth from felled logs was more susceptible to deer browsing than regrowth from the nearby stump. This possibly reflects the dispersion of deer whilst foraging. A single stump would only allow a single deer to browse it at any one time, whereas a long log could be browsed by several animals simultaneously, thereby increasing the incidence of damage to log regrowth.

The susceptibility of the incompletely-felled trees to browsing was considerably greater than the completely felled trees, with almost all of the former trees showing browsing damage to both stump and trunk regrowth. With these trees however, the preference was for the stump regrowth rather than trunk regrowth, reversing the trend observed in the felled trees. Indeed, all new stems on the incompletely-felled trees at the Stream Site, regardless of origin, appear to be at risk of browsing. It is suggested therefore, that browsing damage to willow regrowth by deer may be affected by the damming activities of beavers. Where water levels are raised by dams, and flooding of willows occurs, regrowth following beaver felling may be protected from subsequent deer browsing. It also seems unlikely that other smaller herbivorous mammals could threaten an aquatic willow resource. Thus the only major threat to willow regrowth in flooded areas probably arises from beavers themselves, harvesting new shoots in years following the initial felling. Experience at the study sites has shown that whilst beavers commonly cut small (≤2 cm) diameter shoots at the same time as felling the major trunk of a willow stool, only rarely have they removed the regrowth from felled stumps and trunks (Figure 6.14). The juvenile growth of many species of the Salicaceae contain high levels of secondary compounds such as terpenes and phenolics, which have been demonstrated to deter the grazing of showshoe hares (*Lepus americanus* Erxleben) (Bryant, 1981), and mountain hares (*Lepus timidus* L.) (Tahvanainen *et al*., 1985). It is possible that beavers are also deterred by such chemical defences in juvenile willow, whereas roe deer apparently are not.

These data suggest therefore that under low to moderate deer pressure, and given a sufficiently large supply of willow and other tree species available to beavers, willow regrowth is unlikely to be removed in large enough amounts to prevent willow coppices developing. Tree-felling by beavers tends to occur predominantly in autumn and winter (Northcott, 1971; Svendsen, 1980; Hodgdon & Lancia, 1983) corresponding with tree dormancy. It has been shown that willow cut during these dormant periods display the most rapid regrowth rates, whereas trees cut in summer months tend to show inhibited growth for a number of years (Kindschy, 1989). The same study also demonstrated that the growing season of willow was prolonged by beaver felling, with earlier spring growth initiation and later autumn dormancy of newly sprouted stems evident. Furthermore, our study suggests that where water levels are high or rise as a consequence of beaver dams and willows are flooded, deer browsing on the new stems will be negligible.

Figure 6.14 Harvesting of willow regrowth from a cut stump by beaver at the Stream Site.

When the amount of regrowth of felled willows is standardised, it is clear that considerably more new growth occurs from the trunk of an incompletely-felled tree than from the same length of branch within the canopy of an untouched tree, especially when deer browsing pressure is low. Not only was the growth rate of new stems of the incompletely-felled trees greater than that of the control, but the number of growing stems was also greater. Although direct comparisons cannot be made between the regrowth from a completely felled stump and either a controlled section of incompletely-felled trunk or canopy of a control tree, stumps also sprout abundant new shoots. Shoots frequently reached over a metre in length in one growing season and up to 2.5 m after two years, which compares favourably to figures from France reported by Fustec *et al*. (2001), although the presence of any subsequent deer browsing is not detailed by these authors. It is likely that in the long-term, felled willows will produce a thick shrubby growth form when deer browsing is low, while under high browsing pressures a more upright tree architecture will evolve. Regrowth of red willow (*Salix lasiandra*) felled by beavers in the USA, achieved approximately half the height and approximately six times more annual stem growth than untouched control trees (Kindschy, 1985). Furthermore, roe deer browsing tends to be clumped rather than evenly distributed through a stand (Welch *et al.*, 1988; Gill, 1992a), which when coupled with the felling patterns of beavers is likely to lead to a structural mosaic of favoured tree species.

Hypothesis 6.2 stated that the amount of annual stem regrowth from a measured section of the trunk of incompletely-felled willows will be greater than the annual growth of stems on a similar length branch of an untouched tree. These data indicate that the annual length of stem regrowth from a standardised trunk length of an incompletely-felled willow was approximately 11 times that observed from a similar length of branch within the canopy of an unaffected control tree. In addition, the number of growing shoots was approximately 6 times greater than that in control trees. These data therefore support Hypothesis 6.2, which is accepted.

Hypothesis 6.3 stated that the role of deer browsing would have a greater impact on the regrowth arising from the cut willow stumps following felling than from the trunk of incompletely-felled trees. Deer browse shoots from the tips downward, so it was assumed that any regrowth from the trunk of an incompletely-felled tree would have an advantage in avoiding deer browsing because it would begin growth higher above the ground than stump regrowth. In other words, trunk regrowth would spend a shorter period of time below the browsing height of deer than would stump regrowth, and hence be less vulnerable to damage by deer. The data do not support this hypothesis however, with *c.* 80% of the incompletely-felled willow showing regrowth from trunks suffering deer grazing, compared to only *c.* 20% of cut stumps, so Hypothesis 6.3 is rejected. However, the bases of incompletely-felled trees are extremely vulnerable to deer damage. The reasons why the regrowth from completely severed stumps should be much less prone to deer attack, than that from the bases of incompletely-felled trees is unknown. As both forms of regrowth are initially at the same low starting point above the ground, height should not be an influencing factor. However, if the stump regrowth grows at a faster rate than similar regrowth from the base of an incompletely-felled tree, perhaps because resources are being utilised by a smaller section of tree (*i.e.* the resources responsible for stem growth must be shared between the base and the trunk of an incompletely-felled tree, compared to just the stump of a completely felled tree), then stump regrowth will grow above the grazing height of deer sooner, and be less prone to grazing. This is unable to be verified however, as the lengths of regrowth arising from the bases of incompletely-felled willows were not recorded, so cannot be compared to stump regrowth.

As well as promoting vegetative regeneration of willow these data suggest that beaver felling may also influence sexual reproduction of the trees. Although the datasets are small, they indicate that regrowth from incompletely-felled trees is the first to produce catkins, followed by cut stumps, with control trees the last to flower. In the early part of the growing season, the mean number of catkins present on each tree was also greatest in the incompletely-felled trees. As stated earlier, due to methodological artefacts the diameter, and therefore age, of the trees in each of the three experimental categories fell into distinct groups. The incompletely-felled trees were the largest, followed by the stumps, with controls being the smallest of all. As flowering in trees generally occurs only after a juvenile growth period has been completed (Edlin 1976), the age of the trees involved in our study will clearly influence the presence of catkins. However, the smallest control tree showing catkins had a diameter of 0.04 m, and only one of the six controls was smaller than this. This suggests that at least five of the six experimental control willows were old enough and large enough to flower, and that age / size of tree in this case can be eliminated as a reason for the later and less vigorous flowering of the controls when compared to the larger stumps and incompletely-felled trees. Earlier flowering may offer the willows that have been cut by beavers a competitive advantage, allowing them to set seed earlier in the season, and perhaps allowing seedling recruitment in gaps before tall herbs and unfelled trees limit the amount of sunlight reaching the ground. Willow may therefore respond to felling by beavers, by flowering earlier and more copiously thereby increasing the chance of successful sexual as well as vegetative reproduction.

6.5.2 Aspen regrowth following felling by beavers

Whilst willows felled by beavers produce abundant new shoots, aspen also re-sprouted vigorously, supporting the statement that “few species grow as fast in youth as aspen” (Borset, 1960). Since 11 mature aspen were felled, eighty-five separate suckers sprouted from the root system of the original trees, each with an average height of over 2 m and around 7 m of woody stems per sucker. This indicates that in just 2 years, approximately 600 m of aspen regrowth have occurred following the felling of 11 mature trees. Hypothesis 6.4, that aspen would respond to beaver felling by vigorous suckering from the roots, is therefore accepted.

Although few authors have reported growth rates of aspen following beaver felling, the data in this study compare favourably with the relevant literature available. In Norway, four-year old suckers of European aspen were recorded at heights of 6.7 m, with a second year shoot having reached a height of 2.2 m (Borset, 1960). This latter figure falls within the height range (1.71 – 2.40 m) observed at Bamff of two-year old suckers. Stegeman (1954) measured the growth of aspen (*c.* 6 - 43 years old) in the USA, reporting maximum annual height increment (approximately 0.76 m) in trees 14-years old. The youngest trees in his study showed a mean annual height increment of 0.49 m, approximately half of that observed in the suckering shoots at Bamff. Comparisons between the Bamff data and that of Stegeman (1954) should be viewed judiciously, however, due to the different ages and species of aspen measured. Both of these published papers (Stegeman, 1954; Borset, 1960) and the data presented in this thesis, do suggest that suckering growth is not just abundant, but also rapid in comparison to older, unbrowsed trees.

There was no evidence of beavers harvesting the new shoots, which is surprising given the high preference that beavers have for aspen (Simonsen, 1973; Lahti & Helminen, 1974; Johnston & Naiman, 1990; Gorshkov *et al.*, 1999). Similarly, we observed no deer browsing of aspen suckers, in line with Rackham (1975) and Joys *et al*. (2004), although both roe and red deer have high preferences for aspen (Gill, 1992a), and aspen is often planted as a fodder crop for wild deer (Worrell, 1995b). Avoidance could be due to elevated levels of secondary compounds in the plant tissues produced as a response to the initial felling, in order to deter further browsing. Increases in the concentrations of plant secondary compounds have been documented in numerous plants as an induced defence mechanism following damage by herbivores (*e.g.* Karban & Myers, 1989; Gill, 1992b). The American aspen (*Populus tremuloides*) is known to produce two different types of sucker – an "adult-form" with small leaves and a "juvenile-form" with large leaves (Kramer & Koslowski, 1979). As well as juvenile-form suckers being predominant in areas of heavy beaver felling (Basey *et al.*, 1988), such regrowth has been shown to be avoided by beavers (Basey *et al.*, 1990) and other herbivores (Bryant, 1981). This is possibly due to high levels of an unknown phenolic compound in the bark of juvenile root suckers, since the scent of aspen bark provides the perceptual cue for tree selection by beavers (Doucet *et al.*, 1994b). The contrasting appearance of regrowth and foliage implies that European aspen exhibits a similar suckering strategy. It was originally hypothesised that aspen regrowth following felling by beavers would generally be avoided by grazing beavers and deer (Hypothesis 6.5) due to the reasons outlined above, and the observations at the Bamff estate support this hypothesis.

Despite the vigorous suckering response of aspen following felling observed in our study, it is unlikely that the architecture of regrowth can fulfil the same habitat support function of mature trees. It is also possible that significant amounts of the copious suckering regrowth could die-back due to intraspecific competition for light (*e.g.* Stegeman, 1954). Extensive localised loss of mature aspen due to beaver felling could thus affect associated biota in the short to medium term, although certain management techniques could increase the regrowth of aspen following felling. For example, thinning of young suckers could reduce the effects of light competition and increase growth rates of the remaining stems, and disking (physical disturbance of the soil and roots) 2 - 3 years post-felling can promote suckering (Stegeman, 1954). It is worth considering, however, that riparian aspen communities successfully coexist with high beaver densities throughout Scandinavia, despite the well-documented preference of beavers for aspen (*e.g.* Borset, 1960).

7 Effects of beaver activity on terrestrial and aquatic herbaceous plant and invertebrate communities

7.1 Abstract

The feeding and construction activities of beavers have great potential to increase habitat heterogeneity and consequently increase floral and faunal diversity. Despite the general acceptance of this principle by researchers, relatively few studies have investigated the effects of beaver activity on the biodiversity of aquatic and terrestrial plant and invertebrate communities. The work presented in this chapter represents a case-study to identify the effects of beaver tree-felling, construction and non-woody feeding on elements of the biodiversity of aquatic and terrestrial habitats.

Generally, the highest taxonomic richness, diversity and abundance values were obtained from “beaver-affected” areas when compared to control or reference conditions. In riparian woodland, the mean cover of herbaceous plant species and grasses increased in beaver-created canopy gaps compared to areas that were unaffected by beaver activity. Similarly, higher mean cover of herbaceous species was evident in areas of heavy tree-felling in which felled deadwood was abundant. The Shannon diversity index of the ground invertebrate communities present in such areas was also higher than in unaffected woodland. However, invertebrate taxonomic richness and abundance were highest in areas in which beaver effects were confined to grazing of non-woody species under an intact tree canopy.

In all three aquatic habitats sampled, the species richness of macrophyte communities was greatest outside beaver-proof exclosures than within them. Such localised changes could be attributed to the effects of non-woody grazing by beavers, which is known to have occurred widely at Bamff throughout the year, although the possible role of exclosure artefacts was not satisfactorily eliminated. However, the construction activity

of beavers also affected aquatic biodiversity, with increased macroinvertebrate diversity, richness and abundance observed on caches, lodges and immediately downstream of dams. These increases in macroinvertebrate diversity were attributed to the hydrological effects of beaver dams in streams, as well as the provision of refugia and food sources provided by beaver-created coarse woody debris. Overall, 30% of all macroinvertebrate species sampled were only present in “beaver affected” sites.

The importance of beaver-generated woody debris to the total input of deadwood to both the riparian woodlands and aquatic habitats at Bamff is believed to be considerable. These inputs, together with the effects of beaver-created canopy gaps and herbaceous grazing, increased habitat heterogeneity and plant and invertebrate diversity at Bamff over three years following introduction of beavers.

7.2 Introduction

In their dual roles of keystone species and ecological engineer, beavers have great capacity to influence both the floral and faunal diversity of the riparian landscape, as well as altering the physico-chemical conditions of streams. These effects of beavers on the landscape (which have been considered in detail in Chapter 2) are predominantly the results of feeding and construction activities. As trees are selectively felled by beavers for food, the composition of the riparian forest is altered in terms of tree species, size and location. For example, common species that are preferred by beavers usually decrease in relative abundance, whilst the relative abundance of rarer, unpalatable species increase (*e.g.* Johnston & Naiman, 1990). Furthermore, browsing of trees by beavers can alter the architecture of the stand from an upright canopy to a more shrubby growth form (*e.g.* Kindschy, 1985), and habitat complexity can be further increased by beaver-created standing and felled deadwood and incompletely-felled living trees. Where the canopy is thinned, more light is able to reach the herbaceous ground flora potentially increasing the diversity of the herb layer (Kitchener, 2001). The selective felling of trees by beavers can therefore increase both the floral species diversity and structural heterogeneity of riparian woodlands.

By using felled trees to undertake construction work, such as dams, lodges and caches, beavers further add to the complexity of their habitat, whilst producing conditions beneficial to themselves. As water-levels rise behind beaver dams and riparian woodland is flooded, vegetation succession through a mosaic of terrestrial and aquatic seral stages occurs. Initially flood-intolerant species will die-back to be replaced by moisture-loving marsh species at the pond margins, whilst a hydrosere of macrophyte species will develop in the pond itself. Eventually the pond will silt up to provide nutrient-rich and species-diverse "beaver meadows". The physical structures built by beavers also potentially trap sediment and provide a refuge for a variety of macroinvertebrate species (*e.g.* Clifford *et al.*, 1993), as well as a food source and shelter for a variety of higher organisms such as fish, amphibians and mammals (*e.g.* Patenaude, 1983; Sidorovich, 1991).

Many of the aforementioned beaver-induced changes to the structure and composition of riparian woodland and aquatic habitats have been evident at the Bamff study sites, and have been described in Chapters 4 – 6 of this thesis. The observed increase in architectural and compositional complexity of the tree canopy as a result of tree-felling by beavers, is likely to have had concomitant effects on the composition of herbaceous plant communities and ground-dwelling invertebrates. The accumulation of some of this felled material as woody debris in streams and ponds, in the form of dams, lodges and caches, as observed at Bamff, is likely to have affected the diversity of macroinvertebrate communities present in these waterbodies. The effects of these changes on the biodiversity of the Stream and Lake Sites, however, have yet to be considered. Beavers also spend much of the year feeding on herbaceous terrestrial and aquatic vegetation. Whilst the visual effects of herbaceous grazing appear more subtle than that observed with woody species, any effects on the diversity of the herbaceous communities will be assessed in riparian woodland and aquatic macrophyte beds.

This chapter will investigate the extent and nature of the effects of the feeding and construction activity of beavers on herbaceous vegetation and invertebrate communities, in both riparian woodland and aquatic habitats. Diversity of plant and terrestrial invertebrate communities in beaver-affected areas will be compared to those in nearby controls – namely beaver-proof exclosures - at the same study site. The effects of beaver constructions on macroinvertebrate communities will be examined by comparison of beaver-affected sites (*e.g.* on a cache, immediately upstream of a dam, *etc.*) with habitats or fluvial reaches within the same ponds and streams that have been determined as being representative of reference conditions (*i.e.* unaffected directly by beaver activity). The following hypotheses will be tested:

7.1 The diversity of ground flora in riparian woodland will be increased, and the species composition altered, by the combined effects of tree-felling and summer grazing on herbaceous plant species by beavers.

7.2 Selective feeding on macrophytes by beavers will alter the species composition and increase the diversity of aquatic herbaceous communities.

7.3 Through the construction of dams, caches and lodges, the diversity of macroinvertebrate communities will increase in ponds and streams.

7.4 The diversity of ground-dwelling woodland invertebrate communities will increase as a result of the increased habitat heterogeneity produced by the tree-felling activities of beavers.

7.3 Methods and materials

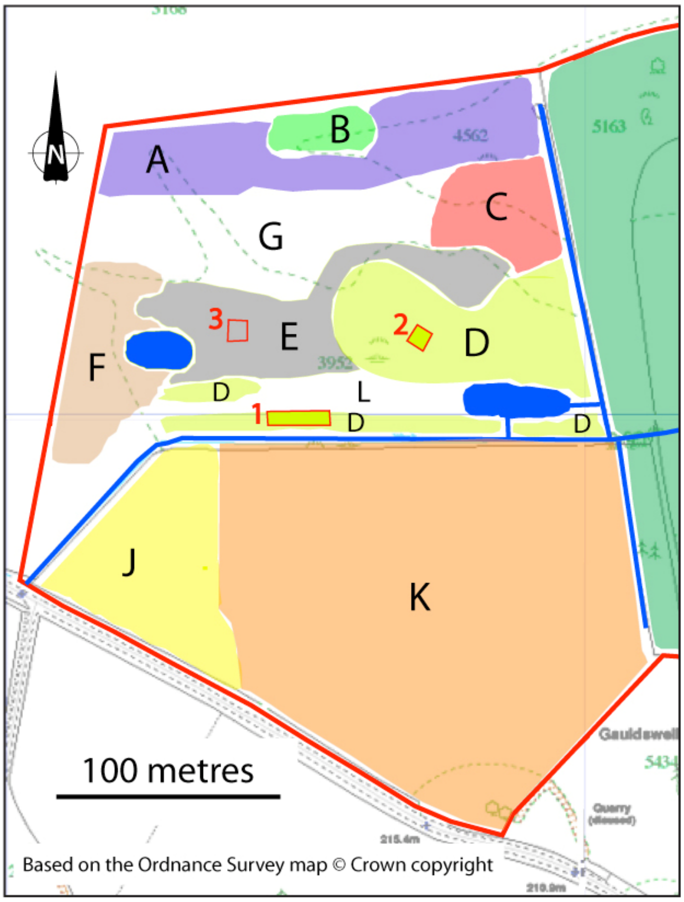
7.3.1 Terrestrial vegetation surveys

In March 2003, three beaver-proof exclosures were built at the Stream Site using softwood fence posts and Rylock®-type stock fencing approximately 0.9 m high, with the bottom wire of the fencing pegged into the ground. Each exclosure was situated in an area of woodland that showed obvious signs of beavers presence (*e.g.* felled trees), but included no felled trees within the exclosures themselves. Within these constraints the locations were chosen randomly. Exclosure 1 was approximately 93 m^2 (*c.* 5.5 m X 17 m) in size and located on the banks of a ditch within Habitat D (see Table 3.1), whilst Exclosure 2 enclosed approximately 100 m^2 (10 m X 10 m) of non-riparian woodland in Habitat D. Exclosure 3 covered 120 m^2 (12 m X 10 m) of non-riparian woodland within Habitat E. Figure 7.1 shows the location of the three exclosures. In order to avoid the influence of areas of trampled vegetation created during the construction of the fences, and to avoid trampling vegetation whilst sampling the communities within the exclosures, narrow boundary strips inside the perimeter of each exclosure were formed. Access to these strips allowed the sampler to observe vegetation within the monitoring area of the exclosures, whilst minimising edge effects of the fences and trampling effects during sampling.

The monitoring areas within each exclosure were divided into 32 fixed 1 m X 1 m quadrats, in which the percentage cover of plant species was estimated and recorded, as well as the percentage cover of the tree canopy above the quadrat. The vegetation height was also measured at six points within each quadrat, by randomly placing a metre rule inside the quadrat and recording the maximum height of vegetation touching the rule. A similar procedure was used to sample the vegetation cover and height outside the exclosures, by randomly selecting eight 1 m X 1 m quadrats at each of the four sides of the exclosure, within *c.* 10 m of the fencing. All measurements both inside and outside of the exclosures were made by a single sampler, in order to eliminate any differences in estimates of percentage cover. All surveys were also conducted in as short a time period as possible (usually 1 - 3 days) in order to minimise any temporal variation in the vegetation communities. Surveys were conducted in midsummer of

Year 1 (August 2003), late-spring of Year 2 (May 2004) and late-summer of Year 2 (September 2004). The construction of the exclosures was such that small herbivores, such as rabbits and voles could pass through the mesh of the fences, and deer could jump over the fence, with only beavers excluded from the areas. Figure 7.2 shows the structure of the fences of Exclosure 2.

Figure 7.1 Map showing the locations of the three exclosures at the Stream Site. The coloured zones correspond to the habitats described in Table 3.1.



Based on the Ordnance Survey map © Crown copyright

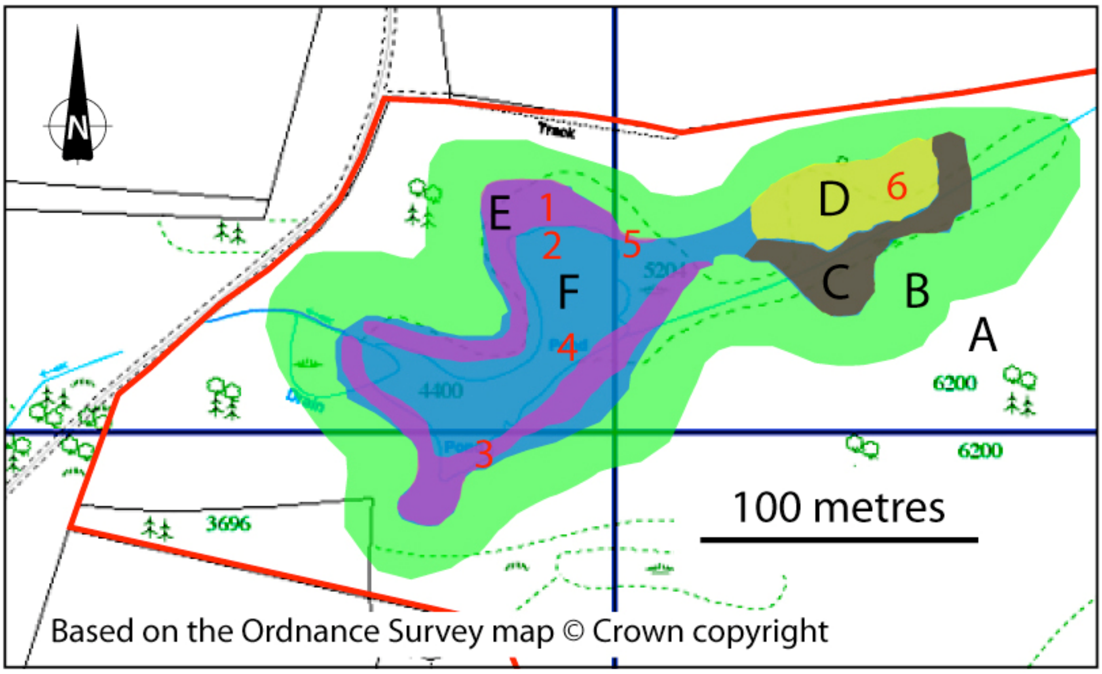
In addition to these surveys, one area each of intact tree canopy, felled trees left *in situ*, and felled and removed trees, were sampled in midsummer of Year 3 (August 2005). The percentage cover of all ground vegetation present in ten randomly placed 1 m X 1 m quadrats was assessed, together with tree canopy cover in each quadrat.

Figure 7.2 Photograph showing the structure of fencing of Exclosure 2 at the Stream Site.

7.3.2 Macrophyte surveys

In May 2003, six exclosures were built using pre-treated softwood fence posts (*c*. 2.5 m long) and galvanised rabbit wire netting approximately 1.8 m high stapled to each post from the top. The exclosures were pre-fabricated on the loch banks and carefully erected within the loch itself, taking care to minimise any damage or disturbance to the macrophyte beds. To facilitate construction, the bottom section of netting (*c*. 15 cm) was not stapled to the posts allowing them to be more easily driven into the loch bed, with this section of wire then being folded over and trodden into the sediment as much as possible, to hinder beavers burrowing under the netting. Upon completion of the exclosure at least approximately 20 – 30 cm of post and netting were emergent from the water surface in order to prevent beavers climbing over the netting, whilst allowing for any increases in water level that may occur during the study. Each exclosure was 2 m X 2 m in size and located within the lochs at the locations shown in Figure 7.3. Five of the six exclosures (Exclosures 1 – 5) were located in the western-most loch, with Exclosures 1, 3 and 5 located in Habitat E (see Table 3.2) characterised by abundant emergent macrophytes, and Exclosures 2 and 4 located within Habitat F which is largely open-water dominated by floating-leaved macrophytes. Exclosure 6 was situated within the floating sedge swamp of Habitat D in the eastern-most loch. Figure 7.4 shows the structure and siting of Exclosure 2 within the open water of the loch.

Figure 7.3 Map showing the locations of the six exclosures at the Lake Site. The coloured zones correspond to the habitats described in Table 3.2.



Based on the Ordnance Survey map © Crown copyright

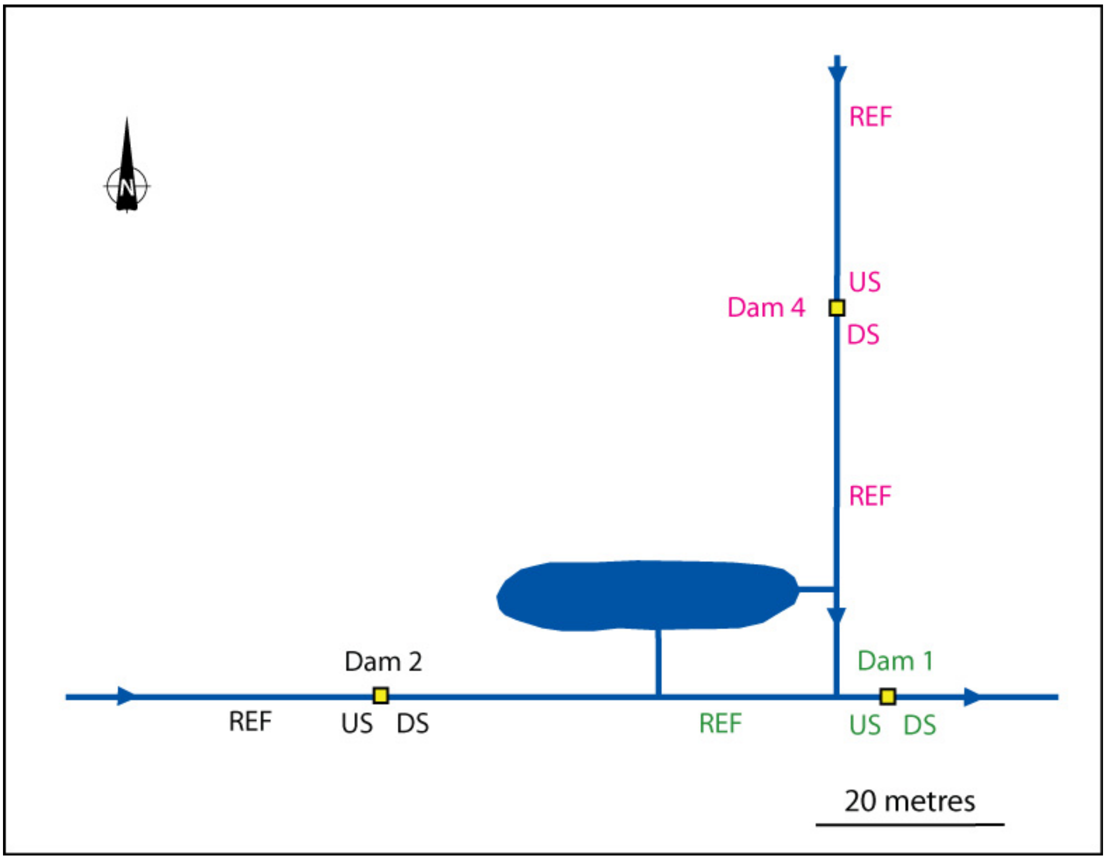
Within each exclosure, the percentage cover of all floating-leaved and emergent macrophyte species present in each of four contiguous quadrats (1 m X 1 m) was assessed and recorded, together with the vegetation height measured at six points in the same manner as in the terrestrial exclosures. The same sampling methodology was employed in four quadrats (1 m X 1 m) amongst the macrophytes surrounding each exclosure. The initial location of these quadrats was such that the macrophyte communities did not markedly differ from those enclosed by the fences, and were situated as near to the exclosures as possible whilst avoiding areas trampled or damaged during the construction of the exclosures. Once such suitable sample areas had been selected they were used during all sampling seasons throughout the study, and avoided under any other circumstances so as not to disturb the vegetation.

Figure 7.4 Photograph showing the structure and siting of Exclosure 2 at the Lake Site.

7.3.3 Macroinvertebrate surveys

Macroinvertebrate communities were sampled by 3-minute kick samples using a kick net (mesh size 500 µm) in two seasons (autumn 2004 and spring 2005). The contents of the net were emptied into sealable plastic sample bags and transported back to the laboratory for preservation in industrial methylated spirits (IMS), and sorted whenever possible within a month of sampling. All specimens were identified to as high a taxonomic resolution as possible (often species) using standard identification keys (*e.g.* Hynes, 1977) and enumerated.

Figure 7.5 Schematic locations of macroinvertebrate sample sites around the dams at the Stream Site. Watercourses and ponds are shown in blue, with flow direction indicated by the arrows.



At the Stream Site, samples were taken for the Dam study from three dams located on two ditches (Dams 1, 2 and 4 as described in section 4.6.3) with one sample each taken from immediately upstream (US) and immediately downstream (DS) of the dams. In addition, two reference sites (REF) were sampled on each ditch at points where the overall character of the stream channel was adjudged to have returned to natural conditions and the influence of the dams was assumed to be negligible. Figure 7.5

shows the sample locations at the Stream Site. At the Lake Site, samples were taken around the outlet dam (Lake Dam as described in Section 4.6.3) from immediately upstream and downstream of the dam, with a single reference site located approximately 25 m downstream. In this latter case, samples were only taken in spring 2005. In all samples, the stream bed, water column and any macrophytes present were disturbed, and in the case of each DS site the dam was also disturbed by kicking, in order to gather any macroinvertebrates present on the structure itself.

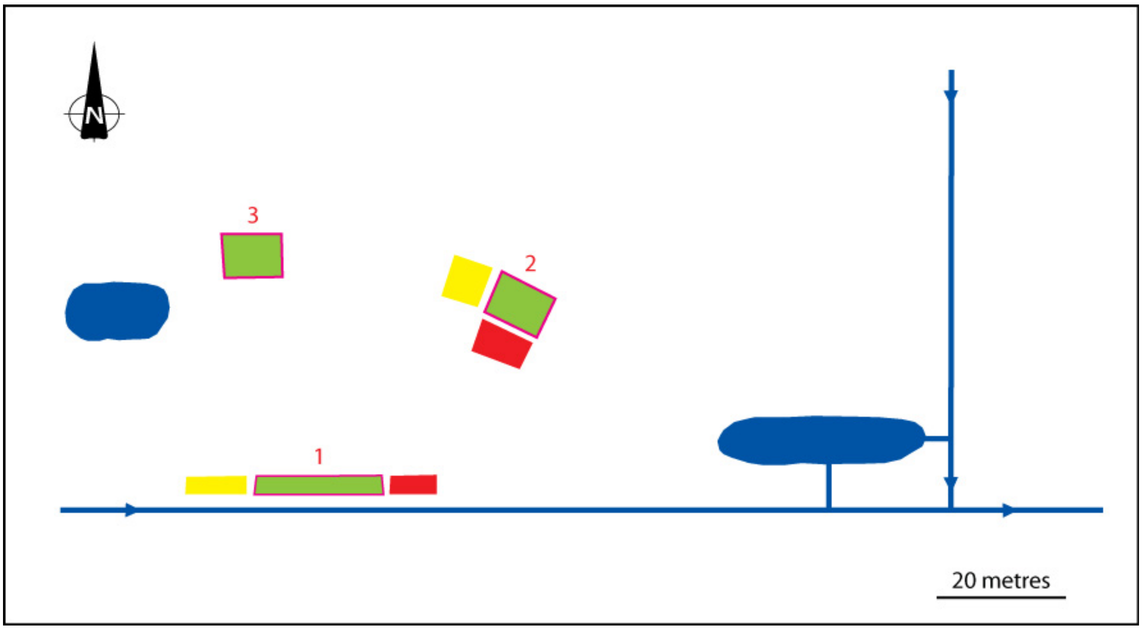
At the Stream Site, the effects of beaver caching activity on macroinvertebrate communities were investigated by sampling three different substrata within the main pond. A single sample was taken from each of three separate caches of woody material (Caches), three separate piles of stripped woody feeding remains (Wood), and three areas of pond characterised by bed sediment with no woody debris (Sediment). Caches and woody debris were sampled by a kick / sweep method, kicking wood piles to release macroinvertebrates into the net which was continually swept through the water column immediately surrounding the sampled woody debris, and through any macrophytes arising from the debris piles. Any small pieces of wood present in the net were visually examined and discarded after any invertebrates had been removed and added to the collected material. In the case of the sediment samples, the pond benthos was disturbed by kicking and the net continually swept through the water column. Areas of floating, submerged or emergent macrophytes present in the water column above the sampled pond bed were also swept through and included in the sample. Samples were taken in both autumn 2004 and spring 2005, and no caches were present at the Lake Site.

Finally, the effects of beaver lodges on the littoral macroinvertebrates were examined by sampling the Lake Site. Both of the natural lodges present at the site (as described in Section 4.6.3) were sampled (Lodges) using the same methodology as for the cache and woody debris samples taken at the Stream Site. Each lodge was sampled once only in both autumn 2004 and spring 2005. In addition, two areas of fringing emergent macrophyte beds (Macrophytes) and two areas of uncolonised bare sediment banks (Sediment) in close proximity to the lodges were also sampled in each season. The single lodge present at the Stream Site was not examined due to the close proximity of several food caches within the pond, which were sampled separately. Also, this lodge was originally artificially constructed especially for the beavers, and although the beavers have since embellished and built-up the existing structure, alterations have been predominantly to the areas of the lodge that lie above the water surface and on the bank. For these reasons, only the lodges at the Lake Site were investigated.

7.3.4 Terrestrial invertebrate surveys

Terrestrial invertebrate communities were sampled at two locations at the Stream Site only, each centred around one of the beaver-proof exclosures (Exclosures 1 and 2) described in Section 7.3.1. At each location three pitfall traps were positioned just inside the monitoring area of the exclosure (Exclosure), three within an area of heavy tree-felling including felled deadwood (Felling), and three within an area in which no felling had occurred (No Felling). Each trap was approximately 1 m from its nearest neighbour, and both the Felling and No Felling areas were within 5 - 10 m of the exclosures. Plastic beakers were used as traps, inserted into holes dug into the soil so that the lip of the beaker was level with the ground surface, and covered with a Perspex lid approximately 1 cm above the trap held in place by tent pegs. The purpose of the lid was to prevent access to the trap by small mammals and amphibians. A small quantity of dilute anti-freeze solution (ethylene glycol) was added to each beaker to act as a killing medium, and the traps left *in situ* for approximately 48 hours. After this period, the contents of each trap were passed through a sieve (mesh size 1 mm) and preserved in small vials of IMS, before identification to as a low a taxonomic resolution as possible generally within one month of sampling. Each trap was reset four times resulting in 90 samples collected in total (5 dates X 3 traps X 3 locations X 2 sites). Figure 7.6 shows the locations of the pitfall traps at the Stream Site.

Figure 7.6 Schematic showing pitfall trap locations at the Stream Site. Green areas indicate "Exclosures", yellow areas "No Felling" and red areas "Felling". (Note that pitfall traps were only sited in and around Exclosures 1 and 2). Watercourses and ponds are shown in blue, with flow direction indicated by the arrows.



7.3.5 Data analysis

Where appropriate, results were tested using the Kruskal-Wallis test, with significant effects being further analysed by *post-hoc* pairwise Mann-Whitney *U* tests (Dytham, 2003). All such tests were performed using Minitab® Release 14. In all cases, the statistical significance of results are reported using the standard convention (* $P<0.05$; ** $P<0.01$; *** $P<0.001$), and unless denoted as such they should be interpreted as not being significant (*i.e.* $P>0.05$). Species diversity was measured by Shannon index (*H'*) (Magurran, 1988) with values being tested for significance by *t*-test, as described in Kent & Coker (1992), and the evenness (E) of ecological communities was calculated using the Buzas & Gibson's evenness measure (Hammer *et al*., 2005). Calculation and testing of diversity indices (*H'* and E) were performed using PAST Version 1.36 software (Hammer *et al*., 2005). LIFE scores (Lotic-invertebrate Index for Flow Evaluation) were calculated according to the method described in Extence *et al*. (1999). A very brief description of the LIFE index is included in the following section (Chapter 7.3.6).

7.3.6 Explanation of terminology

In addition to any previously defined terms in earlier chapters of this thesis, some clarification is necessary for the following terms used throughout this chapter. In the majority of this chapter, "herbaceous" has been used interchangeably with "non-woody" to distinguish only between woody tree canopy species and non-woody understorey species. However, when referring to and discussing the results of the terrestrial vegetation surveys at the Stream Site (*e.g.* sections 7.4.1 and 7.5.1), the non-woody component of the vegetation has been sub-divided into "herbaceous", "*Urtica dioica*" and "grass / rush". In these specific references, "herbaceous" refers to all non-woody, broad-leaved species, with the exception of the highly dominant common nettle (*Urtica dioica*). Further clarification of the exact species composition of the "herbaceous" and "grass / rush" categories is shown in the notes under Tables 7.3 and 7.5.

Reference is made to species richness throughout this chapter which implies the *number of species* (a dimension without units), as used by Magurran (1988). Similarly, family richness and taxonomic richness imply the *number of families* and the *number of taxa* present respectively.

The LIFE index is based on the known river flow regime preferences of different macroinvertebrate species and families, with each taxon attributed to one of six "flow groups". For each taxon present at a site, a matrix table linking the abundance and flow group of that taxon is used to provide a "flow score" for that particular macroinvertebrate. The LIFE index for the whole community is the sum of these individual flow scores divided by the number of taxa used in the calculation (*i.e.* the average flow score per taxon). Further details of these calculations and the flow groups of each macroinvertebrate taxon can be found in Extence *et al*. (1999).

7.4 Results

7.4.1 Terrestrial vegetation surveys

By combining the species cover data for the 32 component quadrats for each exclosure and the area surrounding each exclosure in all three survey seasons, it was evident that the exclosures were generally less species rich than the surrounding woodland (Table 7.1). This relationship was not significant, however, for either Exclosure 2 or 3 when tested by the Mann-Whitney *U* test (P>0.05 in both cases). Unfortunately the significance of the Exclosure 1 data, which show the greatest difference in mean species richness, could not be tested as all three seasonal values within the exclosure were identical. However, combining the species richness values for each exclosure and corresponding areas outside the exclosures for all three sampling seasons into just two categories (Exclosures and Outside Exclosures, N=9 in each case) allowed the data to be tested statistically. In this case, the mean species richness inside the exclosures was 7.9 (±0.8 SE) compared to a mean value of 11.2 (±0.5 SE) outside the exclosures, and this relationship was significant (Mann-Whitney, P<0.01).

Table 7.1 Species richness within and outside each exclosure in three sampling seasons.

Location	**Season 1 (Aug 2003)**	**Season 2 (May 2004)**	**Season 3 (Sept 2004)**	**Mean (± SE)**
Exclosure 1	5	5	5	5.0 (0.0)
Outside Exc 1	14	11	11	12.0 (1.0)
Exclosure 2	10	9	10	9.7 (0.3)
Outside Exc 2	12	11	10	11.0 (0.6)
Exclosure 3	8	10	9	9.0 (0.6)
Outside Exc 3	10	9	13	10.7 (1.2)

Calculation of Shannon diversity index (*H'*) for the plant communities within and outside each exclosure in each of the three seasons, showed that the vegetation was consistently more diverse outside the exclosures than inside them (Table 7.2). However, this greater diversity outside the exclosures was only significant in the case of Exclosure 2 in late-spring 2004 ($P<0.05$), with the results for the same exclosure in late-summer 2004 being of borderline significance ($P=0.058$).

Table 7.2 Shannon diversity index (*H'*) values within and outside each exclosures in three sampling seasons.

Location	**Season 1 (Aug 2003)**		**Season 2 (May 2004)**		**Season 3 (Sept 2004)**	
	H'	***P*-value**	***H'***	***P*-value**	***H'***	***P*-value**
Exclosure 1	1.15	0.358 (**NS**)	1.23	0.356 (**NS**)	0.95	0.572 (**NS**)
Outside Exc 1	1.29		1.37		1.03	
Exclosure 2	1.28	0.158 (**NS**)	1.32	0.027 (*)	1.11	0.058 (**NS**)
Outside Exc 2	1.54		1.65		1.44	
Exclosure 3	1.24	0.242 (**NS**)	1.40	0.251 (**NS**)	1.36	0.929 (**NS**)
Outside Exc 3	1.44		1.56		1.38	

The mean percentage cover values for each of the key vegetation and substrate types inside and outside the exclosures are shown in Table 7.3. This value was derived from the combined mean values for all three exclosures in each of the three seasons, and tested for significance by Mann-Whitney *U* test. Although the only significant difference between the exclosures and outside the exclosures for these key components was the greater cover of the tree canopy within the exclosures, several interesting but statistically insignificant trends were evident. For example, there was a higher percentage cover of both grass / rush and herbaceous species outside the exclosures, compared to inside, although the cover of common nettles (*Urtica dioica*) was approximately equal in both locations. The cover of fallen deadwood and bare earth was generally very low, although it tended to be higher outside the exclosures in both cases.

Table 7.3 Mean percentage cover of key vegetation and substrate types within and outside the exclosures.

Vegetation / substrate type	**Mean (% Cover)**	***P*-value**	**Significance**
Tree canopy			
Exclosures	60.4	0.0004	***
Outside Exclosures	22.9		
Herbaceous species*			
Exclosures	18.0	0.2888	**NS**
Outside Exclosures	23.1		
Grass / rush species**			
Exclosures	16.5	0.3096	**NS**
Outside Exclosures	25.9		
Urtica dioica			
Exclosures	34.6	0.8252	**NS**
Outside Exclosures	35.4		
Fallen deadwood			
Exclosures	0.0	-	**-**
Outside Exclosures	1.0		
Bare earth			
Exclosures	1.0	0.5084	**NS**
Outside Exclosures	1.7		

* Herbaceous species include *Galium aparine*, *Heracleum sphondylium*, *Cirsium palustre*, *Cirsium arvense*, *Ranunculus repens*, *Stellaria media*, *Rumex obtusifolius*, *Lamium album*, *Epilobium montanum*, *Rubus idaeus*, *Pteridium aquilinum*, *Hypnum cupressiforme*, *Taraxacum officinale* and *Polygonum aviculare*.

** Grass / rush species include *Holcus mollis*, *Lolium perenne*, *Deschampsia cespitosa*, *Juncus effusus* and *Holcus lanatus*.

Table 7.4 shows the species richness and diversity of the vegetation communities in three areas of different tree-felling conditions outside the exclosures at the Stream Site. The most species-rich vegetation was present under an intact tree canopy (area B), with the least rich community observed in areas of felling with abundant *in situ* deadwood (area C). The most diverse community according to the Shannon index, however, was in the area of felled and removed trees (area A), with the lowest diversity in the area of felling with *in situ* deadwood (area B). Pairwise comparisons of the Shannon indices for each area, however, showed that no significant differences were present (*P*>0.05 in all three cases), although the higher *H'* value in area A than in area C was of borderline significance (*P*=0.054).

Table 7.4 Species richness and Shannon diversity index (*H'*) of vegetation communities outside exclosures in three areas of different tree-felling conditions.

Area	**Tree-felling conditions**	**Species richness**	***H'***
A	Felled trees removed by beavers	9	1.304
B	No felling	13	1.232
C	Felled trees left *in situ*	7	1.076

The mean percentage cover of the key vegetation and substrate types in the three areas of differing tree-felling conditions showed that the composition of the plant communities varied greatly (Table 7.5). Areas of intact tree canopy (area B) showed the highest cover of grass / rush species (Kruskal-Wallis test, *P*=0.002) and lowest cover of herbaceous species (Kruskal-Wallis, *P*=0.008), with no fallen deadwood. In contrast, the areas of tree-felling (areas A and C) showed much greater cover of herbaceous species, with low levels of grass / rush cover, and a large component of fallen deadwood in area C. Nettles formed a very large part of the vegetation community in all three areas, although it was most important in areas of felled trees with *in situ* deadwood (area C) and least important in clear-felled parts of the woodland (area A).

Table 7.5 Mean percentage cover of key vegetation and substrate types within three areas of different tree-felling conditions outside the exclosures. *P*-values are the result of Kruskal-Wallis tests.

Vegetation / substrate type	**Area**			***P*-value**
	A	**B**	**C**	
Tree canopy	1.0	71.0	0.0	<0.001
Herbaceous species*	38.4	12.0	41.9	<0.01
Grass / rush species**	13.5	33.3	3.5	<0.01
Urtica dioica	49.0	59.5	74.5	<0.05
Fallen deadwood	6.5	0.0	45.5	<0.001
Bare earth	0.0	0.0	0.0	NS

* Herbaceous species include *Galium aparine*, *Heracleum sphondylium*, *Cirsium palustre*, *Cirsium arvense*, *Ranunculus repens*, *Stellaria media*, *Rumex obtusifolius*, *Lamium album*, *Epilobium montanum*, *Rubus idaeus*, *Pteridium aquilinum*, *Hypnum cupressiforme*, *Taraxacum officinale* and *Polygonum aviculare*.

** Grass / rush species include *Holcus mollis*, *Lolium perenne*, *Deschampsia cespitosa*, *Juncus effusus* and *Holcus lanatus*.

The mean vegetation height varied considerably both between sampled areas and, not surprisingly, season (Table 7.6). Within each season, however, at least one of the three areas measured showed significant differences between sward height inside and outside the exclosure. In all of these cases (Exclosure 1 in Year 1, Exclosure 2 in early-spring of Year 2, and Exclosure 3 in both sampling seasons of Year 2) the mean vegetation height was higher inside the exclosures than outside (P<0.001 in all four cases).

Table 7.6 Mean vegetation heights (± 1 SE) inside and outside the three exclosures, as measured in three seasons (N=192 in each case).

Location	**Year 1 Late-summer**		**Year 2 Early-spring**		**Year 2 Late-summer**	
	Mean height (m)	***P*-value**	**Mean height (m)**	***P*-value**	**Mean height (m)**	***P*-value**
Excl 1	0.70 (0.02)	<0.001	0.07 (0.00)	>0.05	0.27 (0.01)	>0.05
Outside Excl 1	0.53 (0.02)		0.08 (0.00)		0.25 (0.01)	
Excl 2	0.72 (0.03)	>0.05	0.09 (0.00)	<0.001	0.27 (0.01)	>0.05
Outside Excl 2	0.83 (0.03)		0.06 (0.00)		0.36 (0.02)	
Excl 3	0.95 (0.02)	>0.05	0.15 (0.01)	<0.001	0.50 (0.02)	<0.001
Outside Excl 3	0.97 (0.02)		0.11 (0.01)		0.40 (0.02)	

7.4.2 Macrophyte surveys

The species richness in all three habitat types was slightly higher outside than inside the exclosures, in both sampling years (Table 7.7). Combining the annual datasets showed the same trend, although the higher species richness outside than inside the exclosures was not significant in any of the three habitats (*P*>0.05 in all cases).

Calculation of the Shannon diversity index (*H'*) for the combined annual data for the macrophyte communities within and outside the exclosures in each of the three habitats, showed that the vegetation was more diverse outside the exclosures than inside them within the emergent macrophytes (Table 7.8). However, in both the open water and sedge swamp habitats the diversity was greatest inside the exclosures. None of these differences were significant (*P*>0.05 in all three cases).

Table 7.7 Species richness within and outside the exclosures in three habitat types.

Habitat	Exclosures	Year 1 (Aug 2003)	N	Year 2 (Aug 2004)	N	Both Seasons	N
Emergent Macrophytes	**Inside**	**7**	12	**8**	12	**8**	24
	Outside	**9**	12	**9**	12	**10**	24
Open Water	**Inside**	**2**	8	**2**	8	**3**	16
	Outside	**2**	8	**3**	8	**4**	16
Sedge Swamp	**Inside**	**3**	4	**3**	4	**3**	8
	Outside	**4**	4	**4**	4	**6**	8

Table 7.8 Shannon diversity index (*H'*) values of the macrophyte communities within and outside the exclosures in three habitat types.

Habitat	Exclosures	*H'*	*P*-value	Significance
Emergent Macrophytes	**Inside**	1.07	0.222	NS
	Outside	1.26		
Open Water	**Inside**	1.06	0.335	NS
	Outside	0.97		
Sedge Swamp	**Inside**	0.74	0.620	NS
	Outside	0.67		

The mean percentage cover of the six dominant macrophyte species inside and outside the exclosures in each of the three habitat types is shown in Table 7.9. No trends in these data were obvious, with some species being more abundant inside the exclosures, and others more abundant outside the exclosures. The only significant differences were the higher percentage cover of bottle sedge (*Carex rostrata*) outside the exclosures in the emergent macrophytes habitat ($P<0.05$), and the lower cover of bogbean (*Menyanthes trifoliata*) outside the exclosures of the sedge swamp ($P<0.05$).

Table 7.9 Mean percentage cover of the six dominant macrophyte species within and outside the exclosures in three habitat types.

Habitat	**Exclosures**	**N**	**Mean percentage cover of species**					
			C. ros	***E. flu***	***I. pse***	***P. nat***	***P. pol***	***M. tri***
Emergent Macrophytes	**Inside**	24	1.1	4.2	55.7	0.0	29.2	0.0
	Outside	24	9.6	6.8	54.0	0.0	15.0	0.5
Open Water	**Inside**	16	0.0	23.1	0.0	42.5	29.1	0.0
	Outside	16	0.0	6.0	0.0	26.3	35.6	0.0
Sedge Swamp	**Inside**	8	40.6	1.2	0.0	0.0	0.0	50.0
	Outside	8	41.9	1.3	0.0	0.0	0.1	10.6

Abbreviations: *C. ros* (*Carex rostrata*), *E. flu* (*Equisetum fluviatile*), *I. pse* (*Iris pseudacorus*), *P. nat* (*Potamogeton natans*), *P. pol* (*Potamogeton polygonifolius*), *M. tri* (*Menyanthes trifoliata*)

The mean vegetation height in the emergent macrophytes and sedge swamp are shown in Table 7.10. In both habitats the mean vegetation height was slightly greater inside the exclosures than outside, but neither trend was significant ($P>0.05$ in both cases).

Table 7.10 Mean vegetation heights inside and outside the exclosures in two habitat types.

Habitat	Exclosures	N	Mean height (m)	SE	Significance
Emergent Macrophytes	**Inside**	72	1.09	0.04	NS
	Outside	72	1.02	0.04	
Sedge Swamp	**Inside**	24	0.66	0.02	NS
	Outside	24	0.65	0.02	

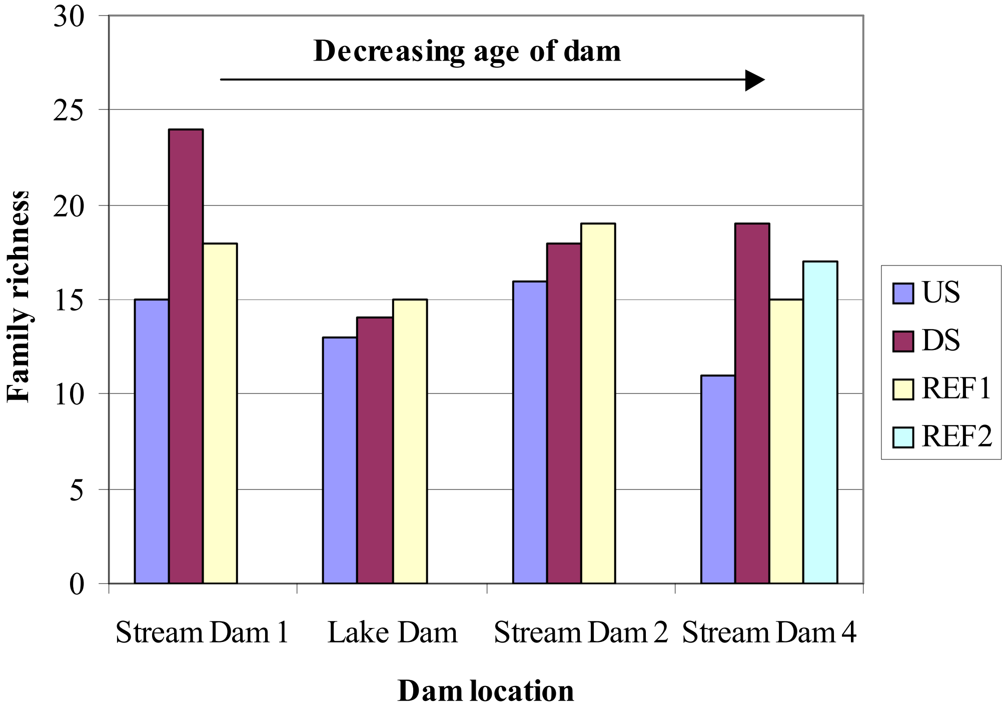
7.4.3 Macroinvertebrate surveys

Species lists for all macroinvertebrate surveys conducted are shown in Apendices B –E.

7.4.3.1 Dams

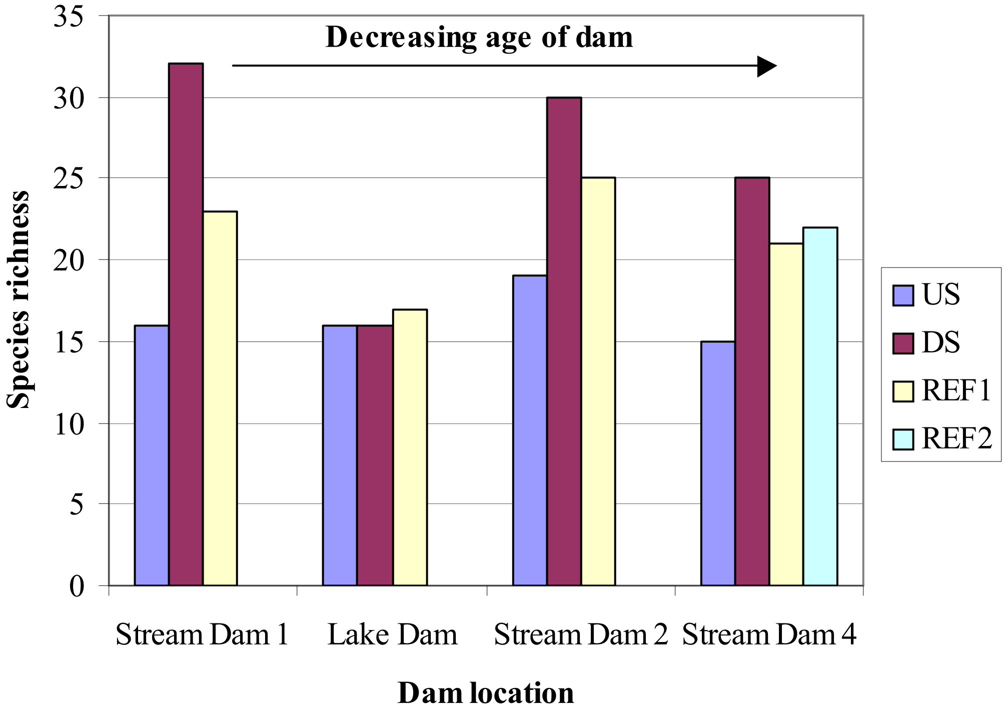
The total number of macroinvertebrate families present at three or four sampling points around each of the four dams was consistently lowest immediately upstream of the dams (Figure 7.7). At two of the dams (Dams 1 and 4 at the Stream Site) the family richness was higher immediately downstream of the dams than at reference sites, although Dam 2 at the Stream Site showed highest family richness at the reference site. There were no significant differences between the family richness recorded at each site, however, for any of the three Stream Site dams (Kruskal-Wallis test, $P>0.05$ in all three cases), although in each case the small sample size (N=2) limited the reliability of such tests. Furthermore, the Lake Site dam could not be tested as only one sample was collected at each sample location. Sample sizes were increased by combining the data for the four dams (both upstream and downstream N=7, reference sites N=9), and on re-testing the data it was found that the family richness was significantly greater at the downstream locations than upstream (Mann-Whitney test, *P*<0.05), although other pairwise comparisons were not significant (*P*>0.05 in both cases).

Figure 7.7 Family richness of macroinvertebrate communities upstream and downstream of four beaver dams. (N=2 for each location at the three Stream Site dams, and N=1 for each location at the Lake Site dam).



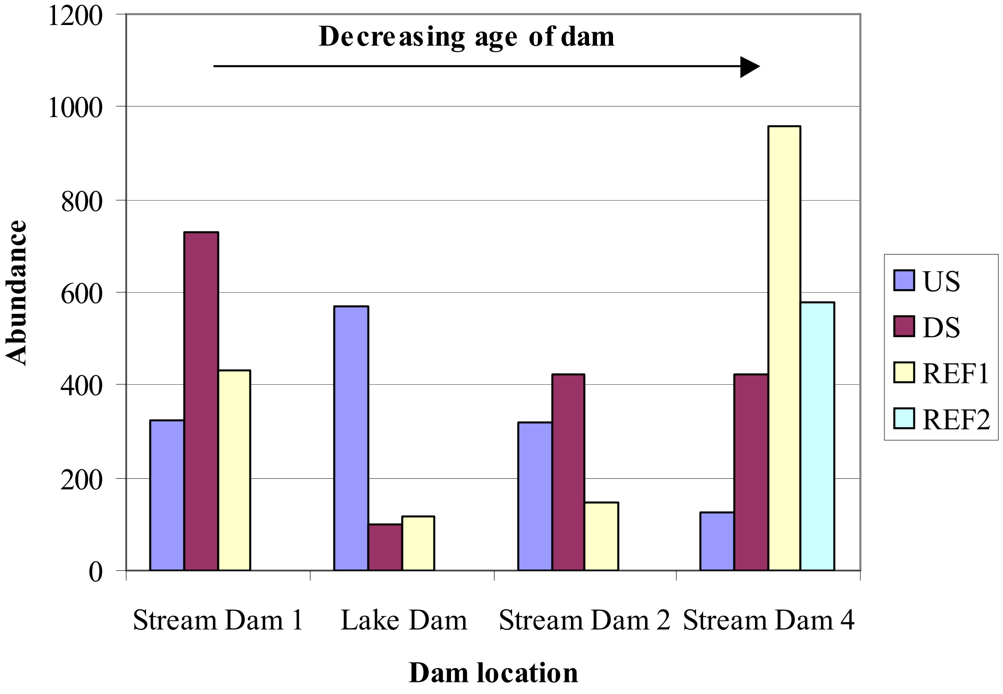
These broad patterns were also evident in the species richness of the macroinvertebrate communities at varying locations around the four dams (Figure 7.8), with the highest values found immediately downstream and the lowest values immediately upstream of three of the four sampled dams. Again, due to the small sample sizes, no significant trends were evident in the data for the individual dams (Kruskal-Wallis, *P*>0.05 in all cases), whilst combining the data also indicated no significant difference between the species richness at each location (Kruskal-Wallis, *P*>0.05).

Figure 7.8 Species richness of macroinvertebrate communities upstream and downstream of four beaver dams. (N=2 for each location at the three Stream Site dams, and N=1 for each location at the Lake Site dam).



Macroinvertebrate abundance patterns showed considerable variation between the different dams, although the abundance was greater downstream of all three Stream Site dams than upstream (Figure 7.9). No significant trends, either on the individual dams or the combined data, were evident however (Kruskal-Wallis, *P*>0.05 in all cases).

Figure 7.9   Macroinvertebrate abundance upstream and downstream of four beaver dams. (N=2 for each location at the three Stream Site dams, and N=1 for each location at the Lake Site dam).



Examination of the overall number of species present in each class / order of macroinvertebrate indicated that the beetles (Coleoptera), caddis fly larvae (Trichoptera), fly larvae (Diptera) and stonefly nymphs (Plecoptera) were the most species-rich taxa in the sampled locations at both the Stream and Lake Site dams (Table 7.11). The only taxon showing significant differences in species richness between locations was Diptera at the Stream Site, however. The number of fly larvae species present immediately downstream of the Stream Site dams was significantly greater than immediately upstream (Mann-Whitney, $P<0.01$), although the other two pairwise comparisons for Diptera at the Stream Site were not significant ($P>0.05$ in both cases). No statistical tests were conducted on the Lake Site data due to the small sample size at each location (N=1).

Table 7.11 Overall macroinvertebrate species richness per class / order at different locations (upstream, downstream and reference sites) around three Stream Site dams and one Lake Site dam.

Class / Order		Stream Site			Lake Site		
		US	DS	REF	US	DS	REF
Platyhelminthes	**Tricladida**	1	1	1	0	1	1
Annelida	**Hirudinea**	2	1	2	2	1	1
	Oligochaetae	1	1	1	1	1	1
Chelicerata	**Hydracarina**	0	1	0	1	0	1
Crustacea	**Amphipoda**	2	2	2	1	2	2
	Isopoda	1	1	1	1	1	1
	Ostracoda	1	1	1	1	1	1
Insecta	**Coleoptera**	3	13	9	4	3	8
	Diptera	4	8	9	7	5	8
	Ephemeroptera	0	1	0	0	0	0
	Hemiptera	2	0	2	0	0	0
	Lepidoptera	0	0	1	0	0	0
	Megaloptera	1	0	0	1	1	0
	Odonata	0	0	2	0	0	0
	Plecoptera	6	6	7	2	3	2
	Trichoptera	4	10	12	7	5	7
Mollusca	**Bivalvia**	1	1	1	1	1	1
	Gastropoda	3	4	4	2	1	1

The macroinvertebrate communities immediately upstream of the Stream Site dams were very similar to the reference sites, in terms of overall number of species present per feeding guild, with predators and shredders dominant. Immediately downstream of these dams, collector-gatherer species become comparatively more abundant (Figure 7.10a). None of the differences between number of species per feeding guild and sample location were significant (*P*>0.05 in all cases), however, except for the higher species richness of collector-gatherers immediately downstream of the Stream Site dams than either immediately upstream or in reference conditions (Kruskal-Wallis, *P*<0.05). At the Lake Site, the downstream community was most similar in composition to the reference site, with collector-gatherers, shredders and predatory species being dominant, but immediately upstream of this dam shredders became comparatively rarer (Figure 7.10b). Again, no statistical tests could be conducted on the Lake Site data due to the small sample sizes (N=1) at each location.

Figure 7.10a Overall macroinvertebrate species richness per feeding guild at three locations around three Stream Site dams. (N=6 for US and DS locations, and N=8 for REF). Abbreviations: Coll Filt = Collector-Filterer, Coll Gath=Collector-Gatherer.

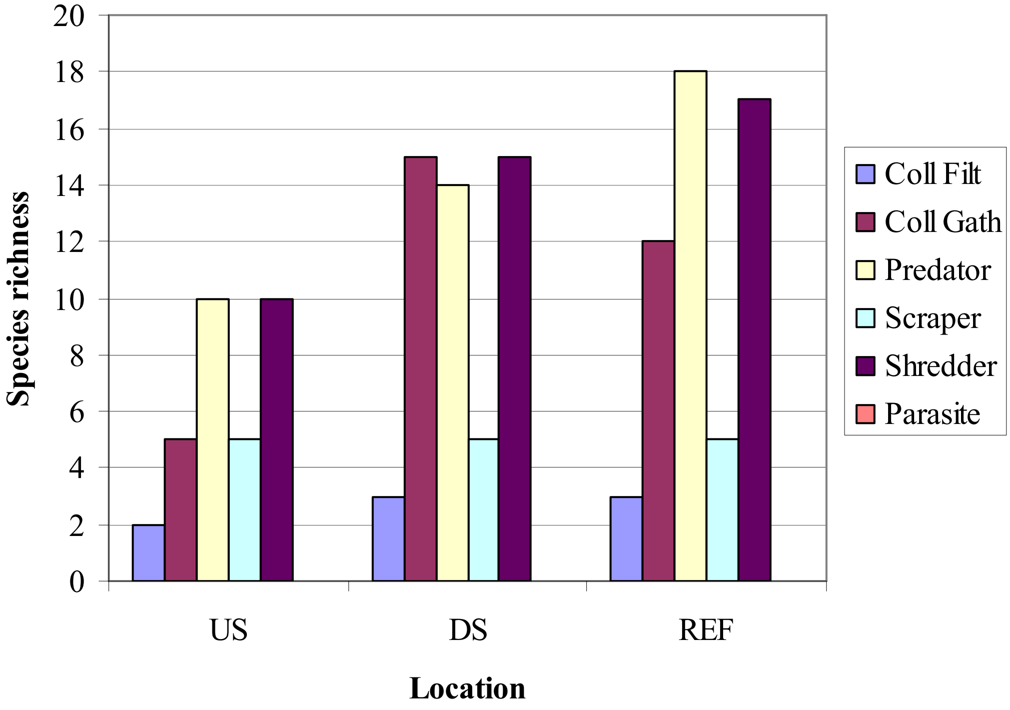
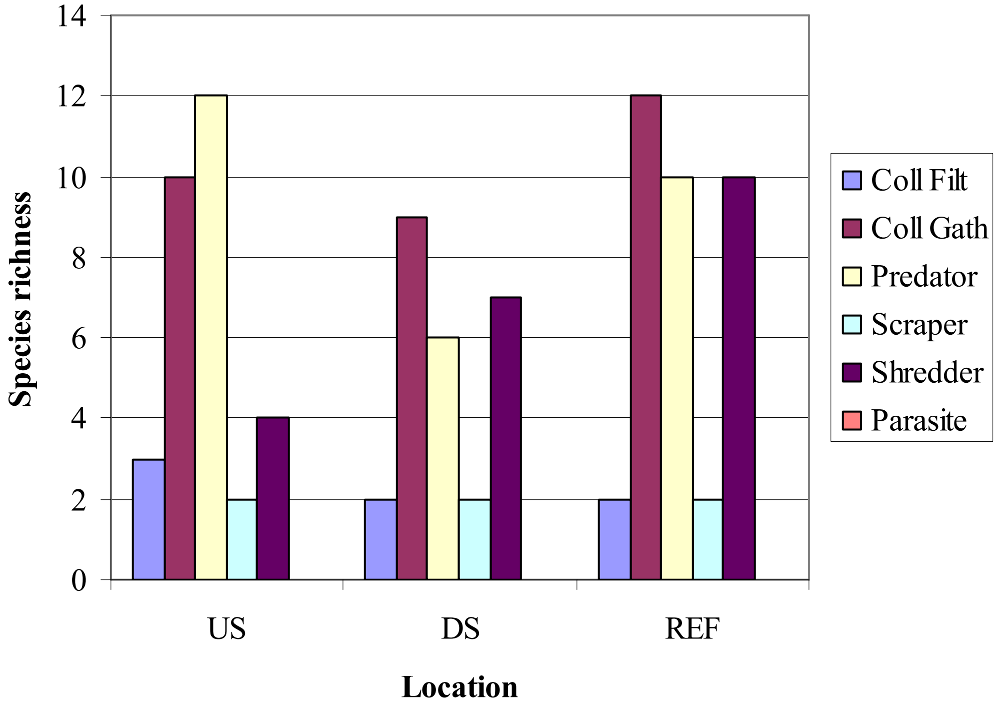
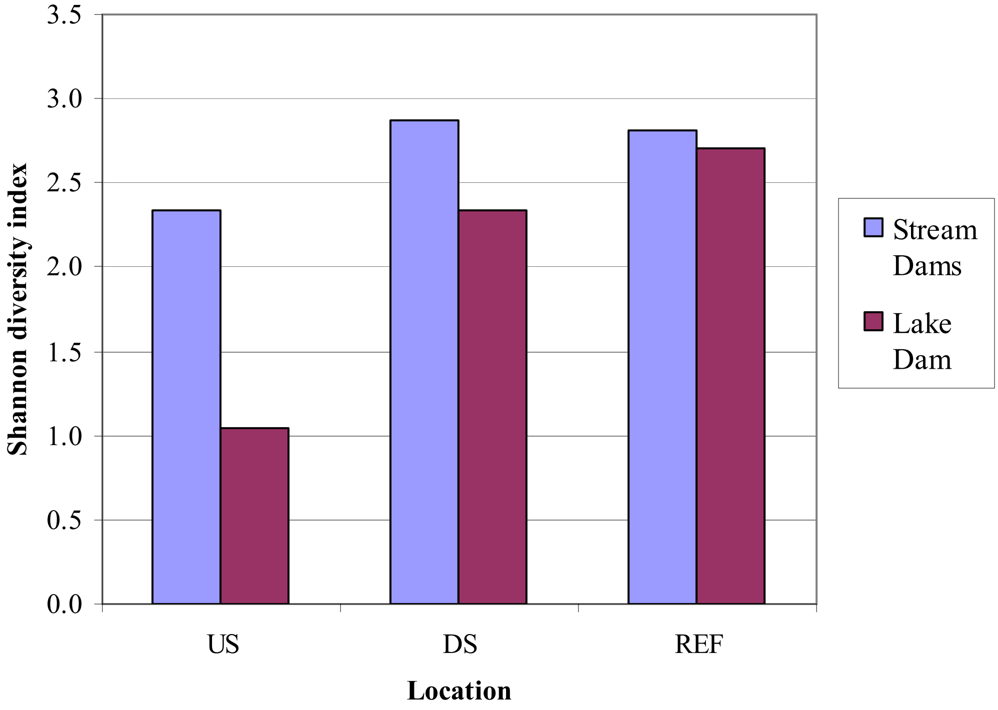


Figure 7.10b Overall macroinvertebrate species richness per feeding guild at three locations around one Lake Site dam. (N=1 for each location). Abbreviations: Coll Filt = Collector-Filterer, Coll Gath=Collector-Gatherer.



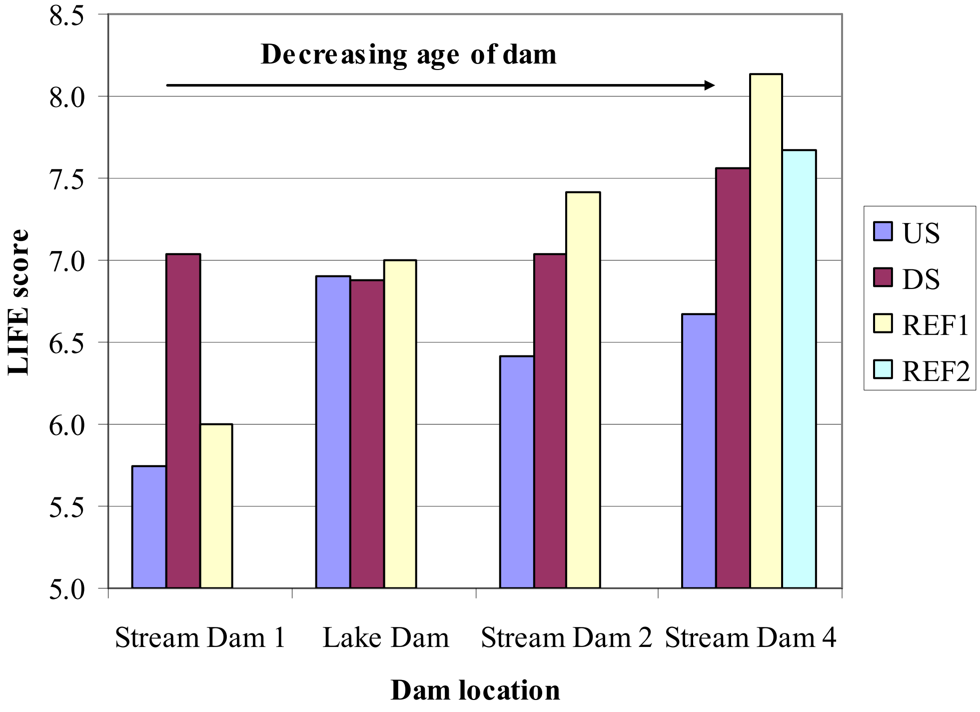
Calculation of the overall Shannon diversity indices (*H'*) for each location at both the Stream and Lake Site dams, showed greater diversity immediately downstream of the dams than immediately upstream at both sites (Figure 7.11). Furthermore, at the Stream Site the diversity immediately downstream of the dams was also greater than at reference sites, although this relationship was not present at the Lake Site. Pairwise comparisons of *H'* values at each location for the Stream Site showed that the macroinvertebrate communities were significantly less diverse immediately upstream of the dams than at either of the other two locations ($P<0.001$ in both cases), but there was no significant difference between the diversity of the reference sites and those immediately downstream of the dams ($P>0.05$). At the Lake Site, macroinvertebrate diversity immediately upstream of the dam was significantly lower than either of the other two sites (*P*<0.001 in both cases), whilst the diversity of the reference site was significantly higher than at either of the dam locations (*P*<0.001 in both cases).

Figure 7.11 Shannon diversity index (*H'*) values of macroinvertebrate communities around the Stream and Lake Site dams.



At the Stream Site the general trend in LIFE score of the macroinvertebrate communities around the dams, was of highest values at the reference sites and lowest values immediately upstream of the dams (Figure 7.12). The only exception to this trend was at Dam 1, where the LIFE score immediately downstream of the dam was highest and the lowest score was immediately upstream of the dam. At the Lake Site, however, no discernible trend was present with LIFE scores at all three locations being approximately equal.

Figure 7.12 LIFE scores of macroinvertebrate communities around three Stream Site dams and one Lake Site dam. (Note y-axis does not start at 0).

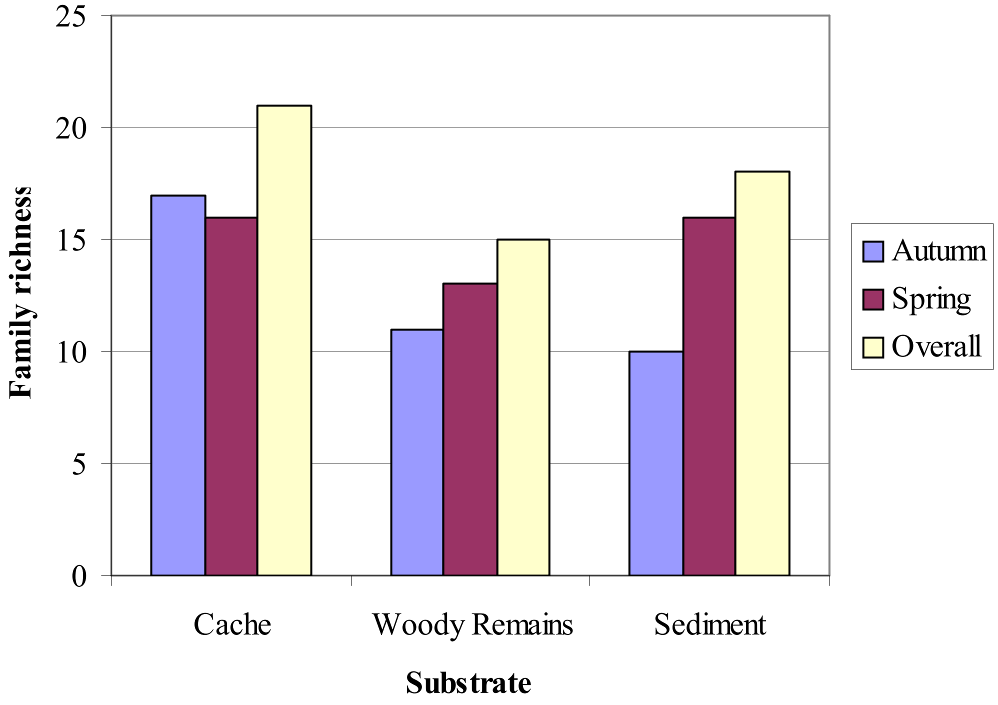


In total 90 species of macroinvertebrate were collected from 23 samples taken around four dams at the Stream and Lake Sites. Of these species, 10 (11%) were found only immediately upstream of the dams, compared to 11 species (12%) found only immediately downstream of the dams and 15 (17%) only at reference sites. A further 28 species (31%) were ubiquitous across the three locations, whilst overall, 25 species (28%) were found only in the immediate vicinity of beaver dams.

7.4.3.2 Caches

The total number of macroinvertebrate families present on caches was generally higher than on either woody remains or sediment in both sampling seasons (Figure 7.13). Combining the seasonal data for each substrate showed this relationship even more clearly, with 21 families present on caches compared to 15 and 18 families on woody remains and sediment respectively. Furthermore, this higher overall family richness on caches was significantly greater than on the other two substrata (*P*<0.05 in both cases), although there was no significant difference between woody remains and sediment (*P*>0.05). It is also interesting to note that the total seasonal family richness was greater in spring than autumn on both woody remains and sediment, but there was little seasonal effect on cache samples.

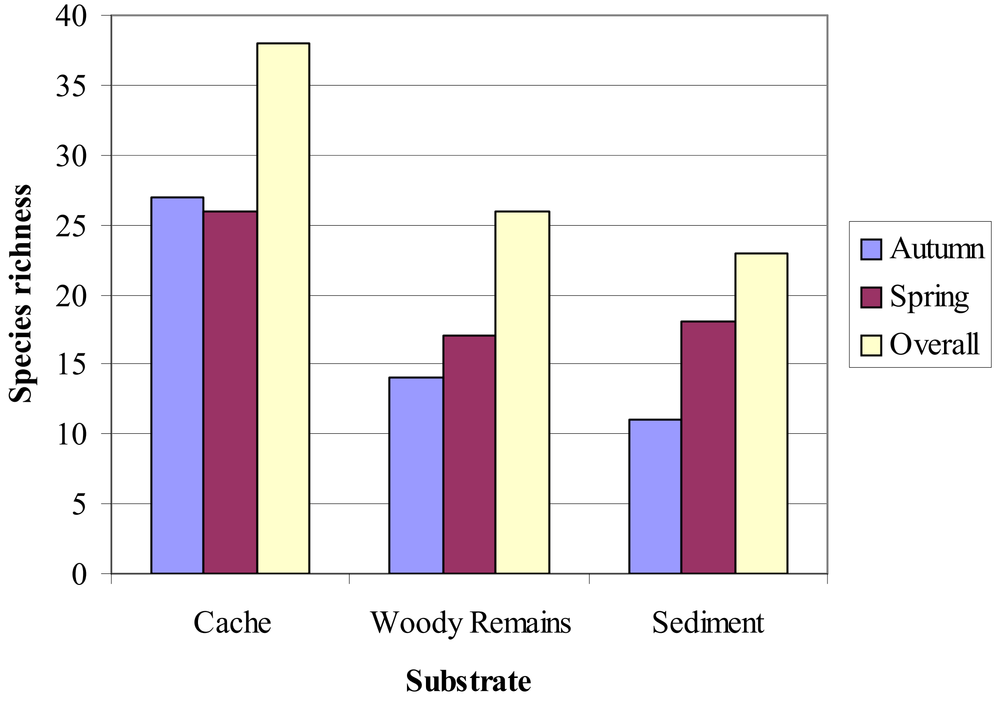
Figure 7.13 Total seasonal (N=3) and overall (N=6) macroinvertebrate family richness on three substrata including caches.



These patterns were also evident in the species richness of the macroinvertebrate communities on the three substrata (Figure 7.14), with the higher overall species richness of the caches (38 species) being significantly greater than on woody remains (*P*<0.05) and sediment (*P*<0.01). Again, no significant difference between the overall species richness on woody remains (26 species) and sediment (23 species) was evident

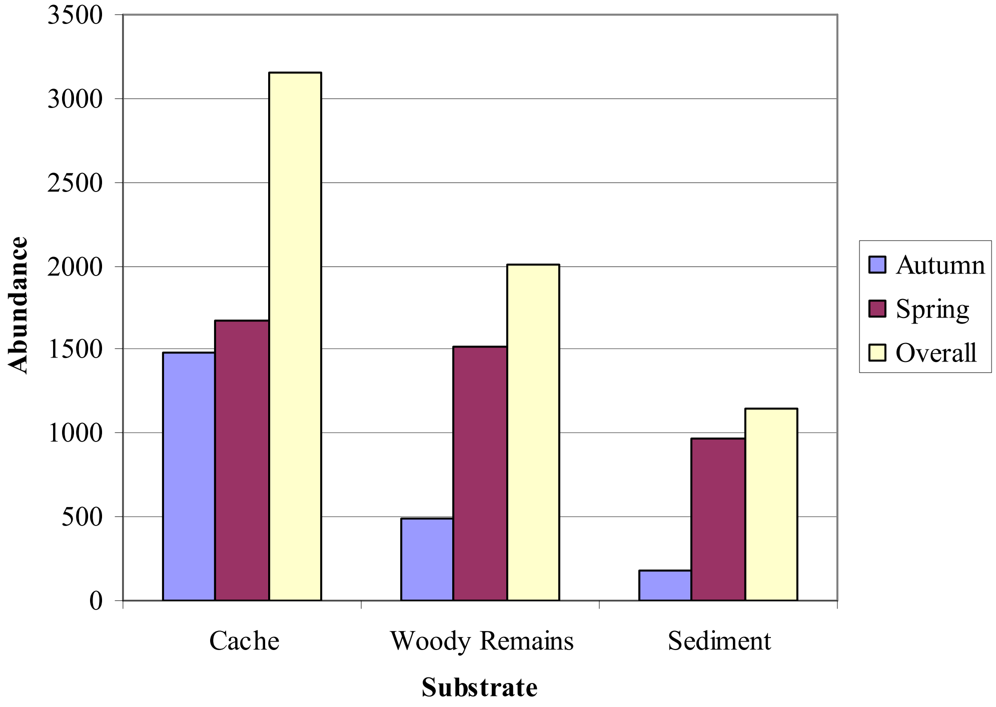
($P>0.05$). The seasonal effect on species richness of the macroinvertebrates on the three substrata was similar to the effect on family richness, as described above.

Figure 7.14 Total seasonal (N=3) and overall (N=6) macroinvertebrate species richness on three substrata including caches.



Seasonal and overall macroinvertebrate abundance patterns mirrored those of species richness, with highest abundances found on caches, followed by woody remains and sediment (Figure 7.15). However, the only significant pairwise comparison between the overall abundance of macroinvertebrates on the three substrata, was the higher abundance on caches than sediment ($P<0.05$). The seasonal increase in abundance from autumn to spring was again most marked on the woody remains and sediment, with little seasonal variation evident on the caches.

Figure 7.15 Total seasonal (N=3) and overall (N=6) macroinvertebrate abundance on three substrata including caches.



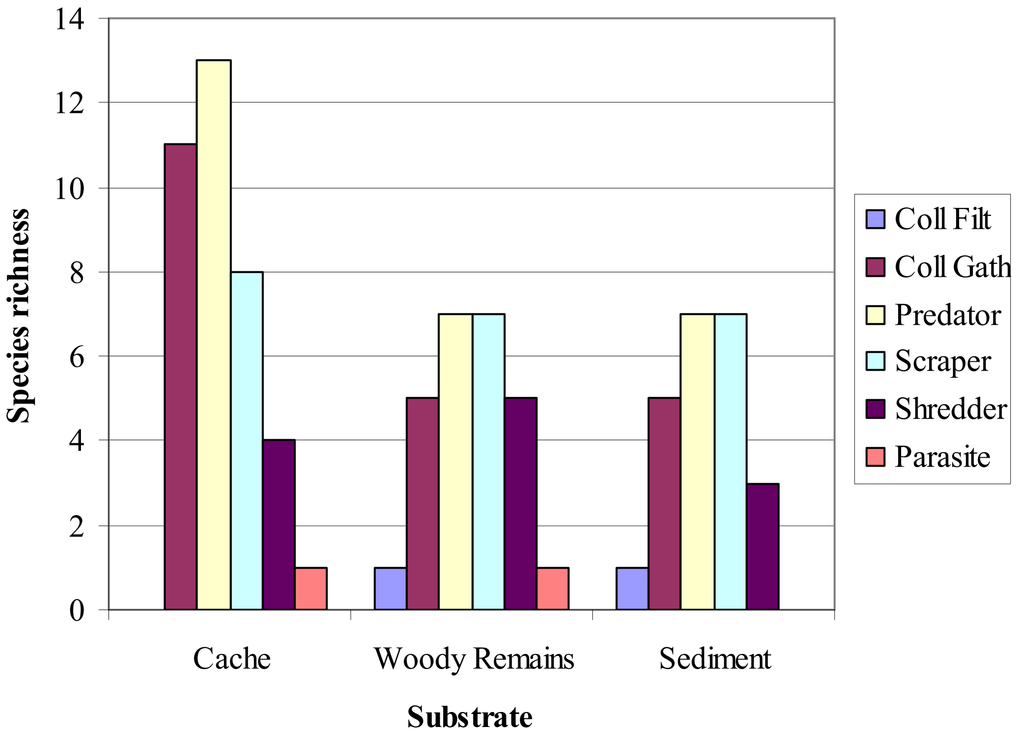
Examination of the overall number of species present in each class / order of macroinvertebrate indicated that the beetles (Coleoptera), bugs (Hemiptera), caddis fly larvae (Trichoptera) and snails (Gastropoda) were the most species-rich taxa in the sampled substrata (Table 7.12). The only taxa showing significant differences in species richness between substrata were the Coleoptera and Hemiptera, however. The number of beetle species present on caches was significantly greater than on sediment ($P<0.05$) and woody remains, although of only borderline significance in the latter case ($P=0.059$). Similarly, the number of water bug species present on caches was significantly greater than on either woody remains or sediment ($P<0.01$ in both cases). For both the Coleoptera and Hemiptera, there was no significant difference between species richness on the woody remains and sediment ($P>0.05$ in both cases).

Table 7.12 Overall macroinvertebrate species richness per class / order on three substrata including caches.

Class / Order		Cache (N=6)	Woody Remains (N=6)	Sediment (N=6)
Platyhelminthes	**Tricladida**	1	0	0
Annelida	**Hirudinea**	3	2	2
	Oligochaetae	1	0	0
Crustacea	**Amphipoda**	2	2	2
	Isopoda	1	1	1
	Ostracoda	1	0	1
Insecta	**Coleoptera**	8	4	3
	Diptera	2	2	2
	Ephemeroptera	1	0	0
	Hemiptera	6	2	3
	Megaloptera	0	0	1
	Odonata	1	1	0
	Plecoptera	0	0	1
	Trichoptera	4	5	2
Mollusca	**Bivalvia**	0	0	1
	Gastropoda	8	5	4

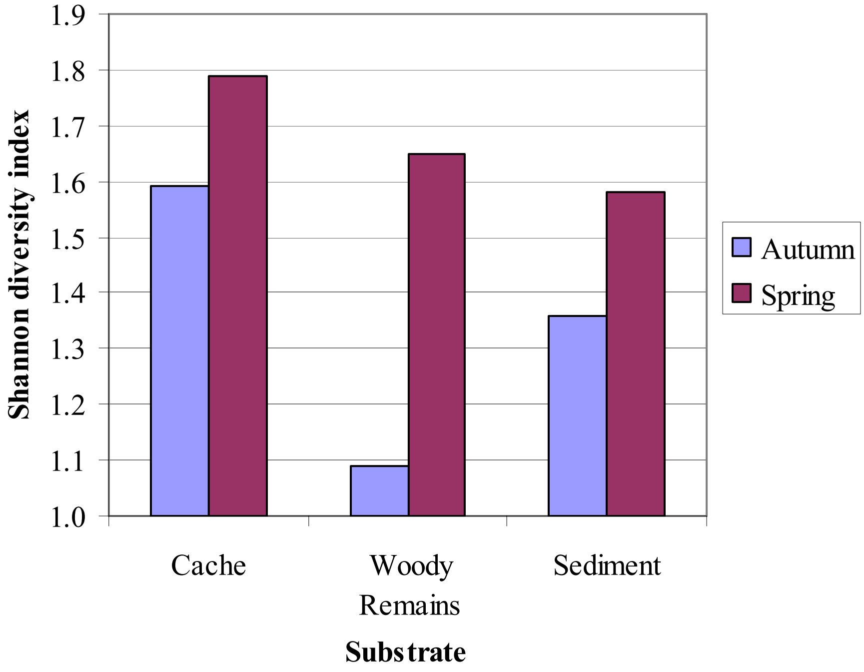
The macroinvertebrate communities on the woody remains and sediment were very similar in terms of overall number of species present per feeding guild, with the exception of the greater importance of shredders on the woody remains. Examination of the data for all three substrata by Kruskal-Wallis test however, showed that only the difference in number of predatory species was significant. *Post-hoc* pairwise Mann-Whitney tests revealed that the species richness of predators on caches was significantly higher than on both woody remains (*P*<0.01) and sediment (*P*<0.05), whilst there was no significant difference between woody remains and sediment (*P*>0.05). Figure 7.16 shows the overall macroinvertebrate species richness per feeding guild on the three substrata.

Figure 7.16 Overall macroinvertebrate species richness per feeding guild on three substrata including caches (N=6 for each substrate). Abbreviations: Coll Filt = Collector-Filterer, Coll Gath=Collector-Gatherer.



Calculation of the overall Shannon diversity indices (*H'*) for each substrate showed great seasonality on all three substrata, with highest diversities evident in spring. Seasonal pairwise comparisons of *H'* values for each substrate showed that the macroinvertebrate communities on caches were significantly greater than on either woody remains (*P*<0.001) or sediment (*P*<0.05) in autumn, and also in spring (*P*<0.001 in both cases). In autumn the diversity of sediment samples was significantly greater than woody remains (*P*<0.001), but this situation was reversed in the spring although not significantly so (*P*>0.05). Figure 7.17 shows the seasonal Shannon diversity indices for the macroinvertebrate communities on the three different substrata.

Figure 7.17 Shannon diversity index (*H'*) values of macroinvertebrate communities on three substrata, including caches, in two sampling seasons. (Note y-axis does not start at 0).

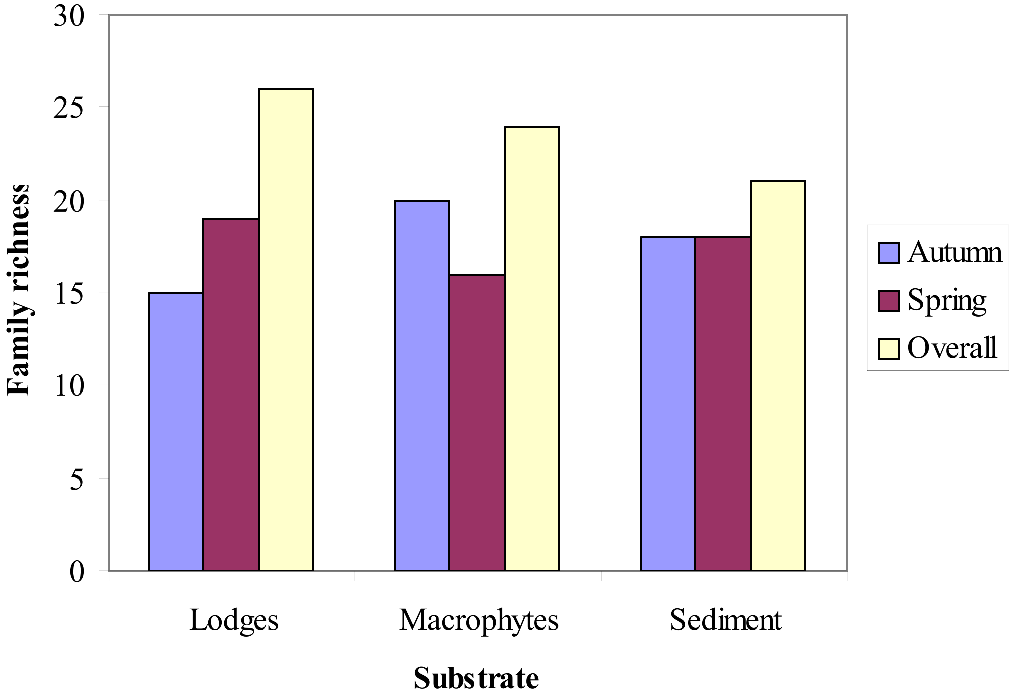


In total 48 species of macroinvertebrate were collected from 18 samples taken in the Cache study. Of these species, 15 (31%) were found only on caches, compared to 1 species (2%) found only on woody remains and 7 (15%) only on sediment. A further 11 species (23%) were ubiquitous across the three substrata. Overall, 25 species (52%) found in the study were associated only with beaver-created woody debris (*i.e.* caches and / or woody remains).

7.4.3.3 Lodges

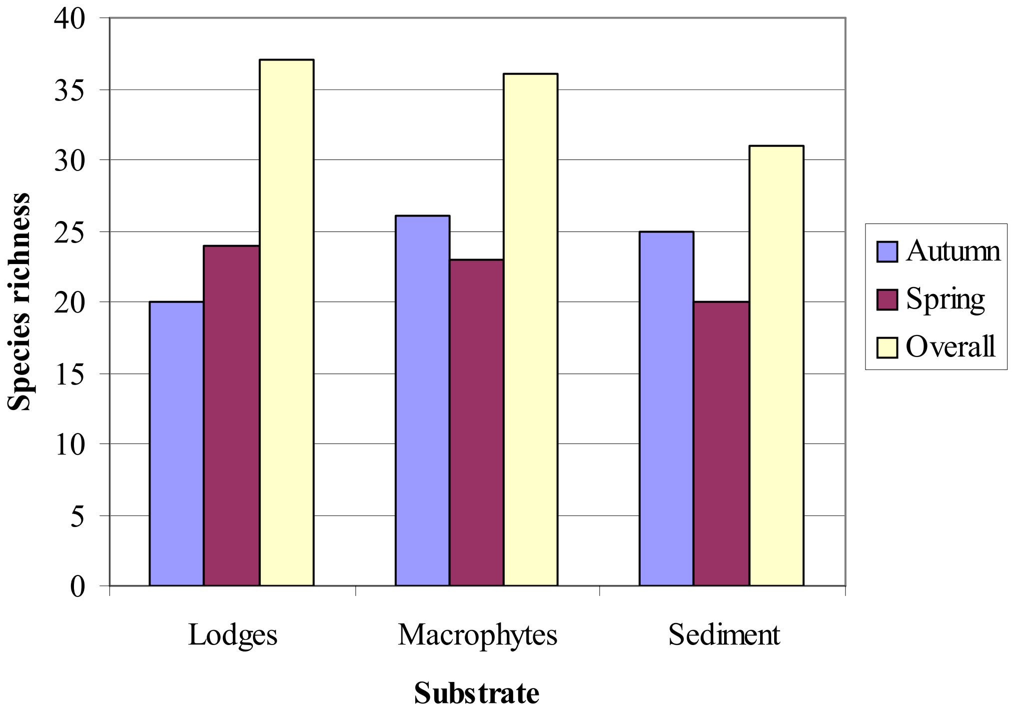
The overall total number of macroinvertebrate families present on lodges (26) was higher than on either macrophytes (24) or sediment (21), however, there was some seasonal variation in the family richness between substrata (Figure 7.18). These differences were not statistically significant (*P*>0.05), however. It is also interesting to note that the total seasonal family richness showed some variation between spring and autumn on both lodges and macrophytes, but there was little seasonal effect on sediment samples.

Figure 7.18 Total seasonal (N=2) and overall (N=4) macroinvertebrate family richness on three substrata including lodges.



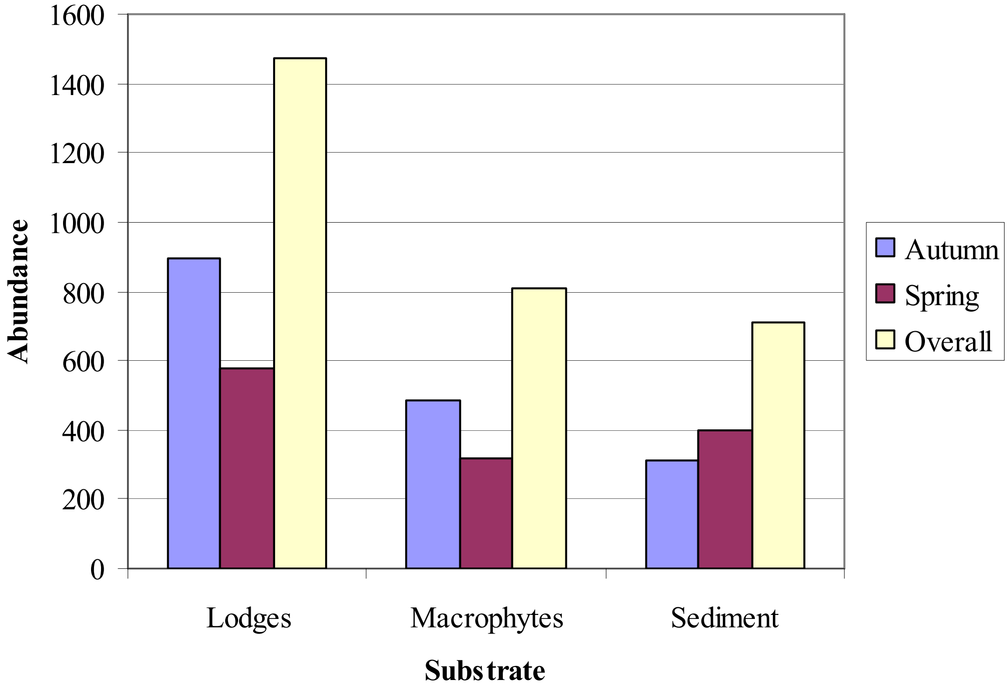
These patterns were also evident in the species richness of the macroinvertebrate communities on the three substrata (Figure 7.19), with the overall species richness of the lodges (37) being greater than on macrophytes (36) or sediment (31), although this trend was not significant (*P*>0.05). Seasonal variation in species richness was evident on all three substrata.

Figure 7.19 Total seasonal (N=2) and overall (N=4) macroinvertebrate species richness on three substrata including lodges.



The overall macroinvertebrate abundance was highest on lodges, then macrophytes, with the lowest overall abundance found on sediment, and generally the seasonal pattern also followed this trend (Figure 7.20). This trend in overall abundance, however, was not significant (*P*>0.05). The seasonal variation in abundance was marked by a decline from autumn to spring on lodges and macrophytes, with a slight increase evident on sediment.

Figure 7.20 Total seasonal (N=2) and overall (N=4) macroinvertebrate abundance on three substrata including lodges.



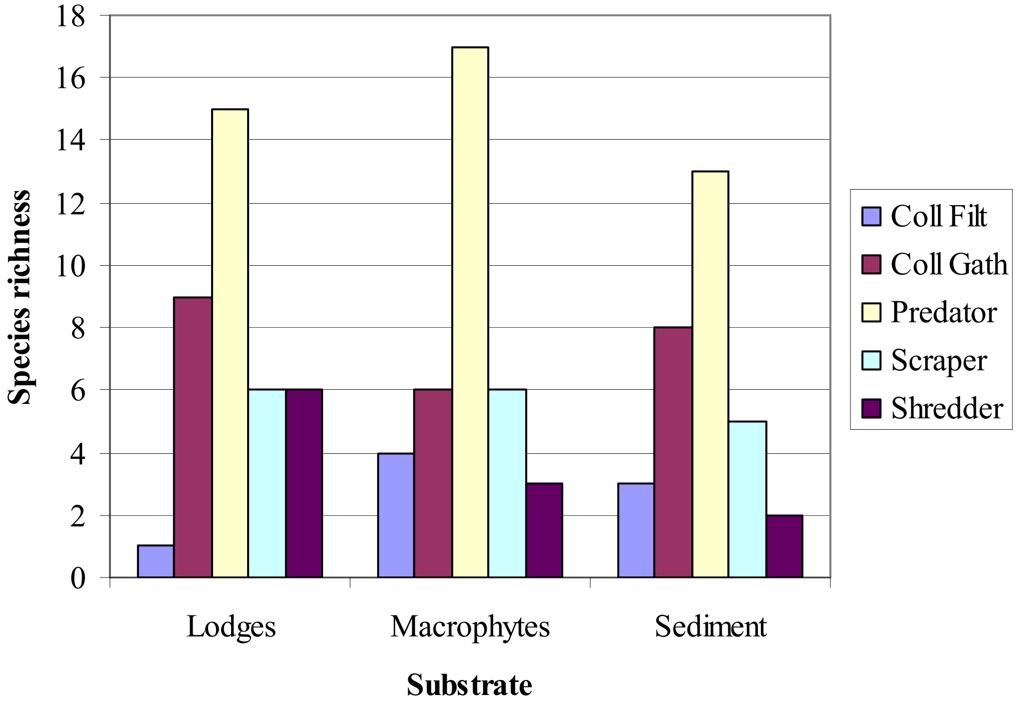
Examination of the overall number of species present in each class / order of macroinvertebrates indicated that the beetles (Coleoptera), bugs (Hemiptera), caddis fly larvae (Trichoptera) and snails (Gastropoda) were again the most species-rich taxa in the sampled substrata (Table 7.13). None of the taxa showed significant differences in species richness between substrata, however.

The macroinvertebrate communities on all three substrata were similar in terms of overall number of species present per feeding guild, with the exceptions of the greater importance of shredders and the lower numbers of species of collector-filterers on the lodges than other areas. However, examination of the data for all three substrata by Kruskal-Wallis test, showed that none of the differences in number of species per feeding guild were significant (*P*>0.05 in all cases). Figure 7.21 shows the overall macroinvertebrate species richness per feeding guild on the three substrata.

Table 7.13 Overall macroinvertebrate species richness per class / order on three substrata including lodges.

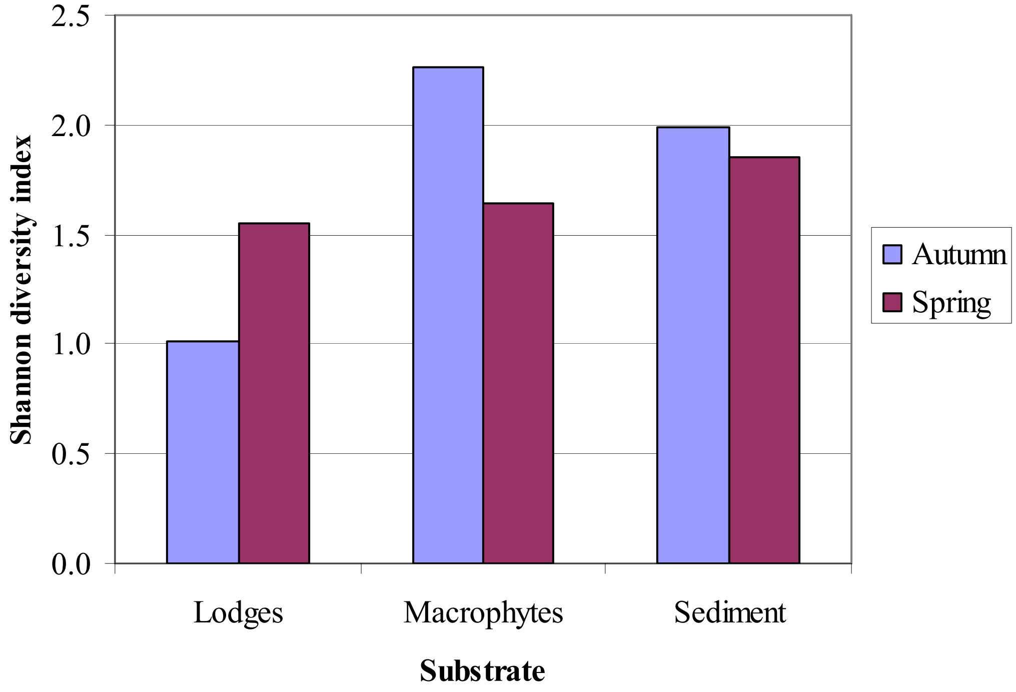
Class / Order		Lodge (N=4)	Macrophytes (N=4)	Sediment (N=4)
Platyhelminthes	**Tricladida**	0	0	0
Annelida	**Hirudinea**	3	3	2
	Oligochaetae	1	1	1
Chelicerata	**Hydracarina**	1	0	1
Crustacea	**Amphipoda**	0	0	0
	Isopoda	0	0	0
	Ostracoda	1	0	1
Insecta	**Coleoptera**	8	8	5
	Diptera	3	4	1
	Ephemeroptera	0	1	1
	Hemiptera	3	4	6
	Megaloptera	1	0	1
	Odonata	1	2	1
	Plecoptera	1	0	0
	Trichoptera	6	6	7
Mollusca	**Bivalvia**	1	1	1
	Gastropoda	5	6	3

Figure 7.21 Overall macroinvertebrate species richness per feeding guild on three substrata including lodges (N=4 for each substrate). Abbreviations: Coll Filt = Collector-Filterer, Coll Gath=Collector-Gatherer.



Calculation of the overall Shannon diversity indices (*H'*) for each substrate showed seasonality on all three substrata except sediment (Figure 7.22). Seasonal pairwise comparisons of *H'* values for each substrate showed that the macroinvertebrate communities on lodges were significantly lower than on either macrophytes in the autumn ($P<0.001$), or sediment in both seasons ($P<0.001$ in both cases). In autumn the diversity of sediment samples was significantly lower than macrophytes ($P<0.001$), but this situation was reversed in the spring although not significantly so ($P>0.05$).

Figure 7.22 Shannon diversity index (*H'*) values of macroinvertebrate communities on three substrata, including lodges, in two sampling seasons.



In total 62 species of macroinvertebrate were collected from 12 samples taken in the Lodge study. Of these species, 12 (19%) were found only on lodges, compared to 13 species (21%) found only on macrophytes and 8 (13%) only on sediment. A further 8 species (13%) were ubiquitous across the three substrata.

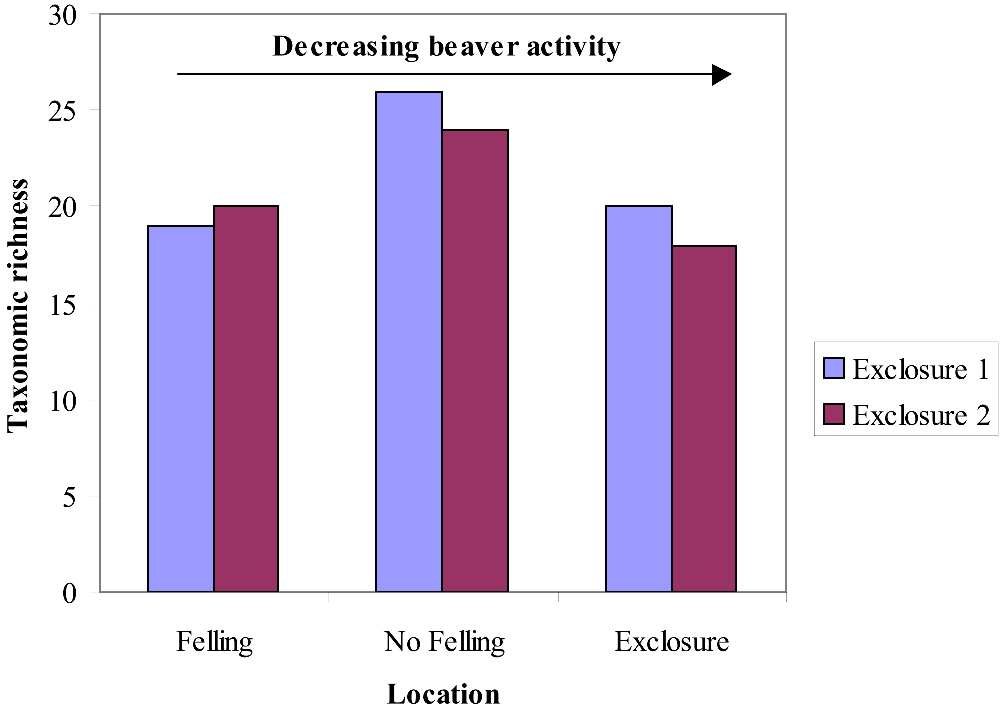
7.4.4 Terrestrial invertebrate surveys

Species lists for the pitfall trap surveys can be found in Appendix F.

In total, 19 and 20 invertebrate taxa were present in areas of heavy tree-felling (Felling) around Exclosures 1 and 2 respectively, compared to 26 and 24 taxa in unfelled areas (No Felling) surrounding the same exclosures. Inside the exclosures themselves

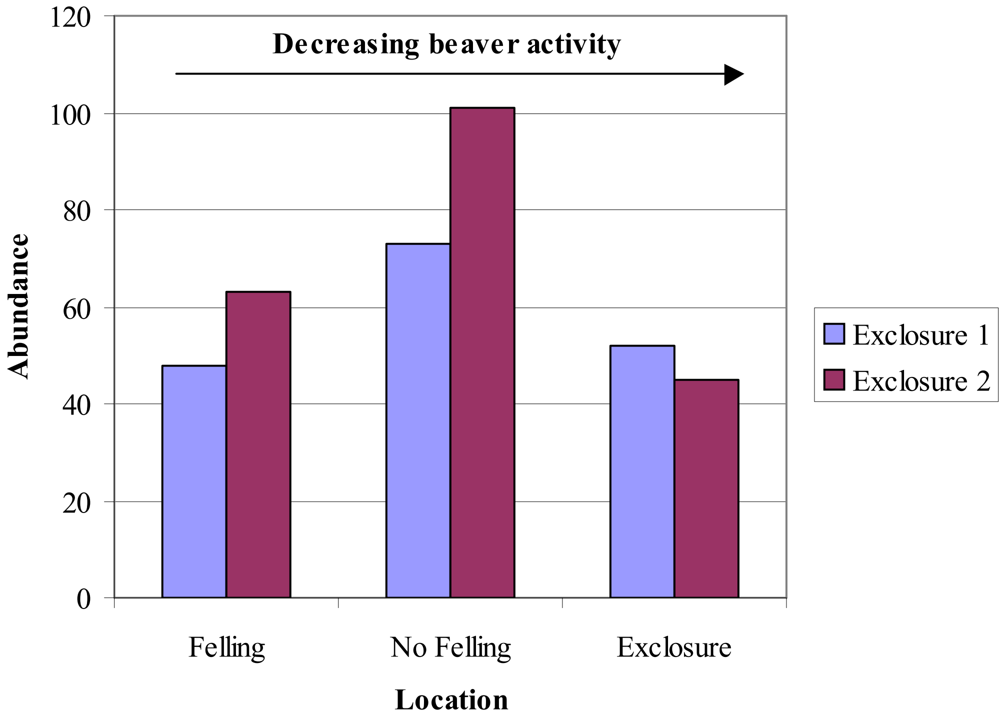
(Exclosures) 20 and 18 taxa were found in Exclosures 1 and 2 respectively. At Exclosure 1, pairwise comparisons of taxonomic richness in each location showed that the richness in the No Felling area was significantly greater than in either the exclosure or felled areas ($P<0.05$ in both cases). No significant differences were evident around Exclosure 2, although the higher taxonomic richness in the unfelled areas than in the exclosure was of borderline significance ($P=0.058$). The taxonomic richness of the invertebrate communities at different locations around the two exclosures is shown in Figure 7.23.

Figure 7.23 Taxonomic richness of invertebrate communities in three areas of differing beaver activity at the Stream Site (N=15 for each bar).



The overall invertebrate abundance was highest in the unfelled areas around both exclosures (Figure 7.24), although this trend was generally not significant ($P>0.05$). Only the pairwise comparison between the greater abundance in the unfelled area around Exclosure 2 and the lowest abundance inside this exclosure was significant (P<0.05), however.

Figure 7.24 Invertebrate abundance in three areas of differing beaver activity at the Stream Site (N=15 for each bar).



The invertebrate communities in the three locations around Exclosure 2 were very similar in terms of overall number of species present per feeding mode, with detritivores being most common followed by carnivores, whilst herbivores and parasites were less common, and fungivores completely absent (Figure 7.25b). However, the only significant pairwise comparison between the taxonomic richness of each feeding mode at each of the three locations around Exclosure 2, was the greater number of carnivorous taxa found in the unfelled area than in the exclosure (*P*<0.01). In the areas surrounding Exclosure 1, the composition of the invertebrate communities were broadly similar in the unfelled area and the exclosure, with detritivory and carnivory again the dominant feeding modes (Figure 7.25a). In the areas of heavy felling around Exclosure 1, however, four feeding modes were approximately equally common. The only significant pairwise comparison between the taxonomic richness of each feeding mode at each of the three locations around Exclosure 1, was the greater number of parasitic taxa found in the heavily felled area than in the exclosure (*P*<0.05).

Figure 7.25a Number of invertebrate taxa per feeding mode in three areas of differing beaver activity around Exclosure 1 at the Stream Site (N=15 for each location).

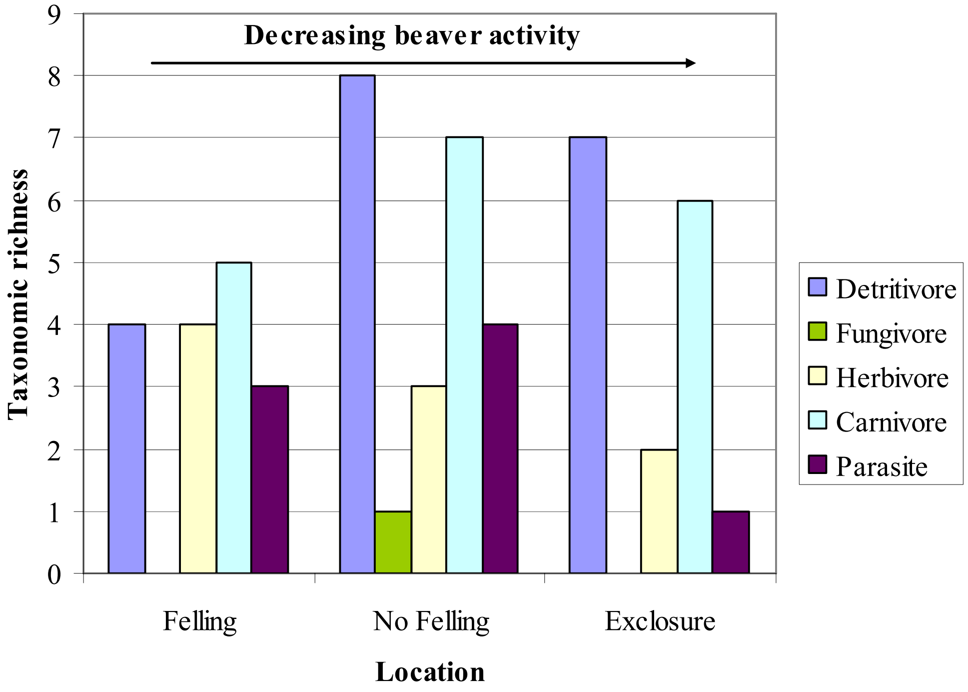
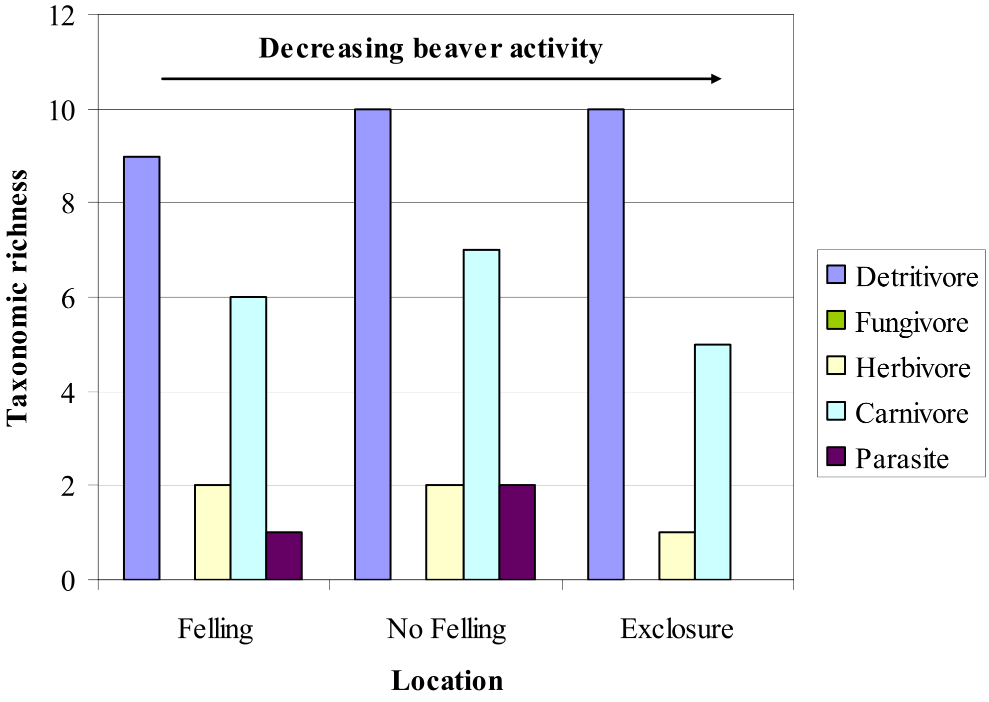


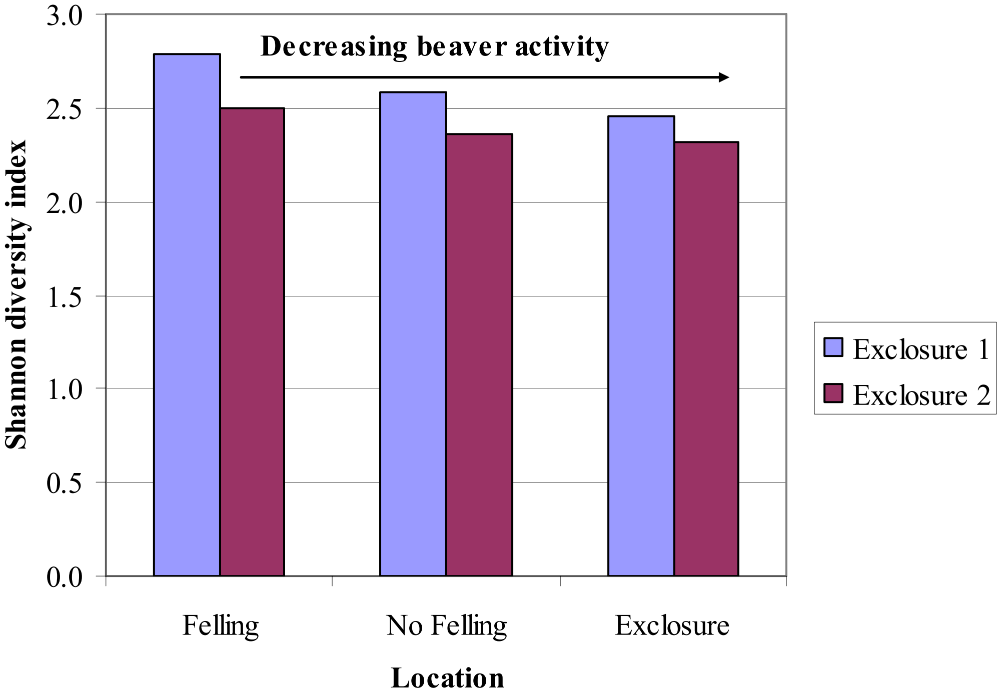
Figure 7.25b Number of invertebrate taxa per feeding mode in three areas of differing beaver activity around Exclosure 2 at the Stream Site (N=15 for each location).



The Shannon diversity indices (*H'*) for each location around both exclosures showed that the greatest invertebrate diversity occurred in the heavily felled areas, followed by the unfelled areas, with lowest diversity within the exclosures themselves (Figure 7.26). Pairwise comparisons of *H'* values for each location around both exclosures generally showed that any differences in diversity were not significant ($P<0.05$). The higher diversity index calculated for the heavily felled area around Exclosure 1 than within this exclosure, however, was of borderline significance ($P=0.052$).

A total of 49 invertebrate taxa were collected from 90 pitfall traps within and around two exclosures at the Stream Site. Of these taxa, 9 (18%) were found only in the heavily felled areas, compared to 12 taxa (24%) found only in the unfelled areas and 4 (8%) only within the exclosures themselves. A further 15 taxa (31%) were ubiquitous across the three different location types.

Figure 7.26 Shannon diversity index values of invertebrate communities in three areas of differing beaver activity surrounding two exclosures at the Stream Site.



7.5 Discussion

7.5.1 The effects of tree-felling and herbaceous grazing by beavers on woodland plant communities

Gaps in woodland tree canopies are created by the tree-felling activities of beavers in a similar manner to that caused by other natural disturbances, such as windthrow, tree senescence, wildfire and dieback due to herbivory or disease, as well as anthropogenic harvesting of trees by foresters. Such gaps can markedly alter the environmental conditions at the level of the forest floor, when compared to those under undisturbed closed canopies. The most obvious difference is an increase in light intensity at the herb layer (*e.g*. Collins *et al*., 1985 *op. cit*. Miller, 1969), which is even evident during the leafless periods of autumn and winter under deciduous trees (Collins *et al*., 1985 *op. cit*. Geiger, 1965). In coppiced woodlands, the midsummer light levels have been recorded as being approximately twenty times greater than under intact canopies, compared to a four-fold increase in spring (Fuller & Warren, 1993).

The creation of canopy gaps also leads to increased soil temperature (Ash & Barkham, 1976) and increased soil moisture (Collins *et al*., 1985 *op. cit*. Minckler & Woerheide, 1965), whilst reduced competition from trees in newly-created gaps leads to greater availability of nutrients to the herb layer (Parsons *et al*., 1994). It is important to note, however, that in gaps created by the felling activities of beavers (and artificial coppice), the trees will still be competing for nutrients as the rootstock remains intact and the tree survives. A variety of environmental conditions and habitats therefore develop when a closed tree-canopy is opened up, which has concomitant effects on the floral communities present in canopy gaps. Whilst sapling growth is encouraged by thinning of the canopy (Runkle & Yetter, 1987), the species richness of the ground flora is also often increased by gap creation (Nash Suding, 2001). Furthermore, the forestry practice of coppicing is well-known for creating a herb-rich understorey that is suppressed under intact tree canopies (Fuller & Warren, 1993).

Indeed, disturbances, such as gap creation, are one of the key factors in structuring plant communities according to the current theory of species richness (*e.g*. Grime, 1979; Begon *et al*., 1996). However, as well as creating canopy gaps, beavers have the potential to further affect the composition of woodland vegetation communities by selectively grazing on herbaceous species during the spring and summer months, feeding upon a wide-range of non-woody species (*e.g*. Kitchener (2001) documents some 149 non-woody species in the diet of beavers). It could be expected, therefore, that the species richness of the herb layer communities in canopy gaps created by beaver felling activity, allied to the effects of herbaceous grazing, would be higher than under intact canopies or areas with no beavers (*i.e.* Hypothesis 7.1).

At the Stream Site at Bamff, the species richness was indeed higher outside the beaver-proof exclosures than inside them, although this relationship was not significant. A similar trend was evident when considering the Shannon diversity indices of the sampled areas. The mean cover of herbaceous species, grasses and bare earth were all higher outside the exclosures, whilst the tree canopy was significantly reduced in the presence of beavers. This suggests that the beavers did encourage a more diverse herb layer to develop, primarily through the creation of gaps in the tree canopy, so Hypothesis 7.1 is accepted.

It is worth noting, however, that the survey methodology did vary slightly between the exclosures and the areas surrounding them. Although the area sampled by the quadrats was identical for each treatment (32 m^2 inside and outside each exclosure), the quadrats inside the exclosures formed a single large area, compared to four smaller areas outside each exclosure. It is common to find increased species richness with increased sampling effort (*e.g.* Magurran, 1988), and the potential influence of different soil conditions, for example, on the plant communities is greater when sampling more locations. In other words, the higher species richness outside the exclosures could be an artefact of the experimental design rather than as a result of beaver-induced changes in the vegetation. As two of the three exclosures (Exclosures 2 and 3) were specifically sited in the centre of areas of approximately visually uniform herbaceous communities, it is anticipated that this effect has been minimised and the overall results are valid.

Alternative methodologies would also have had potential problems, however. For example, if a single large contiguous area was sampled adjacent to the exclosures, analogous to the method employed inside the exclosures, the selection of an "identical" patch of vegetation would be crucial. This problem could be avoided by using four large sample areas, each covering the same area as that within the exclosure, located adjacent to each side of the fencing (in effect, a scaled-up version of the method used in this study). However, this would create two further problems – firstly higher species richness outside the exclosures should be expected as four times the area would have been sampled than inside the exclosures, and secondly the time taken to survey the areas would also increase prohibitively.

When the ground layer communities were compared between areas of different magnitude of disturbance following beaver tree-felling, it was evident that species richness and diversity were lowest where felled trees are left *in situ*, with highest values in nearby unfelled areas. Intermediate richness and diversity were observed in areas where felled trees had been removed from the site of felling by beavers. At first viewing, these results appear to contradict those obtained from within and outside the exclosures at the same site (although again, no results were significant). However, some caution must be used in comparing the results as a considerably smaller number of quadrats (30) were taken than in the exclosure study (576), and sampling was only conducted in late-summer, rather than in both late-spring and late-summer.

Closer inspection of the data revealed that the cover of herbaceous species was actually highest of the three areas in the presence of felled trees (intensive beaver activity), and lowest in the unfelled areas, with grass species showing the opposite trend. Nettles also thrived in the presence of felled wood, presumably at the expense of grasses. Such an association of nettles with deadwood has been noted in other studies (*e.g*. Olsen, 1921) and has been attributed to higher nitrogen and moisture content of the soil – both requirements of *Urtica dioica* - in these locations possibly resulting from the decomposition of the felled wood. The decreased cover of nettles in the "clear-felled" areas could be a result of the mechanical damage caused to the tall-growing plant by the beavers processing and removing large sections of wood from the area. It is possible that this disturbance not only flattened existing nettle plants, but also exposed areas of bare earth to be colonised by opportunistic grass and herbaceous species present in the seedbank. It is also possible that the beavers returned to the felled areas during the spring and summer to feed on non-woody material, perhaps due to a perceived lowered risk of predation. Beavers commonly feed on nettles (*e.g*. Kitchener, 2001), and given the dominance of the species throughout the Stream Site, any effects of beaver grazing is most likely to be evident with this species.

There was also evidence that the architecture of the herbaceous communities had been altered by the felling and feeding activities of the beavers. In the areas surrounding the exclosures the vegetation was significantly shorter than under the closed canopy of the exclosures. Whilst this is likely to be due in part to the reduced cover of tall species (predominantly nettles) and the increasing importance of low-growing herbaceous species, as mentioned above, it is also possibly a result of beaver grazing of the taller species. As no area of non-woody grazing was obvious anywhere at the Stream Site and direct observation of feeding activity not conducted, the true impact of spring / summer grazing by beavers on sward height remains untested.

In summary, the results support Hypothesis 7.1 that beaver activity (tree-felling and possibly non-woody grazing) encourages the development of a more species-rich herbaceous community than would otherwise be present. It is possible that this effect would be more apparent in sites with lower soil-nitrogen levels, as one of the benefits of the canopy gap formation, that of increased light intensity at the ground layer, is likely to have been limited somewhat by the rapidly growing rhizomatous nettle “canopy” that develops at the Stream Site. It is also probable that the herbaceous communities have not yet fully-exploited the beaver-created disturbance, and that diversity will increase with time. For example, Fuller & Warren (1993) state that herbaceous communities often require 2 – 3 years after coppicing of tree canopies to reach peak growth and cover. Furthermore, it is possible that the dominance of nettles will decline through time, due to the effects of growth limitation caused by increased light levels in the felled areas (*e.g.* Olsen, 1921). It seems likely that the effects of beavers grazing on non-woody vegetation would also be more apparent in the presence of a larger population of study animals. For large periods of this study only one beaver was present at the Stream Site, and the population never exceeded two animals – a wild colony would generally contain 4 – 8 animals (*e.g.* Kitchener, 2001; Müller-Schwarze & Sun, 2003).

The effects on species richness observed at the Stream Site can only be attributed to the creation of canopy gaps and grazing on non-woody plants by beavers. Any increases in the level of the watertable due to other beaver activities that were not apparent at the Stream Site, such as damming of streams or direct inundation of riparian woodland, would also add to the disturbance of the vegetation community and potentially increase the species richness and diversity. In one study, a 33% increase in herbaceous plant species richness was found in well-developed beaver-modified (*i.e.* dammed and felled) riparian areas compared to riparian areas without beavers (Wright *et al.*, 2002). Finally, this study has only considered floral diversity and richness, but the provision of felled deadwood in areas of beaver activity is likely to act as a substrate for colonisation of fungi and lichen (*e.g*. Humphrey *et al*., 2002), as are any areas of bare earth created during felling. It seems likely, therefore, that increased diversity and richness of fungal and lichen communities would also occur in areas of beaver activity.

7.5.2 The effects of the feeding activities of beavers on macrophyte communities

Many studies have reported on the succession of vegetation that occurs as beaver ponds develop and wetland areas are formed, leading to increased species diversity within the new heterogeneous habitats (*e.g*. Naiman *et al*., 1986; 1994; Johnston & Naiman, 1987; Sturtevant, 1998). Indeed, in the Upper Volga region of Russia, it has been said that "beaver activity, contributing to the expansion of wetland ecosystems, is now a major factor in the maintenance and increase of the biodiversity of vegetation cover" (Bobrov & Chemeris, 2001). The focus of these studies generally falls on the hydrological and geomorphological changes that result from beavers impounding streams, and the rate of succession can be rapid. For example, beaver ponds in Minnesota, USA, were estimated to encompass almost their entire potential species pool within 40 years (Ray *et al*., 2001), compared to timescales of over 200 years required for ponds in the UK to reach maximum species richness in the absence of beavers (Ray *et al*., 2001 *op. cit.* Hutchinson, 1975). At the Lake Site at Bamff, the beavers occupy a well-developed loch system which has shown little apparent water-level fluctuations during the three years of study, and any effects of the beavers on the hydrology and geomorphology of the habitat is assumed to be minimal.

Beaver-induced disturbances have been seen to elicit changes in the ground flora communities of woodlands (section 7.5.1), through the creation of canopy gaps and possibly by selective grazing on herbaceous plants. Both of these methods of disturbance are also relevant to the activities of beavers within ponds, and will potentially affect the composition and diversity of macrophyte communities within these waterbodies. For example, one study showed that an increase in the abundance and diversity of macrophytes in Danish lakes occurred as a response to beavers creating gaps in the riparian tree canopy (Elmeros *et al*., 2003). Furthermore, although it is acknowledged that herbivory can play an important role in altering macrophyte communities through selective grazing (*e.g*. Lodge, 1991), previous studies have focussed on the effects of grazing by moose (Belovsky, 1981), freshwater snails (Sheldon, 1987) and geese (Kerbes *et al*., 1990). The possible importance of the role of herbivory in structuring macrophyte communities in beaver ponds has largely been ignored by previous studies. Hypothesis 7.2 therefore stated that changes in the species composition and diversity of macrophytes would result from the selective grazing of beavers.

At Bamff, the species richness of macrophyte communities was generally slightly higher in all three habitat types (emergent macrophytes, open water and sedge swamp) outside the beaver-proof exclosures than inside. Unlike the terrestrial exclosures at the Stream Site, none of the Lake Site exclosures are likely to have been affected by beaver-created gaps in the riparian woodland, as they were located either well-away from the shoreline or under intact coniferous canopy. The changes in species richness are therefore attributed to the effects of selective grazing by beavers, as the gaps created by removal of favoured species are exploited by rarer species that have previously been restricted by interspecific competition. This is also reflected in the higher species diversity observed outside the exclosures in the emergent macrophytes. However, the more species-poor open water and sedge swamp habitats show little change in diversity, possibly as a result of there being comparatively fewer species adapted to these habitats present in the loch ready to take advantage of gaps created by the grazing of beavers. Also the existing species are naturally clonal dominants with existing below-ground structures that can refill gaps quicker than new species can colonise them.

Closer examination of the communities within the three habitats showed some interesting results. In the emergent macrophytes, bottle sedge (*Carex rostrata*) increased in mean cover in the presence of beavers, whilst yellow flag (*Iris pseudacorus*) decreased. Both of these species dominated the emergent zone, and being rhizomatous (Stace, 2001) are well-suited to rapidly colonise any gaps in the substrate. It would appear that the beavers are grazing on iris to a greater degree allowing the sedge species to increase cover. This would support the observations made on the beavers' dietary selection of macrophytes at the Lake Site (section 4.7), in which remains of iris were abundant whilst those of sedges were extremely rare.

One species commonly present as remains at beaver feeding stations was bogbean (*Menyanthes trifoliata*), so if this assertion that the food choices of beavers are affecting the composition of macrophyte communities is valid, it would be reasonable to expect some noticeable decline in cover of this species too. Indeed, results from the sedge swamp habitat support this assertion, with bogbean showing a significant decrease in the presence of beaver, whilst *C. rostrata* again showed no significant change in percentage cover.

Another species that has been observed in feeding remains is water horsetail (*Equisetum fluviatile*), although to a considerably lesser extent than either iris or bogbean. In the open water of the loch, the cover of this species was greater inside the exclosures than outside, although no effect of difference was evident in the sedge swamp. It is perhaps possible that this lower abundance outside the deep-water exclosures is due to mechanical damage caused by the erection of the exclosures themselves. Horsetail is more delicate and susceptible to breakage than iris and bogbean (*pers. obs*.), and the exclosures in the open-water involved the most difficulty to install and hence probably impacted most greatly on the vegetation. It is proposed that the community changes in the more robust emergent macrophytes and sedge swamp are responses to beaver grazing pressure, whilst those (minor) changes observed in the open water communities are artefacts of the experimental procedure only. This is in part supported by a study in the Florida Everglades of damage to wetland communities by repeated visits by researchers, which found little evidence of alteration to the species composition or abundance in emergent plants or floating mats of vegetation (Wolski *et al*., 2004). However, this study did not investigate the possible impacts on deeper water macrophyte communities.

Further support for the high preference of beaver for iris comes from the evidence of localised feeding on this plant *inside* one of the exclosures (Exlcosure 1) in the emergent habitat, shortly after the completion of the fences. It is worth noting that community changes outside the exclosures in the emergent zone were still observed despite this short-term interference in the experiment. It also suggests that the beavers may have been following paths through the macrophytes made during the construction of the exclosures, perhaps through curiosity or simply ease of travel. The possibility that researchers can increase the attraction of herbivores to surveyed plants has been postulated elsewhere, and termed the Herbivore Uncertainty Principle (Cahill *et al*., 2001). Some studies have found evidence supporting this theory (*e.g*. Cahill *et al*., 2001) whilst others have not (*e.g*. Schnitzer *et al*., 2002). At Bamff, there was only the aforementioned obvious incidence of beavers following a man-made path through the macrophytes, whilst numerous feeding platforms and trails through the vegetation existed in other areas of the loch. The observed changes in macrophyte communities at Bamff are therefore thought to be due to beavers feeding naturally.

In terms of structural effects on the sedge swamp and emergent macrophytes, no significant differences in vegetation height were observed inside or outside the exclosures, although there was a tendency for the vegetation to be slightly shorter outside. Furthermore, whilst the evidence suggests that localised changes in macrophyte communities have resulted, which could be attributed to grazing of herbaceous species by beavers, there was no noticeable change in species cover in any of the three habitat types over three years when viewed in the larger context of the whole site. The only patches of vegetation in which grazing was obvious tended to be small (*c*. <2 m^2) and scattered throughout the site. Again, it is possible that larger populations of beavers than those at the Lake Site (two animals during the study), could potentially have a more noticeable impact on the vegetation structure. This should be tempered however, with the unusually high pressure that the emergent macrophytes (especially the apparently preferred iris) are under at Bamff, as herbaceous material is believed to be fed upon for much of the year, not just during spring and summer. This was indicated by the absence of woody caches at the Lake Site and the abundance of iris rhizomes in late-winter / early-spring that showed signs of beaver grazing (section 4.7). One of the reasons for the rejection of the Knapdale trial reintroduction was the potential for negative impacts on macrophyte communities to occur (see Appendix A2). From the results of a two-year investigation at Bamff, these fears seem unfounded as no significant deleterious effects of grazing have been apparent, and despite some slight localised positive effects, no noticeable changes in the macrophyte communities across the whole site have occurred.

In summary, slight changes in species composition were observed in emergent macrophytes and the sedge swamp. The nature of these changes, with preferred food items such as iris and bogbean having decreased in cover outside the exclosures, suggests that selective grazing by beavers could be influencing these communities. The possible role of beaver-created gaps in the riparian tree canopy has been eliminated as an influencing factor. It is known, however, that simply enclosing vegetation can influence species composition, as "edge effects" are created (precautions against such effects were taken in the terrestrial vegetation exclosures at the Stream Site) and such effects are likely to have greatest influence in small exclosures, such as those used at the Lake Site. For example, the structure of the fences could provide some shelter from wind or wave action, which given the small size of the exclosures could be important. However, in these affected communities in which it has been proposed the effects of beaver grazing are apparent, the preferred species (iris and bogbean) are both structurally very robust. It seems unlikely that the exclosures offered any significant protection to these species (except from grazing beavers) and edge effects will have been minimal.

In the open water community, however, changes in the percentage cover of the more delicate species present there, could certainly be attributed to exclosure artefacts, such as edge effects or (as mentioned earlier) damage during exclosure construction. Although the general trend in this community was for increased percentage cover inside the exclosures, the lack of any great evidence of grazing on the constituent species through feeding remains, suggests that these trends were due to factors related to the exclosures, not beavers. Due to the uncertain role of exclosure artefacts on the emergent macrophytes, open water and sedge swamp communities, Hypothesis 7.2 has been cautiously accepted, although it is acknowledged that further investigation is necessary to fully validate this hypothesis.

7.5.3 The effects of construction work by beavers on macroinvertebrate communities

The construction activities of beavers can potentially affect macroinvertebrate communities in streams and ponds in several ways. Firstly, hydrological and geomorphological processes can be altered in watercourses by beaver dams, producing a range of environmental conditions and habitat types (*e.g.* Naiman *et al*., 1986; Pringle *et al*., 1988; Butler, 1991; Rolauffs *et al*., 2001; Rosell *et al*., 2005). Much work has been conducted on the numerous fluvial effects of beaver dams – Hammerson (1994) lists 21 environmental changes in streams caused by beaver dams - and are summarised in the excellent review of Gurnell (1997). Secondly, as well as dam-building, other beaver activities can affect the physical and ecological characteristics of streams and ponds. Felled riparian trees may form the basis of incomplete debris dams in streams, whilst caches, lodges and feeding remains act as accumulations of coarse woody debris in both lotic and lentic systems. The potential for beavers to create aquatic patches and increase habitat and species diversity is therefore great, and Hypothesis 7.3 predicted that beaver constructions would lead to increased macroinvertebrate diversity.

Beaver dams create lentic habitats at the expense of riffles or glides, with the upstream community shifting from rheophilus species to lacustrine species (*e.g.* Sprules, 1941; McDowell & Naiman, 1986; Harthun, 1999; Rosell *et al*., 2005 *op. cit*. Margolis *et al*., 2001). This is supported by the data collected at the Stream Site dams at Bamff, which showed lowest LIFE scores immediately upstream of dams, characteristic of communities dominated by taxa common in slow-flowing waters. It was interesting to note that the LIFE score immediately downstream of the oldest dam was higher than that obtained in reference conditions downstream of the dam, a trend not reflected by the other two Stream Site dams. It is unable to be determined from the data, however, whether this is related to the age of the dam or just a site-specific artefact. Sprules (1941) showed that the structure and abundance of macroinvertebrate communities changed over the first year of impoundment upstream of a beaver dam, but as no samples were taken from immediately downstream of the dam any temporal patterns caused by the dam are unable to be determined.

It is also possible that the higher LIFE scores found immediately downstream of the oldest dam than at reference conditions further downstream, are a result of the influence of taxa present on and within the structure of the dam itself. When sampling immediately downstream of all dams, the dam itself was partially disturbed, so it is likely that some invertebrates present on the dam or within its interstices were dislodged and washed downstream into the collected sample. A study of the invertebrate fauna of beaver dams showed that rheophilous taxa accumulate on the structure of the dam, whilst more lentic species were found in downstream reference conditions and in the pond (Clifford *et al*., 1993). It seems reasonable to assume that the development of such a specific dam fauna would take time to develop, and the presence of these taxa immediately downstream of the dam would be most evident in older dams. It may therefore be the case that in future years, as all the Stream Site dams age and develop rheophilous fauna on their structures, higher LIFE scores would be recorded immediately downstream of all the dams.

It was evident that the macroinvertebrate communities were generally more species rich, abundant and diverse immediately downstream of beaver dams, than in either unaffected reaches or immediately upstream of the dams. Furthermore, these changes were most marked in older dams (approximately 2 - 3 years old) than in the youngest dam (*c*. >6 months old). Other studies have recorded densities of invertebrates in beaver ponds 2 - 5 times greater than in riffle sections of the affected stream in spring and summer (McDowell & Naiman, 1986). This apparent disparity could be due to the unusual nature of the dammed streams at Bamff, which are generally narrow and shallow under low flow, with high steep-sided banks limiting lateral flooding of riparian areas. The only dam that has resulted in such flooding is the youngest dam, and again it is possible that in future years increased invertebrate densities will also develop upstream of this dam, in common with some of the published data.

The observed trends in macroinvertebrate community composition, in terms of species richness per feeding guild, only partially reflect those observed in other studies. For example, the low relative importance of shredders in beaver ponds noted by Margolis *et al*. (2001, cited in Rosell *et al*., 2005) is only evident in the Lake Site. The impoundment at the Lake Site (albeit not originally produced by beavers) is by far the oldest pond of those sampled at Bamff, and is perhaps a more accurate reflection of the communities observed in the well-developed beaver impoundments reported in Margolis' study. Other studies noted that collector-gatherers and predators were the most important feeding guilds found in beaver ponds (*e.g*. McDowell & Naiman, 1986), and this is again only evident in the older pond at the Lake Site at Bamff, with the younger Stream Site ponds having lower than expected richness of collector-gatherers. Such taxa feed on fine particulate organic matter (FPOM) derived from sediment or through the action of shredders comminuting coarser particles (CPOM) such as leaf litter. It seems reasonable to expect this food source to increase with time, as sediment and leaf litter accumulate in ponds, so the apparent paucity of gatherers in the Stream

Site ponds could be a reflection of their young age. Another study showed similar community structures in beaver ponds and downstream of dams (Clifford *et al*., 1993), which is evident at the Stream Site dams. However, this particular study also noted the low importance of shredders, except on the dam structure itself, which was not reflected either upstream or downstream of any of the four Bamff dams. Clifford *et al.* (1993) showed that over 90% of the fauna present on the dam structure itself consisted of Simuliidae and Chironomidae, which is evident to some degree at Bamff. For example, 97% of all Simuliidae present in the Stream Site samples were found immediately downstream of a dam, and are likely to have been dislodged from the dam during sampling. Finally, shredders, gatherers and predators were reported to be the most common feeding guilds present in abandoned beaver ponds (Hodkinson, 1975), which is reflected in the data for the well-developed pond of the Lake Site.

As well as alterations to hydrology and geomorphology caused by dams, other beaver constructions act as a source of coarse woody debris in streams and ponds. Beaver caches, lodges, woody feeding remains and even the structure of dams themselves, provide a food source and refuge for macroinvertebrates. The importance of woody debris in aquatic systems and the roles it plays in geomorphology, hydrology and community ecology are well-documented (*e.g*. Gurnell *et al*., 1995; Linstead & Gurnell, 1999; Gregory *et al*., 2003; Harmon *et al*., 2004). However, few researchers have focussed on the effects that beaver-created woody debris has on the macroinvertebrate communities in watercourses by providing food and shelter.

The importance of abandoned beaver lodges in structuring macroinvertebrate communities in macrophyte-impoverished rocky-shored lakes has been documented previously, with higher macoinvertebrate taxonomic richness and abundance observed on beaver lodges than any other littoral habitat (France, 1997a). The data gathered at Bamff suggest that lodges play a similar role in lakes with abundant marginal macrophyte growth. Higher species richness and abundance of macroinvertebrates were present on and around beaver lodges than within either well-developed emergent macrophyte beds or sediment / unvegetated lake margins. However, the Shannon index values were significantly lower on lodges than either other substrate. This index accounts for the evenness (E) of the community (*i.e.* how equally abundant the taxa are) as well as the taxonomic richness, with high diversity being characterised by both high richness and evenness (Magurran, 1988). In the case of macroinvertebrate communities on the lodges, the species richness is high, but examination of the data showed that Chironomidae were present in disproportionately high abundances (*i.e.* low evenness of the community), and this was undoubtedly responsible for the low Shannon index observed on the lodges. Indeed, the lower evenness of the lodge data (E=0.102) than either the macrophyte or sediment habitats (E=0.272 and E=0.227 respectively) was confirmed by specific testing of the data (Buzas and Gibson's evenness measure). The community shift around lodges towards increased numbers of collector-gatherers and shredders suggests that they are providing a source of CPOM and FPOM which is unavailable in other marginal habitats. The coniferous woodland that dominates riparian areas at the Lake Site produces low allochthonous CPOM inputs to the loch (*e.g.* leaf litter), and much of this input would be recalcitrant conifer needles. The results of Margolis *et al.* (2001, cited in Rosell *et al.*, 2005) differ from those obtained around the Bamff lodges by demonstrating a low relative importance of shredders in beaver ponds, despite often high inputs of CPOM, although it is unknown whether lodges were specifically sampled.

The construction of caches within the ponds of the Stream Site also led to increased macroinvertebrate diversity, with the highest species richness, abundance and Shannon index values recorded on caches. The number of species feeding on CPOM (shredders) in the community was approximately the same as on the stripped woody debris and unvegetated areas of the ponds, although the relative importance of collector-gatherers and predators was greatest on caches. This would suggest that the CPOM input from the deciduous canopy surrounding the ponds was sufficiently high as to not be limiting the richness of shredders in the community, and that further inputs in the form of cached woody material had little apparent benefit. However, the supply of FPOM from the cached wood appears to have allowed collector-gatherers to thrive, whilst the matrix of wood provides abundant refugia for ambush predators and their prey. It might also have been predicted that the rough surface of the cache material, when compared to the smoother surface of the debarked woody remains of beaver feeding, would facilitate epiphytic growth (*e.g.* Nilsen & Larimore, 1973), which could be exploited by macroinvertebrates adapted to feed on it (scrapers). However, the importance of scrapers is generally unaffected by the provision of either caches or stripped woody debris in the ponds, which supports work conducted on macroinvertebrate colonisation of woody debris in Canadian lakes (France, 1997b).

In summary, beaver-created woody debris at both Bamff sites has led to a general increase in macroinvertebrate diversity and abundance, and Hypothesis 7.3 is accepted. Of a total of 163 taxa present in 53 samples, 30% were found only in “beaver-affected” sites (*i.e.* immediately upstream or downstream of a dam, or on caches, woody feeding remains and lodges), compared to 26% which were present only in “beaver-unaffected” sites (*i.e.* reference reaches of streams, macrophyte beds, unvegetated lake banks and unvegetated areas of ponds). Following the reintroduction of beavers to Denmark, the taxonomic richness of macroinvertebrates on colonised streams increased from 71 to 81 taxa in just four years (Elmeros *et al.*, 2003). The importance of beaver activities may well have proved even greater if indirect effects on marcroinvertebrates are generated by selective grazing of macrophytes at Bamff.

Only the influence of beaver constructions on aquatic invertebrates has been considered in this section of the thesis, but some effects on terrestrial invertebrates have also been observed. For example, the importance of the emergent woody "cap" or "raft" of caches to the life-cycle of certain fruit flies (*Drosophila spp.*) has been reported (Spieth, 1979). Also, the macroinvertebrate community can be indirectly affected by the terrestrial activities of beavers. Selective felling of riparian tree species can lead to changes in the composition of leaf litter input to streams and ponds, which leads to changes in the macroinvertebrate species assemblages that utilise this CPOM as food (Bailey *et al.*, 2003). It is also apparent that as well as providing spatial habitat heterogeneity, the dynamic nature of beaver constructions introduces temporal heterogeneity, as lodges are enlarged, ponds and meadows develop upstream of dams, and caches are used and replenished. The physical nature of each structure will also vary, providing different habitats and food sources for macroinvertebrates. For example, dams and lodges are characterised by woody material that is well-consolidated with sediment, whereas caches and feeding remains (at least in the short term) are open matrices of wood, providing a much greater surface area for invertebrate colonisation.

Beaver-created coarse and fine woody debris has been estimated to contribute over 50% of the allochthonous inputs to boreal forest streams in Canada, a figure that the authors believe to be a gross underestimate (Naiman *et al.*, 1986). At Bamff, the role of beavers as an agent of woody debris transfer to streams and ponds is likely to be considerable.

Together with increases in macroinvertebrate diversity and abundance associated with these inputs, similar benefits have been reported in amphibians (*e.g.* France, 1997a; Balčiauskas *et al*., 2001), fish (*e.g.* Hägglund & Sjöberg, 1999; Collen & Gibson, 2001), reptiles (*e.g.* Metts *et al*., 2001), birds (*e.g.* Danell & Sjöberg, 1982) and mammals (*e.g.* Sidorovich, 1991). An excellent review of the interactions of beavers with other fauna is provided by Rosell *et al*. (2005).

7.5.4 The effects of tree-felling by beavers on terrestrial ground invertebrate communities

It seems reasonable to assume that the changes in the woodland herbaceous plant communities observed at the Stream Site (section 7.5.1), as a result of the increased habitat heterogeneity caused by the tree-felling and feeding activities of beavers, will lead to increases in the diversity of the ground invertebrate fauna (*i.e.* Hypothesis 7.4). The mosaic of vegetation created, in terms of both species composition and structure, should provide a greater range of physical habitats, microclimates and food sources to be exploited by woodland invertebrates. To a certain extent, this was the observed result at the Stream Site. Both the taxonomic richness and abundance of the ground-active invertebrates were greatest in the areas open to beavers, and in which no felling had occurred but it was assumed some herbaceous grazing had taken place. This assumption is believed to be valid as beaver trails leading from the lodge to (and through) the sampled areas of woodland were present in spring and summer. The taxonomic richness and abundance in both the exclosures and the heavily-felled areas were approximately the same. These results can be interpreted in two diametrically opposing ways.

Firstly, the invertebrate abundance and richness may have increased in unfelled areas that beavers have access to for grazing on herbaceous plants. This increase would be attributed to changes in the species composition and vegetation structure caused by beavers grazing on non-woody plants. The opposing view is that the invertebrate abundance and richness in unfelled areas may have remained static, whilst heavy felling and / or the construction of exclosures had led to decreased richness and abundance in the other two habitats. Whilst it is impossible to determine from the data whether heavy felling was detrimental to ground invertebrate communities in this way, it seems unlikely that the construction of exclosures has had any influence on the results. The exclosures were constructed in March 2003, whilst the pitfall surveys were conducted in September 2004, which should have allowed the generally highly mobile ground invertebrates ample time to recolonise the area after any anthropogenic disturbance has ceased.

The taxonomic diversity of the invertebrate communities, as represented by Shannon diversity index, showed a different trend, however, with the highest diversities being evident in the heavily felled areas and lowest values in the exclosures. As discussed previously (section 7.5.3), this index accounts for the evenness of the community as well as the taxonomic richness (Magurran, 1988), and consequently should provide a more accurate representation of taxonomic diversity than taxonomic richness alone. In the light of these considerations, therefore, Hypothesis 7.4 is accepted, and tree-felling and herbaceous grazing activities do appear to increase the diversity of the ground invertebrate fauna.

There is evidence of community change having occurred in the heavily-felled areas which showed the lowest richness of detritivorous taxa. This is possibly a result of lowered leaf litter input in these areas compared to the intact canopies of the exclosures and unfelled areas, which could also be responsible for the observed lower richness of predators in this area. It is worth considering that only the ground-active invertebrates have been considered in this study, and that other invertebrate groups may show similar (or greater) increases in diversity in beaver-affected woodland. For example, the abundance of felled wood in heavily-felled areas provides a refuge and food source for a wide-range of saproxylic (*i.e.* deadwood dependent) invertebrates (*e.g.* Ratcliffe, 1993; Stevens, 1997; Humphrey *et al*., 2002). A study in Denmark, however, found no notable changes in the diversity of deadwood invertebrates in beaver-cut wood (Elmeros *et al*., 2003), although no details of the amount of deadwood present at the sites prior to reintroduction of beavers are given. At the Stream Site, the amount of fallen deadwood in the woodland created by means other than beavers is very low, so beneficial effects of beavers on invertebrate communities are likely to be most pronounced in the saproxylic taxa, many of which are nationally scarce or threatened (*e.g.* Humphrey *et al*., 2002). As many of these species (*e.g.* wood-boring insects) are unlikely to have been captured by the pitfall traps used to sample the ground-active invertebrates, the true benefits of tree-felling by beavers on woodland invertebrates is likely to have been underestimated in this study. Furthermore, coppiced woodlands are often characterised by a high diversity of flying insects, such as butterflies and moths, which again would not be sampled successfully by pitfall traps (Fuller & Warren, 1993). Further studies at Bamff could indicate that the apparent decline in litter-dwelling detritivorous species, and carnivorous species that prey on them, is balanced or even outweighed by an increase in deadwood-dependent detritivores and their predators.

The use of pitfall traps to sample invertebrate communities has numerous limitations, which are summarised by Southwood & Henderson (2000). For example, catches will often be influenced by species, sex, weather conditions, vegetation cover and trap size / location, as well as by population size. The most active species with a large range (*e.g.* carabid beetles) will inevitably be over-represented compared to less active taxa (*e.g.* molluscs) (*e.g.* Topping & Sunderland, 1992 *op. cit.* Baars, 1979). In summary, even accounting for the limitations of pitfall traps and the focus of the methodology on ground-active invertebrates only, the effect of tree-felling and herbaceous grazing by beavers is to increase the diversity of the woodland ground-invertebrate fauna. Furthermore, it is anticipated that such effects would be more pronounced should other woodland invertebrate communities (*e.g.* saproxylic fauna) be sampled, and a variety of sampling techniques utilised (*e.g.* sweep-nets and suction sampling).

7.5.5 Summary

Four hypotheses were tested at the Stream and Lake Sites, in order to investigate the effects of beaver felling, construction and feeding activities on the biodiversity of terrestrial and aquatic fauna and flora. These hypotheses proposed that floral and faunal diversity would increase in areas of these sites that had been modified by beavers. Generally, the results showed that such beaver activities did lead to increased local biodiversity, in terms of species richness, abundance and diversity, and all four hypotheses were accepted.

Firstly, species richness and diversity of terrestrial non-woody vegetation was found to be higher in those areas immediately surrounding beaver-proof exclosures than inside the exclosures. The mean percentage cover of both herbaceous and grass species increased outside the exclosures, as did bare earth, whilst the tree canopy cover decreased. These changes in the composition of non-woody vegetation were attributed to the creation of canopy gaps by the tree-felling activity of beavers, although the possible role of non-woody grazing was also discussed. Furthermore, in heavily-felled areas in which considerable fallen deadwood was present, the mean cover of herbaceous species and nettles increased, whilst grass cover decreased.

Similarly, the species richness of macrophyte communities in three different habitats was higher outside exclosures than inside, although a corresponding increase in species diversity was only evident within the emergent macrophyte community. Selective grazing by beavers on non-woody aquatic vegetation was believed to be the cause of the observed changes in macrophyte communities, as the effects of beaver-created canopy gaps were eliminated. The most notable changes in species composition were the decreased cover of yellow iris outside the exclosures in the emergent macrophytes, and a similar decrease in bogbean in the sedge swamp. Both species were known to be favoured by grazing beavers at the Lake Site. Despite these localised increases in species richness and diversity, however, there were no noticeable changes in the overall species composition of any of the three habitats over three years of study.

The construction of dams on streams at Bamff, and the resulting hydrological changes that occurred, led to increased macroinvertebrate species diversity, richness and abundance, which was especially marked on older dams. Furthermore, it was suggested that the structure of the dam itself also acted as a unique habitat for colonisation by macroinvertebrates. As well as hydrological effects of the construction activities of beavers on stream invertebrates, lodges, caches and woody feeding remains provide important inputs of coarse woody debris to beaver ponds. The habitat and food supply provided by this beaver-created wood also contributed to an increase in macroinvertebrate species richness, diversity and abundance. Overall, the increased habitat heterogeneity created by beaver dams, lodges and caches led to increased macroinvertebrate richness, diversity and abundance, with 30% of all species collected being present on beaver-affected sites only.

The taxonomic diversity of terrestrial ground invertebrates was highest in heavily-felled areas which incorporated some felled deadwood. Changes in the community composition were also evident in heavily-felled areas, with detritivores less common than in areas under an intact tree canopy, a factor attributed to decreased leaf litter input. Conversely, taxonomic richness and abundance were highest in those areas of intact tree canopy, in which it was assumed beavers grazed on herbaceous species during spring and summer. The possible effects of beaver activity on other types of terrestrial invertebrate communities (*e.g.* saproxylic taxa) were also briefly considered.

Finally, ecosystem engineering by beavers has been shown to have positive effects on the diversity of riparian and aquatic flora and fauna, and such benefits have been utilised by land managers and ecologists for decades, especially in the USA. Bergstrom (1985) documents several cases of beavers being deliberately introduced to degraded stream systems in order to control stream flow, soil erosion and increase the biodiversity of riparian and stream communities. Such actions not only reversed the decline of the degraded ecosystem, but also benefited livestock grazing, fisheries and recreation.

8 Discussion and conclusions: Implications of beaver activity for the landscape of Scottish river corridors, lakes and riparian margins

8.1 Summary of hypotheses tested and major findings

The Eurasian beaver has been absent from the UK for over 400 years after being hunted to extinction after centuries of persecution. The species was only saved from complete extinction by the adoption of hunting bans throughout Europe and the implementation of reintroduction schemes. Currently Britain remains one of very few countries not to restore the beaver to its natural range, despite a recent proposed trial reintroduction in Scotland. The aims of this thesis have been to investigate aspects of the ecological effects of captive beavers within Scottish sites, and to apply them to a wider Scottish context.

The overarching hypotheses of this thesis were two-fold. Firstly, and the main focus of the study, the tree-felling activities of beavers would be controlled by interactions between tree species and size preferences, and tree location. Furthermore, the felling activity would vary seasonally and between years, and could be linked to the amount of construction and caching activity undertaken by the beavers. Secondly, these felling and construction activities would serve to create a mosaic of aquatic and terrestrial habitats, which would lead to increased plant and invertebrate diversity. In the course of this thesis, eighteen specific hypotheses have been tested using data collected over a three-year period at two nearby but contrasting enclosed, semi-natural Scottish areas, each containing small populations of the Eurasian beaver. The following section reviews each of the hypotheses tested in the preceding four chapters (Chapters 4-7) and whether the collected data supported them.

8.1.1 Tree-felling rates and fates

These hypotheses are summarised in Figure 8.1.

Hypothesis 4.1 Tree-felling rates are cyclical, being initially high during the early phases of colonisation, decreasing through subsequent years, and finally increasing again as territories are expanded.

The data for both sites offered partial support for the hypothesis that tree-felling rates by beavers are cyclical. At both sites, the initial felling rate was high and fell dramatically in Year 2, as hypothesised. However, the study period of three years was shown to be too short to establish how long the “consolidation phase” of colonisation would last, and whether felling rates would again increase at the end of this phase as territories expanded. Hypothesis 4.1 could not be accepted therefore at either of the Bamff sites, and it was noted that further years of study would be required to fully test the validity of this hypothesis.

Hypothesis 4.2 Tree-felling rates are a direct product of the degree of construction work and caching behaviour exhibited by beavers.

Comparisons of the calculated annual felling rates to the observed construction and caching activities undertaken at each site showed a good relationship, with highest felling rates corresponding to periods of most intense construction and caching activity. This hypothesis was therefore accepted at both study sites.

Hypothesis 4.3 Marginal habitats (*e.g.* the Stream Site) will require the greatest degree of habitat modification, and hence exhibit higher tree-felling rates, than more optimal habitats (*e.g.* the Lake Site).

The data supported this hypothesis, with greater habitat modifications being undertaken at the Stream Site, and correspondingly higher tree-felling rates observed, than under the more optimal conditions at the Lake Site.

Hypothesis 4.4 The degree of wastage of felled trees will be low overall, but increase as distance from a beaver pond increases. As the ponds are smaller at the Stream Site than at the Lake Site, and hence the amount of woodland in close proximity to the ponds is smaller, it is proposed that wastage will be greatest here.

Wastage of felled trees was indeed found to be higher at the Stream Site than at the Lake Site, where the majority of felled trees were located within the shallow waters of the lochs. Furthermore, as the foraging distance increased at the Stream Site, the degree of wastage of felled trees increased, but only for less preferred species such as birch and alder. This trend was not evident in the felling of preferred willow trees. Despite this caveat, overall the data supported this hypothesis and it was accepted.

8.1.2 Tree-felling patterns and preferences

Hypothesis 5.1 Generic preferences will be exhibited by the beavers, with aspen and willow preferred and elder and coniferous species avoided.

These preferences were supported by the data and the hypothesis accepted. The evidence suggested that beavers forage on a wide range of deciduous species when available, despite abundant preferred species, such as willow, which was believed to be a method of achieving a balanced dietary intake.

Hypothesis 5.2 When constructing dams, proximity of trees should override species or size preferences, with trees nearest the construction site being preferred.

The selection of otherwise unpreferred tree species in close proximity to new beaver constructions, suggested that proximity was the major influencing factor in determining tree-felling patterns when building dams and lodges. In these situations, the usual generic and size preferences appear to be of secondary importance, and this hypothesis was accepted.

Hypothesis 5.3 Size preferences will be exhibited by the beavers, with small trees generally preferred over larger ones.

This hypothesis was accepted at the Lake Site, but rejected at the Stream Site. Possible reasons for this deviation from that predicted at the Stream Site were considered, although a satisfactory explanation was not found.

Hypothesis 5.4 Beavers will exploit areas near to the pond in preference to areas a greater distance away.

At both of the Bamff sites, trees nearer (or within) water were preferred over trees a greater distance from water, with relatively few trees felled further than 50 m from a pond. This hypothesis was therefore accepted at both sites. The data did suggest that resource depletion was occurring in the riparian areas of the Stream Site, with more distant resources being utilised later in the study period.

Hypothesis 5.5 The beavers will act as optimal central place foragers and felling patterns will reflect those predicted by this strategy for single-prey loaders feeding on large items.

This hypothesis was accepted at the Lake Site where the selection of trees did follow the patterns predicted by central place foraging theory. However, the unexpected size-selectivity observed at the Stream Site led to this hypothesis being rejected there. It was proposed that the behaviour of beavers in marginal sites requiring considerable modification is less likely to follow conventional foraging theory than those in optimal sites.

8.1.3 Tree regrowth rates

Hypothesis 6.1 Following felling by beavers, willow trees will show a high incidence of shoot regrowth from cut stumps and the trunks of incompletely-felled trees.

At both sites, regrowth from the cut stumps and felled trunks of willow trees was very common, as was regrowth from the trunks and bases of incompletely-felled willows, so this hypothesis was accepted.

Hypothesis 6.2 The amount of annual stem regrowth from a measured section of the trunk of incompletely-felled willows will be greater than the annual growth of stems on a similar length branch of an untouched tree.

Measurements of the annual length of stem regrowth from a standardised trunk length of an incompletely-felled willow at the Stream Site was approximately 11 times that observed from a similar length of branch within the canopy of an unaffected control tree. In addition, the number of growing shoots was approximately 6 times greater than that in control trees. These data therefore support this hypothesis, which was accepted.

Hypothesis 6.3 Deer browsing will have a greater impact on the regrowth arising from the cut stump of willow trees than that arising from the incompletely-felled willows.

Only *c*. 20% of cut willow stumps showed evidence of deer browsing on stem regrowth, compared to *c*. 80% of incompletely-felled willows, so this hypothesis was rejected.

However, it is worth noting that regrowth arising only from the bases of incompletely-felled willows was very vulnerable to damage by deer (*i.e.* where deer grazing on basal regrowth occurred it was usually severe).

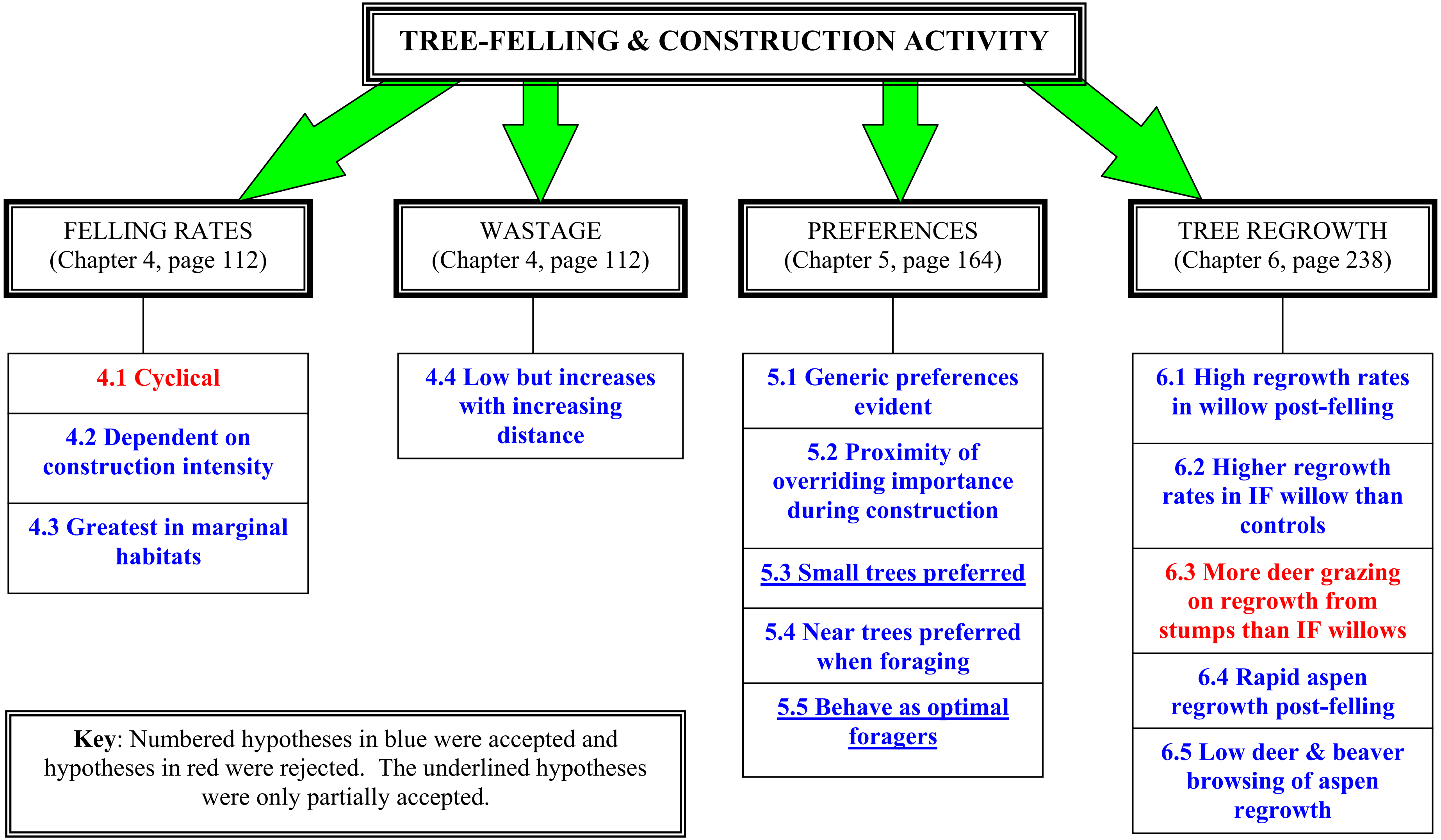
Hypothesis 6.4 Aspen trees will respond to felling by beavers by readily and rapidly suckering from the roots.

After felling by beavers, eleven mature aspen trees responded by producing an approximate total of 600 m of regrowth from 85 new suckers after two years, so this hypothesis was accepted.

Hypothesis 6.5 The incidence of beaver and deer browsing of aspen suckers will be low.

No evidence of browsing of aspen suckers by either deer or beavers was observed at the Stream Site, so this hypothesis was accepted.

Figure 8.1 Summary of hypotheses tested relating to the tree-felling, foraging and construction activities of beavers.



Key: Numbered hypotheses in blue were accepted and hypotheses in red were rejected. The underlined hypotheses were only partially accepted.

8.1.4 Diversity of flora and fauna in beaver-affected habitats

These hypotheses are summarised in Figure 8.2.

Hypothesis 7.1 The diversity of ground flora in riparian woodland will be increased, and the species composition altered, by the combined effects of tree-felling and summer grazing on herbaceous plant species by beavers.

Species richness and diversity of non-woody communities at the Stream Site were higher outside beaver-proof exclosures than inside them, whilst the mean cover of herbaceous species also increased in the presence of felled deadwood in heavily felled areas. These changes were attributed to the creation of newly formed canopy gaps by the beavers, although the possible effects of non-woody grazing were also considered, and this hypothesis was accepted.

Hypothesis 7.2 Selective feeding on macrophytes by beavers will alter the species composition and increase the diversity of aquatic herbaceous communities.

The species richness of macrophyte communities in three types of habitat within the Lake Site was found to be higher outside exclosures than inside them, although only the diversity of emergent macrophytes was increased due to be the selective grazing of beavers. However, the role of possible exclosure artefacts was discussed and could not be entirely eliminated. This hypothesis was therefore cautiously accepted, and certain macrophyte species were noted as being apparently preferred by beavers.

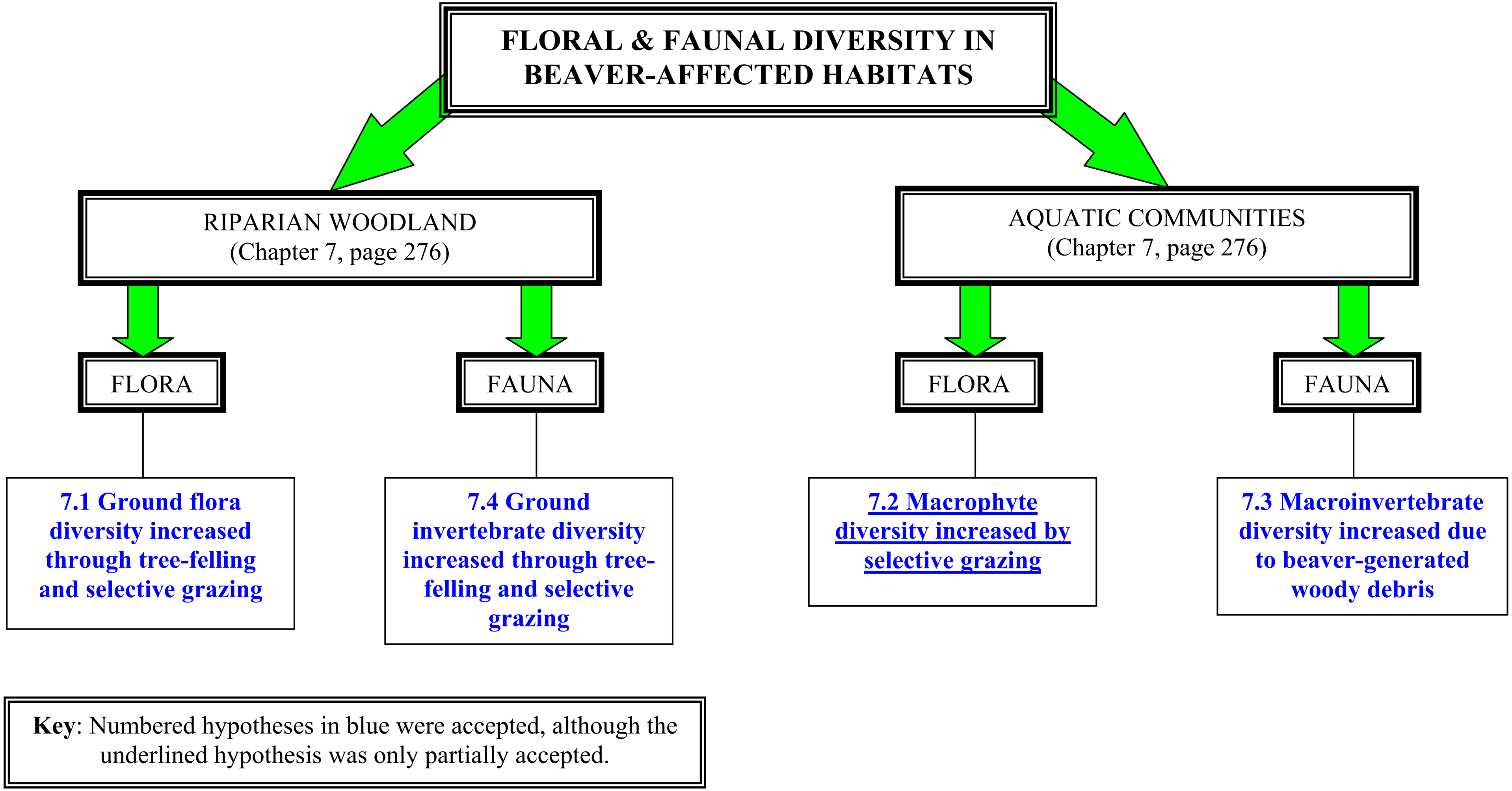
Hypothesis 7.3 Through the construction of dams, caches and lodges, the diversity of macroinvertebrate communities will increase in ponds and streams.

Changes to the hydrology of the streams at both sites caused by dams, and through inputs of coarse woody debris to ponds in the form of caches and lodges, led to increased macroinvertebrate species richness, abundance and diversity. In total, 30% of all species collected in the study were associated only with beaver-affected sites, and this hypothesis was accepted.

Hypothesis 7.4 The diversity of ground-dwelling woodland invertebrate communities will increase as a result of the increased habitat heterogeneity produced by the tree-felling activities of beavers.

The taxonomic diversity (as measured by Shannon diversity index) of ground invertebrates in the heavily-felled areas of woodland at the Stream Site was higher than any other sampled habitat. This was attributed to the effects caused by canopy gap formation, and the provision of felled deadwood. This hypothesis was therefore accepted. However, the abundance and richness of invertebrate communities was found to be highest under intact canopies that had potentially experienced non-woody grazing by beavers.

Figure 8.2 Summary of hypotheses tested relating to the diversity of flora and fauna in beaver–affected habitats.



7.1 Ground flora diversity increased through tree-felling and selective grazing

7.4 Ground invertebrate diversity increased through tree-felling and selective grazing

7.2 Macrophyte diversity increased by selective grazing

7.3 Macroinvertebrate diversity increased due to beaver-generated woody debris

Key: Numbered hypotheses in blue were accepted, although the underlined hypothesis was only partially accepted.

Through these eighteen hypotheses, the following behavioural patterns and potential ecological effects can be concluded. Over a three-year period following introduction of a small number of beavers to the two Bamff sites – the population fluctuated between three and five animals - almost 1,800 trees were felled. The intensity of felling activity varied between the two sites, with two-thirds of all felling having occurred at the Stream Site. This disparity was attributed to the more marginal habitat quality of the Stream Site, which required the undertaking of more habitat modification and construction work than at the Lake Site. For example, maximum felling rates were observed during the initial year of colonisation at the Stream Site (*c*. >300 trees / beaver / calendar year), whilst lowest rates occurred at the Lake Site during the second and third years of occupation (*c*. 55 - 70 trees / beaver / calendar year).

Whilst felling trees, beavers were shown to exhibit preferences for certain tree species, sizes and locations. Aspen and willow were highly preferred species, whilst conifers were almost totally avoided, although a number of different broadleaved species were felled when available. It is interesting to note that on the rare occasions that oak trees were felled at Bamff, they were significantly selected against by the beavers in proportion to their abundance. One of the perceived problems with a trial reintroduction of beavers to the area of Knapdale in western Scotland was potential threats to protected Atlantic oakwoods, which on the above evidence seems unlikely. In terms of size, small trees are generally preferred over larger ones, and foraging tends to occur preferentially within a short distance from ponds (generally <50 m from water). In these respects the beavers were observed to follow the principles of optimal central place foraging, and therefore be broadly predictable. However, it was noted that such optimal foraging only occurred at the Lake Site. The unexpected foraging patterns exhibited at the Stream Site were attributed to the high degree of habitat modification that took place there, with the beavers less selective in terms of tree species and proximity to the construction site being of apparently prime importance.

A further explanation for the higher felling rates observed at the Stream Site is related to caching activity. Numerous winter caches of woody material were formed in the marginal habitat of the Stream Site ponds, whilst none were observed at the more optimal Lake Site. It is believed that an abundant supply of submerged nutritious macrophyte rhizomes, plus accessible inundated live willows, provided the winter dietary requirements of the Lake Site beavers, and rendered cache production unnecessary. Many of the Knapdale lochs also contain extensive macrophyte beds (*e.g.* Murphy *et al.*, 2002), which, it is proposed, could also act as a winter food source to reintroduced beavers.

Given the observed preferences of beavers for willow and aspen, the regrowth of these trees following felling is clearly of importance. This is perhaps especially true of aspen, due to the biodiversity aspects associated with these trees (*e.g.* Cosgrove *et al.*, 2005). It was shown that both trees responded well to felling by producing abundant regrowth – willow by coppicing, and aspen by root sucker production. In the case of willow, regrowth occurred from stumps, trunks and even submerged woody caches and branches incorporated into dams and lodges, and grew rapidly and copiously despite some damage by browsing roe deer. No grazing of aspen suckers by either deer or beavers was recorded, whilst the harvesting of young willow regrowth by beavers was rare. Changes to the architecture of riparian willow groves were discussed (Chapter 6), as a more shrubby growth form was encouraged by beaver felling.

One aspect of the tree-felling activity of beavers is the apparent wastefulness that can occur, especially at greater distances from ponds at marginal sites. For example, approximately 50% of all trees felled at greater distances than *c*. 20 m from a pond at the Stream Site remained either largely or completely intact after felling. Wastage was also most apparent in less-preferred species, such as birch and alder, than in willow. These high figures at a marginal site contrast with the very low wastage of felled trees at the optimal Lake Site, where only approximately 10% of felled trees located within the shallow margins of the lochs are left largely or completely intact after felling. These differences were attributed to the effort involved in carrying woody material over large distances from marginal habitats to a pond post-felling, and the beavers adopting a more vigilant (and less effective) foraging approach at greater distances from safety.

This apparent wastefulness can have certain ecological benefits, however, as unused felled trees are a source of deadwood on the forest floor which can be exploited by specialist saproxylic invertebrate and fungal communities, many of which are of conservation importance (*e.g*. Humphrey *et al*., 2002). As well as increasing terrestrial deadwood, beaver construction activities also provide aquatic sources of coarse woody debris, in the form of caches, woody feeding remains, dams and lodges. Due to the refugia and food supply provided by these allochthonous inputs of wood to the waterbodies of both Bamff sites (as well as the hydrological and geomorphological effects of beaver dams), the diversity, abundance and richness of macroinvertebrate communities was increased. Overall, 30% of all macroinvertebrate species collected were present only in “beaver-affected” sites.

Beavers also affected the herbaceous vegetation communities in riparian woodland and the lochs of the Lake Site, by selective grazing and the production of gaps in the tree canopy. The mean percentage cover of herbaceous species increased in beaver-created canopy gaps, whilst in areas of macrophyte grazing floral richness increased. Furthermore, the diversity of ground invertebrates was highest in areas of heavy-felling, whilst invertebrate richness and abundance was highest in areas of herbaceous grazing with an intact tree canopy. Such effects of tree-felling and non-woody grazing of beavers on plant and invertebrate communities are likely to have concomitant positive effects on higher trophic levels.

The results from the Bamff study therefore show that the potential for beavers to modify their environment through construction and selective grazing is great, particularly at sites of marginal habitat quality. None of the generally perceived problems of beaver colonisation have been apparent at either site however, namely coniferous or deciduous clearfelling, macrophyte depletion, or widespread flooding of land by dams. Instead, the activities have generally led to beneficial aspects, such as increased habitat heterogeneity, increased biodiversity and rapid tree regrowth, and the beavers have lived up to their roles of “keystone species” and “ecosystem engineers”.

8.2 Implications for the wider Scottish landscape

8.2.1 Issues surrounding the feasibility and desirability of reintroducing beavers to Scotland

In Chapter 1.8 of this thesis, the issues pertaining to the feasibility and desirability of reintroducing beavers to Scotland were considered. In many cases, these issues have been explored and documented by specific reports and investigations, and are outside the scope of this research. However, the contents of this thesis are directly relevant to some of the pertinent issues that should be considered prior to any future reintroduction occurring. Using the experience and knowledge gained from this research into the ecological effects of the felling and construction activities of beavers on Scottish sites, the following issues will now be considered and briefly explored.

- **Do suitable habitats for the beaver currently exist in Scotland, and if so what are the locations, sizes and connectivity of these habitats?**
- **Assuming suitable habitat exists, is a reintroduction of beavers to Scotland likely to succeed?**
- **Where should a reintroduced Scottish population of beavers be released?**

8.2.2 Knapdale Forest

The formal application for a trial reintroduction of the Eurasian beaver to Scotland at Knapdale was submitted to the Scottish Executive in January 2002 by Scottish Natural Heritage (SNH). Further information was submitted by SNH in early-2005, with the Minister for the Environment and Rural Development rejecting the proposal later the same year. The reasons stated for this decision were a perceived site-specific problem – fears of possible impacts to specially designated areas of conservation importance in Knapdale forest – and a technical matter – the legality of the proposed exit strategy (see Appendices A1 and A2). Whilst SNH presented a wealth of pertinent information to the Minister, these documents were based on the evidence of other beaver reintroductions across Europe, with predictions of the likely effects of a Scottish reintroduction being based on these reports. As beavers have been absent from the British countryside for around 400 years, the reliance on European experiences of beaver activity was understandable and unavoidable. However, this reliance has often been used by those opposed to the trial reintroduction scheme, who have suggested that the effects of beavers on the Scottish landscape might differ from those witnessed across Europe, and in view of this uncertainty no reintroduction should be permitted. The data presented in this thesis are collected observations and experimental manipulations of Eurasian beavers within Scotland. The major findings can therefore be used to complement those from studies elsewhere in Europe, in order to inform any future reassessment of the proposed trial reintroduction to Knapdale. Comparison of the findings related to the interaction between beavers and their habitat is in broad agreement with those reported in the literature elsewhere.

In order to confidently apply the findings of this study to the proposed Knapdale release site (and avoid the criticisms cited above), the habitat types occupied by the beavers at Bamff must be representative of those occurring at Knapdale. The two Bamff sites are of contrasting nature and quality, and together encompass a variety of habitats. The Stream Site is characterised by a young deciduous plantation surrounding two small ponds and a network of shallow, slow-flowing streams. The tree-canopy is predominantly composed of willow, alder and birch, although a number of other deciduous species, including aspen, and some conifers are also present in smaller quantities. Herbaceous communities are generally dominated by tall herbaceous species, especially nettles, whilst macrophytes are present in limited quantities due to the relatively small size of the ponds. The Lake Site, on the other hand, consists of a mature coniferous plantation surrounding two shallow mesotrophic lochans, with well-developed emergent, floating-leaved and submerged macrophyte communities. One of these lochans contains a large area of young willow carr, and a sedge swamp.

The Lake Site – deemed to be of optimal habitat quality for beavers – offers many of the same habitat conditions provided within the Knapdale lochs and surrounding woodland, whilst the more marginal Stream Site is similar to the habitats present in the riparian areas and instream conditions of many of the shallow streams flowing into and out of the numerous lochs at Knapdale. The Bamff sites are also similar to the Knapdale area in the estimated numbers of roe deer present, and the apparent scarcity of aspen trees, which are much-favoured by beavers and also of great conservation importance. A detailed appraisal of the habitats present at both Bamff sites and Knapdale, has been covered earlier in this thesis (Chapter 3). It is therefore the conclusion of this author, that the habitats are similar enough at Bamff and Knapdale to expect similar behavioural and ecological effects to occur at Knapdale in the event of a future trial reintroduction of the Eurasian beaver.

8.2.3 Other potential Scottish reintroduction sites

Throughout this thesis, comparisons have been made between the Bamff sites and Knapdale. This approach is justified as Knapdale was selected as the site of the recent proposed trial reintroduction of beavers to Scotland, after consideration of many sites and numerous ecological, economic and socio-political factors (see Chapter 1.8 for full details). Although this thesis has concluded that it is unlikely that a trial reintroduction of beavers would cause damage to the qualifying interests of the Taynish and Knapdale Woods SAC, whilst other ecological benefits are likely, the choice of site for any future reintroduction proposal may be focussed elsewhere. It is therefore prudent to briefly consider other Scottish sites that could form part of any future plans to release Eurasian beavers to Britain. Even if Knapdale was again selected as the site of any future trial reintroduction, a consideration of other sites would be beneficial in the event of the trial being successful and a full release across numerous Scottish sites being granted by the Scottish Executive. In this case, a list of favoured release sites would increase the chances of a full reintroduction being successful, when judged both in terms of a surviving and thriving population of beavers, and minimising conflicts with human interests.

As detailed in Chapter 1.8 of this thesis, numerous sites across Scotland were identified as potentially suitable for a trial reintroduction of beavers. Several studies commissioned by SNH (as the proposers of the trial reintroduction scheme) investigated the relative merits and disadvantages of many of these sites, by ranking and comparing them according to many factors (*e.g*. Macdonald *et al*., 1997; Webb *et al*., 1997; Carss *et al*., 1999; Daniels *et al*., 2000). Although detailed descriptions of these studies and the areas assessed by them are beyond the scope of this thesis, certain catchments and regions consistently received recommendations for consideration as candidates for a reintroduction of beavers by the various authors. In general, the studies suggest that the Dee / Don, Ness, Spey and Tay catchments and the Lomond region contain abundant suitable beaver habitat, and that a reintroduction of beavers to these areas would be both feasible and successful.

In particular, the catchments of the Rivers Glass, Farrar and Beauly in the west of the Ness drainage basin are ranked as the best of 13 assessed areas that are believed to be very suitable for beaver colonisation (Carss *et al*., 1999). Further testament to this assessment is the fact that a small number of captive beavers at Aigas in the Beauly area are thriving and breeding successfully (Aigas, 2007). Loch Insh and Insh Marsh in the upper Spey catchment have also been identified as being extremely suitable for beaver colonisation (Macdonald *et al*., 1997; Parker *et al*., 2000), as have the Rivers Tummel and Garry in the Tay catchment (Webb *et al*., 1997; Carss *et al*., 1999; Macdonald & Tattersall, 1999). Finally, in one study the Lomond region was selected as the most suitable for beaver colonisation (Webb *et al*., 1997), with especially good habitat present on Loch Katrine (Carss *et al*., 1999). As an example, Webb *et al*. (1997) attributed a "suitability score" of 33.6 to the Lomond area, compared to 4.1 for the Argyll region, which includes Knapdale. However, the Lomond area has been largely ignored by other researchers investigating the suitability of Scottish sites for a beaver reintroduction, for reasons that are unknown to this author.

This comparison between Lomond and Argyll (and therefore Knapdale) raises an interesting issue – namely that ideal sites for a trial reintroduction may not be well-suited to a subsequent full reintroduction scheme. The assessment of the suitability of catchments or areas for beaver colonisation includes the potential for dispersal of a beaver population within (and outside of) that area, as well as considerations of habitat quality and availability. In terms of a *trial* reintroduction scheme, however, the dispersal of beavers from a release site is seen as disadvantageous, and indeed one of the reasons for selecting the Knapdale site in the 2002 proposal was the natural containment of beavers that the site offered (see Chapter 1.8.3 and Daniels *et al*., 2000). This point serves to highlight the complexities of assessing and ranking "suitable" areas for beaver colonisation, with ecological factors being assessed in parallel with socio-economic issues, as well as the exact purpose of the beaver release (*i.e*. trial study or full reintroduction program).

The socio-economic and political issues that will surround any future trial reintroduction, and possible subsequent full release, of beavers to Scotland are outside of the scope of this thesis, however. In purely ecological terms, studies have suggested that there is sufficient good quality beaver habitat available in Scotland, with good landscape connectivity, to ensure that a full reintroduction would be successful (Macdonald *et al*., 1997; Webb *et al*., 1997). The numerous aforementioned studies that have assessed various sites throughout Scotland, both qualitatively and quantitatively, indicate that the habitats described in this thesis (Chapter 3) are by no means unique to Bamff and Knapdale. Indeed, they are likely to be characteristic of a wide range of riparian woodlands throughout Scotland and the wider United Kingdom, which might be considered suitable alternative sites for any future successful reintroduction of beavers. Furthermore, the Bamff research was conducted in both optimal and more marginal habitats, so the research can successfully be applied to a range of different habitats, not just those likely to be found at potential sites that have been specifically selected for their high suitability for beaver colonisation. The findings of this thesis are therefore relevant, applicable and transferable to many areas of Scotland, not just the Bamff study area and Knapdale. Overall it is the assertion of this thesis that the habitat usage and modification of riparian ecosystems in northern Britain is likely to be similar to that found in this study and the published literature on the subject.

8.3 Future work and research

All of the work conducted throughout this thesis has been based on the activities of a small number of beavers in two sites. The application of these trends and observations to a trial reintroduction of a larger number of beavers (*c*. 20 animals) to Knapdale, or indeed a wider reintroduction programme, could possibly be criticised. However, although the Bamff colonies were small, the sites occupied by them was restricted and relatively small in comparison to unenclosed natural sites, such as Knapdale. Whilst the ecological effects of more beavers might intuitively be expected to be greater than those observed at Bamff, the resources available to the beavers in larger sites would also be greater. For this reason, the behaviour and effects of the Bamff beavers are believed to be representative of larger colonies in larger sites inducing similar densities. Confirmation of this assumption would only be attained by studying the effects of larger colonies within Scotland, and this is recommended for any future reintroduction, as was intended by SNH in their plans for the trial reintroduction scheme. Indeed, it was initially intended that the study animals for this thesis would be the trial reintroduction colonies in Knapdale, which would have circumvented this perceived problem. In addition, more study sites (*e.g.* numerous colonised areas within Knapdale) would have provided a greater range of terrestrial and hydraulic conditions, in which to observe beaver behaviour. The ecological effects of beaver activity across a spectrum of sites ranging from marginal to optimal could then have been assessed, and readily applied to any future release areas.

More specific changes and improvements to the methodologies used throughout this study can also be made. For example, the preference of beavers for woody species was based upon felling surveys. However, as was discussed in Chapter 5, tree-felling occurs for feeding *and* construction, so dietary preferences could be masked in areas or periods of heavy habitat modification. The implementation of cafeteria studies was used to provide evidence of dietary preferences, but a number of different techniques proved unsuccessful. The trialling of more cafeteria methodologies would therefore be beneficial, as would direct or indirect (*i.e.* filmed) observations of beaver behaviour. In the context of a relatively short-term study such as this, however, direct observation was deemed to be overly time-consuming and care would need to be taken to ensure that the beavers were unaware of the observers and were acting naturally. The use of remote film or video cameras on the other hand would have proven prohibitively expensive, as a number of devices would have been required to cover large areas of two study sites.

Regular aerial photography could also have been employed to demonstrate and assess temporal canopy changes at the sites during the study due to beaver activity. Whilst the results may have been a useful visual aid in viewing any landscape changes that occurred, it is unlikely to have yielded more reliable results than the ground surveys of felled and available trees used in this thesis. Again, high financial costs of aerial photography would have limited its usefulness to this study. However, its use in monitoring other larger areas could be advantageous and supplement more restricted field surveys. A further alternative would be to monitor the movement patterns of the beavers, by trapping the animals and fitting radio-tracking devices to them.

Future avenues of study that would complement this research include extending the biodiversity investigations to include saproxylic communities of invertebrates and fungi on felled and standing deadwood created by beavers. The concomitant effects of beaver activity on woodland and riparian mammals and birds could also be investigated, as could any effects of aquatic constructions, such as dams and lodges, on amphibians and fish. Many of the members of these faunal groups are of great conservation interest or functional importance through top-down controls on freshwater and riparian ecosystems, and the effects of beavers on these organisms could therefore be extremely important.

A further improvement to the methodologies used in this thesis would be to extend the time-span from the initial years of colonisation, or to study established colonies of different ages. Neither was possible during this study due to the fixed time-scale of the research and the lack of mature beaver colonies in the UK. Increased timescales would allow patterns of behaviour (*e.g.* felling rates) or environmental responses (*e.g.* tree regrowth rates) to be confirmed or amended, whilst changes in biodiversity would have greater time to be manifested. The investigation into the proposed cyclicity of tree-felling rates (Hypothesis 4.1, Chapter 4, page 115), for example, proved inconclusive and the hypothesis rejected due to the effects of the short study period. The findings were encouraging, however, and the importance of a longer monitoring period than was practical for this three-year thesis, cannot be overstated. It could even be argued that the five-year monitoring program that was integral to the proposed Knapdale trial reintroduction scheme would be insufficient to fully investigate any cyclicity of tree felling rates that may be occurring. Furthermore, the development of beaver-meadows after the culmination of many years of beaver activity, and the associated floral and faunal diversity that occurs in these habitats (as has been documented in many published studies through Europe and the USA) could be investigated given sufficiently long monitoring periods.

Finally, any future studies would benefit considerably from the collection of baseline datasets prior to colonisation by beavers. Many such surveys were conducted at Knapdale (*e.g.* Murphy *et al.*, 2002; Armstrong *et al.*, 2004) and would have proved useful if the trial reintroduction had proceeded as planned. Indeed, the surveys will prove invaluable should a release of beavers to Knapdale occur at any time in the future. Unfortunately, no baseline surveys were possible at Bamff as the beavers had already been present for up to 7 months prior to the commencement of this research project. Consequently difficulties have sometimes arisen in separating the effects of beaver-induced community changes and those occurring as part of natural variation within the sites. The transferability of the baseline data also needs to be considered. For example, the classification of the floral communities at Bamff, and indeed any other future potential release sites, using the established National Vegetation Classification (NVC) (*e.g.* Hall *et al*., 2004) system would make direct comparisons of habitats more reliable. Nevertheless, the findings of this thesis are valid, significant and provide important evidence in predicting the likely effects of beavers on Scottish freshwater systems.

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Appendices

Appendix A1 Letter of rejection of the proposed trial reindroduction of beavers to Knapdale, from the Deputy Minister for Environment & Rural Development

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1 September 2005

John Markland Esq CBE
Chairman
SNH
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EDINBURGH EH9 2AS

Mike Foulis has written to Ian Jardine today to set out the basis for Scottish Ministers' decision not to approve the application from SNH to proceed with a trial re-introduction of the European beaver to Scotland. I thought it would be helpful to you, SNH staff, your partners and other supporters of this project, as well as the public, to provide some further thoughts on how we can build upon the effort you have made in progressing this project.

I want to emphasise my appreciation of the effort which SNH, its Board Members and staff have devoted to developing this proposal in such a constructive manner. I do realise that it has taken a number of years to research, investigate and prepare for this application. Others will now be able to consider whether they want to build upon the foundations you have laid.

In my role as Deputy Minister for the Environment and Rural Development, I share with you the responsibility for addressing the needs of and threats to Scotland's habitats and wildlife. This requires both of us to have a clear focus for the work we choose to undertake in order to achieve the best value from available resources. I was therefore very encouraged to see that the SNH Board has agreed to develop a species conservation framework for Scotland and I share your wish to see priorities clearly set out and effectively managed. I have asked my officials to work closely with those in SNH who are taking forward this important work. There are already some excellent examples of our joint work on species conservation, such as our efforts to safeguard the capercaillie population in Scotland, and the Uist Wader Partnership

I must emphasise that the door is not closed to future reintroductions and I would expect part of the new strategic approach to include evaluation of possible species re-introduction, as well as work on perceived threats, including those from the introduction of invasive non-native species.

I would expect a rigorous appraisal to be made both by SNH and by the Executive of any future reintroduction proposals. Such assessments would need to scrutinise the legal, ecological and management aspects of any proposal, and where appropriate, would need to be accompanied by a well constructed business case. The biodiversity benefits which species expansion or re-introductions can bring to Scotland should be fully explored drawing upon the experience of European Union Member States and wider international knowledge.

As I see it, your proposed framework offers the real prospect of providing a strategic approach for the long-term benefit of Scotland which will help us to meet out obligations to halt biodiversity loss by 2010. In particular, it should help us to address priorities and ensure that the Executive, SNH and other partners make the best use of available resources for the benefit of Scotland and its species. I have asked my officials to keep me informed of the progress of your work on the framework.

It is right and important that SNH is placing on the policy agenda the issue of species that might benefit Scotland or are at risk. In light of the public and media interest in the SNH proposal for a trial re-introduction of the European beaver to Scotland, I am releasing this letter by means of a Press Release and through the Executive's Publications Scheme.

RHONA BRANKIN

Appendix A2 Letter of rejection of the proposed trial reindroduction of beavers to Knapdale, from a senior government official

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1 September 2005

Dr Ian Jardine
Chief Executive
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Dear Ian

I am writing to inform you that Scottish Ministers have decided not to grant SNH's application for a licence under Section 16 (4)(c) of the Wildlife & Countryside Act 1981 for a trial re-introduction of the European beaver.

In reaching this decision, Ministers took full account of all the material supplied by SNH in support of this application, in particular:

The application from SNH dated 7 January 2002 to release the European beaver, Castor fiber, for a trial re-introduction in Knapdale, Argyll.

Annex 2 of the 7 January 2002 application - Trial re-introduction of European beaver to Taynish and Knapdale Woods cSAC -"Appropriate Assessment" dated 12 December 2001.

Annex 3 of the 7 January 2002 application - Business Case for a trial re-introduction.

Letter dated 8 February 2005 from Chief Executive of SNH to Head of the SEERAD Environment Group

Appendix 1 of the 8 February 2005 letter - response to the Minister's letter of 20 December 2002

Appendix 2 of the 8 February 2005 letter -report on local consultation published 30 March 2001 SNH letter.

On the basis of the Executive's assessment across a wide range of policy issues, the conclusion is the licence should not be granted. The principal considerations which led to that decision are set out below.

Implications of Article 6 of the Habitats Directive

In his letter of 20 December 2002 to your Chairman, the then Deputy Minister for the Environment and Rural Development asked SNH to review the impact which this proposal would be likely to have upon the Taynish and Knapdale Woods Special Area of Conservation (SAC). The Minister also sought further information on whether a trial of this type was compliant with Article 6 of the Habitats Directive and I recognise that the supplementary information provided in your letter of 8 February 2005 aimed to address these issues.

The SNH analysis and appropriate assessment contained within Annex 2 of SNH's letter of 7 January 2002 made clear that the impact of the trial would be "certain not trivial" in relation to the Habitats Directive interests of Atlantic oakwoods and "certain" for aquatic plants. Together, these indicated there would be a number of negative effects upon the SAC but led SNH to conclude that a trial of this type would not be in breach of the Directive. This is not a view we share.

We have subsequently discussed with you the relevance of the recent judgment by the European Court of Justice (EC v Government of the Netherlands - the Waddenzee case) where the Court ruled that the test for considering the effects on the integrity of a European site requires there to be no reasonable scientific doubt as to the absence of adverse effects. Ministers fully accept that this ECJ judgement represents a new development. However, viewing the application in light of this judgement, and given that the appropriate assessment identifies the certainty of impact on the features for which the SAC was designated, it appears to us that there is a significant risk that a decision by Scottish Ministers to grant a licence for re-introduction of beavers to this site, could be held to be unlawful in terms of Article 6.

Consideration of Article 12 of the Habitats Directive

The release of the European beaver in Scotland would grant the species full legal protection under the Wildlife & Countryside Act 1981 in accordance with the relevant provisions of the Habitats Directive. This means that options to remove, and certainly to kill, any beaver that is either outwith the trial site or is causing more damage than might initially have been considered, as suggested in Appendix 1 of the SNH letter of 8 February 2005, are limited.

For those Member States with significant beaver populations - Austria, Sweden, Finland, Estonia, Latvia, Lithuania, and Poland - legal provisions have been made through their Accession Treaties to allow those States to remove the level of protection which the European beaver enjoyed in these countries. These measures are now reflected in the consolidated version of the Habitats Directive, which indicates willingness by the European Commission to amend the protected status of the species to reflect their high and healthy populations in certain Member States. But these circumstances do not apply in Scotland, nor has it been demonstrated in the SNH application or supplementary material how the provisions of Article 12 can be satisfied in the event that beavers re-introduced to Scotland had to be killed because of problems they posed in and around the trial site.

In short, we have identified no provision within current UK legislation or European Directives that would allow the exit strategy outlined by SNH to be undertaken in a lawful manner.

Impact upon salmon interests

It is important that the lessons of any trial can be applied across Scotland. While SNH recognises that the trial site at Knapdale does not contain a river in which Atlantic salmon are present, the justifications for selecting this site, set out in your application of 7 January 2002, was the need for natural containment which could not be met on a typical salmon river. However, this means that the site selection would leave open some important questions about the transferability of the trial results to the rest of the country as a whole, particularly given the importance of salmon fisheries for the Scottish economy. While the Norwegian salmon/beaver study quoted in the additional information supplied is informative, it is not a detailed investigation and in our view further trials in Scottish salmon streams would be necessary before any wider reintroduction programme could be sensibly considered.

The additional information relating to Salmon does not give consideration to the issue of the salmon parasite Gyrodactylus salaris (Gs). The UK is currently free of Gs and the Executive would need to be convinced that this parasite would not be introduced into Scottish river systems as a consequence of any reintroduction of beavers. A stringent quarantine process would need to be in place to ensure that the beavers would be free of the Gs parasite before they left Norway.

The Economics and Financing of the Trial

On balance, Ministers were doubtful whether the benefits of this proposal would exceed the likely costs and also questioned the relative priority of this initiative as compared with other species measures. The Deputy Minister has written separately today to your Chairman, indicating her support for your plans to develop a species conservation framework, which has the potential to help both SNH and the Executive to direct future effort to achieve the greatest beneficial effect.

CONCLUSION

After consulting with a wide range of policy interests within the Executive and recognising and appreciating the considerable effort which SNH have made in bringing forward an ambitious project, we have nevertheless concluded that your application to re-introduce the European beaver to Scotland on a trial basis at the site proposed should be refused.

Since there has been significant public interest in this proposal, this letter is being released by means of a Press Release and through the Executive's Publications Scheme.

MIKE FOULIS

Appendix B Macroinvertebrate surveys: Stream Site dams

	Autumn										**Spring**									
	Dam 1			**Dam 2**			**Dam 4**				**Dam 1**			**Dam 2**			**Dam 4**			
Species	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**
Oligochaeta spp.	0	7	0	3	0	0	0	0	0	13	183	14	12	6	33	11	1	0	0	11
Polycelis spp.	0	0	0	0	0	0	0	0	0	0	169	23	4	15	4	0	0	0	0	0
Erpobdella octoculata	0	6	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Indet. *Erpobdella spp.*	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Glossiphonia complanata	3	0	0	0	0	0	0	0	0	1	2	1	0	0	4	3	1	0	0	3
Planorbis carinatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Planorbis planorbis	0	2	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippeutis complanatus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Radix peregra	6	0	31	5	0	1	0	0	0	0	2	1	8	5	2	0	0	0	0	2
Potamopyrgus jenkinsii	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physa fontinalis	18	10	3	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0
Sphaeriidae spp.	0	0	0	5	0	3	4	0	0	50	0	0	0	5	2	34	7	1	3	2
Ostracoda spp.	21	0	0	1	0	1	0	0	0	0	5	2	0	0	0	0	0	0	131	4
Asellus aquaticus	7	58	10	41	7	2	1	0	0	24	77	64	113	44	77	3	4	1	0	43
Crangonyx pseudogracilis	0	4	0	1	5	0	0	0	0	0	80	88	162	91	11	0	0	0	0	0
Gammarus pulex	0	0	0	0	0	0	1	2	0	2	40	0	0	91	17	7	37	6	17	108
Hydracarina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Chironomidae spp.	2	5	0	2	1	4	16	3	1	52	2	9	11	27	59	12	70	69	159	125
Ceratopogonidae	1	0	0	0	0	0	0	0	0	0	4	0	0	0	1	0	0	0	0	1
Pedicia spp.	1	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	1	2	0
Elaeophilia spp.	0	0	0	1	0	0	1	0	0	0	0	0	1	4	0	8	1	0	1	0
Hexatoma spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dicranota spp.	0	0	0	1	0	0	6	0	1	0	2	0	0	0	0	3	24	0	12	1
Tipula spp.	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Simuliidae spp.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	83	0	3	0
Ptychopteridae spp.	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	4	0	0	0	0
Hemerodromia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Gyrinus caspius	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Haliplus confinis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Appendix B Macroinvertebrate surveys: Stream Site dams (continued)

	Autumn										Spring									
	Dam 1			Dam 2			Dam 1				Dam 2			Dam 1			Dam 2			
Species	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**
Ilybius spp.	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agabus sturmii	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0
Agabus paludosus	0	0	0	0	0	0	0	0	0	0	5	0	0	1	0	0	0	0	0	0
Agabus spp.	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	2	0	0
Dytiscus marginalis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Graptodytes / Stictonectes spp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hydroporus palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hydroporus pubescens	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydroporus nigrita	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Rhantus spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anacaena globulus	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3	0
Helophorus longitarsis / griseus / minutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hydrobius fuscipes	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Limnebius truncatellus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Indet. *Hydrophilidae spp.*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydraena rufipes / britteni / riparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Elmis aenea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnius volckmari	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Oulimnius spp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Helodes spp.	3	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	4	0
Plectrocnemia conspersa	0	0	0	0	0	0	1	0	0	0	2	0	0	3	4	5	2	0	15	3
Indet. *Polycentropodidae spp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	2
Drusus annulatus	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	0	1	0	0	0
Glyphotaelius pellucidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Halesus digitatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Halesus radiatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Halesus digitatus / radiatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Limnephilus centralis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix B Macroinvertebrate surveys: Stream Site dams (continued)

	Autumn										Spring									
	Dam 1			**Dam 2**			**Dam 1**				**Dam 2**			**Dam 1**			**Dam 2**			
Species	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**
Limnephilus extricatus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus hirsutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Limnephilus lunatus	0	0	0	0	0	0	0	0	0	0	6	14	22	8	0	0	0	1	0	0
Limnephilus marmoratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Micropterna lateralis	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	6	0
Micropterna sequax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	0	8	0
Potamophylax latipennis	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0
Potamophylax cingulatus / latipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
Stenophylax permistus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Indet. *Limnephilidae spp.*	1	1	0	0	0	0	0	0	0	0	1	5	2	9	7	0	2	3	1	0
Crunoecia irrorata	0	0	0	0	0	0	1	0	23	0	0	0	0	0	0	0	0	0	20	0
Beraea maurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	1	0
Beraea pullata	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	5	0	0	0	0
Baetis rhodani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Leuctra hippopus / moselyi	0	0	1	1	0	0	18	2	18	1	3	0	1	0	0	0	1	0	14	0
Leuctra inermis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Leuctra nigra	0	0	0	0	1	0	16	0	0	12	2	0	0	5	6	3	38	2	42	33
Indet. *Leuctridae spp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Nemurella picteti	3	0	0	0	13	1	0	0	11	0	43	1	0	6	6	0	17	15	301	11
Nemoura avicularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	8
Nemoura cinerea	0	0	0	0	0	0	0	0	0	0	0	1	3	22	4	0	0	1	0	0
Nemoura cambrica / erratica	0	0	0	0	0	4	10	0	12	22	20	0	0	0	0	11	5	4	130	6
Nemoura erratica	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nemoura spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	0	0	0
Indet. *Nemouridae spp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49	0	0	9	11	29
Callicorixa praeusta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Notonecta glauca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Appendix B Macroinvertebrate surveys: Stream Site dams (continued)

	Autumn										**Spring**									
	Dam 1			**Dam 2**			**Dam 1**				**Dam 2**			**Dam 1**			**Dam 2**			
Species	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**	**DS**	**US**	**REF**	**DS**	**US**	**REF**	**DS**	**US**	**REF1**	**REF2**
Gerris lacustris	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Velia caprai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sialis lutaria	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyrrhosoma nymphula	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coenagrion hastulatum	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphula nympheata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix C Macroinvertebrate surveys: Lake Site dam

	Spring		
Species	**DS**	**US**	**REF**
Oligochaeta spp.	12	13	25
Glossiphonia complanata	0	2	1
Helobdella stagnalis	0	3	0
Gyraulus albus	0	1	0
Bathyomphalus contortus	0	8	0
Sphaeriidae spp.	13	528	20
Ostracoda spp.	1	1	2
Gammarus pulex	25	0	0
Hydracarina spp.	0	3	0
Chironomidae spp.	27	2	8
Ceratopogonidae	1	1	1
Pericoma spp.	1	0	0
Hexatoma spp.	1	0	5
Dicranota spp.	1	0	5
Ptychopteridae spp.	0	0	7
Ceciomyiidae spp.	0	0	1
Hemerodromia spp.	0	0	1
Indet. *Diptera spp.*	0	0	6
Haliplus obliqus	0	1	0
Dytiscus marginalis	0	1	0
Hydroporus palustris	0	4	0
Limnius volckmari	4	0	7
Esolus spp.	2	0	0
Oulimnius spp.	0	0	2
Helodes spp.	6	0	20
Plectrocnemia conspersa	1	0	0
Holocentropus picicornis	0	1	0
Indet. *Polycentropodidae spp.*	0	0	1
Triaenodes bicolor	1	0	0
Athripsodes spp.	0	1	0
Chaetopteryx villosa	1	0	0
Beraea maurus	0	0	1
Nemoura cambrica / erratica	0	0	1
Indet. *Nemouridae spp.*	0	0	1
Sialis lutaria	1	1	0

Appendix D Macroinvertebrate surveys: Stream Site caches

	Spring									Autumn								
	Caches			Woody Remains			Sediment			Caches			Woody Remains			Sediment		
Species	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Oligochaeta spp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polycelis tenuis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erpobdella octoculata	2	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1
Glossiphonia complanata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Helobdella stagnalis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Theromyzon tessulatum	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Anisus leucostoma	13	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Planorbis planorbis	0	10	7	2	1	0	1	2	0	0	0	0	0	0	0	1	0	0
Planorbis carinatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Gyraulus albus	0	8	9	0	0	0	0	0	0	4	1	5	0	2	4	0	0	0
Gyraulus laevis	0	0	0	3	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Radix peregra	74	611	170	141	126	77	20	38	26	59	96	269	138	74	196	131	245	27
Stagnicola palustris	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physa fontinalis	8	11	1	1	7	2	2	0	1	22	13	44	2	10	26	22	31	10
Sphaeriidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ostracoda spp.	6	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Asellus aquaticus	247	18	1	48	14	3	5	7	0	53	75	226	147	67	208	102	56	79
Crangonyx pseudogracilis	130	14	1	6	4	2	2	1	0	167	170	216	32	236	183	43	41	99
Gammarus pulex	0	0	0	0	0	0	0	0	0	0	28	0	79	0	0	26	0	0
Chironomidae spp.	31	1	0	0	0	0	2	1	1	10	6	11	0	5	1	1	1	12
Chaoborus spp.	52	0	2	16	11	17	17	24	21	90	11	14	24	16	10	0	0	0
Haliplus ruficollis group	1	0	1	0	2	0	0	0	0	4	0	0	0	0	0	0	0	0
Haliplus confinis	0	1	8	0	0	2	0	0	1	0	0	1	0	2	0	0	0	0
Haliplus lineatocollis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hydrobius fuscipes	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ilybius spp.	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilybius ater	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agabus spp.	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Agabus / Platambus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Appendix D Macroinvertebrate surveys: Stream Site caches (continued)

	Spring									**Autumn**								
	Caches			**Woody Remains**			**Sediment**			**Caches**			**Woody Remains**			**Sediment**		
Species	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Agabus sturmii	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dytiscus marginalis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hydroporus palustris	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0
Limnephilus lunatus	0	0	0	0	0	0	0	0	0	6	7	11	1	8	1	5	2	6
Limnephilus auricula	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	5
Limnephilus marmoratus	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Limnephilus rhombicus	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0
Limnephilus vittatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0
Limnephilus flavicornis / marmoratus / politus / stigma	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Micropterna lateralis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Indet. *Limnephilidae spp.*	0	0	0	0	0	0	0	0	0	8	3	11	0	9	7	3	4	3
Cloeon dipterum	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemoura avicularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Sialis lutaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Indet. *Coenagriidae spp.*	0	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Hesperocorixa linnaei	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocorixa sahlbergi	0	8	0	0	0	0	0	0	0	2	1	3	1	2	8	0	0	0
Callicorixa praeusta	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sigara distincta	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Sigara dorsalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sigara semistriata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sigara selecta / stagnalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Corixa punctata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Indet. *Corixidae spp.*	44	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Notonecta glauca	0	4	0	0	0	0	0	0	0	0	1	5	0	0	0	0	0	0
Notonecta spp.	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Appendix E Macroinvertebrate surveys: Lake Site lodges

	Autumn						**Spring**					
	Lodges		**Macrophytes**		**Sediment**		**Lodges**		**Macrophytes**		**Sediment**	
Species	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**
Oligochaeta spp.	0	4	3	0	0	19	2	46	3	1	12	29
Indet. *Planariidae spp.*	0	0	0	0	0	0	0	1	0	0	0	0
Erpobdella octoculata	0	3	1	0	0	0	0	0	0	1	0	0
Glossiphonia complanata	1	3	0	0	10	3	0	0	3	2	2	4
Helobdella stagnalis	1	7	0	0	1	7	1	3	11	1	8	6
Anisus leucostoma	4	8	0	134	0	0	0	0	0	0	0	0
Bathyomphalus contortus	4	0	96	0	15	32	6	40	20	22	11	25
Gyraulus albus	0	0	0	0	0	0	0	1	0	1	0	0
Radix peregra	1	0	4	4	0	0	0	0	3	0	0	0
Stagnicola palustris	0	0	1	0	1	0	0	0	1	2	1	0
Acroloxus lacustris	3	0	0	0	1	0	0	0	1	2	4	2
Sphaeriidae spp.	172	11	19	25	8	37	106	42	10	19	3	48
Ostracoda spp.	2	27	0	0	3	2	0	1	0	0	0	1
Chironomidae spp.	11	616	54	1	124	9	275	7	118	66	62	129
Ceratopogonidae spp.	0	0	9	0	0	0	0	0	2	1	0	0
Chaoborus spp.	0	0	3	0	0	0	2	0	4	0	0	0
Dixella spp.	0	0	3	0	0	0	0	0	0	0	0	0
Ptychopteridae spp.	0	0	0	0	0	0	0	1	0	0	0	0
Limnius volckmari	0	0	0	0	0	0	0	1	0	0	0	0
Haliplus confinis	0	0	0	0	0	0	0	1	0	0	0	1
Haliplus ruficollis / wehnckei	0	0	0	3	0	0	0	0	0	1	0	0
Haliplus ruficollis group	0	0	2	0	0	0	0	0	0	0	0	0
Anacaena globulus	1	0	0	0	0	0	0	0	0	0	0	0
Hydrobius fuscipes	0	0	0	1	0	0	0	0	0	0	0	0
Agabus spp.	1	0	12	0	0	0	0	0	0	0	0	0
Ilybius spp.	0	0	0	2	0	0	0	0	0	0	0	0
Acilius canaliculatus	0	0	0	0	0	0	0	0	1	0	0	0
Acilius sulcatus	0	1	0	0	0	0	0	0	0	0	0	0
Hydroporus palustris	0	0	0	0	2	0	3	12	0	0	0	0

Appendix E Macroinvertebrate surveys: Lake Site lodges (continued)

	Autumn						**Spring**					
	Lodges		**Macrophytes**		**Sediment**		**Lodges**		**Macrophytes**		**Sediment**	
Species	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**
Hydroporus angustatus	0	0	0	0	0	0	0	0	0	0	7	0
Hydroporus erythrocephalus	0	0	0	1	0	0	0	0	3	0	0	0
Hydroporus gyllenhalii	0	0	6	0	0	0	0	0	0	0	0	0
Hydroporus incognitus	0	0	0	0	0	1	0	0	0	0	0	0
Rhantus exsoletus	0	1	0	1	0	0	0	0	0	0	0	0
Hydrocyphon spp.	0	1	0	0	0	0	0	0	0	0	0	0
Gyrinus distinctus	0	0	0	0	0	3	0	0	0	0	0	0
Athripsodes aterrimus	0	0	0	0	0	0	0	0	0	0	1	0
Athripsodes cinereus	0	0	0	0	0	3	0	0	0	0	0	0
Athripsodes bilineatus	0	0	0	0	5	0	0	0	0	0	0	0
Athripsodes albifrons / bilineatus / commutatus	0	0	0	0	0	0	4	0	0	0	0	0
Athripsodes spp.	0	0	0	0	0	0	0	0	0	0	0	6
Triaenodes bicolor	0	0	5	0	0	2	0	0	0	0	1	0
Anabolia nervosa	0	0	0	0	0	0	1	0	0	0	0	0
Glyphotaelius pellucidus	0	0	0	0	0	0	1	0	0	0	0	0
Limnephilus affinis / incisus	0	0	0	0	0	0	1	0	0	0	0	0
Limnephilus flavicornis / marmoratus	0	0	0	0	0	0	1	0	0	0	0	0
Limnephilus flavicornis / marmoratus / politus / stigma	0	0	0	0	0	0	1	0	0	0	0	3
Limnephilus rhombicus	0	0	1	0	0	0	0	0	0	0	0	0
Indet. *Limnephilidae spp.*	0	0	1	0	0	0	0	0	0	0	0	0
Holocentropus stagnalis	0	0	0	0	0	0	0	0	0	2	1	0
Plectrocnemia conspersa	0	0	1	0	1	0	0	0	0	0	0	0
Plectrocnemia geniculata	0	0	0	0	0	0	0	0	2	0	0	0
Plectrocnemia spp.	0	0	0	0	0	0	0	0	1	0	0	0
Agrypnia obsoleta	0	0	0	0	0	0	0	0	2	0	0	0
Agrypnia obsoleta / varia	0	0	0	0	0	0	1	0	0	0	0	0
Oligotricha striata	0	0	0	0	0	0	1	1	0	0	0	0

Appendix E Macroinvertebrate surveys: Lake Site lodges (continued)

	Autumn						**Spring**					
	Lodges		**Macrophytes**		**Sediment**		**Lodges**		**Macrophytes**		**Sediment**	
Species	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**
Cloeon dipterum	0	0	14	0	0	2	0	0	0	0	0	0
Indet. *Nemouridae spp.*	0	0	0	0	0	0	0	1	0	0	0	0
Sialis lutaria	2	0	0	0	3	3	2	1	0	0	0	6
Coenagrion hastulatum	0	0	48	4	1	0	1	0	0	1	0	0
Coenagrion puella	0	0	0	0	0	0	0	0	1	0	0	0
Coenagrion spp.	0	0	0	0	0	0	0	0	0	0	0	2
Indet. *Coenagriidae spp.*	0	0	0	0	0	0	0	0	3	6	1	0
Cymatia bonsdorffii	0	0	0	0	0	0	0	0	0	0	1	0
Hesperocorixa sahlbergi	0	0	7	15	2	1	0	0	0	0	0	0
Hesperocorixa spp.	3	0	0	0	0	0	0	0	0	0	0	0
Sigara dorsalis	0	4	0	0	0	3	0	0	0	0	0	0
Sigara fossarum	0	0	0	0	0	3	0	0	0	0	0	0
Sigara spp.	0	0	0	0	0	0	0	0	0	0	0	2
Indet. *Corixidae spp.*	0	1	1	0	0	0	0	0	0	0	0	0
Gerris lacustris	0	0	0	0	1	0	0	0	0	2	1	0
Notonecta glauca	1	0	1	3	1	0	0	0	0	0	0	0
Notonecta spp.	0	1	0	0	0	0	0	0	0	0	0	0
Microvelia reticulata	0	0	1	0	0	0	0	0	0	0	0	0
Hydracarina spp.	0	0	0	0	0	3	1	11	0	0	10	8

Appendix F Terrestrial invertebrate surveys: Stream Site

All figures represent the total number of invertebrates captured in 15 pitfall traps (*i.e.* 3 traps on 5 dates).

Species	**Total Abundance**					
	Exclosure 1			**Exclosure 2**		
	Felling	**No Felling**	**Exclosure**	**Felling**	**No Felling**	**Exclosure**
Indet. *Cryptostigmata spp.*	0	2	0	0	0	0
Indet. *Acari spp.*	0	3	4	0	2	0
Indet. *Linyphiidae spp.*	3	2	6	3	2	1
Melogona scutellare	0	0	0	0	0	1
Craspedosoma rawlinsii	0	0	0	0	1	0
Nanogona polydesmoides	0	0	0	0	1	0
Indet. *Carabidae spp.*	1	0	2	6	10	4
Indet. *Curculionidae spp.*	1	0	0	0	0	0
Hydroporus ferrugineus	0	1	0	0	2	0
Anacaena globulus	4	0	0	0	0	0
Indet. *Hydrophilidae spp.*	1	9	1	1	0	0
Indet. *Silphidae spp.*	1	0	0	0	0	0
Indet. *Staphylinidae spp.*	3	5	2	19	17	1
Indet. *Tenebrionidae spp.*	0	0	0	1	4	0
Indet. *Polyphaga spp.*	0	0	0	0	1	0
Indet. *Entomobryoidea spp.*	6	3	12	2	4	1
Indet. *Neelidae spp.*	0	0	0	1	0	0
Indet. *Sminthuridae spp.*	0	1	1	1	0	3
Indet. *Anisopodidae spp.*	0	0	1	0	0	0
Indet. *Cecidomyiidae spp.*	1	2	0	0	0	0
Indet. *Ceratopogonidae spp.*	1	0	0	0	1	0
Indet. *Chironomidae spp.*	0	0	0	1	0	0
Indet. *Culicidae spp.*	1	0	0	0	0	0
Indet. *Dolichopodidae spp.*	4	11	5	2	7	2
Indet. *Dryomyzidae spp.*	0	0	3	0	0	0
Indet. *Empididae spp.*	0	0	1	1	1	0
Indet. *Lauxaniidae spp.*	4	1	0	0	0	0
Indet. *Lonchopteridae spp.*	0	1	0	0	1	1
Indet. *Phoridae spp.*	3	3	0	1	1	2
Indet. *Piophilidae spp.*	0	0	1	0	0	0
Indet. *Tipulidae spp.*	1	0	0	0	0	0
Arion ater agg.	5	3	2	1	1	0
Arion spp.	0	0	0	2	0	1
Cochlicopa lubrica	0	0	0	5	12	8
Retinella radiatula	0	1	0	5	2	4
Indet. *Psyllidae spp.*	1	0	0	0	0	0
Indet. *Cicadellidae spp.*	0	3	1	0	0	0
Indet. *Chalcidoidea spp.*	0	1	0	0	0	0
Indet. *Platygasteridae spp.*	0	3	0	0	0	0
Indet. *Proctotrupoidea spp.*	0	1	0	0	0	0
Indet. *Trichogrammatidae spp.*	0	1	1	0	1	0
Trichoniscoides albidus	0	1	1	0	0	1
Cylindroiulus nitidus	0	1	0	0	0	0

Appendix F Terrestrial invertebrate surveys: Stream Site (continued)

Species	**Total Abundance**					
	Exclosure 1			**Exclosure 2**		
	Felling	**No Felling**	**Exclosure**	**Felling**	**No Felling**	**Exclosure**
Cylindroiulus punctatus	0	0	0	1	1	0
Ommatoiulus sabulosus	0	0	0	1	1	1
Ophyiulus pilosus	0	0	1	2	0	1
Indet. *Julidae spp.*	0	0	0	0	1	0
Oligochaetae spp.	4	3	1	0	1	1
Nemastoma bimaculatum	0	1	0	0	0	0
Oligolophus meadii	0	1	0	0	0	0
Oligolophus tridens	1	7	3	6	22	10
Brachydesmus superus	0	2	3	0	2	2
Polydesmus angustus	0	0	0	0	1	0
Polydesmus spp.	0	0	0	0	1	0
Indet. *Histrichopsyllidae spp.*	2	0	0	1	0	0