Felling and foraging: results of the first year of beaver (*Castor fiber*) activity in an enclosed Scottish site

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Abstract: A trial reintroduction of the European beaver (*Castor fiber*) to Scotland has been proposed and is awaiting Scottish Executive approval. Currently, no data have been published on the actual effects of beavers on the Scottish landscape, although many authors have predicted potential impacts. Such predictions have been based on the impacts of the beaver in other European countries. The aim of this study is to provide a better predictive capability as to the potential effects on tree felling immediately following beaver reintroduction by using data of beavers in captivity. In 2002, four European beavers were released into two large, semi-natural enclosures – the Willow Carr Site and the Lake Site - in eastern Scotland. This paper represents data from the first year of a three-year monitoring programme to investigate the felling and feeding activities of these beavers. In absolute terms, willow (*Salix* spp.) were the favoured species at both sites, being felled in the greatest numbers, followed by alder (*Alnus* spp.) and birch (*Betula* spp.). In terms of relative abundance, only the selections against birch at both sites, and for willow at the Lake site, were found to be significant. No size-selectivity at the Willow Carr Site was evident, but significantly smaller than average trees of all three genera were felled at the Lake Site. Decreased felling activity was observed with increasing distance from the lodge at the Willow Carr Site, whilst most trees felled at the Lake Site were situated within the shallow margins of the lakes. Approximate felling rates were 0.5 and 0.8 trees per beaver per day, at the Willow Carr Site and Lake Site respectively.

Keywords: *Castor fiber*, beaver diet, reintroduction, Scotland, feeding preferences.

Introduction

The European beaver (*Castor fiber*) was a common sight along British watercourses until the sixteenth century (Conroy & Kitchener 1996), when hunting and habitat loss finally extirpated the species from the United Kingdom (UK), and indeed throughout the majority of their natural range. Following several successful recent reintroductions of the species throughout Europe (Nolet & Rosell 1998), a trial reintroduction of free-ranging beaver from a Norwegian donor population to the Knapdale area of Scotland was proposed by Scottish Natural Heritage (Gaywood 2001). This proposal is currently awaiting Scottish Executive approval. However, a captive population of four adult individuals from natural European stock was established early in 2002 into a semi-natural environment on a privately owned estate in eastern Scotland. These beavers – three females and a single male – were placed in pairs, in two large enclosures. Here, space is presumed non-limiting and the beavers have been left largely free of human disturbance (Ramsay 2002).

The activities of beavers affect the landscape, which in turn affects the flora and fauna that share the habitat with them. The beaver therefore acts as a keystone species (Kitchener 2001). Furthermore, they have also been described as ecosystem engineers due to the direct physical mechanisms used by beavers to modify the ecosystem (Jones et al. 1994). Such physical effects on the environment include damming of streams, wetland creation, and tree felling. The foraging and feeding behaviour of the European

beaver are integral aspects to its roles of keystone species and ecosystem engineer. 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).

Whilst previous studies have modelled and predicted the extent of such potential ecological effects of reintroducing the European beaver to Scotland (Macdonald & Tattersall 1999, Rushton et al. 2000, South et al. 2000), no studies have been conducted on the actual effects of beaver activity in Scotland. Furthermore, any future reintroduction of beavers to Scotland will be subjected to very close scrutiny in the period immediately following release of the animals. 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). The studies of the reintroduced beavers in the Biesbosch area of the Netherlands offer a notable exception (Nolet et al. 1994).

The aim of this study is to provide a predictive capability as to the likely effects of beaver foraging and felling activity immediately following reintroduction into the UK, based on data gathered on captive beavers in Scotland. The preferences for certain woody species, the tree size-selectivity exhibited, and the distances foraged over by beavers in two enclosed sites in Scotland during the first year of colonisation have been investigated here. From these data, approximate tree felling rates have also been derived. This paper represents the first phase of a three-year monitoring programme.

Methods and materials

The Bamff estate is located in eastern Scotland near Blairgowrie, approximately 25 miles northeast of Perth (figure 1). Situated in the foothills of the Highlands, the estate comprises 525 ha of hills, forest and farmland, with the highest point

Figure 1. Location of the study area.

rising 425 m above mean sea level. 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.

The beavers are located in two large enclosures located approximately 0.9 km apart. The first site ("Willow Carr Site") is an area of young willow plantation and meadow of approximately 13 ha, containing two small purpose-built ponds and a network of drainage ditches (photo 1). The predominant tree species are willow (*Salix cinerea*, *Salix aurita* and *Salix caprea*), birch (*Betula pendula* and *Betula pubescens*) and alder (*Alnus glutinosa* and *Alnus incana*). In March 2002, a male and female beaver from Norway were introduced to this site. In late January 2003 the male died and was not replaced.

The second site ("Lake Site") consists of two small artificial lakes linked to each other by a short channel, surrounded by mature conifer

Photo 1. The Willow Carr Site. *Photograph: Kevin Jones*.

plantation comprised predominantly of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and European larch (*Larix decidua*), covering approximately 9 ha. Large areas of willow and birch scrub, bog vegetation and fringing macrophytes, especially yellow flag (*Iris pseudacorus*), are also present at this site (photo 2). Two young female beavers, each approximately 14 months old, were introduced to the Lake Site in July 2002 and have thrived since that date.

In early spring 2003 at the Willow Carr Site twenty 10x10 m random quadrats were used to assess tree species composition. Where possible, deciduous trees were recorded to species although in some cases some deciduous trees were only recorded to genus. The genera of conifers were not recorded. Within the quadrats the girths of all trees were measured at the point of beaver activity (approximately 30 cm up the trunk) or in the case of felled trees immediately below the cut, and the approximate distances from the nearest pond were estimated.

Similarly in spring 2003 tree composition of the Lake Site was assessed by using ten 10 m wide belt transects stretching 50 m from the lake bank into the surrounding woodland. The transects were spaced regularly around the lake margin. Again deciduous trees were recorded to species although in some cases some deciduous trees were only recorded to genus. The genera of conifers were not recorded. Within the transects girths of all trees were measured in the same way as at the Willow Carr Site. The approximate distance from the shore of all trees was also measured.

In addition, at both sites complete surveys of all cut tree girths and genera (both within and outside the random quadrats at the Willow Carr Site c.q. transects at the Lake Site) were conducted in late January 2003. The distance of all felled trees from the water's edge was also

Photo 2. The Lake Site. *Photograph: Nigel Willby*.

measured at the Lake Site during the complete survey.

The preference of beavers for a particular genus 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 random quadrats at the Willow Carr Site and the belt transects and complete survey of felled trees at the Lake Site. The index used was:

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

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:

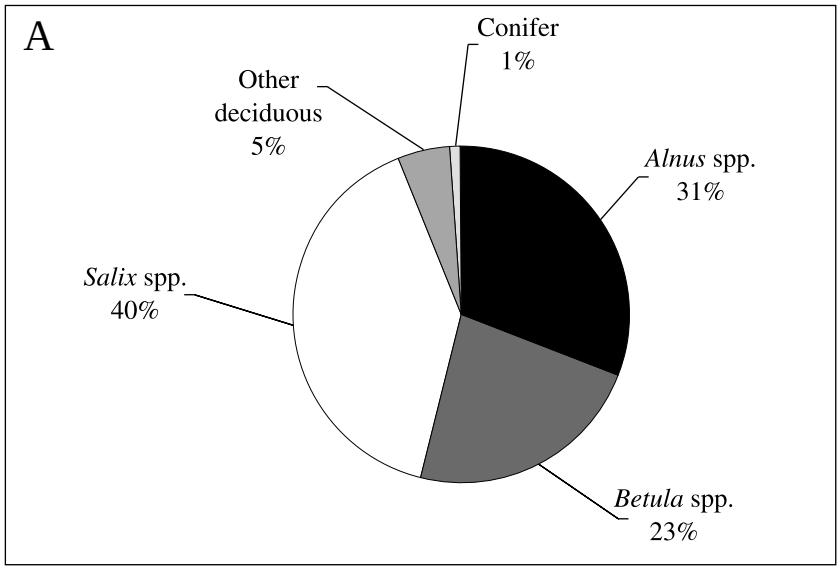
$$X^2=(ln\ Q)^2 / [1/x_i + 1/(m - x_i) + 1/y_i + 1/(n - y_i)]$$

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 mean values for both available and felled trees at the Willow Carr Site were from the random quadrats. The data used to calculate the mean values for available trees and felled trees at the Lake Site were from the belt transects and the complete survey respectively. The tree size-selectivity data were tested for statistical significance using the Mann-Whitney U-test.

Results

At the Willow Carr Site willow, birch and alder are dominant with only a small number of conifers present (figure 2A). At the Lake Site coniferous woodland dominates with smaller amounts of willow, birch and alder mainly on the lake shoreline and within the lake shallows (figure 2B). These shallows have in part been created by a beaver dam at the lake outlet, which has raised the water level by approximately 0.1 m.

The complete surveys of all felled trees at both sites indicated that 298 trees were felled at the Willow Carr Site, and 320 trees were felled at the Lake Site. Dividing these data by the number of beavers present at each site, and the number of days elapsed between the release of the beavers and the time of the full survey (324 and 205 days at the Willow Carr Site and Lake Site respect-



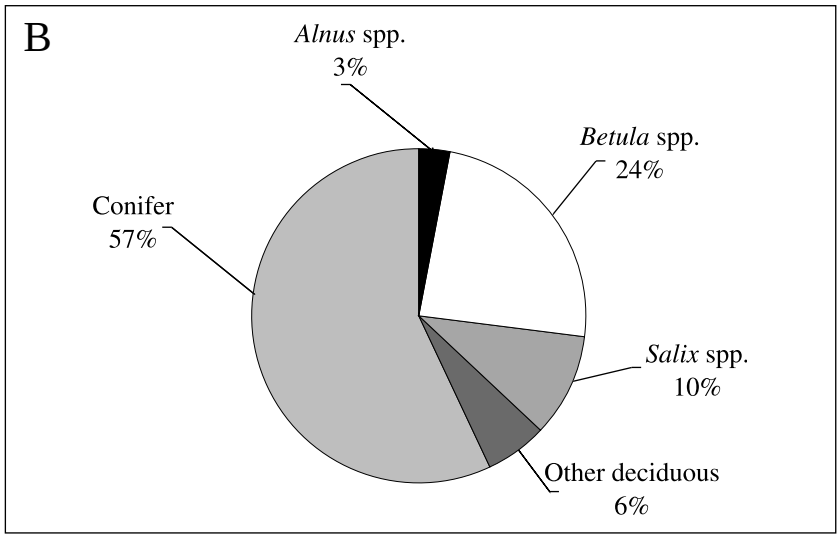


Figure 2. Tree species composition at (A) the Willow Carr Site (*n*=348), and (B) the Lake Site (*n*=578).

ively), yields approximate felling rates of 0.5 trees per beaver per day at the Willow Carr Site and 0.8 trees per beaver per day at the Lake Site.

At both sites, only trees of three genera were felled: *Alnus* spp., *Betula* spp. and *Salix* spp., whilst conifers were avoided except for occasional incidences of bark stripping. Of the felled trees only the selections against birch at both sites ($P<0.05$ at the Willow Carr Site and $P<0.001$ at the Lake Site) and for willow at the Lake Site ($P<0.001$) are statistically significant (table 1). Whilst available genera were of broadly similar size classes at both sites, the degree of size-selectivity varied between the sites (table 2). The beavers at the Willow Carr Site showed no preference in tree size for any of the three genera that were felled. At the Lake Site smaller trees were selected than the average size available for all three genera that were felled. At the Willow Carr Site trees at the larger end of the size range (6-12 cm in diameter) made up the majority of the felling, whilst smaller diameter classes of trees (4-10 cm in diameter) were chosen at the Lake Site (figure 3).

The foraging distances at the Willow Carr Site show decreased felling activity with increasing distance from the ponds (figure 4A). At the Lake Site there was an apparent locational preference for trees situated in the shallow margins of the lake itself (figure 4B). Maximum and mean distances from the water's edge travelled by beavers to fell trees were 49 m and 24 m at the Willow Carr Site, and 2 m landward and 10 m into the water at the Lake Site.

Discussion

The European beaver is known to have a very broad diet and Kitchener (2001) documented 80

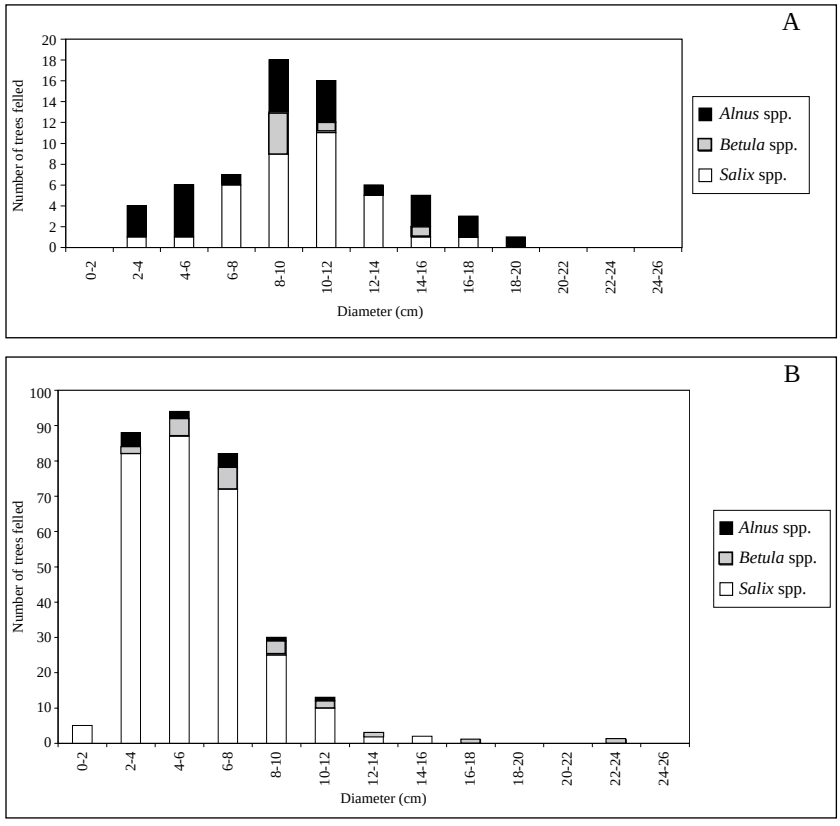


Figure 3. Diameters of felled trees at (A) the Willow Carr Site (n=66), and (B) the Lake Site (n=320).

Table 1. Genus electivity indices (*ln Q*). *** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; NS = not significant ($P>0.05$).

Site	Species	Abundance	Use	% Abundance	% Use	*ln Q*	X^2	*P*
Willow Carr	*Alnus* spp.	107	25	30.7	37.9	0.32	1.29	NS
	Betula spp.	79	6	22.7	9.1	-1.08	5.81	*
	Salix spp.	144	35	41.4	53	0.47	3.04	NS
Lake	*Alnus* spp.	18	12	3.1	3.8	0.19	0.26	NS
	Betula spp.	137	23	23.7	7.2	-1.39	34.21	***
	Salix spp.	60	285	10.4	89.1	4.25	356.89	***

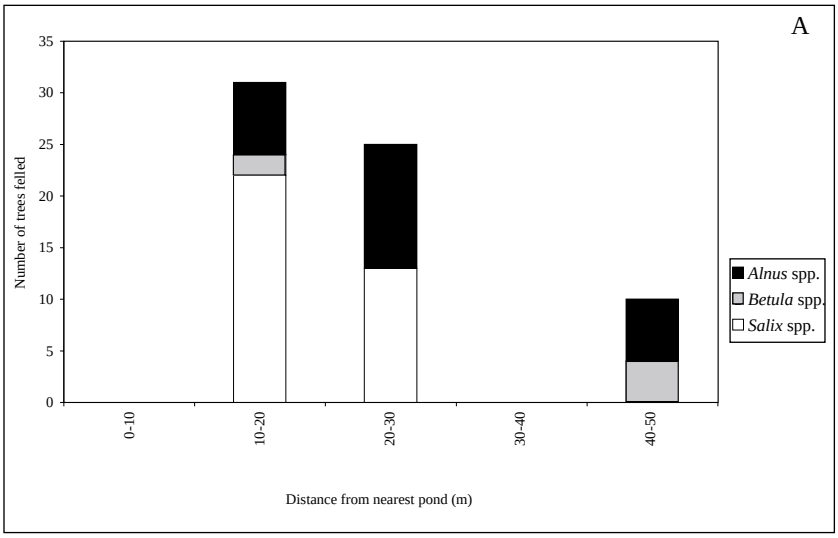
Table 2. Mean available and felled tree sizes at the Willow Carr Site and the Lake Site. *d* = mean diameter (cm); *sd* = standard deviation; *** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; NS = not significant ($P>0.05$).

Site	Species	Available trees			Felled trees			*P*
		n	*d*	*sd*	*n*	*d*	*sd*	
Willow Carr	*Alnus* spp.	107	11	±5	25	10	±5	NS
	Betula spp.	79	10	±4	6	11	±2	NS
	Salix spp.	144	9	±3	35	10	±3	NS
Lake	*Alnus* spp.	18	15	±5	12	6	±3	***
	Betula spp.	137	14	±8	23	9	±5	**
	Salix spp.	60	9	±3	285	6	±2	***

woody species in its diet, although marked preferences for certain genera and species have been recorded (Bryant & Kuropat 1980). 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 Willow Carr Site at Bamff and none at the Lake Site. These trees did not fall into any of the random sampling quadrats. We noted, however, that all of these trees were felled soon after the beavers were introduced to the site, suggesting high species preference despite the low availability.

Willow species are also highly preferred by beavers (Nolet et al. 1994, Lapinski & Stalinski 2001) and data from the Lake Site strongly support this preference, with *Salix* spp. making up 89% of all the felled trees, but only 10% of the trees available. At the Willow Carr Site this positive preference for *Salix* spp. also exists but not significantly so, indicating that either a larger dataset is required to reveal a significant preference or that preference is site or beaver specific. Such differences in preference between individual beavers or beavers from different regions have been observed in other studies (Shelton 1966, cited in Müller-Schwarze & Sun 2003). In absolute terms the data from both sites indicate that willow is felled in the greatest amounts, followed by alder and birch. Furthermore, the significant negative electivity indices for *Betula* spp. at both sites indicate a negative preference for birch by the beavers, even when relative abundance is accounted for.

It is also interesting to note the relatively large amount of alder felled at both sites given the well-documented low preference of beavers for *Alnus* spp. (Nolet et al. 1994). This finding may be due to the role of alder as a construction material rather than as a food item (Pinkowski 1983). It could be reasonable to assume that dam and lodge building activities would be most marked during the first year of colonisation of a new territory, and that the relatively large amounts of alder felled during



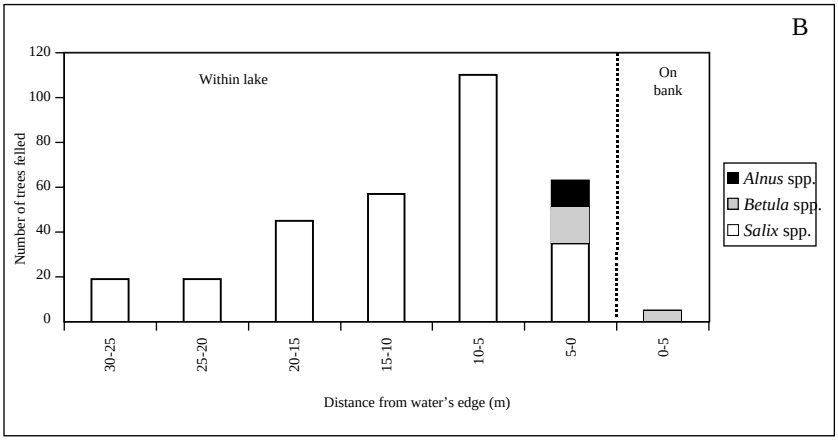


Figure 4. Foraging patterns at (A) the Willow Carr Site (*n*=66), and (B) the Lake Site (*n*=318).

this study could be due to such a construction phase. Small dams have been built at both of the study sites, as well as a relatively large bank lodge at the Lake Site.

Another interesting, but unquantified, aspect of the feeding behaviour of the beavers has been the stripping of small patches of bark from conifers at the Lake Site. Such behaviour has been documented in the European beaver (Simonsen 1973) and the American beaver (*Castor canadensis*; Svendsen 1980), and is thought to be a mechanism by which the nutritional quality of a tree is tested (Jenkins 1980). It is also possible that the ingestion of small amounts of coniferous sap and bark helps to provide a balanced diet (Jenkins 1979).

Beavers are known to select trees by size as well as species, with smaller trees being felled before larger ones (Simonsen 1973, Jenkins 1979). The general trend at the Lake Site supports this pattern of selection, and, in all three genera felled by beaver smaller trees are preferred. At the Willow Carr Site, however, beaver do not exhibit any significant size-selectivity. This lack of distinct size-selectivity could be due to the greater role played by alder in the felling behaviour at this site. If alder is largely

being utilised for construction, size may simply be of lesser importance than when felling for food.

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). Our preliminary data support this observation. At the Lake Site the vast majority of felling occurs within the aquatic zone, with no incidence of the beavers browsing further than five metres from the shoreline. At the Willow Carr Site this aquatic supply of woody material is not present and the beavers are forced to browse further from the safety of the small ponds and drainage ditches.

Conclusion

This paper documents the first year (2002-2003) of beaver felling and foraging activity following reintroduction to an enclosed Scottish site. During this period an average of 0.5 trees and 0.8 trees per beaver per day were felled at the Willow Carr Site and Lake Site respectively. Woody species felled included willow, birch and alder with a strong preference for *Salix* spp., a negative preference for *Betula* spp., and complete avoidance of conifer felling. Felling was undertaken for lodge and dam construction as well as feeding activity. Collation of data from the winter of 2003-2004, when construction activities have to date not been apparent, will allow us to determine the relative importance of felling for feeding and building. Although the felling and foraging activities may not be sustained long-term, an understanding of the initial impacts is important for trial reintroduction projects where public scrutiny may be intense. Whilst these results may not be directly transferable to other Scottish sites or other European regions with markedly different environmental conditions, they do however give an indication of the preference for specific woody species and tree sizes, and the possible levels of felling activity by reintroduced beaver.

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Samenvatting

Vellen en foerageren: resultaten van het eerste jaar van activiteiten van bevers (*Castor fiber*) in een omrasterd gebied in Schotland

Een proef-herintroductie van de Europese bever (*Castor fiber*) in Schotland is voorgesteld en wacht op goedkeuring door de Schotse overheid. Op dit moment zijn er geen gegevens gepubliceerd over de effecten van bevers op het Schotse landschap, hoewel veel auteurs potentiële effecten hebben voorspeld. Dergelijke voorspellingen zijn gebaseerd op de effecten van bevers in andere Europese landen. Doel van deze studie is om met gebruik van gegevens van bevers in gevangenschap betere voorspellingen te kunnen doen van het potentiële effect van bevers op het vellen van bomen direct na de herintroductie van de dieren. In 2002 zijn vier Europese bevers uitgezet in twee grote, omheinde, semi-natuurlijke gebieden in het oosten van Schotland: de *Willow Carr Site* en de *Lake Site*. Dit artikel presenteert de gegevens van het eerste jaar van een driejarig monitoringprogramma, dat zich richt op de vel- en foerageer-activiteiten van deze bevers. In absolute zin zijn op beide lokaties wilgen (*Salix* spp.) in de grootste aantallen geveld, gevolgd door els (*Alnus* spp.) en berk (*Betula* spp.). In termen van relatieve dichtheid zijn alleen de negatieve selectie van berk in de Willow Carr Site en de positieve selectie van berk in de Lake Site significant. In de Willow Carr Site is geen voorkeur voor boomgrootte aangetoond. In de Lake Site zijn de gevelde bomen van alle soorten significant kleiner dan gemiddeld. In de Willow Carr Site nam het aantal gevelde bomen af bij toenemende afstand tot de beverburcht, terwijl in de Lake Site de meeste gevelde bomen in de ondiepe randen van de meren groeiden. Per bever zijn per dag gemiddeld 0,5 bomen geveld in de Willow Carr Site, en 0,8 bomen in de Lake Site.

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