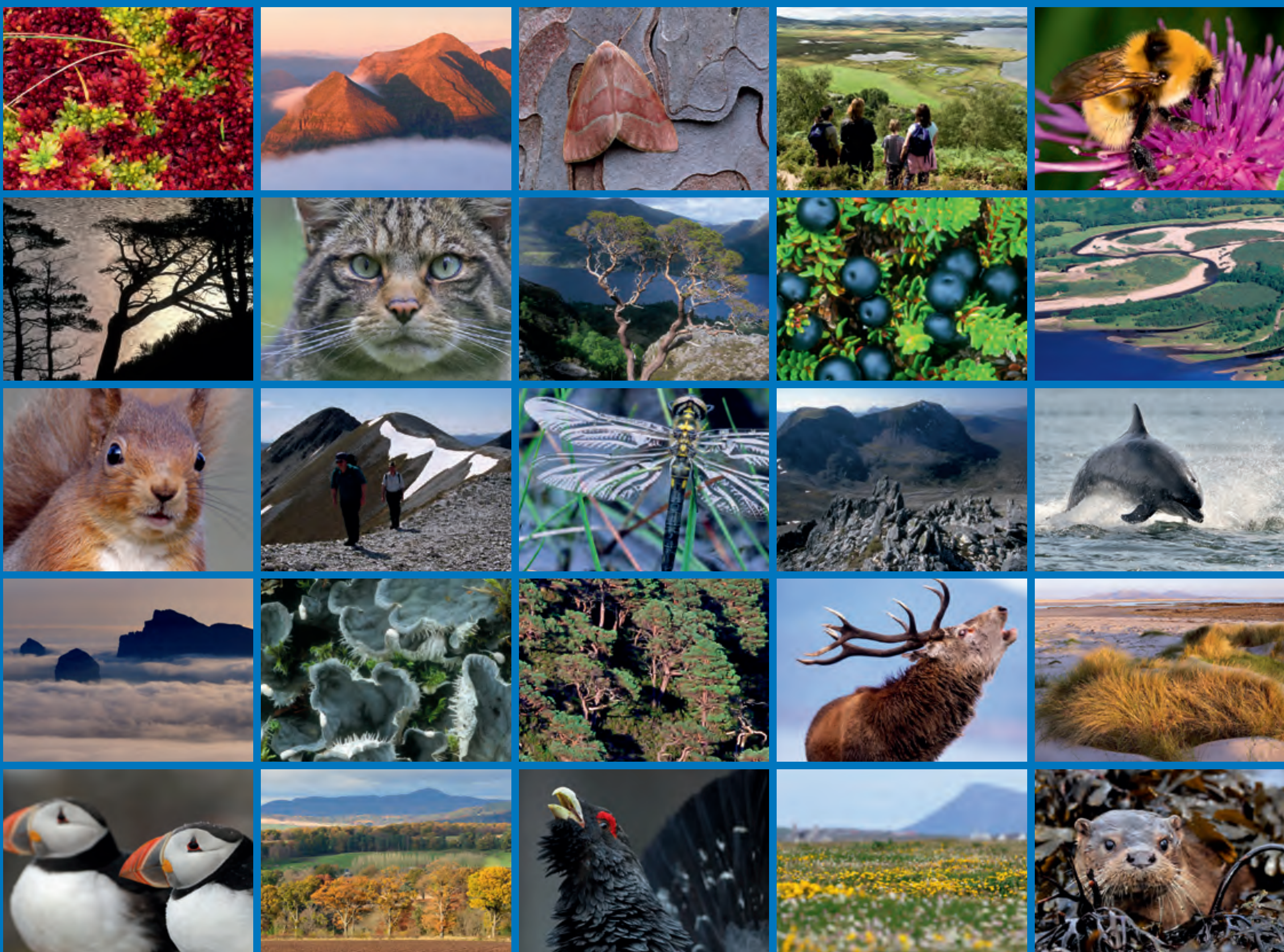
Scottish Natural Heritage
Commissioned Report No. 525

The Scottish Beaver Trial: Woodland monitoring 2011



COMMISSIONED REPORT

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For further information on this report please contact:

Jeanette Hall & Martin Gaywood
Scottish Natural Heritage
Great Glen House
INVERNESS
IV3 8NW
Telephone: 01463 725000
E-mail: beavers@snh.gov.uk

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Summary

The Scottish Beaver Trial: Woodland monitoring 2011

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Background

In 2008, the Scottish Government approved a licence to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), to undertake a five-year trial reintroduction of the European beaver (*Castor fiber*) to Scotland after an absence of more than 400 years. In May 2009, three beaver family groups were introduced to Loch Coille-Bharr, Loch Linne/Loch Fidhle and Creagmhor Loch/Loch Beag on land managed by Forest Enterprise Scotland (FES) at Knapdale, Argyll. Since 2009, additional releases have also taken place, and by November 2010, beaver groups were established in these three lochs and Lochan Buic. This is the third annual report that describes the effects of beavers on riparian woodland at Knapdale, and summarises effects observed up until November 2011 and attempts to identify trends that are emerging with increasing time since the reintroduction process began.

Main findings

- 31 transects comprising 111 (4×10 m) permanent vegetation plots have been established between zero and 30 m of the water's edge on five lochs at Knapdale.
- Six of these plots have since been excluded from the monitoring data either because of beaver induced flooding, or human activity, leaving a total of 105 monitoring plots.
- Downy birch was the dominant species on most plots, although alder, hazel, ash, rowan and willow also occurred as co-dominants or dominants with restricted distributions.
- In November 2011, 29 months after their release, beavers had directly affected trees in 46 (43.8%) out of the 105 continuously monitored vegetation plots. Of the individual trees marked in all plots, 13.0% had been gnawed or felled.
- Plots used by beavers included more birch and willow, but less alder, than an average plot.
- At November 2011, slightly fewer beaver effects had occurred in plots within 0-4m of water and only slightly more occurred at 6-10, 16-20 or 26-30m from water. Beavers had not affected trees any further from their lodges in 2011 as compared to November 2010.
- There has been a slight decrease in the mean stem diameter of trees affected by beavers from 5.0cm in November 2010 to 4.7cm in November 2011.
- A comparison of the tree and shrub species used by beavers with their abundance indicates that willow and rowan are preferred species and alder and hazel avoided species. Birch is both the most abundant species and the species most often used by beavers, but is used at a frequency commensurate with its abundance. There have been no changes in beaver species preferences.
- The degree, characteristics and any resprouting of beaver-cut stumps, are important for the long-term dynamics and sustainability of the beaver interaction with woodland. By November 2011, resprouting stems were apparent from the stump or base of 35% of

trees that had been directly affected by beavers, which was less than the previous year. However, the remaining resprouted shoots were longer and more numerous than previously.

- The most vigorous resprouting was observed on ash, willow and rowan; poorer resprouting was observed on birch and very poor resprouting was observed on alder and hazel, although these latter species were rarely affected by beavers anyway.
- Trees most strongly affected by beaver activity continue to be rowan growing within 4 m of the water (40 % affected, mostly felled) and willows growing from 6 – 30 m from the water (30 % affected). Both of these species are vigorous resprouters.

For further information on this project contact:
Jeanette Hall, Scottish Natural Heritage, Great Glen House, Inverness, IV3 8NW.
Tel: 01463 725000
For further information on the SNH Research & Technical Support Programme contact:
Knowledge & Information Unit, Scottish Natural Heritage, Great Glen House, Inverness, IV3 8NW.
Tel: 01463 725000 or research@snh.gov.uk

This project is part of the independent monitoring programme for the Scottish Beaver Trial coordinated by SNH in collaboration with a number of independent monitoring partners. For further information go to:
www.snh.gov.uk/scottishbeavertrial
or contact:
Martin Gaywood, Scottish Natural Heritage, Great Glen House, Inverness, IV3 8NW
Tel: 01463 725230 or beavers@snh.gov.uk

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Acknowledgements

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1. BACKGROUND

1.1 Overall background to the trial release of beavers

The European beaver, *Castor fiber*, became extinct in Scotland by the end of the 16^{th} century as a result of hunting combined with habitat loss (Kitchener and Conroy, 1997). Over recent years the potential for restoring this species to the natural fauna has been investigated. These investigations have resulted in a suite of information about the scientific feasibility and desirability of conducting such a reintroduction. Relevant documents published by Scottish Natural Heritage (SNH) can be viewed at the 'Other work on beavers' page at:

http://www.snh.gov.uk/protecting-scotlands-nature/safeguarding-biodiversity/reintroducing-native-species/scottish-beaver-trial/other-work-on-beavers/

Article 22 of the European Council Directive 92/43/EEC *on the Conservation of Natural Habitats and of Wild Flora and Fauna* (the 'Habitats Directive') requires the UK government to consider the desirability of reintroducing certain species (listed on Annex IV), including European beaver.

The Species Action Framework, launched in 2007 by Scottish Ministers, sets out a strategic approach to species management in Scotland. In addition, 32 species, including the European beaver, were identified as the focus of new management action for five years from 2007. SNH works with a range of partners in developing this work and further information can be found at

http://www.snh.gov.uk/protecting-scotlands-nature/species-action-framework/

In May 2008, the Minister for Environment approved a license to allow a trial reintroduction of up to four families of European beaver to Knapdale Forest, mid-Argyll. The licence was granted to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), who are working on behalf of the 'Scottish Beaver Trial' partnership. The trial site, Knapdale Forest in Argyll, is managed by Forest Enterprise Scotland (FES). Animals were caught in Norway in 2008, quarantined for six months and released in spring 2009. The initial release sites were Loch Coille-Bharr, Loch Linne/ Loch Fidhle and Creagmhor Loch/ Loch Beag, immediately to the west of Creagmhor Loch. Further releases took place during 2010 at Lochan Buic/Lily Loch

One condition of the licence is that SNH coordinates an independently conducted monitoring programme in collaboration with the project partners. The trial will therefore involve a number of independent monitoring sub-projects in order to address the primary aims, and at the end of the trial the outputs of the monitoring will be assessed and a decision made by Scottish Government on the next stage. This is a progress report on the woodland monitoring sub-project, which is being conducted by The James Hutton Institute (formerly Macaulay Land Use Research Institute) in partnership with Scottish Natural Heritage.

1.2 Summary of likely beaver impacts on woodland

Beavers are ecosystem engineers and can produce both direct and indirect effects upon woodlands. The most obvious direct effect is felling of trees. In other parts of their range, particularly during autumn and winter, beavers gnaw and fell trees for food and to obtain timber for the construction of lodges and dams. In the short term at least, tree felling can reduce the biomass of standing, living trees and change the age and size structure of woodlands. Longer-term changes may involve a shift in tree species composition. Many riparian tree species in Europe and North America evolved in the presence of beavers and other browsing herbivores and, given suitable conditions, respond to browsing of woody stems by producing abundant new growth. This can lead to the production of denser stands of woody vegetation producing abundant foliage, which can offer a valuable food resource not only to beavers but also to browsing ungulates and herbivorous insects (Jones *et al.* 2009). However, the recovery of vegetation from beaver browsing and felling will be dependent upon the interaction of new shoots with subsequent browsing by both beavers and sympatric ungulate browsers (Hood and Bayley, 2009). Some woody species may also respond to browsing by altering the nutritional and anti-herbivore defensive chemistry of new growth, which can alter the food quality of this plant material for herbivores, sometimes in unpredictable ways (Veraart *et al.* 2006).

Because plant species differ in their tolerance of browsing and their competitive abilities, as well as their palatability to herbivores, sustained browsing of riparian woodlands by beavers may also alter their floristic composition. As well as herbivorous animals, human interests can also be influenced by changes in the structure and floristic composition of riparian woodlands: the appearance of loch and river shores can change, with significant aesthetic consequences, access to the water from land may be hindered or facilitated and changed levels of shade on smaller watercourses may influence water temperatures, which in turn can affect the reproduction and survival of commercially and recreationally valuable fish species.

Many internationally important species of lichen rely on a continuity of old tree stems in open woodland. By maintaining a cycle of felling and re-growth, beaver activity may result in a loss of this habitat in riparian zones, or at least suppress future development of such habitat.

The most obvious indirect effect of beaver activity on lochside woodlands is flooding caused by beaver dams. Beavers build dams to raise the water level of lochs and watercourses but also to expand their potential foraging area into inundated woodlands and other habitats. Most tree species are intolerant of sustained flooding, and so flooding can increase the amount of standing dead timber but possibly also favour flood-tolerant species such as willows.

2. AIMS AND OBJECTIVES

The overall aim of this work is to monitor the effect of the introduced beavers on woodland in the area of the trial release, in order to inform any future decisions on future plans for the species in Scotland.

The objectives of this monitoring work are to:

1. Carry out a sample-based assessment of the composition and structure of the loch-side woodlands around the beaver release site;
2. Assess the nature and extent of beaver effects on the loch-side woodlands, again based on a representative sample of survey plots;
3. Assess seasonal variation in the effect of beavers on woody vegetation.

In addition to these objectives, we will ultimately identify any changes in the nature of the beavers' effects on the woodland that become apparent during the course of the monitoring program from 2009-2014. It is particularly relevant to identify temporal shifts in:

i) The nature of foraging activity and impact as compared to that observed immediately after colonisation (i.e. changing preferences for tree species and size classes within locations.
ii) The spatial location of impacts
iii) The use of sprouts from previously beaver-affected trees.

This report covers the monitoring of beaver effects on woodlands undertaken at two sampling times (April 2011 and November 2011), and quantifies the effects of beavers since the previous monitoring visit in November 2010 (Moore *et al.* 2011), up to a point 29 months after the release of beavers. Where possible, comparisons will be drawn between recent beaver effects and those during previous monitoring periods. Most comparisons are made between the results in November 2011 and November 2010 (Moore *et al*. 2011), which were collected on a standardised set of plots.

It is not intended to try to assess the effect of beavers on the woodland ground flora or on epiphytic species. It is likely that the presence of beavers will affect these species – either directly through grazing or indirectly through changing the woodland structure – but confidently demonstrating such an effect was deemed to be extremely difficult or impossible and would have demanded greater resources than were available. Much of the loch-side vegetation in the trial area had been managed prior to the reintroduction to improve the habitat in preparation for the trial beaver release. As a result, the ground flora is already developing in response to this management. Distinguishing any change which may result from beaver activity from this background change is likely to be extremely challenging – especially over such a short period as five years.

3. METHODS

3.1 Site description and beaver releases

The loch-side and riparian woodland at Knapdale has been described by Armstrong *et al.* (2004) (Loch Linne and Loch Fidhle) and Brandon-Jones *et al.* (2005) (all loch-side and riparian woodland within the FES land at Knapdale). Most of the release sites (excluding Lochan Buic and Lily Loch) lie within the Taynish and Knapdale Woods Special Area of Conservation (SAC; EU code UK0012682), which comprises 44 % broadleaf woodland as well as water bodies, extensive conifer plantations and smaller areas of bogs, marshes, water-fringed vegetation, fens, heath and scrub. One main reason for the designation of the area as an SAC is the presence of old sessile oak (*Quercus petraea*) woods with *Ilex* and *Blechnum*. In the years leading up to the Scottish Beaver Trial, extensive areas of conifer plantation have been cleared from Knapdale, particularly near the lochs, and in most places, dense downy birch (*Betula pubescens*) regrowth has taken their place.

A decision was taken to restrict woodland monitoring with permanent plots to the strip of woodland within 30 m of loch shores, as it was anticipated, based on other studies of *C. fiber*, that most beaver effects would occur in this zone (Haarberg & Rosell 2006). Most woodlands in this zone at Knapdale are dominated by mature and regenerating birch and common alder (A*lnus glutinosa*). In many areas, willow species, particularly goat willow (*Salix caprea*) are abundant and rowan (*Sorbus aucuparia*) is widespread throughout the site, both as mature and sapling trees. Hazel (*Corylus avellana*) and ash (*Fraxinus excelsior*) are also common in some areas around the loch shores. Aspen (*Populus tremula*) is highly favoured by European beavers elsewhere, but is very rare at Knapdale and only occurs on rocky terrain, where it is largely inaccessible to beavers. *Q. petraea* is common and widespread at Knapdale, but within 30 m of the water it is limited to steep, often rocky terrain where the shore is precipitous and unsuitable for beavers.

Three family groups, comprising eleven beavers, were released at Knapdale in late May 2009. One group was released in each of Loch Coille-Bharr (four animals), Loch Linne/Loch Fidhle (four animals; these lochs are continuous with one another) and Creagmhor Loch (three animals). Beavers were released into artificial straw bale lodges situated in areas that were expected to provide suitable browsing habitat nearby and minimise the likelihood of disturbance to the animals. These artificial lodges were located at the southern ends of Loch Coille-Bharr and Creagmhor Loch and on the island in Loch Linne/Fidhle. Subsequently, one Loch Linne beaver died, and all three beavers disappeared from Creagmhor Loch, although the adult male was subsequently recaptured and returned to the site. Prior to April 2010, the male at Creagmhor Loch was removed on welfare grounds because of ill health and subsequently died at Edinburgh Zoo. By this time, the family from Loch Coille-Bharr had established themselves in a lodge on the eastern shore of the small Dubh Loch to the east of Loch Coille-Bharr. These animals had also dammed the point where Dubh Loch naturally drains to Loch Collie-Bharr, flooding the surrounding broadleaf woodland and significantly expanding the area of Dubh Loch.

To reach the trial's aims of having established four pairs of beavers at Knapdale, two new pairs were released in 2010: i) in May one pair was released onto a small un-named lochan (British National Grid coordinates NR 78908 88570) just to the south of Lochan Buic, called Lily Loch for the purposes of this report. This loch lies outwith the Taynish and Knapdale SAC but within the Forest Enterprise Scotland land-holding. ii) in June 2010 a further pair was released onto Creagmhor Loch. The male from the Lily Loch pair died a few days later and the female moved herself to the nearby Lochan Buic. Another male beaver was released into that loch in September 2010. In anticipation of the 2010 releases, a number of additional monitoring transects were established around Lily Loch and Lochan Buic in April 2010, and no new sampling areas have been established since (see 3.2.1 below).

At November 2010, there were beaver pairs/families established on four loch complexes at Knapdale: Loch Coille-Bharr/Dubh Loch, Loch Linne/Loch Fidhle, Creagmhor Loch/Loch Beag and Lochan Buic/Lily Loch. The first two families each successfully produced at least one kit in 2010. These same families have also produced a further kit each during the summer of 2011, although only that produced by the Loch Linne/Loch Fidhle pair has survived. During the summer of 2011 the pair of non-breeding beavers on Creagmhor Loch built a further lodge at the south-eastern end of the small loch to the east of Creagmhor Loch; this loch is now known as Loch Beag (Figure 1).

3.2 Field Methods

3.2.1 Location of transects

Seventeen transects, each comprising from one to four plots, with 65 plots in total, had been established at Knapdale in November 2009 (Moore *et al.* 2010). Those transects were positioned, radiating perpendicularly from the water's edge, around all lochs known to have been used by beavers at that time, so that all shores, other than those too steep to be used by beavers, were included. By November 2009, the lack of beaver field signs suggested that some of these areas were yet to be visited by beavers. To increase the likelihood that a reasonable number of transects would subsequently be visited by beavers, the choice of locations was further guided by the locations of active beaver lodges and the distribution of existing signs of beaver herbivory. A further 13 transects (43 plots) were established in April 2010, and one further transect (3 plots) established in November 2010, making a total of 111 plots across 31 transects. Most transects established in 2010 were positioned to monitor the impact of the newly released beavers at Lily Loch/Lochan Buic. Plot locations are indicated in Figure 1, which also shows the six plots that have been modified whether due to i) beaver induced flooding (2 plots), or ii) damage by forestry activities (1 plot), or iii) their locations coincided with areas of no trees (3 plots: see Table 2). No further sampling plots have been added since November 2010. Figure 1 illustrates the locations of all lodges used by beavers during the survey period reported here, including one newly formed in Summer 2011 on Loch Beag.

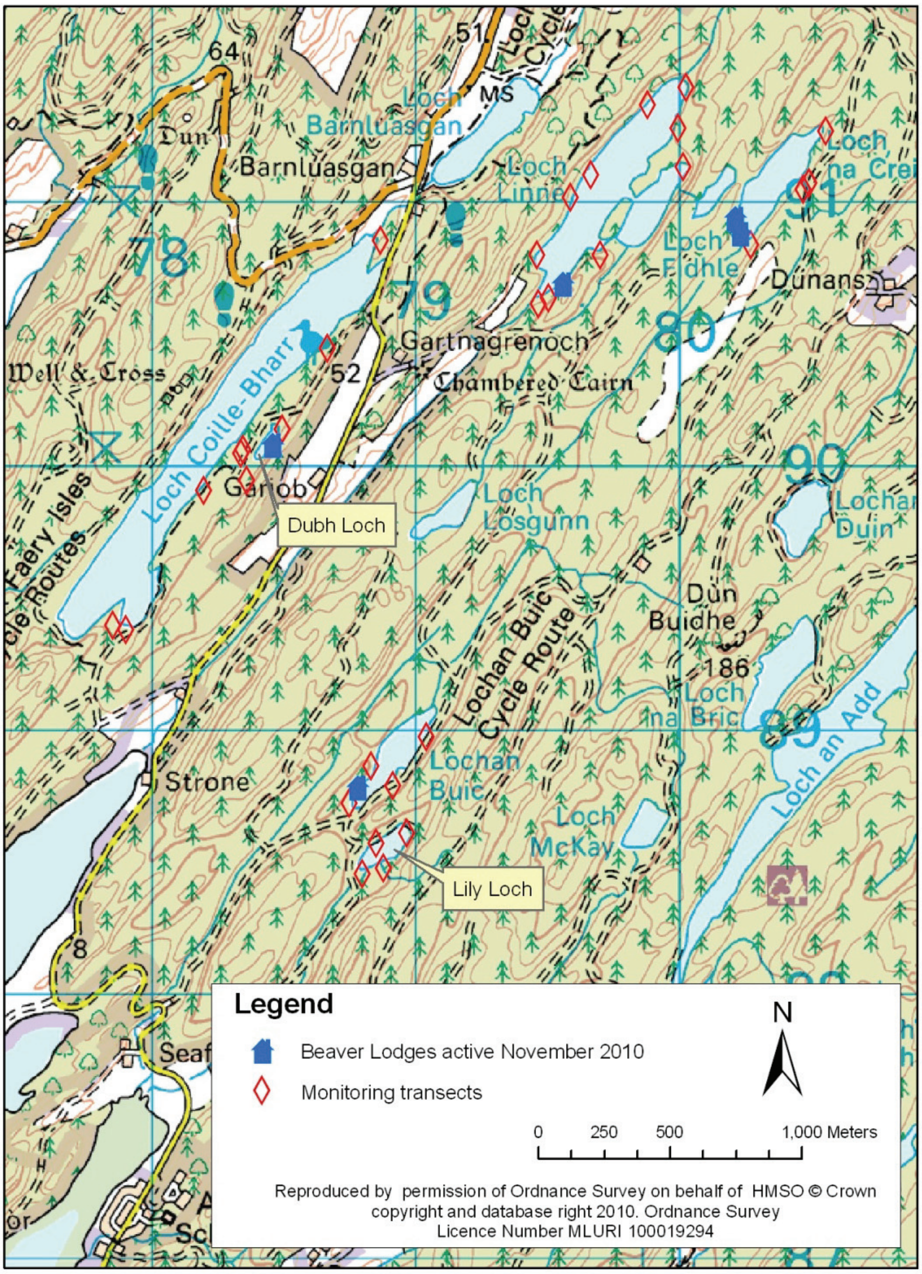


Figure 1. Locations of monitoring transects and active beaver lodges at Knapdale, November 2011.

Complete transects extend perpendicularly from the water's edge for 30 m (Figure 2). In most cases, four rectangular plots are positioned along each transect, each 10 m wide (along the side parallel to the water's edge) and 4 m deep (along the side parallel to the transect). Plots are placed along the transect from 0 – 4 m, 6 – 10 m, 16 – 20 m and 26 – 30 m from the water. All four corners of each plot are marked with permanent wooden posts, and one post is marked with a numbered aluminium tag (at point A, Figure 3). The geographic coordinates of each plot are also recorded at this point using a global positioning system (GPS). Where the loch shore is indented or projects into the loch beyond a straight line along the edge of the first plot, all land and trees up to the water's edge is considered to be part of the plot, and if necessary the position of the plot is adjusted such that its total area remains 40 m^2 (e.g. Figure 3). In sites where the woodland is flooded it is not always possible to access, nor to identify, the edge of the loch. In these instances, the transect is started at the closest point to the water body that allows safe working.

On some sections of loch shore, deciduous broadleaf woodland extends for less than 30 m from the water before conifer plantations, paths, roads or inaccessible terrain are encountered. In these cases, transects included fewer than four plots. Where transects crossed small paths, it was occasionally necessary to shift a plot one or two metres towards or away from the water.

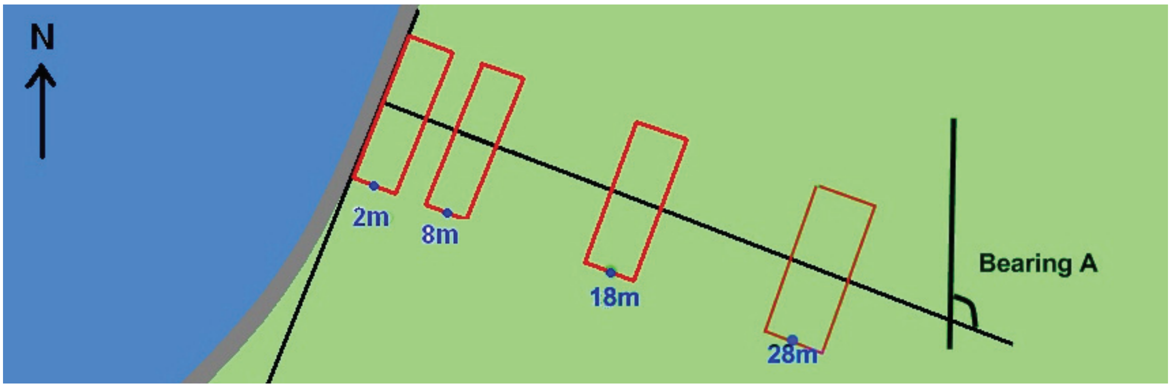


Figure 2. Schematic illustrating the arrangement of survey plots (red rectangles) along a transect, relative to a nearby loch (blue shading). Blue text indicates the distance of the midpoint of each plot from the water's edge.

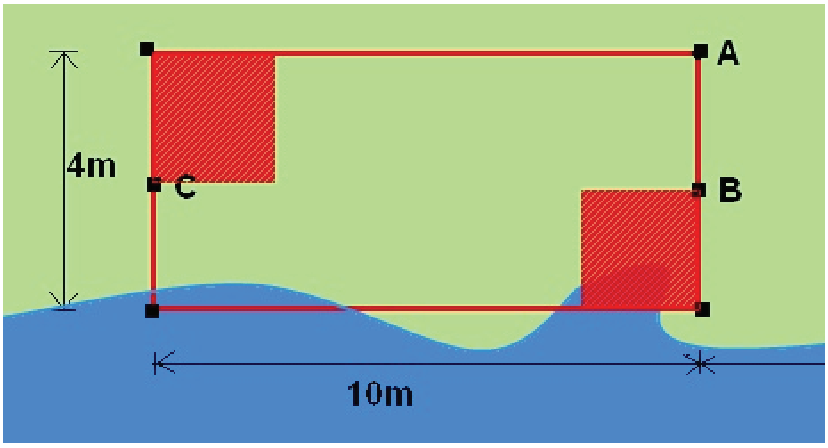


Figure 3. Dimensions of permanent vegetation plot, position of subplots for ground cover description within the plot (solid red squares) and several point locations referred to in the text

3.2.2 Plot measurements

Each plot was delineated with a line extended around its four corner posts while observers were on site. The slope of each plot, from its lowest to highest point, was measured using a clinometer, and where this was greater than zero, the aspect of the slope was also measured using a compass. Percentage vertical canopy cover and ground surface area covered by standing water were estimated to the nearest 5 % and recorded for each plot. Several measurements were taken from a point midway along the right hand side of the plot when viewed from the waterside (point B, Figure 3). Percentage horizontal vegetation density was measured across the plot from point B by estimating the percentage area obscured of a 50 × 50 cm white board held by an assistant facing the observer from point C (figure 3). This was repeated with both the board and the observer's eyes at four different levels above the ground: 0 – 50 cm, 50 – 100 cm, 100 – 150 cm and 150 – 200 cm. At each visit, in each plot, one photograph was taken from point B, facing across the plot towards point C, with a camera supported 1.6 m above the ground by a monopod. The camera used was a Nikon Coolpix 5400, with its zoom set to the widest lens angle possible (28 mm). All photographs are archived at The James Hutton Institute and will form a sequence of photographs describing visual changes to the plots over the course of the Scottish Beaver Trial.

3.2.3 Subplot measurements of ground cover

Ground cover was described in two subplots within each plot. Subplots measured 2 × 2 m and were positioned in the front right-hand corner and back left-hand corner of the plot (when facing the plot from the water) as illustrated in Figure 3. For each plot, percentage cover of the following types was estimated to the nearest 5 %:

- standing water
- rock
- bare earth or mud
- grasses, sedges or rushes
- leaf litter
- woody litter (from small twigs to logs)
- ferns (including browned-off bracken)
- bryophytes
- dwarf shrubs (primarily *Calluna vulgaris, Myrica gale* and *Vaccinium* spp.)
- herbs

Because litter, for example, could overlie an area of grass which might overlap a layer of moss, the sum of all estimates in a plot was allowed to exceed 100 %. Tree seedlings less than 1.3 m in height were also counted in each subplot.

3.2.4 Measurements of woodland and beaver effects

All trees greater than 1.3 m in height, regardless of stem diameter, were marked and recorded in each plot, along with stumps and fallen timber from trees which would originally have met this criterion. Working from one end of the plot to the other, each stem, or in the case of easily grouped clumps of smaller stems of a single species, each clump of stems was permanently marked with a uniquely numbered aluminium tag. Tags were affixed as close to the ground as possible, using either a small aluminium nail or, for some smaller stems, a length of wire encircling the stem. For each stem, stump or group of stems, an observer recorded the species; measured the diameter at height 20 cm[1] (or lower if a bifurcation occurred at 20 cm or if beavers had severed the stem below 20 cm) of each stem or stump using calipers; recorded whether the stem or stump was alive, dead or indeterminate; and assigned the stem(s) to one of the 11 categories listed in Table 1.

[1] The usual forestry convention is to measure Diameter at Breast Height (DBH, generally taken to be 1.3m). 20cm was chosen as the average height of beaver browsing and thus most likely to influence beaver browsing preferences.

Table 1. The eleven status classes used to classify trees and tree parts in the plots, and the codes used to record them

Code	Status
BCut	Site on a tree where a minor branch has been removed by beavers, typically overhanging the water
Blog	Large log felled by beavers
BP	Tree partially felled by beavers i.e. the xylem has been incompletely severed, some phloem remains continuous between the stump and the upper part of the tree, but the upper part of the tree has fallen over and is resting on the ground or on other trees
BSt	Stump of a tree felled by beavers
BUp	Upright tree gnawed by beavers; this included trees with a single bite-mark through to trees that are near toppling
LogUp	Upright stems growing from a log or horizontal tree trunk previously felled by beaver
NLog	Naturally fallen log
NP	Naturally partially fallen tree
NSt	'Natural' tree stump – resulting from windfall or decay, but also including stumps sawn by humans
Up	Upright tree, unaffected by beaver gnawing, n.b. trees need not be vertical to qualify, some 'upright trees' are inclined at angles as low as 10 degrees from the ground
Gone	Trees that had previously been tagged but which could not be found on subsequent visits

In a number of cases, trees branched at a point closer to the ground than the height at which stem diameters were measured (20 cm); in these cases diameters were recorded for all stems at that height. Instances were also observed where trees branched at a point higher than 20 cm, but beavers severed the branched stems above the branching point. In those cases, in addition to the 20 cm diameter observers also measured the diameter where the stem was severed by beavers, and recorded this hierarchy of branching (see Annex 1 for details). In some instances, secondary and even tertiary branching events were recorded below beaver gnawing.

Some tree stems and logs were leaning, either naturally, or because they had been incompletely gnawed and partially felled by beavers or because they had been completely severed by beavers but were still supported above the ground by surrounding vegetation. The angle these stems made with the ground was recorded. From trees and stumps that had been gnawed by beavers, observers recorded the percentage of the circumference of the stem that had been gnawed. In the case of stumps of trees felled by beavers, this was almost always 100%. From stumps felled by beavers and partially felled and upright trees gnawed by beavers, observers also recorded the height above the ground at which gnawing had occurred. For stumps, this was taken from the highest part of the stump remaining. From upright trees, this was taken from the vertical midpoint of the gnawing. The lengths and diameters of any logs lying within the plot were also recorded, but only that part of the log lying within the plot boundary was included.

Observers also recorded any coppice resprouting from stumps or trees gnawed by beavers. All new shoots were counted and recorded separately as:

- "low shoots": shoots originating from stumps or below the gnawing damage on trees gnawed but not felled by beavers, or
- "high shoots": shoots originating from logs or above the gnawing damage on the stems of upright or partially felled trees gnawed by beavers.

The average and maximum shoot lengths were both recorded, and whether or not the longest shoot had been browsed. Where coppice resprouting had occurred and it had subsequently been browsed, observers recorded the extent of browsing effects on these shoots attributable to deer (roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and sika deer *Cervus nippon* are present at Knapdale) and/or to beavers on a three-point scale: 0 = none; 1 = detectable, less than half of shoots browsed; 2 = substantial, more than half of shoots browsed. Previous bark stripping by deer was evident on the trunks of many willows throughout Knapdale.

A series of illustrations of trees that have experienced a variety of beaver effects and an example datasheet recording all required data about these trees was produced for observers' reference in the field. Many permutations of tree growth form and beaver effect are more easily described by these illustrations than in text. This sheet is included as Annex 1 at the end of this report.

3.1.5 Comprehensive mapping of beaver effects

In addition to the establishment and monitoring of permanent vegetation plots, a further approach was trialled in 2010 to assess the distribution of beaver impacts. At Creagmhor Loch, an attempt was made to locate, tag and record the nature of the effects on all trees affected by beavers (Moore *et al*. 2011). This approach was discontinued in 2011.

3.1.6 Timing of measurements

The fieldwork reported here was conducted in April and November 2011. Field visits have been planned for two time periods in each year of the monitoring programme so that observers are able to assess the full extent of coppice resprouting throughout the growing season from trees and stumps felled by beavers, as well as any beaver and deer herbivory that these shoots have suffered. This timing of survey also allows partitioning of the intensity of beaver gnawing among the two times of year: November-April and April-November. These periods coincide approximately to the periods of dormancy and growth of trees respectively. It is anticipated that spring fieldwork will reveal the full extent of tree felling and bark feeding that has occurred on dormant trees through the preceding winter and that autumn fieldwork will also allow the determination of the net biomass gain of new shoots resulting from the interaction of growth and browsing.

3.3 Analysis and presentation of results

The abundance of trees within plots was considered in two ways. First, the number of stems were counted, and second, the basal area of each stem was calculated (basal area = $\pi \times$ stem radius^2) and these were summed to give a total stem basal area (at height 20 cm) for each plot. These totals included the stumps of trees recently felled by beavers, so as to provide the closest approximation of the plot structure 'pre-beaver', but excluded branches and logs felled by beavers and naturally felled logs and natural stumps.
Distances of transects from active lodge sites were calculated in a geographic information system by tracing the shortest path possible across the surface of the water body fronted by the two locations.

Where comparisons were made between trees directly affected by beavers and the total tree sample, the former category included all trees gnawed by beavers, whether they were still standing or whether only a stump remained.

Where possible, data are analysed in order to provide a comparison with previous time periods, in order to document temporal changes in the effects of beavers.

4. RESULTS

4.1 Details of transects and plots

The locations of the 31 transects and 111 plots established by November 2010 are listed in Table 2, and their locations are illustrated in Figure 1. Seven different species were recorded as dominant or co-dominant species in at least one plot, however it should be noted that plot 244, which was dominated by *Q. petraea*, included only a single tree. Also two of the marked plots, plots 285 and 290 did not contain any trees. *B. pubescens* was dominant in the majority of vegetation plots. Note that species dominance in Table 2 has been determined on the basis of number of stem diameters recorded, which may overestimate the abundance of *C. avellana* and to a lesser extent *Salix*, because many stems may have been recorded from a single stool or plant.

Table 2. Numbers and date of establishment of each transect/plot and the permanent tag numbers, British National Grid reference, initial distance from the water's edge[2], dominant woody species and presence or absence of beaver browsing in each plot within each transect in 2010 and 2011

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species‡	Beaver sign# 2010	2011
1. Dubh N	11/09	211	NR 78494 90138	0 m	BETPUB	Y	Y
		212	NR 78500 90140	6 m	BETPUB	Y	Y
		213	NR 78509 90139	16 m	BETPUB	N	N
		214	NR 78512 90162	26 m	BETPUB/SORAUC	N	N
2. Linne SW	11/09	3015	NR 79461 90798	0 m	BETPUB	N	Y
		3016	NR 79457 90799	6 m	ALNGLU/BETPUB	Y	Y
		217	NR 79450 90808	18 m	ALNGLU/BETPUB	Y	Y
		218	NR 79445 90814	26 m	BETPUB	N	Y
3. Coille-Bharr SE	11/09	219	NR 77900 89380	0 m	BETPUB/ALNGLU	N	N
		220	NR 77899 89375	6 m	BETPUB	N	N
		221	NR 77892 89369	16 m	BETPUB	N	N
		222	NR 77885 89361	26 m	BETPUB	N	N
4. Creagmhor S	11/09	223	NR 80271 90836	0 m	BETPUB	N	N
		224	NR 80272 90834	6 m	BETPUB	Y	Y
		225	NR 80265 90823	16 m	BETPUB	N	N
		226	NR 80258 90815	26 m	BETPUB	N	N
5. Fidhle N	11/09	227	NR 80014 91133	0 m	BETPUB	N	N
		228	NR 80018 91141	6 m	BETPUB	N	N
		229	NR 80021 91149	16 m	BETPUB	N	N
		230	NR 80027 91157	26 m	BETPUB	N	N
6. Dubh S	11/09	231	NR 78360 89946	0 m	BETPUB	N	Y
		232	NR 78359 89946	6 m	Salix/BETPUB	Y	a
		233	NR 78353 89929	16 m	Salix/BETPUB	Y	Y
		234	NR 78355 89924	26 m	Salix/BETPUB	Y	Y
7. Linne SW	11/09	235	NR 79588 91016	0 m	BETPUB/ALNGLU	Y	Y
		236	NR 79576 91020	6 m	Salix/BETPUB	Y	Y
		237	NR 79575 91022	16 m	Salix/BETPUB	Y	Y
		238	NR 79592 91033	26 m	BETPUB	N	N
8. Linne W	11/09	239	NR 79665 91103	0 m	CORAVE	Y	Y
		240	NR 79665 91097	6 m	CORAVE	N	Y
		241	NR 79645 91126	16 m	CORAVE	N	N
		242	NR 79640 91118	26 m	CORAVE	N	Y
9. Coille-Bharr SSE	11/09	243	NR 77851 89397	0 m	ALNGLU/BETPUB	N	Y
		244	NR 77846 89391	6 m	QUEPET	N	N
		245	NR 77843 89387	16 m	BETPUB	N	Y
		246	NR 77823 89384	26 m	BETPUB	N	N

[2] Some of the plots have since flooded in the vicinity of beaver dams

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species[‡]	Beaver sign[#] 2010	2011
10. Creagmhor E	11/09	247	NR 80471 91047	0 m	BETPUB/FRAEXC	Y	Y
		248	NR 80472 91039	6 m	BETPUB	Y	Y
		249	NR 80475 91031	16 m	BETPUB	Y	Y
		250	NR 80484 91026	26 m	BETPUB	N	N
11. Coille- Bharr E	11/09	251	NR 78195 89908	0 m	ALNGLU/SORAUC	N	N
		252	NR 78202 89905	10 m	BETPUB/SORAUC	N	N
		253	NR 78209 89899	20 m	BETPUB/SORAUC	N	N
12. Creagmhor N	11/09	254	NR 80555 91267	0 m	BETPUB	N	N
		255	NR 80561 91273	6 m	BETPUB	Y	Y
		256	NR 80567 91281	16 m	ALNGLU/BETPUB	Y	Y
		257	NR 80574 91285	26 m	BETPUB	N	N
13. Creagmhor NE	11/09	258	NR 80492 91072	0 m	BETPUB/SORAUC	Y	Y
		259	NR 80493 91073	6 m	BETPUB	N	N
		260	NR 80501 91064	16 m	BETPUB	N	N
		261	NR 80510 91058	26 m	BETPUB	N	b
14. Linne N	11/09	262	NR 80026 91434	0 m	ALNGLU	N	N
		263	NR 80029 91439	6 m	BETPUB	N	N
		264	NR 80037 91451	16 m	ALNGLU/BETPUB	N	N
		265	NR 80043 91459	26 m	BETPUB	N	Y
15. Linne SE	11/09	269	NR 79466 90614	0 m	ALNGLU/BETPUB	Y	Y
		270	NR 79463 90611	6 m	BETPUB	Y	Y
16. Linne SE	11/09	271	NR 79503 90635	0 m	BETPUB	Y	Y
		272	NR 79506 90626	6 m	BETPUB	Y	Y
		273	NR 79512 90619	16 m	BETPUB	Y	Y
		266	NR 79518 90614	26 m	BETPUB	Y	Y
17. Coille- Bharr N	11/09	276	NR 78867 90853	0 m	ALNGLU	N	N
		277	NR 78873 90863	6 m	ALNGLU	N	N
		278	NR 78877 90863	16 m	ALNGLU/Salix	N	N
		279	NR 78882 90873	26 m	BETPUB	N	N
18. Lilly NW	4/10	201	NR 78851 88572	0 m	ALNGLU/Salix	N	Y
		202	NR 78849 88578	6 m	ALNGLU	N	Y
		203	NR 78844 88583	16 m	BETPUB	N	N
19. Linne NE	4/10	204	NR 79994 91278	0 m	BETPUB	Y	Y
		205	NR 79998 91276	6 m	BETPUB	Y	Y
		206	NR 80007 91276	16 m	BETPUB	N	N
		207	NR 80017 91276	26 m	BETPUB	N	N
20. Lilly N End	4/10	280	NR 78965 88611	0 m	ALNGLU	N	N
		281	NR 78968 88615	6 m	ALNGLU/BETPUB	N	Y
		282	NR 78975 88619	16 m	ALNGLU	N	N
		283	NR 78986 88623	26 m	BETPUB	N	N
21. Linne NW	4/10	284	NR 79879 91366	0 m	ALNGLU/CORAVE	Y	Y
		285	NR 79877 91369	6 m	-	-	c
		286	NR 79870 91374	16 m	CORAVE	N	N
		287	NR 79864 91381	26 m	CORAVE	N	N
22. Lilly SE	4/10	288	NR 78879 88477	0 m	Salix	N	N
		289	NR 78884 88473	6 m	ALNGLU	N	N
		290	NR 78881 88462	16 m	-	-	c
		291	NR 78885 88451	26 m	BETPUB	N	N
23. Lilly SSE	4/10	292	NR 78798 88455	0 m	ALNGLU/Salix	N	N
		293	NR 78798 88450	6 m	BETPUB	N	N
		294	NR 78803 88441	16 m	BETPUB	N	N
		295	NR 78809 88430	26 m	BETPUB	N	N
24. Lochan Buic SW	4/10	296	NR 78747 88723	0 m	BETPUB/Salix	N	Y
		297	NR 78738 88715	6 m	BETPUB	N	N
		298	NR 78730 88719	16 m	BETPUB	N	N
		299	NR 78726 88719	26 m	BETPUB	N	N
25. Lochan Buic NE	4/10	2101	NR 79040 88975	0 m	BETPUB/ALNGLU/ CORAVE	Y	Y

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species‡	Beaver sign# 2010	2011
		2102	NR 79054 88964	6 m	ALNGLU/BETPUB		d
		2103	NR 79067 88965	16 m	CORAVE	N	N
		2104	NR 79063 88977	26 m	BETPUB/CORAVE	N	N
26. Linne E	4/10	274	NR 79699 90798	0 m	BETPUB	Y	Y
		275	NR 79705 90794	6 m	BETPUB	Y	Y
		300	NR 79710 90785	16 m	BETPUB	Y	Y
		2105	NR 79718 90780	26 m	BETPUB	N	N
27. Dubh W	4/10	2705	NR 78346 90062	0 m	BETPUB/SORAUC	Y	a
28. Dubh SW	4/10	2706	NR 78338 90049	0 m	BETPUB/SORAUC	Y	Y
29. Coille Bharr NE	4/10	2894	NR 78665 90445	0 m	ALNGLU/CORAVE	N	Y
		2895	NR 78670 90441	6 m	ALNGLU	N	N
		2896	NR 78675 90437	16 m	ALNGLU/SORAUC	N	N
		2897	NR 78703 90399	26 m	BETPUB/SORAUC	N	N
30. Lochan Buic E	4/10	2921	NR 78914 88790	0 m	BETPUB/Salix	N	N
		2922	NR 78915 88785	6 m	BETPUB/CORAVE	N	N
31. Lochan Buic W.	11/10	3221	NR 78832 88864	0 m	ANLGLU/BETPUB	N	Y
		3223	NR 78828 88863	6 m	BETPUB	N	Y
		3223	NR 78817 88862	16 m	BETPUB	N	N

Footnote to Table 2: * From nearest edge to water ‡ Species codes are listed in Table 4. # Beaver sign includes any gnawing or felling of woody vegetation up until Nov 2010 or Nov 2011 respectively. Other changes to the status of plots a: Plot now flooded due to beaver activity, b: Plot partially bulldozed by forestry activities, c: No trees occurred in this plot, d: Location of plot 2102 coincided with a track.

Beaver activity was recorded in 15 plots for the first time, during the year Nov 2010- Nov 2011.

4.2 Ground cover in subplots

Results for ground cover estimates and seedling counts in the two subplots in each vegetation plot in November 2011 are presented in Table 3. It was not anticipated that any major changes in ground vegetation would take place across any single year but these data are presented for completeness. Towards the end of the trial, a full statistical comparison will be made, in order to quantify any effects of beaver activity on the ground cover parameters. It should be borne in mind that the results of these ground cover surveys are very season-specific, and quite different results might be returned at other times of the year. It is notable that only 9 seedlings of woody plants were recorded across all plots.

Table 3. Mean percent ground cover of ten categories estimated in November 2011 in two 2 × 2 m subplots in each plot and mean number of woody seedlings per subplot.

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryophytes	Dwarf shrubs	Herb	Seedlings
1; 0m	97.5	0	0	0	0	0	0	2.5	0	0	0
1; 6m	25	0	0	5	17.5	5	7.5	45	5	2.5	0
1; 16m	0	0	0	0	45	5	27.5	80	0	1.275	0
1; 26m	0	0	0	0	37.5	10	17.5	90	0	2.5	0
2; 0m	2.5	0	5	45	22.5	7.5	1.275	40	25	0	0
2; 6m	5	0	5	27.5	22.5	20	2.5	55	0	5	0
2; 18m	0	0	5	17.5	22.5	20	2.5	85	0	1.25	0
2; 26m	2.5	0	5	27.5	40	35	5	80	0	1.25	0
3; 0m	0	0	0	57.5	30	6.25	2.5	35	5	1.25	0
3; 6m	0	0	0	47.5	12.5	3.75	3.75	70	0	0	0
3; 16m	0	0	0	42.5	27.5	7.5	3.75	70	0	1.25	0

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryophytes	Dwarf shrubs	Herb	Seedlings
3; 26m	0	0	0	47.5	35	12.5	2.75	30	0	1.25	0
4; 0m	5	0	0	65	3.75	1.25	0	40	1.25	0	0
4; 6m	1.25	0	2.5	85	3.75	2.5	0	30	1.25	2.5	0
4; 16m	0	0	0	3.75	17.5	22.5	1.25	92.5	0	0	0
4; 26m	0	0	1.25	20	20	20	1.25	92.5	0	0	0
5; 0m	0	0	0	45	15	5	7.5	65	3.75	1.25	0
5; 6m	0	0	2.5	47.5	10	15	2.5	52.5	12.5	3.75	0
5; 16m	0	0	0	92.5	2.5	1.25	2.5	15	25	0	0
5; 26m	1	0	2.5	72.5	5	3.75	5	32.5	0	0	0
6; 0m	100	0	0	77.5	0	0	0	0	0	0	0
6; 6m	100	0	0	42.5	2.5	17.5	0	0	0	0	0
6; 16m	87.5	0	0	40	0	7.5	0	7.5	0	0	0
6; 26m	27.5	0	17.5	32.5	3.75	12.5	1.25	30	0	1.25	0
7; 0m	0	0	2.5	6.25	17.5	5	40	80	7.5	2.5	0
7; 7m	0	2.5	2.5	2.5	50	25	10	65	5	1.25	0
7; 16m	0	7.5	0	0	42.5	3.75	2.5	72.5	37.5	1.25	0
7; 26m	0	17.5	0	0	27.5	2.5	20	55	40	0	0
8; 0m	0	0	2.5	75	30	0	0	25	0	0	0
8; 6m	0	0	22.5	40	50	1.25	1.25	31.25	0	5	0
8; 16m	0	0	0	47.5	45	5	1.25	22.5	0	3.75	0
8; 26m	0	2.5	5	45	40	2.5	3.75	37.5	0	5	0
9; 0m	2.5	0	7.5	62.5	10	5	0	31.25	0	7.5	0
9; 6m	0	0	5	97.5	50	1.25	0	11.25	0	3.75	0
9; 16m	2.5	0	2.5	40	12.5	2.5	1.25	72.5	0	0	0
9; 26m	0	0	0	8.75	30	20	3.75	97.5	0	1.25	0
10; 0m	0	0	12.5	60	7.5	5	2.5	60	0	1.25	0
10; 6m	0	0	0	62.5	15	2.5	8.75	37.5	0	12.5	0
10; 16m	0	0	5	75	7.5	0	2.5	47.5	0	3.75	0
10; 26m	0	0	2.5	35	10	2.5	3.75	40	0	10	0
11; 0m [a]	10	0	0	20	5	5	0	90	0	0	0
11; 10m	0	0	0	22.5	22.5	5	6.25	65	2.5	0	0
11; 20m	0	0	0	32.5	40	7.5	1.25	85	12.5	0	0
12; 0m	5	0	15	75	1.25	0	0	7.5	0	10	0
12; 6m	1.25	0	2.5	80	5	3.75	12.5	82.5	0	3.75	0
12; 16m	10	0	5	32.5	10	2.5	15	50	5	2.5	0
12; 26m	2.5	0	0	52.5	5	0	10	40	25	2.5	0
13; 0m	0	0	0	55	5	8.75	3.75	75	7.5	3.75	0
13; 6m	0	0	0	72.5	5	7.5	3.75	45	36.25	0	1.5
13; 16m	0	0	0	17.5	25	20	5	80	1.25	1.25	0
13; 26m[b]	-	-	-	-	-	-	-	-	-	-	-
14; 0m	2.5	2.5	2.5	92.5	5	0	2.5	7.5	0	2.5	0
14; 6m	5	0	92.5	3.75	1.25	12.5	15	0	2.5	0	0
14; 16m	0	0	2.5	87.5	10	1.25	7.5	8.75	0	7.5	0
14; 26m	0	0	0	92.5	7.5	2.5	1.25	25	0	2.5	0
15; 0m	0	0	5	50	2.5	2.5	0	55	0	0	0
15; 6m	0	0	2.5	70	5	12.5	0	17.5	0	0	0
16; 0m	0	0	2.5	52.5	5	3.75	5	87.5	11.25	0	0
16; 6m	0	0	2.5	12.5	12.5	10	21.25	60	5	0	0
16; 16m	0	0	0	75	5	30	7.5	12.5	0	0	0
16; 26m	0	0	0	32.5	12.5	1.25	15	67.5	0	0	0
17; 0m	0	0	17.5	77.5	12.5	0	1.25	2.5	0	5	0
17; 6m	50	0	7.5	77.5	7.5	0	2.5	2.5	0	3.75	0
17; 16m	12.5	0	35	52.5	10	3.75	0	3.75	0	7.5	0
17; 26m	0	0	0	60	17.5	20	2.5	55	0	2.5	1
18; 0m	0	0	0	60	40	6.25	1.25	25	20	0	0
18; 6m	0	0	0	77.5	20	5	1.25	42.5	0	3.75	0
18; 16m	1	0	32.5	8.75	55	2.5	2.5	62.5	0	8.75	0

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryophytes	Dwarf shrubs	Herb	Seedlings
19; 0m	0	0	2.5	47.5	2.5	1.25	47.5	12.5	0	0	0
19; 6m	0	0	0	75	7.5	7.5	5	60	1.25	0	0
19; 16m	0	0	2.5	85	7.5	2.5	17.5	60	2.5	0	0
19; 26m	0	10	0	5	22.5	2.5	12.5	95	22.5	0	0
20; 0m	0	0	5	92.5	5	1.25	0	0	0	8.75	0
20; 6m	0	0	7.5	80	25	0	0	23.75	0	12.5	0
20; 16m	5	0	0	90	17.5	2.5	0	5	0	7.5	0
20; 26m	0	0	25	13.75	50	35	1.25	50	0	5	0
21; 0m	0	0	0	67.5	20	0	8.75	17.5	2.5	3.75	0
21; 6m	0	0	0	15	20	0	82.5	2.5	0	0	0
21; 16m	0	0	0	60	10	2.5	45	22.5	0	2.5	0
21; 26m	0	0	7.5	2.5	77.5	1.25	40	12.5	0	1.25	1.5
22; 0m	0	0	7.5	67.5	60	1.25	0	15	0	1.25	0
22; 6m	0	0	0	85	40	2.5	0	18.75	0	5	0
22; 16m	10	0	0	90	10	0	0	10	0	11.25	0
22; 26m	20	0	10	27.5	30	2.5	0	17.5	0	17.5	0
23; 0m	1.25	0	2.5	92.5	15	1.25	0	7.5	0	0	0
23; 7m	0	0	0	92.5	22.5	0	0	25	0	0	0
23; 16m	0	0	1.25	1.25	30	5	2.5	97.5	0	0	0
23; 26m	0	0	2.5	23.75	25	32.5	0	75	0	0	0
24; 0m	0	0	0	22.5	15	0	0	92.5	0	0	0
24; 6m	0	0	0	87.5	12.5	16.25	0	75	0	1.25	0
24; 16m	0	0	0	8.75	50	50	0	100	0	2.5	0.5
24; 26m	0	0	10	5	50	25	1.25	51.25	0	2.5	0
25; 0m	0	22.5	2.5	30	45	12.5	0	22.5	1.25	2.5	0
25; 6m [c]	-	-	-	-	-	-	-	-	-	-	-
25; 16m	0	0	0	57.5	20	0	1.25	60	0	3.75	0
25; 26m	0	0	0	42.5	32.5	22.5	8.75	55	0	2.5	0
26; 0m	15	0	0	16.25	17.5	16.25	40	20	6.25	0	0
26; 6m	0	0	2.5	10	10	17.5	22.5	85	2.5	0	0
26; 16m	0	0	2.5	6.25	22.5	55	2.5	77.5	8.75	0	0
26; 26m	0	0	0	1.25	47.5	50	1.25	95	1.25	0	0
27; 0m[d]	-	-	-	-	-	-	-	-	-	-	-
28; 0m	97.5	0	0	0	0	0	0	2.5	0	0	0
29; 0m	0	0	0	42.5	60	6.25	2.5	55	0	0	0
29; 6m	0	0	0	82.5	22.5	0	5	20	0	1.25	0
29; 16m	0	0	7.5	32.5	15	2.5	21.25	22.5	0	8.75	0
29; 26m	2.5	0	5	2.5	30	6.25	10	67.5	0	3.75	0
30; 0m	0	0	5	50	12.5	2.5	3.75	72.5	0	3.75	0
30; 6m	0	0	0	55	20	11.25	0	55	0	6.25	0
31; 0m	0	0	0	85	20	6.25	3.75	37.5	2.5	0	0
31; 6m	0	0	0	27.5	10	3.75	0	92.5	0	0	0
31; 0m	0	0	0	1.25	27.5	10	6.25	100	10	0	0

4.3 Vegetation composition and structure in plots

The numbers of stems of tree and shrub species, and their basal areas, in the final set of plots that were established by November 2010 are shown in Table 4. These represent a consistent baseline data-set for availability of trees to beavers, against which future comparisons can be made. Fourteen tree and shrub species were identified in the vegetation plots. However, because they were not in leaf during fieldwork, willows could only be identified to genus, meaning that species diversity has been underestimated. However, most *Salix* at Knapdale is believed to be *Salix caprea*. Numerically, *B. pubescens* is clearly dominant, and only *A. glutinosa, C. avellana, Salix* spp. and *S. aucuparia* can also be considered abundant. In much of the following analysis, these five species, and *Fraxinus*, have been considered individually, with the remaining species grouped in the category ‘other’. When total basal area was considered, the dominance of *B. pubescens* over *A. glutinosa* was less marked. This result can be largely explained by the widespread occurrence of dense thickets of young, small birch trees which have grown in place of recently cleared conifer plantations throughout Knapdale. The substantial contribution made by *A. glutinosa* to the total basal area despite its more modest stem count, reflects the fact that this species most commonly occurs as large trees right at the water’s edge.

Table 4. Total number of upright stems and total basal area of all tree and shrub species recorded in plots at November 2010. Asterisked rows indicate species categories that were summed and treated as a single category in most data summaries and analyses.

	Common name	Code	Species	Stem Count	Total basal area (cm^2)	Median diameter (cm)
*	Sycamore	ACEPSE	*Acer pseudoplatanus*	2	4	1.5
	Black alder	ALNGLU	*Alnus glutinosa*	534	112,100	5.0
	Downy birch	BETPUB	*Betula pubescens*	2986	121,403	3.0
	Hazel	CORAVE	*Corylus avellana*	375	12,065	3.0
*	Hawthorn	CRAMON	*Crataegus monogyna*	5	162	2.0
*	Douglas fir	PSEMEN	*Pseudotsuga menziesii*	1	3	2.0
	Ash	FRAEXC	*Fraxinus excelsior*	58	10,595	7.0
*	Holly	ILEAQU	*Ilex aquifolium*	1	79	10.0
*	Bog myrtle	MYRGAL	*Myrica gale*	11	37	2.0
*	Sitka spruce	PICSIT	*Picea sitchensis*	26	7,216	5.5
*	Sessile oak	QUEPET	*Quercus petraea*	6	1,444	2.0
*	Wild rose	ROSACI	*Rosa acicularis*	1	1	1.0
	Willow	Salix	*Salix* spp.	509	15,260	4.0
	Rowan	SORAUC	*Sorbus aucuparia*	395	7,736	2.0
	TOTAL			4,910	288,105	

Because beavers are expected to have the greatest effect on woodland near to the water’s edge, different tree and shrub species may vary in their susceptibility to beaver herbivory if their distributions differ in relation to distance from water. Figure 4 shows how the abundance of each species differs with distance from the water. The density of *A. glutinosa, C. avellana* and *F. excelsior* decrease and the density of *B. pubescens* increases with distance from water. It is clear that the greatest number of large *A. glutinosa* were found near the water’s edge. *S. aucuparia* was most abundant within 4 m of the water.

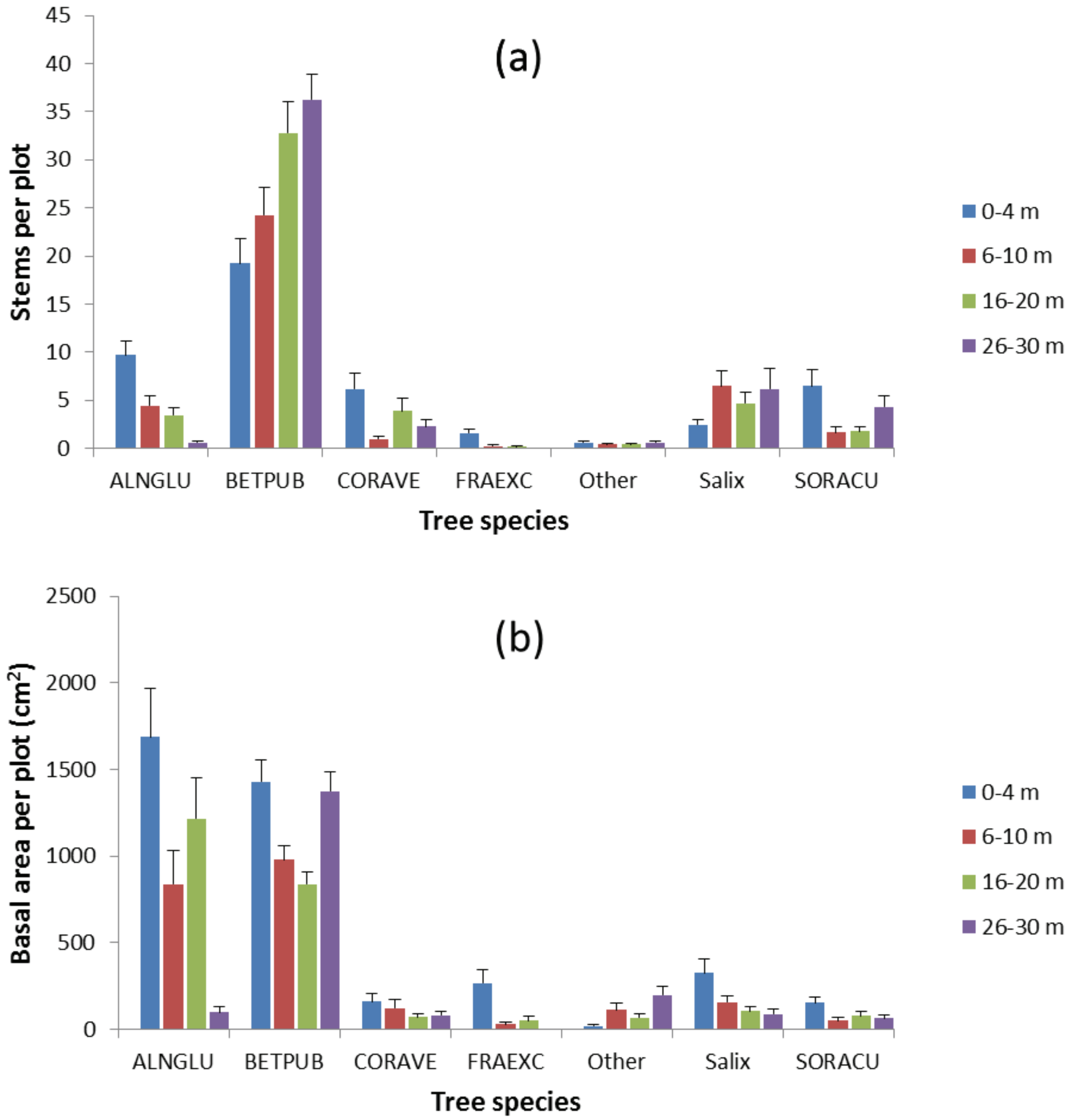


Figure 4. (a) Mean number of stems per plot and (b) mean total basal area per plot for six common tree and shrub species in plots located at increasing distances from the water's edge. The less common tree and shrub species are pooled in the 'other' category. Error bars indicate 1 standard error.

4.4 Beaver effects

4.4.1 Use of transects by beavers

The establishment of transects was partly guided by existing beaver effects, making these data unsuitable for a formal analysis of the factors influencing beaver preferences for vegetation communities present in different transects. However, up to November 2010, 17 of the 31 (54.8%) transects included trees that had been gnawed by beavers and a further 7 hitherto unused transects had been used by November 2011, meaning that 77.4% had been used by that time. The intensity of beaver effects on each transect remains variable.

4.4.2 Use of plots by beavers

Of the 108 plots surveyed in November 2010, data for 105 of them were also available in 2011. In the interim two had been flooded due to beaver damming and one partially bull-dozed. In November 2010, 30.5% had signs of beaver effects on trees, and this had increased to 43.3% by November 2011 (Table 2). The additional plots established in 2010 were, like those previously set up, sited in anticipation of the establishment of further beavers released in these areas, and hence the plots are not an unbiased or random sample of the woodland at Knapdale.

A comparison of plots used by beavers with plots not used by beavers informs us how vegetation community and proximity to water influence the likelihood that a plot will be used by beavers. Figure 5 compares the abundance of each of the major tree and shrub species in plots not used by beavers to their abundance in plots that were used by beavers. These data, collected in November 2011, suggest that beavers preferentially used plots dominated by dense birch and that they avoided plots dominated by large alder trees. Comparing these data with those from November 2010 suggests that the preference for dense birch plots has declined between the two sampling dates. This may reflect a relative shift away from greater activity in construction of lodges during initial establishment, to a greater preponderance of foraging activity, particularly in those areas in which the breeding pairs produced kits. Through 2011, plots used by beavers continued to be characterised by substantially more stems of *Salix* and rowan than plots that were not used.

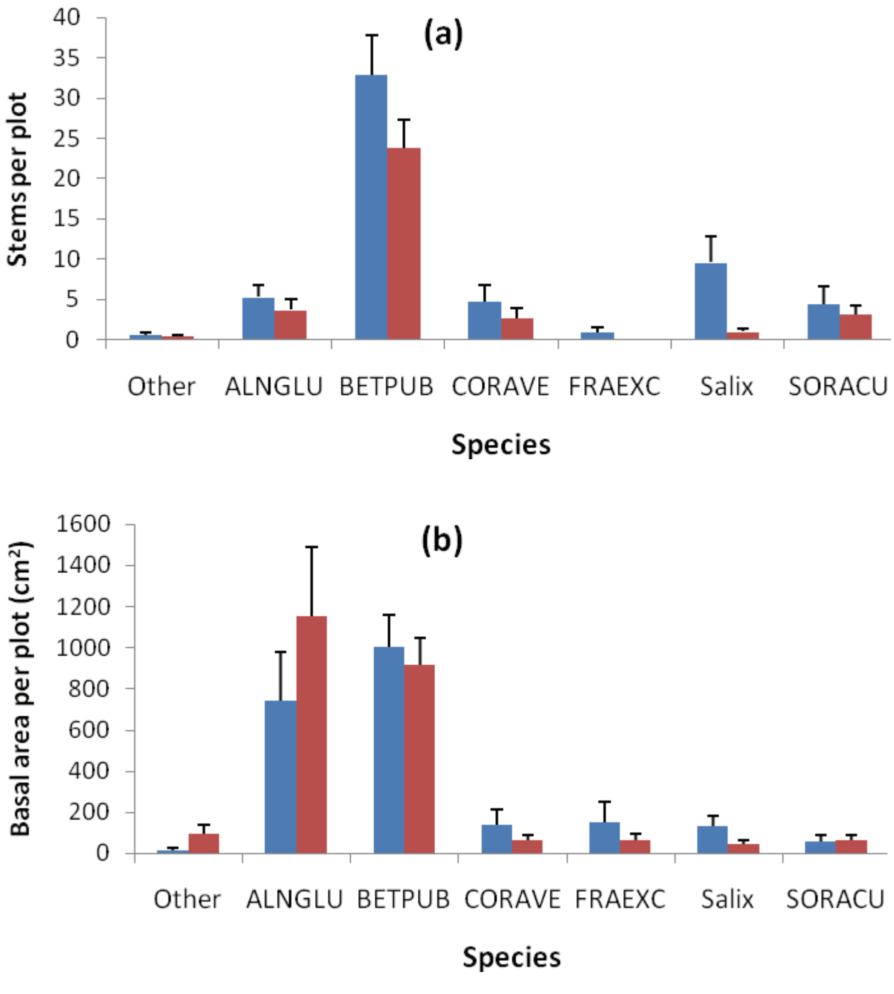


Figure 5. (a) Mean number of stems per plot and (b) mean total basal area of each tree & shrub *species in plots without (red; n = 59) and with (blue; n = 45) evidence of beaver*

browsing up to November 2011. The less common tree & shrub species are pooled in the 'other' category. Error bars indicate 1 standard error; species codes from Table 4.

Of the 15 plots newly used by beavers in 2011, 73.3% were either 0m or 6m from the water (Table 2). The dam at Dubh Loch has substantially expanded the area of that water body into the surrounding woodland and across a nearby Forestry Commission road and walking track. Since November 2009, the beavers had continued to improve the dam, consequently expanding the flooded area as reported previously (Moore *et al.* 2010, 2011). This flooding has prevented access to some of the plots established in that area (Table 2).

Figure 6 illustrates how beaver effects varied with the plots' proximity to water. It was reported previously (Moore et al. 2011), that between 2009 and 2010 there had been a slight tendency for beaver effects on trees to be occurring slightly further from the water's edge. This would be expected because although beavers would prefer to forage close to water which permits escape from predators, as the beavers deplete their preferred food sources at these locations they might be forced to forage elsewhere. A comparison of the incidences of beaver herbivory per plot up to November 2010 and between November 2010 and November 2011 showed a further tendency for greater incidences of herbivory in plots that were further away from the water's edge. However, there was a large variability in the new incidences of herbivory among plots and this putative spatial shift in beaver activity is not yet statistically proven, in that the interaction between year of measurement and incidences per plot was not statistically significant.

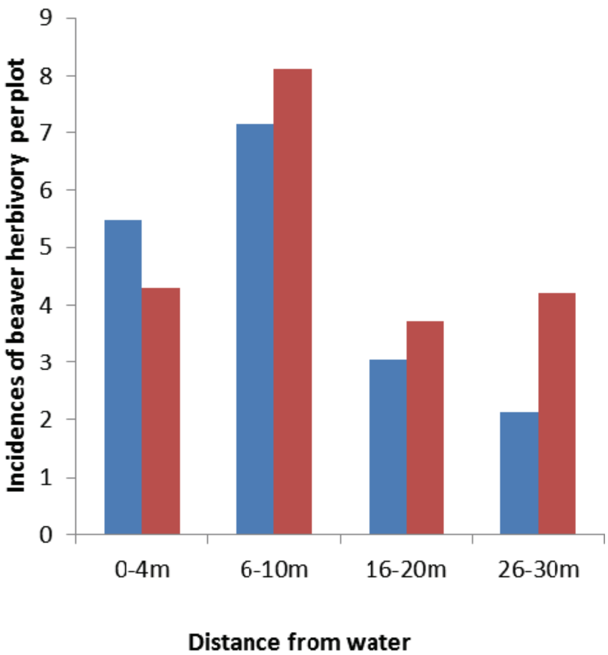


Figure 6. Distribution of beaver effects, expressed as mean number of new incidences per plot, with plot distance from water's edge, occurring in the period up to and including November 2010 (blue bars) and the period November 2010-November 2011 (red bars).

A second important facet of the spatial distribution of the effects of beavers on trees, is the possibility that the distance at which they forage from their lodges would increase as the preferred food types that are close to them are depleted. The consistent recording of the same set of plots in November 2010 and November 2011 permits a comparison of the distance of these plots from the nearest beaver lodges, how this has changed over time and in relation to the plot characteristics. A REML-GLM[3] analysis of the distances between the lodges and the plots was conducted, entering 'lodge' as a random effect and whether or not the plot was dominated by preferred or heavily used species, (defined as stems of either *Salix*, or *Betula pubescens* or when these occurred in combination with each other or *Sorbus aucuparia*) and whether the plot showed signs of browsing imposed during the year prior to assessment in November 2010 and November 2011. Not unexpectedly, beavers used plots closer to their lodges (Fig 7: $F = 38.4$, df = 1,215, $P<0.001$). The distances from the lodges to plots that were dominated by tree and shrub species considered to be preferred by beavers were shorter than those to plots that were dominated by un-preferred species (Fig 7: $F = 14.1$, df = 1,215, $P<0.001$). But although the overall pattern of plot use is that beavers use plots close to their lodges that contain their preferred species (Fig 7), this effect is not statistically significant ($F = 2.41$, df = 1,214, $P=0.12$). There was no significant change in these patterns of plot-use by beavers between November 2010 and November 2011, ie no interaction effects involving autumn of measurement. Overall the results suggest that beavers are in general continuing to exploit the woodland resources by using plots containing preferred species that are closer to their lodges. This emphasises the importance of the beavers' decision in where to situate their lodges. There is a slight tendency for beavers to use plots that are further from the water's edge compared to the previous year up to November 2010. However neither of these slight shifts in plots affected by beavers is as yet statistically significant. It is notable that the Creagmhor Loch beavers have built a new lodge on the neighbouring Loch Beag. Of the sixteen monitoring plots on Creagmhor loch, only two were used at all by beavers between November 2010 and November 2011. The plots on Creagmhor Loch were not particularly distant from the original lodge constructed compared to those plots associated with the other lodges.

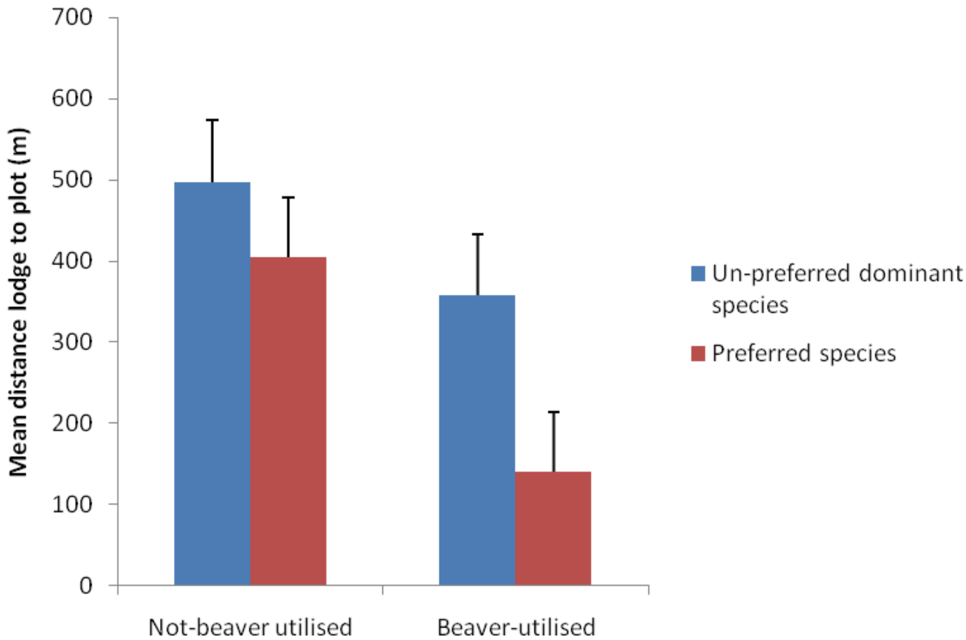


Figure 7. The mean distance from the four main beaver lodges to their corresponding monitoring plots in relation to whether or not the plots were utilised by beavers and whether the plot consisted of a dominant species that was unpreferred (blue bars) or preferred or frequently used by beavers (red bars). The data cover the periods up to November 2010, and between November 2010 and November 2011, although no difference between time periods was detected.

[3] Residual Maximum Likelihood – Generalised Linear Model. Used to test for effects of possible explanatory variables.

4.4.3 Use of tree and shrub species by beavers

Different tree and shrub species differ in their abundance and spatial distribution at Knapdale but also in their suitability as food sources for beavers. Consequently, it is expected that the proportional use of preferred species should be greater than their proportional availability and, conversely, that of avoided species should be less than their availability. It is clear that the majority of direct beaver effects observed at Knapdale were on *B. pubescens* (Figure 8).

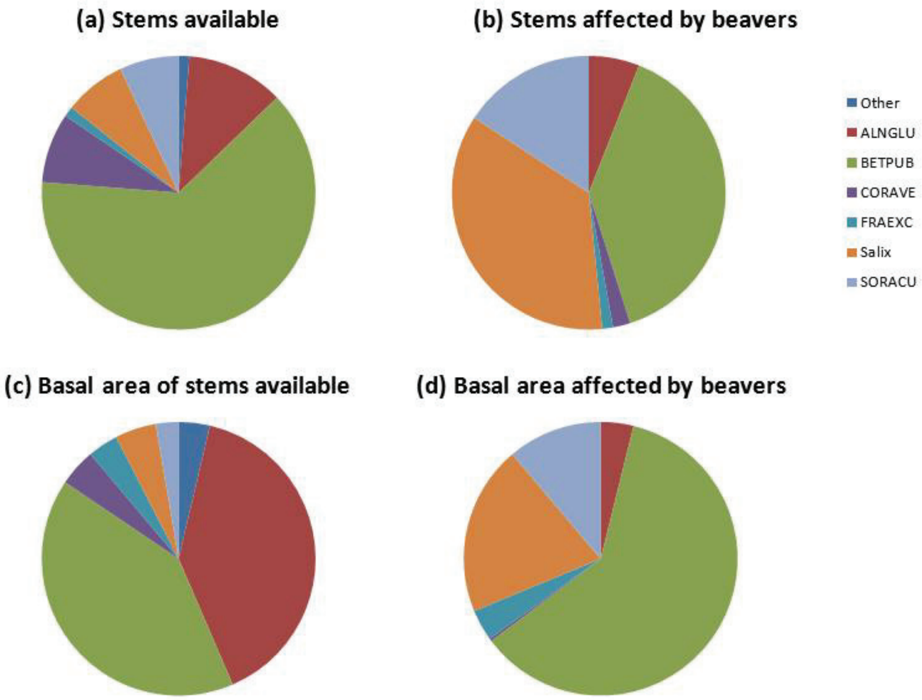


Figure 8. Proportional composition by species of (a) total number of stems in plots at Knapdale and (b) total number of these stems gnawed by beavers attributable to major species, and proportions of (c) total summed basal area of stems in plots at Knapdale and (d) total summed basal area of these trees chewed by beavers. These data include all stems recorded up to and including November 2011. The less common tree and shrub species are pooled in the 'other' category. Species codes can be found in table 4.

Figure 8 shows that although fewer individual stems of *B. pubescens* were browsed than expected from its availability, the total basal area of browsed *B. pubescens* was greater than expected. This finding suggests that beavers tended to favour large birch trees over the small birch trees typical of dense stands of birch growth. Figure 8 also strongly suggests that *A. glutinosa,* and large trees in particular, were avoided by beavers, while *Salix* and *S. aucuparia* were fairly strongly preferred relative to their availability, both on the basis of tree numbers and basal area. *F. excelsior* was used at a rate similar to its abundance, while *C. avellana* was used much less than would be expected from its abundance, and when it was used, only very small branches were gnawed. It should be noted however that the apparent availability of *C. avellana* is somewhat misleading; it is less widespread than other species, but a very large number of small stems was often recorded growing from only a few stools. This overall pattern of tree selection relative to availability is similar to the conclusions of previous reports (Moore *et al*. 2011), but a fuller analysis based on foraging in individual years, rather than effects accumulated across years, will be undertaken towards the end of the trial reintroduction.

4.4.4 Use of individual trees by beavers

The majority of marked and measured stems in the plots in November 2011 were still standing trees unaffected by beavers. However, stems, stumps and branches were recorded in all 11 status categories (Table 5). By November 2010, 10.2 % of trees in the plots had been directly affected by beavers, however these accounted for only 4.8 % of the total basal area. By November 2011, 13.0% of the trees in the plots had been affected by beavers (Table 5).

Table 5. Eleven status classes used to classify trees and tree parts in the plots, codes used to record them, and the numbers of each class recorded in vegetation plots in November 2010 and changes recorded in 2011.

Status	Code	Count 2010	Count 2011	Diff 2010-2011	Total basal area 2010 (cm^2)	Total basal area 2011 (cm^2)
Site where a minor branch removed from standing tree	BCut	7	11	+4	6	38
Log felled by beavers	BLog	26	39	+13	2 273	2669
Tree partially felled by beavers	BP	33	41	+7	3 774	4156
Stump of tree felled by beavers	BStump	379	490	+111	8 229	9887
Upright tree gnawed by beavers	BUp	62	55	-7	2 441	4219
Upright stems growing from a log	LogUp	28	28	0	251	250
Naturally fallen log	NLog	39	42	+3	13 212	12139
Naturally partially fallen tree	NP	1	2	+1	1 809	1828
Natural tree stump	NStump	9	26	+17	264	558
Felled Stump	HumanSt	0	2	+2	*	41
Tree pushed down by beaver tree	Bent	*	21	n/a	*	93
Base of Tree Affected	Base	*	30	n/a	*	4657
Upright tree, unaffected by beavers	Up	4422	4212	-210	271 707	264608
Tagged 2009, 2010 missing 2011	Gone	20	69	+49	20	743
TOTAL (excl. 'Gone')		5 006	4999		303 966	305143

Up to November 2011 beaver gnawing occurred at a variety of heights on the tree stem, mostly between 0 and 70 cm (Figure 9). The mean height of gnawing was 34.4cm, approximately the same as in 2010 (mean 29.4cm), although fewer stems were gnawed at ground level compared to 2010. It is likely that as the beaver reintroduction trial proceeds, the height of beaver gnawing will be increasingly influenced by the availability of regrowth following previous beaver activity.

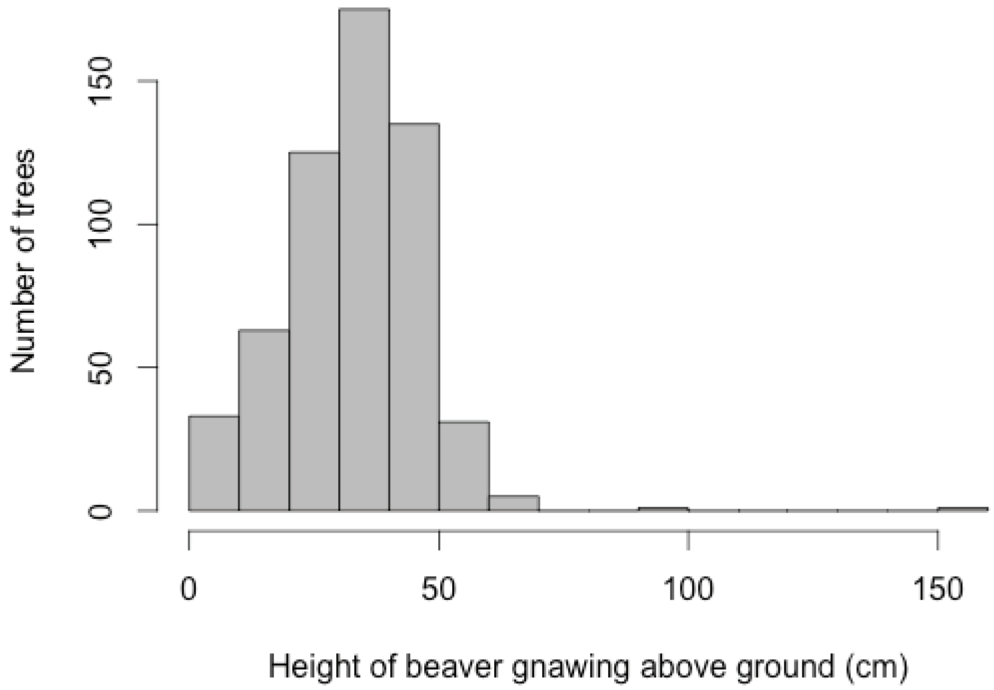


Figure 9. Histogram illustrating the distribution of heights of beaver gnawing above the ground up to 2011. Size classes are labelled with their upper limits.

The ultimate effect of beavers on woodland structure at Knapdale will be strongly influenced by which individual trees beavers fell. Figure 10 compares the distribution of stem diameters amongst all trees measured in the vegetation plots and among trees gnawed or felled by beavers up to and including November 2011. Numerically, the vegetation surrounding the lochs at Knapdale is dominated by small trees, reflecting the extensive areas of recent regrowth of birch, in particular, described by Brandon-Jones *et al.* (2005).

It seems that beavers use very small trees (diameter ≤ 2 cm) less than their availability would dictate, and mostly use trees of diameter 2 – 6 cm. The distribution of sizes of stems gnawed by beavers as measured in November 2011, was approximately the same as measured in November 2010 (Figure 10, Moore *et al*. 2011), but there was a slight reduction in the mean diameter of the gnawed trees (2010: Mean = 5.08cm, SE = 0.183; 2011: Mean = 4.77cm SE = 0.153; P=0.067). Trees larger than 6 cm diameter were gnawed approximately in proportion to their abundance. In our sampling plots, very few trees of diameter ≥ 20 cm were observed to have been directly affected by beavers. However trees of this size and considerably larger were commonly observed both as stumps and partially felled trees throughout the trial area more widely, particularly close to the water.

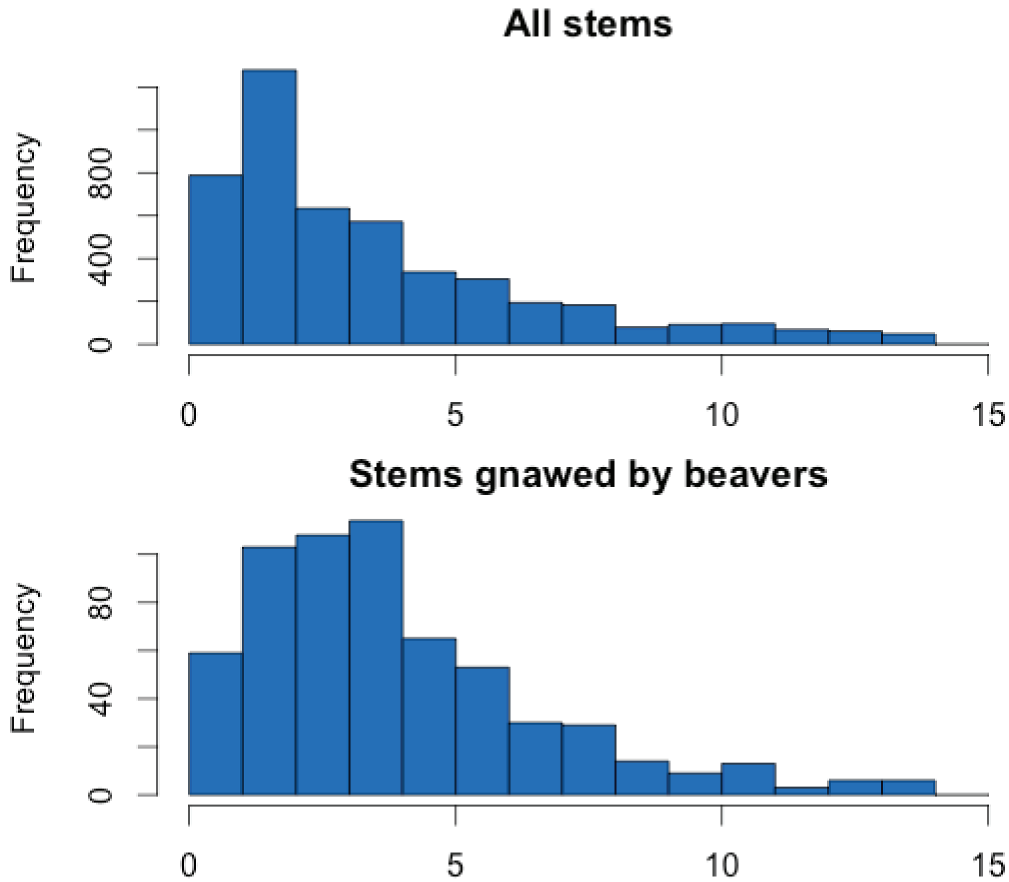


Figure 10. Frequency histograms illustrating the distribution of stem diameters of all trees and shrubs recorded in plots at Knapdale (top) as at November 2010, and the distribution of stem diameters of trees gnawed or felled by beavers up to November 2011 in the plots (bottom). These histograms are truncated; beavers also use some trees larger than 15 cm diameter.

4.5 Resprouting and subsequent deer and beaver browsing

An important factor that will influence the effects of beavers on riparian woodland in the medium to long-term is the resprouting of stumps of felled trees. The key rationale for conducting two monitoring sessions in the woodland each year is to estimate both rates of browsing by deer and beavers on new shoots during the non-growing season as well as rates of browsing and net growth during the growing season. In November 2009, no new sprouts were observed on beaver stumps in the permanent plots, and little significant resprouting was observed elsewhere in the trial site (Moore *et al.* 2010). As expected this situation had changed little by April 2010, as the intervening winter period was not favourable for plant growth. The patterns of resprouting occurring on trees directly affected by beavers, in particular stumps and partially felled trees, observed in November 2010 showed that the mean number of shoots growing from the stumps or bases of trees previously felled by beavers observed was 4, but the median and modal values were zero. So although relatively few of the trees had resprouted, some had produced large numbers of resprouted shoots. This remains the situation as at November 2011 (Figure 11), and the lengths of those resprouted shoots remain fairly short, most of them are 10mm or less (Figure 12).

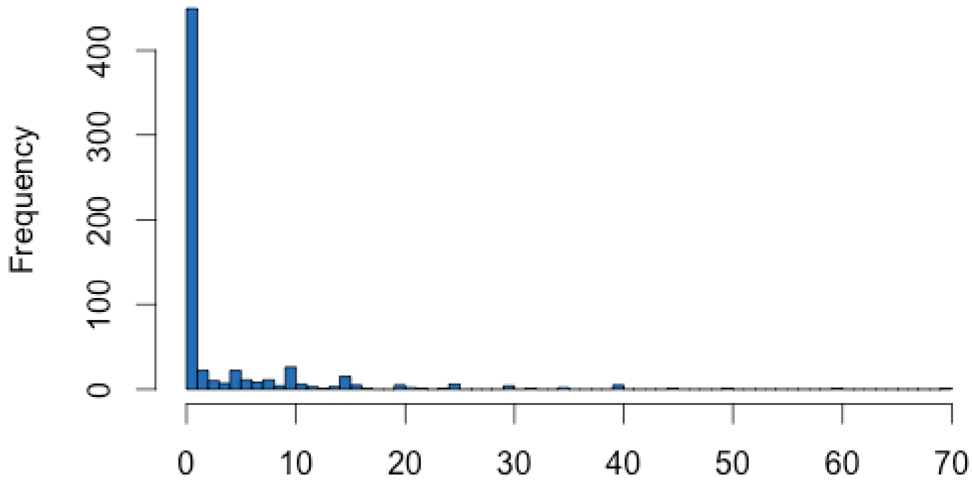


Figure 11. Histogram illustrating the distribution of numbers of new shoots observed, in November 2011, growing from the stumps of trees previously felled by beavers.

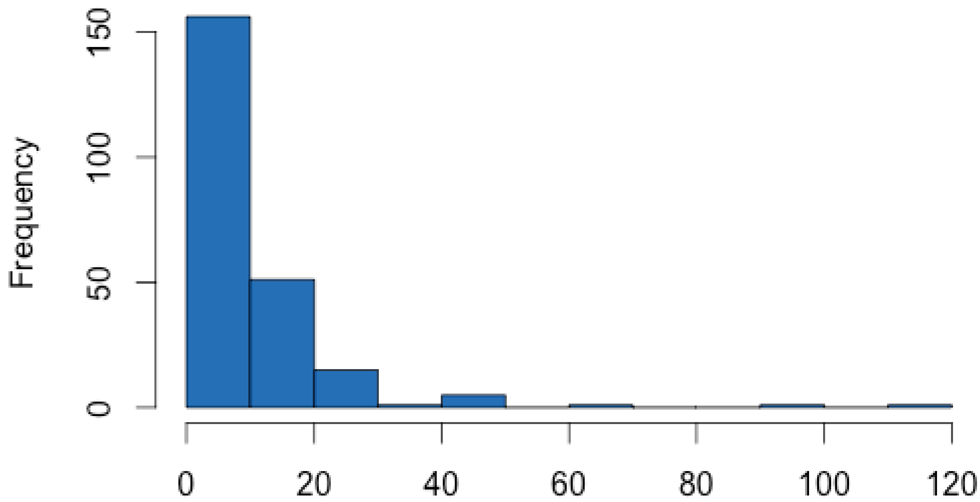


Figure 12. Histogram showing distribution of average shoot lengths (in mm) resprouting from the stumps and bases of all trees gnawed by beavers, November 2011. Instances where no resprouting was observed are not included.

Figure 13 shows resprouting rates by species, demonstrating some strong differences. Ash, willow and rowan are reliable resprouters, which generally produce large numbers of thick shoots. Fewer birch stumps had apparently resprouted in 2011 in comparison to 2010, and this may be due to the senescence of previously resprouted stumps, and the concomitant senescence and disappearance of the many thin, wispy shoots previously recorded in 2010. Many of the remaining resprouted shoots showed signs of frost damage (Figure 14a) and many of the stumps remaining from previous felling activity by beavers had become rapidly overgrown with moss (Figure 14b). Hazel and alder are thus far fairly poor resprouters. Monitoring in April 2011 found browsing on beaver-affected stumps to have been still fairly uncommon, but nonetheless increasing in occurrence at Knapdale in parallel with the increase in availability of resprouted shoots. Furthermore, these signs of recent herbivory by both deer and beavers are more readily distinguishable both from each other and from non-browsing shoot damage, probably because browsing had occurred outside of the growing season, when shoots were already dormant and consequently the shoots have not withered in response to browsing.

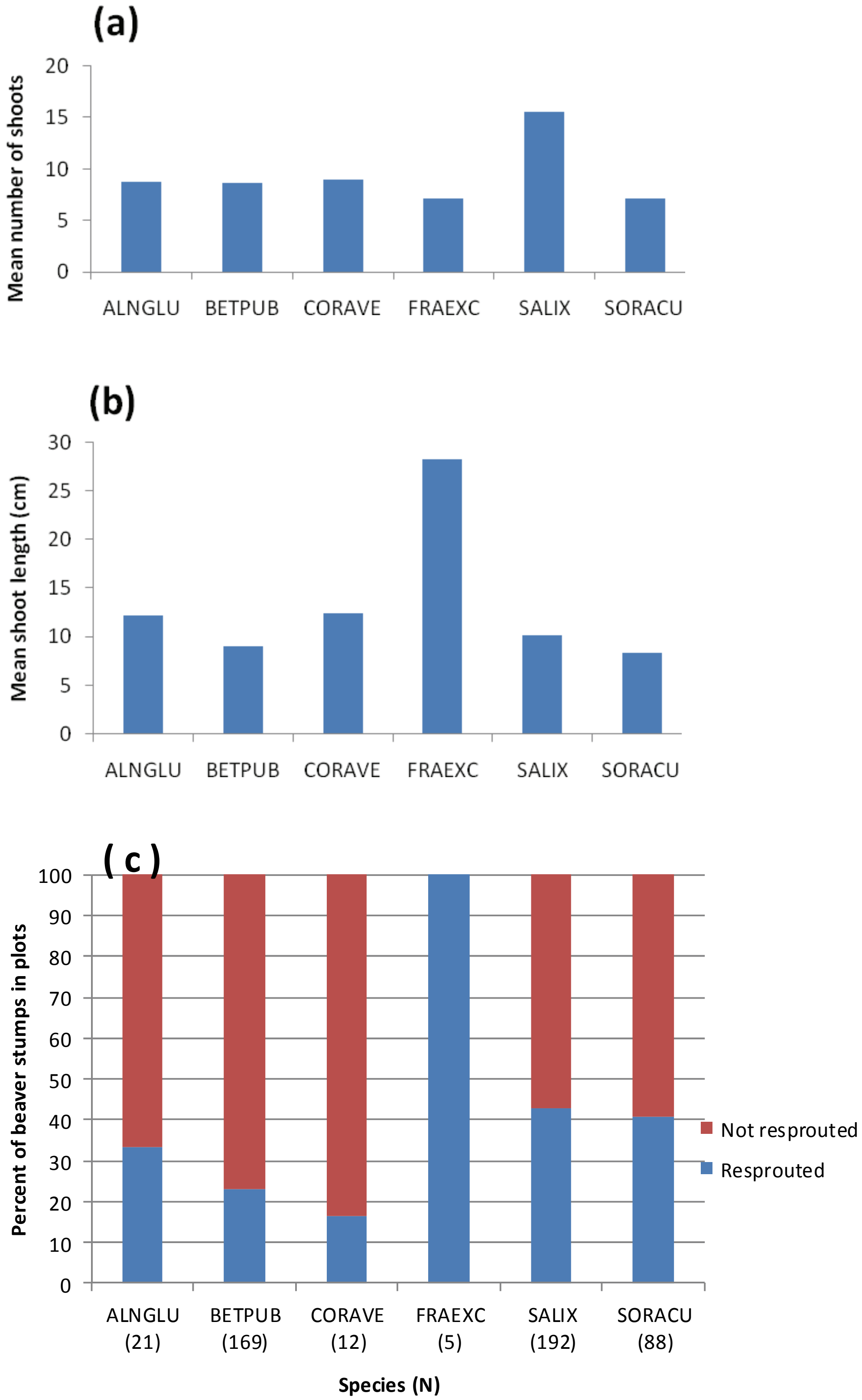


Figure 13. (a) Mean number of shoots and (b) mean length of shoots in mm observed growing from the stumps and base of trees gnawed by beavers in November 2011 and (c) percentage of beaver stumps with and without new resprouting shoots. Number of stumps observed is indicated under species labels.

Figure 14. a) frost damage causing browning to resprouting shoots and b) a stump over-grown by moss.

4.6 Seasonal differences in beaver effects

Because trees in the plots are individually permanently marked and monitored for the duration of this study, all beaver effects that occur after initial marking of these trees can be detected.

Because of the constancy of the composition of the sample of plots recorded in November 2010 and November 2011, the seasonal variation in the effects of beavers on the trees can now be assessed by comparing the frequency of effects of beavers between these dates. During summer and autumn, beavers are expected to feed more on forbs and aquatic macrophytes in addition to the foliage of deciduous trees and to direct their diet more towards the bark and small twigs of woody vegetation as other foods become less available through winter (Krojerová-Prokešová *et al.* 2010). November 2010-April 2011 coincides with the period of winter dormancy of the vegetation and April-November 2011 represents the summer growth period. A greater proportion of the trees changed status during the summer period than the winter period for all species except *S. aucuparia* (Figure 15). This result may be due to the felling and browsing of trees by beavers during the summer months to provide cached food resources and material for lodge-building.

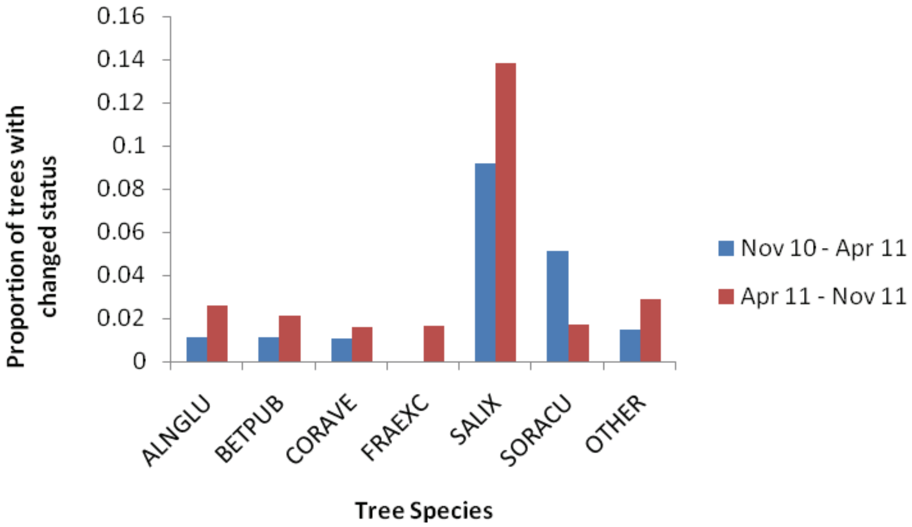


Figure 15. The proportion of stems of each species that changed status between monitoring sessions in November 2010 and November 2011. The descriptions of status are in Table 5. Species codes and the numbers of trees of each species are summarised in Table 4. The less common tree and shrub species are pooled in the 'other' category.

5. DISCUSSION

The fieldwork reported here was conducted 24 and 30 months after the initial reintroduction of beavers to Knapdale in early summer 2009. Over that period there has been some instability in the numbers and locations of beavers, so any interpretation of trends in beaver foraging patterns should still be treated with some caution. However where possible we have drawn comparisons between the situation in November 2010 and November 2011, during which period the precise sample of plots remained fairly constant. Beavers had gnawed and felled a substantial number of trees in marked plots by November 2010, presumably partly for immediate consumption of their inner bark, twigs, shoots and leaves and partly for construction of lodges and dams and for caching under water. In November 2010, 10.2% of trees had been gnawed or felled by beavers, whereas using a comparable method of analysis, this figure had risen to 13.0% by November 2011. The limited information available to date suggests that beavers at Knapdale affected a greater proportion of the available trees and shrubs during the summer months than during the winter months, for almost all species. Herbivory of the upper parts of trees would be expected to yield greater energy and nutrient gains during the summer when they are in leaf. Some of the harvested material would have been cached underwater by beavers. Food caching is a behavioural characteristic that is advantageous to beavers that regularly experience harsh winters, when access to food resources or travel opportunities may restricted by ice for long periods, or the costs of swimming at low temperatures may become too high (Nolet and Rosell 1994). The proportion of the beavers' diet that is comprised of food from other sources such as grasses, forbs and shrubs, or aquatic vegetation is unknown, but likely to be higher during the summer. During the period of this study, and since their effect up to November 2010 were reported, beavers have continued to actively enhance their lodges and a dam, both of which use mainly poles from harvested stems, rather than large tree trunks.

The effect of beavers on Knapdale already extends beyond the direct effects of gnawing and felling of trees. A substantial area has been flooded by a beaver dam at Dubh Loch and vegetation changes can be expected in the flooded woodland. Beavers browse throughout the flooded area, further from Dubh Loch than would otherwise be expected. Flood-tolerant species such as willows and alder may survive there while less flood tolerant species may die but persist for some time as standing dead timber. Ultimately, the vegetation may shift from broadleaf deciduous woodland to swamp or bog.

5.1 Woody vegetation at Knapdale

Since the initial survey undertaken in November 2009 (Moore *et al.* 2010), the number of monitoring plots at Knapdale has been almost doubled, however the mixture of woodland types included in the sample has not changed substantially. The most numerous species in vegetation plots, by a considerable margin, was *B. pubescens*. Dense stands of young regrowth of this species, as well as larger, old trees, occur throughout the area. In many places birch has rapidly colonised areas from which conifer plantations were removed to meet Natura Special Area of Conservation obligations in earlier years. These early successional woodlands are dynamic communities and it will be of great interest to monitor their development in the presence of beavers. *A. glutinosa* is also widespread and common at Knapdale, but in contrast to *B. pubescens*, it occurs primarily as large trees at the water's edge, and for this reason accounts for a similar large proportion of total tree basal area. *Salix* spp., *C. avellana*, *F. excelsior* and *S. aucuparia* were also common in plots and have previously been identified as important components of European beaver habitat elsewhere in Europe (Haarberg & Rosell, 2006, Macdonald *et al*. 1997).

5.2 Beaver browsing preferences and effects

Because the positioning of transects was partially guided by pre-existing beaver herbivory, the plots selected are not an entirely unbiased sample of loch shore, however the number of transects established at Knapdale is now such that all vegetation types are represented and a clear picture of beaver preferences is emerging.

Based upon a comparison of the sizes of trees used by beavers with those available, the preferred tree size for beavers was from 3 – 6 cm diameter, and smaller trees were less preferred, although still commonly used. The mean diameter of stems eaten by beavers has decreased slightly in the last year. The beavers also used some large trees in the plots including those up to 30 cm diameter. Outwith the plots many still larger trees were also observed to have been affected by beavers. A study of foraging by beavers in Telemark, Norway (the source of the reintroduced beavers) found that beavers there tended to use smaller trees than is the case at Knapdale to date (Haarberg & Rosell, 2006). In Telemark, 95 % of cut stems were ≤ 5 cm diameter and these accounted for 47 % of the basal area affected, whereas only 70 % of cut stems were ≤ 5 cm at Knapdale, accounting for only 15 % of affected basal area. This difference may reflect the fact that the habitat at Knapdale has no recent beaver browsing history, whereas past beaver effects in Telemark may have resulted in fewer large trees being available to foraging animals. This has some implications for the woodland structure. First, beavers may not, at least so far, be playing a strong direct role in thinning the dense birch regrowth stands around the lochs which often comprise very small (diameter 1 - 2 cm) trees, and second, their focus on larger trees may significantly reduce the standing biomass of these communities and increase the amount of light reaching smaller trees and the ground. It is clear that beavers will fell or attempt to fell even very large trees.

There have been no changes in the tree and shrub species utilised by beavers at Knapdale. Results show that beavers continue to exhibit a strong preference for willow and rowan in relation to their availability. They avoid alder, and other species are used largely in proportion to their availability. In numerical terms, birch remains the species most frequently used. Haarberg & Rosell (2006) found in Telemark that beavers' species preferences could be ordered willow > rowan > birch > *Prunus* > others > alder > conifers, which is almost perfectly consistent with patterns observed at Knapdale. Note that the alder present in Telemark was *Alnus incana,* not *A. glutinosa*.

Results to date confirm observations from other populations that beaver effects are confined to areas close to water, primarily within 10 m of the shore. Beaver effects were distributed slightly further inland in the November 2010 monitoring period compared with the previous (2009) period, and this trend has continued in the November 2011 monitoring results, with a slight increase in beaver observations in the plots other than those immediately at the water's edge. Some minor beaver activity has been recorded up to 50 m away from the lochs. Where conditions allow, beavers will feed from the water on overhanging branches and trees growing right at the water's edge. Opportunities for this type of feeding seem to be limited at Knapdale, as loch shores are sometimes steep or rocky and often are vegetated with large mature trees such as birch and alder rather than by dense thickets of preferred species such as willow or aspen. Many parts of Knapdale are not suitable for assessing how far beavers forage from the water, because the narrow strip of broadleaf woodland along the edges of the lochs, is hemmed in by dense conifer plantation. The persistence of this and other shifts in the activity of beavers will be revealed by further monitoring, particularly in response to local depletion of preferred species, and expansion of the beaver population. One striking observation supported by casual observations as well as by previously reported plot data is that foraging beyond 20 m from the water was primarily (and exclusively, in the case of the plots), targeted at *Salix* trees (Moore *et al.* 2011). There was no indication from comparisons of the plot monitoring data between years, that plots further from beaver lodges were being increasingly used with time since the release of beavers. It appears that the siting of beaver lodges is a critical factor in determining the beavers' future food supply, foraging ecology and the impacts of their foraging.

In most areas, the majority of felled biomass has been removed for construction, caching or eating elsewhere, or consumed on the spot by beavers. Even some very large trees have been almost entirely removed. As a consequence, the riparian woodland is not generally becoming cluttered with dead wood, and indeed in parts it is beginning to feel more open, particularly when larger, spreading, waterside trees are removed.

It was reported previously that 44% of beaver-affected trees showed evidence of resprouting by November 2010 and that no resprouting was observed in November 2009 (Moore *et al.* 2011). This indicates a lag between tree felling and resprouting for most trees. Timing and likelihood of resprouting may also be sensitive to the time of year at which beaver impacts occur. Those stumps that had resprouted in the November 2011 survey had produced more resprouts which had on average grown in length since the November 2010 survey. However, the percentage of beaver-gnawed stumps that were resprouting was only 35% in the November 2011 survey, and this was be due to senescence of some of the previously recorded resprouts, many of which were very thin. Rowan, willow and ash are still proving to be the most vigorous resprouters, but it is notable that a smaller proportion of beaver-gnawed willow, rowan and birch were resprouting in 2011 than in the previous year. Although resprouting is widespread, it appears that much of it is resulting in many very thin shoots which may have a high rate of senescence and turnover, and be of little significance to beavers or to the structure of the woodland. The resprouting stems appear to be susceptible to frost damage. Further surveys will reveal the extent and the development of resprouting; of particular interest is the rate at which resprouting can provide future browsable stems for beavers and other herbivores such as deer. There were, as yet, rather few incidences of beaver or deer rebrowsing on these resprouted shoots.

5.3 Assessment of monitoring methodology and future monitoring plans

Ideally, this woodland monitoring program would have commenced with a survey of baseline vegetation conditions in the plots before beavers were reintroduced. Uncertainty surrounding several aspects of the releases made this impractical, however. For example, the precise locations of the artificial lodges used for the releases was not known long in advance and the use of space by beavers post release could not be confidently predicted, making siting of transects too speculative to be justified. Despite the absence of such baseline data, the persistence of stumps of trees felled by beavers prior to the first survey has allowed the reconstruction of an almost complete picture of woodland structure and species composition prior to the release. All stumps of trees felled by beavers in vegetation plots were identified, tagged and measured. Estimates of stem density and total basal area in each plot will only differ from the true baseline figures if trees branched above the site of beaver gnawing but below 20 cm. Other measures that may have changed from their baseline values since the beavers' introduction include estimates of canopy cover, estimates of horizontal vegetation density and estimates of ground cover, particularly where beavers had caused flooding or canalisation. Any direct effects of beavers on trees that have occurred since monitoring plots were established will have been detected.

Overall, the permanent woodland monitoring plot methodology is serving its purpose well. Tree tags and plot markers have proven robust and durable. Some transects established on Lily Loch and Loch Coille-Bharr are arguably of marginal interest now that beavers have established patterns of movement focussed on other lochs, however low-level beaver activity continues to be detected on these lochs (as of April 2011) and they will continue to be monitored for the duration of the Scottish Beaver Trial.

6. CONCLUSIONS

By November 2010, 31 transects had been established around the shores of Loch Coille-Bharr, Dubh Loch, Loch Linne, Loch Fidhle, Creagmhor Loch, Lily Loch and Lochan Buic at Knapdale. Transects extended 30 m inland from the shore and most comprised four 4 × 10 m permanently marked plots. In each plot, all trees, stumps and branches, dead or alive and standing or felled were permanently marked with uniquely numbered metal tags, identified to species (or for *Salix*, genus), and their diameter measured. All beaver effects on these trees were recorded. More than half of these plots were established in November 2009 and have now been monitored in five periods. The remainder were established April 2010 in anticipation of further beaver releases plus a further transect of four plots was established in November 2010. These plots will continue to be monitored six monthly throughout the Scottish Beaver Trial to describe the effects of beavers on woodland structure and composition.

There have been no major changes to the patterns of tree use since the report was made for 2010. However, we can now show that there has been a minor shift of beaver activity to plots further from the water's edge, although the majority of activity remains within 10m of the shores of the lochs. There appears to have been no detectable shift by beavers towards using plots that are farther from their lodges, although the Creagmhor beavers have built a new lodge on a neighbouring loch. Most effects were observed on transects less than 500 m from active beaver lodges. The utilisation of different species by beavers remains the same as previously reported, with preferences for willow and rowan. At least 16 tree and shrub species were recorded from plots, but only six occurred in substantial numbers. These were *B. pubescens, A. glutinosa, C. avellana, F. excelsior, S. aucuparia* and *Salix* spp. Most plots were dominated by *B. pubescens*, often in conjunction with one or more other species, and the birches were numerically the most used by beavers.

By November 2011, beavers had been present at Knapdale for 29 months and had produced noticeable effects on woody vegetation. Trees had been gnawed or felled by beavers in 43% of the 105 plots that could be monitored. Up to November 2010 10.2% of trees within our sample plots had been affected by beavers and this increased to 13.0% by November 2011. Within the plots that were used by beavers, in some, only one or two stems were affected whereas in others over 60% of the stems present had been affected. Plots used by beavers included more *B. pubescens* and *Salix*, but less *A. glutinosa* than an average plot. Although beaver effects were detected to greater distances from the shore, 72 % of effects occurred within 10 m of the water. Beavers continue to favour trees of diameter 3 - 6 cm.

Thirty five percent of trees felled by beavers were resprouting with new shoots in November 2011. *Salix*, *F. excelsior* and *S. aucuparia* were particularly vigorous resprouters. The structure of riparian woodland at Knapdale in future will be strongly influenced by the interaction between the growth of new shoots from beaver stumps and subsequent browsing of these shoots by deer and beaver. However, results to date suggest that although resprouting may be profuse, it may take longer than anticipated for it to generate regrown stems that may be utilised by beavers. The continued monitoring of resprouting is an important component of future work.

7. REFERENCES

Armstrong, H.M., Poulsom, L., Simson, P., Wilson, J. and Tracey, D., 2004. Testing methods for monitoring beaver impacts on terrestrial vegetation in Knapdale. *Scottish Natural Heritage Commissioned Report No. 026.*

Brandon-Jones, L., Bryce, J. and Gaywood, M., 2005. The Scottish Beaver Trial: Survey of riparian woodland at Knapdale 2003-2004. *Unpublished report to Scottish Natural Heritage.*

Haarberg, O. and Rosell, F., 2006. Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. *Journal of Zoology*, 270, 201-208.

Hood, G.A. and Bayley, S.E., 2009. A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. *Forest Ecology and Management*, 258, 1979-1989.

Jones, K., Gilvear, D., Willby, N. and Gaywood, M., 2009. Willow (*Salix* spp.) and aspen (*Populus tremula*) regrowth after felling by the Eurasian beaver (*Castor fiber*): implications for riparian woodland conservation in Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19, 75-87.

Kitchener, A.C. and Conroy, J.W.H., 1997. The history of the Eurasian Beaver *Castor fiber* in Scotland. *Mammal Review*, 27, 95-108.

Krojerová-Prokešová, J., Barančeková, M., Hamšíková, L. and Vorel, A., 2010. Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. *Journal of Zoology*, 281, 183-193.

Macdonald, D.W., Maitland, P., Rao, S., Rushton, S., Strachan, R. and Tattersall, F., 1997. Development of a protocol for identifying beaver release sites. *Scottish Natural Heritage Research, Survey and Monitoring Report* No. 93.

Moore, B.D., Iason, G.R. and Sim, D., 2010. The Scottish Beaver Trial: Woodland monitoring 2009. *Scottish Natural Heritage Commissioned Report No. 393.*

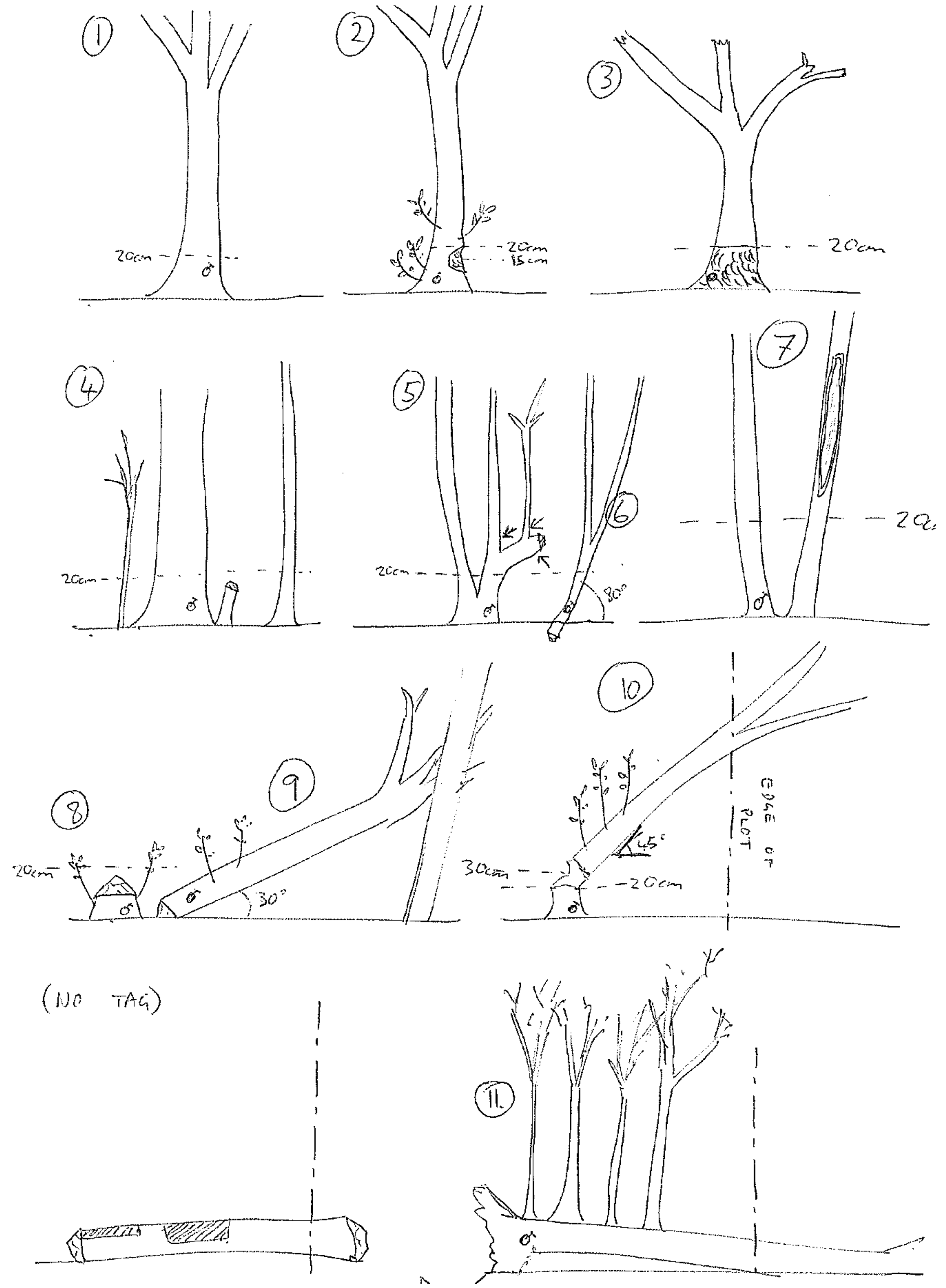
Moore, B.D., Sim, D.A. and Iason G.R., 2011. The Scottish Beaver Trial: Woodland monitoring 2010. *Scottish Natural Heritage Commissioned Report No. 462.*

Nolet B.A. and Rosell, F., 1994.Territoriality and time budgets in beavers during sequential settlement. *Can Journal of Zoology*, 72, 1227-1237.

Veraart, A.J., Nolet, B.A., Rosell, F. and de Vries, P.P., 2006. Simulated winter browsing may lead to induced susceptibility of willows to beavers in spring. *Canadian Journal of Zoology*, 84, 1733-1742.

ANNEX 1: ILLUSTRATIONS OF BEAVER EFFECTS ON TREES

Reference illustrations used in the field encompassing most tree, stump and log forms encountered with various types of beaver effect. Accompanying example datasheet with entries corresponding to numbered illustrations.



Scottish Beaver Trial: Woodland Monitoring. 302-460. Autumn 2009. Version 2.

Loch: COILLE BHAR Transect: 7 Distance: 0 to 4 m. Page 1 of 1
Plot Tag: 235

Tag No.	Species or count	Diam.(20cm)	Status	Angle	Alive Y/?/N	bark rmvd	low shoot	high shoot	avge. shoot	Deer	Beav	Height chopped	log length
#[a]	CODE	cm	[b]	deg	Y/?/N	%[c]	count[d]	count[e]	cm	0/1/2[f]	0/1/2[f]	cm	m[g]
1	SORACU	15	Up		Y	0	0	0	--	--	--	--	--
2	BETPUB	10	B, Up		Y	50	2	2	20	0	0	15	--
3	QUEPET	20	B, Up		N	100	0	0	0	0	0	20	--
4	BETPUB	15,3,1	Up		Y	0	0	0	0	0	0	--	--
	"	2	B, St		Y	100	0	0	0	0	0	15	--
5	Salix	5	Up		Y	0	0	0	0	0	0	--	--
	"	8											
	"	5, 3	Up		Y	0	0	0	0	0	0	--	--
	"	6	B, St		Y	100	0	0	0	0	0	30	--
6	"	4	B, Br	80	Y	0	0	0	0	0	0	--	3
7	SORACU	4	Up		?	0	0	0	0	0	0	--	--
		4	Up		?	deer	0	0	0	0	0	--	--
8	ALNGLU	15	B, St		Y	100	2	--	20	1	0	15	--
9	"	15	B, Log	30	Y	0	--	2	20	1	0	--	3
10	SORACU	20	B, P	45	Y	100	0	3	50	0	0	30	2
—	BETPUB	25	B, Log	0	?	20	--	0	0	0	0	--	2
11	SALCAP	30	N, Log	0	Y	0	0	0	0	0	0	--	4
		3,3,4,5	Up		Y	0	0	0	0	0	0	--	--

a: bracket paired stumps & logs; **b:** For stumps, logs & partially felled, indicate B (beaver) or N (natural) then Up=upright; St=stump; P=partially felled; Log; Branch **c:** % of circumference or % of log w/in plot, "deer" for old deer bark stripping; **d:** <30cm; **e:** >30cm; **f:** 0=none, 1=detectable, 2=significant; **g:** within plot boundaries.

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Policy and Advice Directorate, Great Glen House,
Leachkin Road, Inverness IV3 8NW
T: 01463 725000

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