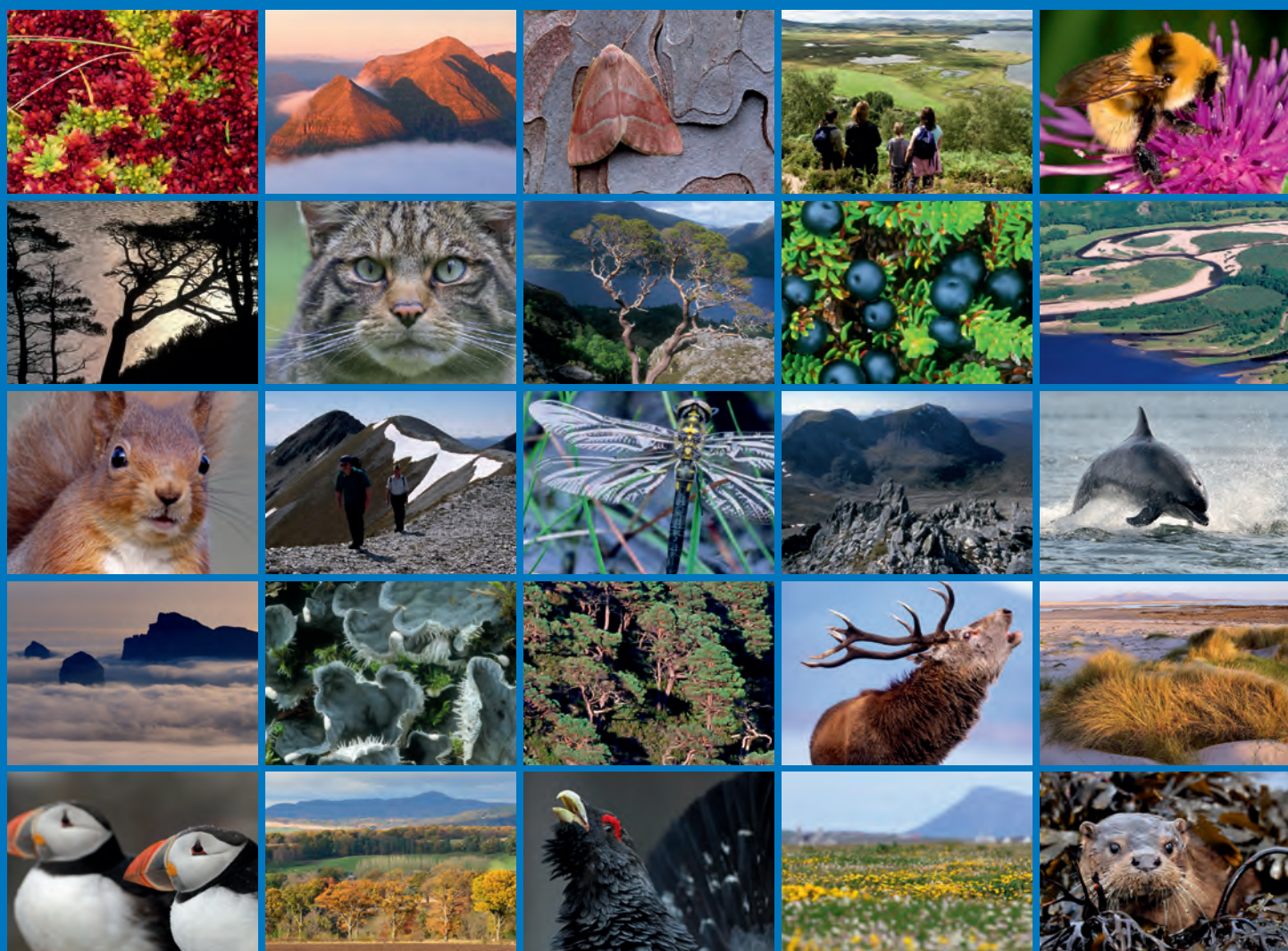


# The Scottish Beaver Trial: Fluvial geomorphology and river habitat 2008-2013, final report





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# COMMISSIONED REPORT

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**Commissioned Report No. 683**

**The Scottish Beaver Trial:  
Fluvial geomorphology and river habitat  
2008-2013, final report**

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## COMMISSIONED REPORT

# Summary

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## The Scottish Beaver Trial: Fluvial geomorphology and river habitat 2008-2013, final report

**Commissioned Report No. 683**

**Project No: 7062**

**Contractor: Centre for River Ecosystem Science, University of Stirling**

**Year of publication: 2015**

### **Keywords**

Fluvial; geomorphology; stream; river; habitat; woody; debris; sediment; beaver.

### **Background**

A five year trial reintroduction of the European beaver in Knapdale, Argyll, began in spring 2009. An independent monitoring programme was established to investigate the effects beavers might have upon particular aspects of the natural heritage were they to be released more widely in Scotland. The aspects studied included: semi-aquatic and aquatic macrophytes; damselflies and dragonflies; fish; water chemistry; hydrology; and fluvial geomorphology and river habitat. In addition to extensive surveys at the beginning and end of the trial period, interim monitoring was undertaken to establish the rate of any changes related to beaver activity. This report describes the extensive final survey and analysis of the data on fluvial geomorphology and river habitat collected during the trial period.

### **Main findings**

- Beavers appear to have explored much of the stream network, but have largely chosen not to exploit the river and riparian resources available and have therefore had limited influence on the fluvial geomorphology and river habitat in the trial area.
- Some dams were constructed where streams enter or leave lochs, where gradients were low and flows sluggish. No streamside lodges were constructed during the trial. Data collected during the 2013 survey indicate that little change in stream habitat has occurred since 2008 and there is no evidence of a reach-scale beaver activity effect on physical habitat.
- Changes in the density of woody debris features are the combined result of a small beaver impact and a naturally high background level of woody debris input, flux and loss during storm events. The assessment of reaches under different flow and turbidity conditions may have contributed to slight variations in the way that woody debris was recorded.
- Although beavers have significant potential to modify fluvial habitat through dam building, the evidence gathered during the Knapdale trial suggests that the incidence of dam

building will be low when populations are small and have ready access to well-vegetated standing waters.

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*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:*

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## 1. INTRODUCTION

A five year trial reintroduction of the European beaver (*Castor fiber*) in Knapdale, Argyll began in spring 2009. The trial investigated the potential to return the species to Scotland after a 400 year absence following unsustainable levels of hunting (Kitchener and Conroy, 1997).

The joint licence application for a trial, submitted in 2007 by the Royal Zoological Society of Scotland and the Scottish Wildlife Trust, identified the opportunities that a scientifically monitored, time-limited trial could provide. Those relevant to the area of study covered by this report include:

- studying the ecology of the beaver in the Scottish environment;
- assessing the effects of beaver activity on the environment, including a range of land uses; and
- generating information that could inform further releases of beavers in sites with different habitat characteristics.

Other suggested areas of study included: beaver health; public health; socio-economic effects; and the impact on specific species of conservation concern.

The ecological effects of the reintroduced beavers on the environment were monitored from 2009 to 2014, principally through the use of repeated ecological surveys. Pre-reintroduction baseline data were collected in 2008, and similar data had been collected in 2002. Surveys covered the breadth of the freshwater and woodland ecosystems present at the site including aquatic and semi-aquatic macrophytes, damselflies and dragonflies, fish, fluvial geomorphology, river habitat, riparian habitat, loch and stream hydrology and water chemistry.

This report details the results of the fluvial geomorphology and river and riparian habitat monitoring, undertaken by the University of Stirling. The report provides a full and impartial analysis and interpretation of the data. Interim monitoring reports, produced during the trial, can be found on the SNH website: [www.snh.gov.uk/scottishbeavertrial](http://www.snh.gov.uk/scottishbeavertrial).

A summary of the aims of the hydromorphology and river and riparian habitat survey is given in Section 1. Methods for the baseline and repeat surveys, as developed by Gilvear & Casas-Mulet (2010), are described, along with survey dates, in Section 2. An overview of the survey results from the five year period is presented in Section 4, together with general observations made during the survey.

## **2. AIMS AND OBJECTIVES**

### **2.1 Aims**

The monitoring programme for fluvial geomorphology and river and riparian habitat was designed with the aim of monitoring the effects of beaver activity across the stream network. Its purpose was to detect changes in stream hydromorphology and stream and riparian habitat that may have occurred as a result of the reintroduction of beavers to Knapdale. The surveys therefore needed to incorporate habitat attributes potentially influenced by beaver activity including:

- in-channel fluvial features and substrate types;
- bankside vegetation presence and structure;
- wider riparian woodland and wetland habitat features;
- hydraulic meso-habitats;
- bank morphology and stability, e.g. bank erosion; and
- the extent and significance of natural additions of woody debris, e.g. log jams

To distinguish changes in these attributes associated with the effects of beavers from natural 'background' changes, parallel monitoring of sites with low or zero beaver presence was required.

### **2.2 Objectives**

#### *2.2.1 Survey design development*

In developing a robust survey methodology, the following challenges had to be addressed (Gilvear and Casas-Mulet, 2010):

- Uncertainty about precisely where beavers would establish territories following their release.
- The related uncertainty about precisely where the beavers would have a direct physical effect through localised foraging.
- How to assess indirect effects, for example the potential downstream effects that may have arisen when sediment was trapped behind a beaver dam.

#### *2.2.2 Monitoring strategy implementation*

The monitoring, specifically the collection of baseline data, had to be sufficiently flexible to accommodate the potential for beavers to move and to establish territories across the Knapdale area. This flexibility would allow monitoring resources to be moved from areas where the ecosystem was unaffected by the reintroduction to other areas that would provide an insight into the effects of beaver activity.

#### *2.2.3 Data analysis*

The data had to be presented in an easily digestible and reproducible format, and an analysis undertaken of the significance of any underlying trends in the data that may indicate a response of the environment to beaver activity.

#### *2.2.4 Recommendations*

A further objective was to provide an insight into the ecology of the beaver in the riverine environment in Scotland and inform future management elsewhere in Scotland.



### **3. METHODS**

#### **3.1 Extent of baseline surveys**

To provide the flexibility required for monitoring the influence of the beavers before knowing where they would establish their territories, the baseline surveys were both detailed and extensive. This ensured that the baseline data would be available for wherever felling or other beaver related activity subsequently occurred, as well as documenting the habitat characteristics of a relatively unstudied stream network.

Between November 2008 and January 2009, 55 reaches covering 21.5 km of streams in the Knapdale area were surveyed to produce a baseline data set. Where appropriate, the reaches coincided with those used in previous surveys undertaken in 2002 (Gilvear, 2002). Most reaches were 450–500 m long, but 18 were shorter as the confluence with a larger watercourse or the tidal limit of the stream prevented a full reach length from being surveyed. Since the primary focus of the investigation was on trends in habitat and associated features at individual sites over time in relation to levels of beaver activity, rather than a comparison of absolute values between sites, no correction was made to allow for the non-standard length of some reaches. The spot-check locations for all of the survey reaches are shown in Figure 1.

#### **3.2 Methodology**

The monitoring strategy was developed by Gilvear and Casas-Mulet (2010) at the outset of the trial. A number of established and bespoke data collection methods were included as part of the baseline survey design. Table 1 provides a summary of the information collected. Further information is given below.

##### *3.2.1 River Habitat Survey*

River Habitat Survey (RHS) is an established, rapid and repeatable method of providing quantifiable information about stream habitat, specifically the presence, abundance and structure of habitat within river corridors (Fox *et al.*, 1998; Raven *et al.*, 1998). It aims to document features of value to wildlife and provide an assessment of river habitat quality (indexed by the Habitat Quality Score).

For the purposes of the Scottish Beaver Trial, RHS was undertaken during the winter months allowing the channel habitat structure to be clearly documented. This is not possible under the very dense woodland cover of the summer months.

##### *3.2.2 Modified geomorphic assessment*

Data on stream dynamics and geomorphological features were collected using a standard fluvial audit approach. For the purposes of the baseline survey, improvements were made to the survey sheets (Gilvear and Casas-Mulet, 2010) to facilitate data collection. Measurements of channel morphology included: left and right bank top height; bankfull channel depth; and bankfull width. The RHS definition of banktop was used, i.e. the first major break in slope marking the point at which floodwater would normally spill out of the channel (bankfull). Whether bed material was consolidated or unconsolidated was recorded at spot-checks. Unconsolidated substrate is easily mobilised. The bed material was recorded as 'Consolidated' where the substrate had an armour layer or was compacted. A Wolman pebble count (of approximately 100 particles) was undertaken in each reach, when appropriate (i.e. where bedrock or fine sediment did not dominate). Wolman describes a method of sampling coarse river-bed material that has become the standard approach for characterising river substrate (Wolman, 1954).

### 3.2.3 *Inventory of instream woody debris and geomorphic features*

An inventory of woody debris and fluvial features was created. Information included the location and size of each feature. Fluvial features included gravel bars and bank erosion. Individual woody debris features (>1 m<sup>2</sup> coverage or 1 m member length) were measured (length and width), georeferenced, photographed and classified according to type (leaf (L), twig (Tw), branch (Br), trunk (Tk)) and channel coverage (full width (FW), half width (HW), marginal (M)). Woody debris features were inspected for beaver teeth marks. It was considered appropriate to go beyond the simple *presence/absence* recording used in RHS because of the potential activity of beavers.

### 3.2.4 *Riparian vegetation*

The characterisation of both left bank (LB) and right bank (RB) broadleaf tree vegetation included horizontal distance from the stream (0–1 m, 1–5 m, 5–10 m, 10–15 m, >15 m) and vegetation distribution and density (none, none-CP (indicating the presence of coniferous plantation immediately next to the stream), isolated, scattered, semi-continuous, continuous).

### 3.2.5 *Fixed point photography*

A comprehensive catalogue of georeferenced photos, taken looking both upstream and downstream from each spot-check, was established during the trial.

### 3.2.6 *River corridor features and tree canopy*

A survey of fallen trees, wetland features and the composition of the tree canopy within the river corridor was undertaken in 2008. Based on the findings of Jones *et al.* (2003), a 25 m wide river corridor (12.5 m either side of the stream) was surveyed. At each spot-check the number of fallen trees and branches within the corridor was recorded. These were classified by type (branch or tree), size (small <1 m, medium 1–5 m, large >5 m) and, where identifiable, species. The relative canopy cover for live trees was also recorded. The main species relevant for inclusion in this assessment were: downy birch (*Betula pubescens*); black alder (*Alnus glutinosa*); willows (*Salix* spp.), plus other broadleaf species (e.g. hazel (*Corylus avellana*) and sycamore (*Acer pseudoplatanus*)). Trees were classified by structure (Tree (T), Shrub (S)) and percentage canopy cover. The approach adopted thus provided greater detail for the baseline dataset than relying on RHS alone. Birch and willow species in particular are an important element of beaver diet (Jones *et al.* 2003) and woodland monitoring by the James Hutton Institute subsequently confirmed the extensive use of these tree species in the vicinity of lochs by beavers at Knapdale (Iason *et al.*, 2014).

The size and location of wetland features within the river corridor were also recorded.

### 3.2.7 *Salmonid habitat assessment*

An assessment of hydraulic habitat was undertaken at each spot-check, allowing the mapping of six different habitat types: riffle; riffle-run; glide; deeper glide; pool; and bedrock/cascade. Fish populations and spawning activity have been monitored since the outset of the trial as part of a separate study (Argyll Fisheries Trust, 2010) and any changes over the trial period will be presented in a forthcoming report (Argyll Fisheries Trust, in prep.).

Table 1. Table summarising the data collected during the baseline survey of stream reaches in the Scottish Beaver Trial area using the Modified Geomorphic Assessment

<b>Reference information</b>	
Spot-check code	Unique identifier for each individual spot-check
RHS reach	Number identifying the reach being surveyed
Photo reference	Unique identifier for each photo taken
Easting	OS grid easting reference (OSGB36)
Northing	OS grid northing reference (OSGB36)
Water course	The name of the water course when available
Tributary to	The loch that the stream flows into
Date	Date on which the data was collected
<b>Channel Dimensions / Characteristics</b>	
Standard RHS methodology records channel dimensions at one location for each reach. The modified survey records the following information every 50 m:	
Bankfull width, LB Bank top height, RB top height	Bankfull as delimited by the first major break in bank slope (bank top) or occasionally by the limit of terrestrial vegetation, marking the point at which floodwater would spill out of the channel
Bankfull depth 1, 2 & 3	Bankfull channel depths were recorded at equal intervals across the wetted channel width
Bed material type	Bed material classified 'consolidated' or 'unconsolidated'
<b>Bankside vegetation</b>	
Standard RHS records vegetation structure at 10 spot-checks within each 500 m reach but only notes the presence of alder species. Information on vegetation structure is not linked to species relevant to beaver foraging. To rectify this, information on vegetation structure was collected along a 25 m transect across the river corridor perpendicular to the stream. Information on the total buffer width was also collected.	
LB & RB vegetation width	Riparian broadleaf woodland was characterised for the right and left banks in terms of width (0-1m, 1-5m, 5-10m, 10–15m, >15m)
LB & RB vegetation distribution	Broadleaf tree distribution was recorded for the right and left banks as either none, none-CP (indicating the presence of coniferous plantation immediately next to the stream), isolated, scattered, semi-continuous or continuous.
LB & RB <i>Alnus</i> structure / cover	The structure (tree/shrub) and percentage cover of three key broadleaf tree genera ( <i>Alnus</i> , <i>Betula</i> and <i>Salix</i> ) were recorded for the right and left banks at each spot-check
LB & RB <i>Betula</i> structure / cover	
LB & RB <i>Salix</i> structure / cover	
LB & RB other broadleaf structure / cover	The structure (tree/shrub) and percentage cover of <i>Corylus sp.</i> and <i>Acer sp.</i> were recorded for each bank.
Number of fallen branches	The number of fallen branches were tallied for three size classes; small (<1 m), medium (1–5 m) and large (>5 m)
No. fallen trees	The number of fallen trees were tallied for the three size classes; small (<1 m), medium (1–5 m) and large (>5 m)
Dominant species amongst fallen trees	Where a number of fallen trees were observed, the dominant species was recorded

### **Instream habitat**

A change in the hydraulic features of meso-scale habitat will occur in, and adjacent to, any reaches affected by beaver dam building activity. River Habitat Survey provides information on presence and extent of flow types and channel features, but it does not map the location of meso-habitats. To address this, the following information was recorded:

Flow type (salmon habitat)	Hydraulic habitat assessment was undertaken recording six different habitat types (riffle, riffle-run, glide, deep glide, pool and bedrock/cascade).
Bed material	Two Wolman pebble counts (approx.100 particles), were undertaken within every 500 m reach, using a standard pebble plate. Pebble counts were located at spot-checks 1 and 6 except where conditions did not allow, e.g. in bedrock reaches or those with heavily silted substrates.

### **Woody debris features**

The standard RHS only reflects the presence/absence of woody debris features. As woody debris is expected to be influenced by beaver activity the following data was recorded:

WD feature code	Unique identifier for each woody debris feature
WD feature composition	Woody debris features were classified by type: leaf (L), twig (Tw), branch (Br) or trunk (Tk)
WD channel overage	The proportion of channel covered by the woody debris was recorded as full-width (FW), half-width (HW) or marginal (M)
WD feature length, WD feature width	Woody debris dimensions, length and width (m), were recorded
WD feature photo reference	A photograph of the feature was taken and recorded

### **River corridor features**

RC feature code	Unique identifier for each river corridor feature
RC feature type	Pond, wetland, fallen tree, felled tree
RC feature length, feature width	The length and width of the feature were recorded
RC feature location	OS grid reference for the feature location
RC feature photo reference	A photograph of the feature was taken and recorded

### **Erosion/Deposition features**

As part of the modified geomorphic assessment the location of areas of major bank erosion and sediment deposition were recorded, characterised, photographed and georeferenced:

ED feature code	Unique identifier given to each individual erosion and deposition feature
ED feature type	The geomorphological term for the feature was recorded
ED feature substrate	The substrate; cobble, pebble, sand, earth – was noted
ED feature location	Channel position of the ED feature; left bank (LB), right bank (RB), in channel (Ch)
ED feature length, feature width	The length and width of the feature were recorded
ED feature location	Grid reference for location of feature

### 3.3 Repeat surveys

#### 3.3.1 Interim surveys

By 2010, the approximate locations of present and probable future beaver activity were evident. Interim surveys were undertaken in 2010 and 2011 to collect data from a subset of 12 of the baseline reaches, located in close proximity to the resident beaver populations. Surveys covered 4.8 km of stream (Table 2). The spot-check locations for these reaches are shown in yellow in Figure 1. Following the release of some more beavers, an additional three reaches in the vicinity of Lochan Buic were included in the 2012 interim survey raising the surveyed length to 5.9 km. Spot-check locations for these reaches are shown in red in Figure 1. Interim surveys were undertaken in November of each year. Details of the subset of reaches are presented in Table 3.

Interim surveys included the RHS methodology, fixed point photography and the inventory of in-stream wood and geomorphic features. Additionally, a survey of riparian felling, not relevant during the baseline survey, was undertaken. This survey documented the number and location of felled trees, categorised by size and (where possible) species, at locations of beaver activity within the river corridor zone. Of the baseline survey methodologies, these approaches were considered most relevant given the limited nature of the interaction between beavers and their Knapdale environment; specifically, the construction of lodges on the loch shorelines rather than on the stream network, and the relative absence of feeding, felling and dam building activity on the stream network.

#### 3.3.2 Trial-end surveys

The final re-survey covered a total of 17.7 km of river corridor across the Knapdale area and was undertaken in November 2013. In addition to re-surveying the interim survey reaches, a partial resurvey of the majority of the baseline reaches was undertaken. This marked the completion of a five year period of monitoring as part of the Scottish Beaver Trial. The following assessments were included in the 2013 re-surveys, and provided a comprehensive 'end of trial' dataset relevant to the behavioural effects of the introduced beavers:

- RHS on interim survey reaches only;
- Modified Geomorphic Assessment;
- fixed point photography;
- inventory of instream wood and geomorphological features;
- river corridor (fallen trees); and
- riparian felling.

Many elements of the baseline survey were designed to provide useful data in the event of beavers establishing territories on the stream network. It was not necessary to repeat many of the baseline surveys because beaver activity within the trial area was predominantly focused around the lochs. The repeated elements of the baseline survey presented in this report, covered features relevant to analysing the impacts of the beavers. Additional data collected during the baseline year are available in shapefile format.

### 3.4 Survey dates and locations

Table 2. Breakdown of the survey data collected during the trial and the stream length (km) included in each survey

	2008	2010	2011	2012	2013
River Habitat Survey	21.45	4.80	4.80	5.85	5.85
Modified Geomorphic Assessment	21.45	4.80	4.80	5.85	17.65
inventory of in-channel features	21.45	4.80	4.80	5.85	17.65
fixed point photographic survey	21.45	4.80	4.80	5.85	17.65
river corridor fallen trees	21.45	0.00	0.00	0.00	17.65
river corridor tree canopy survey	21.45	0.00	0.00	0.00	0.00
salmonid habitat assessment	21.45	0.00	0.00	0.00	0.00
riparian felling survey	21.45	4.80	4.80	5.85	17.65

Table 3. Details of the stream reaches surveyed during interim years including the RHS reach number, associated beaver family, description and location

RHS reach no.	Associated beaver family	Description	NGR (start)	NGR (finish)
1	Creagmhor/Un-named (North)	Creagmhor Loch outflow	180237	179968
2	Creagmhor/Un-named (North)	Creagmhor Loch outflow	690828	690515
			179968	179692
			690515	690196
12	Linne/Fidhle	Loch Fidhle southern end inflow	179383	179632
			690269	690574
13	Linne/Fidhle	Loch Fidhle southern end inflow	179634	179798
			690572	690818
14	Creagmhor/Un-named (North)	outflow from Un-named (North) into Loch Fidhle	180002	180069
			691042	690990
16	Linne/Fidhle	Loch Linne northern end inflow	180005	180087
			691450	691555
36	Dubh/Coille-Bharr	Loch Coille-Bharr outflow	177628	177313
			689682	689425
37	Dubh/Coille-Bharr	Loch Coille-Bharr outflow	177902	177636
			689862	689673
40	Dubh/Coille-Bharr	Loch Barnluasgan outflow into Loch Coille-Bharr	179066	178834
			691053	690863
41	Dubh/Coille-Bharr	Loch Barnluasgan northern end inflow	179456	179709
			691422	691741
42	Linne/Fidhle	Loch Linne outflow	179425	179103
			690590	690269
43	Linne/Fidhle	Loch Linne outflow	179103	178774
			690266	689886

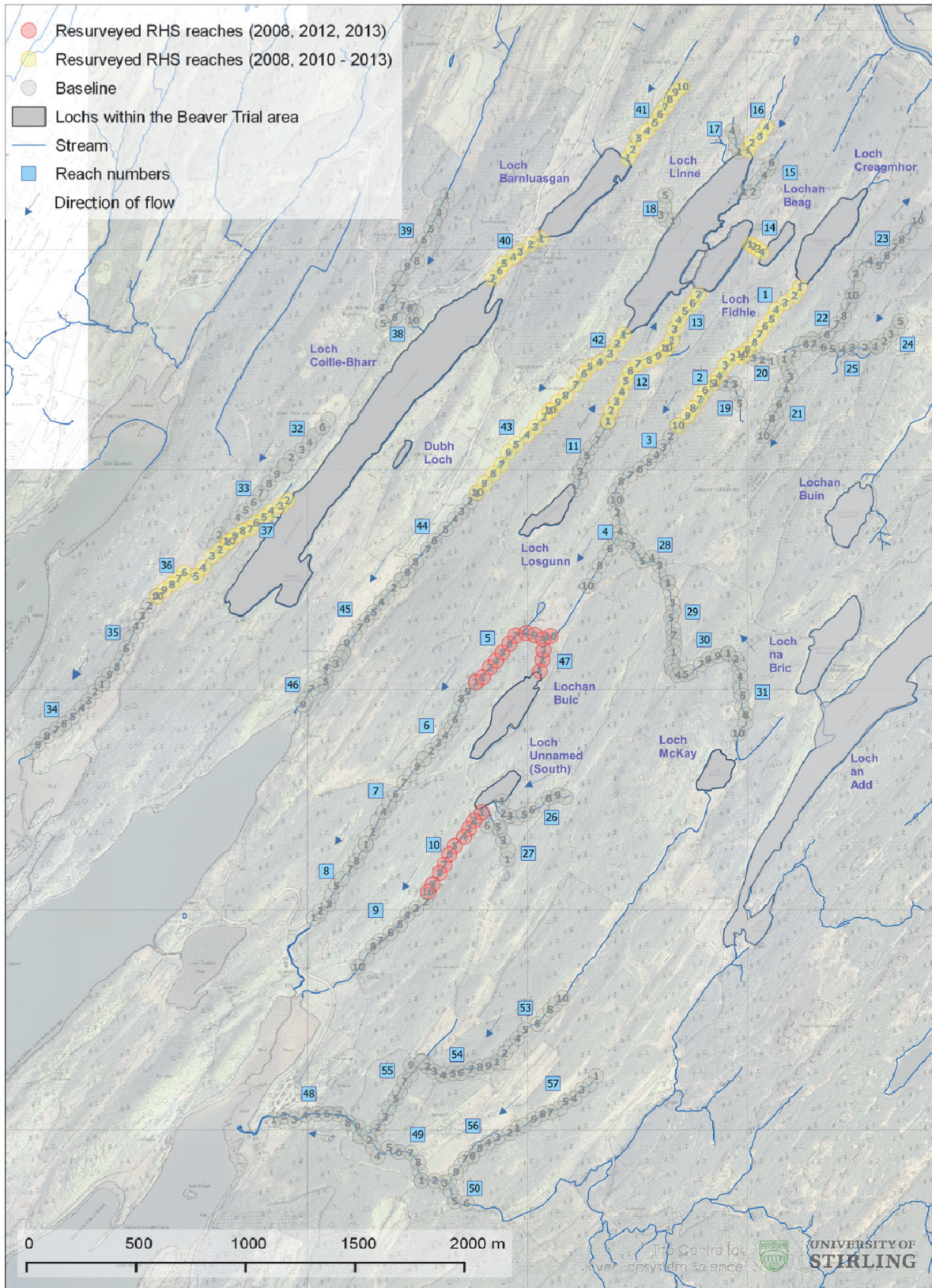


Figure 1. Spot-check locations on interim survey reaches. Mapping data reproduced by permission of Ordnance Survey on behalf of HMSO. © Crown Copyright. All rights reserved.

## 4. RESULTS

### 4.1 Ranking of sites

In order to analyse the data to illustrate the influence that the activity of beavers may or may not have had, reaches were divided into four levels of potential activity based around the proximity and availability of habitat resources. A simple ranking exercise was undertaken on the subset of annually surveyed reaches. Reaches were grouped based on the answers to the following questions, indicating either observed or potential beaver activity:

- Is the reach within 500 m of a beaver occupied loch?
- Is the reach with 1000 m of a beaver occupied loch?
- Is the reach downstream of a beaver occupied loch?
- Has dam building been observed within the reach?
- Is the reach downstream of dam building activity?
- Is there accessible native woodland habitat within the reach?
- Has felling been observed in the reach?

Results from the grouping exercise are presented in Table 4.

Table 4. Ranking of subset of reaches based on potential and observed activity levels

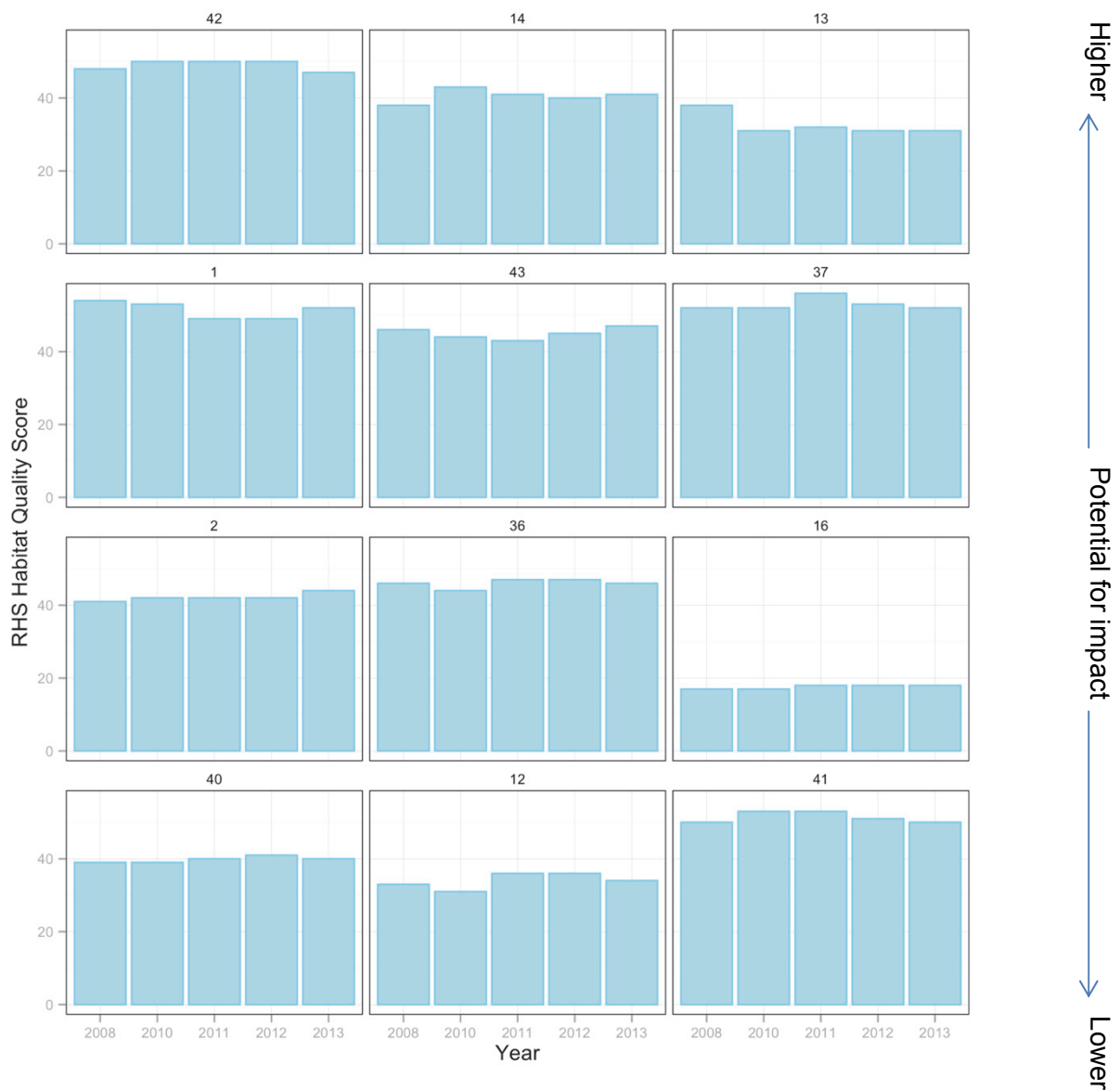
Reach	Within 500m of occupied Loch	Within 1000m of occupied Loch	Downstream of occupied Loch	Dam building observed	Downstream of dam building	Accessible native woodland	Felling activity observed	Level
42	✓	✓	✓	✓	✓	✓	✓	High
14	✓	✓	✓	✓	✓	✓	✓	High
13	✓	✓	✓	✓	✓	✓	✓	High
1	✓	✓	✓		✓			Moderate
43		✓	✓		✓			Moderate
37	✓	✓	✓		✓			Moderate
2		✓	✓		✓			Low
36		✓	✓		✓			Low
16	✓	✓					✓	Low
40		✓			✓			Very Low
12		✓						Very Low
41					✓			Very Low

### 4.2 Stream habitats

Stream habitat monitoring, undertaken at the reach scale using RHS, allowed habitats to be documented. The data collected were used to calculate Habitat Quality Scores (HQS). This index provided a general indication of the habitat diversity present within a reach, based on a tally of the natural features recorded. Scoring features included gravel bars, eroding cliffs, large woody debris, waterfalls, back waters and floodplain wetlands. The diversity of bed substrate and flow types also contributed, as did bankside vegetation and land use. The scores, calculated for each of the 12 annually surveyed reaches, are shown in Figure 2. The scores for reaches with a complete set of spot-checks are similar to the modal value of 40-50 for comparable stream types in the RHS database (Raven *et al.*, 1998). The scores



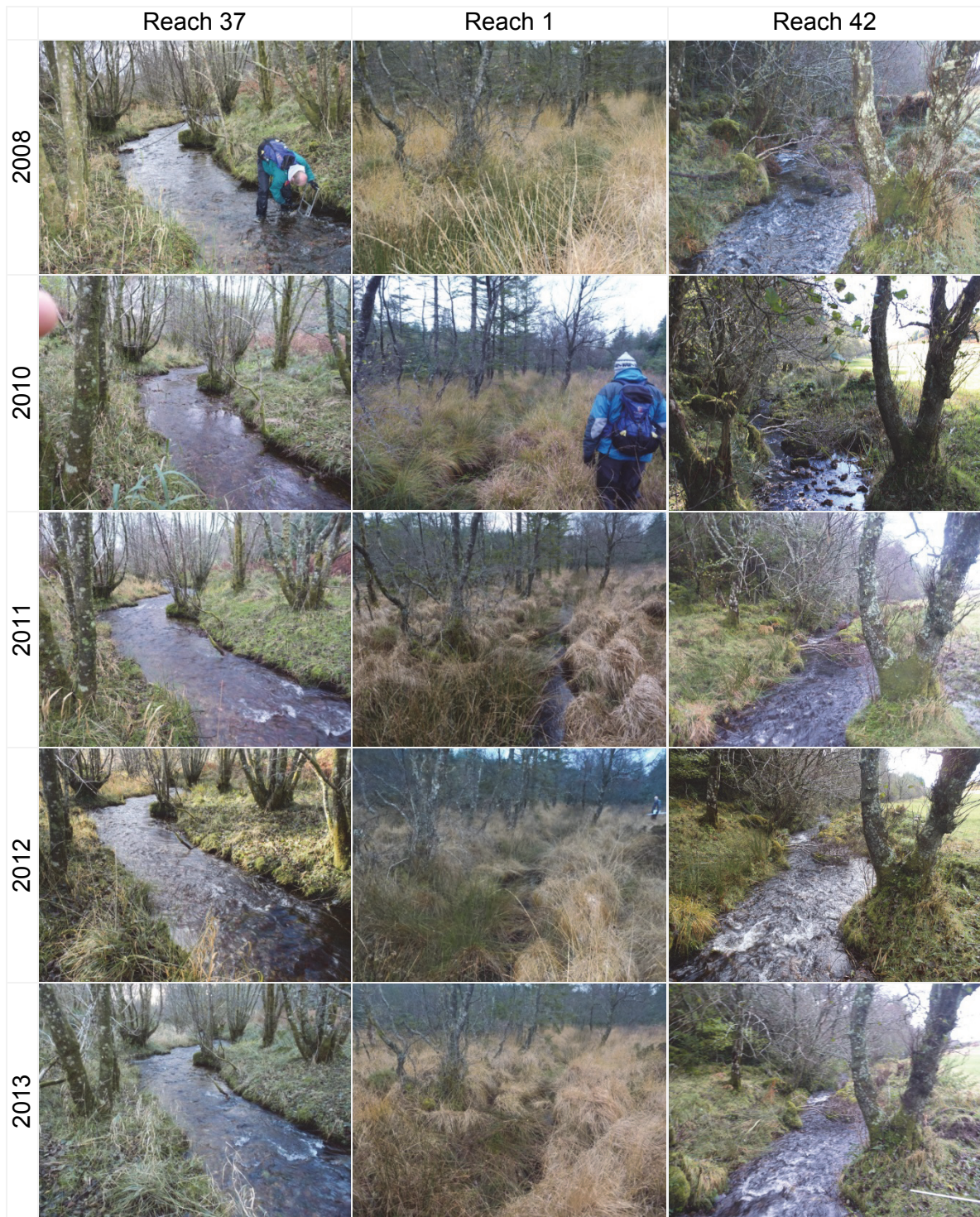
support the field observations that there was no trend of change in habitat structure or diversity for the duration of the trial. Within-reach variability in HQS is relatively small and can be accounted for by natural (non-beaver) or surveyor variability.



**Figure 2. Habitat Quality Scores for each of the reaches surveyed annually between 2008 and 2013**

Note: The RHS HQS score is based on a summation of the spot check data for a reach. Since the focus is on trends in HQS scores at individual reaches over time rather than a comparison between reaches no correction has been made for shorter reaches that contained less than the standard 10 RHS spot checks.

Riparian habitats were also documented using photography. A large library of photographs was compiled, a selection of which is presented in Figure 3. They show typical reaches typical of streams across the area and illustrate the stability of habitat structure including riparian vegetation and instream features.



*Figure 3. A comparison of stream habitat at locations fixed for the duration of the trial.*

As described above, no individual reaches suggest a change in habitat quality over time as described by the HQS based on RHS data. The same is true when the data are grouped by beaver activity level (Figure 4).

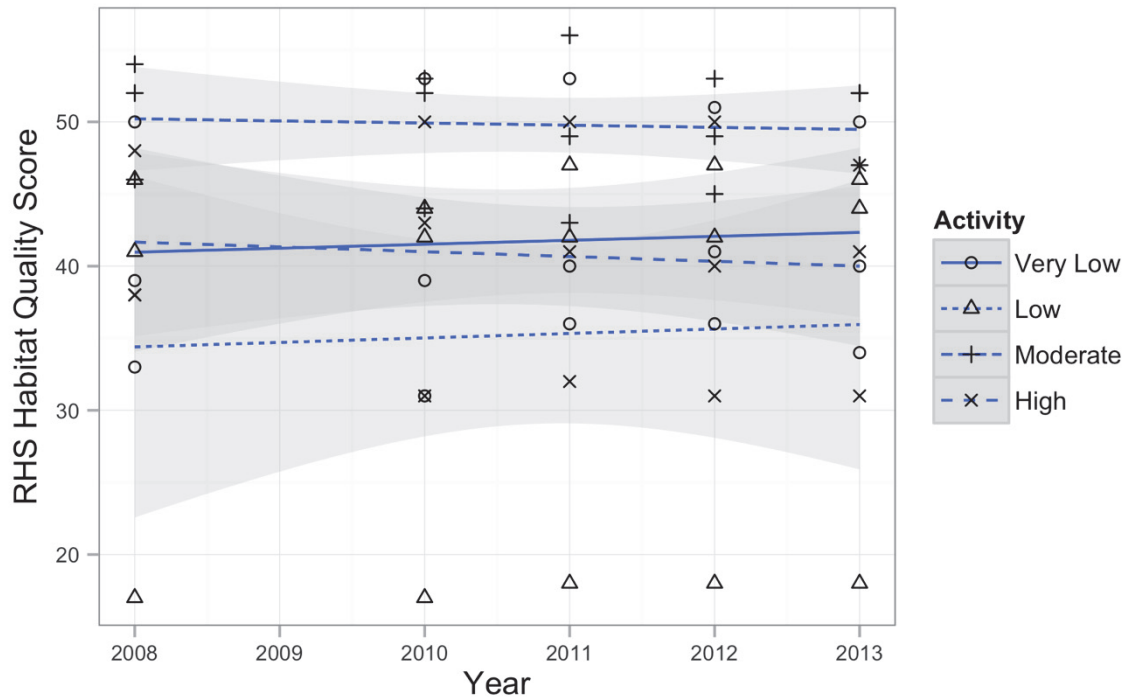


Figure 4. Relationship between Habitat Quality Scores for different levels of beaver activity over the course of the Scottish Beaver Trial

To provide statistical support to the inference drawn from Figure 4, a linear mixed-effects model was fitted to the data. The model incorporated a correlation structure to account for the fact that the same reaches were surveyed repeatedly over the course of the trial. The output from the model is presented in Figure 5. The non-significance of the interaction terms between activity levels and time in the output indicates that there is no detectable effect of beaver activity on the Habitat Quality Scores, based on the data available. The analysis was done using the nlme package (version 3.1-117) in R (version 3.1.0).

R Output

Linear mixed-effects model fit by REML

Data: data.lf

AIC	BIC	logLik
288.9878	310.4515	-133.4939

Random effects:

Formula: ~1 | Reach

(Intercept) Residual

StdDev: 9.837425 2.015658

Correlation Structure: ARMA(1,0)

Formula: ~Time | Reach

Parameter estimate(s):

Phi1

0.3987081

Fixed effects: hqs ~ Activity \* Time

	Value	Std.Error	DF	t-value	p-value
(Intercept)	40.87672	5.847595	44	6.990347	0.0000
ActivityLow	-6.69752	8.269748	8	-0.809882	0.4414
ActivityModerate	9.39610	8.269748	8	1.136202	0.2888
ActivityHigh	1.08306	8.269748	8	0.130967	0.8990
Time	0.23429	0.399733	44	0.586127	0.5608
ActivityLow:Time	0.13285	0.565308	44	0.235009	0.8153
ActivityModerate:Time	-0.34299	0.565308	44	-0.606728	0.5471
ActivityHigh:Time	-0.65941	0.565308	44	-1.166469	0.2497

Correlation:

	(Intr)	ActvtL	ActvtM	ActvtH	Time	ActL:T	ActM:T
ActivityLow	-0.707						
ActivityModerate	-0.707	0.500					
ActivityHigh	-0.707	0.500	0.500				
Time	-0.205	0.145	0.145	0.145			
ActivityLow:Time	0.145	-0.205	-0.103	-0.103	-0.707		
ActivityModerate:Time	0.145	-0.103	-0.205	-0.103	-0.707	0.500	
ActivityHigh:Time	0.145	-0.103	-0.103	-0.205	-0.707	0.500	0.500

Standardized within-Group Residuals:

Min	Q1	Med	Q3	Max
-1.5996931	-0.3716962	-0.1020187	0.5137113	2.0016340

Number of Observations: 60

Number of Groups: 12

Figure 5. Statistical output from the linear mixed effects model investigating the relationship between the Habitat Quality Score and beaver activity

### 4.3 Stream dynamics

The survey results for reaches 48–57 in the Barnagad Burn catchment were excluded from the analysis because high levels of suspended sediment meant that it was not possible to collect a reliable inventory of fluvial features. There is no evidence that the beavers ventured into this catchment, and the character of the river is sufficiently different for it to be of limited value for comparison purposes.

The pebble count data collected from fixed locations on reaches within the area of the beaver trial are presented in Figure 6. The data show very little change in the composition of bed substrate, indicating no major shift in substrate type. No consistent siltation or coarsening of bed sediments are indicated by the profile graphs. This is most obvious for reaches that are relatively uniform such as 42, 13, 36 and 16. A few reaches, e.g. reach 37, appear to show a difference between 2008 and 2013 for one or both samples. This can be explained by the high diversity of bed substrates and features present at these locations meaning that slight differences in the spatial extent of the pebble count can lead to a change in the profile.

The spatial extent and density of erosion and deposition features are shown in Figure 7. Features recorded during interim surveys (2010–2012) are shown for the subset of reaches only. The map clearly indicates the very low density of features present. An average of less than one feature per reach precludes statistical analysis of the data, but there is clearly no indication of an increase in channel instability. By nature, the features in the Knapdale area are generally small and relatively transient. Small erosion scars or slumping banks rapidly re-vegetate. Deposition features are small and easily submerged at moderate to high flows.

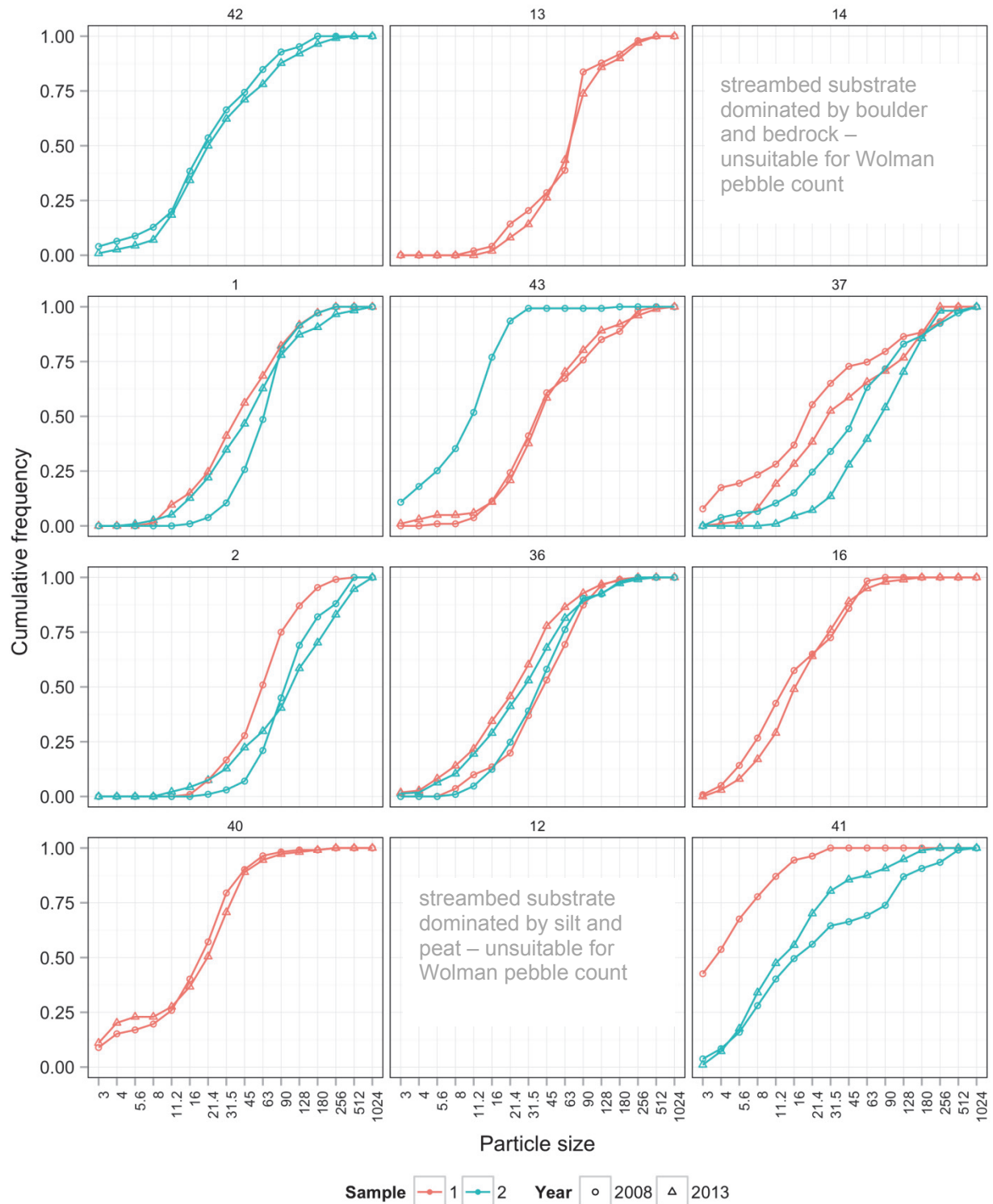


Figure 6. Cumulative frequency plots for the pebble count data collected at fixed locations on the reaches within the area of the Knapdale trial. Note: Surveys were undertaken at the start (2008, pre beaver) and end (2013) of the trial. Only one pebble count was undertaken in some reaches, either because the reach was shorter than 10 spot-checks or because gravel habitat was only present on a proportion of the reach. Not all pebble count locations were resurveyed in 2013.



#### 4.4 Woody debris

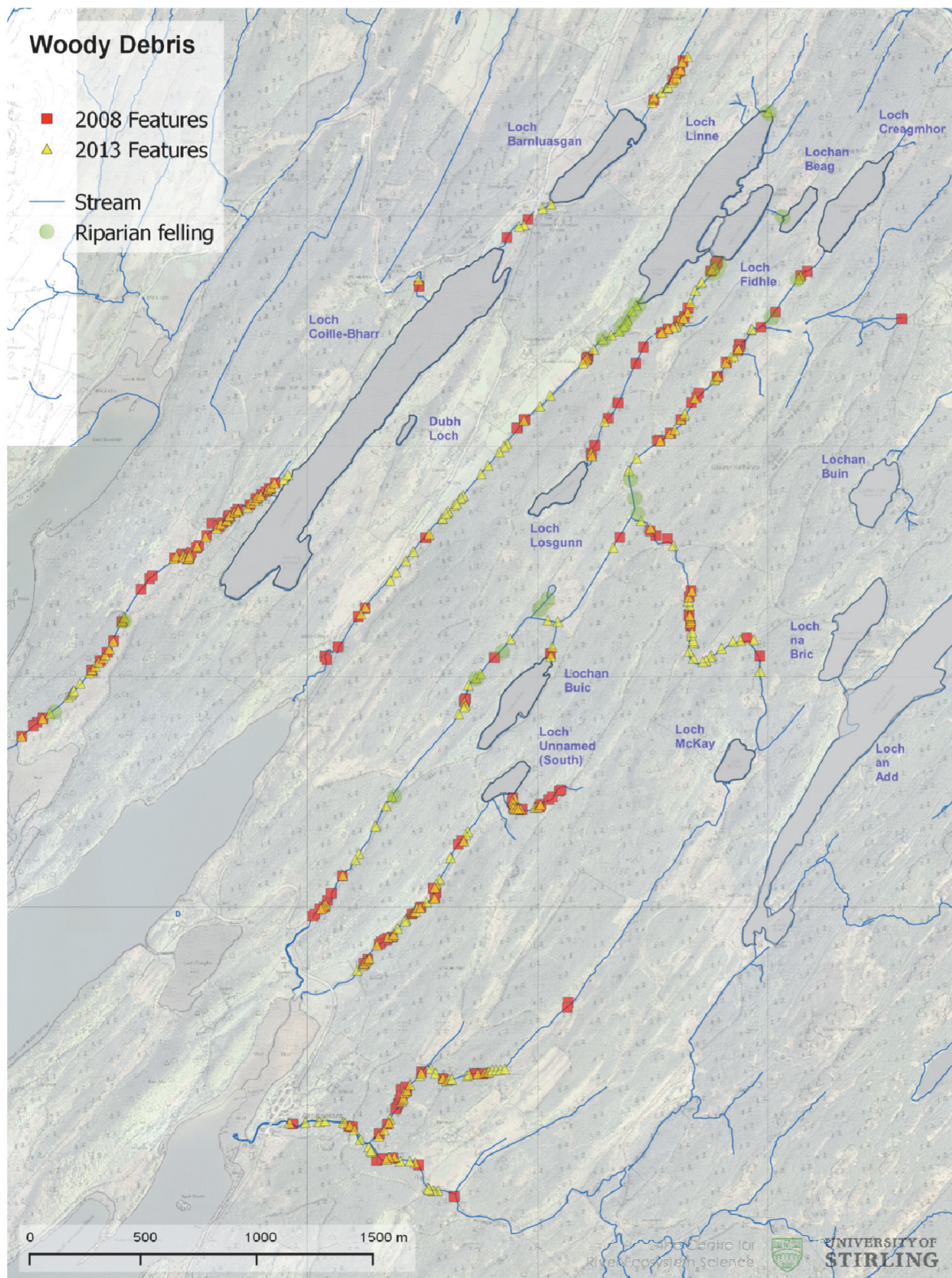


Figure 8. The location and number of woody debris features recorded in 2008 and 2013. Mapping data reproduced by permission of Ordnance Survey on behalf of HMSO. © Crown Copyright. All rights reserved.



Figure 8 illustrates the location and number of woody debris features recorded in the re-surveyed reaches at the beginning and end of the trial. The spatial extent of the features was broadly equal, although the density increased in some reaches. There was an increase in the total number of features recorded from 186 in 2008 to 313 in 2013. In particular there was an increase in the number of records of woody debris downstream of Loch Linne where some riparian felling occurred close to the loch outlet.

The number of woody debris features present over the course of the trial varied strongly at some sites but was largely stable at others. Those recorded were a mixture of consolidated features, accumulations of loose and more transient material, and individual items. The change in the number of woody debris features over the course of the trial can be seen in Figure 9.

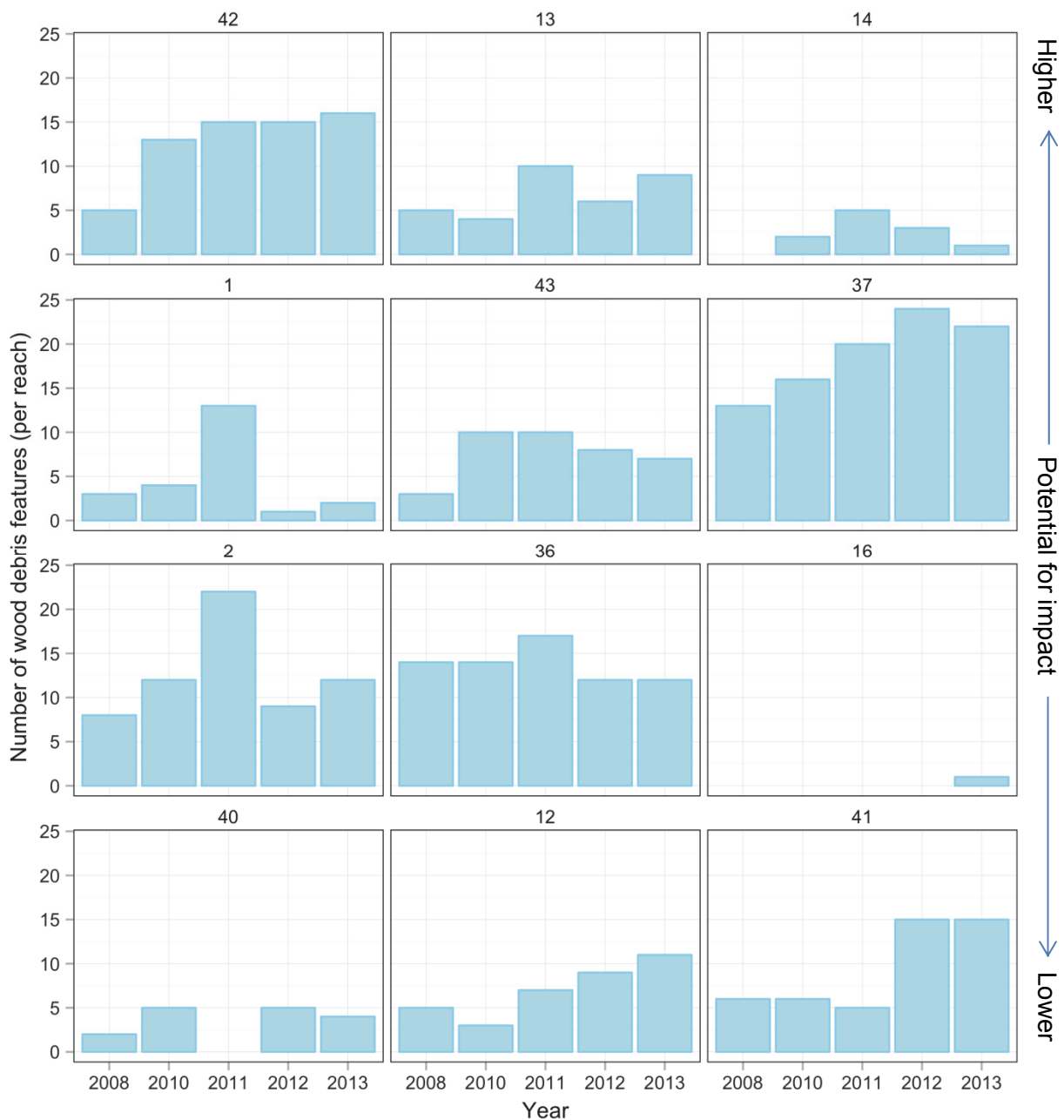


Figure 9. The number of woody debris features recorded for each of the reaches surveyed annually between 2008 and 2013

The trend in the number of woody debris features through time varies from reach to reach. There was an increase in the number of features recorded in some reaches, e.g. 12, 16, 42, but this was not apparent in all reaches. Moreover, obviously cut beaver wood was rarely observed outwith the beaver dams. To compare reaches directly and assess whether changes in the occurrence of features could be attributed to the potential impact of beavers, the number of features were converted to a score of density per 100 m. When the reaches were then grouped according to the level of beaver activity, the general trend (apart from 'low' beaver activity) was for an increase in the density of features, although there was variability amongst the reaches within each group (Figure 10). The fact that reaches assigned to very low, moderate and high levels of activity all showed a similar average trend suggests that any apparent trend was unrelated to beaver activity. This most likely reflected the general influence of major storms in winter and spring of 2012 whose influence was potentially greater due to the weakening of branches by unusually high snow accumulation in the winters of 2009/10 and 2010/11.

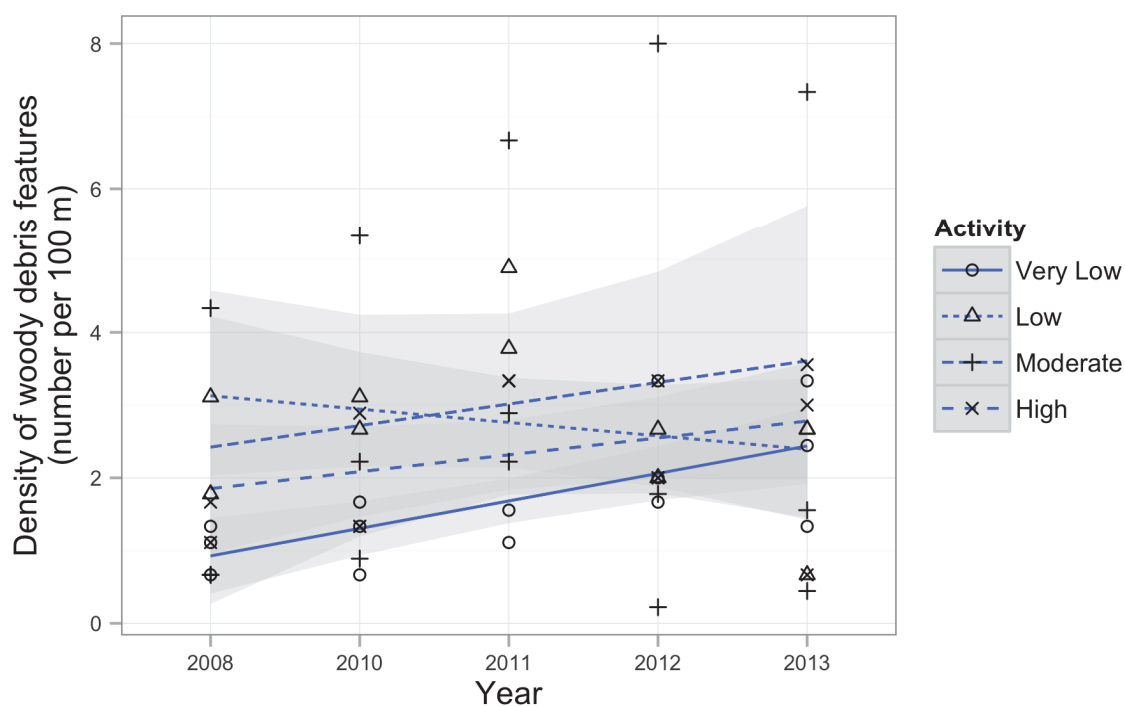


Figure 10. The trend in number of woody debris features over the duration of the trial. The data suggest a slight overall increase, but due to high variability amongst the reaches the effect is not statistically significant

To test the statistical significance of the trend and, more specifically, to test for a difference in the rate of increase in the presence of features between different activity levels, a linear mixed-effects model was fitted to the data. To account for the fact that reaches were repeatedly surveyed over the course of the trial, a correlation structure was incorporated into the model. The output is given in Figure 11. The model suggests that, based on the data available, it is not possible to confirm that the observed trend represents a true increase, although this trend would be significant at a threshold of  $p = 0.1$ . Perhaps more importantly, there is no statistical evidence that any of the different beaver activity levels responded differently through time.

R Output

Linear mixed-effects model fit by REML

Data: wd.allyears

AIC	BIC	logLik
185.8512	205.9662	-81.92558

Random effects:

Formula: ~1 | Reach

(Intercept) Residual

StdDev: 1.490896 1.028268

Correlation Structure: ARMA(1,0)

Formula: ~Time | Reach

Parameter estimate(s):

Phi1

0.3420052

Fixed effects: Density ~ Time \* Activity

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.6018063	1.1118528	38	0.5412644	0.5915
Time	0.3589973	0.2037344	38	1.7620843	0.0861
ActivityLow	1.7901940	1.7065295	8	1.0490261	0.3248
ActivityModerate	1.4237708	1.5715373	8	0.9059733	0.3914
ActivityHigh	0.7369953	1.6090752	8	0.4580241	0.6591
Time:ActivityLow	-0.3997090	0.3170988	38	-1.2605186	0.2152
Time:ActivityModerate	-0.0587884	0.2881240	38	-0.2040384	0.8394
Time:ActivityHigh	-0.0750409	0.2999804	38	-0.2501528	0.8038

Correlation:

	(Intr)	Time	ActvtL	ActvtM	ActvtH	Tm:ACL	Tm:ACM
Time	-0.550						
ActivityLow	-0.652	0.358					
ActivityModerate	-0.707	0.389	0.461				
ActivityHigh	-0.691	0.380	0.450	0.489			
Time:ActivityLow	0.353	-0.642	-0.619	-0.250	-0.244		
Time:ActivityModerate	0.389	-0.707	-0.253	-0.550	-0.269	0.454	
Time:ActivityHigh	0.373	-0.679	-0.243	-0.264	-0.576	0.436	0.480

Standardized within-Group Residuals:

Min	Q1	Med	Q3	Max
-1.487025500	-0.489330269	0.005685075	0.469677668	2.186147713

Number of Observations: 54

Number of Groups: 12

Figure 11. Statistical output from the linear mixed effects model to investigate the relationship between the woody debris features and beaver activity

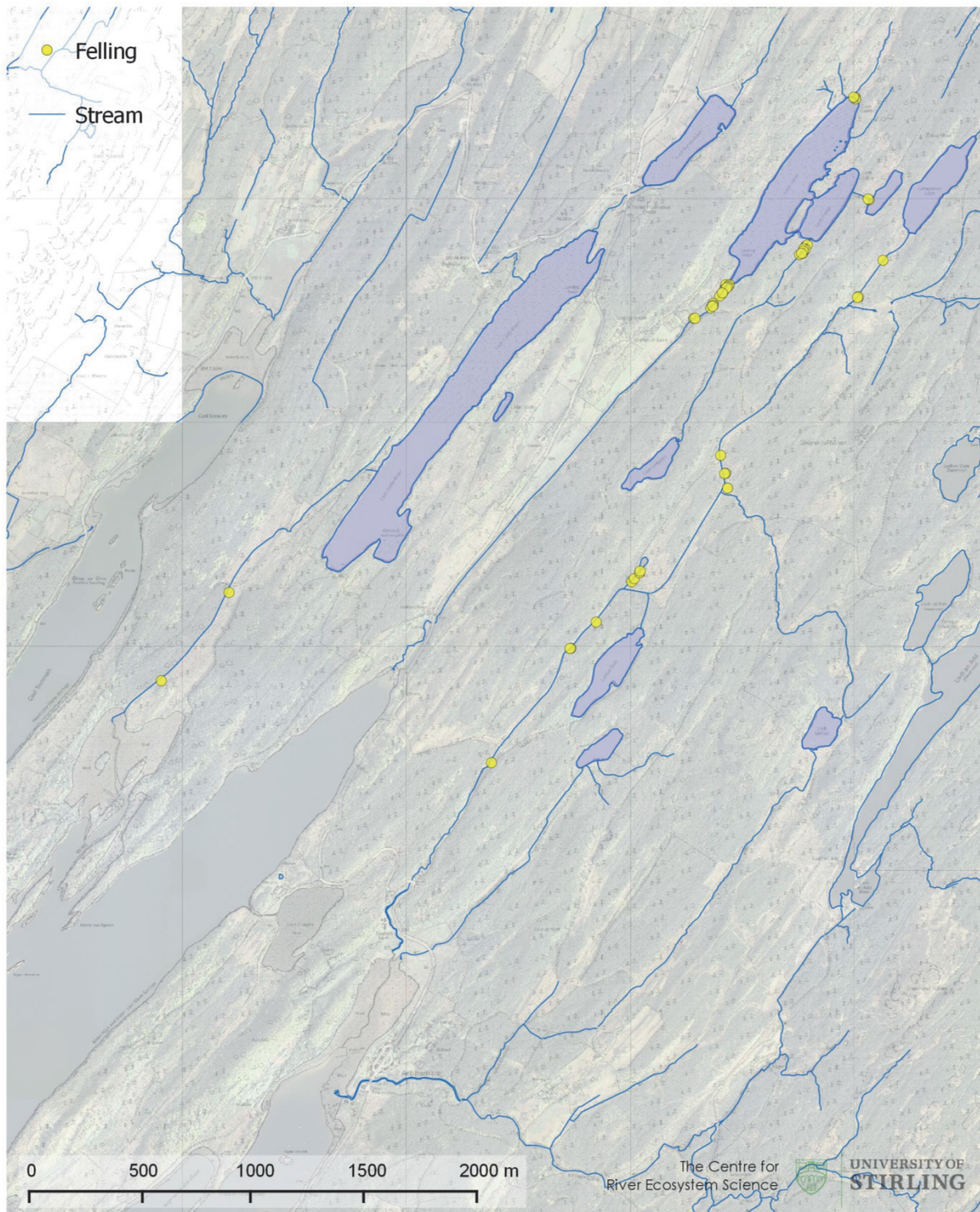
Field observations indicated that, although features can be relatively transient, most notably smaller loose accumulations of twigs and leaves, for the relatively low energy Knapdale streams, larger features and individual pieces can remain *in situ* for a number of years ( Figure 12). Additionally, even where there is a turnover of material, features persist at some locations.



Figure 12. Fixed point photography showing the relative stability of woody debris. The upper panel is from reach 36 and the lower from reach 2.

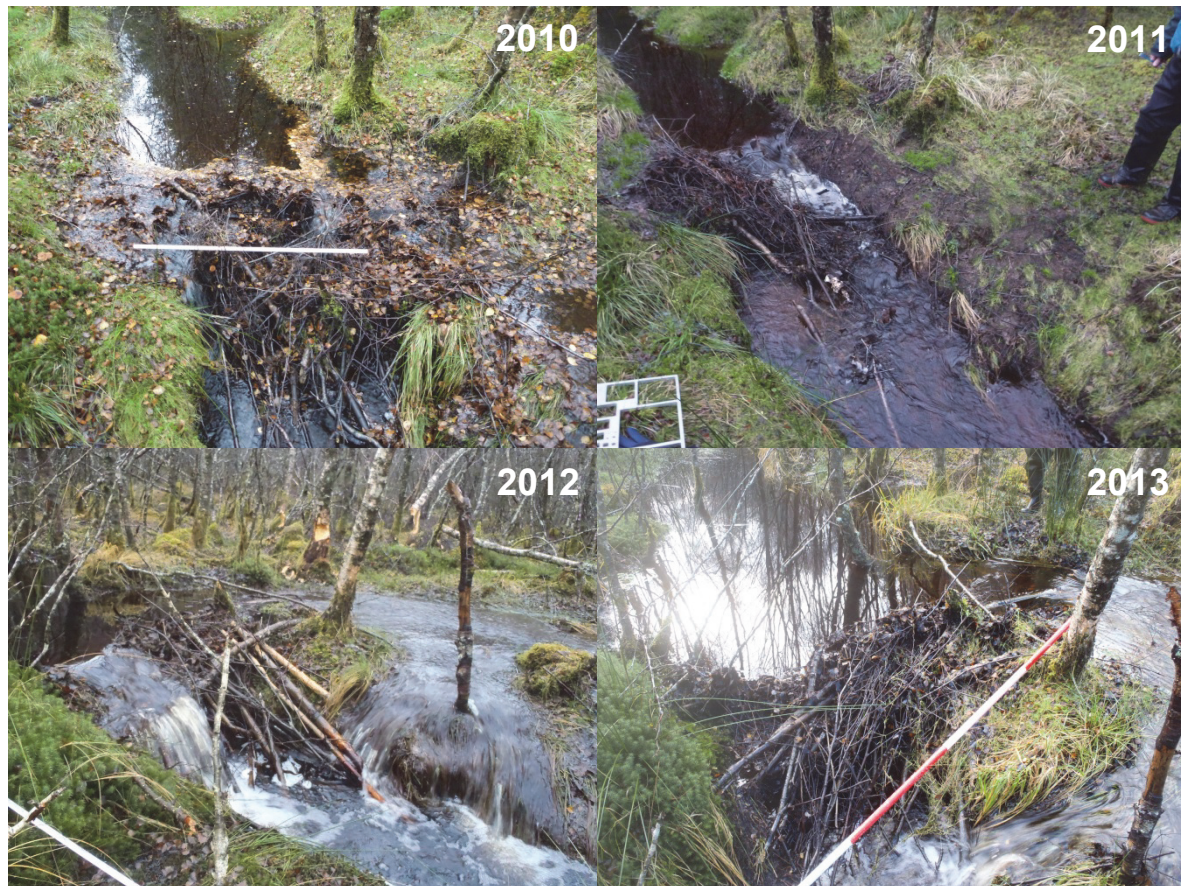
#### 4.5 Beaver felling and dam construction

In addition to monitoring the potential effects of beaver activity on stream morphology and habitat, data on riparian felling and dam construction by beaver were collected. The recorded instances of riparian felling are shown in Figure 13. Other than near the shoreline of Loch Linne and Loch Fidhle, and on the outflow of Un-named Loch (North), symbols indicate the felling of single stems or small trees.



*Figure 13. The location of observed riparian felling on the stream network in the Scottish Beaver Trial area*

Three dams were constructed on survey reaches within the area of the trial. The beginnings of a dam on the outflow of Loch Linne were removed by Scottish Beaver Trial field staff early in the trial to comply with the conditions of the release licence. A dam at the outflow of Un-named Loch (North) was constructed at the start of a small stream that connects the Loch with Loch Fidhle over a distance of approximately 150 m. The proximity of the dam to the loch shore and the small size of the stream meant that this dam had very little measurable effect on the stream. The third dam, constructed on the inflow to Loch Fidhle (reach 13), had measurable but localised effects on the stream. In November 2013, the dam was 60 cm high and ponded water behind it for 55 m upstream. The phases of dam construction are shown in Figure 14.



*Figure 14. Fixed point photography of dam constructed on the inflow to Loch Fidhle (reach 13)*

The dam was constructed on a sluggish, slow flowing section of channel near the outflow of Loch Fidhle. Although there was a build-up of leaf litter, the already fine substrate did not accumulate and is unlikely to change dramatically.

Figure 15 shows the change in stream morphology at this site over the period of the trial. A transition to more lentic habitat and an increase in marginal wetland, attributable to a raised valley floor water table, is evident.

Other instances of dam building within the trial area were associated with the unmapped outflow of Dubh Loch into Loch Coille-Bharr where beavers began construction of a dam in October 2009 that ultimately raised water levels upstream by over 1 m. On Loch Linne two low dams 20 m apart were constructed in August 2009 but were situated upstream of reach 42 before the loch outflow formed into a clear channel. These may have been trial structures constructed in advance of the main (but subsequently removed) dam 200 m

downstream. No attempt was made to remove these structures due to their inaccessibility but they were no longer present in May 2011, possibly as a result of damage by thawing ice. It is also understood that in September 2014 beavers dammed the outflow of Un-named Loch (South) in reach 10 (Roisin Campbell-Palmer pers. comm.).



Figure 15. The impact of dam construction on stream habitat of inflow to Loch Fidle (reach 13).

## 5. DISCUSSION

### 5.1 Effectiveness of monitoring

The monitoring of instream and riparian stream habitat during the trial was successfully implemented. This discussion is shorter than it would have been had the beavers exploited the stream habitat available.

The recording of felling in the river corridor at a number of locations confirmed that beavers investigated some of the streams. There were relatively low rates of riparian zone felling along the majority of the streams. This was consistent with the observations of other monitoring partners in the Scottish Beaver Trial i.e. that beaver activity had been focussed on loch and loch shore habitat (Willby *et al.*, 2014) and adjacent woodland (Iason *et al.*, 2014). It endorses the decision to (a) reduce the extent of stream monitoring and to (b) reallocate resources to collecting loch data where more sizeable beaver effects were generating results that were more likely to provide an insight into the ecology of the beaver in the Scottish landscape.

The stream monitoring that was undertaken after the baseline survey focused on stream reaches close to the lochs with resident beaver populations. Beaver activity in the stream environment was low, even at sites with the most suitable habitat and situated in close proximity to occupied territories. Thus, any effects were likely to be small. The size of the trial (e.g. the number of beavers and the number of streams with repeat surveys) may mean that there is not enough power to detect any of these beaver-related effects. Even so, the results of the monitoring, together with some more qualitative observations, warrant discussion. Where possible, this has been developed into conclusions relevant to making decisions about the future of the beaver in Scotland.

### 5.2 Effects on stream habitat

The analysis of habitat data indicated that the beavers in the Knapdale trial had no significant reach-scale effects on instream or riparian habitat during the monitoring period. Within-reach variability in Habitat Quality Score was relatively small suggesting that any beaver-related trend would likely be detectable. Instead, the variability was predominantly attributable to differing flow conditions at the time of survey, leading to the recording of different flow types. The difficulty of relocating the precise position of RHS cross-sections, due to the effect of dense tree cover on GPS reception, may have introduced additional variability, as may inter-surveyor variability. However, the methodology can accommodate this type of error, allowing confidence in the conclusion that there has been no significant change in the type and diversity of habitats present at the reach scale. The fixed-point photographs presented in Figure 3 are typical of the majority of stream reaches and support the indications given by the Habitat Quality Scores. The modification of stream habitat by beavers in Knapdale occurred at a very low frequency and, even in those reaches affected, modifications rarely extended beyond a single spot-check. However, the potential for beavers to modify fluvial habitat in alternative settings through a greater occurrence of dam construction should not be doubted (Burchsted & Daniels, 2014).

Figure 16 illustrates changes to small headwater agricultural streams at a site on Tayside associated with extensive felling and dam building by beavers and monitored over a 12 year period. Here there have been major changes in the riparian habitat and distribution of flow types, the retention of coarse and fine organic matter and fine sediment, and landscape scale changes in physical habitat heterogeneity (Law & Willby, *subm*). In this case the animals occurred at high densities due to partial containment, had limited access to larger areas of standing water, and tree felling by beavers was the major agent of wood input to watercourses. The use of RHS in this situation would, without question, have registered major changes in fluvial geomorphology.





*Figure 16. Examples of modification of stream habitat on Tayside associated with dam building by beavers. All pictures from Bamff Estate near Alyth. Clockwise from top left: woody debris input to stream prior to dam building; creation of shallow water wetland through low 100 m long dam on stream headwater; mature (7 year old) pond formed on a cascade dam system on steeper gradient channel; three year old dam on cascade system reinforced after flood damage. All pictures © Nigel Willby.*

### **5.3 Effects on drivers of stream habitat**

As well as using RHS to monitor stream habitat, potential drivers of reach scale change, specifically the presence of instream woody debris, deposition and erosion features, were surveyed. As well as being important habitats in their own right, these features have the potential to alter in-stream hydraulics and instigate habitat change that should ultimately be reflected to changes in HQS.

Felling activity has the potential to contribute to the amount of woody material present in a river both directly through the building of dams and food caching, and indirectly through felling in the riparian zone. However, over the course of the trial, riparian felling was relatively low and generally restricted to discrete patches or individual trees within the river corridor. Exceptions to this occurred where the riparian corridor overlapped the shoreline of Loch Linne, Loch Fidle and Un-named Loch (North).

Dead and live wood, including tree trunks, stumps, twigs and branches, are naturally occurring components of stream habitat, and are essential to the natural functioning of stream ecosystems. It is widely referred to as large woody debris (LWD) and can form features as single pieces, but commonly coalesce to form jams that may span the channel, impound water and retain smaller items of organic matter such as leaves, and introduce hydraulic diversity. It provides important services, including the provision of habitat and food for fish and invertebrates, the diversification of processes of sediment transport, and is part of the nutrient cycle.

Although beaver cut wood was seen in the channel at some locations, any increase attributable to beaver felling was swamped by the variability attributable to natural inputs of wood, fluxes of wood and degradation processes. These include dying trees falling over, broken branches and windthrow as well as decay and the break up and dispersal of features. Storms were reported in the weeks prior to the 2011 survey, and the reports were supported by field observations of storm damage. Further storms were also reported prior to the 2012 and 2013 surveys. Storms are likely to contribute to the turnover of features both through an increase in the input of woody material and the breakdown and dispersal of existing in-stream features during high flow events. In some reaches, new woody debris features introduced by the 2011 storms persisted. Others were relatively transient with densities having returned to pre-storm levels. This was most obvious through sections of birch woodland where branches were already relatively rotten before falling into the streams.

The rate of input of beaver-generated wood to the streams of Knapdale was small compared with the inputs through these other natural processes, e.g. windthrow during storms. Since small-scale aggregations of wood are typical of forested stream ecosystems any additional inputs associated with beaver activity are likely to be of low consequence.

No marked changes in the presence of fluvial features or the general geomorphological character of the streams surveyed were observed during the course of the trial. The data collected revealed the reaches to be relatively stable, as would be expected for catchments dominated by hard limestone and igneous rocks (Peach, 1911) and supporting extensive forest cover. The number of features remained low throughout the trial and the composition of bed substrate was relatively stable. Extensively modified sections of channel present within the trial area, most notably altered by straightening and ditching for forestry purposes, also showed very little morphological or ecological change.

#### **5.4 Effects of dam building**

In the trial area, the building of a total of six dams was recorded up to October 2014. Of these, the major structure on the Loch Linne outflow was removed and the secondary structure did not survive, possibly due to the effects of thawing ice. The total recorded density of dams at Knapdale was 0.3 per km, which lies at the lower end of the range of 0.14 to 22.00 dams / km recorded for beavers in Russia and North America (Zavyalov, 2014). In the US, Burchsted & Daniels (2014) quote densities commonly exceeding 10 dams / km of channel. In contrast to Knapdale, Law & Willby (subm) found that at one site on Tayside with a history of beaver occupation since 2002, the frequency of dam building on small headwater agricultural streams had reached 5 dams / km by 2012, with widespread associated effects on stream morphology, habitat heterogeneity and fine sediment and organic matter retention (see Figure 16). However, the animals were within a large enclosure, and so some caution is needed in comparing these observations from those taken from completely free-living animals.

Beaver dams have the potential to interrupt the downstream conveyance of sediment that naturally occurs during high flows. As a result, beaver dams are widely recognised as important sediment sinks (Meentemeyer & Butler, 1999). In larger streams and rivers with higher sediment loads, dam building might be expected to have a destabilising effect on channel morphology through longitudinally decoupling geomorphic processes (Burchsted & Daniels, 2014). It was not possible to investigate this as part of the Scottish Beaver Trial, principally because the incidence of dam building was so low and beavers tended to construct dams on small, low-energy, already silty channels and thus influenced only very short lengths of stream. Since the geomorphic effects of beaver dams tend to increase with their age and height (Malison *et al.*, 2014; Burchsted & Daniels, 2014) it is probable that the relatively young age and low height of most dams at Knapdale also serves to reduce their influence. The extensively forested nature of the Knapdale stream catchments also meant that sediment input was naturally very low. However, localised effects (i.e. spot-check scale)

included increasing the diversity of marginal stream habitat and diversifying flow patterns, consistent with the positive effects of beaver dams on habitat heterogeneity reported on much larger scales elsewhere (Smith & Mather, 2013; Burchsted & Daniels, 2014).

### **5.5 Future scenarios at Knapdale and implications for stream geomorphology**

The resources associated with standing waters and the adjacent woodland are likely to sustain the current low density Knapdale beaver population without further utilisation of stream habitat. Since beavers are highly territorial, any increased survivorship of kits to adult stage may result in the establishment of new territories. This would require exploration of the stream network by dispersing animals that may result in the wider incidence of small-scale habitat modification. However, the standing water resource currently includes several lochs unoccupied by beavers (Losgunn, Barnluasgan, Un-named Loch (South) and McKay) all of which offer suitable habitat and an abundance of palatable macrophytes (Willby *et al.*, 2014). Provided that beavers successfully discover these lochs, extensive use of the stream system remains unlikely in the near future.

If the population size increases in parallel with a reduction in the quality of existing territories (e.g. due to over-exploitation of the lake macrophyte resource) it is possible this would increase further the motivation of beavers to establish territories on the stream system. The existing examples of dam building in Knapdale, although few, include a notable change in habitat at one site (Dubh Loch) which clearly indicates that the Knapdale beaver population has both the propensity and resources (typically small willow and birch) for dam construction. Any large-scale expansion of beavers into the Knapdale stream system would therefore be expected to produce changes in fluvial geomorphology typical of forested stream catchments elsewhere. However, provided animals retain access to young willow and birch and the beaver population does not increase dramatically, it seems highly unlikely that the frequency of dam building will approach that commonly observed in headwater streams in the US.

### **5.6 Wider implications of findings for beaver reintroduction in Scotland**

The present observations suggest that, where beavers occur at low density and in close proximity to well-vegetated standing waters, the effects on stream systems will be limited since felling activity is likely to be associated with loch shorelines and there is little requirement to raise water levels through dam building. If the productivity of such populations is sufficient, additional territories are likely to be formed via the colonisation of other standing waters and adjoining riparian habitat, rather than through the energy-costly modification of watercourses. Such conditions might potentially apply across much of the north and west of mainland Scotland. According to the temporal resource variability hypothesis, animals exploiting highly seasonal resources are also likely to meet their nutritional requirements within smaller home range sizes. Since beavers at Knapdale exploit deciduous macrophyte species (Willby *et al.*, 2014), whilst beaver ranges elsewhere have been shown to shrink with increasing temporal resource heterogeneity (McClintic *et al.*, 2014), it is possible that beaver home range sizes that include lakes will typically be small with the effects on surrounding running water systems being reduced accordingly.

Elsewhere in Scotland, away from high concentrations of shallow, well-vegetated standing waters, beavers are likely to associate with margins and backwaters in the lower lying reaches of larger rivers or small floodplain stream systems. Here, low stream power favours the accumulation of finer sediment and the growth of willows with smaller stem sizes that are preferred by beavers (Jones *et al.*, 2009; Campbell *et al.*, 2012). Studies of the distribution of the Eurasian beaver in different European countries typically highlight a preference for riverine willow scrub above all other types of riparian habitat (John & Kostkan, 2009; Fustec *et al.*, 2001). The increased input of wood to river systems is likely through either direct felling, caching, or on smaller agricultural streams, dam building (although current evidence indicates that dam building on Tayside outwith known hotspots of beaver activity has been

rare to date; Campbell *et al.*, 2012). Beavers will make a more significant contribution to inputs of wood in such systems than on rivers with more extensively wooded margins where inputs via windthrow, bank erosion and storm damage will naturally dominate. The middle to upper courses of large rivers of upland character may offer less suitable habitat for beavers due to higher channel mobility, faster and more highly variable flows, coarse alluvial substrates and natural dominance of the riparian zone by mature black alder. Studies of species- and size-specific felling rates suggest that such trees are unlikely to be used widely by beavers due to their large size and low palatability (Gerwing *et al.*, 2013; Iason *et al.*, 2014).

## 6. CONCLUSIONS

The approach used to monitor the stream network, including RHS, the modified fluvial audit, and the inventory of features, provided a robust method for observing and documenting habitat change. The surveys undertaken on the stream network represent, both spatially and temporally, one of the more intensive applications of the RHS methodology in the UK. The results of the analysis of the quantitative environmental data reflect the qualitative observations of the riparian and in-stream habitat.

Baseline surveys estimated the natural levels of woody debris in streams. Further surveys revealed that woody debris features varied in both size and persistence. Windthrow was a source of in-stream wood during the trial, although statistical analysis suggests that this was not true for all reaches. This is most likely due to the differing riparian habitat of each reach. Beaver-generated in-stream wood was recorded but was not found to increase the density of features above the natural background level and was a minor source of material relative to the input caused by wind damage to trees.

Channels were found to be geomorphologically stable, with less than one erosion or deposition feature per 500 m length for the duration of the trial. This is consistent with small streams flowing through well-vegetated river corridors in well-forested catchments. High flows capable of generating new erosion and deposition features are rare and features are rapidly recolonized by vegetation. This pattern remained unchanged throughout the duration of the Scottish Beaver Trial.

Incidences of riparian felling indicated that beavers explored much of the stream network in the trial area. It is also clear that the beavers did not exploit the available resources within the river and riparian zones, other than where they overlapped with loch shorelines. Elsewhere on the stream network, riparian felling was isolated and infrequent and may have represented no more than single visits to a location.

Dams were constructed on inflows and outflows in close proximity to lochs where the flow was slow or sluggish. No streamside lodges were constructed during the period of the trial.

From the data collected it has not been possible to ascertain whether the stream habitat of the Knapdale area was unsuitable for beavers, or simply less attractive than the loch habitat and its associated woodland, which appeared to meet the resource requirements of the current population. If the population was to increase at Knapdale, then the movement of animals into stream systems and associated habitat modification may be expected.

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