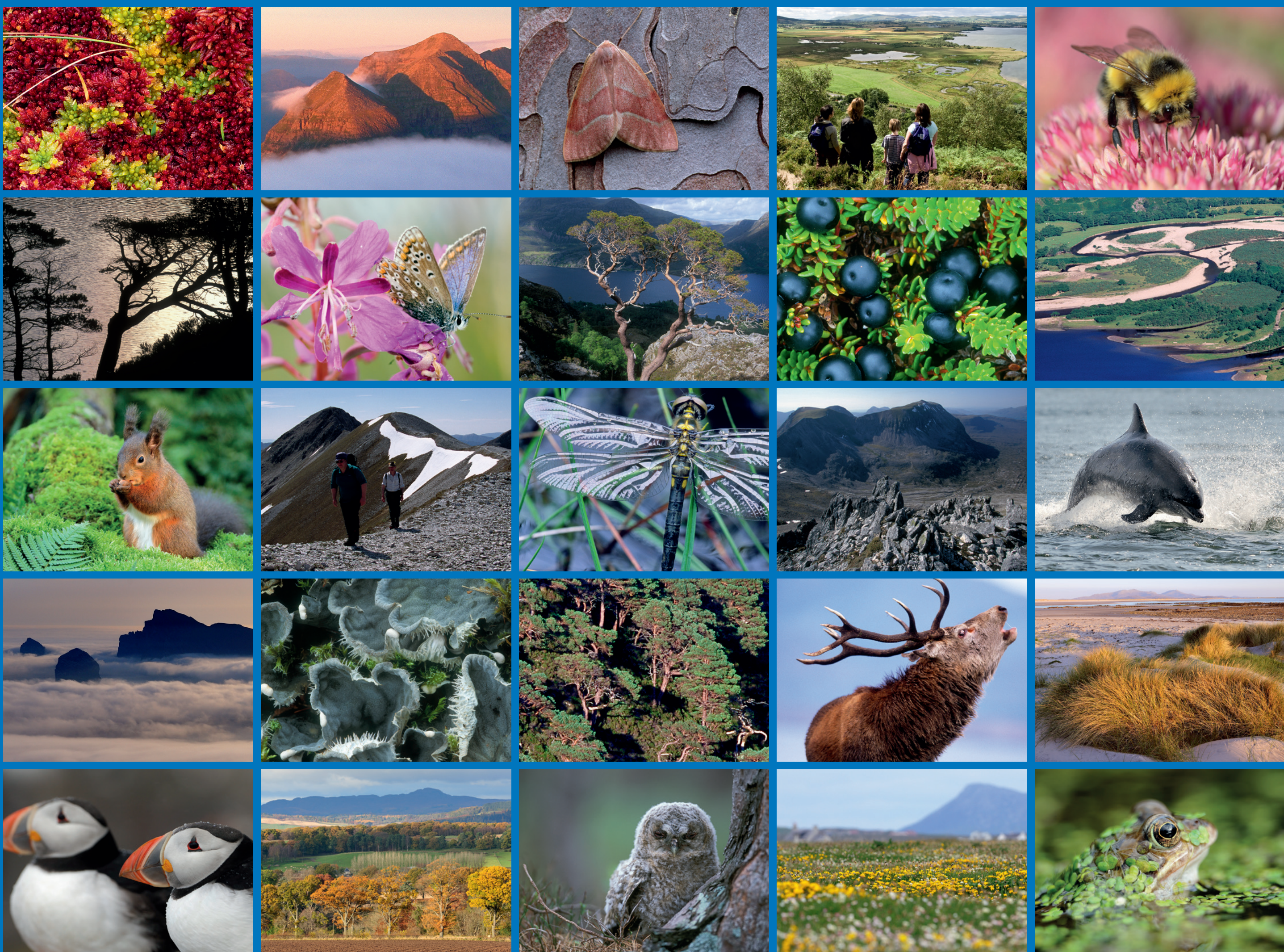
Scottish Natural Heritage
Research Report No. 1013

Survey of the Tayside area beaver population 2017-2018



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RESEARCH REPORT

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Survey of the Tayside area beaver population 2017-2018

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RESEARCH REPORT
Summary

Survey of the Tayside area beaver population 2017-2018

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Keywords

Castor fiber, density models, Eurasian beaver, management, population estimates, population dynamics, Tayside distribution

Background

There is a long, documented history of the Eurasian beaver *Castor fiber* and its former abundance throughout Britain (Coles 2006), and it is generally believed to have become extinct in Scotland, through over-hunting, by the 16th century (Kitchener and Conroy 1997). In 2009, an official trial reintroduction of beavers, the Scottish Beaver Trial (SBT), took place in mid-Argyll, though it later became apparent that a larger number of beavers existed through unauthorised releases in the Tayside area of Perthshire, with confirmed reports of their presence from around 2006. For the purposes of this survey 'Tayside' refers to the total catchments of the Rivers Tay and Earn.

The largest beaver population in Scotland currently occurs in Tayside. A full survey was first undertaken in 2012 (Campbell et al. 2012). Scottish Government announced in November 2016 that it was minded to retain the Eurasian beaver in Scotland. The decision was informed by 20 years of work on beavers and beaver reintroduction issues, summarised in the SNH '*Beavers in Scotland'* report (Gaywood 2015). The 2012 survey estimated that there were 38-39 groups of beavers present in the Tay catchment, equating to approximately 146 individual beavers (range 106 - 187). Further records were collated and presented in the final report of the Tayside Beaver Study Group (TBSG) published in 2015 (TBSG 2015), and more recent records received from the public were collated by SNH. The TBSG report highlighted the need for a resurvey of the Tay catchment to help inform decision-making for beaver management and clarify the current conservation status of the species. The need for a resurvey has also been confirmed by the current Scottish Beaver Forum. This report describes the findings of this survey, using density mapping of field signs and reports of beaver activity; makes comparisons with the 2012 survey; and estimates the current population size and distribution. It included surveys in catchments adjacent to Tayside, including sections of the Forth/Teith, Tay coastal catchments and the South Esk. Recommendations for future research and potential management strategies are also made.

Main findings

– Beaver activity was recorded throughout large parts of Tayside.

- Beavers are spreading in distribution and are present outside the catchments of the Tay and Earn. Small numbers of territories occur within the Forth catchment from Loch Achray in the Trossachs, parts of the Teith and Devon, and the main stem of the Forth near Stirling.
- No evidence of beaver presence was found on the South Esk nor in several freshwater bodies associated with the lower Forth and Forth estuary, including Loch Leven.
- Distribution in Tayside ranged from as far north as Dunalastair Water, extending out to the River Dochart and River Lyon in the west, over to Forfar Loch in the east and down to Loch Earn in the south.
- 114 active beaver territorial zones were identified in this study, giving a conservatively estimated number of approximately 433 beavers (range 319 – 547). This number is based on a previously reported European mean group sizes of 3.8±1.0 animals per territory, which was also used in the 2012 SNH survey. Some identified zones may constitute multiple families and additional active territories, along with dispersing singletons, are likely to exist both within Tayside, especially on minor watercourses, and outside of the Tayside catchment which it was not feasible to cover during this survey.
- Out of the 114 beaver territories defined using the 2017/2018 survey data, 100% were contained within the areas identified as 'Potential Beaver Woodland' and 95% were contained within the 'Potential Core Beaver Woodland', as defined by previous SNH GIS mapping exercises (Stringer et al. 2015).
- Potential management issues were recorded at a total of 159 points, across 21 territories, ranging from dam building, collapsed burrows, tree felling, crop feeding and damage to fence lines.
- A total of 86 dams, or sites where dams had been removed, were recorded. Of these, 41 dams occurred within one private estate.
- There was an increase in both beaver distribution and density compared to the 2012 survey although spatial variability was evident, with areas of expansion and infilling, along with smaller areas of habitat abandonment potentially through culling.

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List of abbreviations

BDA	Beaver Dam Analogues
BRAT	Beaver Restoration Assessment Tool
CDE	Clinton Devon Estate
EPS	European Protected Status
GPS	Global Positioning System
LLTNPA	Loch Lomond & the Trossachs National Park Authority
NFUS	National Farmers Union Scotland
OS	Ordnance Survey
SBT	Scottish Beaver Trial
SNH	Scottish Natural Heritage
SWBG	Scottish Wild Beaver Group
TBSG	Tayside Beaver Study Group

1. INTRODUCTION

1.1 Background

Archaeological evidence of the Eurasian beaver *Castor fiber*, such as preserved gnawed timber and bones, carvings and historical references, testify to their former abundance throughout Britain (Coles 2006). By the 15th century, the trade in beaver furs in Scotland was no longer economically viable due to over-exploitation. While oral tradition suggests small numbers may have survived in and around the Loch Ness and Lochaber areas until the late 17th century, there is no further mention of their presence after this time (Coles 2006). The Eurasian beaver is therefore believed to have become extinct in Scotland, through over hunting, by the 16th century (Kitchener and Conroy 1997).

Both Eurasian and North American *C. canadensis* beavers tend to colonise suitable habitat in a linear manner (i.e. dispersal generally follows water courses) though they can travel over land between catchment basins (Halley et al. 2012; Simunková and Vorel 2015). Dispersal distances for individuals can range from a few kilometres to tens of kilometres, depending on a range of factors including population density and habitat availability (Zurowski and Kasperczyk 1990; Fustec et al. 2001). It has been estimated that ~80% of dispersing beavers attempt to establish territories within 5 km of their natal territory (Nolet and Baveco 1996; Saveljev et al. 2002), though much greater distances (80 km+) have been recorded. Beavers are highly territorial, living in family units which actively defend their territories largely through chemical communication and aggression. Beaver territories tend to be linear and range from 0.5 km to 20 km (average 3 km) of shore or riverbank (Macdonald et al. 1995; Herr and Rosell 2004; Campbell et al. 2005). In high quality habitat, beaver families can occupy home ranges of 0.5-0.7 km of bank, with ~150-200 m long gaps between adjacent territories (Novak 1987). In poor quality habitat beaver territories can be larger and more widely spaced. The size and numbers of beaver territories depends on a number of factors including the density of beaver populations, habitat quality, the number of family members and their settlement pattern (Campbell et al. 2005).

Since the 1900s, following a historic decline primarily due to hunting, beaver numbers have recovered throughout much of their former range in Europe through protective regimes, hunting regulation, active reintroductions and natural recolonisation. The first known beaver translocation, from Norway to Sweden, occurred in 1922, and since then, there have been more than 205 recorded translocations which have returned beavers to 25 nations where they were formerly extinct (Halley et al. 2012). Such reintroductions have been a mix of official and unofficial/illegal releases, for example in Belgium (Verbeylen 2003). There are currently estimated to be approximately 1.04 million Eurasian beavers distributed throughout much of their former native range (Halley et al. 2012). The case for reintroducing the Eurasian beaver to Scotland has been debated for over 20 years, and in 2009 a trial reintroduction started in Knapdale forest, mid-Argyll, the Scottish Beaver Trial (SBT). Findings from the scientifically monitored trial have been published. Outside of this official process, beavers appeared, through unlicensed releases, in parts of the Tay and Earn catchments (referred to as Tayside in this report) and successfully bred over many years. The largest beaver population in Scotland now occurs on Tayside.

A full survey was last undertaken in 2012 which estimated that there were 38-39 active groups of beaver present in Tayside (Campbell et al. 2012). Since this survey additional active territories have been reported, along with known beaver culling undertaken by some land-owners experiencing conflicts with this species (TBSG 2015). Therefore, the need for a resurvey of Tayside to help inform decision-making for beaver management and clarify the current conservation status of the species was required.

Scottish Government announced in November 2016 that it was minded to retain the Eurasian beaver in Scotland. The decision was informed by 20 years of work on beavers and beaver reintroduction issues, summarised in the SNH ‘Beavers in Scotland’ report (Gaywood 2015, 2018). The decision further specified that beaver populations in Knapdale and Tayside would be allowed to extend their ranges naturally, but that further unauthorised releases would be an offence. Ongoing beaver conflict concerns primarily in agricultural areas of Tayside, together with an over-arching need to assess the current conservation status of beavers, led to a decision to organise a resurvey to help inform decision-making for beaver management. This report describes the methodologies and results of this resurvey to determine the current distribution, territory number and associated population estimate. Recommendations for future research and potential management strategies are made.

1.2 Objectives of the study

i. To undertake a field survey that will enable beaver field signs to be recorded and mapped, the locations and numbers of likely occupied beaver territories to be established, and the numbers of beavers to be estimated in the relevant catchments (Tayside, plus nearby catchments with confirmed or anecdotal records).

ii. To provide digital outputs that includes suitable georeferenced data compatible for SNH GIS, and for future use in relevant national biological databases.

iii. To allow for a direct comparison of survey results from the current survey with the results from the 2012 survey, in particular noting changes in territory numbers (and therefore beaver numbers), range etc.

2. METHODS

2.1 Field surveys

2.1.1 Survey area

The 2017/2018 survey area included those areas surveyed previously in 2012: the River Tay; the River Tummel; the River Isla (and its tributaries including the River Ericht, Dean Water, Kerbet Water, Burn of Kilry and Lunan Burn with Loch Clunie, Marlee Loch and Rae Loch); the mouth of the River Almond; the River Earn (and its tributaries including the Farg, Dron Burn and Pow Water); and the Invergowrie Burn. Water courses were prioritised to ensure these areas were resurveyed first.

The survey area was then expanded to include water courses with suitable habitat (based on hydrology and vegetation availability) beyond the points beavers had been previously found, plus additional areas in which beavers have been reported since 2012. In order of priority, tributaries and water bodies directly associated with the Rivers Tay, Earn, Isla and Tummel were surveyed. For these rivers, lower order water-courses (drainage ditches, for example) were also surveyed where beaver field signs were found in the vicinity and/or activity had been recorded. Following initial findings of this Tayside survey and previous reports of some beaver activity in surrounding water courses, the decision was made to extent the survey to the Forth and South Esk catchments. A similar methodology was taken with first order water courses and any lochs surveyed first.

Lastly OS maps and SNH beaver woodland maps and GIS suitability layers (SNH Potential Beaver Woodland and Potential Core Beaver Woodland datasets, Stringer et al., 2015) were consulted and a sample of other water bodies (Pitcairnie and Dupplin Loch, Monikie Reservoirs, Pond of Drummond) identified as having suitable habitat were also selected and searched.

Overall the Tayside catchment landscape spans an area ca. 5,000 km², of predominantly prime agricultural land with around 2,000 km² of arable farmland (TLBAP 2016). Urban areas also lie in the lowlands and flood plain, with large areas of the riparian zone used as salmon fishing beats. Further up the catchment, land-use is a mosaic of mixed agriculture, deciduous and plantation forest. The extensive rivers and burns throughout the Tay catchment are vast by UK standards and have a total combined length of over 5,000 km. Several standing waters also dominate the landscape and range in size from small ponds to large lochs utilised for recreational purposes such as fishing, wildlife-watching, boating or shooting waterfowl (TLBAP 2016). Many freshwater areas are designated sites for natural heritage interests throughout the catchment, for example; Sites of Special Scientific Interest (SSSIs), Special Areas of Conservation (SACs) and Special Protection Areas (SPAs), thereby tending to offer favourable habitat for beavers, including wetlands, marshes and reed beds.

The Forth catchment includes an area of approximately 1,029 km^2 and includes major tributaries such as the River Teith (SEPA, 2011). The upper Forth includes the Loch Lomond and Trossachs National Park. The headwaters are dominated by heather moorland and semi-natural woodland, going into predominantly agriculture, mainly arable farming land in the middle and lower reaches. Stirling and Alloa represents the major urban areas. The South Esk catchment drains an area of about 564 km^2. Land-use is predominantly rough grazing and forestry in the upper catchment, and agriculture in the lower catchment. The River South Esk is a Special Area of Conservation for its populations of freshwater pearl mussel (*Margaritifera margaritifera*) and Atlantic salmon (*Salmo salar*).

A total of over 1000 km of connecting water course bank (river, burn, loch etc.) and approximately 310 km of non-contiguous water course bank (using spot-checks) were surveyed over a period of over 180 person-days across all the catchments. Reports of beaver sightings from the Tayside Beaver Study Group (TBSG), stakeholders (e.g. National Farmers Union Scotland [NFUS], Loch Lomond and the Trossachs National Park), and members of the public (largely via SNH Area Office record keeping), were also investigated as far as was feasible. This resulted in areas being investigated outside of the Tayside catchments. The full area surveyed is illustrated in Annex 1.7.

It should be noted that the main aim of this report is to provide a detailed overview beaver presence on the Tayside, Forth and South Esk catchments, rather than to record every sign of beaver activity. However, given the extent of watercourses within these catchments (in particular lower order burns and extensive artificial drainage systems) it was not physically possible to survey every area of freshwater. The survey was as robust and comprehensive as possible, and all optimal beaver habitat areas were investigated. However, it should be noted that sub-optimal and some highly-modified water courses may have been missed, therefore resulting in a possible underestimation of beaver territories/numbers, although such water courses are less likely to have permanent beaver presence. Higher order water courses, areas of known or recently reported beaver activity and areas of suitable habitat were prioritised even though beavers may occupy minor and artificial water courses, especially in areas of higher population densities.

2.1.2 Survey methods

Beavers display quite distinct and obvious field signs, although at low densities and within more naturalised water courses these may be relatively inconspicuous and mistaken for other species. Mapping field signs can help to identify beaver distribution, allow an assessment of their habitat use and an estimation of the number of active territories present within an area.

As far as possible, water courses were surveyed for field signs at least 2 km from the last recorded beaver field signs or until suitable habitat ended, for example at steep waterfalls, open moorland or significant hydroelectric dams. Two people (RCP and KW) undertook the majority of the field survey work, with assistance from Coral Edgcumbe, Donald Malone, and Gerhard Schwab, between 17 April 2017 and 25 January 2018.

This survey used field sign data and maps previously produced by Campbell et al. (2012). Following the 2012 survey, further beaver records were collated and presented in the final Tayside Beaver Study Group published in 2015 (TBSG 2015). The TBSG decided against recommending a full resurvey at that time. However, between April 2013 and November 2014, 38 cases of beaver activity were reported to the TBSG. Eleven of these reports were in areas not previously identified within the 2012 survey. These reports, along with more recent records of sightings and management conflicts provided by the public, have been collated by SNH and were used to target areas surveyed in this report.

Beaver activity was recorded by following the methods used in Campbell et al. (2012) to allow direct comparison with the previous beaver distribution study in Tayside. Field surveys involved surveying a water course from canoe or on foot depending on accessibility, though the majority were undertaken on foot. As noted in Campbell et al. (2012), canoe surveys are more likely to reveal more waterside activity with the potential for underreporting inland activity, whilst the opposite tends to be true for surveys on foot. However, this is highly dependent on the structure and size of the watercourse, and the extent of bankside vegetation growth.

Beaver field signs (see Annex 1 for type of signs recorded) were logged using one of two GPS devices. A handheld GPS (Garmin eTrex) recorded beaver signs as a single GPS point with a linear resolution of 10 m. A Trimble Geo7x GPS device was also used to provide a more detailed approach to surveying in the form of line data. This device involved the recording of a “feeding line”, commencing at the site of the first beaver feeding sign during a survey and ending after no subsequent feeding signs were observed for 10 m along that stretch of water course. In data processing this line was split into points at 10 m intervals to be comparable to point data collected (Annex 1 for full method). Point data were also collected using the Trimble device, specifically the location of features such as lodges, dams and burrows etc. This allowed the classification of large stretches (up to hundreds of metres) of continuous beaver activity of the same feeding intensity (low, medium, high) more efficiently.

For each data point or feeding line collected by either device, the following information was recorded and was re-evaluated every 10m during the survey:

1. Activity type
2. Ordnance Survey (OS) grid reference
3. Photo No. (if appropriate)
4. Estimated age (fresh, old or mix of both)
5. Distance from water (m)
6. Area affected (m)
7. River width and approximate depth (m)
8. Land use (along water course and surrounding area)
9. Beaver activity effort (low, medium or high)
10. Management impact (low, medium or high)
11. Any other comments

This information was used to help further delineate separate beaver territories based upon expert judgment following modelling. Gaps in recorded beaver field sign activity may relate to the lack of suitable habitat as opposed to an indication of beaver absence. Therefore, gaps in suitable foraging habitat that would also equate to gaps in beaver activity, were not interpreted as a boundary between family group territories. Therefore, as described in Campbell et al. (2012), gaps in beaver activity were also cross-referenced with habitat type (particularly an absence of woody vegetation) based on SNH core beaver habitat maps and aerial images in Google Maps, to refine delineation of active territories.

’Beaver activity effort’ was categorised as: low (e.g. <5 small (<10cm diameter) tree trunks/woody stems within 10m radius); medium (e.g. 5-10 small diameter trunks/stems within 10m radius); or high (e.g.10+ small diameter trunk/stems within 10m).

‘Management impact’ (i.e. the perceived impact on freshwater/land use) was categorised subjectively based on the perceived impact at the time of survey as: low if affecting a small area and/or could have been easily mitigated without excessive costs or resources (e.g. small scale tree felling); high if a large area was affected and/or mitigation was resource intensive (e.g. flood bank collapse, multiple collapsed burrows or flooding of large area of crops); with medium ranging between these.

2.2 Processing and analysis

Field data collected as outlined in Section 2.1. were quality assured, processed and backed-up weekly. All subsequent mapping and analysis was undertaken in ArcGIS 10.2.2 for Desktop. Figure 1 provides a workflow summary of the data processing and analysis. In addition to primary data collected as part of the field survey, previous survey data and associated datasets held by SNH were supplied for analysis under GIS Data Supply licence 83737. All backdrop mapping layers used OS data (© Crown copyright [and database rights] 2018 OS 100017908).

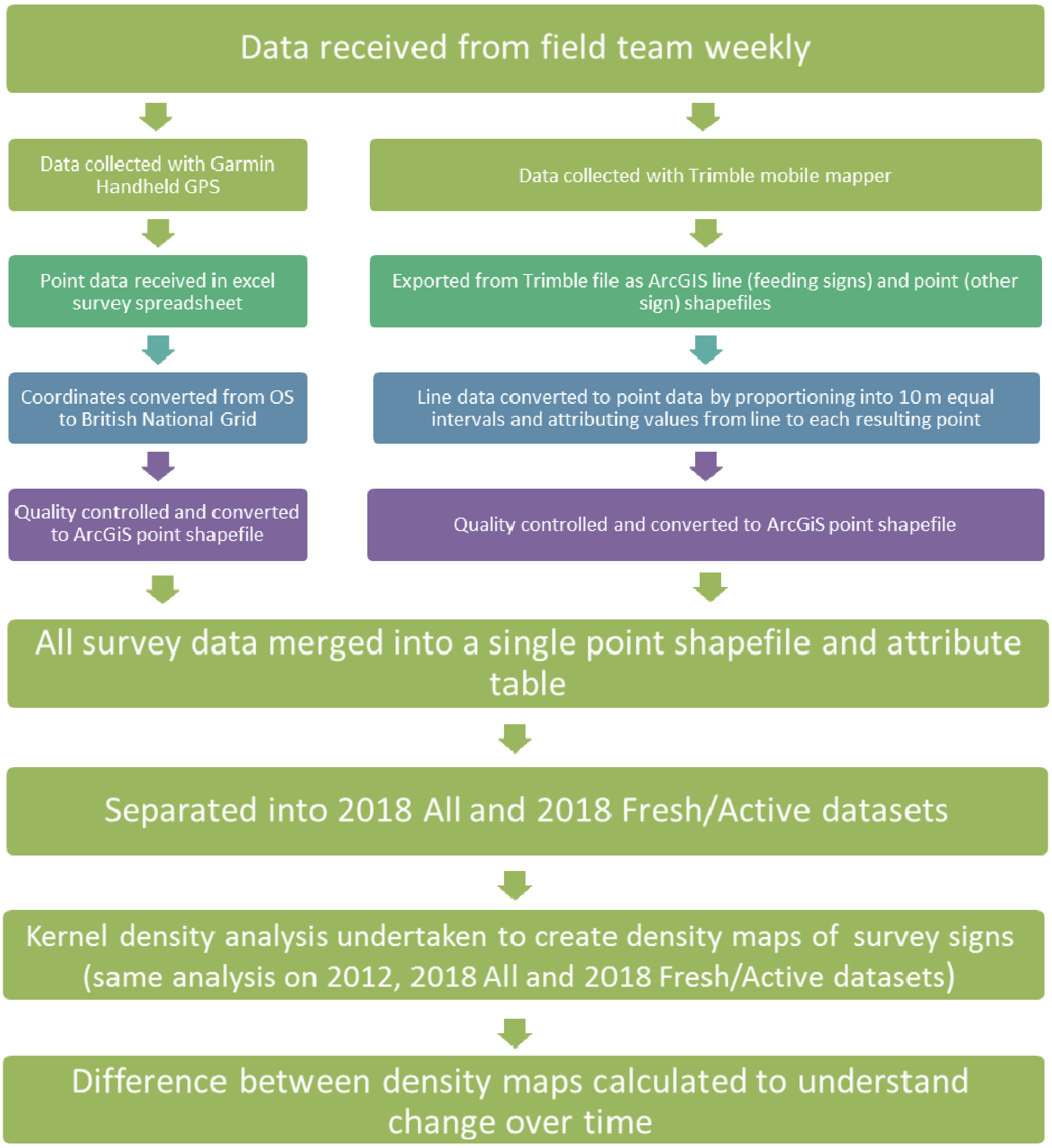

Figure 1. Flow chart summarising data processing and analysis workflow used. Full details and ArcGIS methodology provided in Annex 1.3.

2.3 Territory definition and population estimate

2.3.1 Overview

Territory and group size vary greatly within beaver populations (Wilsson 1971; Nolet and Rosell 1994; Herr and Rosell 2004). Territory size is not necessarily correlated with beaver group size or reproductive rate (Campbell et al. 2005).

Beaver territories have been defined previously using a number of methods: scent mound mapping as indicators of territory borders (Campbell et al. 2005); biologging (GPS/RF tags) individuals (Campbell et al. 2005; Graf et al. 2016); riverbank length with minimum convex polygons or kernel methods (Herr and Rosell 2004); or patterns of beaver field sign density (Fustec et al. 2001).

Early colonisation is often slow and represented by low numbers of pioneer individuals. As mating opportunities increase, new territories become established and population density increases. In expanding beaver populations, active territories tend to be further apart as family units select the highest quality habitat (Nolet and Rosell 1994), but as population density increases infilling occurs, territories come closer together and territorial behaviours (including aggression and scent marking) increase (Hartman et al. 1995; Rosell 2002). During spring, scent marking tends to increase in frequency, especially at higher population densities. This is also the time that sub-adults, after reaching sexual maturity (~20 months), disperse from their natal territories to seek territories and mating opportunities of their own (Hartman 1997). At higher population densities dispersal may be delayed with individuals as old as seven years remaining with their parental families to assist with kit rearing and natal territory defence as new territories become scarcer (Mayer et al. 2016). As beaver populations establish, population growth can increase more rapidly until carrying capacity is reached (Hartman 1994). At carrying capacity beaver populations will have a regulatory effect on numbers, especially on survival of dispersers (Parker and Rosell 2012; Campbell et al. 2005). At this stage in population development, territories tend to be smaller and fecundity is reduced, though this can vary between sites and be influenced by other factors (Campbell et al. 2005).

Beavers live in family groups, made up of an adult breeding pair typically with two generations of non-breeding offspring, ranging from two to seven individuals (Wilsson 1971). To determine total population numbers, active territories were assumed to represent one beaver family group. Campbell et al. (2012) previously estimated the number of beavers present (excluding evidence of single animals) based on multiplying identified territories by a mean of 3.8±1.0 (standard deviation) individuals (Rosell et al. 2006), and this rationale is applied here. This European average group size takes into account non-breeding territories.

2.3.2 Determination of territories from survey data

Due to the significant increase in beaver signs and territories since the 2012 survey and the requirement to provide a quantitative analysis of change in territory numbers since then, it was decided that an automated classification approach, based upon density and location of recorded signs be used to model the spatial distribution and number of territories. Kernel density analysis was undertaken and then combined with expert knowledge of the survey area to reach a final estimate of territorial zones. Kernel density analysis calculates the density of features in a neighbourhood around those features, thereby allowing the identification of spatially explicit clusters of beaver activity which it is argued relates to territorial zones.

The methodological workflow behind this territory modelling is outlined below in Figure 2, illustrating how the outputs from kernel density analysis were converted to territorial zones. The full method, including step by step analysis is detailed in Annex 1.4. All analysis was undertaken using ESRI ArcGIS 10.2.2. for Desktop. It is recognised that any such landscape scale modelling involves spatial uncertainty. However, it is argued that this uncertainty will be significantly less than the change observed between surveys. Additionally, the model was run on the 2012 dataset to compare territory number results to those determined qualitatively by Campbell et al. (2012).

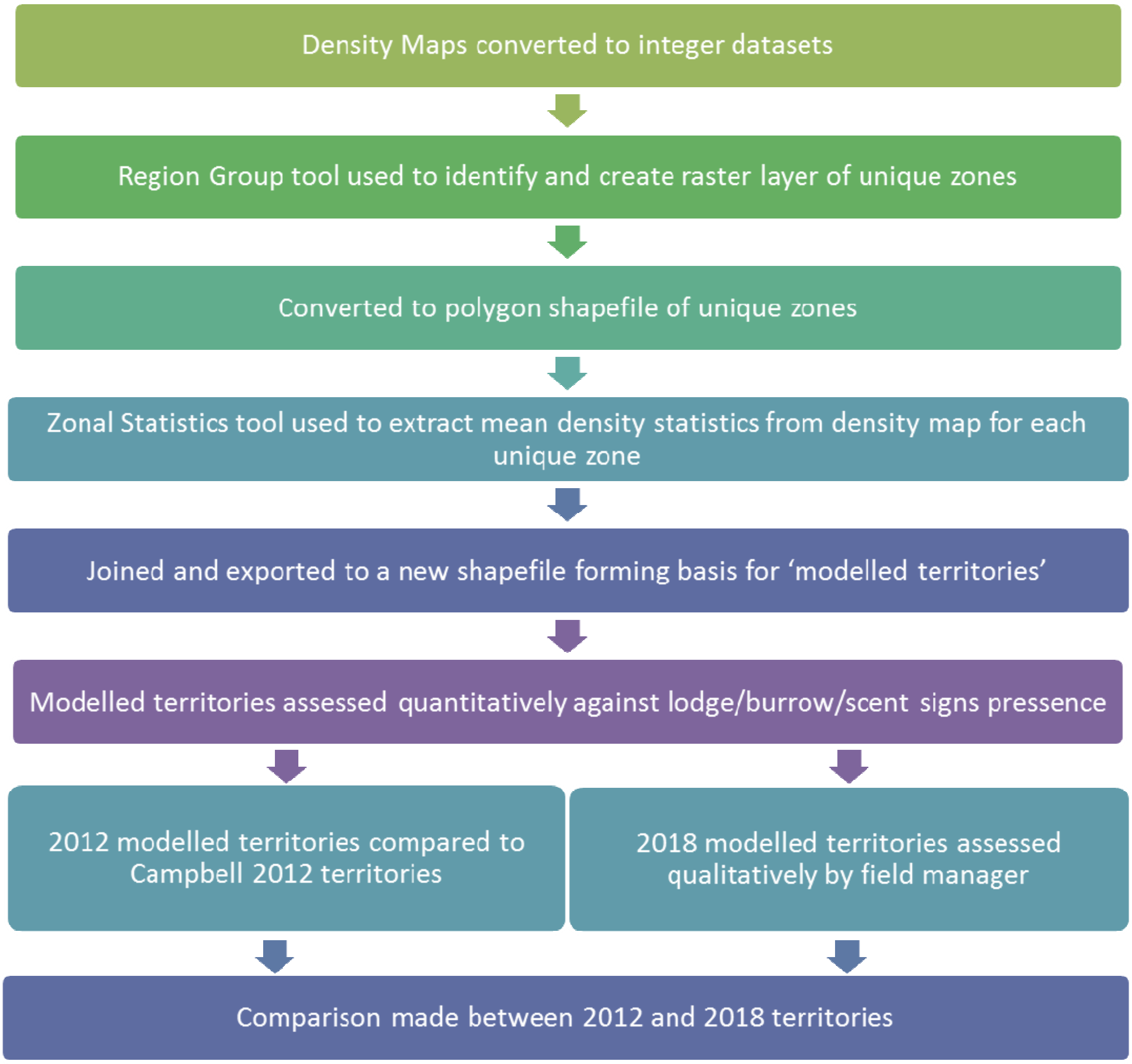

Figure 2. Flow chart illustrating the process of modelling zones of territory based upon density of survey points and subsequent interpretation. Full method and selection criteria in Annex 1.4.

3. RESULTS

3.1 Field signs

Beaver field signs (old and fresh) were only recorded within the Tayside and Forth catchments, no field signs were found in the River South Esk catchment. Field surveys resulted in a total of 23,670 data points being recorded (following data processing), covering a range of beaver field sign types (see Annex 1 for the types of field signs recorded). At some points multiple signs were recorded, making a total of 29,036 signs.

3.1.1 Type of field signs

By far the most dominant field sign recorded was woody feeding (including felled trees, cut or gnawed branches, and/or feeding on shrubs, n = 22,315 points), with fresh feeding on vascular plants the second most common (n = 5,594) (Figure 3). The distribution and density of feeding signs can be seen in Annex 2.1.

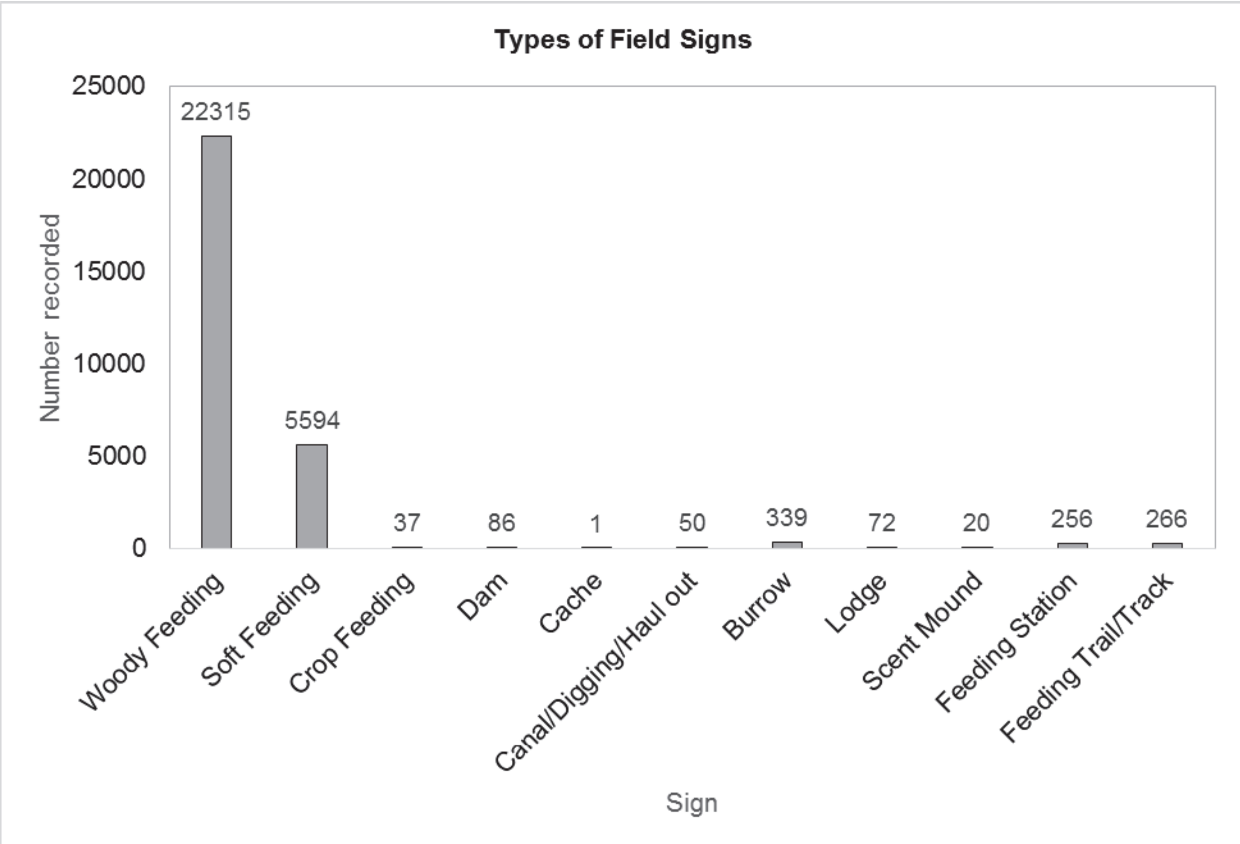

Figure 3. Types of beaver signs recorded (descriptions in Annex 1).

3.1.2 Effort expended on field signs

A subjective measure of beaver activity was made by the experienced survey personel, by estimating the amount of effort (low, medium or high) the beavers expended in producing the field signs recorded (see section 2.1.2). Overall most effort expended was ranked as low (~63%), including field signs such as foraging on small diameter sapling and/or ‘soft feeding’. Effort ranked as high represented ~9% of recorded field signs, consisting mainly of foraging on large diameter trees and fresh damming activity (Figure 4). Annex 2.2 shows how these measures of activity were distributed in the catchments.

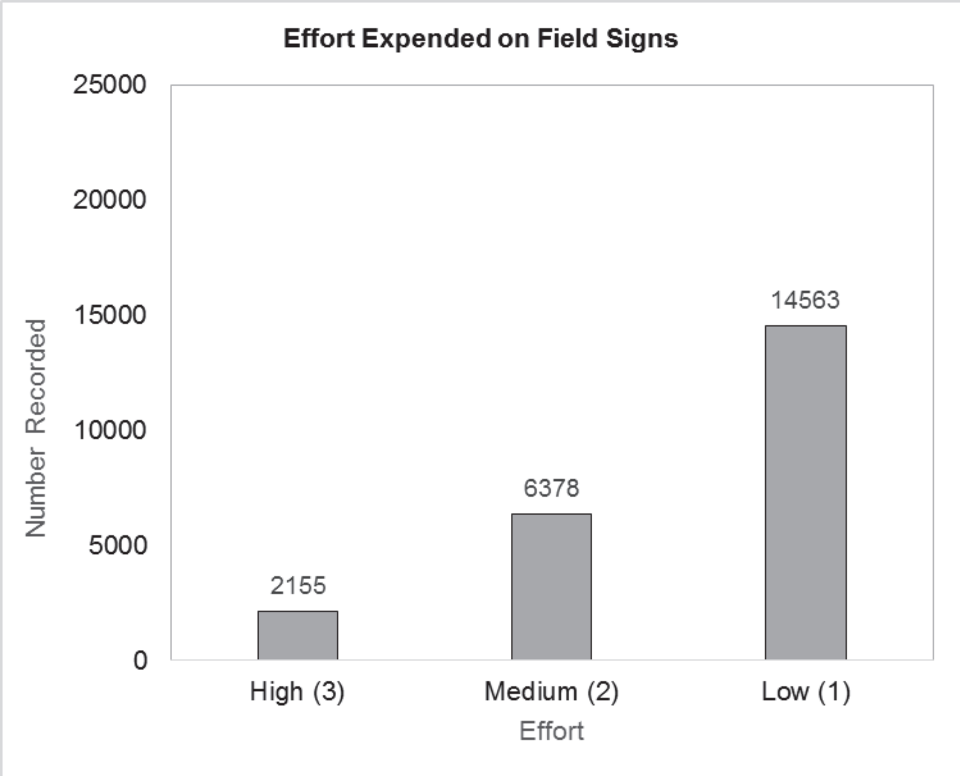

Figure 4. Number of beaver field signs requiring high, medium or low effort to be expended into the activity.

3.1.3 Lodges and burrows

A total of 72 beaver lodges were recorded during surveys. The majority (64%, N = 46) of these were in active use whereas 36% (N = 26) had been abandoned. Beaver territories contained between one and four lodges.

If the terrain is suitable, burrows are made with no over ground lodge structure. Beavers will reside in burrow systems dug into friable substrate instead of, or in addition to, a lodge. Therefore, the absence of a lodge does not mean beavers are not residing and breeding within a given area. A total of 339 beaver burrows were found. A mapped overview of the distribution of lodges and burrows can be found in Annex 2.3. However, it should be noted that burrows, in particular, can often be missed as entrances tend to be submerged, therefore these figures should not be considered as total counts. For similar reasons, distribution and population censuses should not be based on lodge/burrow records.

3.1.4 Damming activity

A total of 86 beaver dams or recently removed dams were recorded. It should be noted that 41 of these were located within one privately owned estate in Alyth where beavers had previously been held as part of a collection. Out of the remaining 45 dams, 25 were fresh/currently actively maintained, and 18 were inactive or breached dams (Annex 2.4).

3.1.5 Age of field signs

Field signs at a site could vary in their age classification (old, new or a mixture of both). Most sites of beaver activity (15,575, 68%) consisted of a mixture of both new and old field signs. A total of 25% (5,833) of all activity was classed as old and the remaining 7% (1682) was new beaver activity. Annex 2.5 details their distribution across the Tayside catchment representing their former and current distribution.

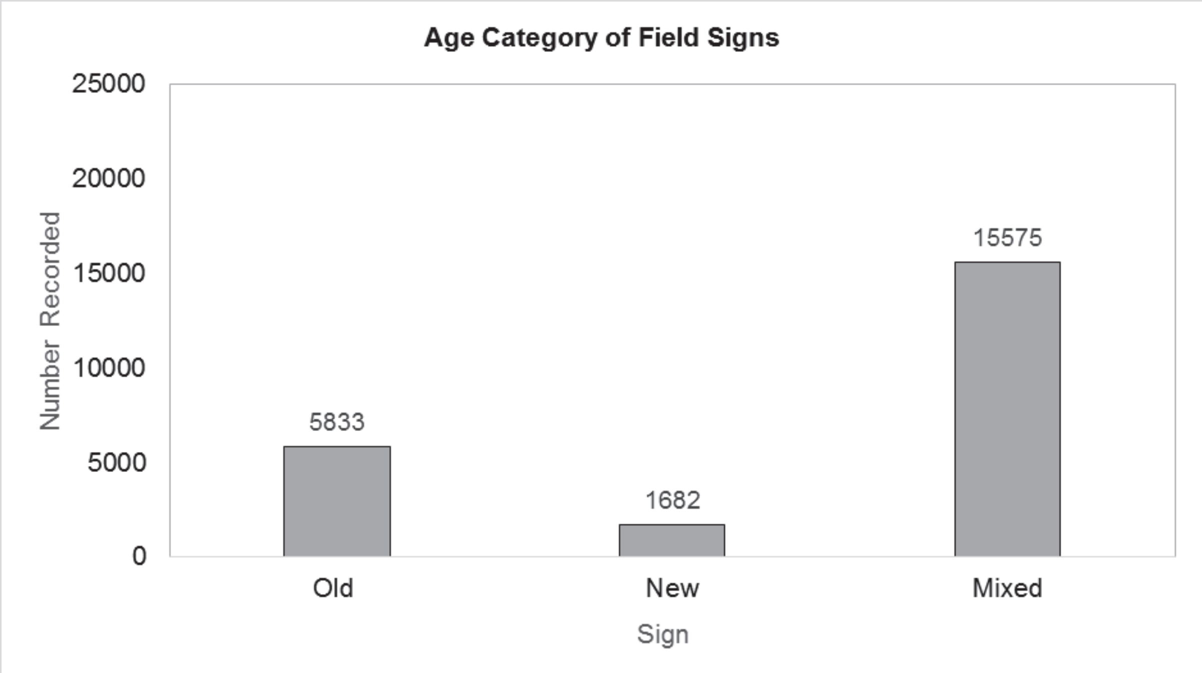

Figure 5. Number of beaver field signs recorded in each age category (old, new or a mix of old/new).

3.1.6 Land use

The majority (55%, 13,103) of records of land use with recorded beaver activity occurred within riparian deciduous woodland. Agriculture was the second most common land use recorded (37%, 8,798). The remaining land uses recorded, in order of magnitude, were fishing/recreational/amenity areas, grassland, residential/urban/garden areas, wetland/marsh, nature reserves and coniferous/commercial woodland (Figure 6).

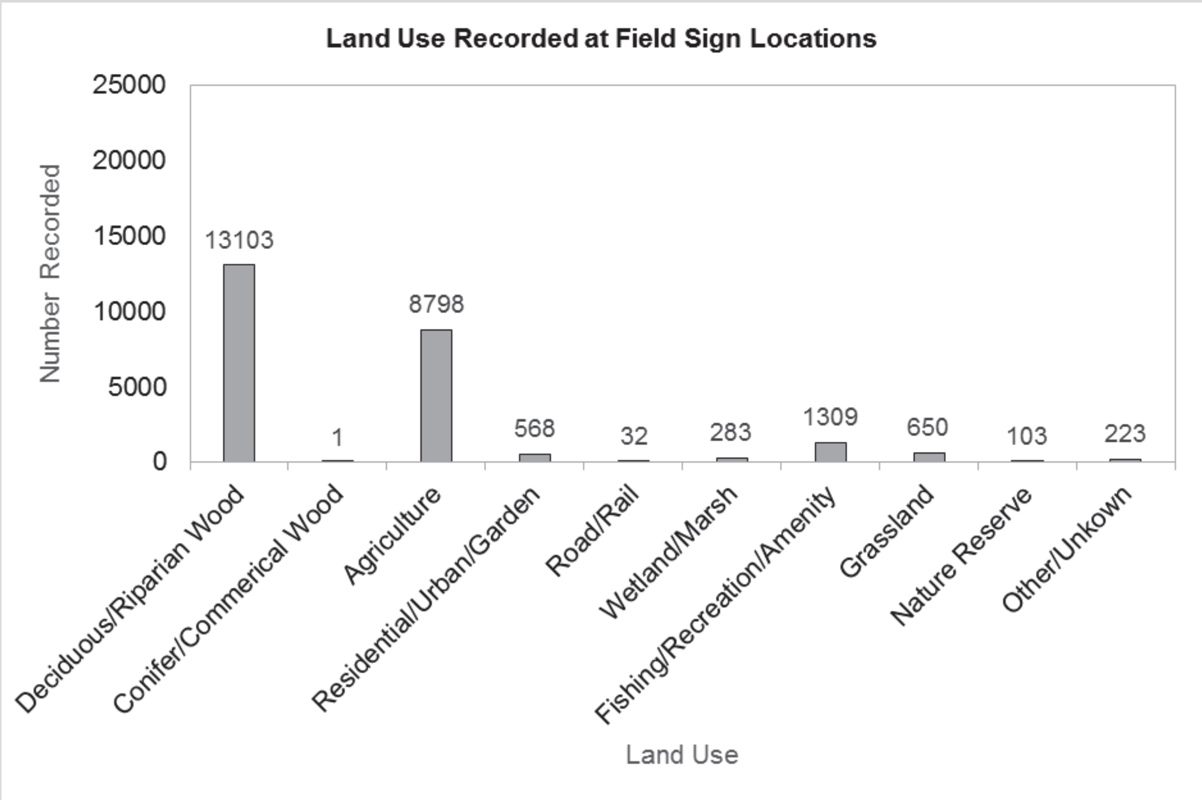

Figure 6. Distribution of land uses associated with recorded beaver activity.

3.1.7 Impact of potential management concern

The potential impact of beaver activity on land management varied greatly, from negligible to obvious impacts. Measuring this impact involves a level of subjectivity, so the perceived impact (referred to as 'management impact' in the dataset) was recorded by surveyors as far as possible using a simple score of 'low', 'medium', or 'high', without obtaining the views of the land-owners/managers in question.

A total of 159 potential management issues were logged during surveys. The majority (61%) were represented on agricultural land use. The remaining issues were recorded on deciduous woodland (25%), residential/urban/garden (10%), fishing/recreation/amenity (3%) and wetland/marsh (1%). Potential management issues were recorded across a total of 21 identified territories.

Three main types of potential management issues arising from beaver activity were identified out of 159 recorded observations. Damming and flooding accounted for most (27%), followed by active management/removal of beavers (24%) and digging into soft substrates (21%). Agricultural crop raiding accounted for 12% of all issues, in addition to residential/urban/garden and fishing/recreation/amenity (8%) and road/rail infrastructure conflicts (8%).

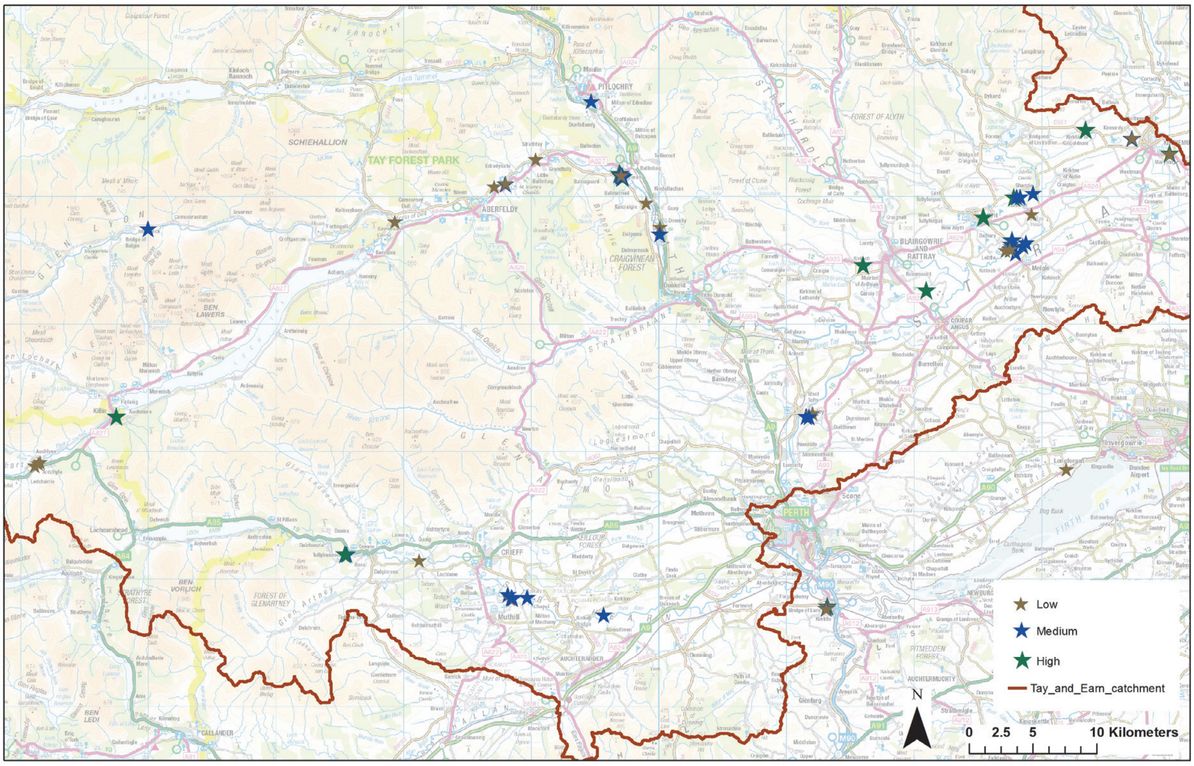

Figure 7. Mapping of 159 identified management conflict locations and their perceived impact (many of them occur in the same areas and are therefore displayed overlaid on the map). Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

3.2 Territories and numbers

3.2.1 Territories

Territory modelling results are presented below along with numerical comparisons between 2012 and 2017/2018 datasets. Additionally, 2017/2018 territory assessment and ground-based validation was undertaken by RCP, based on additional reports and site visits carried out for SNH casework.

Modelled territories based upon density mapping of survey signs indicated there were 88 territorial zones (Annex 2.6). However, it was recognised that some known territories were not accounted for using this approach for a range of reasons including: (1) difficulties in determining between continuous or high density areas of beaver activity; (2) the resolution required for landscape scale modelling may not pick up locally separate populations i.e. in neighbouring lochs/reaches; (3) occasionally it was not possible to carry out full surveys in all areas due to access constraints, resulting in a reduced recording of field signs; (4) the visibility of field signs during the summer surveying period was more limited.

Therefore, to refine and fill in any known gaps to provide a territory number and spatial distribution, modelled results were interpreted using a combination of local and expert knowledge. These full results, presented in Figure 7, give a minimum total territory number of 114. Full methods are included in Annex 1.4, whilst Annex 2.6 shows all territories classified by method of determination (model, splitting of modelled territories based upon expert judgement and additional territories based on expert judgement). The 114 active beaver territories recorded in this give a conservatively estimated number of 433 beavers (range 319 – 547). This number is based on European mean group sizes of 3.8 ± 1.0 animals per territory (Rosell et al., 2006). The distribution of territories across the main catchments is described in Table 1.

Table 1. Distribution of territories by catchment (SEPA catchment ID numbers refer to those used in the SEPA GI02 GIS data layer).

Catchment	SEPA Catchment ID	Number of Territories
Tay	46	73
Earn	48	21
Carse	43	2
Mouth of Tay/Perth	45	4
Mouth of Earn	47	4
Devon	54	2
Forth and Teith	56	5
Stirling	53	1
Allan Water	55	2

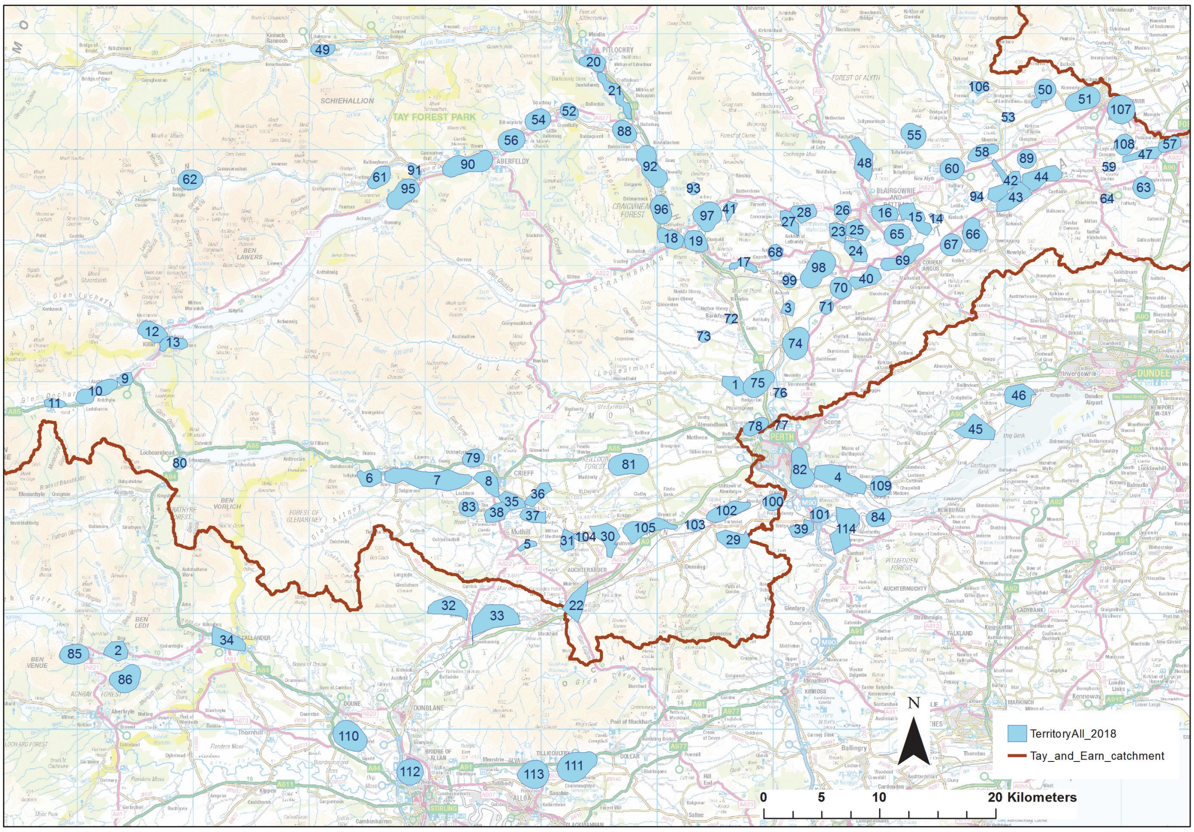

Figure 8. The recorded distribution of total beaver territories (114) from the 2017/2018 survey. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

3.2.2 Relationship between territories and vegetation layers

A comparison of Figures 8 and 9 illustrates that there is some agreement between the suitable habitat identified within the SNH Potential Beaver Woodland and Potential Core Beaver Woodland datasets and the presence of beaver territories. Out of the 114 beaver territories defined using the 2017/2018 survey data, 100% were contained within the areas identified as ‘Potential Beaver Woodland’ and 95% (N = 108) were contained within the ‘Potential Core Beaver Woodland’, as defined by previous SNH GIS mapping exercises (Stringer et al. 2015). These results point to the key role that suitable vegetation plays in determining the spatial extent of beaver territories, and the role such vegetation datasets will play in understanding possible future population ranges.

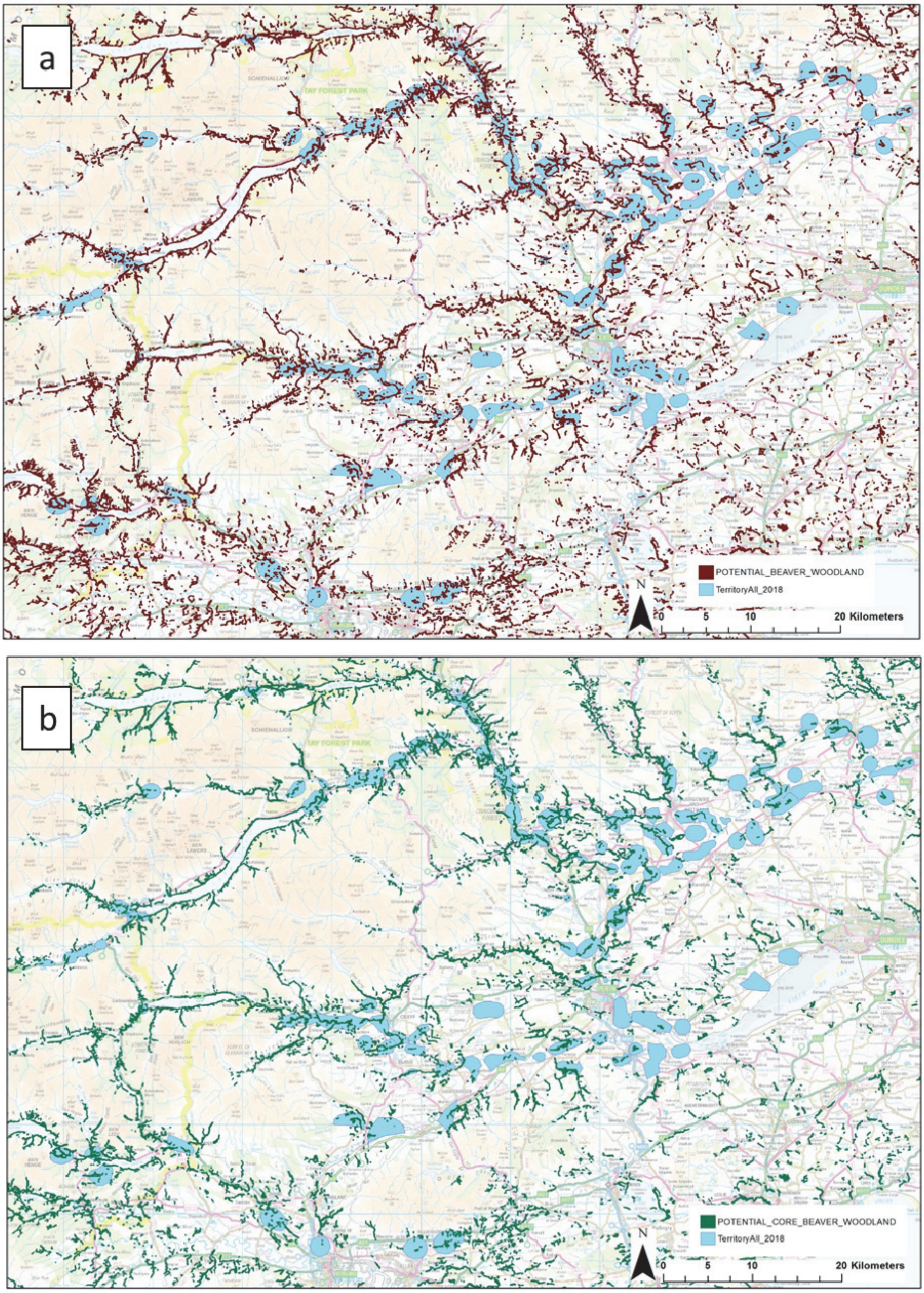

Figure 9a, b. Territories (2017/2018) in relation to (a) SNH Potential Beaver Woodland and (b) SNH Potential Core Beaver Woodland GIS layers. Woodland layers have enlarged layer borders to aid with visualisation. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

3.2.3 Survey signs and territory example areas

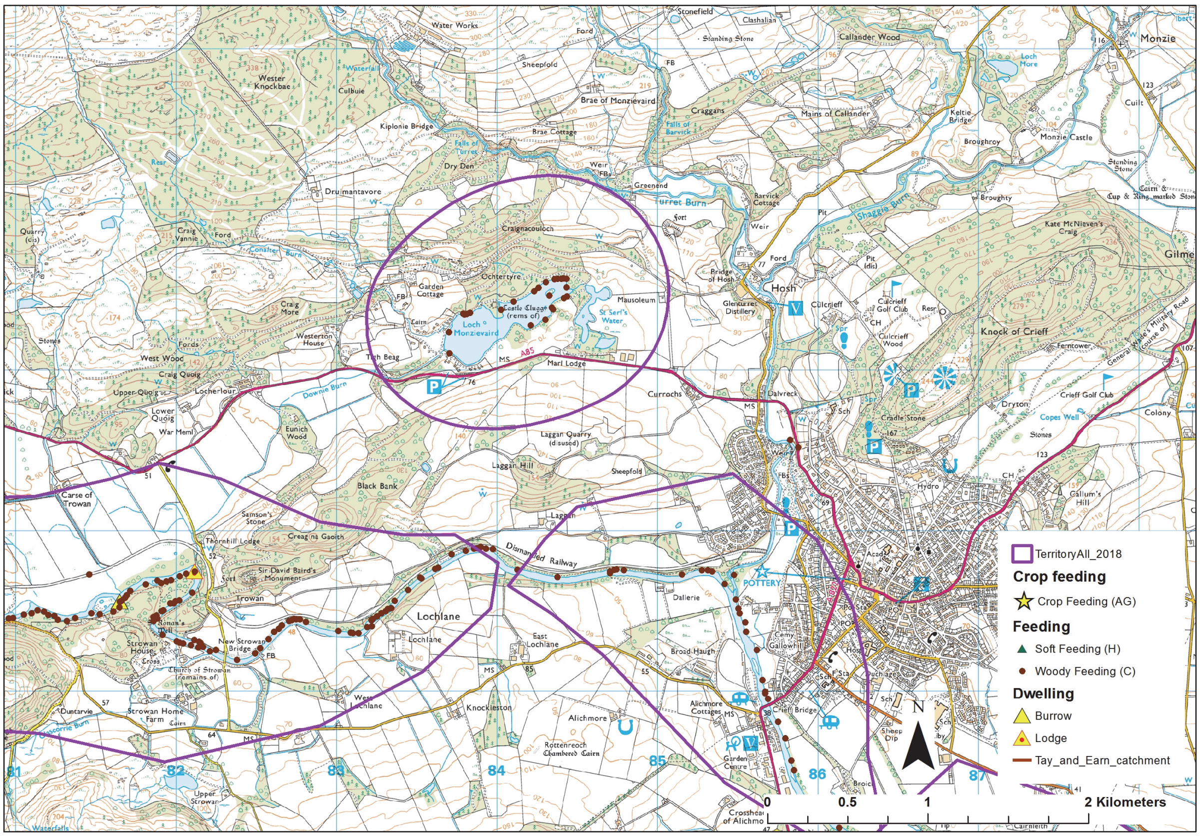

Figure 10. Example of survey results for the Crieff area. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

Figure 10 shows an example of territories and survey signs for the Crieff area. The distribution of field signs are likely to represent multiple beaver territories, and demonstrate how the definition of territories may be complex. Beaver territory number 63 (Top circle in Figure 10) is relatively straightforward to define. A single beaver family will tend to occupy a whole loch (Loch Monzievaird in this instance), rather than co-exist with other non-related beavers given their highly territorial behaviours. On very large lochs (e.g. Loch Tay), as population densities increase, family groups may split a loch but still actively defend borders against each other. However, the lower two territories are more complex. The modelling approach to field sign density mapping has defined this as a single territory, although the associated polygon is quite extensive. Continual field signs and suitable beaver habitat along this section of the River Earn, could represent a large beaver group occupying this section. Even so, given the average length of shoreline typically determined to represent a beaver territory (~3km of shoreline Rosell and Pedersen 1999), Ground based calibration has estimated that this is two territorial areas.

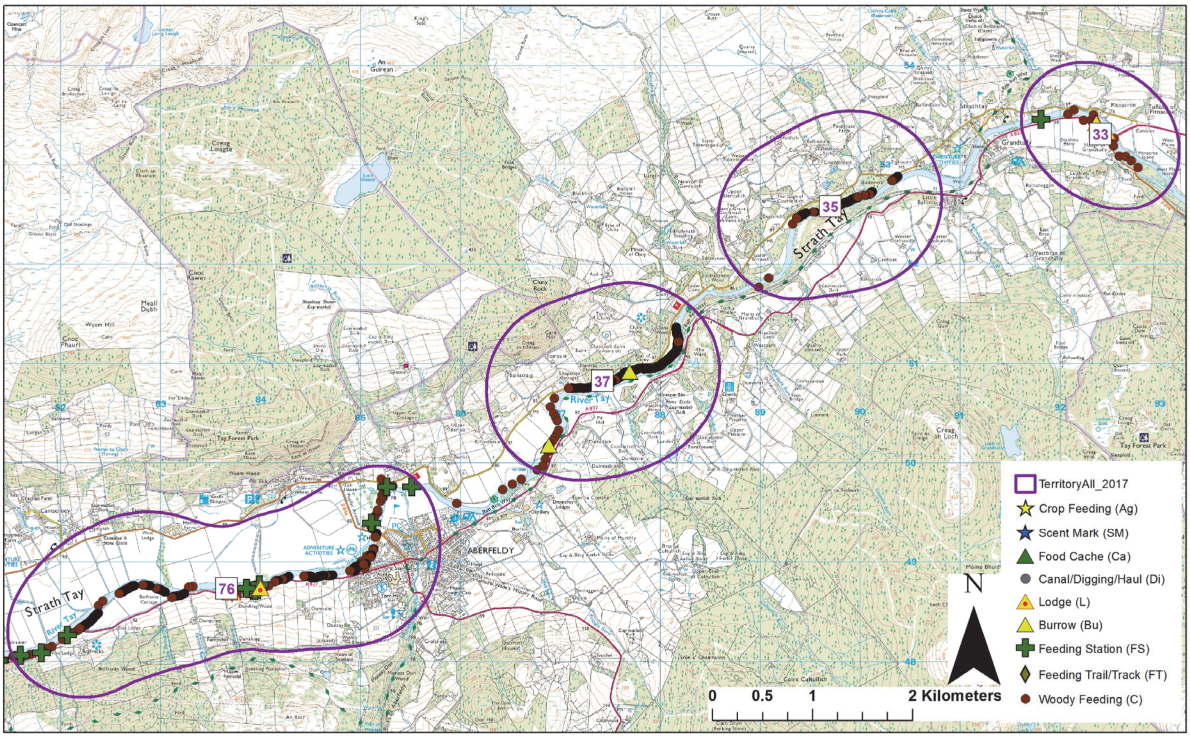

Figure 11. Example of survey results for a section of Strath Tay. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

Figure 11 illustrates a section of Strath Tay where four beaver territories were defined using the automated method described in Annex 1. This enlarged, detailed map of recorded beaver field signs displays several suspected beaver territories. Although it could be theoretically possible for field signs to represent fewer but larger beaver territories, it was decided, given the recorded field sign distribution and type, and suitable habitat, that for the four separate beaver territories could be supported along this section of the River Tay.

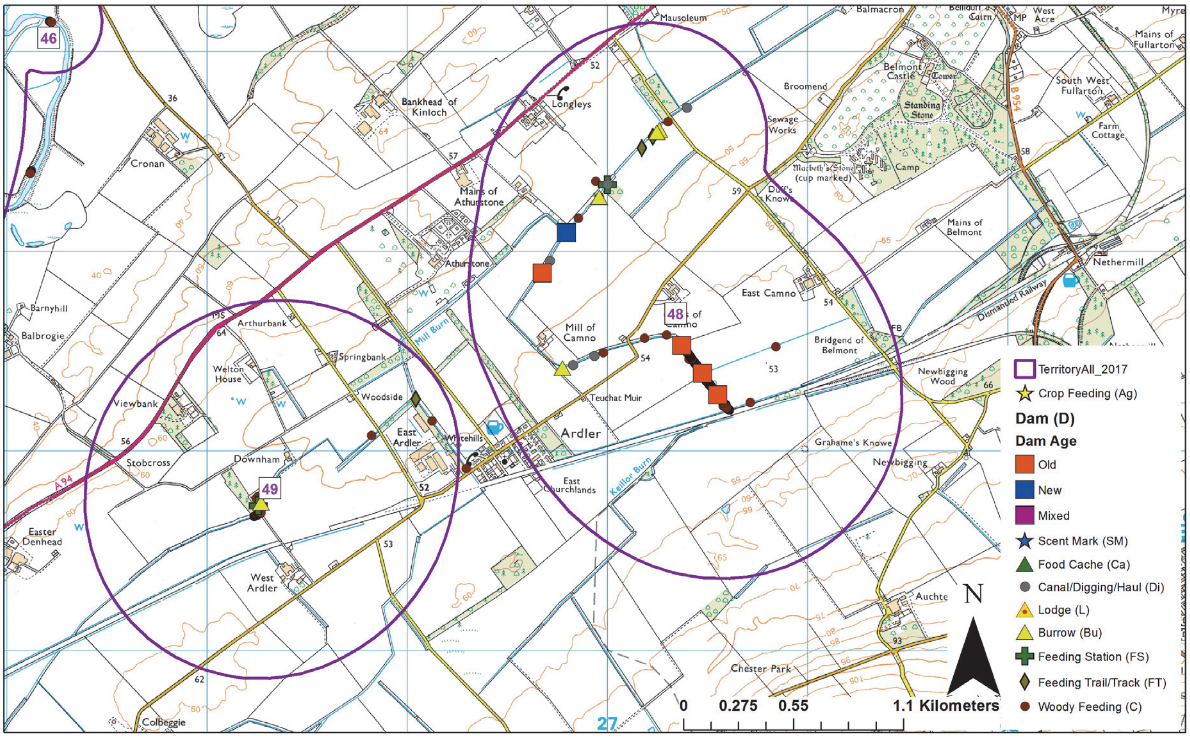

Figure 12. Example of survey results for the Ardler area. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

An example of survey results and territory definition for the Ardler area is presented in Figure 12. This area represents a highly arable agricultural landscape which includes numerous artificial drainage ditches in which water flow is managed in order to ensure optimal and functional crop growing systems. There is a reported long-standing issue of beavers repeatedly damming these ditches leading to ongoing, resource investment by land owners who regularly remove multiple dams. Natural, lower order burns and artificial ditches were surveyed in this area, with beaver field sign recorded (Figure 12). Given the habitat quality suitability for beavers it was determined that a family group was residing in territory 48. This is likely to be a breeding territory. An additional territory was judged to be situated to the west (territory 49), given the distribution of field sign intensity and suitable habitat availability. Whilst it is feasible that the field signs recorded as territory 49 may represent the outer activity of group members from territory 48, given the time of beaver occupation at this site and known breeding, it is more likely that two territories exist in this area, with territory 49 either representing a more recently forming pair or established family.

3.3 Change since 2012 survey

3.3.1 Change between 2012 and 2017/2018

At the landscape scale, there has been a large increase in beaver activity across the Tayside and adjacent catchments (from a minimum of 38 to 114 territories) between the 2012 and 2017/2018 surveys. This is illustrated by field sign density mapping presented in Figure 13. Figure 13b for 2017/2018, which includes fresh, mixed and old signs, unsurprisingly exhibits a much greater density than Figure 13c map for 2017/2018 which displays only points where fresh/mixed signs were included. However, within this overall trend of increased beaver activity, there is spatial variability; both in terms of areas of change since 2012 and in terms of old signs, that were recorded in 2017/2018 when no signs were recorded in 2012, indicating beaver is no longer present at that location.

The majority of reaches surveyed in 2017/2018 exhibited an increase in density of surveyed points (individual data points) of recorded beaver activity. Previously many of these areas had had no beaver activity reported. This is demonstrated in Figure 14 which shows changes in the field sign density between 2012 and 2017/2018. However, Figure 14 demonstrates that there are also around ten areas that have exhibited a reduction in field sign density, and in some cases a complete absence of fresh beaver signs in 2017/2018.

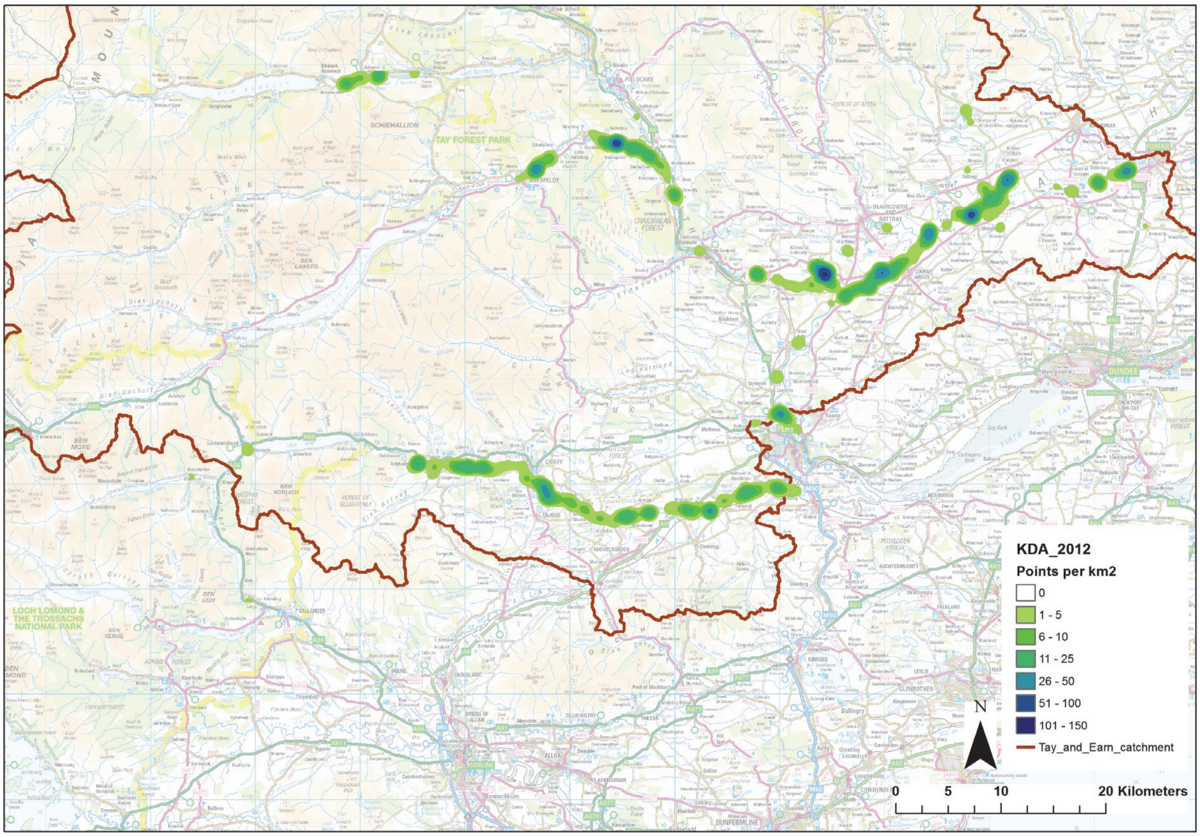

Figure 13 a. Density maps of beaver activity from the 2012 survey. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

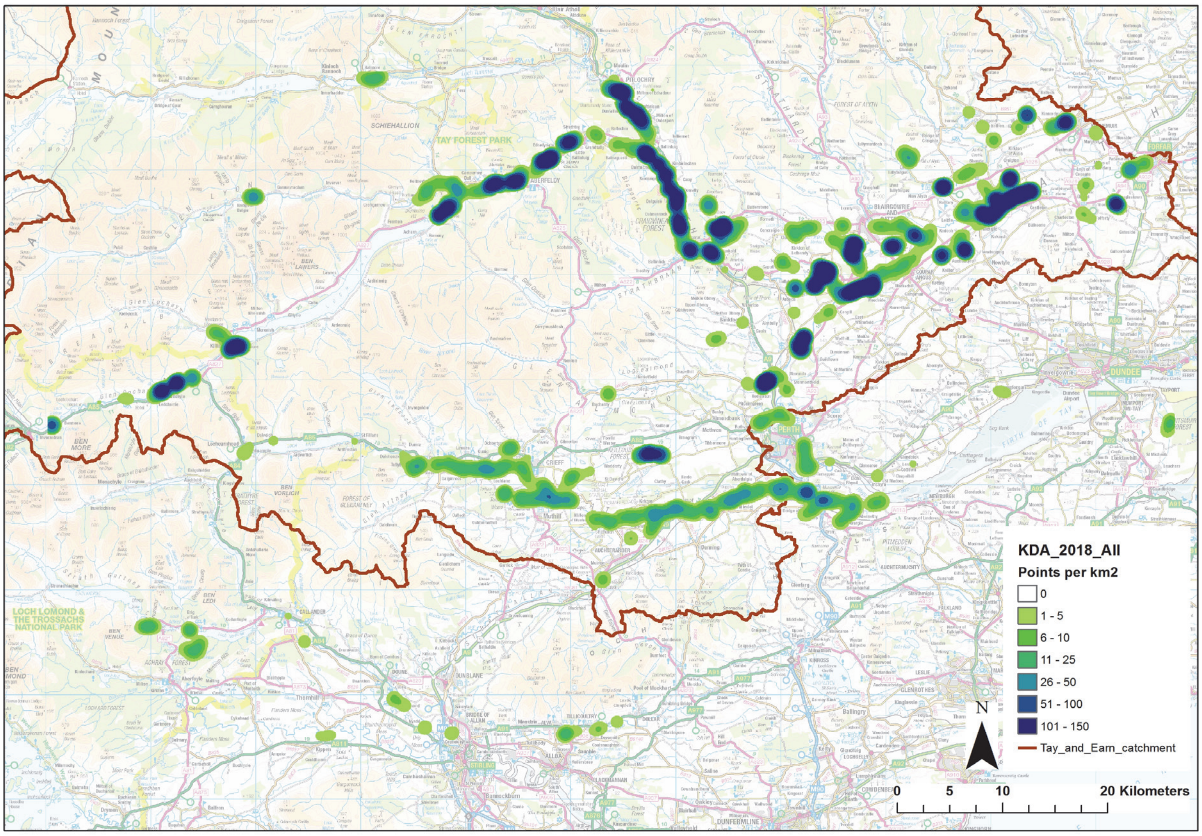

Figure 13 b. Density map of beaver activity from the 2017/2018 survey showing all signs. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

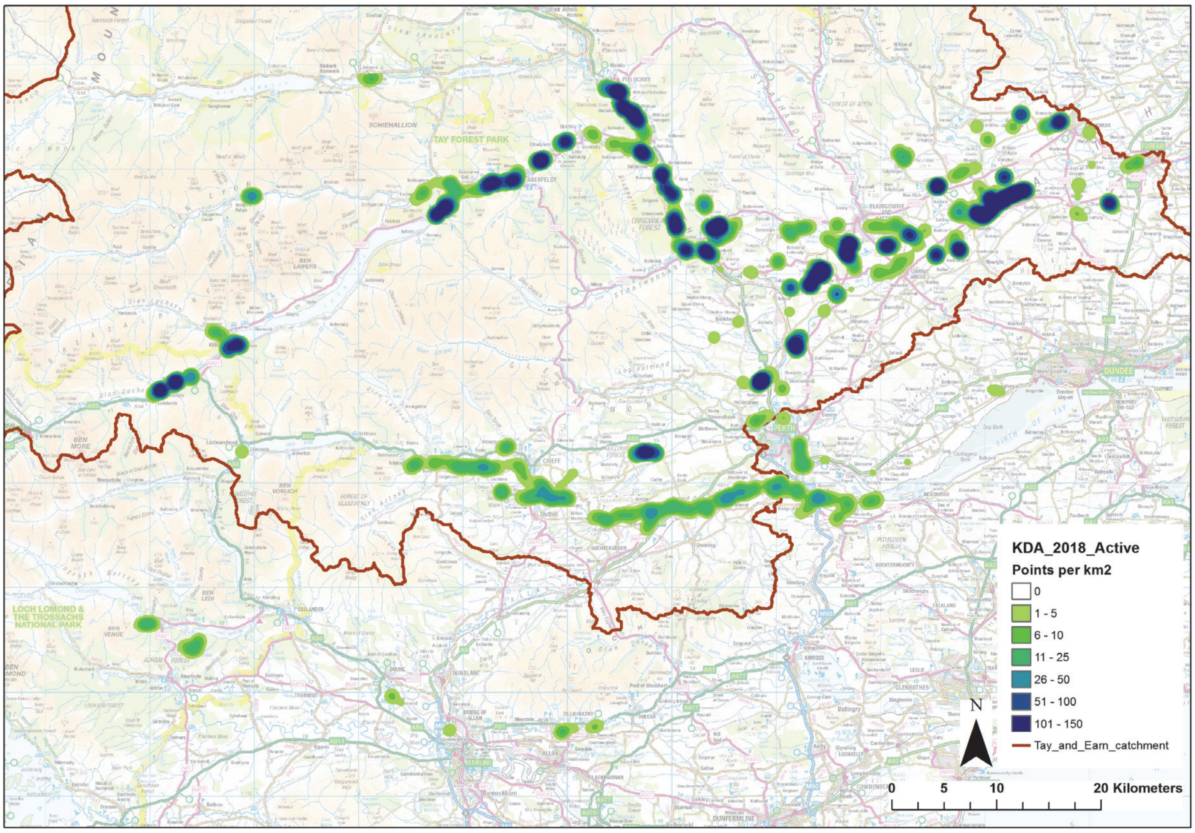

Figure 13 c. Density maps of beaver activity from the 2017/2018 survey (fresh and mixed age signs). Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

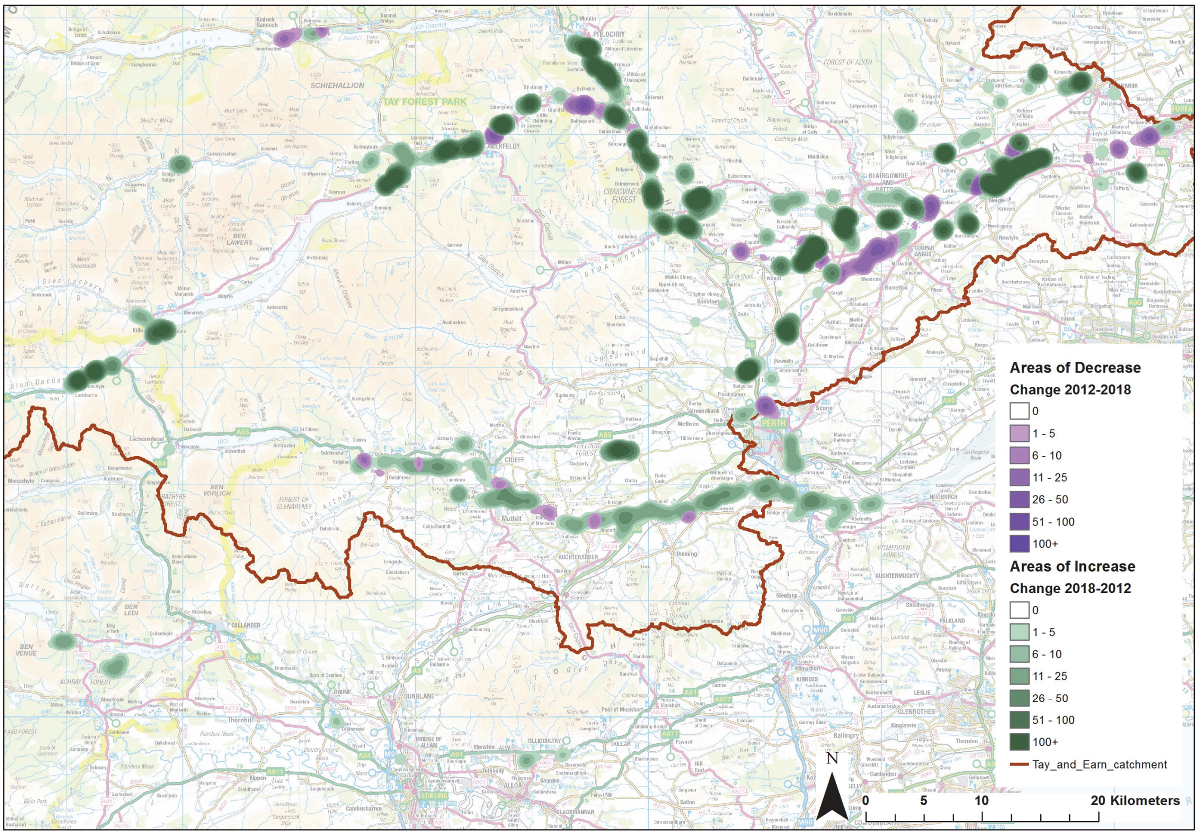

Figure 14. Areas of increased beaver field sign density (Green) and reduced field sign density (Purple) between 2012 and 2017/2018 surveys. Change is measured in number of field sign data points per km^2. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

3.3.2 Change in territories

Campbell et al. (2012) reported that there were 38-39 beaver territories within Tayside, with additional areas of outlying low intensity activity. Whilst there is spatial variation, this value is broadly supported by an independent analysis undertaken as part of this current study. The kernel density based modelling approach outlined in the results section and Annex 1, run on the dataset from Campbell et al (2012), determined there were 40 spatially distinct territorial zones or 'modelled territories', although some of these had very low densities of surveyed activity.

Undertaking the same analysis on the 2017/2018 data, combined with local and expert judgement, resulted in the identification of 114 territorial zones, some of them outwith Tayside. This represents an increase of approximately 75-76 territories when comparing to the 2012 survey estimate, or 74 based on the re-analysis of the 2012 dataset within this report. Figure 15 displays the mapped locations of the estimated beaver territories both in 2012 and 2017/2018.

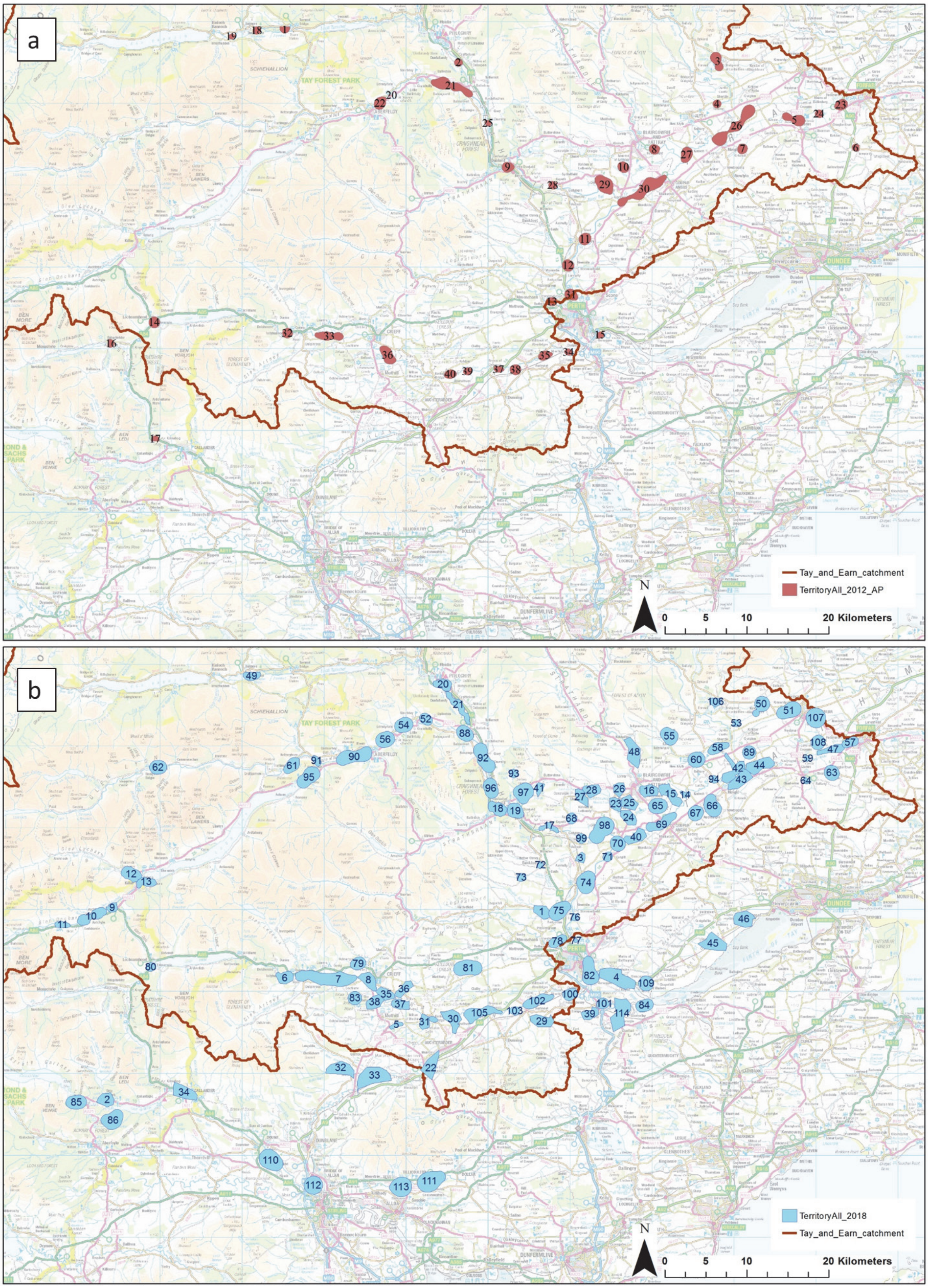

Figure 15 a, b. Comparison of 2012 and 2017/2018 beaver territory extent and number. Contains OS data © Crown copyright [and database rights] 2018 OS 100017908.

4. DISCUSSION

4.1 Population estimates in Tayside and adjacent catchments

One hundred and fourteen active beaver territories were recorded in this study, giving a conservatively estimated number of 433 beavers (range 319 – 547). This number is based on European mean group sizes of 3.8±1.0 animals per territory. However, it should be noted that Scotland has milder climates (with longer associated vegetation growing season) than many of the countries from which these group sizes where recorded from. It is unlikely that the Tayside and Forth populations are operating at carrying capacity, culling in some areas has undoubtedly removed animals and therefore created vacant territories. Such activity has prevented the carrying capacity being reached and therefore stabilisation of the population in these areas. The population may respond to this culling by changing their reproductive patterns through breeding as yearlings (although these individuals, and any of their offspring, tend to have reduced chances of survival) (Müller-Schwarze 2011). It is also important to note that the estimated population figures are conservative, as some territories could have been missed during the survey, especially on some of the lower order and artificial watercourses. Any territory-based survey techniques are limited in estimating total beaver population sizes as they may miss singletons and/or dispersers travelling through the catchment, although by using an average group number and surveying in winter/early spring these methods should take singletons into account.

Beaver populations have been recorded across the Tayside catchment for several years now, therefore it is not unexpected that dispersal to neighbouring catchments has and is occurring. The data presented here should be viewed as a snap shot in time, with colonisation of other catchments part of an ongoing natural process. Dispersing sub-adults tend to colonise habitats close to their natal territory, although they are capable of travelling tens of kilometres per day (Nolet and Rosell 1994; Saveljev et al. 2002) and may move hundreds of kilometres in a season to find suitable territories (Hartman, 1995). Several studies have found that after such initial population establishment, dispersers tend to infill habitats within an occupied area, before expanding into new catchments (Fustec et al. 2001; Barták et al. 2013). Simunková and Vorel (2015) found that there is more rapid population growth when the proximity of source populations (i.e. maternal territories) is small. This applies to the current Tayside population. Additionally, they found that animals dispersing long-distance are more influenced by mating opportunities, rather than purely influenced by habitat selection, so that during an initial phase of population growth individuals will make longer journeys to seek mating opportunities (Halley & Rosell 2002). This natural ecology and dispersal capabilities of beavers, makes it very plausible that colonisation of closely associated catchments, such as Tayside and the Forth which will have multiple potential crossover points (Stringer et al. 2015). Colonisation of the Forth is therefore likely to be a result of natural colonisation, especially given proximity of the catchments at several points and extensive flooding occurring over the last few years. It should be noted that beavers do not require permanent water courses for dispersal and will even follow damp ditch-type systems.

Currently beaver population density within the Forth catchment is low, although suitable habitat exists throughout, so an increase in numbers and distribution is likely to occur. This low density has meant reported beaver conflicts are low, although this is expected to rise and require ongoing management as the population increases. Agricultural, and in time urban, land-use will be expected to experience the most significant conflict issues, in line with those currently experienced across the Tayside catchment. Similar experiences are likely to occur in the South Esk catchment in time.

The number of beavers present in a family unit can be difficult and time consuming to determine, so beaver population size is typically expressed by the number of active territories (Rosell et al. 2006). Beaver family groups will utilise a number of burrows and/or lodges within their territory. These may also be used seasonally and depend on bank substrate. Therefore, the number of burrows and lodges should not be used as a measure of group size. Scent marking plays an important role in territory defence and maintaining territorial boundaries in beavers, and is most common between April and May (Rosell and Nolet 1997). Therefore, we used the approach of collecting field signs and assessing their abundance and distribution to define beaver territories then multiplied this number up by an average group size estimated from the literature. The group size estimate will therefore significantly affect the estimated total population. Assessing group size in beavers is generally done through one of three methods; removal trapping/culling, mark and release, or observational censuses. The size of an average beaver family, derived from a review of 13 beaver studies in Europe and observations of beavers living at high densities in Norway, has been estimated at 3.8±1.0 individuals, with a range of 2.4-5.5 (Rosell and Parker 1995; Rosell et al. 2006). A pilot study which looked at the occupancy of known breeding lodges in Tayside recorded a mean group size of 5.0±1.6 individuals (Campbell-Palmer et al. 2015). However, this Tayside sample targeted known breeding lodges for observation whereas not all territories will contain breeding family groups. Groups sizes of 3.5 individuals are used as an average number per active territory in annual Bavaria population estimates (Schwab, personal communication). This number takes into account both breeding territories, those with single individuals or newly formed pairs, also these below average figures take into account territories held by dispersing individuals and non-breeding pairs.

4.2 Land use impacts and future management

It has been documented that beavers tend to select habitats with predominantly deciduous tree cover (demonstrated in this study), lakes/lochs, narrower river widths (≤15 m), and accessible banks with substrate that they can manipulate (Pintos et al. 2009). However, the adaptive capabilities of this species should not be underestimated, particularly as populations reach carrying capacity when they can demonstrate a high degree of plasticity in selecting a range of habitat conditions and modifying them accordingly (Pinto et al. 2009). Beaver activities can conflict with human interest and land use, imposing a cost (time and financial), especially in intensively managed landscapes such as parts of Tayside. SNH's 'Beavers in Scotland' report provides a more detailed review of land use impacts and future management options in Scotland (Gaywood 2015). Beavers are not confined to areas of wilderness or wild landscapes, they can readily adapt to highly developed urban and agricultural landscapes where suitable freshwater and vegetation features are available.

In studies across Europe most beaver activity occurs in close association with the water's edge, for example 95% of beaver foraging activity in Denmark was within 5 m of water (Elmeros et al. 2003), in Russia 99% of beaver cut stems were within 20 m of shoreline (Baskin and Sjöberg 2003). At Knapdale, Scotland, most field signs (the majority were foraging signs) were recorded within 20 m of the shoreline, although some were occasionally found at least 50 m away (Harrington et al. 2015). Beavers will feed on a range of crops, and will also dam areas, dig and create canals to access crops more readily (Nolet and Rosell 1998; Campbell et al. 2012). The majority of human-beaver conflicts therefore occur within a relatively narrow strip of habitat adjacent to freshwater habitats. In Bavaria, over 90% of beaver conflicts occur within 10 m of the water's edge, while 95% occur within 20 m (Schwab et al. 1994). Although conflicts will also occur further away from freshwater, they will be rare and usually in association with a high value food resource, for example, an isolated tree stand.

In this study, most perceived land use impacts occurred on agricultural land. These may represent areas of higher 'visibility' meaning that such impacts are more obvious and therefore more routinely recorded than other sites less often visited by people. However, such modified systems also represent the types of habitats where beaver activity can impact most significantly. For example, field drainage systems may allow little flexibility in water level rises so that even small dams can have significant effects on waterlogging. In more naturalised systems, or agricultural landscapes which are not farmed close to the water's edge, beaver damming will usually not result in any significant conflict in the immediate riparian zones. The presence of such riparian habitat can create a 'buffer', resulting in a decreased risk of conflict in any land use further from the watercourse.

Any future management strategy in Scotland, or elsewhere in Britain, should adopt a practical approach that is flexible and open to adaptation as populations are restored. The provision of a broad range of management options and tools, acceptable to both landowners and to wider society, should be investigated (Hartman 1999; Campbell-Palmer et al. 2015). Some of the key issues to consider and potential management options have been set out in the SNH 'Beavers in Scotland' report (Gaywood 2015). Long-term beaver management is best focused where practicable on the establishment of buffer zones of native riparian vegetation along freshwater courses, although this option will be more difficult where essential infrastructure (for example) is protected by raised flood banks, where heavily modified or managed watercourses are common, or the associated land use is judged to be too commercially important for the establishment of buffer zones. It is important that, where undesirable impacts result from beaver activity, these are dealt with promptly and competently.

It is important to note that only negative management issues were recorded in this survey. This was a subjective categorisation undertaken by experienced personnel, although it is accepted that management impacts may vary by perception. Using walk-through surveying techniques results in only visible impacts on the day of survey being captured. Therefore, this methodology excludes management history and previous mitigation investment for any particular site, unless there are obvious signs such as removed dam material still visible.

The Eurasian beaver is known to have numerous and predominantly beneficial impacts on biodiversity and environmental ecosystem services, if reintroduction is allowed (Law et al., 2017, Puttock et al., 2017). Recent work, especially in a Scottish context, has summarised that beaver activities have an overall positive effect at numerous levels from the creation of dead wood, sediment and nutrient trapping, habitat creation and maintenance, to water quality improvements (Gaywood 2015; Gaywood 2018; Stringer and Gaywood 2016). Such positive impacts have not been reported in this survey and, whilst not detracting from negative impacts to individual landowners, should not be ignored in terms of relevance to Scotland, especially on a landscape scale.

4.3 Damming activity

Damming activity is one of the main ways beavers can modify their habitats. The extent of damming activity will depend greatly on hydrology and beaver population density (Halley and Rosell 2002, but also SNH 'Beavers in Scotland' report for a more detailed review of how damming activity may impact on land use practices in Scotland, Gaywood 2015). In brief, Eurasian beavers tend to dam on shallow, narrow watercourses, on average 0.36±0.14 m in depth by 2.5±1.1 m in width with the maximum width of most water-courses dammed tending to be <6 m (Hartman and Törnlöv 2006). The gradient of the watercourse tends to influence dam building, with damming on gradients of >2.5% less likely (Schulte 1989; Hartman and Törnlöv 2006).

Results from the 2017/2018 survey of Tayside demonstrate that relatively few dams have been constructed or permitted in Tayside, given the number of territories and the likely number of animals. This may be due to the following reasons: (1) Most freshwaters where beaver territories exist are deep and wide meaning that the beavers do not feel the need to dam, for reasons of safety or to access food; (2) most territories do not lie in low order tributaries, where shallow water might trigger dam building responses; (3) damming activity has been occurring but dams are being removed. A minority of landowners, particularly in agricultural areas with numerous land drainage systems, have reported significant damming requiring regular removal with significant resource investment. However, as has been discussed, Tayside is not yet approaching carrying capacity and there are very many smaller, shallower and steeper channels that may well be dammed if/when they become occupied beaver territories.

As beaver populations grow and their densities increase, successive generations are forced to travel greater dispersal distances and/or occupy 'suboptimal' habitats in more minor watercourses. This is in fact occurring within Tayside, where increasing numbers of beavers are now occupying smaller tributaries and artificial drainage systems, associated with some of the larger river systems where they have been resident for many years. These provide suitable habitat for beavers, as some of these watercourses can be easily dammed, banks tend to be suitable for burrowing and can provide a ready supply of food. Since beavers often need to modify such habitats, particularly to stabilise and deepen water levels, this tends to lead to increased conflicts with people. Damming activity is one of the most common causes of conflict, especially in flatter landscapes, and require reactive management. Land drainage systems are essential for many agricultural practices in this area, and their failure or blockage can cause significant problems, including increased ground water levels and direct flooding of crops (Schwab and Schmidbauer 2003).

4.4 Burrowing activity

A detailed review of how burrowing can impact upon land use is also included in the SNH Beavers in Scotland report (Gaywood et al., 2015). Overall there is very little information from Europe on the collapse of beaver burrows in livestock or equestrian pastures. There have been a few anecdotal reports from Bavaria of calves falling into beaver burrows, and some injuries have been recorded where hooves have broken through into burrows (Schwab, G. personal communication). However, the major problems with beaver burrows appear to be agricultural machinery becoming stuck and burrows under roads or in flood banks collapsing, rather than causing injury to livestock.

Results from this survey confirmed the presence of 329 burrows in the surveyed area. However, it is likely that the majority of burrows are rarely seen due to their submerged entrances lying below the water line, unless water levels fall and/or burrows collapse. Therefore, results almost certainly underestimate the number of burrows that exist within the surveyed area.

4.5 Future perspectives on beaver population growth in Scotland

It is now evident that beavers exist outwith Tayside and the official reintroduction trial site at Knapdale, mid-Argyll (Figure 7). Beavers are now present within the Forth catchment. Given the close association (distance, connectivity and flood events over last few years) with the Tayside catchment, the apparent population growth on Tayside and the dispersal capabilities of beavers, the spread into the Forth catchment can be attributed to natural population expansion.

Catchment divides are penetrable for beavers, though large distances with inhospitable habitat types will slow colonisation. Overland dispersal is less common for beavers, however large distances to cross watersheds have been documented (Hartman 1995; Saveljev et al. 2002). Initial GIS-based assessments by SNH indicated a high degree of potential interconnectivity between catchments for dispersing beavers, including between the Tay, Earn and neighbouring catchments such as the Forth (Stringer et al. 2015). Although there does not appear to be beaver activity in the River South Esk currently, this is likely to change over time given the proximity and availability of suitable habitat.

Annual population growth rates in beavers have been recorded between 5-34% (Balodis et al. 1999; Gorshkov 2006; Heidecke et al. 2009; Sluiter 2003). While rates of range expansion have been recorded at 1.5 and 19.7 km per year (Hartman 1995; Barták et al. 2013), these will vary greatly depending on a range of factors including the stage of population development, habitat quality and interconnectivity.

There were some areas where no signs were recorded in 2012, and only old signs were found in the 2017/2018 survey. There are two possible explanations for this. Firstly, these areas were not discovered in the 2012 survey, or secondly, in the five years since 2012 there have areas where beaver has expanded into and then either abandoned or been removed.

Although undoubtedly beavers have now established within Tayside and are extending in distribution, unregulated culling may be impacting on densities in some areas. This may particularly be the case in those areas that are well connected, within suitable habitats and where higher densities have been recorded previously. In other areas, particularly those where the population is expanding in both range and distribution, previous recording of activity is most likely to represent dispersing individuals that have moved on to alternative areas in search of mates' or have died (e.g. Tentsmuir in Fife). The number of beavers said to have been dispatched to date range widely from 50-240 or more, but such reports are completely unvalidated making it impossible to determine what impact this has had to date, and how viable culling could be as a future management technique.

Beavers can have significant impacts in highly modified, agricultural systems. However lethal control can be an ongoing population management requirement as it results in the breaking up of family groups, the creation of territory gaps and therefore opportunities for dispersing individuals to continually recolonise areas. Culling in spring has been demonstrated to effectively reduce beaver population densities (Parker et al. 2002), although currently no timing restrictions exist on lethal control in Scotland. This situation will change once, and if, beavers become European Protected Species.

Out of the 114 beaver territories identified in this study, 100% included 'Potential Beaver Woodland' and 95% (N = 108) included 'Potential Core Beaver Woodland' as defined by previous SNH GIS mapping exercises (Stringer et al. 2015). These results point to the key role, suitable vegetation plays in determining beavers' spatial extent and points towards the role such vegetation datasets will play in understanding possible future population range. However, as beaver densities rise, beavers will occupy increasingly more 'unsuitable' habitats. Their ability to adapt to varying habitats should not be underestimated, dispersing individuals especially are likely to at least seasonally reside in areas outside of 'Potential Beaver Woodland', as they can survive without the presence of trees. This stage in population development will be accompanied by increasingly likely human-beaver conflicts.

4.6 Study limitations

Field survey work began in mid-April offering the ideal opportunity to observe beaver activity, particularly bankside structures and woody feeding. As the vegetation growth season progressed, and because of the required extension of field survey time due to the abundance of field signs, later surveys where not completed until well into July. At this time, bankside vegetation growth in some areas was at its maximum, making it difficult to detect many beaver field signs, although feeding on herbaceous species in such areas may have been more prominent. Also, water level ranged greatly during this period (from excessively dry periods to heavy rains), and burrowing activity during periods of high water levels is likely to have been under recorded.

Not all watercourses could be accessed safely by the field team. In such circumstances spot check surveys were made where possible, although such watercourses were usually steep, rocky, and fast flowing, and likely to be unsuitable for beaver occupation. Such watercourses may have been traversable by beavers and so there is a possibility that a relatively insignificant number of family units were missed.

It is more likely that active territories were missed on minor and/or artificial drainage systems given the extremely large number of such watercourses within the Tayside. With growing beaver population size and densities, infilling of habitat occurs so that later territories will form in unoccupied areas, with earlier colonisers tending to select the most favourable habitats (Campbell et al. 2005). As such areas tend to represent 'suboptimal' habitat for beavers, they are increasingly likely to modify such habitats to suit their needs, for example damming to create deeper water, which in turn may generate greater human-beaver conflicts. Therefore, there may have been under-reporting of beaver active territories and associated management issues, although we are confident that the main conflict types have been captured. Also, territories with management issues are more likely to be reported by the general public, and those less likely to present conflicts may be under-reported.

The vast majority of surveying was conducted on foot rather than from canoe. Localised patches of beaver activity were often discovered inland away from the waters' edge such as woody foraging and agricultural crop feeding. Such areas when viewed from the water were only visible if worn foraging trails were still prominent. Surveying on foot in such cases therefore allowed us to assess the extent of beaver activity more fully. However, Campbell et al. (2012) reported surveys were considerably more rapid via canoe and allowed a much clearer view of burrows and scent mounds on the banking. Furthermore, surveying from canoe facilitated sightings of feeding on very small diameter woody stems such as willow (*Salix spp.)* at the waters' edge. Therefore, scanning the banks for field signs from the position of a beaver's point of view definitely had its advantages. Overall, it is therefore recommended that future surveys use a combination of both options depending on the time of year and type of watercourse. For example, walking would be more suitable in months of low bankside vegetation and on narrower watercourses. Canoeing would be more advantageous during periods of high vegetation cover (though the value of undertaking surveys during such times may be more limited) and on large water bodies.

As with any wildlife population densities will vary greatly over time and with habitat quality (Novak 1987). One of the greatest areas of uncertainty in determining territories via spatially discrete zones of activity is that, where there are continuous stretches of river with high intensity activity recorded, it is hard to differentiate between territories. Such areas may contain significantly more than the mean number of 3.8 individuals used in this report (Rosell et al. 2006). With continued population expansion over time this uncertainty will most likely increase and so should be incorporated into any future sampling strategy and population size calculations.

4.7 Recommendations for further research and monitoring

Given the significant potential for beaver to impact upon land use and modify habitats on a landscape scale, their presence and subsequent management requirements need due consideration. The provision of accurate and up to date population information (distribution, number, colonisation rates etc.) will obviously help inform future decision-making and the management of beavers in Scotland. However, the collection of such data can be time consuming and resource intensive. Obtaining total numbers is problematic and involves some degree of estimation of territory boundaries and family size. Annual re-surveying may be excessive, and a more useful investment of resources could be to monitor beaver impacts rather than determine numbers, and the colonisation of new areas and/or active lodge counts in autumn. However, in Lower Frankonia in Germany, annual surveys are undertaken, with volunteer support, to determine if existing recorded territories are still occupied. Therefore, most time is spent on surveying any new territories which establish due to the expansion of populations – such a strategy may represent a sensible and manageable approach in Scotland.

One immediate objective for the authors and SNH is to run the Beaver Restoration Assessment Tool (BRAT). BRAT was developed in North America (Macfarlane, et al. 2017) to determine the potential for rivers to support beaver dams. It was considered that beaver dams and artificial dams, termed beaver dam analogues (BDAs), might help to enhance aggradation in deeply incised and degraded arid streams (Pollock et al., 2014). The BRAT model does not seek to predict where dams will be constructed, rather it quantifies the dam capacity in a given reach by considering the local hydrological and vegetation conditions. Although the model is not predictive in terms of beaver expansion, it has been shown by Macfarlane et al. (2017) that sites with higher capacity are preferentially sought out for dam building over those reaches with lower capacity, and therefore reaches which are predicted to have high capacity are more likely to be dammed.

The BRAT model has been used to help design restoration efforts by targeting the construction of BDAs in specific areas. At Bridge Creek, Oregon, beavers colonised reaches where BDAs had been constructed, resulting in the increased efficacy of the structures and enhanced aggradation (Pollock et al., 2014; Bouwes et al., 2016). In addition to the geomorphic improvement that dams and BDAs offer, these structures also led to the creation of juvenile steelhead (*Oncorhynchus mykiss*) rearing habitat and consequently a significant increase in steelhead recruitment and overall population size (Bouwes et al., 2016). The BRAT model has further been deployed in a range of different river systems to aid both beaver recolonisation and BDA-led restoration. More recently the output from the BRAT model has been used to model the potential for beavers to offset climate driven reductions in snow pack in Utah (Hafen K., 2017; Wheaton, et al., 2017). BRAT similarly provides an essential tool for predicting other ecosystem services that beavers may offer such as flood peak attenuation.

The BRAT model not only provides an invaluable tool for designing effective, empirically based, restoration strategies but it also indicates where beaver dams might cause potential management conflict issues. Understanding and pre-empting where these conflicts are likely to arise will help to mitigate the potential harm that beavers may cause whilst helping to direct their behaviour to areas that might more effectively provide the range of ecosystem services that may be desired from beaver dam construction.

It is recommended that any future survey work is undertaken earlier in the season, or during late autumn to allow counts of active lodges. It should be emphasised that given the successful expansion of beavers on Tayside, any future field survey should be done over a longer period, or be concentrated on the edge of expansion zones.

The 2017/2018 and 2012 Tayside survey results also provide a wealth of opportunities for more detailed research into beaver population dynamics (both spatial and temporal) in the catchments, with widespread relevance for other areas in Great Britain and Europe where beaver reintroduction is ongoing. There may, however, be some limitations resulting from the lack of information on the composition of the original founders, the intensity of any culling that has taken place, and the extent of any further unofficial animal releases. Even so, the dataset collected could facilitate further research into the environmental impacts (both positive and negative) of what is now an extensive wild beaver population.

The data collected can also help to inform and direct future management strategies as well as public engagement activities. As a specific recommendation, the current impacts of beavers, combined with the ongoing development of vegetation suitability and dam capacity modelling, will allow GIS-based models of beaver impact and risk to be created and further refined, highlighting areas of specific future management issues and opportunities, not just within Tayside, but more broadly if necessary.

5. CONCLUSIONS

This report covered three main objectives;

I. The field survey mapped a range of beaver activity, both fresh and old field signs, to estimate the current number of active beaver territories (Figure 7). It is estimated that the minimum number of beaver occupied territories is 114 in the surveyed area, which (assuming an average of 3.8 ± 1 beavers per territory) can be estimated to represent approximately 319 – 547 individuals. The vast majority of these territories reside within the River Tay catchment with current distribution ranging from Dunalastair water, extending out to the River Dochart and River Lyon in the West, over to Forfar Loch in the East and down to Loch Earn in the South. A smaller number of active territories were recorded within the Forth catchment, from Loch Achray in the Trossachs, parts of the River Teith and Devon, to the main stem of the River Forth into Stirling. There was no evidence of beaver activity currently on the River South Esk.

II. Digital outputs and appropriate georeferenced data compatible for SNH GIS were provided for use in relevant national biological databases.

III. Comparisons between the 2012 (Campbell et al. 2012) and this 2017/2018 survey found a significant increase in the number and distribution of beaver territories. This represented both an extension of distribution range, infilling between previous territories and the establishment of new territories overall. In some areas, namely parts of the lower River Earn and River Isla which are associated with prime agricultural land-use, negative changes in densities of signs were recorded. This may represent areas in which culling has been known to have occurred.

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ANNEX 1: FIELD SIGN CODES AND METHODS

Annex 1.1 Field sign codes used

Annex 1.1 Field sign codes and descriptions used during current survey, adapted from Campbell et al. (2012).

Code	Sign	Description
C	Woody Feeding	Cutting or gnawing of woody vegetation (shrubs, saplings and trees)
H	Soft Feeding	Feeding on herbaceous vegetation
Ag	Crop Feeding	Feeding on agricultural crops. The area affected was measured as m²
D	Dam	Dams were classified as active/maintained or old/breached. Height and width were recorded in m.
Ca	Cache	Cut, stored woody vegetation
Di	Canal/Digging	Beaver digging into substrate or creation of canals leading inland to access more foraging grounds
Bu	Burrow	Entrances may be below normal water levels and can extend inland forming complex underground systems
L	Lodge	Burrows where the nest chamber has breached the surface and has been built up using sticks and mud
SM	Scent Mound	A pile of material (usually mud) scrapped together by the beaver on which a distinctive scent (castoreum/ anal-gland secretion) is deposited
SS	Scent Site	A small area of concentrated multiple scent mounds
FS	Feeding Station	This is a location at the edge of the water where a beaver repeatedly takes material obtained elsewhere to consume
FT	Feeding Trail	Created by the frequent passing of a beaver on land running from the water inland

Annex 1.2 Field surveying and data collection

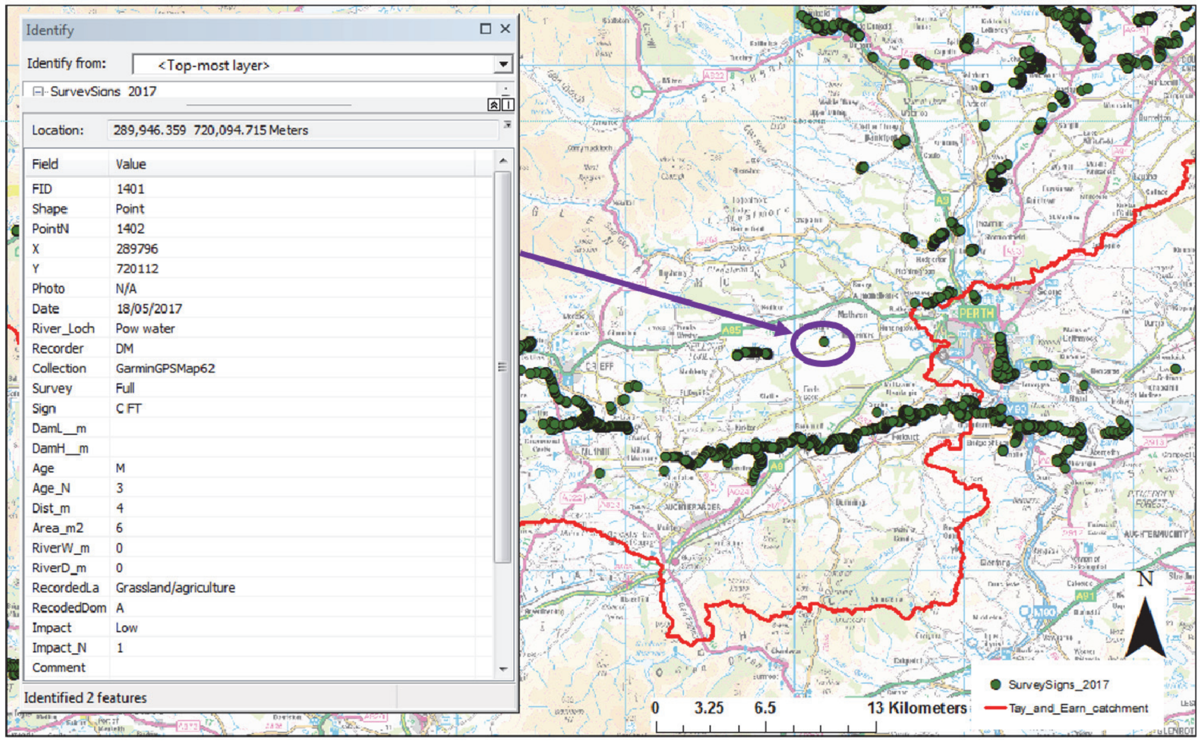
1. Survey areas were prioritised to ensure all areas surveyed in Campbell et al. (2012) were covered. This included the River Tay, the River Tummel, the River Isla (and its tributaries including the River Ericht, Dean Water, Kerbet Water, Burn of Kilry and Lunan Burn with Loch Clunie, Marlee Loch and Rae Loch); the mouth of the River Almond; the River Earn (and its tributaries including the Farg, Dron Burn and Pow Water); and the Invergowrie Burn. In addition the River South Esk and any main tributaries starting from the closet point to the River Isla were surveyed, along with the River Forth.
2. The survey area was then expanded to include tributaries and water bodies directly associated with the Rivers Tay, Earn, Isla and Tummel within Tayside, and the Allan Water, River Devon and Teith within the Forth catchment. After this associated lower order water courses where surveyed if beaver field signs were found in the vicinity and/or activity had been recorded. Lastly OS maps were consulted and those water bodies identified having suitable habitat were selected and surveyed.
3. Any reports of beaver records were followed up as far as possible. This included spot check surveys of any sites reported to SNH.
4. Our survey locations also extended 2 km upstream from the last recorded beaver field sign on the watercourse. At times this was not possible due to the difficulties of the terrain and in such cases spot checks were made every few hundred metres using binoculars.
5. Survey work was organised by main-river and associated tributaries on a week by week timetable for logistical purposes. For example, the Tummel and its tributaries and surrounding water bodies were focused on during week 1. Once these had been covered, the remaining weeks of field work targeted any missed gaps, smaller water courses with suitable habitat and follow ups to any new beaver activity recordings were undertaken.
6. Data collection involved field staff walking a linear stretch of water course (canoeing was used to a lesser extent depending on accessibility) and recording field signs.
7. Beaver field signs (see Annex 1 for type of signs recorded) were logged using one of two GPS devices. Data was collected directly using a Trimble Geo7x GPS device or a Garmin handheld GPS. The Trimble device involved recording a “feeding line”, commencing at the site of the first beaver feeding sign during a survey, and ending after no subsequent feeding signs were observed for 10 m along that stretch of water. Point data were also collected using this device, and the location of features such as lodges, dams and burrows etc. recorded. A handheld GPS recorded beaver signs as single GPS points with a resolution of 10 m.
8. For each data point or feeding line collected by either device, the following information was recorded and checked every 10 m during the survey: Activity type; OS grid reference; Photo number; Estimated age of field sign (fresh, old or mix); Distance from water (m); Area affected (m); River width and approx. depth (m); Surrounding land use type; Beaver activity effort (low, medium or high); Management impact (low, medium or high); Any other comments
9. Beaver activity effort was categorised as low (e.g. <5 small diameter trunks/ woody stems within 10m radius); medium (e.g. 5-10 small diameter trunks/ woody stems within 10m radius); or high (e.g.10+ small diameter trunks/ woody stems within 10m).
10. Management impacts were categorised subjectively, based on the perceived impact at the time of survey, as low if affecting a small area and/or could have been easily mitigated without excessive costs or resources (e.g. small scale tree felling); high if a large area was affected and/or mitigation was resource intensive (e.g. flood bank collapse, multiple collapsed burrows or flooding of large area of crops); medium if ranging between these.
11. Data were collated and passed on for analysis on a weekly basis.

Annex 1.3 Core data processing and analysis workflow used

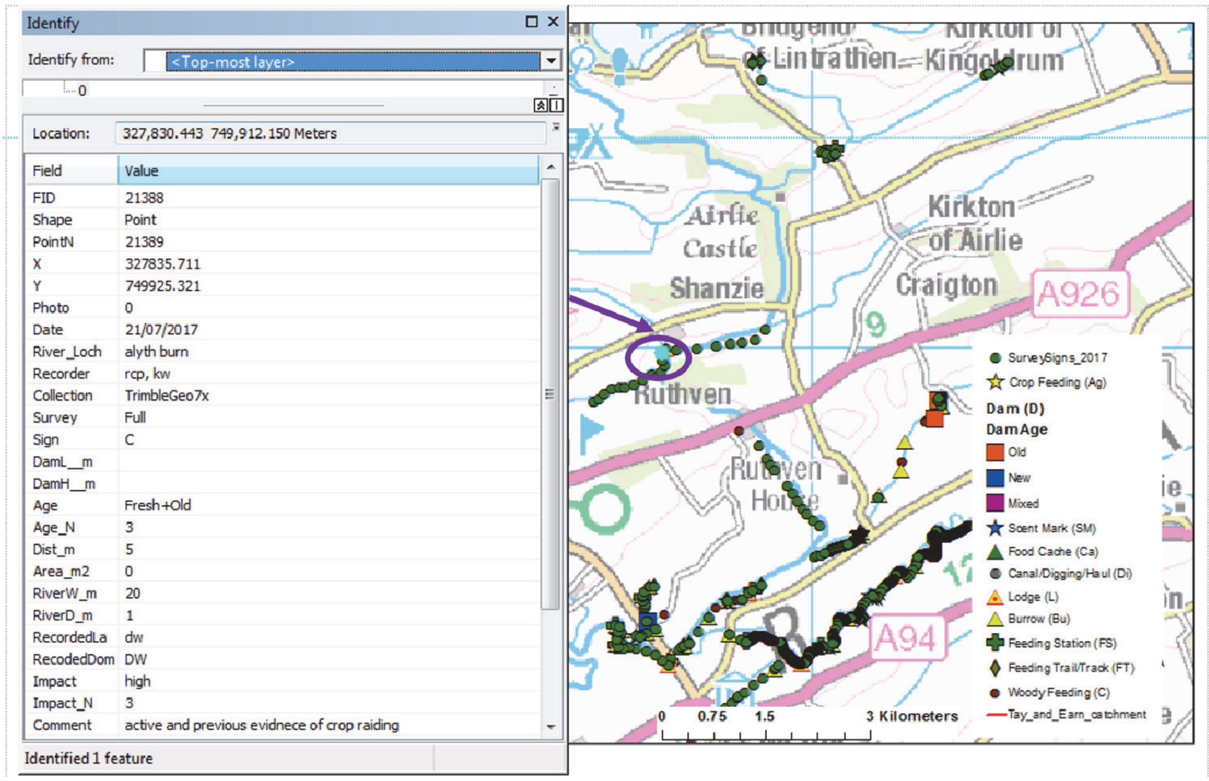
1. Field data were collected weekly from the field team (via email)
2. For data collected with the Garmin handheld GPS, data were received in an Excel spreadsheet and coordinates were converted from OS GB grid-references to British National Grid eastings/northings.
3. For data collected with the Trimble mobile mapper, data were received as a Trimble file and exported using Trimble software as ESRI line (feeding signs) and point (all other data) shapefiles.
4. All data were imported into GIS software (ArcGIS 10.2.2 for Desktop was used for all analysis).
5. Point data (from both the Garmin handheld GPS and Trimble mobile mapper) were converted and saved as ESRI point shapefiles.
6. Line data (from the Trimble mobile mapper) were split into equal 10 m intervals using 'COGO' toolbar 'proportion' and 'split into COGO lines' functions before being converted to a point shapefile using the 'feature to point' function. 10 m was chosen to be comparable to the sampling frequency used for point data.
7. All data were visually quality controlled to ensure they fell along the river lines surveyed. Spot quality control checks were also made i.e. checking that the data for a point indicates it is for the river reach where it is displayed on the map.
8. All survey data were merged into a single point shapefile (and associated attribute table database).
9. For the analysis of the 2017/2018 survey data, the dataset was separated into '2018 All' and '2018 Fresh/Active' datasets. '2018 All' included all data collected during the 2018 survey. However, it was recognised that if only 'old' signs were recorded at specific survey points then these may not represent active beaver sites. Therefore, for the '2017 fresh/active' data subset only points where mixed or fresh/new signs were recorded were used in any analysis. Data were separated using the 'Definition Query' function within layer properties.
10. Data were plotted against OS backdrop mapping (for which OS data © Crown copyright [and database rights] 2018 OS 100017908 applies) using British National Grid geographic projection.
11. The Definition Query function was used to display and obtain summary statistics for various subsets of data i.e. age, sign type, impact etc., as described in the main part of this report.
12. Kernel Density (Spatial Analyst Tool) was used to visualise patterns of survey point distribution. Kernel Density calculates a magnitude per unit area from point or polyline features using a kernel function to fit a smoothly tapered surface to each point or polyline (http://pro.arcgis.com/en/pro-app/tool-reference/spatial-analyst/kernel-density.htm). This was displayed in 'heat maps' allowing easy spatial identification of areas of beaver activity. A 1 km^2 search radius was used to determine the heat maps.
13. The same Kernel Density analysis was undertaken on the 2012 survey dataset provided by SNH (Tayside_Beaver_Survey_2012, and described in Campbell et. al 2012).
14. The 2012 dataset was subtracted from the 2017/2018 fresh/active dataset using the raster calculator function to visualise areas of increased beaver point density (based on surveyed areas). Similarly, the 2017/2018 fresh/active dataset was subtracted from the 2012 dataset and presented separately to clearly visualise areas of decreased beaver point density.

Annex 1.4 Territory definition method

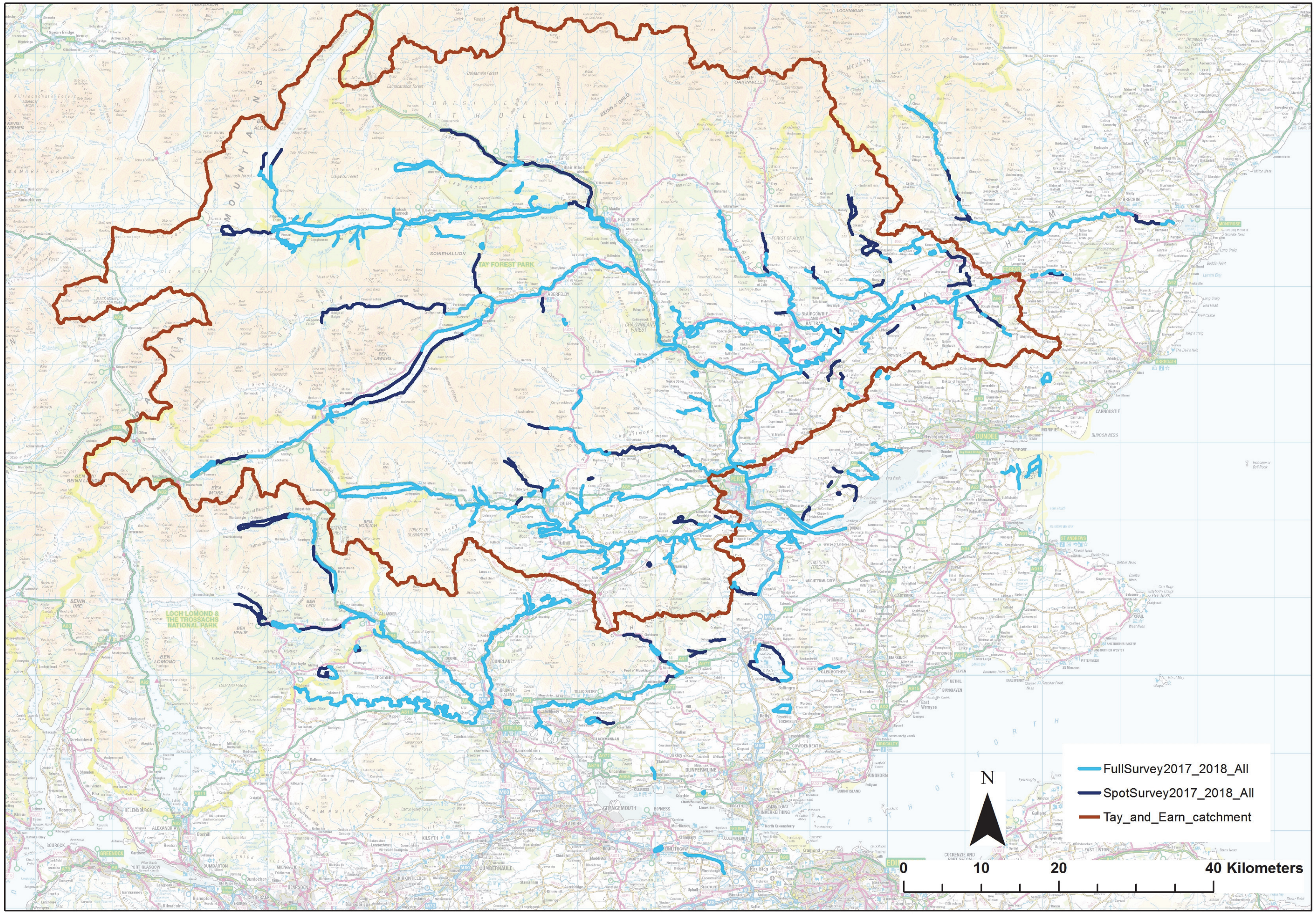
1. All analyses was undertaken in ArcGIS 10.2.2 for Desktop using data outputs created in the previous analysis described in Annex 1.3
2. Kernel Density plots (2012 and 2018 fresh/active) were converted to integer (whole number) datasets to facilitate analysis. The Int (Spatial Analyst) function was used, threshold 100000.
3. The Region Group (Spatial Analyst) function was used as a tool by which to identify spatially independent regions, as density clusters and to assign a unique number to each region (these numbers were eventually used as unique identifiers for each beaver territory). Within this function, 'Eight Neighbours' and 'Cross' zone grouping options were selected and values of '0' indicating no grouping were excluded.
4. The resulting 'Region Group' raster layer was converted to a polygon using the 'raster to polygon' function.
5. The 'zonal statistics to table' function was used for 2012 and 2018 fresh/active integer datasets to acquire a mean point density for each region.
6. The Zonal statistics were joined to the Region Group polygons using the 'join by attribute' function and the unique region numbers. The output was then exported to a new shapefile.
7. Territories and associated point density data were then plotted to allow visual comparison.
8. 2012 territories were plotted against those defined in Campbell et al. (2012) and the numbers compared.
9. 2017/2018 territories were assessed using the presence of various key field signs by Rosin Campbell-Palmer and local experts. The majority of territories were defined using the modelling approach, but where analysis was believed to have missed or combined territories, additional territories (Expert additional) or splitting of modelled territories (Expert split) was undertaken (steps 11-13).
10. Additional territories were included from known historical recording and/or local knowledge followed up by ground truthing by survey staff. In addition to these some territories were included from the recording of small number of field signs that didn't translate into separate territories through the density modelling approach, but that field survey staff could establish was an active territory though access for full survey recordings were not possible (e.g. terrain, access issues).
11. A number of territories produced by the modelling were further split using ground truthing of known beaver families (mainly those observed in previous trapping or observational studies or through local knowledge), through the recording of scent marking borders and/or using hydrological features such as the natural divide between two lochs. From an ecological perspective beaver territories will naturally follow such natural features.
12. Division of territories was harder on linear, riverine systems, for these the modelling approach predominated as time and resources did not permit a greater determination of family boundaries (through family composition observations), therefore potential for underestimation of territories may have occurred/been more likely along main rivers with greater beaver densities i.e. along the River Earn, lower River Tay.
13. The method of beaver territory determination and analysis is presented in the figures of Annex 2.6.
14. This combined modelling and expert knowledge formed the basis of the final territory layer TerritoryAll_2018.
15. A comparison in total number of territories (2012 versus 2018) made numerically allowing estimates of population size to be made based upon collected survey data.



Annex 1.5 Example of the database details behind each recorded survey point on the GIS. OS data © Crown copyright [and database rights] 2018 OS 100017908.

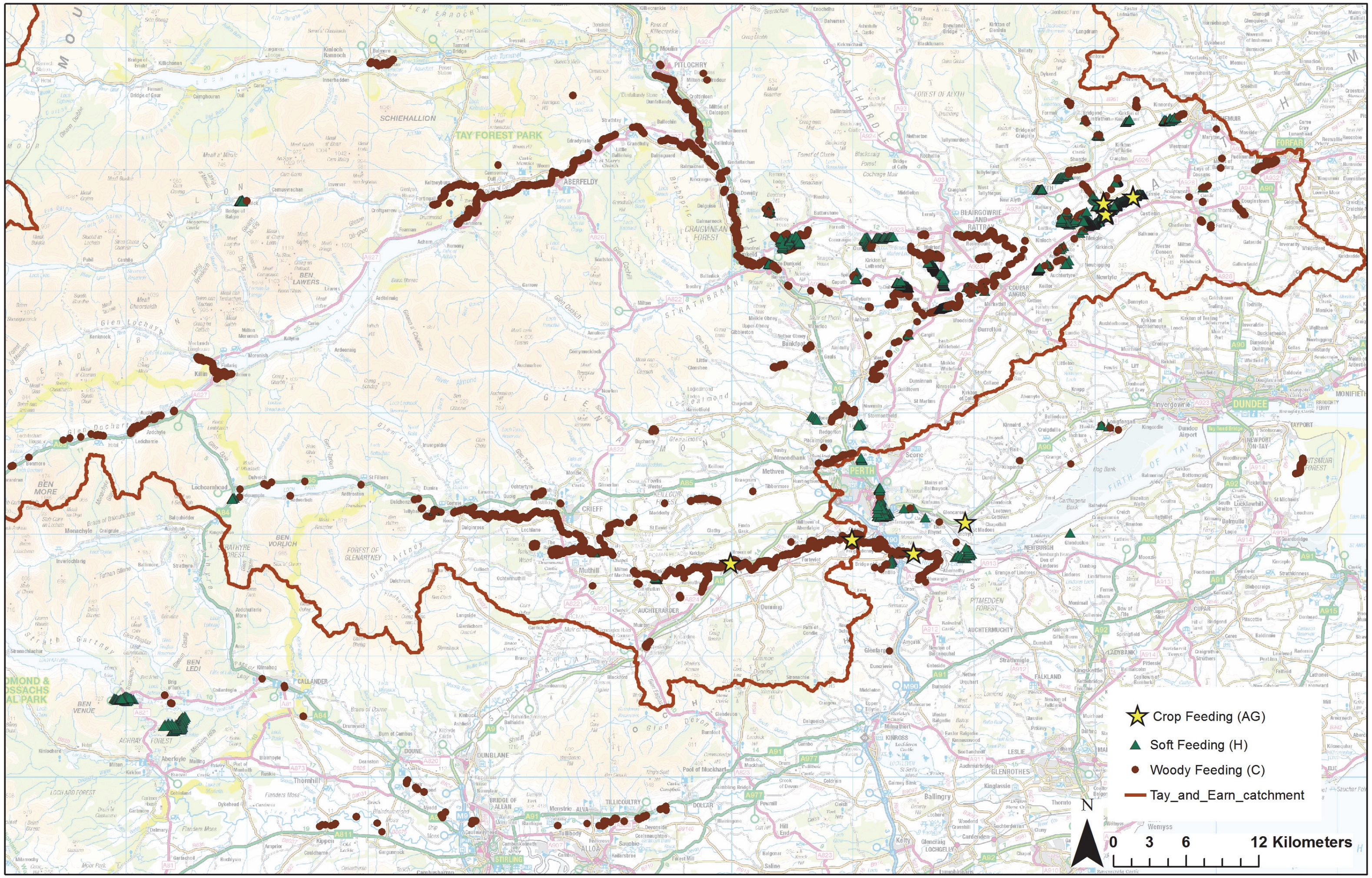


Annex 1.6 Example of the database details behind a survey point where a 'high' management impact has been identified by the field team. OS data © Crown copyright [and database rights] 2018 OS 100017908.

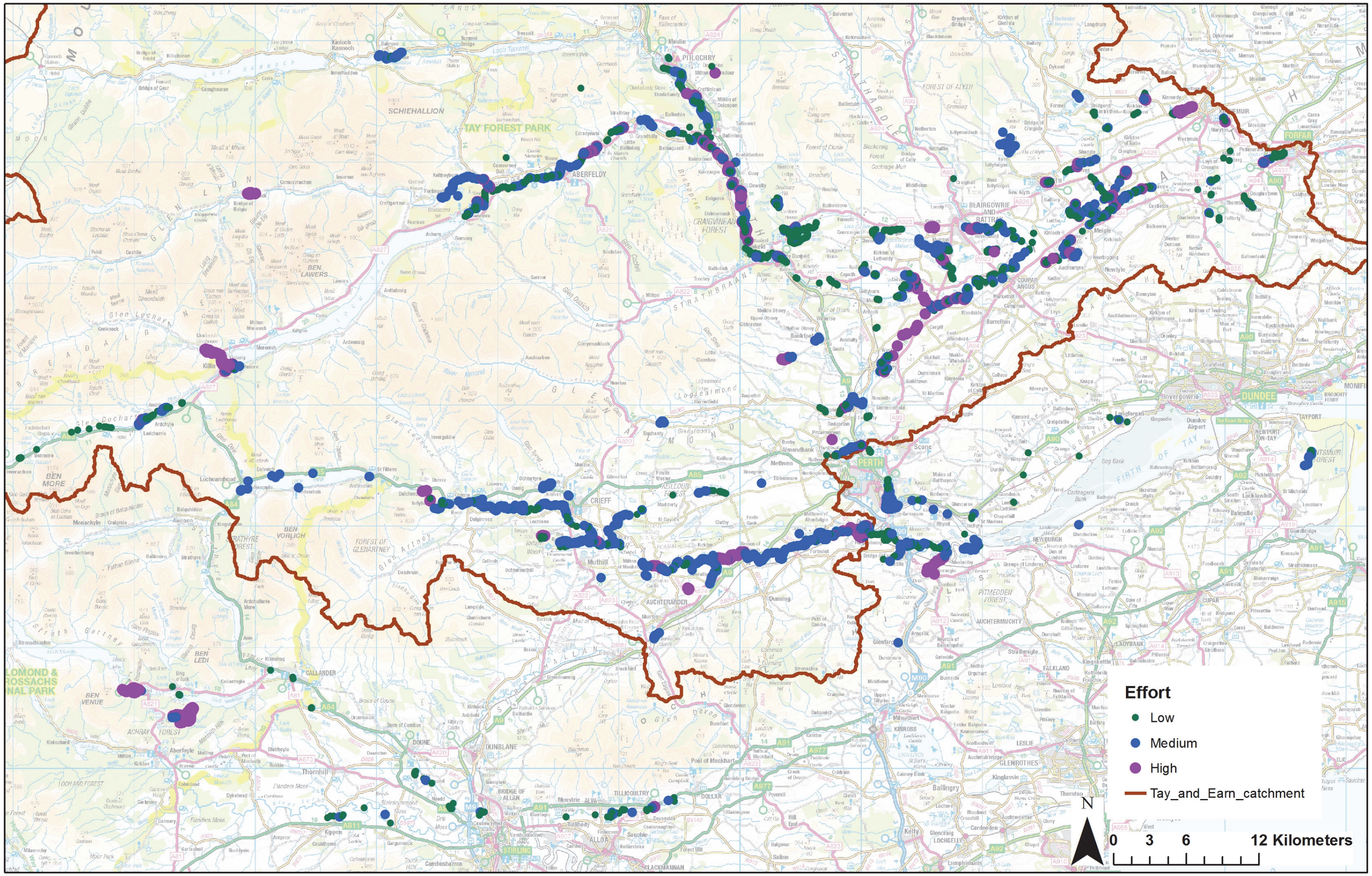


Annex 1.7. Mapped total surveyed area 2017/2018, including both full (light blue) and spot (dark blue) surveys. OS data © Crown copyright [and database rights] 2018 OS 100017908.

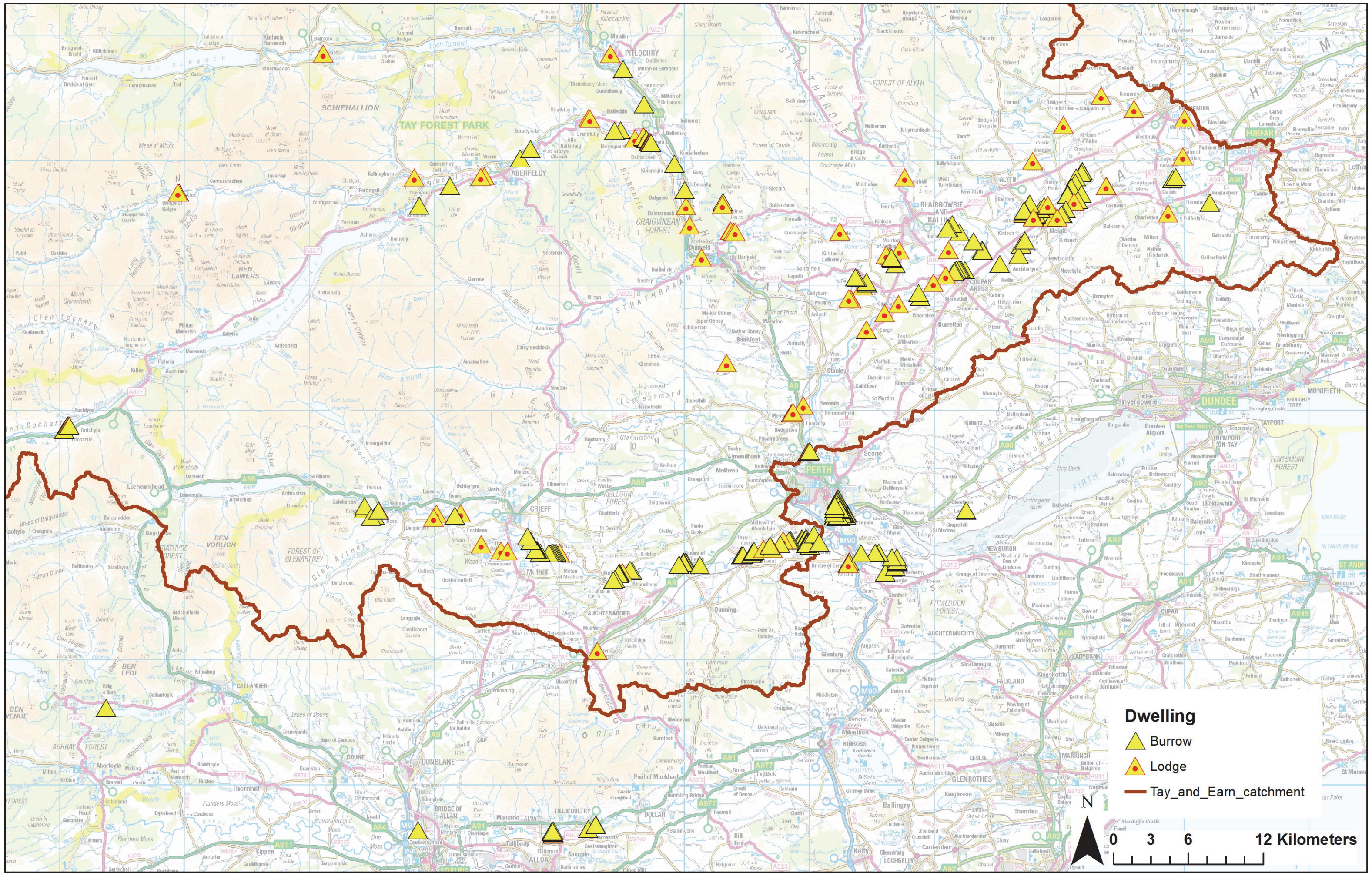
ANNEX 2: FIELD SIGN DISTRIBUTION MAPS



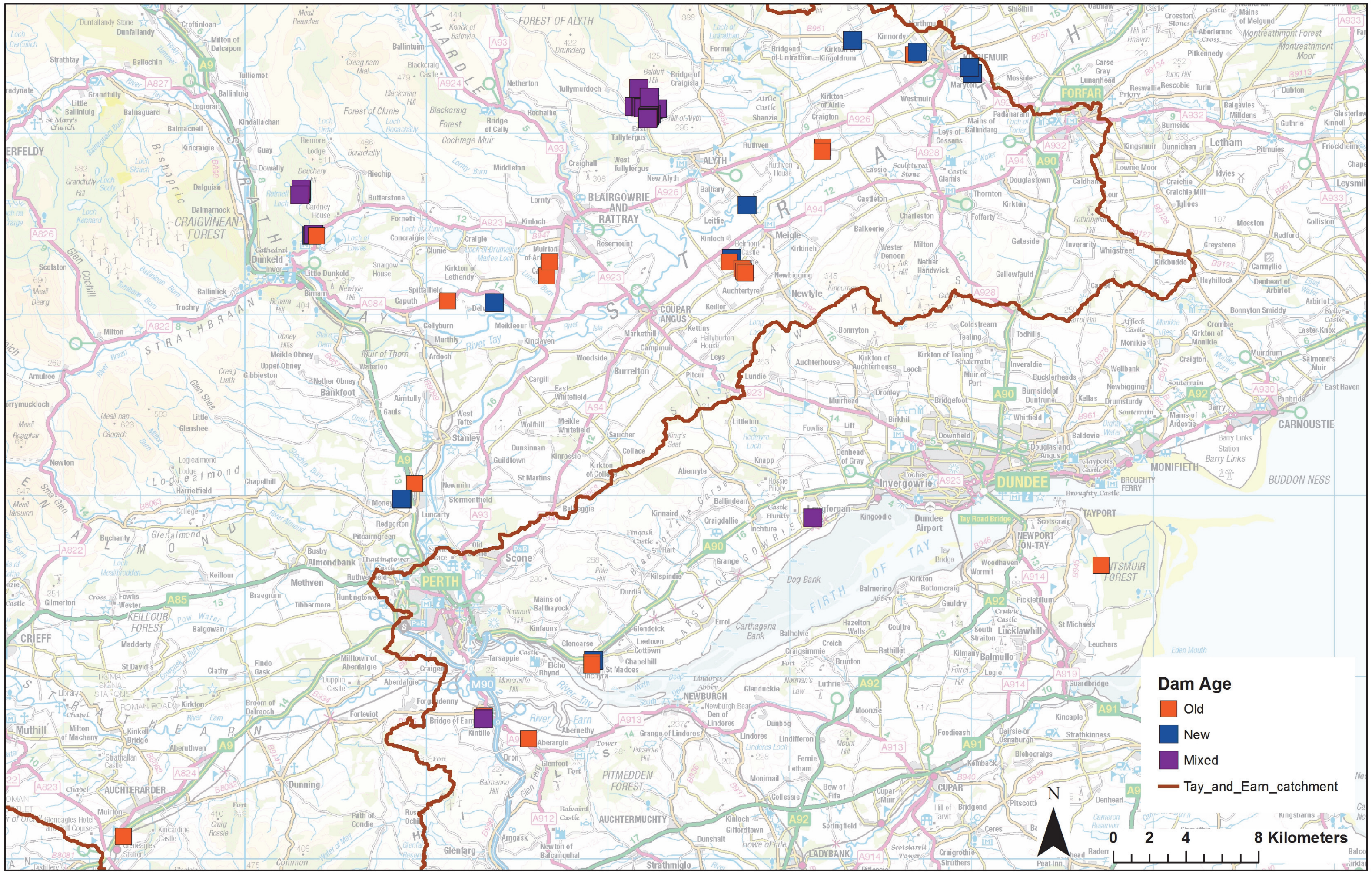
Annex 2.1 Mapped distribution of beaver feeding signs in Tayside area, 2017/2018. OS data © Crown copyright [and database rights] 2018 OS 100017908.



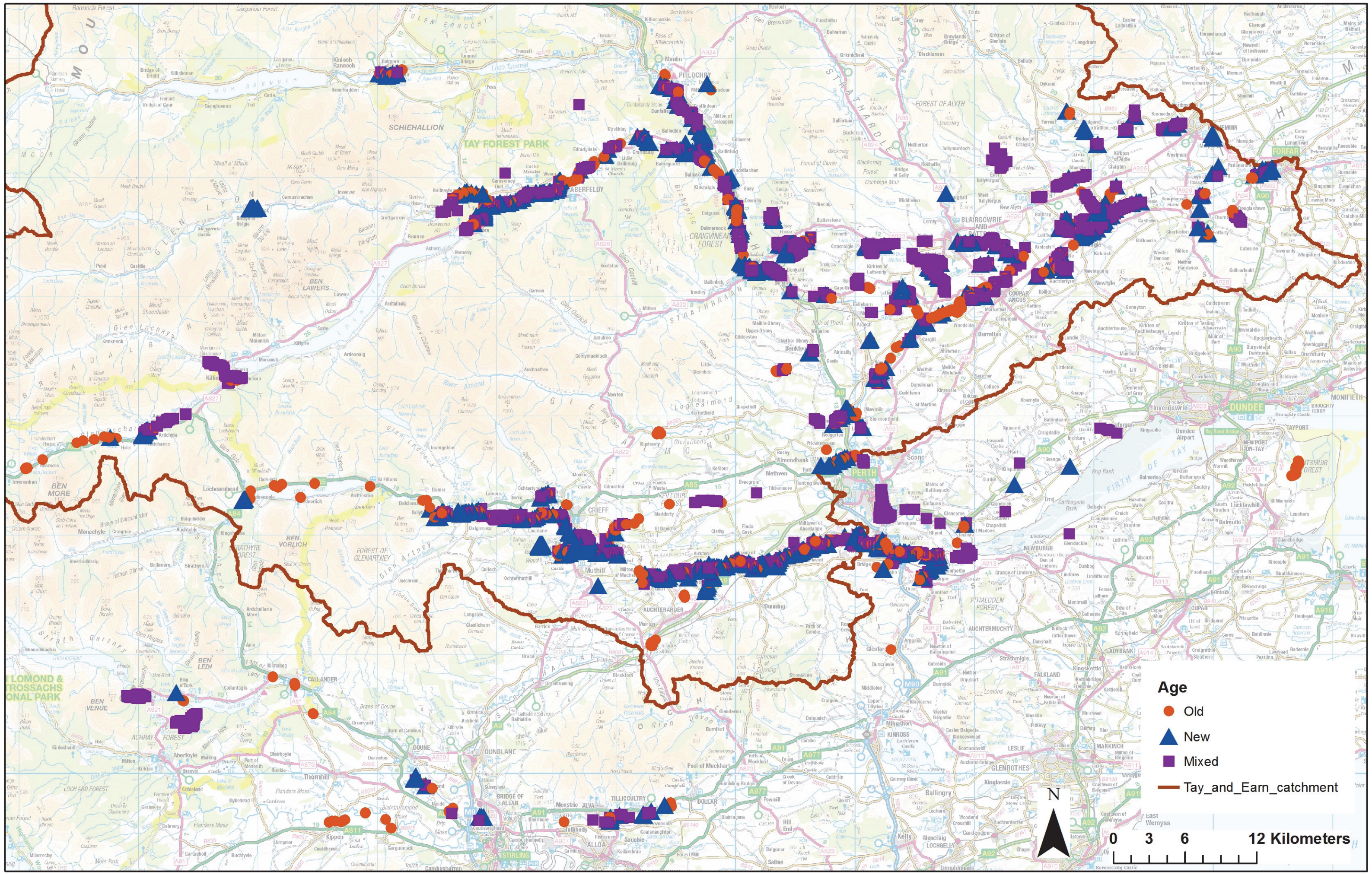
Annex 2.2. Mapped distribution of beaver activity effort categories (low, medium, high) for field signs (i.e. the effort that the beaver invested into the activity) in Tayside area, 2017/2018. OS data © Crown copyright [and database rights] 2018 OS 100017908.



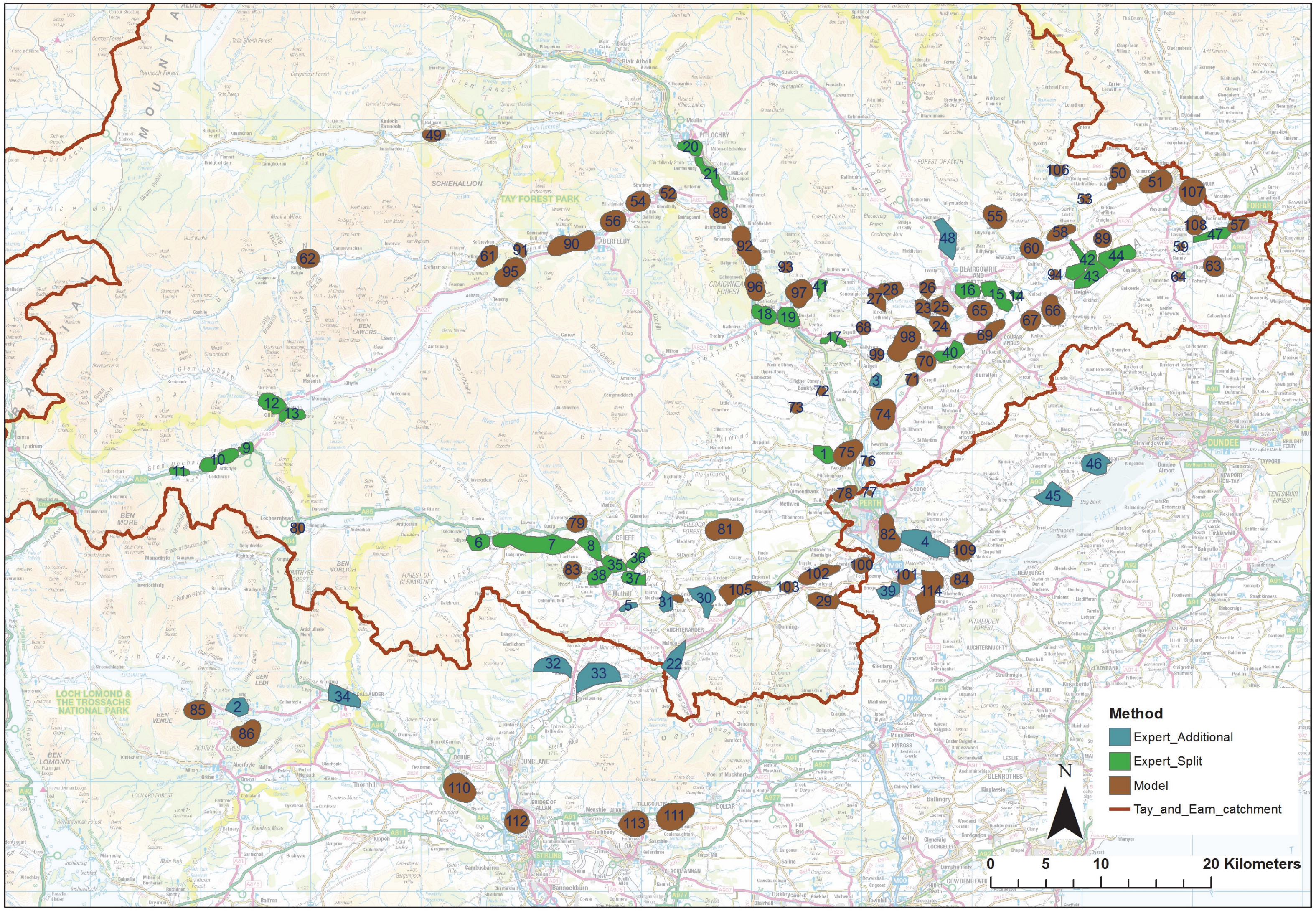
Annex 2.3. Map of the distribution of beaver burrows and lodges recorded in Tayside area, 2017/2018. OS data. © Crown copyright [and database rights] 2018 OS 100017908.



Annex 2.4. Map of beaver dam locations (active, breached and sites where dams had been obviously removed) and their respective ages (old, new or a mix of old and new) in Tayside area, 2017/2018. OS data © Crown copyright [and database rights] 2018 OS 100017908.



Annex 2.5. Map showing the distribution of old, new and mixed beaver field signs in Tayside, 2017/2018. OS data © Crown copyright [and database rights] 2018 OS 100017908.

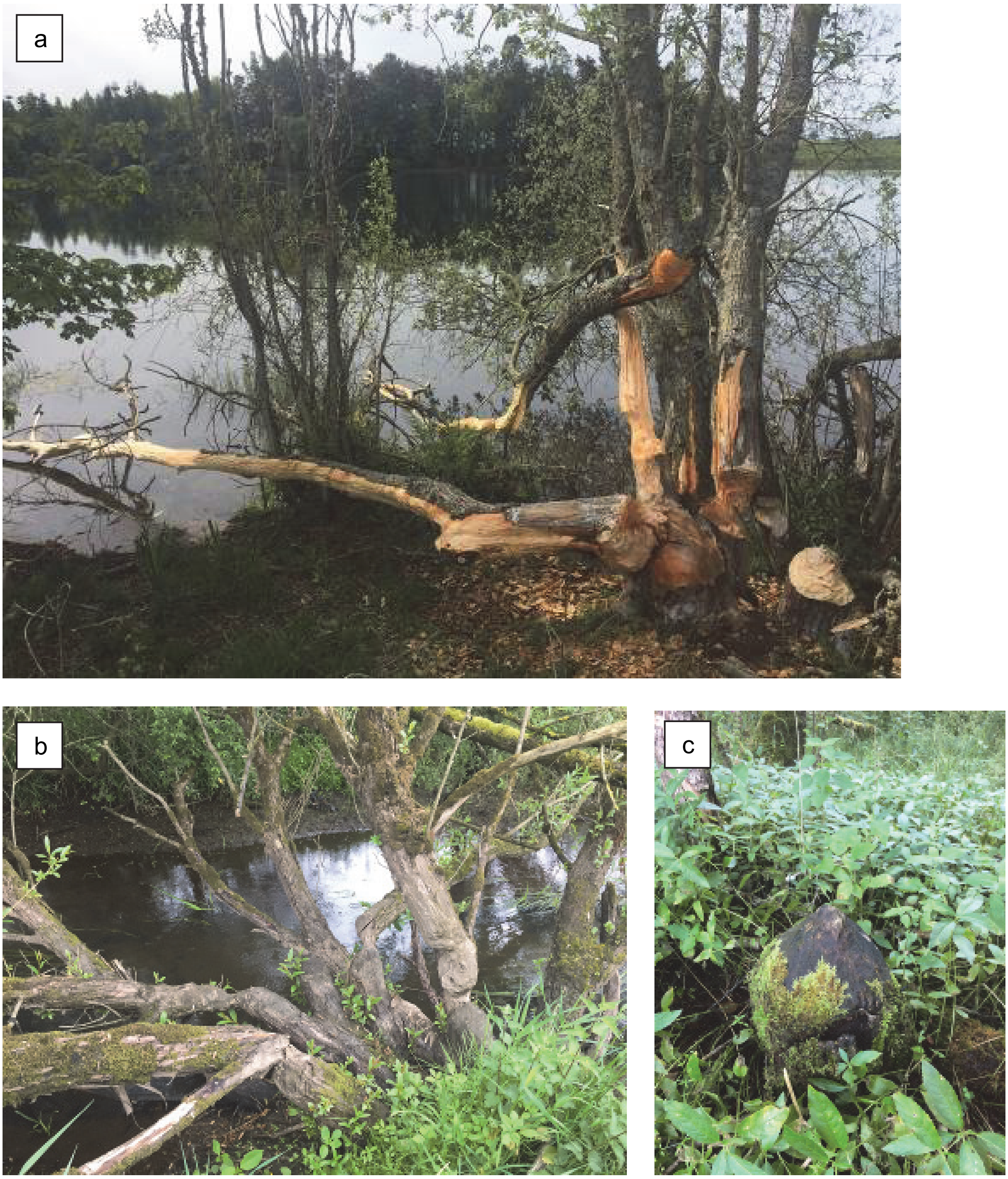


Annex 2.6. Map showing 2017/2018 territories and method of determination. OS data © Crown copyright [and database rights] 2018 OS 100017908

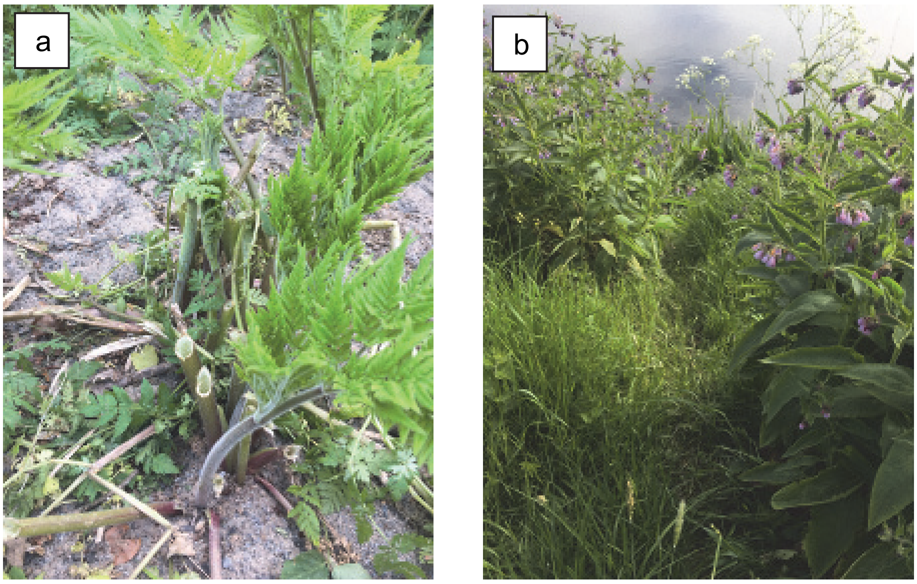
ANNEX 3: SURVEY PHOTOGRAPHS

The following images and their descriptions represent a sample of the typical field signs, land use types, and land use impacts recorded during the survey.

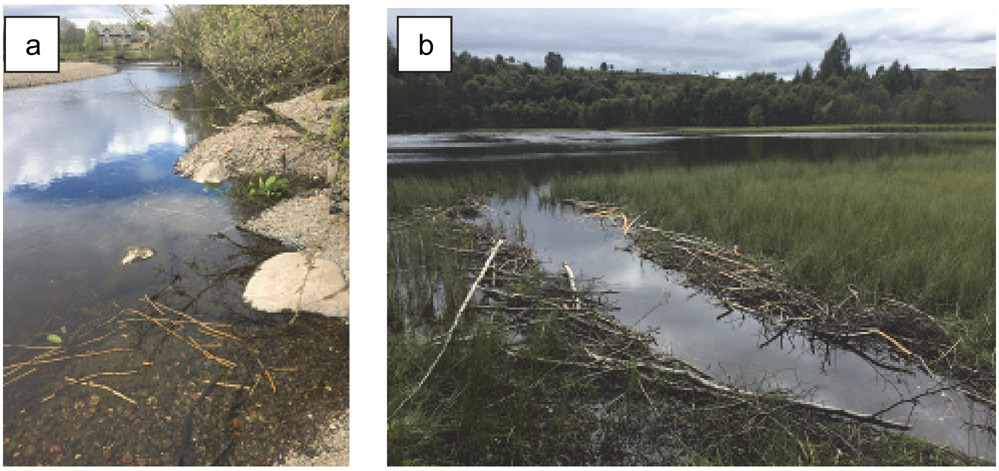
Typical field signs



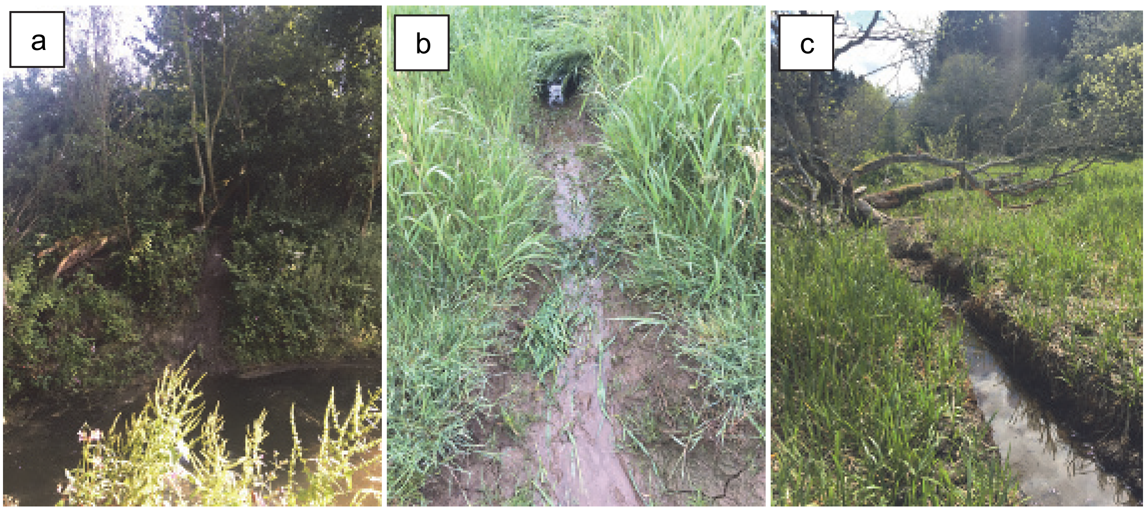
Annex 3.1 a, b, c. Woody foraging, consisting of felled stems/trunks, gnawed side branches and/or feeding on shrubs. Age was classed as fresh (a), old (b + c), or mixed.



Annex 3.2 a, b. Feeding on herbaceous plants (recorded as 'soft feeding') was evident on a wide range of species through flattened forage trails, cut stems and feeding remains.



Annex 3.3 a, b. Feeding stations were distinguished largely through discarded peeled sticks and/or piles of vegetation, often associated with the water's edge but also found inland.



Annex 3.4 a, b, c. Beaver forage trails (a + b) and canals (c) tend to lead inland from the watercourse. These are typically associated with other foraging field signs.

Annex 3.5 a, b, c. Residential structures included lodges (a + c) and burrows (b). A beaver territory will typically have numerous burrows. They may have no lodges (just burrows), or can have several lodges and/or a mix of lodges and burrows largely depending on bank substrate and structure

Annex 3.6. Scent marking activity. This typically occurs on bankside substrate and/or vegetation that a beaver has pulled into a mound structure. Scent mounds tend to be found along the shoreline. They may be singular or multiple mounds with a distinctive smell.

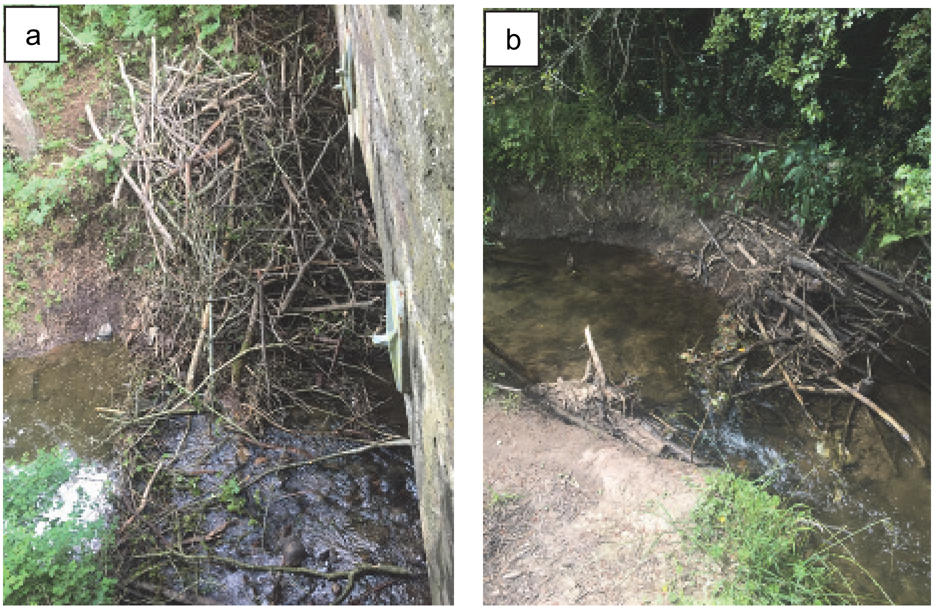
Land use types in Tayside

Annex 3.7 a, b, c, d. Freshwater habitats in which beavers were recorded in Tayside varied from: (a) artificial drainage ditches associated with arable land ; small burns with a range of depth and associated riparian vegetation (not illustrated); (b) urban areas and hard infrastrucutre; and (c and d) larger rivers lined with deciduous woodlanda and grazing pasture.

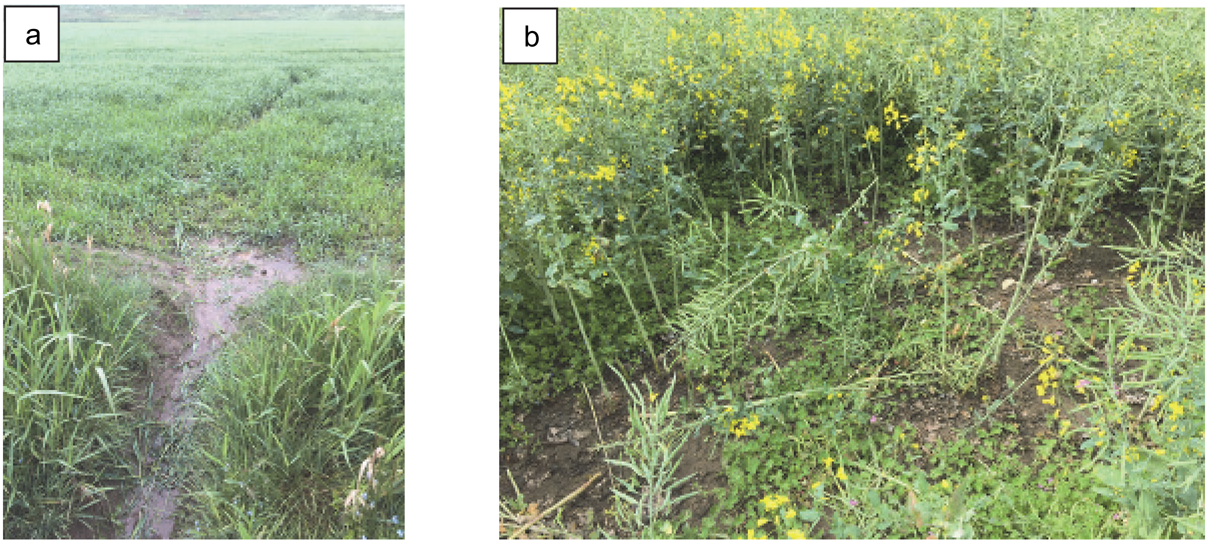
Land use impacts

The following images are samples of land use impacts of some of the beaver activity encountered during suveys.

Annex 3.8 a, b. Damming impacts varied according to location, hydrology and surrounding land use. Greatest impact tended to be associated with narrower, straight watercourse sections which tended to display multiple dams. Impounded water was recorded flooding tracks, waterlogging crops and impeding land drainage pipes.

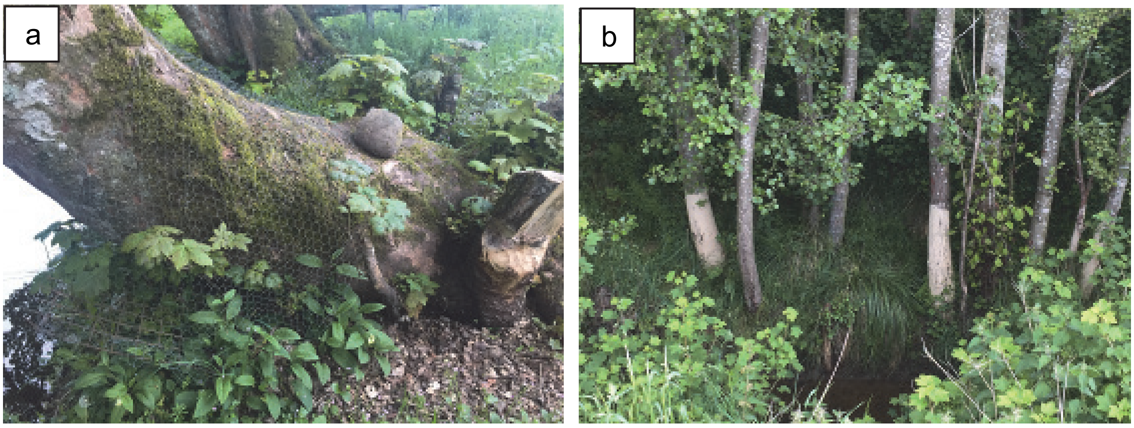


Annex 3.9 a, b. Dam breaching resulting from high water flows (b) and partial removal by people (a) was evident at several sites.



Annex 3.10 a, b. Crop feeding was recorded at several sites with old, worn forage trails evident (a). In other sites forage trails were new and presumably varyied seasonally. Small areas of crop feeding were recorded across several crop types at the end of forage trails (b).

Annex 3.11. Flooding of crops through beaver damming, especially of small water courses and/or land drainage ditches, is likely to become a more significant conflict issue as population densities and beaver occupy in lower order water courses increase.



Annex 3.12 a, b. Tree protection measures had been used at several locations, often associated with gardens or public buildings e.g. village halls. This always took the form of mesh wire potection (a), apart from one site where the Tayside Beaver Study Group had previously trialled deterrent paint (b).

Annex 3.13 a, b. Conifer felling and ring barking on mature trees was evident, although not in significant amounts.

Annex 3.14 a, b, c, d. Collapsed burrows were recorded at several locations, often associated with arable land and/or flood banks.

Annex 3.15. There were a small number of records of trees felled onto fencelines with varying levels of damage to infrastructure.

Annex 3.16. A burnt out beaver lodge, implying a conflict issue.

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