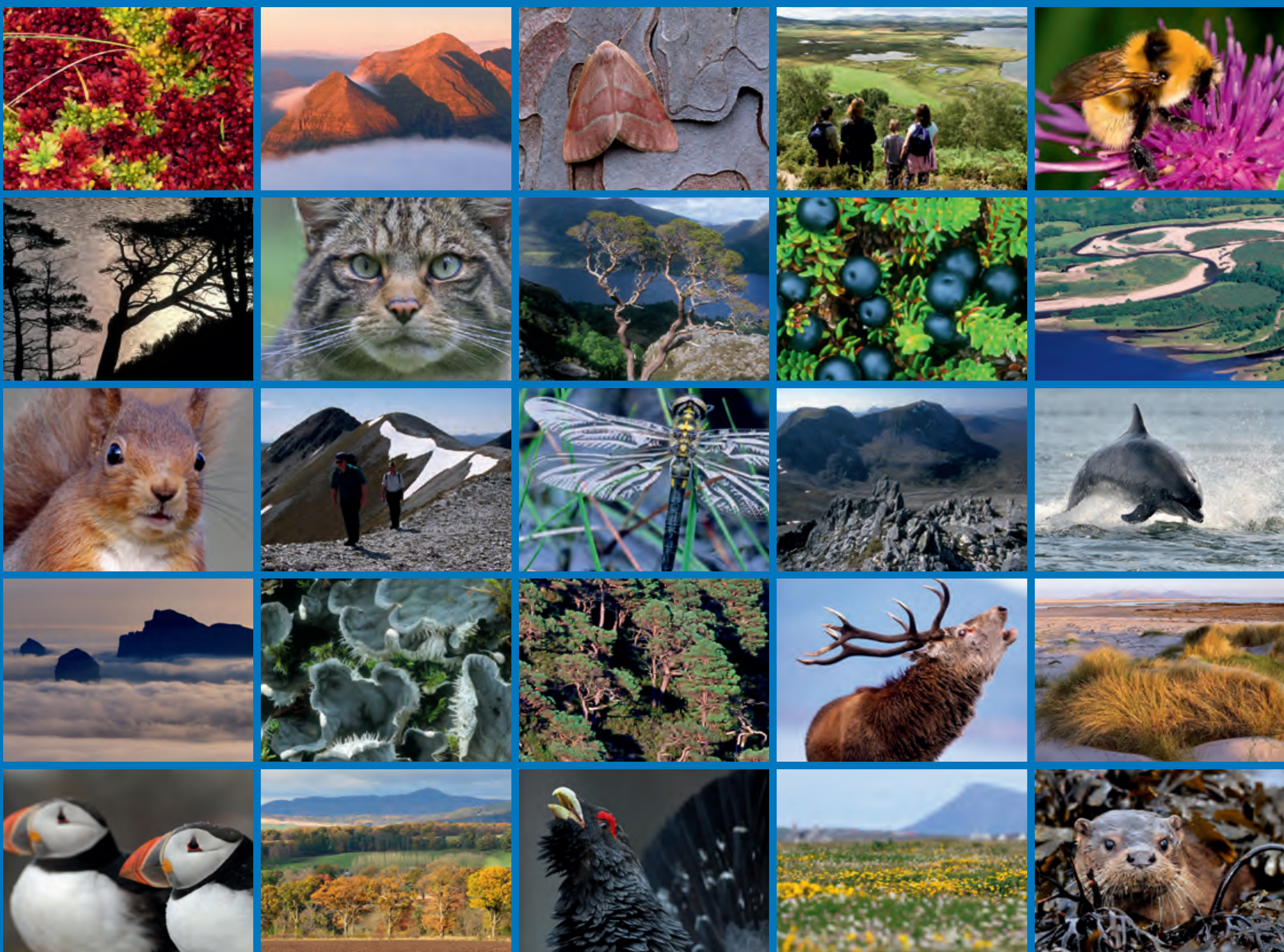
Scottish Natural Heritage
Commissioned Report No. 685

The Scottish Beaver Trial: Ecological monitoring of the European beaver Castor fiber and other riparian mammals 2009-2014, final report



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COMMISSIONED REPORT

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The Scottish Beaver Trial: Ecological monitoring of the European beaver *Castor fiber* and other riparian mammals 2009-2014, final report

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COMMISSIONED REPORT

Summary

The Scottish Beaver Trial: Ecological monitoring of the beaver *Castor fiber* and other riparian mammals 2009-2014, final report

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Beaver; monitoring; Knapdale; Scottish Beaver Trial; reintroduction; population.

Background

In 2008, the Scottish Government approved a licence for the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), to undertake a five-year trial reintroduction of the European beaver *Castor fiber* after an absence of over 400 years. The aims of the trial (which has now been completed) included an assessment of the ecology of the beavers, and their impacts on the Scottish environment. The success or failure of the trial will be based on a number of specific criteria, which relate to the ability of the reintroduced population to sustain itself, the effects of the beavers on biodiversity, the economic effects of the beavers, and the cost of their reintroduction and ongoing management.

In order to effectively assess the Scottish Beaver Trial (SBT), Scottish Natural Heritage (SNH) coordinated a monitoring programme, in collaboration with a number of independent organisations. A core element of this was the monitoring of the beaver population itself. SNH worked in partnership with the Wildlife Conservation Research Unit at the University of Oxford (WildCRU) in order to ensure the monitoring of the beavers, and other riparian mammals present at Knapdale, was suitable and appropriate. WildCRU were responsible for the independent analysis of data received on the ecology of the released beavers. The aim of this report is to report on and summarise the data gathered on the ecology of the beaver population and other riparian mammals over the duration of the trial; to present analyses that address the relevant success and failure criteria of the trial, and address key ecological questions relevant to the study of the ecology and biology of the European beaver in the Scottish environment. This final report collates ecological monitoring data from the beginning (June 2009) to the end of the trial (to June 2014).

Summary of findings

- A total of sixteen beavers in five families or pairs were released during the trial (fifteen in the first year and one in the second). The aim was to establish a minimum of four breeding pairs in the release area by May 2011. Of the released individuals, three deaths (all males) were recorded during the first year of the trial, and five animals went missing (four over the first two years, and one in the fourth year). As of June 2014, eight of the released beavers were known to be alive and present in the release area.

- A total of fourteen wild-born beavers were recorded over the four ‘kit emergence periods’ monitored. Litter size varied between one and three kits per reproducing pair. Four wild-born individuals survived to at least one year old, three survived to become a sub-adult (at two years old). Two kits (in separate years) were predated, eight went missing before they were one year old and are almost certainly dead. Either one or two wild-born animals remain at the release site.

- In comparison with other reintroductions (across taxa), post-release mortality, based on known deaths, was low. Kaplan-Meier survival estimates, however, were imprecise due to the high censoring (loss of animals) rate (considering the potential biases in the data, *S* could vary between 0.38 and 0.74, with a 95% CI of 0.19, 1). Mortality of established adult animals was low. Compared with other beaver populations, the proportion of females breeding was high, and although litter size was relatively low, it was probably comparable with that of the source population in Norway. Kit loss, however, (in some years) was very high (100% of kits lost in 2012 and 2013).

- The beaver population currently at Knapdale appears to be stable, but not increasing. The population did not reach predicted size (probably due to low reproductive success, i.e. high kit mortality, and possibly low litter size).

- It is important to consider that the beaver population at Knapdale was not intended to be self-sustaining, and thus that, as a management recommendation, supplementation would be needed to sustain a population at the release site. However, population viability modelling suggests that, even with supplementation, the existing population will not be viable unless kit mortality decreases. Small sample size was necessary for the trial purposes, but small sample size effects do mean that these results may not be relevant for beavers at other sites, or for other beavers at Knapdale. With this in mind, our recommendation is that any future release of beavers (at Knapdale or elsewhere) is monitored to assess on-going reproductive success, and thus to re-assess likely population growth as part of an iterative adaptive management approach.

- Beavers at Knapdale currently comprise three groups (of between two and four members, plus potentially any kits born in the summer of 2014) and one single male, covering a total area of 367 ha, at a density of approximately one beaver family per 5 km of waterway edge. Monitoring of where these beavers settled, what area they used, and what habitats they used, suggest that translocated individuals have successfully established at Knapdale.

- ‘Family’ home range sizes were smaller than in Norway (the origin of the source population) but within the range reported for beavers generally. For the most part, beavers appeared to settle on the loch on which they were released (although some used a neighbouring loch more intensively) and home range size appeared to vary according to loch size, with the longer lengths of waters’ edge habitat of the larger lochs simply being used less intensively. It is probably reasonable to assume that beavers released on other loch systems in Scotland will, for the most part, settle on the loch on which they are released (particularly if the landscape allows local-scale shifts of home range boundaries). Release site fidelity on rivers might be different.

- As expected, field signs (which comprised mostly cut, felled or gnawed trees or branches) were located predominantly within 20 m of the waters’ edge, although some field signs were occasionally found at least 50 m from the waters’ edge. With a view to management and mitigation of undesirable impacts (should they occur), beaver ‘habitat use’ at 50 m or more from the waters’ edge should be anticipated (where riparian habitat extends this far) but is likely to be only occasional. There was no evidence of progressive spread further from the waters’ edge over the five years of the trial.

- All beaver families built at least one permanent lodge. Dam and canal building was variable among families/lochs, and canal building was also variable among years, which appears, from other studies, to be normal for beavers. Although it is probably not possible to predict beaver construction activities at a local scale, their impacts (if any) can usually be managed and mitigated.

- Woodland habitat types were used approximately in proportion with their availability in the beaver's home range. There was some evidence that the Loch Linne family preferentially used riparian woodland areas dominated by downy birch (*Betula pubescens*) where it occurred with eared willow (*Salix aurita*), and that the Dubh Loch family preferentially used riparian woodland areas dominated by downy birch with rowan. Downy birch alone was the most dominant broadleaved tree species within all beaver home ranges but it appeared to be used either in proportion with, or slightly less than, its availability. These results are in accordance with those of the woodland monitoring (and broadly in accordance with other European studies) that suggest a preference for willow, and possibly also rowan.

- Because there was no increase in the number of families over the duration of the trial, we are unable to describe how beavers might spread in the landscape at Knapdale or elsewhere. Information from the literature on other beaver reintroductions, and natural recolonisations, suggests that beavers usually undergo an expansion in range before increasing in density.

- During the trial, sub-adults (translocated individuals and wild-born individuals) did leave their family groups, presumably as part of the natural dispersal process. At Knapdale, the very low numbers of sub-adults and the time period over which they left mean that it is unlikely that they would have met and formed new breeding pairs. However, the size of the population on the Tay suggests that new families have established there.
- Detailed behavioural information from a subset of beavers provided no evidence that translocated beavers were behaving 'abnormally' in any way.

- There was no evidence that beaver reintroduction has had a negative impact on the presence of otters in the area.

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This project is part of the independent monitoring programme for the Scottish Beaver Trial coordinated by SNH in collaboration with a number of independent monitoring partners. For further information go to:
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1. INTRODUCTION

1.1 Background

The European, or Eurasian, beaver *Castor fiber* became extinct in Scotland around the 16th century as a result of over-hunting. Over recent years the potential for restoring this species to the natural fauna has been investigated. These investigations have resulted in a suite of information with regard to the scientific feasibility and desirability of conducting such a reintroduction. Relevant documents published by Scottish Natural Heritage (SNH) can be viewed at www.snh.gov.uk/scottishbeavertrial.

The work undertaken is in line with obligations on the UK Government, under Article 22 of the European Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Flora and Fauna (the 'Habitats Directive'), to consider the desirability of reintroducing certain species (listed on Annex IV), including European beaver.

The Species Action Framework, launched in 2007 by Ministers, and completed in 2012, set out a strategic approach to species management in Scotland. In addition, 32 species, including European beaver, were identified as the focus of new management action for five years from 2007. SNH worked with a range of partners in developing this work and further information can be found at www.snh.gov.uk/speciesactionframework.

In May 2008, the Scottish Government Deputy Minister for the Environment approved a licence to allow a trial reintroduction of up to four families of European beaver into Knapdale Forest, mid-Argyll.

The licence was granted to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), who managed the 'Scottish Beaver Trial' (SBT). The trial site, Knapdale Forest in Argyll, is owned by Forest Commission Scotland (FCS). Several families of animals were caught in Norway during 2008 and quarantined for six months. Three families were released in spring 2009, and a further two pairs in May and June 2010. The second of the latter two pairs was released at the beginning of the second year of the trial, under agreement from the Scottish Government, as a replacement for the first family that failed to establish (see Section 2). The release was followed for a five-year period, with a monitoring programme that ran until Spring 2014.

The licence issued by the Scottish Government to the RZSS and SWT came with a number of conditions, a key one being that the monitoring of the project must be independently coordinated by SNH. As part of this process, SNH, therefore, entered a partnership with the Wildlife Conservation Research Unit (WildCRU) at the University of Oxford to support, enable and report on the ecological monitoring of the beaver population and other riparian mammals during the trial period. This is just one element of a wider monitoring programme, coordinated by SNH, which included: beaver health, terrestrial vegetation, aquatic and semi-aquatic macrophytes, fish, Odonata, water chemistry, hydrology, riverine geomorphology, socio-economics, public health and scheduled monuments. These monitoring projects were led by other Independent monitoring partners (details of the entire monitoring programme are given at http://www.snh.gov.uk/protecting-scotlands-nature/reintroducing-native-species/scottish-beaver-trial/the-monitoring-programme). Throughout the 5-year trial period, the various monitoring elements were coordinated, and annual Research and Monitoring Co-ordination Group meetings were held so that information could be efficiently shared by those involved with the monitoring programme.

1.2 Relevant success and failure criteria

The licence application sets out *success criteria* for the project, some of which are specific to the ecology of the beaver (rather than the wider socio-economic and other environmental aspects of the trial), and thus are particularly relevant to the ecological monitoring work carried out. These are, that:

- **Survival of introduced animals is similar to that of successful reintroduction programmes elsewhere in Europe at a similar stage of population establishment.**
- **A stable or increasing core population is achieved within the limits of the study site.**

There are also *failure criteria.* The failure criteria specific to the ecology of the beaver are, that:

- **Mortality levels preclude establishment of a population.**
- **Significant and unsustainable damage is incurred by the ecosystem within the study site.**

1.3 Relevant objectives of the Scottish Beaver Trial

Specific *relevant objectives* of the Scottish Beaver Trial, as set out in the original licence application submitted by SWT and RZSS, were to *'study the ecology and the biology of the European beaver in the Scottish environment'* and thus to *'generate information during the proposed trial release that will inform a potential further release of beavers at other sites with different habitat characteristics.'*

Further, although not stated explicitly initially as an objective of the ecological monitoring, for any reintroduction it is important to be able to assess post-release behaviour of animals. With both animal welfare and future success (of further releases, if the decision is made to reintroduce beavers) in mind, and given the disturbance that animals are subject to during capture, quarantine and release, it is crucial to be able to assess whether or not individual animals were negatively affected by the process, and how well they have adapted to their new environment. This question can be addressed by assessing the health of the animals and their stress levels, as well as various demographic parameters (such as survival and reproductive success), but behaviour is also key (partly because aberrant behaviours can be relatively easily detected).

An additional aim of the ecological monitoring project (Campbell *et al.* 2010 p3) was to *'ensure the methodology includes the collation of suitable data which will allow the refinement of the existing beaver population model commissioned by SNH (Rushton et al. 2002), thereby improving our ability to predict future trends in beaver populations should the trial support the case for further reintroductions.'*

1.4 Addressing relevant success/ failure criteria, and objectives of the trial

Relevant success and failure criteria of the trial were addressed by analysis of beaver demographics and (observed and future predicted) population growth, as compared with information derived from other beaver reintroductions elsewhere in Europe. The assessment of 'significant and unsustainable damage to the ecosystem' was primarily addressed by other monitoring partners, but was supported by limited monitoring of other riparian mammals. The number of 'other riparian mammals' that we were able to monitor was limited by resources. Therefore, we chose to concentrate on the otter because it is a qualifying feature of the Taynish and Knapdale Woods Special Area of Conservation. We included American mink and water vole because field signs for these two species can potentially be detected while carrying out otter surveys, and thus without the requirement for additional resources. The water shrew is designated as a Species of Conservation Concern in the UK but we are not aware of any water shrew records from Knapdale so this species was not included in the monitoring programme.

The broader trial objective of studying the ecology of beavers in the Scottish environment, was addressed by assessing home range size and location of beaver families, spatial organisation, and habitat use. To address the additional, but important, objective of assessing the behaviour of translocated beavers (above), we equipped a subset of individuals (for a limited period of time) with GPS tags and/or time-depth recorders, to assess activity patterns, nightly distances travelled and diving behaviour; where possible, these data were compared with comparable data from the source population in Norway.

The original monitoring protocols for this work were detailed in Campbell *et al.* (2010), and methods refined over the first two years of the trial, as appropriate (discussed in Harrington *et al.* 2012). In ensuring that the relevant key ecological and behavioural information was collected, the aim throughout was to achieve a balance between data collection, animal welfare and maintaining natural behaviours within the population. The health of the beavers at Knapdale was reported on by the Royal (Dick) School of Veterinary Studies, Edinburgh University, and published in Goodman (2014).

This final report supersedes all previous annual reports and covers monitoring of the ecology of released beavers and other riparian mammals to the end of the Scottish Beaver Trial (June 2014). In the first section of the report, we provide a brief overview of the animals present at Knapdale. The following four sections of the report address beaver demographics, ecology and behaviour, and monitoring of other riparian mammals. In the final section, we offer recommendations that we hope will contribute to the decision-making process.

2. ANIMALS AT KNAPDALE

Between May 2009 and September 2010, a total of 16 beavers were released into Knapdale Forest, mid-Argyll (Fig. 1, 2).

Figure 1. Location of the Scottish Beaver Trial release area in Knapdale Forest, mid-Argyll. Base map © 2015 Google.

Most individuals were released as either breeding pairs or families (breeding pairs with their juvenile/sub-adult offspring, Table 1) with one solo male released to pair with a female that had lost her partner. Each breeding pair/family was released at a separate release site, with only one release site per loch. The aim was to establish a minimum of four potential breeding pairs in the release area by May 2011. This is a summary of the animals released during the trial, their fate and wild-born beavers born during the trial (Table 1, 2). Note that pairs/families are referred to throughout by the name of the main loch on which they occur, although in the third year of the trial there was an exchange of individual beavers between pairs (see Table 1, footnote e).

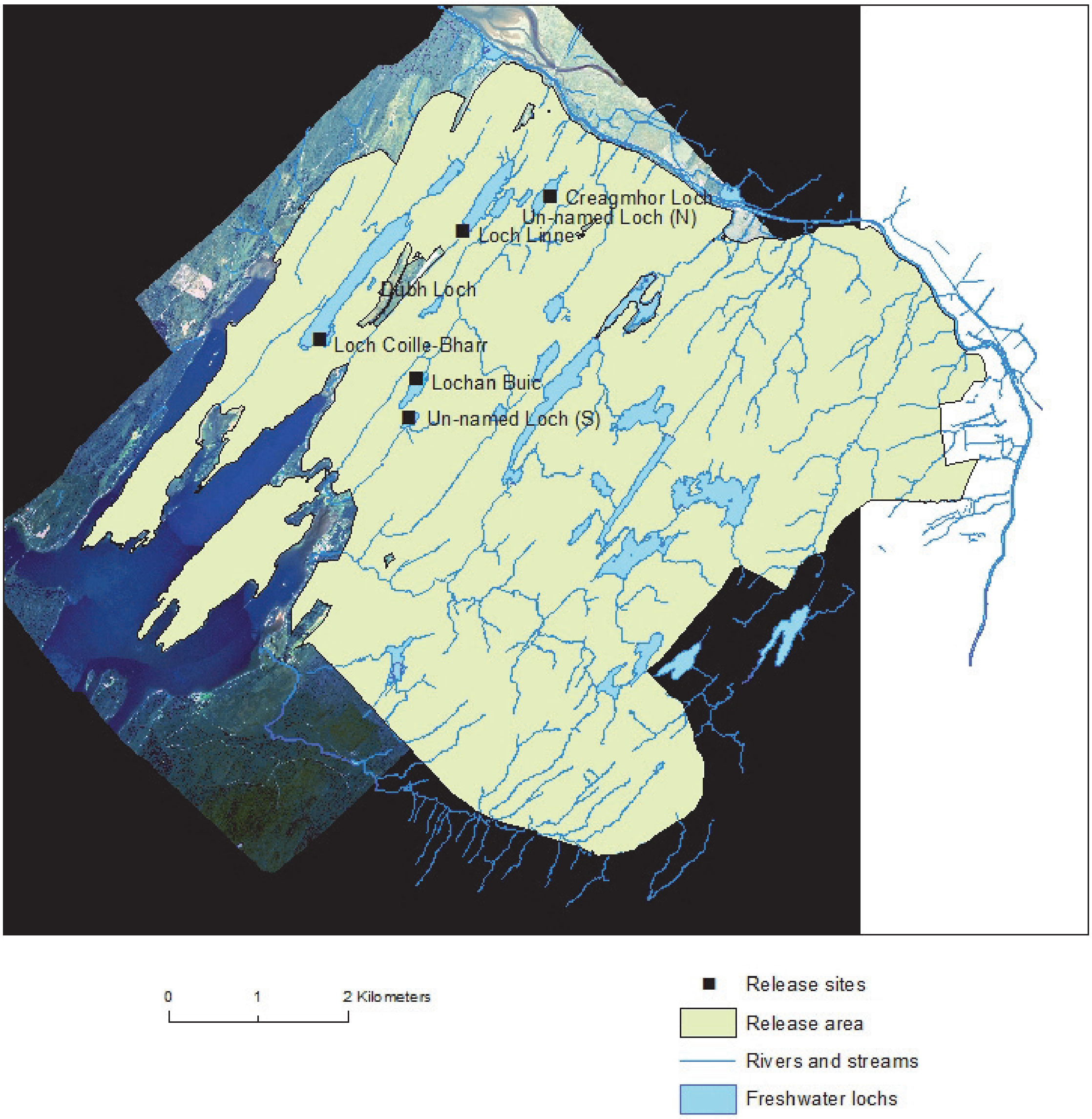

Figure 2. Scottish Beaver Trial release area in Knapdale Forest, mid-Argyll, showing release sites for each beaver pair/family. The underlaid aerial photograph shows the location of the Loch Sween (a sea loch - in dark blue). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

*Table 1. Fate of beavers released in Knapdale, Argyll (2009 – 2014). Released animals known to be alive and present at the release site at the end of the trial are highlighted in grey. The mother of the translocated yearlings and sub-adults is shown in superscript. Last confirmed sightings were camera trap records *, direct observations [†], or live trap records [t]. Final fate indicated is as of April/May 2014.*

Name	Sex	Age[a]	Release data	Release loch	Current loch	Last confirmed sighting	Fate
Andreas Bjorn	M	5+	31/05/2009	Creagmhor Loch		11/12/2009[t]	Withdrawn from programme Dec 2009; died in captivity May 2010
Gunn Rita	F	5	31/05/2009	Creagmhor Loch		05/06/2009[b]	Missing
Mary Lou [Gunn Rita]	F	1	31/05/2009	Creagmhor Loch		15/07/2009[b]	Missing
Frank	M	Unk	30/05/2009	Loch Linne	Loch Linne	19/05/2014*	Alive
Frid	F	Unk	30/05/2009	Loch Linne	Loch Linne	06/05/2014*	Alive
Biffa [Frid]	M	2	30/05/2009	Loch Linne		08/09/2010[†]	Missing
Biffa's brother [Frid]	M	2	30/05/2009	Loch Linne		-	Dead (shortly after release)
Bjornar	M	Unk	30/05/2009	Loch Coille-Bharr	Loch Coille-Bharr/Dubh Loch	10/05/2014*	Alive
Katrina	F	Unk	30/05/2009	Loch Coille-Bharr	Loch Coille-Bharr/Dubh Loch	24/04/2014[†]	Alive
Millie [Katrina]	F	2	30/05/2009	Loch Coille-Bharr	Loch Coille-Bharr/Dubh Loch	24/04/2014[†]	Alive
Marlene [Katrina]	F	2	30/05/2009	Loch Coille-Bharr		05/06/2009 (08/2009)[c]	Missing
Tallak	M	5+	04/05/2010	Un-named Loch (South)		11/05/2010	Dead (c. 2 weeks post-release)
Trude	F	2	04/05/2010	Un-named Loch (South)	Lochan Buic	28/05/2014[†]	Alive
Eoghann[d]	M	2	23/06/2010	Creagmhor Loch	Lochan Buic	28/05/2014[†]	Alive
Elaine[d]	F	2	23/06/2010	Creagmhor Loch	Un-named Loch (North)	03/02/2013*	Missing
Christian	M	3	21/09/2010	Lochan Buic[e]	Un-named Loch (North)	24/05/2014*	Alive

[a] Estimated age at time of release; post-mortem tooth sectioning revealed Andreas Bjorn to be > 7 years old, and Tallak to be 13-14 years old (Frode Bergan, Telemark University College, unpub. data).
[b] Roisin Campbell-Palmer pers. comm.
[c] Telemetry signals suggested that Marlene was on a nearby sea loch in August 2009, but this was not confirmed visually.
[d] This pair were released to as a replacement for the loss of the original Creagmhor family that did not settle in the release area.
[e] Christian was released to provide a mate for Trude following the death of Tallak; he was released into Lochan Buic where Trude had established a small burrow and was regularly observed feeding. Christian was released at the far end of the loch at an artificial lodge where his scent had been placed prior to release - the two beavers paired up on the night of Christian's release and remained together until the end of Year 2, but moved to Un-named Loch (North) at some point during 2011 (at about the same time Eoghann moved from Creagmhor Loch to Lochan Buic and subsequently paired with Trude – the precise timing of the swap and the details of the sequence of movements of the two males are not known).

*Table 2. Wild-born beavers in Knapdale, Argyll (2009 - 2014). Wild-born animals known to be alive and present at the release site at the end of the trial are highlighted in grey. Last confirmed sightings were camera trap records * or direct observations † († = trapped). Final fate indicated is as of April/May 2014; the missing 2 year old probably dispersed but missing kits are almost certainly dead.*

Name	Sex	Year of birth	Mother	Loch	Last confirmed sighting	Age at last confirmed sighting	Fate
Barney	M	2010	Frid	Loch Linne	17/05/2014*	almost 4	Alive?[3]
2	?	2010	Katrina	Dubh Loch	04/07/2012†	2	Missing
Logan	M	2011	Frid	Loch Linne	07/05/2014*	almost 3	Alive?[3]
4	M	2011	Katrina	Dubh Loch	28/08/2011†	0	Predated as a kit
5	F	2012	Frid	Loch Linne	22/08/2012	0	Predated as a kit
6	?	2012	Katrina or Millie[1]	Dubh Loch	24/07/2012†	0	Missing[4]
7	?	2012	Katrina or Millie[1]	Dubh Loch	16/08/2012†	0	Missing[4]
8	?	2012	Katrina or Millie[1]	Dubh Loch	16/08/2012†	0	Missing[4]
Woody	F	2012	Trude[2]	Lochan Buic	08/07/2013†	1	Missing
10		2013	Millie	Dubh Loch	18/07/2013†	0	Missing
11		2013	Millie	Dubh Loch	23/07/2013†	0	Missing
12		2013	Trude	Lochan Buic	13/08/2013†	0	Missing
13		2013	Trude	Lochan Buic	19/08/2013†	0	Missing
14		2013	Frid	Loch Linne	22/07/2013†	0	Missing

[1] Maternity unknown (kits were lost before being captured and thus genetic testing is not possible)
[2] Film footage suggested that this female was pregnant in 2011, but no kits were seen; Elaine (the female beaver at Un-named Loch (North)) was also thought to be pregnant in 2012, and there were signs that she was pregnant in 2011, but no kits were observed; Elaine is now dead or missing (see Table 1).
[3] At least one sub-adult is alive on Loch Linne – identity is unconfirmed, it may be Barney or Logan. (The last confirmed observation of Barney and Logan together was 04/04/2012 and the last sighting of one of these individuals was May 2014).
[4] Last record of all 3 kits together was on 24/07/2012; last record of 2 together 16/08/12.

3. DEMOGRAPHY AND POPULATION GROWTH

3.1 Aims

To address the success and failure criteria set out for the trial, it was necessary to monitor a number of population parameters and to assess initial population growth rates. These data can be compared with the early stages of other reintroduction projects elsewhere, with a view to assessing the relative success of the trial in Knapdale.

We also compared observed population growth during the trial with that predicted, prior to the trial, on the basis of population models (as published in Rushton *et al.* 2002). However, the number of beavers released was small (the trial population was not intended to form a self-sustaining reintroduction), and the trial itself was of limited duration, therefore, estimated population parameters were imprecise, and it was not possible to ascertain whether observed phenomenon (e.g. low reproductive success) were typical of beavers at Knapdale, or whether they were rare chance events. These issues are discussed further below.

The Scottish government will decide on the future of beaver reintroduction to Scotland, and on the future management of the Knapdale population. To help inform management, we also used a simple population viability analysis package to explore likely population growth at Knapdale 30 years into the future, and thus population stability under a number of different potential demographic scenarios.

3.2 Methods

Monthly observations and annual trapping

To verify presence of individuals at the release site for management purposes, SBT carried out monthly visual checks of all occupied lochs. These data were used to assess survival (post-release survival of translocated animals and survival of wild-born young), size and composition of family groups, and population growth.

All translocated animals were marked prior to release with both PIT tags (used to verify the identity of animals when trapped) and ear tags that could be read using binoculars. Observations were carried out on all lochs from a boat, canoe or from the land each month, combined with images from trail cameras. Spotlights were used for observations in the dark, where animals had been habituated. Identity and location was recorded for all animals observed (one record per animal per month); unidentified animals were also recorded, and sex and/or age class (adult or young) estimated if possible.

Additionally, monitoring protocols required all animals known to be present at the release site, to be trapped annually, to monitor the health of translocated individuals (reported on in Goodman 2014), to replace lost ear tags and mark wild-born individuals with ear tags. Note that successful monthly observations were dependent on effective marking of all individuals (both translocated and wild-born), and capture and marking wild-born animals was a high priority.

Where possible, animals were trapped using the Norwegian method of trapping from a boat as described in Campbell *et al.* (2010). This method was preferred because it allows targeted captures, and reduces individual recaptures and overall capture time, but was possible only on Loch Linne, Lochan Buic, Loch Coille-Bharr and Creagmhor Loch. On some of the smaller lochs (e.g. Dubh Loch and Un-named Loch (North)), where use of a boat was not feasible, Bavarian cage traps were used (see Campbell *et al.* 2010 for details). With animal welfare in mind, cage trapping at a specific location ceased if an individual was recaptured three times within a one-month period, and resumed (in an attempt to capture animals not yet trapped) after a period of not less than two weeks, but not more than two months. Late February to late spring, when females may be pregnant, was avoided for intensive cage trapping efforts. Otherwise, trapping was carried out by SBT when it fitted in with other monitoring activities. The number of traps used and the number of hours that traps were open, as well as trap locations of all captured animals, were recorded.

Summer lodge/den counts

To report the number of females that successfully bred, and estimate the number of young per female, SBT carried out direct observations of all active lodges or dens (see Rosell *et al.* 2006) where the presence of pregnant females was suspected, over the duration of the kit emergence period each year. Observations were carried out by one or two observers from 8 - 12 pm, fortnightly, between mid-July and the end of August (in Year 3) extended to the end of September (in Year 4)[1]. Trail cameras around the lodges were also used to detect kit presence in the later years of the trial. The number and age-class (adults, sub-adults, yearling, new kits) of all animals seen emerging from, and returning to, the lodge were counted.

The timing of the trial (with the official end of the trial monitoring in May 2014) meant that lodge/den counts were not carried out in 2014. Reproductive data were therefore only available for four years of the trial (2010 – 2013 inclusive).

Note on radio-telemetry and tracking dispersers

Ideally, the movements of all released individuals (and all wild-born animals approaching dispersal age) would have been tracked to allow an estimate of the proportion of animals dispersing from their family groups within, or from, the release site, as well as how far they disperse. However, although the original monitoring protocols (see Campbell *et al.* 2010) had included the use of VHF telemetry, difficulties associated with radio-tracking in the Knapdale environment coupled with concerns regarding the time and personnel required, meant that animals were not radio-tracked after the first year of the trial[2]. ARGOS tags deployed on a small number of animals by SBT for management purposes (they were not deployed for ecological monitoring) were not sufficiently accurate to be of any use in locating dispersers, and limited resources did not allow for the use of GPS tags over the duration of the trial. It was not possible, therefore, to determine whether ‘missing’ animals (those not seen during monthly observations) had dispersed or died[3].

Analyses

Kaplan-Meier survival analyses were run in R (version 3.0.2, R Core Team 2013), using the package “OIsurv” (Diez 2012). Population viability analyses were carried out using VORTEX (a generic population viability analysis software package; Lacy and Pollak 2014). Demographic parameters that were not available from the trial were taken from South *et al.* (2000) and Nolet and Baveco (1996); additional comparative data from the source population in Norway was obtained from Campbell (2010).

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[1] One kit was first seen emerging from the den in mid-September in 2011 (preliminary Year 3 data), which was later than originally expected and therefore, the period for den counts was extended from mid-July - end of August (see Harrington *et al.* 2011) to mid-July - end September.

[2] Although it should be noted that even when animals are equipped with VHF transmitters, it is extremely labour intensive and often not possible to follow dispersing animals.

[3] Although there was some information on the presence of beavers outside the release site from field sign searches (see section 4.10), these observations were limited and animals were not caught or identified (because they had moved on by the time field signs were observed/reported).

3.3 Overview of monitoring results

Over the duration of the trial, 3,462 animal observations (including direct observations and camera trap captures) were made but this figure is inflated by the inclusion of repeat observations of focal animals that were attempted in Year 1 (focal observations were discontinued as a monitoring method due to the disturbance they caused to animals, and excessive time requirements for field teams). In comparison, only 366 observations were made in Year 5 (suggesting the need for closer to 2,000 observations over the duration of the trial) when only monthly checks of all animals were made. In total, over the 5 year trial, 1,309 (approximately 38%) of all observations were unidentified, but this was only 12% in Year 5.

372 separate trap events[4], covering a total of 3,968 trap hours, were recorded – this effort resulted in 80 captures. Most translocated animals that settled and remained at the site (see Table 1) were captured most years (with the exception of Bjornar only captured in 2011 and Eoghann only captured in 2010 and 2011); of the 14 wild-born kits recorded during the trial, only 3 were captured and marked.

3.4 Survival of translocated animals

A crude estimate of minimum survival of released animals to the current time is given by the number known to be currently alive, still being monitored and present within the original release area (eight) (Fig. 3), divided by the total number of animals released (16). On this basis, minimum survival to the end of the trial is 0.50. This includes only known survivors (for this analysis, missing animals are considered dead), and treats all released individuals equally, although, in reality, staggered releases over the first two years of the trial (Table 1, Fig. 3) mean that some individuals have survived five years post-release whereas others have only, thus far, survived four years post-release.

[4] For each trap event the number of traps, locations targeted and duration of trapping varied according to current conditions, and specific targets (the aim was to trap all individuals once each year, therefore which individuals were targeted was dependent on success of the previous trap event).

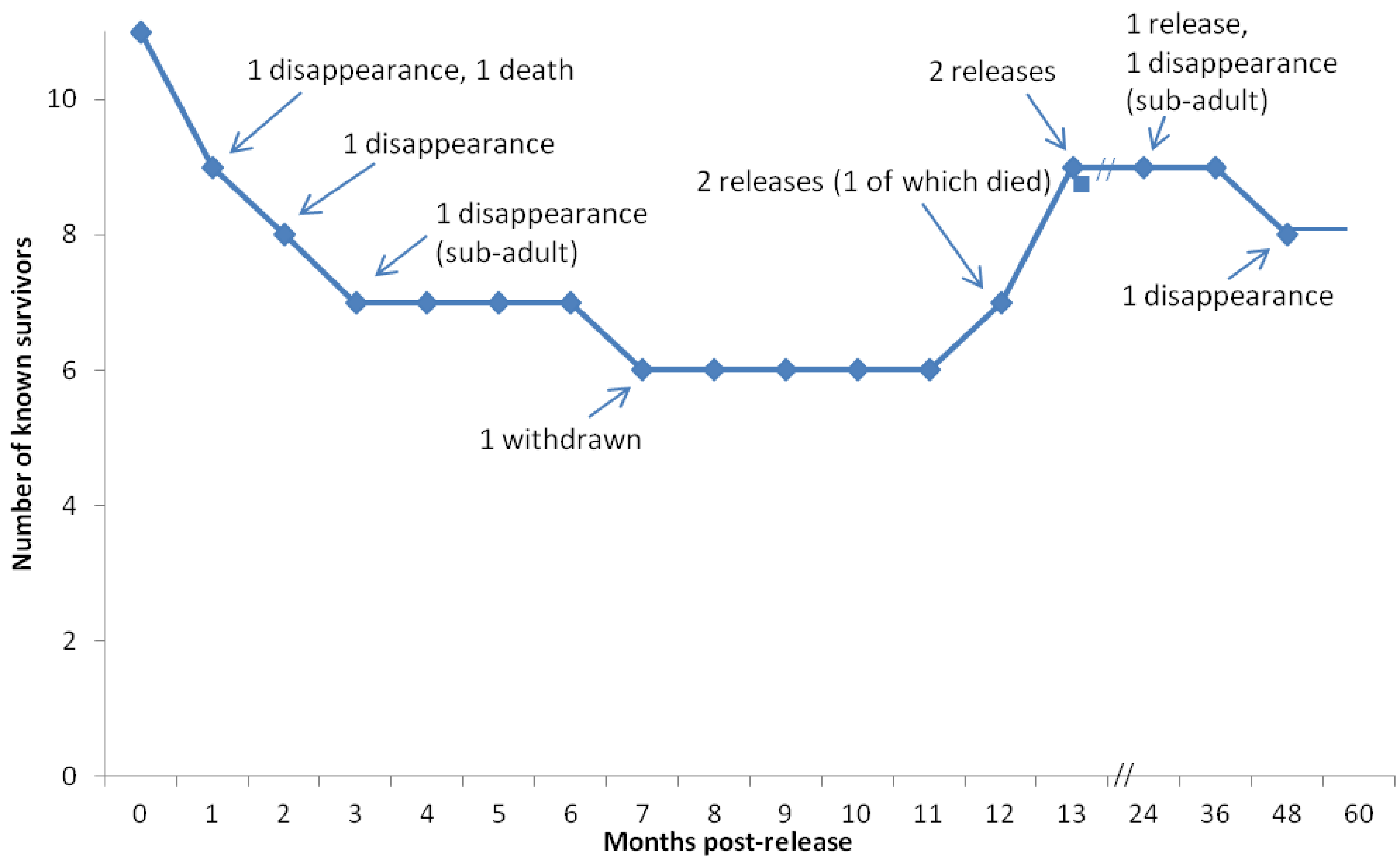


Figure 3. Number of beavers known to be surviving at Knapdale over time since their initial release. Missing animals, in this case, are not counted and are presumed dead. (Note the scale change after 13 months).

Kaplan-Meier estimates of the probability of survival (*S*) take account of the different release times of individuals and the loss of animals to monitoring (i.e. those that are lost and for which fate is unknown). *S* at the end of the five-year trial is estimated as 0.68 (95% confidence intervals 0.44, 1, Table 3), with a mean survival across all individuals of 42.9 months (± SE 8.3; NB. this is a restricted mean, with an upper limit of 60 months). However, the small size of the population being monitored means that the variance estimate may underestimate the actual variance, and the high censoring rate (loss of animals to monitoring) means that *S* may be biased if censored (missing) animals are more or less likely to die than are the others still being monitored (i.e. if all missing animals are actually dead, survival estimates will be too high). To illustrate the effect of the unknown fate of missing animals in this population, we estimated *S* for two extreme hypothetical scenarios: one where all missing animals were assumed to be dead, and a second where all missing animals were assumed to be alive (as recommended by Winterstein *et al.* 2001, Fig 4). Within these two extremes, *S* at the end of the trial was estimated to vary between 0.38 and 0.74 (combined 95% confidence interval 0.19, 1), with mean survival times of between 27.7 and 46.1 months (restricted mean, with an upper limit of 60 months).

Table 3. Kaplan-Meier estimates[1] of the probability of survival of translocated beavers at time t, where t = time in months since release.

T	*S*	SE	lower 95% CI	upper 95% CI
1	0.91	0.09	0.75	1
6	0.78	0.14	0.55	1
12	0.68	0.15	0.44	1
24	0.68	0.15	0.44	1
36	0.68	0.15	0.44	1
48	0.68	0.15	0.44	1
60	0.68	0.15	0.44	1

[1] Note that if all, or a high proportion of, the missing animals are dead, these estimates will overestimate the probability of survival.

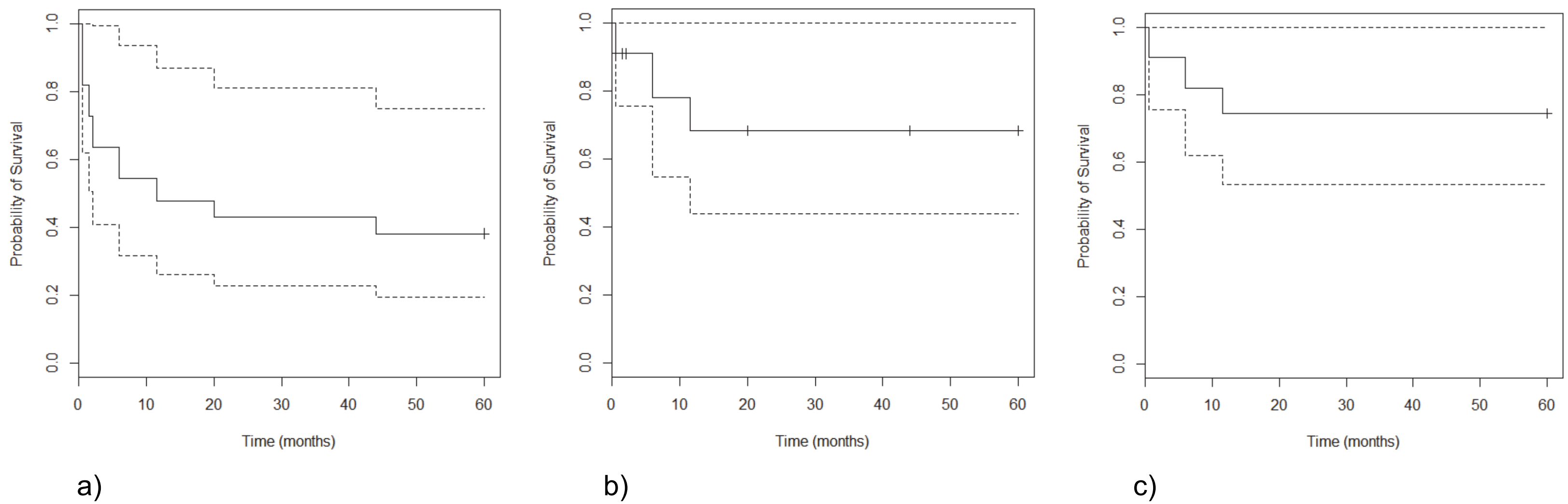


Figure 4. Kaplan-Meier estimates of the probability of survival of translocated beavers against time (in months) since release (shown with 95% confidence intervals). b) shows estimates based on actual beaver histories as in Table 1, and takes account of the loss of animals during the trial, compared with a) which shows a 'lower bound' that assumes all missing animals are dead, and c) which shows an 'upper bound' that assumes all missing animals are still alive.

Regardless of the imprecision of survival estimates, there is a clear pattern to survival over time that is common in translocation projects, insofar as most losses occurred within the first few months after release and survival tended to stabilise over time.

3.5 Reproduction

No reproduction was expected in Year 1 (summer 2009) because no females were released (in May 2009) that were pregnant. During Year 1, females of the Linne and Dubh Loch families may have become pregnant following mating in the winter of 2009/10, and thus could have produced kits at the beginning of Year 2 (summer 2010) but the Buic pair and the Creagmhor pair had only just been released and so could not have reproduced. Thereafter, (from the winter of Year 2, with kits potentially produced at the beginning of Year 3 - summer 2011), four mature breeding pairs were present (but only two produced kits in 2011). In Year 3 and Year 4, three of four beaver pairs successfully reproduced; litter size (produced in Year 4 and Year 5) ranged between one and three kits. Throughout the trial, thus far, annual reproductive rate has ranged between 0.5 and 1.25 (i.e. the mean litter size for all pairs of beavers present in a year - defined as the proportion of pairs that successfully reproduce x the mean litter size, Table 4). Success of reproduction in Year 5 was not assessed because the trial ended before any young would have been born; at this time three mature breeding pairs were present.

Table 4. Beaver reproduction in Knapdale (2009-2014). Data are number of pairs that could reproduce (N), proportion of pairs successful (p.pairs), mean litter size of successful pairs (ml), reproductive rate (Rr); where reproductive rate is defined as p.pairs x ml, and litter size is the number of emerging kits (as in Nolet et al. 2005).

Year	N	p.pairs	ml	Rr
2009	0	-	-	-
2010	2	1.0	1	1.0
2011	4	0.5	1	0.5
2012	4	0.75	1.67	1.25
2013	4	0.75	1.67	1.25

3.6 Survival of young wild-born animals

Of the total fourteen kits born at Knapdale between summer 2010 and summer 2013, only four (0.29) are known to have survived to 1 year of age (Table 5). Of the four wild-born individuals that survived to become yearlings, two or three (0.5 – 0.75) survived to become sub-adults (2 years old), although only one now appears to remain at the release site (at Loch Linne, aged either 3 or 4 years) (Table 5).

*Table 5. Known survival of wild-born beavers in Knapdale (2010-2013). Y = yes, survived, N = not survived (dead or missing – confirmed deaths are marked with a *), ? = uncertain status (see footnote).*

Name	Year of birth	Loch	Survival to 1 year	Survival to 2 years	Survival to 3 years	Survival to 4 years
Barney	2010	Loch Linne	Y	Y	?[1]	?[1]
2	2010	Dubh Loch	Y	Y	N	
Logan	2011	Loch Linne	Y	?[1]	?[1]	
4	2011	Dubh Loch	N*	-	-	
5	2012	Loch Linne	N*	-		
6	2012	Dubh Loch	N	-		
7	2012	Dubh Loch	N	-		
8	2012	Dubh Loch	N	-		
Woody	2012	Lochan Buic	Y	N		
10	2013	Dubh Loch	N			
11	2013	Dubh Loch	N			
12	2013	Lochan Buic	N			
13	2013	Lochan Buic	N			
14	2013	Loch Linne	N			

[1] One or both of these two individuals is still alive and present at Loch Linne, it is not currently clear whether one or two wild-born animals are present, or, if only one, which one.

3.7 Mortality

Of the total 16 animals released, three deaths were recorded (all during the first year of the trial, and all male), equating to a post-release mortality rate of 0.19 (or approximately 20%). Andreas Bjorn was found in poor body condition and withdrawn from the programme in December 2009 (seven months post-release) and died five months later in captivity of bacterial myocarditis (inflammation of the heart, Goodman 2014). Tallak died several weeks post-release and post mortem results suggest that he did not feed, most likely due to an individual failure to adapt to his new environment (Goodman 2014). Andreas Bjorn and Tallak were both older males (at least 7, and at least 13, years old, respectively, Frode Bergan, Telemark University College, unpub. data[5]). The only younger (two year old) male to die post-release, died 24 hours after release; this animal was found to have lung, liver and kidney congestion suggestive of sub-acute circulatory failure[6] (Goodman 2014). Beaver health was being monitored by the Royal (Dick) School of Veterinary Studies, University of Edinburgh; further details are available in Goodman (2014).

Of the 14 kits born at Knapdale (up to and including summer 2013), two were known to have been predated (one in summer 2011 and one in summer 2012). This equates to a total kit mortality rate (including only confirmed deaths, over all four years monitored) of 0.14; and yearly kit mortality rates of between 0 (in 2010) and 0.5 (in 2011). It is not clear, however, whether the one predation event observed per year in 2011 and 2012 is likely to increase proportionally with an increase in the number of kits produced, or whether they were both rare chance events. All three of the kits from Dubh Loch in 2012 and all five kits from Dubh Loch, Lochan Buic and Loch Linne in 2013, are now missing. It is unknown whether these animals have died (although it is probable that young missing kits are dead), and, if so, what the cause of death might have been.

[5] Animal age was confirmed by cementum analysis of teeth taken from the carcasses; from a welfare point of view it would be ideal to know the age of the animals before the decision was made to trap them from the wild for translocation, but this was not possible in this case.
[6] There was no evidence of infection or degenerative disease (Goodman 2014).

3.8 Comparisons with beaver reintroductions elsewhere in Europe

Although there have been a number of beaver reintroductions throughout Europe (reviewed in Halley and Rosell 2002; Dewas *et al.* 2012), few documents provide detailed data on survival, population demography or population growth during the first few years of the release. For three reintroduction projects (see Table 6), survival of translocated individuals at one year post-release varied between 64 and 86% - this fits relatively well with our estimates of the probability of survival at one year post-release (0.68) for Knapdale, especially considering that the higher values reported in the literature account only for known deaths and do not include 'lost' animals. Known mortalities at Knapdale within the first year of release (although not all occurred in the same calendar year) totalled 19% of all animals released, which is similar to the 14% reported from the Vistula Basin, Poland, and 20% from Peene valley, Germany, respectively (see Table 6), and much lower than the 33% first-year mortality reported for Biesbosch, Netherlands (Nolet and Baveco 1996). Bajomi (2011) reported an extremely low mortality rate of 2%, but this only included deaths directly connected with the reintroduction process (e.g. deaths during transport, or due to stress-related causes post-release).

The best documented reintroduction of beavers is the Biesbosch population reintroduced to the Netherlands between 1988 and 1991 (Nolet and Baveco 1996; Nolet *et al.* 2005). The beaver population in the Biesbosch experienced low reproductive rates in the initial years of establishment (thought to be due to low quality food associated with climatic changes, and/or perhaps at least partly a temporary response to translocation). Although litter size in Biesbosch was not statistically different to that in an established population in Germany (Elbe region), the proportion of females breeding was half (or less than half) of that in the Elbe region (Nolet and Baveco 1996), and in a reintroduced population in Poland (see Table 6). Whilst reproductive success also appears to be low in Knapdale, the situation differs from that in Biesbosch in that the proportion of females breeding at Knapdale appears to be high (although sample size is small), but litter size seems to be low compared with both the Biesbosch (reintroduced) population (2.4) and the Elbe (established) population (1.98, Nolet and Baveco 1996). Interestingly, litter size also appears to be relatively low in the source population in Norway, with mean values of 1.4 – 2.0 (depending on age of the female, with particularly low values recorded for younger females) and litters of more than 3 kits rarely observed (Campbell 2010). We were not able to find any information on survival of wild-born kits in other reintroduction projects but post-emergence survival of young animals in the source population is reported to be very high: 89% of 140 offspring observed survived to 3 years of age (Campbell 2010).

Summarising beaver reintroduction projects across Europe, Macdonald *et al.* (1995) reports that reintroduced populations generally increase at a rate of 20 – 34% annually once they have started to breed, which is much higher than the rate at which established populations grow, reportedly between 0 and 15% annually. Thus far there has been negligible population increase at Knapdale.

Table 6. Survival, reproduction and annual population increase at Knapdale compared with other beaver reintroductions in Europe and the source population in Norway.

Population	Parameter			
	Survival of translocated animals, one year post-release[1]	**Proportion pairs breeding**	**Litter size**	**Annual population increase**
Biesbosch, Netherlands (1988-1991)[a]	64.3%	31%	1-5 (mean=2.4, n=12)	
Peene valley, Germany (1970s)[b]	80%		-	34%
Vistula Basin, Poland (1970s/80s)[b]	86% 60% in mountains	60%	-	20%
Knapdale (this study)	68%	50-75%[2]	1-3 (mean=1.4, n=10)	-9 - +22%[3]
Source population, Norway	-	-	1-4 (mean=1.4-2.0, n=Unknown)	-

Source: [a]Nolet and Baveco 1996, [b]Macdonald *et al.* 1995

[1] Where reintroductions occur within a specified release site, estimates of post-release survival are usually defined by 'known survivors' and are thus affected by both known deaths and missing animals (i.e. they are estimates of minimum survival). For Knapdale we provide an estimate of survival that accounts for missing animals as well as known deaths. For Biesbosch, one loss was also reported, although the majority of losses were known deaths. For Peene valley and Vistula Basin, survival is based only on losses due to recorded deaths (and thus both may be over-estimated).

[2] For years when there were 4 mature pairs present

[3] From 2011 to 2014, see Figure 6

3.9 Population growth at Knapdale

Over the duration of the trial, the number of beaver 'families' present at Knapdale remained constant at four, and although the size of three of the four families appeared, in earlier years, to be increasing due to wild births, there was little or no overall net increase in family size (due to loss of kits in later years, and disappearances of wild-born sub-adults, Table 2, 5, 7). A total of 14 kits were produced but only one (possibly two, see Table 5) was confirmed to remain in the population by the end of the trial. The Creagmhor 'family' now appears to comprise only a single male. Overall population growth has therefore been negligible over the five years of the trial (Fig 5, 6).

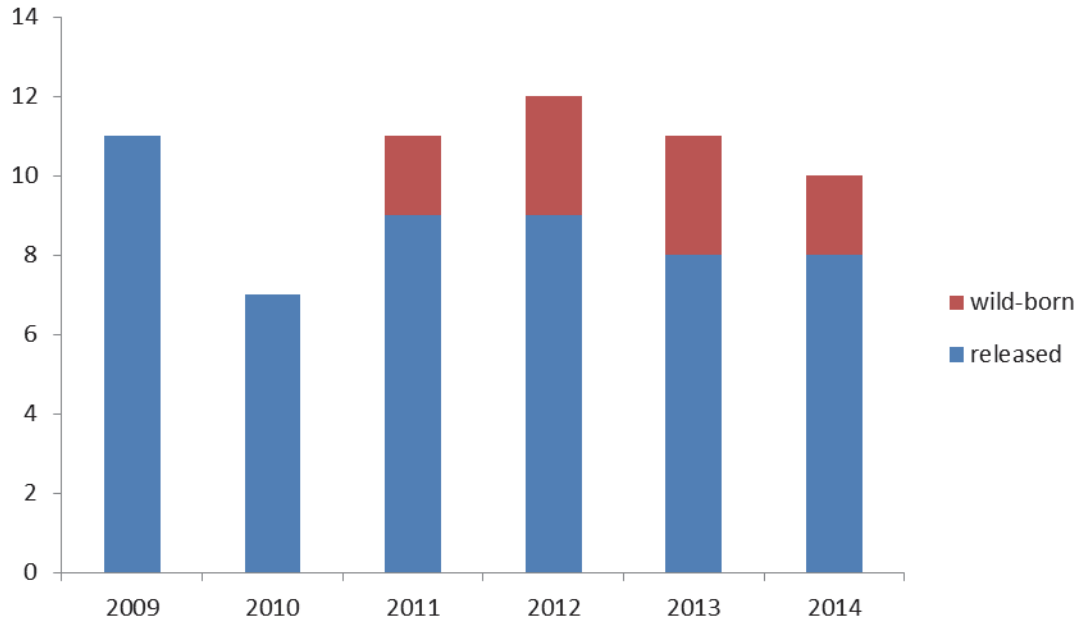


Figure 5.Total number of beavers present in Knapdale on 1st June of each year. (Note that this assumes two wild-born animals were alive on Loch Linne in 2013 and 2014).

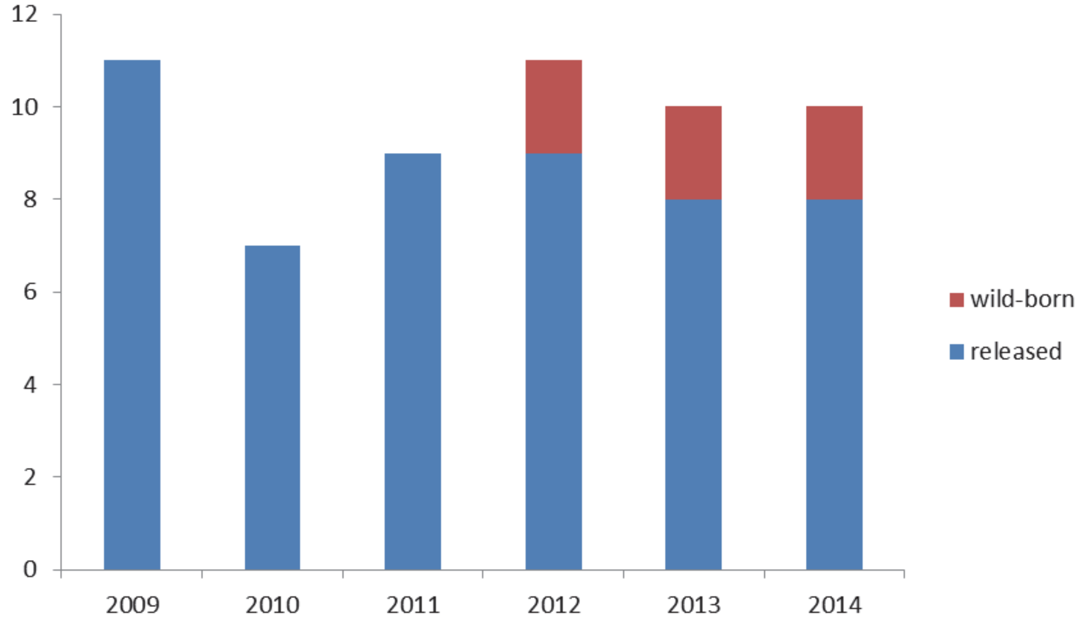


Figure 6. Total number of sub-adult and adult beavers (including all beavers two years of age or older, i.e. breeders and non-breeders in family groups) present in Knapdale on 1st June of each year. (Note that this assumes two wild-born animals were alive on Loch Linne in 2013 and 2014).

A total of three or four sub-adults (two released, one or two wild-born) may have dispersed, but the low numbers and the fact that they (presumably) left the occupied area in different years mean that the chances of individual beavers (of opposite sex) meeting and forming new families is low. The geography of the site (with beavers spread among three separate catchments, see Fig. 10) will also have an impact on the chances of dispersing animals meeting (in this case, only two of the lochs – Creagmhor Loch and Lochan Buic – are connected by waterways). The two most recent presumed/possible dispersals were the wild-born two year old of unknown sex from the Dubh Loch (last seen in July 2012) and (possibly) one of the wild-born male sub-adults from Loch Linne (either Barney or Logan, last seen together in May 2012, i.e. one of these individuals might have dispersed at any time since then, although Logan, at that time, would only have been 1 year old, see Table 2).

Population structure

Beavers were released in five 'family' groups (of between two and four individuals); three families (released in 2009) included one to two sub-adults each, the other two 'families' (released in 2010) were released as breeding pairs (the following discussion excludes the first Creagmhor family, released in 2009, that did not settle and establish a home range at the site, see Table 1, and Harrington *et al.* 2011, 2012). Of the two families with sub-adults that settled at the release site, one sub-adult in each family – Marlene from the Dubh Loch family, and Biffa from the Linne family - had dispersed by the end of the second year post-release[7] (one of the sub-adults – Biffa's brother from the Linne family - also died shortly after release); only the Dubh Loch family still includes one of the released sub-adults – Millie[8] - at the end of the fourth year post-release (Table 7).

By the end of the trial (June 2014), and not including kits that might have been born in the summer of 2014, maximum family size was three. The Linne family included at least one of their wild-born sub-adults (age 3 or 4 years), but no 2-year old subadults, and no yearlings (the kit born in summer 2012 was predated as a kit, and the kit born in 2013 is missing, see Table 2)[9]. Since the disappearance of the wild-born sub-adult on Dubh Loch (during summer 2012), the Dubh Loch family consisted only of the three adults (all three kits from summer 2012, and both kits from 2013, are now missing, fate unknown, Tables 2 and 7). Trude from the Buic family was suspected pregnant in summer 2011 (note that the male partners of the Buic and Creagmhor pairs exchanged places sometime between April and October 2011), but neither successfully produced kits that year. Trude produced one kit in summer 2012, that went missing as a yearling, and two kits in 2013 that went missing as kits. There were signs that Elaine from the Creagmhor pair was suspected to be pregnant in both 2011 and 2012, but no kits were ever observed and this female has now disappeared or died (see Tables 1 and 2), leaving only the adult male (Christian) at Creagmhor Loch. Only one 'family' currently includes wild-born animals, and, whilst the dispersal of sub-adults is completely natural and to be expected at from about 2 years of age, there is no evidence that sub-adults dispersed and formed new, additional families (see above). The loss of the female from the Creagmhor family means that, at the end of the trial, there were effectively only three breeding pairs.

[7] Marlene disappeared the same summer of her release (see Table 1).
[8] Millie is now (at the end of Year 3) considered an adult; she gave birth to either some or all of the kits at Dubh Loch in the summer of 2012 (it is not known whether Katrina, the older female, also gave birth that year, Table 2, 3).
[9] It is currently unclear whether there are one or two sub-adults present, and, if only one, which individual it is (the sub-adult Barney, or Logan the yearling from 2012, see Table 2).

Table 7. Changes in beaver family composition (post-kit emergence) at Knapdale (2009 – 2014), as of summer each year. Non-breeding beavers that are 2 years of age or older are considered sub-adults; breeding animals are considered adults. (This summary excludes the original Creagmhor family that failed to settle).

Family	**2009**[1]	**2010**	**2011**	**2012**	**2013**	**2014**
Linne	Adult male Adult female 2 sub-adults	Adult male Adult female 1 sub-adult 1 kit	Adult male Adult female 1 yearling 1 kit	Adult male Adult female 1 sub-adult 1 yearling 1 kit (predated)	Adult male Adult female 1 or 2 sub-adults 1 kit	Adult male Adult female 1 or 2 sub-adults [this year kits unknown]
Dubh Loch	Adult male Adult female 2 sub-adults	Adult male Adult female 1 sub-adult 1 kit	Adult male Adult female 1 sub-adult 1 yearling 1 kit (predated)	Adult male 2 Adult females[2] 1 sub-adult[3] 3 kits	Adult male 2 Adult females[2] 2 kits	Adult male 2 Adult females[2] [this year kits unknown]
Buic	-	Adult male Adult female	Adult male Adult female[4]	Adult male[5] Adult female 1 kit	Adult male Adult female 1 yearling 2 kits	Adult male Adult female [this year kits unknown]
Creagmhor	-	Adult male Adult female	Adult male Adult female[4]	Adult male[5] Adult female[4]	Adult male	Adult male

[1] as released.
[2] Millie (released as a sub-adult,is now a breeding female in the group; it is not clear whether Katrina is still breeding).
[3] This wild-born sub-adult (unconfirmed sex) went missing in the summer 2012.
[4] Suspected pregnant but no kits produced.
[5] Male partners exchanged places between the Buic and Creagmhor pairs in early summer - autumn 2011.

3.10 Did the trial population reach predicted population size during the trial?

Prior to the trial, Rushton *et al.* (2002) used VORTEX[10] to assess likely population growth at Knapdale over the five years of the trial. Using three sets of population parameter estimates (high, medium and low, see Table 8) and 200 simulations per scenario, Vortex predicted that, in all cases, the population would persist with population sizes of 48, 26 and 14, respectively. In reality, although the population at Knapdale did persist for the duration of the trial, the evidence available suggests that it did not reach the predicted population size. Even the low parameter scenario (equivalent to the lowest levels recorded in published studies, Rushton *et al.* 2002) exceeds the population of nine or ten animals known to be present at the end of the trial (although the 6 or 7 missing animals mean that the Knapdale population over a larger area could number a maximum of 16). Thus, although persistence is to some extent a measure of success, limited population growth suggests only partial success.

There were a number of differences between the modelled population and the actual trial population. Rushton *et al.* (2002) used a starting population of 12 individuals (6 males, 6 females, three of each aged 2 and 7) and set the proportion of females breeding at 0.5 to account for the fact that some adult females remain in their natal group and do not breed until they are 3 years or older. In reality, the number of animals released (considering only those that settled and stayed at the release area for at least the first year – i.e. excluding the original Creagmhor family, the two males that died shortly after release and Marlene who disappeared less than one month post-release, see Table 1) was only 10 (5 males and 5 females in total), and the population has only been reproducing for 4 years (and for some pairs only 3 years). The VORTEX model was therefore rerun for the purposes of the current study using the medium and low parameter scenarios used by Rushton *et al.* (2002) with an initial population size of 5 males and 5 females (and assuming animals of unknown age were 5 years old) – this model run predicted a population size of 18.9 (± SD 3.5) or 11.8 (± SD 2.5), respectively, at four years post-release (Fig. 7). The low parameter scenario predicted a population size of about 10 adults (which almost matches reality) but also predicted the presence of 1 or 2 yearlings in the population (which is not currently the case) – this suggests that even the low parameter scenario used by Rushton *et al.* (2002) overestimates reproductive success, due to either lower than expected litter size, or lower than expected survival of young, occurring in reality.

Table 8 shows the parameters used in the Rushton *et al.* models compared with demographic parameters actually observed at Knapdale. This shows quite clearly the differences between estimated and observed litter size and juvenile mortality, both of which have obvious effects on population growth and thus presumably account for the mismatch between observed and predicted short-term population growth. In a more complex spatial model, Rushton *et al.* (2002) found that litter size was a significant predictor of population size after 5 years, but juvenile mortality was not (neither was adult mortality). However, in his simulations, Rushton *et al.* used input values of between 0.29 and 0.55 for juvenile mortality, whereas, in reality, annual juvenile mortality at Knapdale during the trial was much more variable, and ranged between 0 and 100%.

[10] VORTEX is an individual-based simulation of life events in wildlife populations. VORTEX models population dynamics, over an annual cycle, as discrete, sequential events that occur according to user-specified probabilities. The simulation of the population is iterated many times to generate the distribution of fates that the population might experience. http://vortex10.org/Vortex10.aspx

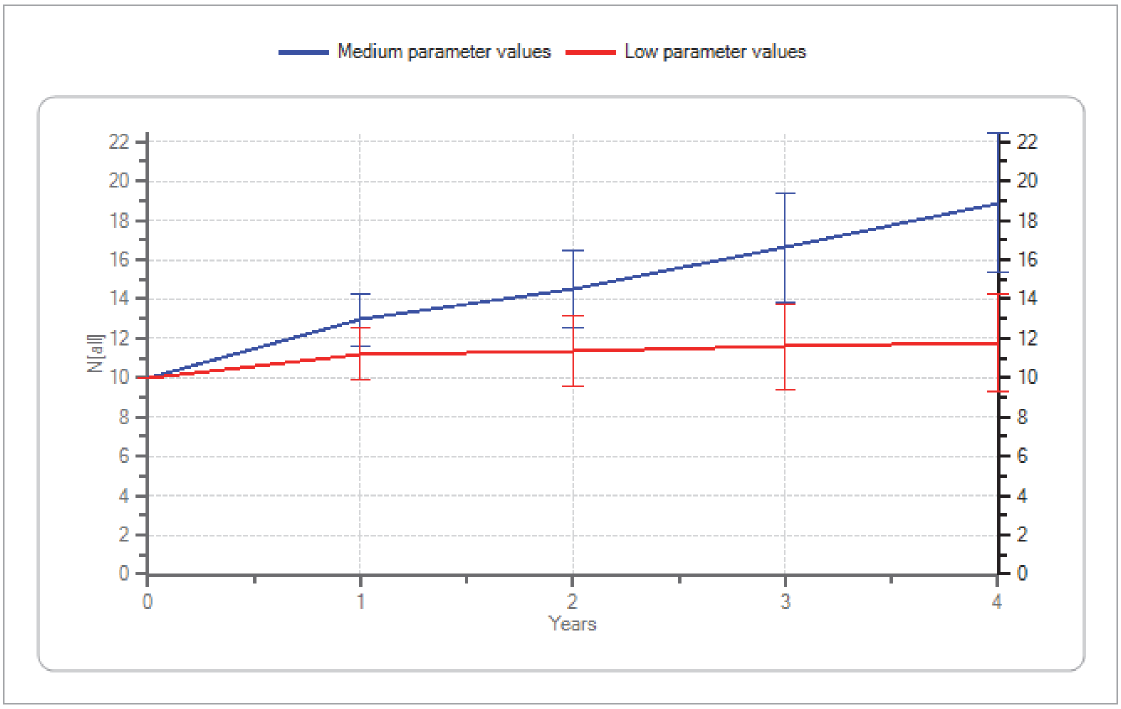


Figure 7. Mean (± SD) predicted population sizes from 1000 replicate VORTEX simulations starting with 5 males (2 x 2 year olds, 1 x 3 year old, and 2 x 5 year olds) and 5 females (3 x 2 year olds, 2 x 5 year olds), using parameter values as in Rushton et al. (2002), and run for 4 years (to enable comparison with the four years of reproduction monitored at Knapdale). Note that even the low parameter scenario slightly overestimates the total known population size at Knapdale at the end of the trial.

Table 8. Demographic parameter estimates used by Rushton et al. (2002) to model population growth at Knapdale prior to the trial, compared with demographic parameters actually observed at Knapdale.

Parameter	High	Medium	Low	**Observed, at Knapdale**
Litter size frequency distribution				
n=1 kit	17%	20%	23%	**70%**
n=2 kits	50%	55%	59%	**20%**
n=3 kits	17%	16%	15%	**10%**
n=4 kits	8%	5%	3%	**0%**
n=5 kits	8%	4%	0%	**0%**
Female breeding probability	0.7	0.5	0.31	**0.5-0.75**
Annual mortality probabilities				
Sub-adult and adult[1]	0.063	0.070	0.077	**-**[2]
Yearling	0.190	0.350	0.500	**0.5 – 0.75**[3]
Juvenile	0.290	0.325	0.360	**0-1.0**

[1] Mortality probabilities as used by Rushton *et al.* were the same for sub-adults and adults so there was no need to define the age at which a beaver became an adult for the purposes of the model; adults were defined, in the model, simply by the age at which they first bred.
[2] Note that because the aim of the model was to assess population growth of the animals that survived the initial translocation process and settled at the release site, we did not include early post-release mortalities in these estimates of mortality probabilities (translocation survival can be included in the model as a separate parameter). There was therefore no estimate of sub-adult or adult mortality available.
[3] This is not an annual estimate of yearling mortality but loss of yearlings over the duration of the trial (see Table 5).

3.11 Population persistence into the future at Knapdale

The small sample size and short monitoring period of the trial mean that it is difficult to infer likely future prospects for the beaver population at Knapdale. As was suggested for the reintroduced population at Biesbosch, low reproductive success may be a temporary response to translocation, or it may be a feature of the particular individuals released (due to, for example, their age). Alternatively, low reproductive success may be a (temporary or permanent) feature of the site (for example, either weather- or habitat-related). These alternative suggestions have quite different, and obvious, implications for the future viability of beavers at Knapdale. However, it is not possible to distinguish between these hypotheses without further monitoring of the individuals currently present, as well as the release and monitoring of further individuals.

To assess the relative likelihood of population persistence at Knapdale under different life history scenarios, we used VORTEX (as above) to simulate likely population growth over the longer term (30 years). Because the trial was not intended to produce a self-sustaining population we assume that supplementation would occur and that this would probably involve the release of up to 20 more animals (i.e 10 pairs). There are essentially two possibilities: 1) that the low reproductive success observed thus far <u>does not</u> improve in future years with the release of more animals (i.e is site-related), 2) that the low reproductive success observed thus far <u>does</u> improve in future years with the release of more animals (i.e. is individual- or year-related). Within these two alternative possibilities, we outlined four life history scenarios, as follows:

- Reproductive success remains unchanged
- Average litter size increases
- Kit mortality decreases
- Litter size increases and kit mortality decreases

As in Rushton *et al.* (2002) we modelled beavers in VORTEX as a single, freely interbreeding population. The main assumption of this approach is that any unpaired adult will be able to breed with any other unpaired adult of the opposite sex, which is currently unrealistic at Knapdale (given the low densities present), and so simulations may produce overly optimistic predictions (because the model may over-estimate the ability of unpaired individuals, in reality, to find each other and breed). Another disadvantage of VORTEX is that it is unable to represent beaver family structure explicitly – however, other parameter values (female breeding probability or age at which female first breeds) can be adjusted to account for the fact that a proportion of adult females remain within their natal group and do not breed until they are 3 years of age, or older. Environmental variation was incorporated as the standard deviation in the proportion of females breeding and the standard deviation in age-specific mortality rates.

Model verification

To verify that the model could recreate actual population growth at Knapdale, we initially ran the model for 4 years using model parameters estimated from the population at Knapdale (Table 9) to see how well the predicted population growth matched what had actually happened at Knapdale during the trial. For this four year model, we set kit mortality at 71.4% (± 0%) to reflect the actual loss (assumed mortality) of 10 of 14 kits born over the duration of the trial, and a starting population of total 10 individuals with ages as above (to reflect the released individuals that remained at the release site for at least the first year of the trial): 5 males (2 x 2 year olds, 1 x 3 year old, and 2 x 5 year olds) and 5 females (3 x 2 year olds, with the age of Frid kept at 5 years old to allow her to continue to reproduce in the model, and the age of Katrina adjusted to 8 years so that she would only reproduce for two years in the model). This model predicted a population size of 9.9 ± 2.0, comprising about 8 adults and 1 or more young, which matches reality well (except that in the actual population at Knapdale there are no individuals less than 2 years of age). The 'mismatch' in predicted and actual population size appears to arise because we used a value of 71.4% mortality for kits every year (above), whereas in reality kit mortality in the last year was 100%.

Table 9. Parameter values used in VORTEX simulation models. Parameters were taken from the trial population at Knapdale where possible, but we also used information from the population in Norway (the source of the Knapdale beavers) where it was useful, otherwise parameter values were used as in Rushton et al. (2002), the source of all parameter estimates (and brief justification) are given in the table.

Parameter		**Notes**
Minimum breeding age – females	4 years	Rushton *et al.* (2002) set female first breeding age at 2 years on the assumption that beavers can physically breed from this age. However, none of the females at Knapdale appeared to breed before 4 years of age. It is possible that this was an effect of the translocation rather than age per se. Nevertheless, breeding success in Norway is low for females of 2 – 3 years. Rushton *et al.* adjusted the proportion of females breeding to take account of the fact that some sexually mature females remain in their natal group and do not breed until they are older – increasing the age of breeding has a similar effect.
Minimum breeding age – males	2 years	As in Rushton *et al.*
Maximum breeding age – females	10 years	Rushton *et al.* used 15 years but given that females in Norway produce few kits over the age of 8 years, 15 seems rather high. Note that Katrina (unknown age, estimated at least 5 years old in 2009) appears to have been usurped by her 4 or 5 year old daughter Millie in 2012, whereas Frid (also estimated at least 5 years old in 2009) was still breeding in 2013.
Maximum breeding age – males	15 years	As in Rushton *et al.*
Maximum litter size	3	This is actual maximum litter size recorded at Knapdale. In Norway only 1 litter over 3 was recorded[1]. This is lower than the maximum litter size of 5 used by Rushton *et al.*
Sex ratio at birth	50%	As in Rushton *et al.*
% adult females breeding (± SD)	75% (± 10%)	This is the actual % of breeding pairs that successfully produced kits (per year) at Knapdale for the two years when there were 4 pairs of animals ≥ 4 years of age present. Actual SD unknown.
Distribution of litter sizes (n=1, 2, or 3)	70%, 20%, 10%	Actual litter sizes recorded at Knapdale
Age-specific mortality, mean per year (± SD): 0-1 1-2 2-3 3-4	 57.5% (± 43.5%) 37.5% (± 2.2%) 7.0% (± 1.1%) 7.0% (± 1.1%)	0-1: Assuming all kits that disappeared died, mortality was as follows: 0, 50, 80, 100% over the 4 years monitored 1-2: Actual loss of 1 or 2 of 4 yearlings over the duration of the trial (not enough data to assess per year), SD as in Rushton *et al.* NB. this is similar to medium scenario used by Rushton *et al.* 2-3 and >4: as in Rushton *et al.*
Initial population size	Females: 2 x 7 year olds, 1 x 9 year old; Males: 1 x 3 year old, 1 x 7, 1 x 8, 2 x 9	Current population size at Knapdale (not including the older female Katrina who is apparently no longer breeding and not seen since April, and counting only 1 sub-adult at Loch Linne). Assuming unknown age translocated animals were 5 years old at the time of translocation (2009).

[1] Campbell 2010

Model simulations

Simulations (see Table 10) were run using a starting population as it currently is at Knapdale (see Table 1), supplemented with a total of 20 further individuals[11] released over one to 5 years (10 pairs in 2016, 5 pairs in 2016 and 2018, or 4 pairs every year for 5 years from 2016). Supplements were modelled with 100% survival, assuming that if animals did not survive and settle at the site they would be replaced[12]. Each simulation was run over 30 years, with 1,000 iterations. No catastrophes were included. Carrying capacity was set at 500 to allow hypothetical unlimited population growth. We set the value for carrying capacity high (as in Rushton *et al.* 2002) so that simulated population growth is unrestrained – this approach reveals the point at which predicted population size exceeds local carrying capacity (the estimated carrying capacity of Knapdale is 90 individuals, Rushton *et al.* 2002) and thus indicates when beavers might be expected to disperse and spread beyond the site.

Model outputs are shown in Table 10 and Fig. 8. The first point to note is that in the absence of any improvement in reproductive success, simulations predict that population size will begin to decline as soon as supplementation stops. This seemed to be the case regardless of the actual number of additional beavers added to the population or the duration over which supplementation occurred (simulations with more than 20 individuals added to the population are not shown). There was little apparent difference among the alternative supplementation regimes, and the relative advantage of each may involve logistical, as well as biological, considerations. In terms of improving reproductive success, kit mortality is obviously more important than litter size (i.e. it is almost irrelevant how many kits are born, if mortality levels reach 100%), although simulations showed that increasing litter size would influence population growth rates if kit mortality also declined. Further simulations would be useful to identify reproductive parameter values ('indicators of success') at which population persistence could be ensured.

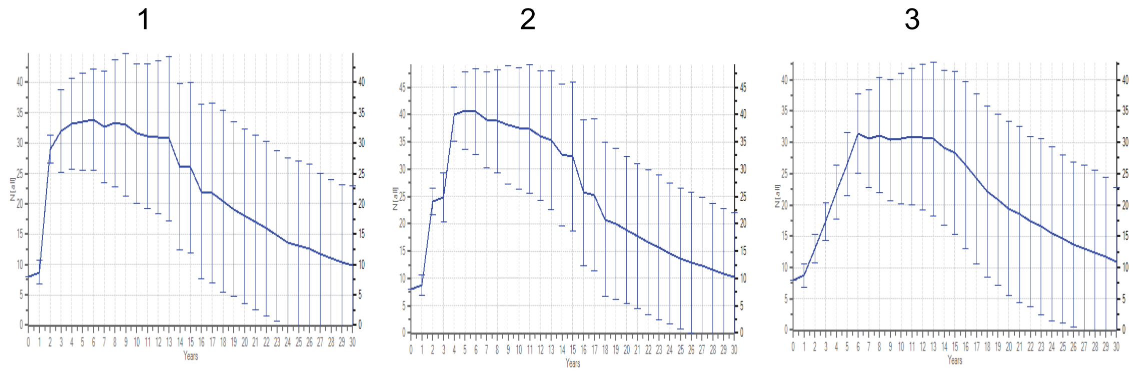
[11] Note that although not intended as a self-sustaining population, in the absence of supplementation, the current Knapdale population would go extinct in all scenarios.

[12] An alternative approach would be to include post-release survival as 0.68 (as estimated from survival analysis); there are a number of reasons why this step is probably not necessary: 1. This is an imprecise estimate of survival, 2. Applying post-release survival essentially has the effect of reducing the size of the population at the beginning of the period simulated, so the immediate loss of animals can more easily be accounted for by altering the starting population size (although this does not allow variation in post-release survival, and 3. Management actions (presuming the aim is to achieve a self-sustaining population) that counteract any early losses of animals are likely.

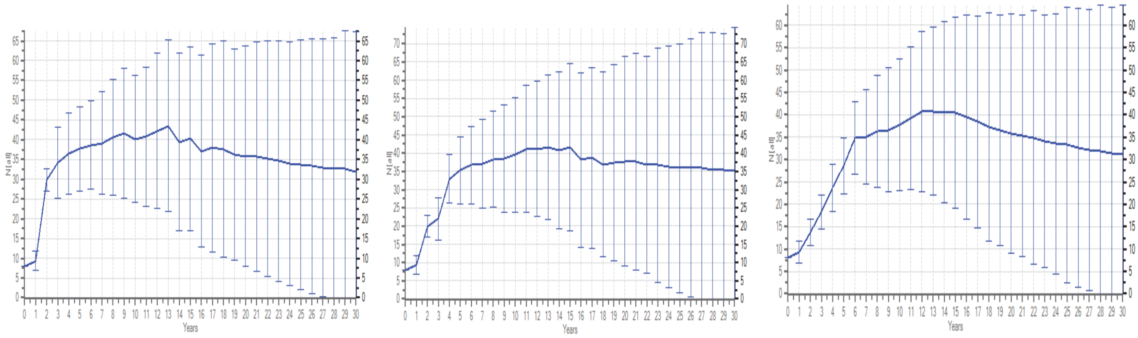
Table 10. Predicted population dynamics (probability of extinction, time to extinction, and population growth rate) and final predicted population size after 30 years, based on VORTEX model simulations (with 1,000 replicates) under four possible hypothetical life history scenarios and three supplementation scenarios.

Scenario Description	Supplementation	Probability of Extinction	Mean time to first extinction[1] (years)	r (mean growth rate) (SD)	Predicted population size[2] (mean ± SD for extant populations)
Reproductive success unchanged	10 pairs	0.899	13.4	-0.062 (0.24)	6.57±4.01
	5 pairs x 2 years	0.268	24.4	-0.001 (0.23)	14.60±12.0
	4 pairs x 5 years	0.237	24.7	0.001 (0.24)	13.84±11.4
Increased litter size. Distribution: (10, 70, 20%)	10 pairs	0.106	24.11	0.301 (0.31)	35.67±35.5
	5 pairs x 2 years	0.116	23.46	0.033 (0.27)	39.76±39.6
	4 pairs x 5 years	0.103	24.98	0.029 (0.25)	34.72±33.4
Decreased kit mortality (33±2%)	10 pairs	**0**	-	0.064 (0.22)	59.04±20.7
	5 pairs x 2 years	**0**	-	0.064 (0.16)	58.03±19.8
	4 pairs x 5 years	0.001	30.00	0.064 (0.12)	58.3±20.0
Increased litter size and decreased kit mortality (as above)	10 pairs	**0**	-	0.122 (0.20)	323.5±76.5
	5 pairs x 2 years	**0**	-	0.120 (0.15)	304.1±73.1
	4 pairs x 5 years	**0**	-	0.118 (0.11)	286.5±72.9

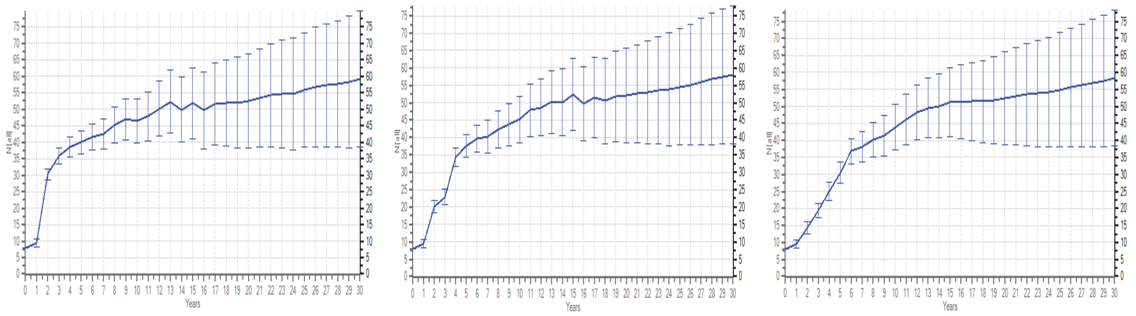
[1] of populations going extinct
[2] this is mean of extant populations (and thus differs from graphs which show all populations, including those that went extinct)



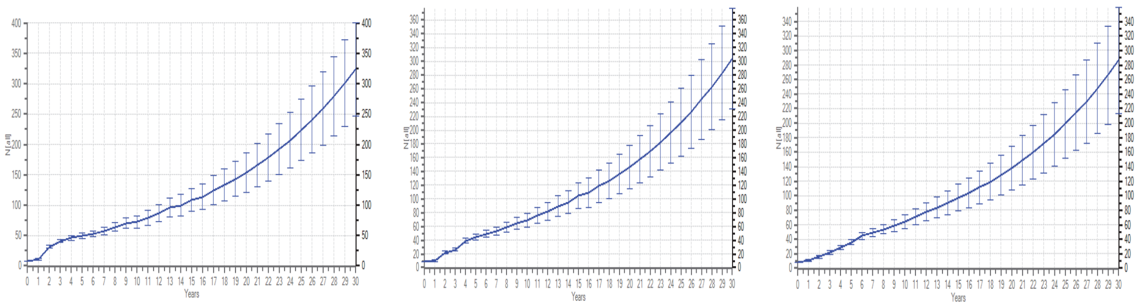
a) Reproduction remains unchanged – all populations decline to low levels when supplementation stops, and have a high risk of extinction after about 20 years



b) Increased litter size – although the populations seems to stabilise, population size is very small, hugely variable, and liable to extinction



c) Decreased (and low variability) kit mortality – population size increases slowly but remains below carrying capacity (note that, in this scenario, yearling mortality is still quite high)



d) Increased litter size and decreased kit mortality – population size increases with little chance of extinction, and likely spread beyond the release site

Figure 8. Predicted population size (mean ± SD of all populations) of beavers at Knapdale over the next 30 years, based on VORTX model simulations (run with 1,000 replicates) under four possible hypothetical life history scenarios (a – d) and three supplementations scenarios (1 – 3) (see text and Table 10), assuming a starting population as exists at Knapdale in 2014. The y axis shows the number of beavers, and x axis represents 0 to 30 years (where year 0 is 2014).

3.12 Questions relevant to the success/failure criteria of the trial

The purpose of monitoring population demography at Knapdale was to address the success / failure criteria, as far as was possible within the confines of the trial population size and duration. The trial was designed to be practical, logistically manageable, reversible, and of an appropriate duration to inform a general decision on beaver reintroduction throughout Scotland, and thus was necessarily small (in terms of population size) and short (in terms of duration). It was also designed to look at beaver interactions with a number of environmental parameters which are reported elsewhere. The trial was not intended to be a founder population, and thus should not be expected to be self-sustaining. The limited size and duration of the trial mean that inevitably it cannot be used for estimating robust population parameters, but the information obtained was nevertheless useful in a number of ways. The comments below, in response to the specified success/failure criteria, must be considered with these limitations in mind.

Are survival/mortality/reproductive rates similar to that of successful reintroduction programmes elsewhere in Europe at a similar stage of establishment?

Survival (of translocated animals) was influenced predominantly by early post-release mortality and animal losses. Early losses of animals (within seven months of release, most within two to three months) were relatively low (c. 20%) (compared with reintroductions in general, Harrington *et al.* 2013), and estimated survival at one year post-release compared favourably with other beaver reintroduction projects. Mortality of established adult animals was low.

In general, beaver reproduction at Knapdale has been slow to establish, due in part to some animals not being present until 2010, as well as new pairings (see Table 1), and, possibly, inexperience (for some beaver pairs – the Buic and Creagmhor pair), or even old age of the mother (which may be applicable to Katrina – the adult female released at Loch Coille-Bharr/Dubh Loch - and perhaps also Frid on Loch Linne). Comparative data are also sparse. Reproductive success appears to be low, but differs from that reported in the Biesbosch reintroduced population – the proportion of females breeding was higher at Knapdale than at Biesbosch (where it was very low compared with established populations), but mean litter size was lower than at Biesbosch (but possibly comparable to that recorded in the established source population in Norway).

The lack of comparative data mean that it is not possible to fully answer this question. However, our experience of reintroductions in general (across taxa) suggest that early post-release losses were within the range that might be expected. Reproductive rates (section 3.5) and survival of wild-born animals (section 3.6) warrant further attention.

Is the core population stable or increasing?

The beaver population currently present at Knapdale appears to be stable, but not increasing. Limited growth of the sub-adult and adult population would have been expected over the duration of the trial because of the length of time required for a wild-born beaver to reach sub-adulthood and the small number of families. The loss of sub-adults and low survival of wild-born kits in the last two years of the trial meant that population growth indicated in the second and third year of the trial did not continue in later years. The population did not reach predicted size due to low reproductive success (low litter size and high kit mortality).

Are mortality levels likely to preclude establishment of a population?

Mortality of established animals appears to be relatively low thus far. All beavers appear to be in good health and body condition (Goodman 2014), which suggests that the population could potentially grow. However, loss (presumed mortality) of kits appears to be high and largely responsible for the lack of population growth observed thus far. Population modelling suggests that, even with supplementation, the population will not be viable unless kit mortality (or variance in kit mortality) decreases.

In summary, if the decision is made to retain beavers at Knapdale, with the aim of establishing a self-sustaining population there, supplementation will be necessary. Further monitoring will also be necessary to assess reproductive success and the factors that influence it, with a view to informing longer-term management of the population.

3.13 Comments on the wider implications for the rest of Scotland

The low numbers of beavers released at Knapdale mean that estimation of population parameters (particularly age-specific survival of wild-born animals, and reproductive rates) are imprecise and probably biased by the large influence of chance events (e.g. predation of kits) or demographic effects (e.g. age of the breeding females). Whilst preliminary analyses presented here may suggest limited potential for population growth, these results may not be relevant for other beavers at other sites (or even for different beavers at Knapdale). The Tayside beaver population was estimated to comprise 38-39 beaver occupied territories in 2012 (Campbell *et al.* 2012). It is not possible to calculate population growth rate of the Tayside population because their founder population size and release years remain unknown, however, lodge counts conducted on the Tay catchment in 2013 and 2014 suggested an average litter size of 1.9 (±1.1) (with a range in litter size of 1 – 4, and most lodges producing 2 – 3 kits), and kits were produced at 0.83 and 0.88 lodges observed (n = 11 and 18, respectively; Campbell-Palmer *et al.* 2015). These values are higher than observed at Knapdale but it is not possible to attribute the difference to region specifically because the provenance of the Tayside beavers (most likely Bavarian) also differs from that at Knapdale.

4. ECOLOGICAL DATA

4.1 Aims

One of the main aims of the beaver ecology monitoring was to document where beavers settled, what size of area they occupied and what habitats they used. The original monitoring protocols (in Campbell *et al.* 2010) included radio-tracking, and focal observations, of individual beavers but problems associated with telemetry signals in a hilly environment with abundant water, disturbance of beavers, and the resource requirements of such intensive methods, led to these methods being discontinued after the first year of the trial. Field signs, in contrast, are non-intrusive, they are easily detectable and identifiable, and can be recorded at any time of day. Field signs provide clear evidence of the areas occupied, and used, by beavers but have the disadvantage of unknown individual identity. However, at Knapdale, the four beaver pairs/families still occupy discrete areas, and, therefore, combined with monthly observations (see section 3.2) to verify individual locations, field signs can provide a simple outline of the area used by a beaver pair/family, as well as the intensity of use of (terrestrial[13]) areas within it. Beaver field signs also have the advantage of providing additional information beyond location, such as on damming and canal building activity.

The main focus of this section is on beavers that settled within the release area, but occasional field sign searches beyond the release area were also carried out in an attempt to locate animals that did not settle, and dispersers. The aim in this section, was thus, to estimate beaver density within the trial area, to describe family home ranges, to map and describe evidence of other beaver activities (e.g. dam building, and the development of scent marking behaviour), to assess habitat preferences, and (where possible) to provide evidence of dispersal events beyond the release area.

4.2 Methods

Field sign surveys

A 40 m wide margin along the water's edge around each loch/river known to contain beavers, as well as surrounding riparian corridors within the trial area (as shown in Fig. 9), was searched (on foot or by boat) for field signs each season (Spring = Mar, Apr, May, Summer = June, Jul, Aug, Autumn = Sept, Oct, Nov, Winter = Dec, Jan, Feb) from January 2011 (Year 2) to the end of the trial (in June 2014), and their locations recorded. Field signs recorded included: dwellings (lodges and burrows), signs of construction activity (dams and canals), feeding signs[14], and signs of other activities (e.g. scent marking activities) (see Table 11). One location per 10 m length of river/loch bank was recorded for clusters of field signs of the same type. For feeding signs, only fresh signs (i.e. those left within the last 3 months) were recorded; for other field signs (e.g. lodges, burrows, or scent mounds), only those with evidence of recent (within the last 3 months) use were recorded. Field signs were marked with natural wool (that would decompose over time) to enable surveyors to distinguish fresh from older, previously recorded, signs in successive surveys. Field sign surveys were also carried out over the first two years of the trial, but in Year 1 and the summer and autumn of Year 2, they were carried out monthly and covered a margin of only 5 m from the waters' edge, and prior to March 2010 were not carried out systematically (discussed in Harrington *et al.* 2011). Tree species (for any felled, cut or gnawed tree or branch) was recorded in Year 1 and 2, but not in later years[15].

[13] Field signs provide only occasional evidence (in the form of macrophyte 'mats') of aquatic habitat use.
[14] Note that felled trees and cut branches may be used for construction as well as for food.
[15] To reduce overlap and redundancy in the monitoring work, the beaver ecology monitoring did not collect data on the size, number or species of felled trees beyond January 2011 – the impact of

There were also occasional searches beyond the occupied/release area for missing animals.

Table 11. Field signs recorded (revised January 2011)

Type	Feature	Including
Dwelling	Burrow	
	Lodge	
Construction	Dam	
	Canal	
Feed Sign	Food cache	Underwater stores of cut saplings and branches outside the lodge/burrow
	Tree/branch cutting	Felled trees/saplings Cut tree stumps Gnawed trees Cut branches Stripped branches/sticks
	Feeding stations	
	Foraging trail	
	Other	Grazed area = cropped (by beavers) ground vegetation Aquatic macrophyte mats
Activity	Tracks	
	Scent mound or marking	Single mark, or recent marking of a larger, frequently used mound etc.

beavers on the riparian woodland was monitored by the James Hutton Institute (JHI), see section 4.9 and Iason *et al.* 2014.

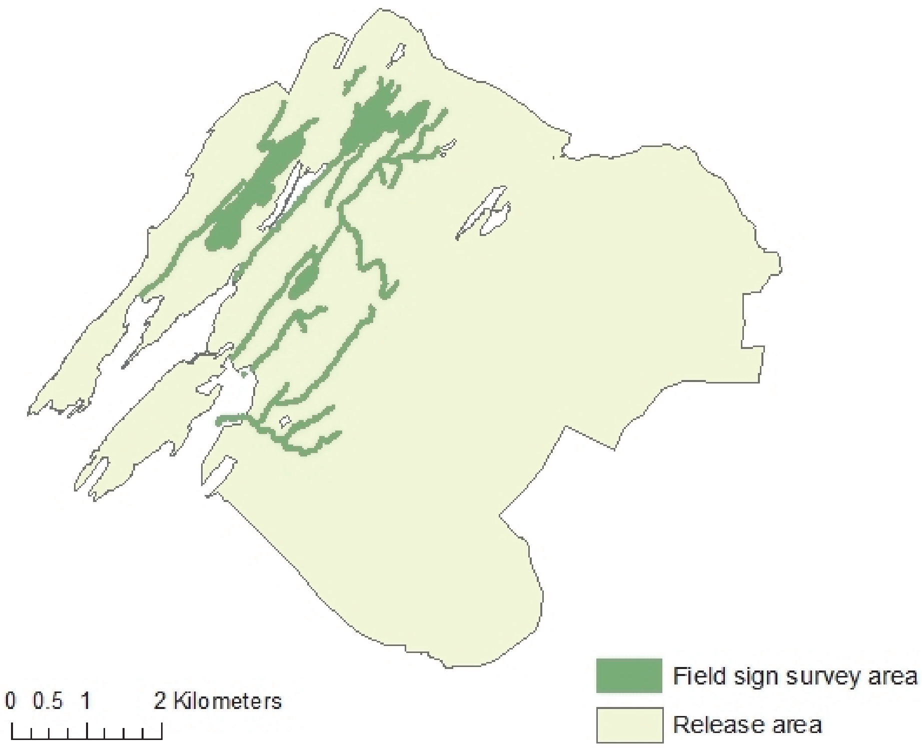


Figure 9. Schematic showing the areas surveyed for field signs within the release area (based on a 40 m buffer around each loch occupied by beavers), Knapdale, Argyll. Since January 2011, these areas have been surveyed seasonally (in Year 1, a smaller area – based on a 5 m buffer – was surveyed monthly – see text). Note that the survey area only covers part of the release area but was designed to cover an area slightly larger than the area actually used by beavers to cover both their current activity and any potential increase in area used. Individual release sites were within the area surveyed, and are shown in Figure 2.

Analyses

The total area occupied by beavers in the final year of the trial was estimated using the smallest convex polygon that enclosed all beaver field sign locations recorded in that year. The length of 'occupied' loch/river bank was measured as the length of waterway edge within that convex polygon.

To estimate territory sizes of established pairs/families, we used all field sign locations and measured the length of waterway edge covered for each pair/family, for each of the last three years of the trial (Year 3 – Year 5, inclusive) combined. We restrict our analysis to these years because two beaver pairs were not released until the second year of the trial, and field sign survey data, prior to March 2011 (Year 2) were not comparable to those collected later. From Year 3, all beaver pairs/families could be considered to be 'established', at least in a locational sense (some movements of male beavers between lochs still occurred in Year 3, see Table 1). In all cases, field signs were inferred as belonging to a particular family on the basis of location – this is currently possible at Knapdale because the majority of field signs occur in relatively clear clusters. Outlying field signs (see 4.10), which were few, were not included in home range estimates. Observational locations were not used because they added little, or no, additional information, and they did not, in any case, occur beyond the area covered by field signs. Two features of the area occupied by beaver pairs/families were quantified: the total length of waters' edge (loch or river bank) occupied (all 3 years combined), and the distance (mean and maximum) away from the waters' edge that the occupied area extended to (for each of Year 3 - 5)[16]. To visually assess differences in the distribution of field signs, we also plotted field sign locations for each year (Year 3 - 5) separately.

Habitat selection can be considered at a number of different hierarchical levels, whereby first order selection refers to the location of the species' range, second order selection to the location of individual or group home ranges, and third order selection to habitat use within the home range (Johnson *et al.* 1980). In the case of reintroduction, animals are usually released within their species' range, and, to a certain extent, home range placement is dictated by release site selection (assuming that released animals settle at their release sites, which is not always the case, but was approximately the case at Knapdale, see Figure 2 and 10). The most relevant question at Knapdale, therefore, related to habitat use by beavers within their established home ranges. We assessed habitat use (focusing specifically on terrestrial habitats) at the level of the beaver family/pair, and quantified use by counting the proportion of feeding sign locations that occurred within each habitat type. As for territory size, we used all field signs from the last three years of the trial (Year 3 – 5) combined. We used two different datasets to quantify habitat availability: the Knapdale riparian woodland 2005[17] dataset (Brandon-Jones *et al.* 2005), which records the dominant tree species within riparian broadleaved woodland[18], and the Native Woodlands of Scotland Survey (NWSS) dataset, which categorises all native woodland by dominant habitat type[19]. Both datasets are broad scale. The advantage of the Knapdale woodland survey is that it uses the same species categories as in the more detailed woodland monitoring carried out by the James Hutton Institute (JHI), so it allows a direct comparison of habitat selection at different scales. NWSS offers a different perspective and potentially further information on the use of woodland habitats beyond that defined simply by tree species. Because we were interested in the details of habitat use by each family, we described habitat use for each beaver family/pair separately and inferred that there was some level of preference for a specific habitat type when proportional use was greater than proportional availability.

All spatial measurements were calculated in ArcGIS 10.2 (www.esri.com), using the Fresh water features layer of the Ordnance Survey MasterMap[20]. The convex polygon enclosing all field signs was generated using the Minimum Bounding Geometry function in the Features

[16] In previous annual reports we presented 100% minimum convex polygons, and, in accordance with Herr and Rosell (2004), measured the length of waterway contained within that polygon. We also calculated 100% restricted edge polygons (REPs) (using a restriction distance of 0.2) to provide estimates of pair/family territory area. However, the geometry of lochs and waterways at Knapdale, and the fact that beavers use a narrow strip of (non-overlapping) river/loch bank, meant that this step was not necessary and did not provide any additional information beyond that provided by a direct calculation of the area of waters' edge occupied. A direct measurement of length of waterway occupied, as well as distance away from the waters' edge provided a more accurate representation of the area actually used by beavers in this landscape.
[17] Updated in 2011.
[18] All riparian broadleaved woodland within 100 m of freshwater bodies and water courses was mapped as polygons of relatively homogeneous woodland, and habitat (we used the habitat category 'dominant tree species') assessed within a representative 25 x 25 m quadrat (full details in Brandon-Jones *et al.* 2005).
[19] Mapped, as for the Knapdale riparian woodland survey, as polygons of woodland type; data held in the Forestry Commission's Spatial Data Repository, available with metadata and further information from http://scotland.forestry.gov.uk/supporting/strategy-policy-guidance/native-woodland-survey-of-scotland-nwss
[20] Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2013 Ordnance Survey 100017908.

toolset, in Data Management Tools. The lengths of water's edge were calculated by retrieving the perimeters of polygons describing freshwater lochs, measuring the length of any other rivers or streams occupied using the measurement tool, and summing all individual sections of the area occupied. The distance of field signs from the waters' edge (defined as the nearest loch or stream) was calculated using the Near function in the Proximity toolset, in Analysis Tools, using a 50 m search radius[21]. Distances were summarised per year, and compared among years. For the purpose of habitat analysis, 'home range' was defined by a polygon delineating a cluster of field signs presumed to belong to a single beaver family or pair (see Figure 10) with a 10 m buffer (using the Minimum Bounding Geometry function), the proportions of each habitat type within the buffered home range were calculated by clipping the woodland dataset by the new 'home range' polygon (using the Clip tool in the Geoprocessing toolbox) and summing the area of each habitat type included, and the proportions of locations within each habitat type were calculated by creating a Spatial Join between the field signs for a family and the clipped woodland dataset which matches each field sign location with the habitat type within which it falls. Statistical analyses (where appropriate) were carried out in R (version 3.0.2, R Core Team 2013).

For comparison with the first two years of the trial, which could be considered to represent a 'settlement' phase, we report length of loch/river bank occupied during Year 1 (for the Linne and Dubh Loch families) and Year 2 (for the Buic and Creagmhor pairs), as originally reported in Harrington *et al.* (2012). Length of loch/river bank occupied is not affected by the differences in sampling strategy, or survey 'margin', among years, and thus offers a useful comparison over the duration of the trial. For descriptions of beaver activities and habitat use, Year 1 and 2 field sign data were included where appropriate (in all analyses the years included is stated in the text). For all tree felling, gnawing and branch cutting, tree species was recorded in Year 1 and 2, and these data are also reported for additional information.

4.3 Overview of fieldsigns recorded

Over the duration of the trial, over 5,600 field signs and their locations were recorded. Most field signs (95% of all field signs) were feeding signs, the vast majority of which (80% of feeding signs) were evidence of gnawed or cut branches, or felled trees. Feeding stations, food caches and foraging trails were also frequently found (19% of feeding signs). Very few scent mounds or scent marks were recorded (n = 16 records over 5 years, < 0.1% all field signs).

4.4 Density of beavers within the release area

In the final year of the trial, the four beaver families covered a total area of 366.9 ha, incorporating seven lochs, of which six were utilised (within this polygon, only Losgunn, the small loch north of Lochan Buic, appeared to remain unused by beavers Figure 10). The current 'beaver range' incorporates approximately 20 km of loch or river bank, which equates to a density of c. 0.2 beaver families per km of waterway edge (or, on average, one beaver family per 5 km of waterway edge) – although this is a slight underestimate because almost 6 km of streams and rivers between the north-easterly lochs and Lochan Buic in the south were unoccupied at the end of the trial (see Figure 10). There was little change in the total area occupied over the duration of the trial, except that Un-named Loch (South) (where Trude and Tallak were originally released at the end of Year 1) was not occupied by the end of the trial.

---

[21] For the Dubh Loch family, the selection radius limit was removed to allow for the altered loch edge due to increasing water levels as a result of beaver damming (see Willby *et al.* 2014). For all family/pairs, all distances were checked to ensure that they were mapped to the correct (i.e. the occupied) polygon (loch).

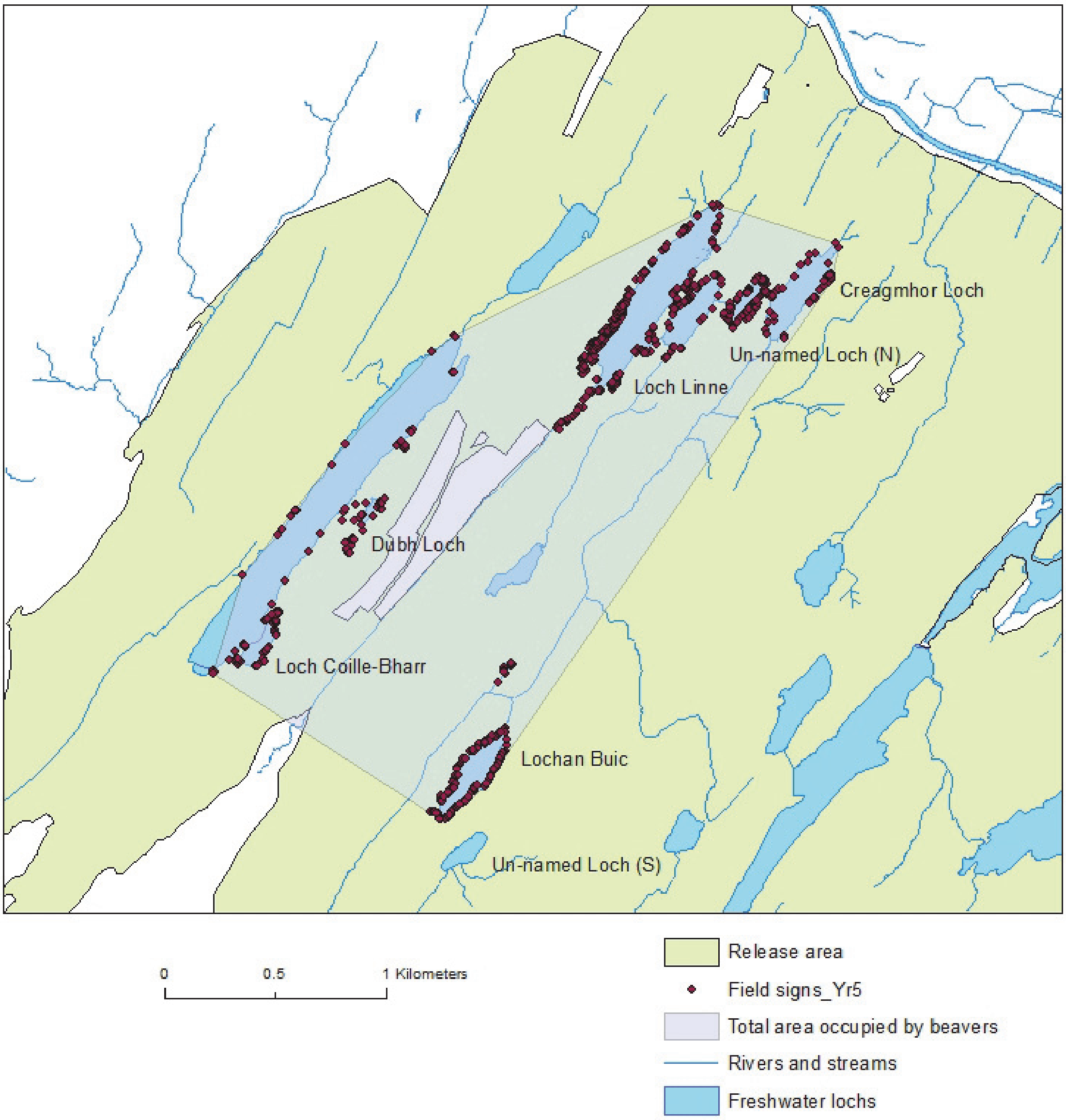


Figure 10. Area occupied by beavers at Knapdale, Argyll, in the final year of the trial. Note that Un-named Loch (South) now falls outside the occupied area. The grey-lined polygons within the occupied area are privately owned areas excluded from the release area. Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2013 Ordnance Survey 100017908.

4.5 Number and size of established territories

Beavers remained in four discrete family territories throughout the duration of the trial, although there were changes in the membership of two of those territories in Year 3 (see Table 1). There have been some minor shifts in focus of activity (see Figures 12 below), but otherwise, with the exception of Un-named Loch (South), all lochs on which beavers were released remain occupied.

For Years 3 – 5 combined, the length of waters' edge used by a beaver pair/family ranged between 1.8 and 4.7 km for different families (Table 12), and the median (and maximum) distance of field sign's from the waters' edge, ranged between 1.7 and 20.9 m (maximum 28.4 and 130.7 m) (Table 12). With the exception of field signs located to the south of Dubh Loch, most (82 – 98%) were located within 20 m of the loch/river bank (Fig. 11). Given that most field signs recorded were felled trees, gnawed or cut branches, it is not surprising that this finding is broadly in accordance with Iason *et al.* (2014) who reported most effects of beavers on trees occurring within 10 m of the waters' edge (assessed between 0 and 30 m from the waters' edge). However, to capture the majority of field signs, a wider search band width was clearly required (i.e at least 20 m), and initial survey protocols that required searching a band of 5 m from the waters' edge would have captured less than half (35 – 48%) of all field signs. In quantifying the length of loch/river bank used, we made no attempt to identify and subtract unused areas within the perimeter of the occupied loch, which meant that there was, by definition, no annual change in the length of waters' edge occupied, except minor changes in the length of in/outflow streams used. There was variation in the spatial distribution of field signs within the area used – for example, in the use of Creagmhor Loch by the Creagmhor pair (who predominantly used Un-named Loch (North), see Fig 12) - but no clear or apparently consistent temporal trend (except that, in all cases, field signs appeared to be most abundant in Year 4, Fig 12).

Distance of field signs from the waters' edge differed significantly among years, for all beaver families (Kruskal-Wallis rank sum test[22]: Linne family – K-W chi-squared = 18.39, $p < 0.001$; Dubh Loch family – K-W chi-squared = 39.1, $p < 0.001$; Buic family – K-W chi-squared = 15.2, $p < 0.001$; Creagmhor pair - K-W chi-squared = 12.1, $p = 0.002$; in all tests df = 2), being on average further from the water's edge (for 3 of the 4 beaver pairs/families[23]) in Year 4 than in either Year 3 or Year 5, but did not increase over progressive years as might be expected if resources were progressively depleted. Iason *et al.* (2014) also found no tendency for beavers to forage on woodland vegetation further from the water over the duration of the trial (although these authors did find an increase over time in the use of vegetation plots containing un-preferred tree species, suggesting that preferred tree species were being depleted). The consistency of temporal pattern in field sign distribution (with respect to their distance from water) between three family groups suggests that annual variation might be explained by weather effects, although some variation may also be due to temporary changes in family composition.

The area of loch occupied per beaver pair/family ranged over an order of magnitude, between 4.3 and 34.6 ha (Table 12). Although area used per beaver pair/family appeared to be positively related to family size (Fig. 13a), we suggest that this is a coincidental relationship (due to chance and small sample size) and that a simple positive (geometric) relationship between area used (equivalent to perimeter of the loch, Fig. 13b) and area of the loch is more likely (i.e beavers used the entire perimeter of the loch on which they settled, which was the loch on which they were released or its nearest neighbour, regardless of the size of that loch). Campbell *et al.* (2005) also found no correlation between territory size and group size in either the reintroduced Biesbosch population or in Norway. Similarity in estimates of the areas used by beavers one year post-release with estimates of area used

[22] Non-parametric statistics used because of skewed distribution of distance data.

[23] For the Dubh Loch family, field signs appeared to be located furthest from the waters' edge in Year 3, and distance appeared to decrease over the following years – however, this family occupy a loch that has been increased considerably in size by water level rises resulting from damming (see Willby *et al.* 2014), but distances were measured according to the waters' edge as mapped prior to the trial. Distances measured therefore reflect the changing position of the loch edge, as well as distance from the 'new' waters' edge.

in Year 3 – 5, when they could be considered to be 'settled'[24], suggest that, in the absence of neighbours, beavers settle and rapidly establish a home range.

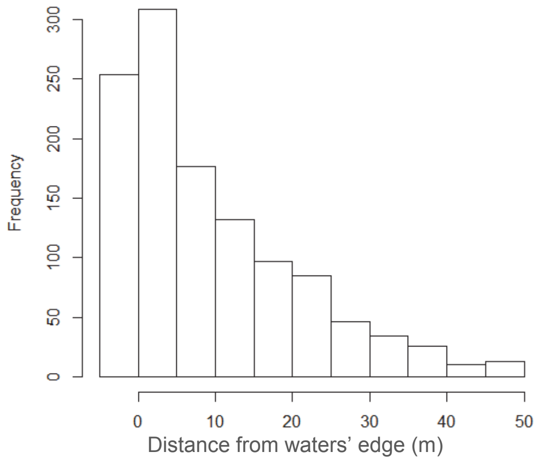
Table 12. Annual family territory/home range sizes (Year 3-5), with estimated home range length at one year post-release (Year 1 for the Loch Linne and the Dubh Loch families, Year 2 for the Buic family and the Creagmhor pair, from Harrington et al. (2012) presented for comparison. Distance data are median, maximum (number of field signs).

Family	**Area used by beavers**		**Estimated home range length (km) (1 yr post-release)**	**Area of occupied loch/s (m^2)**
	Loch/river bank length (km)	**Distance from waters' edge (m)**		
Linne	3.8	5.6, 49.4[1] (1183)	3.5	174,616
Dubh Loch	4.7	20.9, 130.7[2] (719)	4.5	345,544
Buic	2.4[3]	1.7, 28.4 (486)	3.0	43,954[4]
Creagmhor	1.8[5]	6.5, 42.8 (556)	1.5	65,393

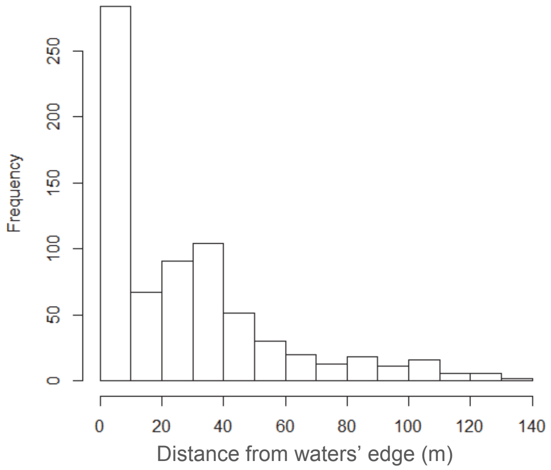
[1] Note that distance was measured within a limit of 50 m from the waters' edge.
[2] Note that this is likely to be an overestimate because distance is measured from the original waters' edge as mapped in the Ordnance Survey Mastermap water layer, but Dubh Loch has been substantially increased in size as a result of beaver damming (see Willby *et al.* 2014) which would account for much of the distance as measured here.
[3] Including c.1 km of connecting streams/rivers.
[4] Un-named (South) Loch has an area of 15,762 m^2, and a perimeter of 577 m, but was only used in Year 2 of the trial (see Fig. 12).
[5] Including c. 48 m stream connecting the 2 lochs (Unamed loch (North) and Creagmhor)

Territory sizes reported here for the Buic family and the Creagmhor pair were smaller than average territory sizes reported for beavers in Norway by Herr and Rosell (2004) (4.4 ± 1.4 km) but individual territory sizes as small as 1.58 km have been recorded in Norway (Campbell *et al.* 2010), so it seems that 1.8 km in Knapdale is not exceptional.

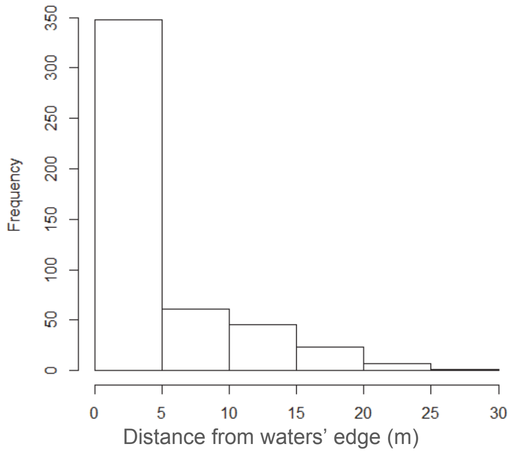
[24] Differences may be due to measurement error as well as differences in the actual area used by beavers.



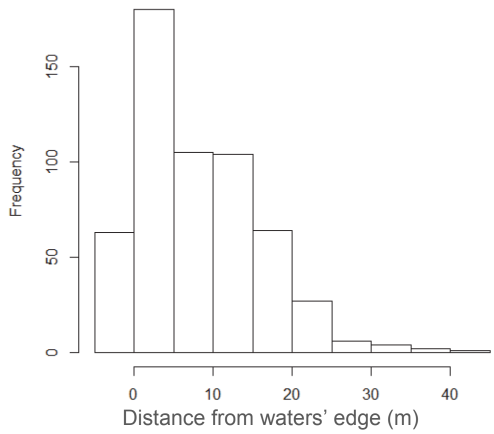
a) Loch Linne



b) Dubh Loch (and Loch Coille-Bharr)



c) Lochan Buic



d) Creagmhor Loch and Un-named Loch (North)

Figure 11. Distribution of distance of field signs from waters' edge for all four family territories, for Year 3 – 5 combined.

4.5.1 Linne family

YEAR 3 | **YEAR 4** | **YEAR 5**

1 adult ♂	1 adult ♂	1 adult ♂
1 adult ♀	1 adult ♀	1 adult ♀
1 yearling	1 sub-adult	1 or 2 sub-adults
1 kit	1 yearling	1 kit (disappeared)
	1 kit (predated)	

Dubh Loch family

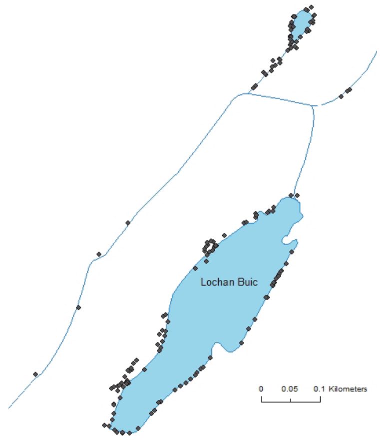
YEAR 3 | **YEAR 4** | **YEAR 5**

1 adult ♂	1 adult ♂	1 adult ♂
1 adult ♀	2 adult ♀	2 adult ♀
1 sub-adult	1 sub-adult (dispersed?)	2 kits (disappeared)
1 yearling	3 kits (disappeared)	
1 kit (predated)		

Figure 12. Schematic showing field sign locations for all beaver pairs/families (Linne and Dubh Loch family) at Knapdale, 2012-2014. Year 3, 4 and 5 are depicted to show annual changes occurring during a period when the beavers could be considered to have established a stable home range. Note different scale (the scale bar in all figures represents 0.2 km). Lodge and dam locations are shown in Figure 19 and 20, respectively. Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

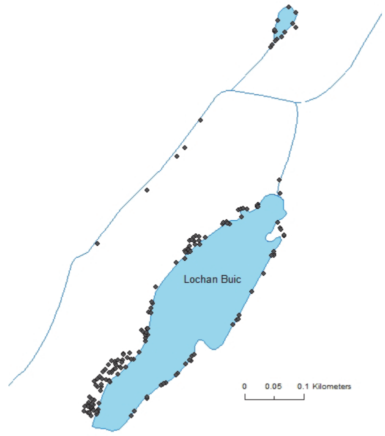
4.5.2 Buic family

YEAR 3



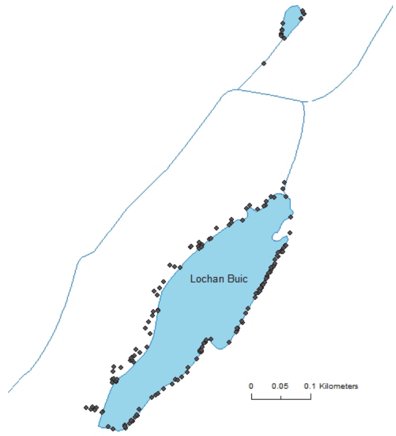
1 adult ♂
1 adult ♀

YEAR 4



1 adult ♂
1 adult ♀
1 kit

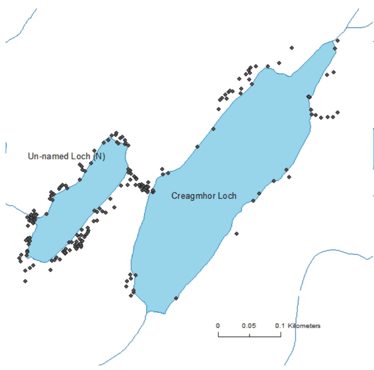
YEAR 5



1 adult ♂
1 adult ♀
1 yearling (died?)
2 kits (disappeared)

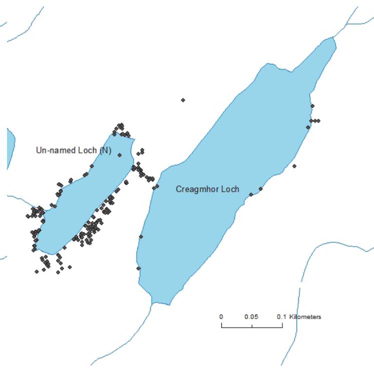
Creagmhor pair

YEAR 3



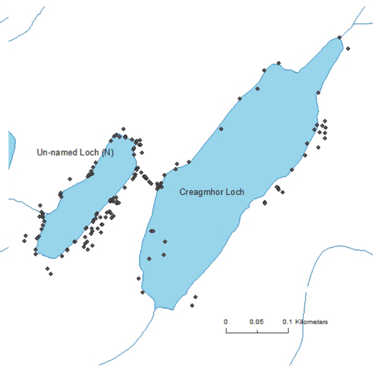
1 adult ♂
1 adult ♀

YEAR 4



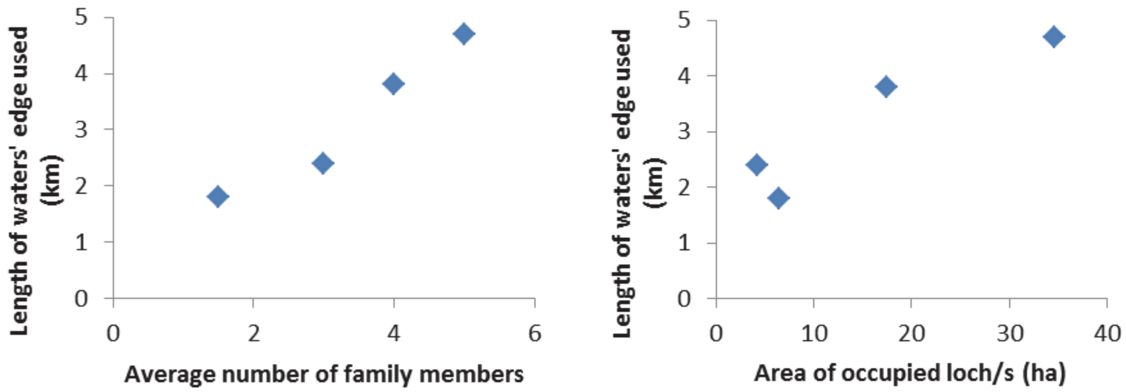
1 adult ♂
1 adult ♀ (disappeared)

YEAR 5



1 adult ♂

Figure 12 cont. Schematic showing field sign locations for all beaver pairs/families (Buic family and Creagmhor pair), Knapdale, 2012-2014. Year 3, 4 and 5 are depicted to show annual changes occurring during a period when the beavers could be considered to have established a stable home range. Note different scale (the scale bar in all figures represents 0.2 km). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.



a) b)

Figure 13. Length of waters' edge used by translocated beaver pair/families in relation to a) the number of family members, and b) the area of the occupied loch/s. Note that in some cases two lochs were occupied by a pair/family, but with the exception of Un-named Loch (South) all occupied lochs included the loch onto which the beavers had originally been released. The apparent relationship between area used and family size is probably coincidental (see text).

4.6 Seasonal area use

In our second annual report (see Harrington *et al.* 2012), we carried out a preliminary analysis of seasonal home ranges, and suggested that winter home ranges might be smaller than those used in other seasons. However, for all families, the presence of outlying points in winter suggested that perhaps the difference was in reduced intensity of use rather than a reduction in the area used *per se*. However, when combining data from all families over the last three years of the trial, and using number of field signs recorded as an indicator of beaver activity[25], we could not detect a difference among seasons (GLM[26]: $F_{season} = 0.31$, $p = 0.58$, df = 1, 41). Plots of field signs by seasons did not reveal any consistent seasonal patterns, and there was no evident separation of specific areas of their home range used in different seasons (Fig. 14-17).

Across all families and all years, there was little difference in type of field sign detected among season, except that there appeared to be slightly fewer feeding stations recorded, and a slightly greater proportion of tree or branch cutting, in autumn (Fig. 18). The woodland monitoring did not detect any seasonal differences in the impact of beavers on trees, but they defined seasons differently and compared impact over the summer months (April – October) with that incurred over the winter months (November – March) (Iason *et al.* 2014) and so 'autumn' activity as defined by the ecological monitoring (as September, October and November) may have occurred in both periods of the woodland monitoring. Further analysis would be required to assess whether the higher proportion of tree and branch cutting in autumn was consistent among lochs and over years, and whether it represented a statistically and biologically meaningful difference. However, the field sign surveys were not designed to provide detailed information on beaver activity. The feature 'tree/branch cutting'

[25] The number of field signs is approximately equivalent to the number of 10 m sections of loch/river bank in which signs were recorded, except that signs of different types – see Table 11 – were recorded separately, so each 10 m section of loch/river bank could be counted more than once.
[26] Model run using the *lme* function, in the Package *nlme* (Pinheiro *et al.* 2014), with Season and Year included as fixed effects, and Family as a random effect.

is useful for efficient data collection and the provision of broad-scale information on the use of space by beavers, but it potentially encompasses a range of behaviours including feeding and construction activities, and so is not suitable for detailed behavioural analysis and does not warrant further analysis at this stage. Elsewhere beavers tend to cut more trees in autumn to make food caches for the winter (e.g. Nolet 1997; Rosell and Czech 2000) and so it is likely that further study at Knapdale would reveal similar seasonal effects.

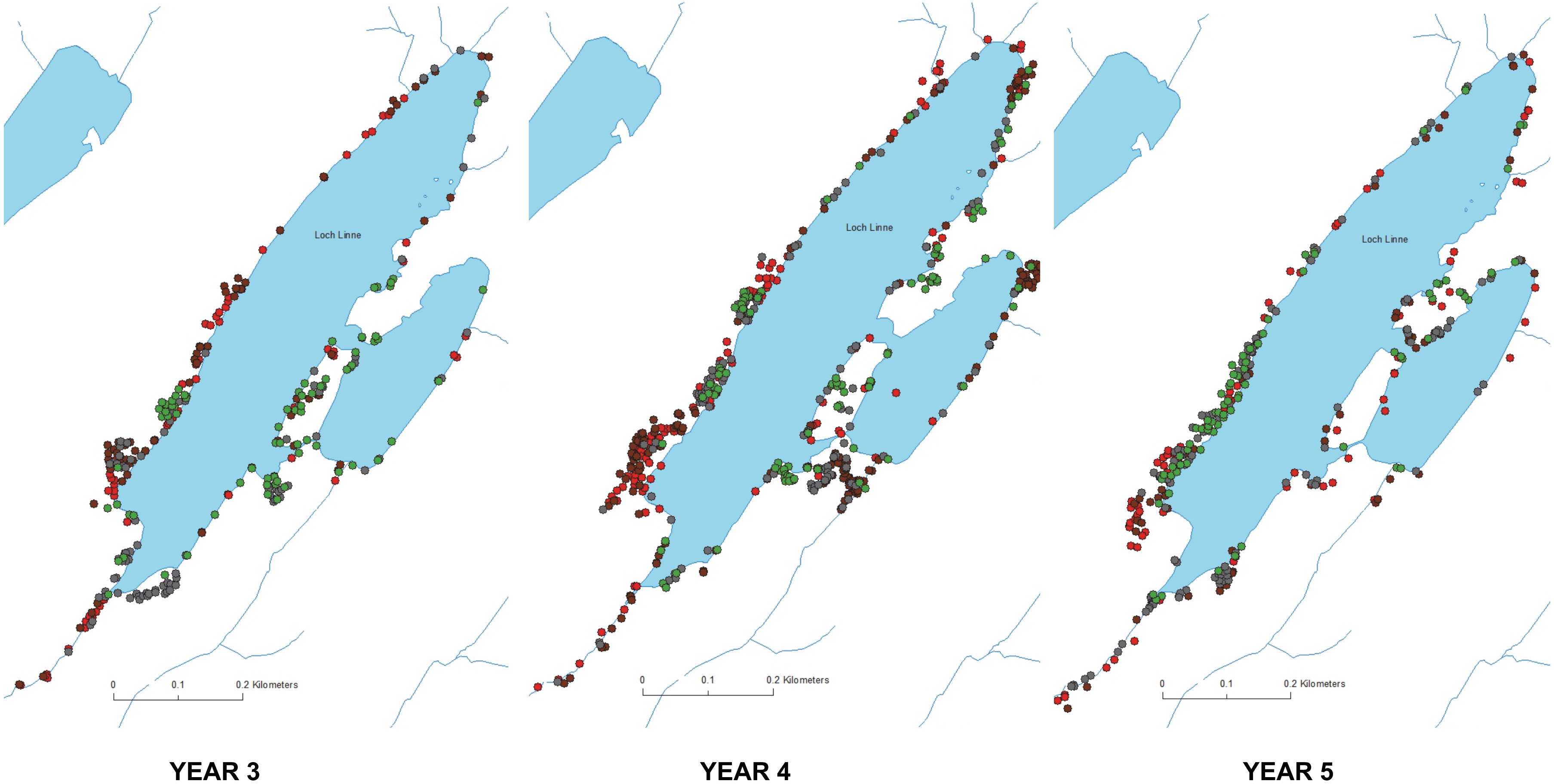


Figure 14. Schematic showing field sign locations for the Linne beaver family, Knapdale, 2012-2014, in summer (red), autumn (brown), winter (grey), and spring (green). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

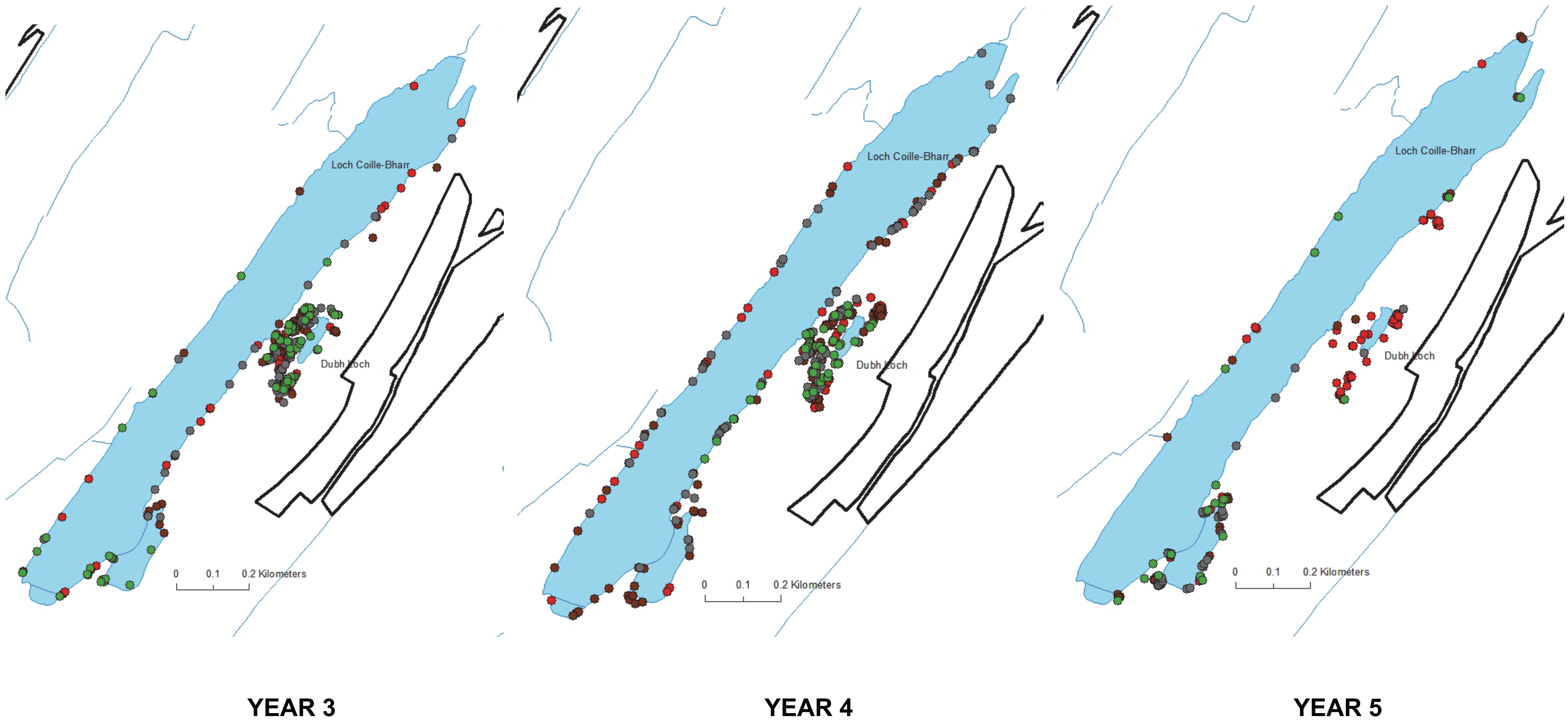


Figure 15. Schematic showing field sign locations for the Dubh Loch beaver family, Knapdale, 2012-2014, in summer (red), autumn (brown), winter (grey), and spring (green). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

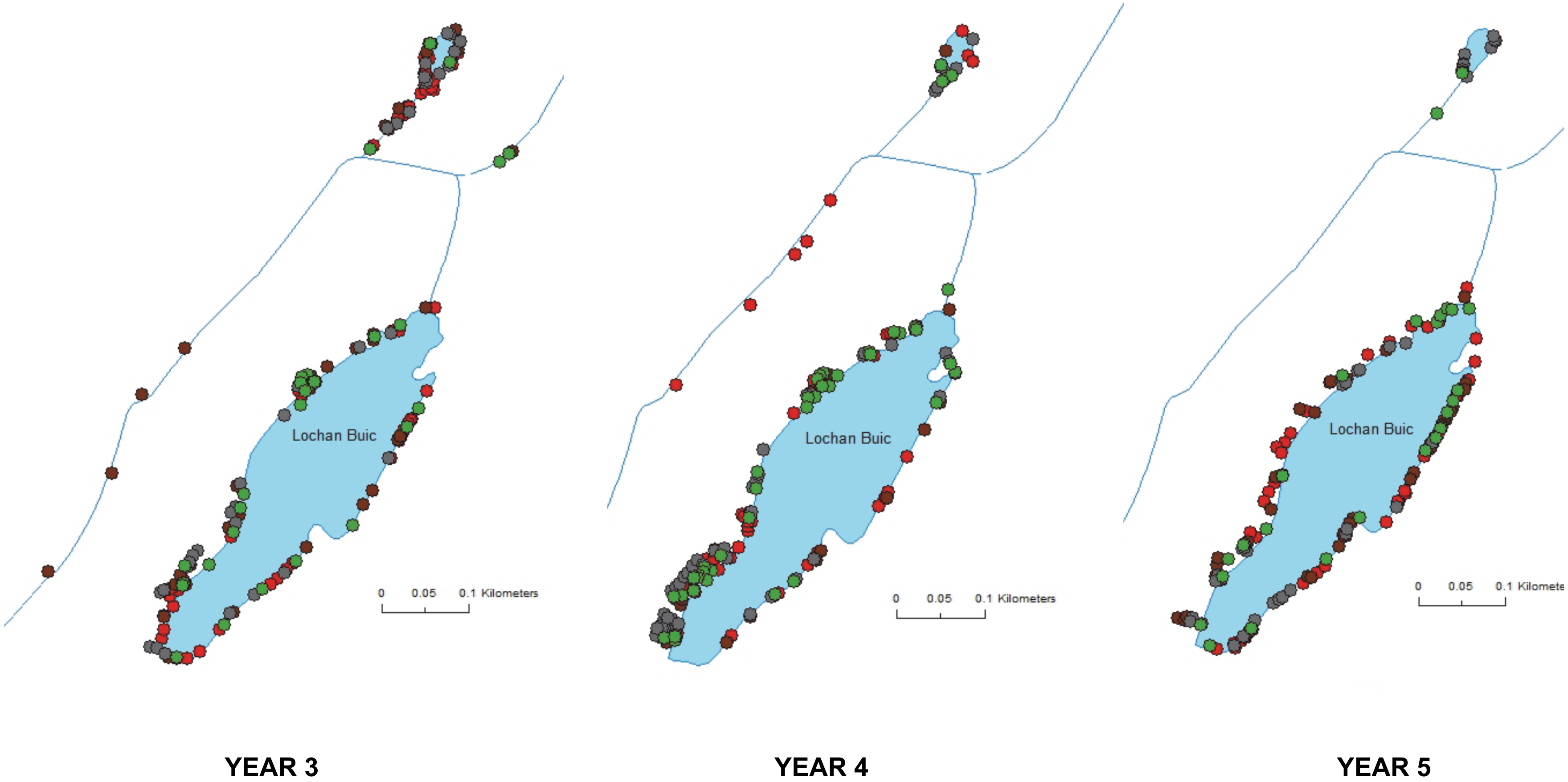


Figure 16. Schematic showing fieldsign locations for the Buic beaver family, Knapdale, 2012-2014, in summer (red), autumn (brown), winter (grey), and spring (green). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

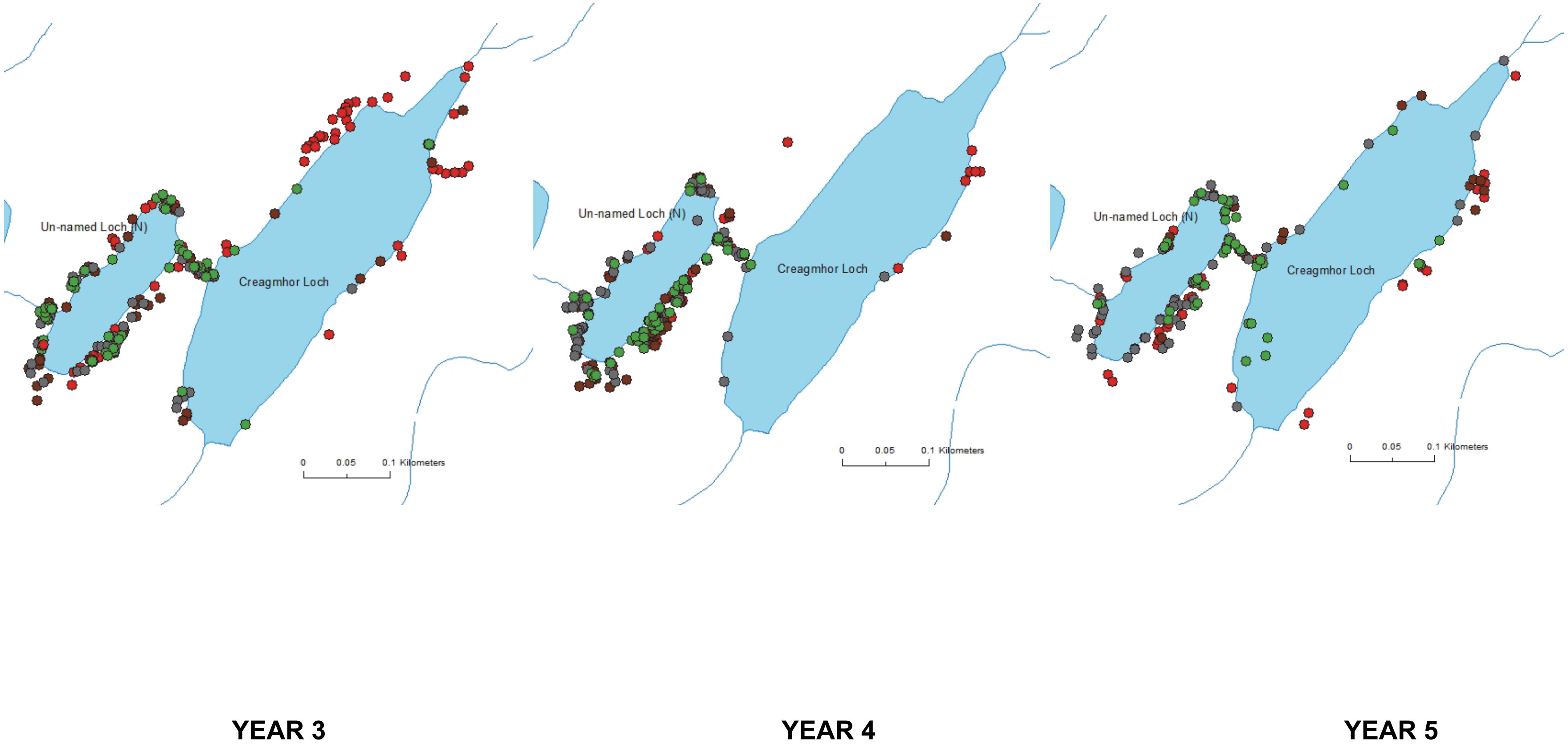


Figure 17. Schematic showing field sign locations for the Creagmhor beaver pair, Knapdale, 2012-2014, in summer (red), autumn (brown), winter (grey), and spring (green). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

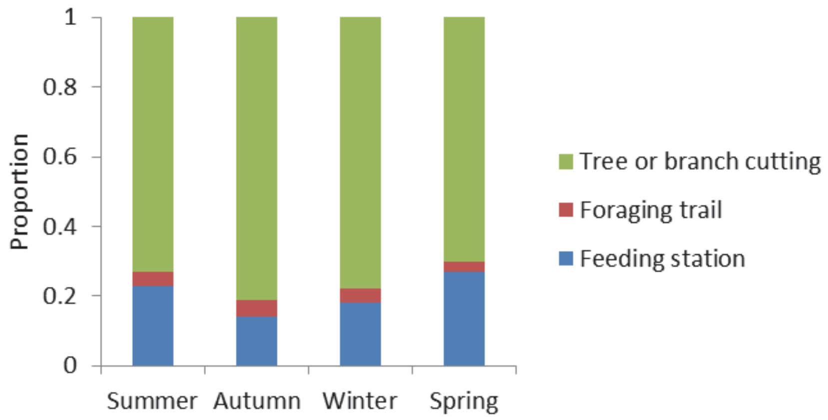


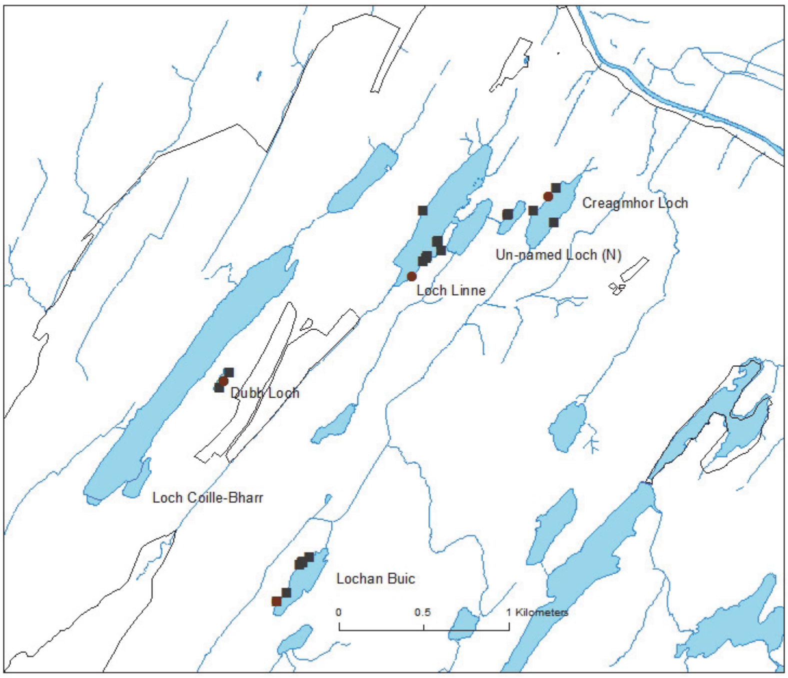
Figure 18. Types of field sign recorded at Knapdale, Year 3 – Year 5, by season (showing the three most frequently recorded types of field sign – all other field sign types appeared to be recorded occasionally in all seasons).

4.7 Dwellings and construction activities

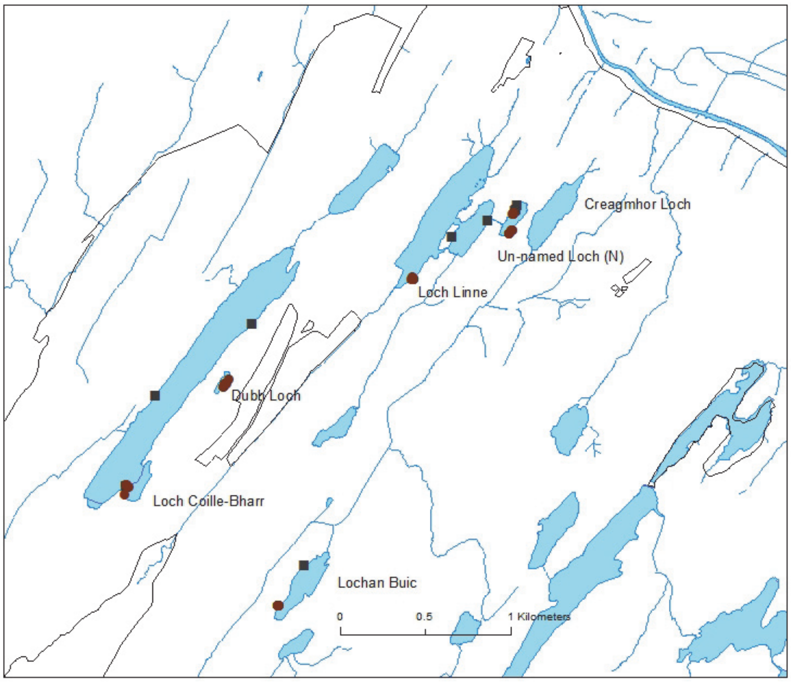
Burrows and lodges

Each pair of beavers built one to three lodges, resulting in a total of seven beaver lodges being constructed at Knapdale (Fig. 19). European beavers reintroduced to Polish lakelands also built two or more lodges per site, which they used either in different ways (e.g. a different lodge may be used by the mother and her young), or under different circumstances (e.g. seasonally; Zurowski 1992). At Knapdale, the second lodge was sometimes built on a second loch, and sometimes at the opposite end of the same loch. The Dubh Loch family, for example, were released on Loch Coille-Bharr, where they originally built a lodge, but built a second lodge on the smaller Dubh Loch, that became the centre of their activity. The female Elaine and her first male partner (Eoghann) were released on Creagmhor Loch and built a lodge there, before expanding their range to include Un-named Loch (North) where a second lodge was built (first recorded in the summer of 2010) on the northwest bank, and a third in Year 3 (summer 2011, at about the same time as the male occupants of this loch changed – see Table 1) on the south bank of Un-named Loch (North). The Linne family, and the Buic family (who exchanged male occupants with the Creaghmor pair), used a single lodge throughout the trial. All lodges were continually 'improved' with the addition of fresh materials (mud and cut branches), over the duration of the trial (during all seasons). Improvements were almost always made at the waters' edge, and may have been maintenance behaviours to counteract water erosion, adjustments in response to changes in water level, or lodge extensions (Müller-Schwarze & Sun 2003). In addition, all beaver pairs/families dug one or two burrows that were located away from the lodge; although only one of these (on Un-named Loch (N)) appeared to still be used in the final year of the trial, suggesting that these are temporary structures. In Poland, Zurowski (1992) noted that single beavers often lived in burrows, and that lodges were usually associated with reproduction. All beavers at Knapdale were released as mature pairs, which may have explained why lodges were immediately built on all lochs (all occupied lochs had lodges in construction within a year of release). A number of 'attempted' burrows were also recorded, particularly in the first two years of the trial, that were not completed due to unsuitable terrain (e.g. underlying rock) – some of these probably represented the start of lodge building or temporary burrows[27].

[27] Lodges are constructed by first digging a bank hole (tunnels in steep slopes, with the entrance underwater), which is then turned into a lodge by piling sticks over and around the entrance, and over the 'roof' of the bank hole (Müller-Schwarze & Sun 2003).



a)



b)

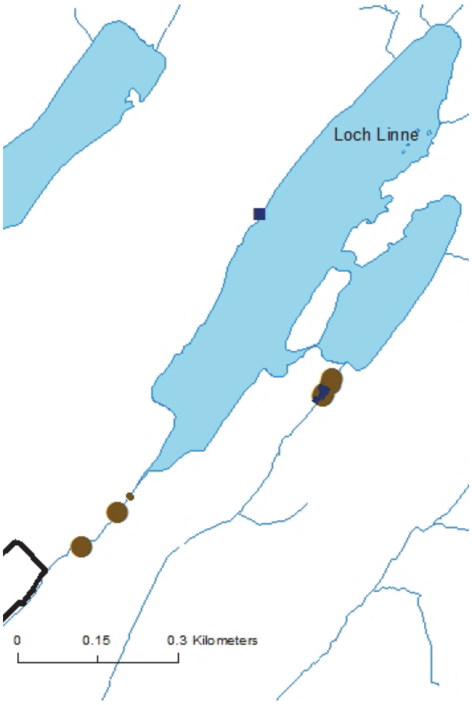
Figure 19. Lodge (brown circles) and burrow (black squares) locations, at Knapdale a) in the first two years of the trial, and b) during Year 3 - 5. Several of the burrows recorded in the first two years of the trial were 'attempted burrows' (see text). No active burrows or lodges were recorded on Creagmhor Loch after Year 2. Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

Dams and canals

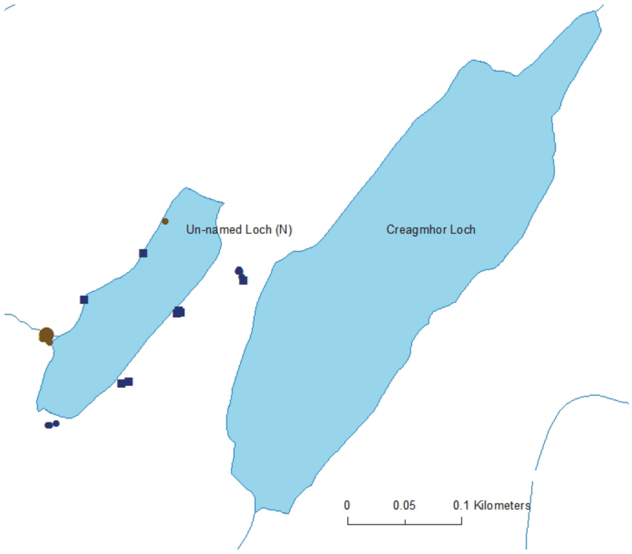
Beavers build dams to impound or to retain water, to create feeding areas, provide safe refuge (and keep the lodge entrance under water), and facilitate travel and movement of logs and branches (Müller-Schwarze & Sun 2003). Similarly, canals are constructed to ease the transport of logs and branches from foraging sites to the lodge or dam (Müller-Schwarze & Sun 2003).

Five main locations, on three lochs, were dammed throughout the trial (Fig. 20): two dams on Dubh Loch (one on the north-east bank, the other on the waterway connecting Dubh Loch and Loch Coille-Bharr), two dams on Loch Linne (both on the outflows of the main loch and the smaller south-east section, respectively) and one on Un-named Loch (North) on the western outflow that drains down a steep (impassable to beavers) bank to Loch Linne. Canal-building activities differed among the occupied lochs and were clearly most extensive on Dubh loch and Un-named Loch (North) (Fig. 20). No dams and only one canal were built on Lochan Buic.

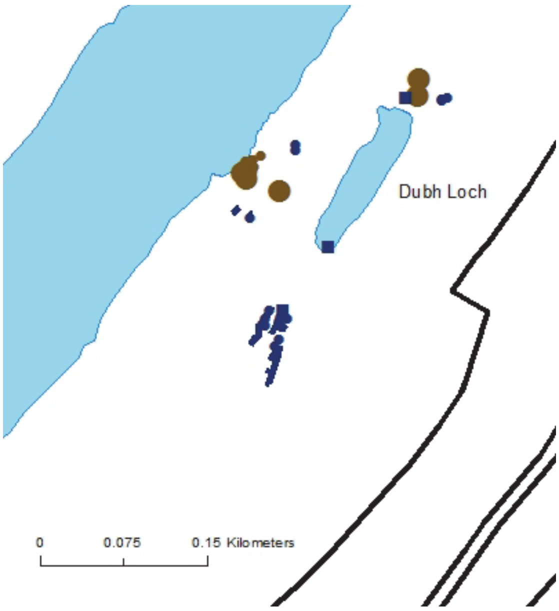
Canal construction on Dubh Loch and on Un-named Loch (North) was most extensive in Year 4 (as was all other beaver activity recorded by field signs, above), but although there initially appeared to be an apparent increase in canal building activity over time, this did not continue into Year 5 on Dubh Loch and was not the case on Un-named Loch (North) (Fig. 21) (the two lochs on which canal building was most extensive). An increase in the impact of beavers on trees (especially those close to water) in Year 4 was also noted by Iason *et al.* (2014). It is not clear what caused this apparent increase in activity and impact in a single year of the trial, but it may have been influenced by weather or by temporary changes in beaver population size or structure.



Loch Linne

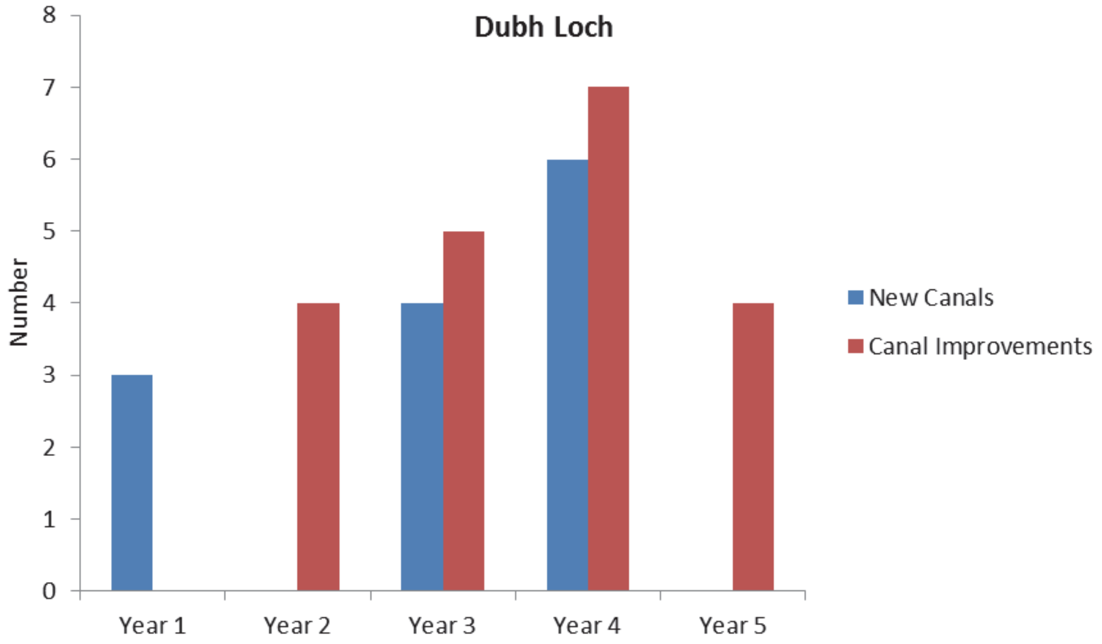


Un-named Loch (North)



Dubh Loch

Figure 20. Locations of dam (brown circles) and canal building (blue squares and lines) over all years of the trial. Note that the outline of Dubh Loch is, in reality, now much extended and extends much further south than indicated here (see Willby *et al.* 2014). *(Canals were recorded as both points and lines in the GIS database). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.*



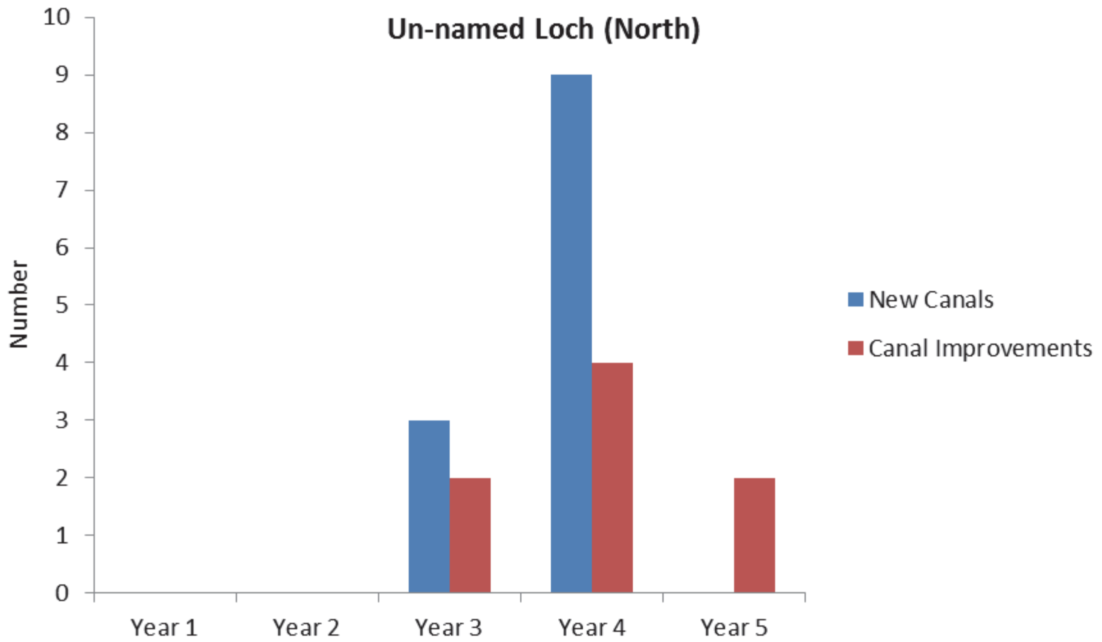


Figure 21. Canal building activity at Knapdale, over successive years of the trial, 2009-2014.

4.8 Scent marking activity

Beavers, like many other mammals, use chemical signals to communicate with one another, but they are unique among mammals in building mud piles on which they deposit secretions, forming ‘scent mounds’ (Müller-Schwarze & Sun 2003). Scent mounds are usually placed strategically throughout the beavers’ territory.

There was relatively little evidence of scent marking over the duration of the trial. Scent mounds or marking were recorded at Loch Linne, Dubh Loch, Lochan Buic and on the stream that flows from Creagmhor Loch to Lochan Buic (Fig. 22). No scent marking was recorded on Creagmhor Loch or on Un-named Loch (North). All scent marking events were recorded in spring or summer. Scent marking tends to increase as population density increases (Rosell & Nolet 1997), and so low scent marking activity in this case was probably due to low population density.

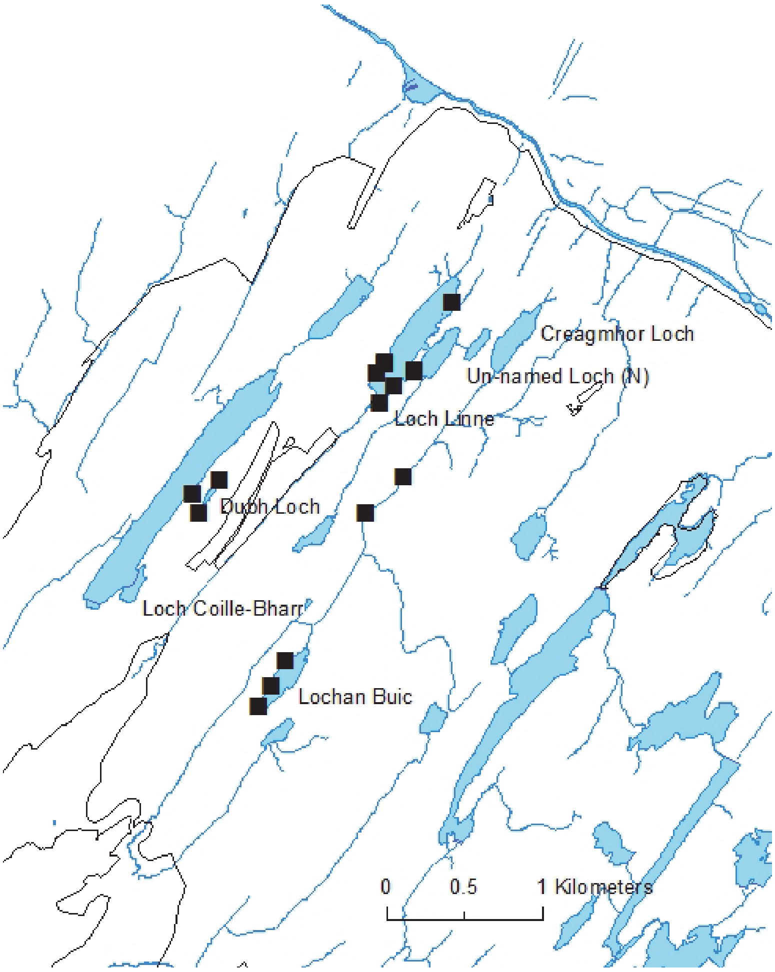


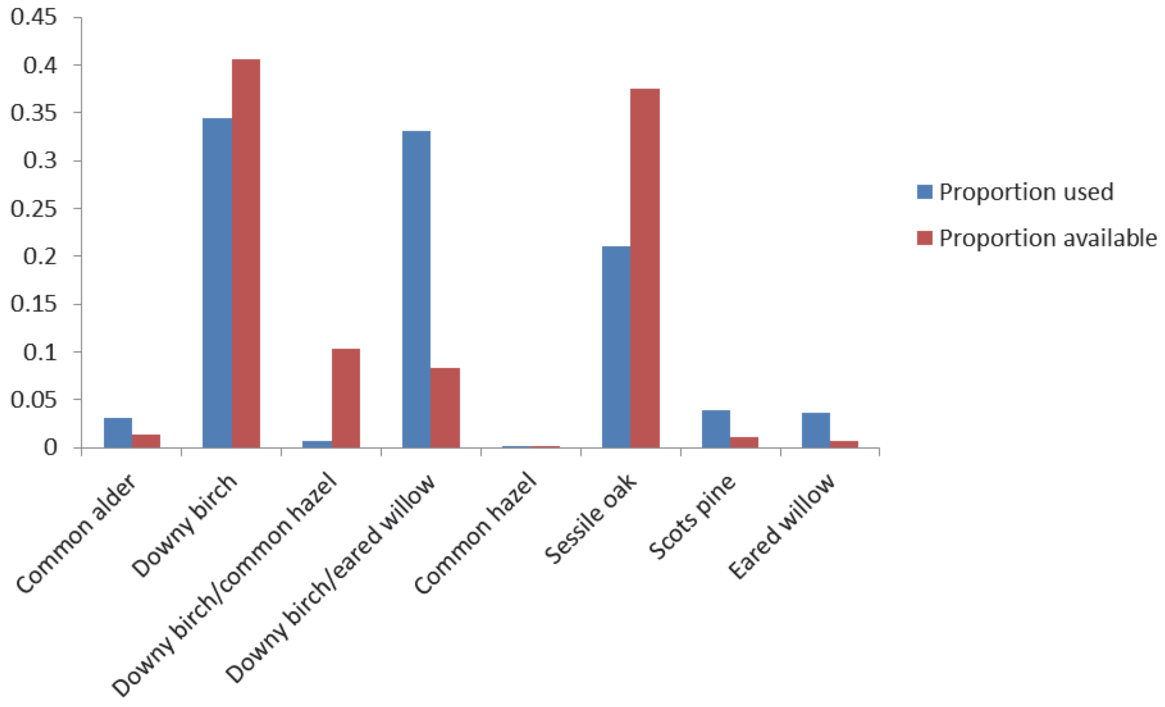
Figure 22. Scent marking activity at Knapdale over the duration of the trial. Note that each location was recorded only once; there was no evidence of maintenance or of fresh depositions. Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

4.9 Habitat use

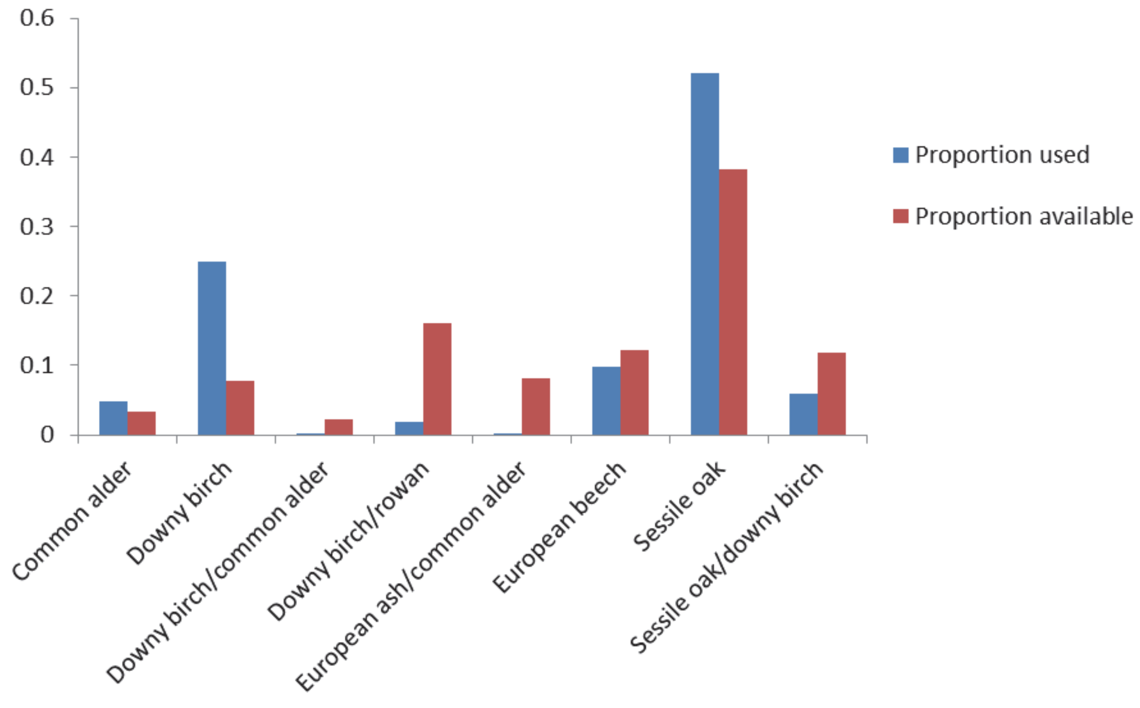
Detailed habitat descriptions of the loch-side habitat within the release area are given in Brandon-Jones *et al.* (2005) and in Iason *et al.* (2014). The loch-side area is comprised predominantly of broadleaf woodland, and, prior to the trial, by extensive conifer plantations (much of which were cleared, before beavers were released, and have been replaced by dense downy birch *Betula pubescens* regrowth). The wider release area, similarly, comprises extensive conifer plantations with blocks of native woodland, as well as smaller areas of bogs, marshes, water-fringed vegetation, fens, heath and scrub (Iason *et al.* 2014). Old sessile oak woods are present and are one of the main defining features for the Taynish and Knapdale Woods being a Special Area of Conservation.

The most dominant broadleaved tree species within all beaver home ranges was downy birch (and, for Linne Loch and Dubh Loch/Loch Coille Bharr, sessile oak); the Dubh Loch family appeared to show some preference (insofar as proportional use was greater than proportional availability) for downy birch, but all other beaver families appeared to use woodland dominated by this species in proportion with (or slightly less than) than its availability (Fig. 23). The Dubh Loch family showed an apparent preference for areas with sessile oak but the habitat data used in the analysis probably did not provide an accurate representation of habitat availability in the last three years of the trial because of the recently flooded area around this loch (as a result of beaver damming, see Willby *et al.* 2014). The Loch Linne and Dubh Loch families showed a clear preference for wet woodland and a minor preference for some of the upland woodland types (birchwood, oakwood and ashwood). There was some evidence that the Linne family preferred woodland dominated by downy birch and eared willow, *Salix aurita*, together, and eared willow where it was the dominant tree species (Fig. 23). The Creagmhor pair occupied a less diverse deciduous woodland (only downy birch and sessile oak, *Quercus petraea*, occurred as dominant species, and only upland birchwood as a woodland habitat type) – this pair appeared to use upland birchwood preferentially. We were unable to assess habitat preferences for the Buic family because only one dominant species type – downy birch– was present within their home range. The Buic family range differed from the others in woodland habitat type and was comprised predominantly of non-native woodlands, with a small proportion of wet woodland, and a very small proportion of fen, marsh and swamp – all habitat types appeared to be used approximately in proportion to their availability. Throughout, interpretation of the use of woodland habitats was hindered by the large proportion of uncategorised areas in the NWSS dataset. In the first year of the trial, cut trees and branches (n = 2,207 feeding signs) consisted of 39% downy birch, 32% willow, 18% rowan; 4% alder, 2% hazel, and 2% oak.

These findings, which provide an approximation of broad-scale habitat use, are broadly in accordance with the more detailed analyses of the effect of beavers on riparian woodland carried out by the James Hutton Institute (JHI). They report that downy birch is the most dominant tree species on most of their monitoring plots, and they suggest that beavers strongly preferred willow. Although birch was the species used most commonly by beavers, it was generally avoided, but there was some evidence of selection of large birch trees (see Iason *et al.* 2014 for further details). They also found that beavers strongly avoided alder. Hazel was used roughly in proportion with its availability (and increasingly over time), but only very small stems were gnawed. Sessile oak was poorly represented in the JHI monitoring plots and therefore categorised as 'other' species, with a number of low abundance species. The JHI woodland monitoring differs from the assessment of habitat use by beavers included here in both the scale of the monitoring and the detail. The JHI monitoring is based on detailed monitoring of 31 transects comprising 111 (4x10 m) permanent vegetation plots between zero and 30 m from the water's edge distributed across the five lochs used by beavers at Knapdale (i.e. they assess use and availability of individual trees). Whereas assessment of habitat use by beavers reported here is carried out at the level of the beaver family within their entire home range but at a broad scale. Broad scale habitat availability data describes areas by the dominant broadleaved tree species, or woodland habitat type, present – it only tells us about the ‘patch’ that the beaver is in, it tells us nothing about the beavers’ fine scale habitat use within that patch (i.e. beavers may be cutting and foraging on a tree species that occurs rarely within a patch dominated by a different tree species. For example, beavers may use areas dominated by downy birch – which is likely given their abundance – but may actually be feeding on willow).

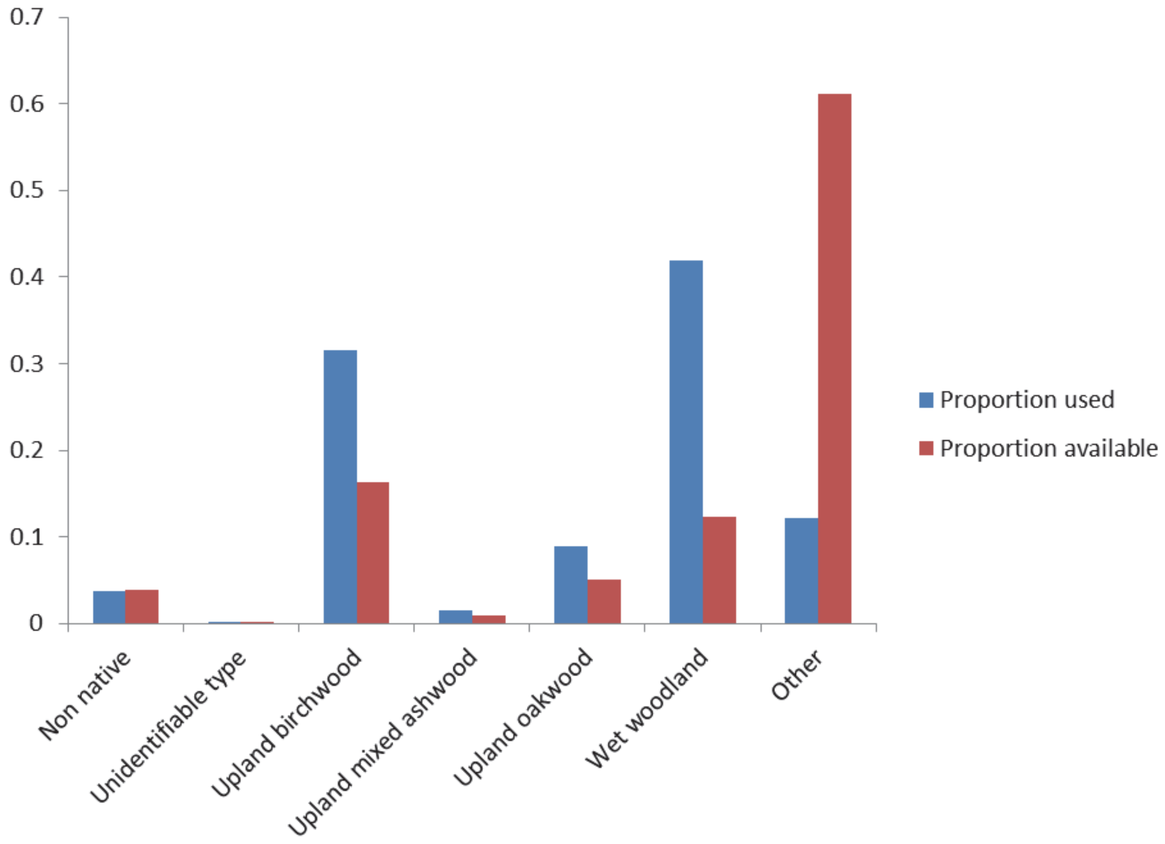


Linne family

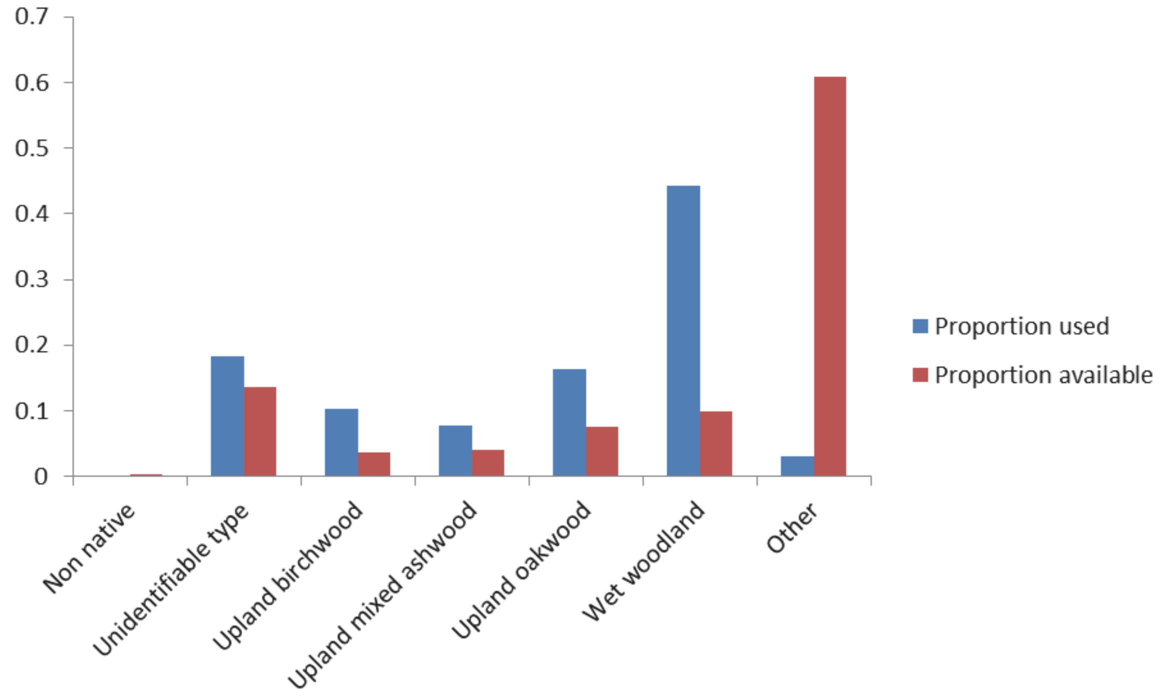


Dubh Loch family

Figure 23a. Proportional composition of riparian broadleaved woodland (by dominant tree species) within family home ranges, and proportional use by beavers (as revealed by field sign locations). The Buic family and the Creagmhor pair are not shown because their home ranges included only one or two (respectively) dominant species (see text).

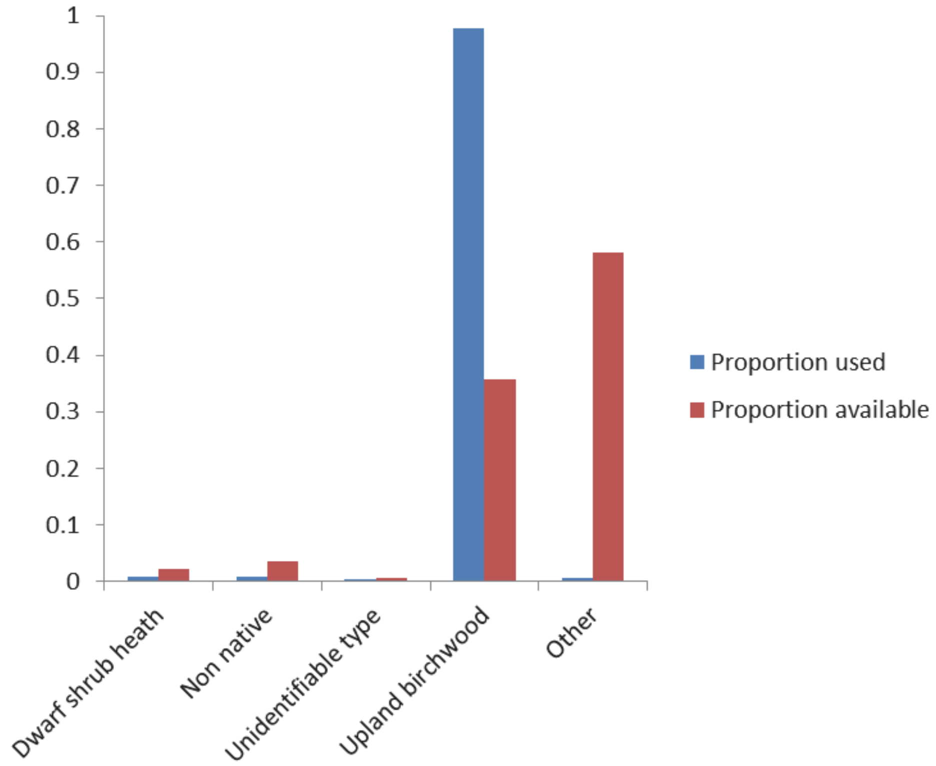


Linne family

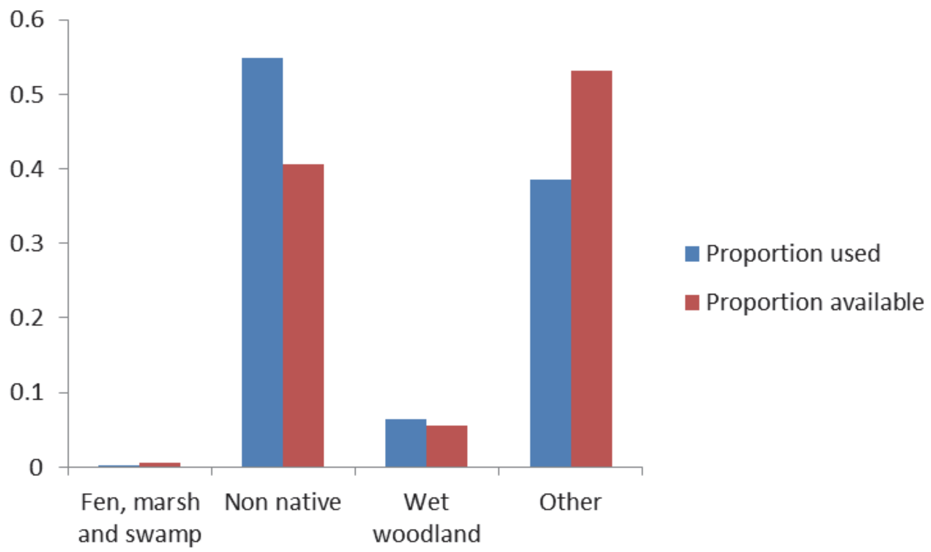


Dubh Loch family

Figure 23b. Proportional composition of native woodland habitat (by dominant habitat type) within family home ranges, and proportional use by beavers (as revealed by field sign locations). 'Other' represents areas not categorised within the NWSS dataset (see text).



Creagmhor pair



Buic family

Figure 23b (cont.). Proportional composition of native woodland habitat (by dominant habitat type) within family home ranges, and proportional use by beavers (as revealed by field sign locations). 'Other' represents areas not categorised within the NWSS dataset (see text).

4.10 Dispersal by sub-adults and identification of fieldsigns outwith the release area[28]

In the first two years of the project, two dispersal events of a subadult away from the natal group were recorded. One was dispersal of a two year old female (Marlene) in the Dubh Loch family, and the other a two year old male (Biffa) in the Linne family. Marlene was tracked via VHF telemetry south-west to a watercourse in the vicinity of the Fairy Isles and then to a nearby sea loch in August 2009 (two months post-release). She has not been seen since. Biffa remained with the Linne family for almost two years (1 year, 10 months) post-release. He was last seen in February of 2011.

During Year 3, the wild-born two year old (unknown sex) in the Dubh Loch family also appeared to disperse. That animal has not been seen since summer 2012. It is also possible (although unconfirmed) that one of the wild-born males (at either one or two years old) from the Linne family dispersed the same summer.

Dispersal of beavers from the release site constitutes important ecological information that will be crucial to the long-term management of the Knapdale population, and to assessing how beaver populations elsewhere might spread if a decision is made to reintroduce beavers elsewhere in Scotland. However, although we are able to report the proportion of sub-adults that leave their family group and at what age this occurred (assuming that these individuals have dispersed and not died), we are currently unable to estimate dispersal distances or to otherwise describe dispersal movements. Although SBT sought reports of beaver signs in Argyll outwith the trial area in the final years of the trial, none of the reports received could be verified as actual beaver presence. Beaver presence was positively identified on Shuna Island and the river Add (in November 2011), but there were no beavers there at the time of the search.

The average dispersal distance of beavers (in established populations) on the Elbe, Germany was 26 km (Heidecke 1984, cited in Macdonald *et al.* 1995) and in Switzerland most beavers dispersed 10-20 km from their natal site, but occasionally travelled up to 120 km (Stocker 1985, cited in Macdonald *et al.* 1995).

4.11 Summary and considerations regarding further beaver releases at Knapdale or elsewhere in Scotland

Within the broad remit of studying '*the ecology and biology of the European beaver in the Scottish environment*', the important (and answerable) questions relate to where the beavers settled in relation to their release sites, the size of the area occupied by beavers, the habitats used, and the extent of the beavers' various construction activities (lodge building, dam building etc.) over the duration of the trial. The extensive quarterly field sign surveys carried out by SBT over the five years of the trial, provided sufficient data to allow us to answer these questions, as applied to the release site at Knapdale. Applying these findings to '*a potential further release of beavers at other sites with different habitat characteristics*' is more difficult simply because the trial took place at a single site (as would be expected of a trial release) and so did not encompass any variability in landscape or habitat. However, the beavers on Tayside offer some insight into what might be expected in other systems. Here, we summarise the ecological data presented, and highlight what is, and what is not, known, with respect to what has actually happened at Knapdale, and what might be predicted to happen elsewhere.

[28] This section includes only individuals that dispersed from the release site at an age at which they would be expected to leave their natal (or family) range and after they had (in the case of translocated animals) spent some time within an established home range with their family. Early post-release dispersal from the release site post-release is a different process that occurs in response to translocation, represents a failure to settle at the release site, and can occur in any age animal. Cases of post-release dispersal are described in Annex 2.

Beavers released at Knapdale tended to settle either where they were released, or near to where they were released, and, for the most part, to remain within the pairs or family groups within which they had been translocated. There were, however, some local shifts in the centre of their activity (and, in one case, a change in mating partners). Three of the four beaver 'families' settled on the nearest neighbouring loch (that then became the focus of their activities) to that onto which they had originally been released. Two of the three pairs/families that settled on a neighbouring loch continued to use the original release-site loch (albeit less intensively), one beaver (a single female, Trude) did not use the original loch (Un-named Loch (South)) once it had moved. The reason for abandoning the Un-named Loch (South) is not known but may have been due to local-scale habitat effects (habitat data available within either the Knapdale woodland survey or the native woodland survey were not sufficiently fine-scale to make relevant comparisons among lochs), or perhaps a response to the death of the male beaver on that loch (possibly the female was simply searching for a new mate). The natural differences in the size of lochs meant that beaver pairs/families occupied home ranges that varied considerably in size, with larger lochs apparently used less intensively. However, the pattern of field sign locations suggested that, even on the larger lochs, beavers used, or at least visited, most of the entire perimeter of the occupied loch (with the possible exception of a small stretch of loch bank on the north west bank of Loch Coille-Bharr dominated by upland oak, and on the south east bank of Creagmhor Loch, see Figure 12). Despite the relatively large variation in home range sizes (the Dubh Loch family home range was over twice that of the Buic family, measured in length of waters' edge, and over four times the area, measured as the loch area occupied), all home range estimates were well within the range of beaver home range sizes reported in the review by Macdonald *et al.* (1995). Beaver territory size depends on food quality (Macdonald *et al.* 1995) and dispersion (McClintic *et al.* 2014), and may be related in more complicated ways to long-term resource defence (e.g. Campbell *et al.* (2005) found that territory size in Norway and the Netherlands was positively related to the proportion of deciduous habitat, which they hypothesised was associated with the slow renewal rate of woody plants). The patterns observed at Knapdale suggests that, at least for low density reintroduced populations, the size and shape of water bodies (insofar as beavers can easily reach, and thus potentially defend, the whole perimeter of the larger loch by 'criss-crossing' the loch by water, see e.g. Fig. 25d) also influences home range size. Within loch systems elsewhere in Scotland it is probably reasonable to assume that pairs of beavers will, for the most part, settle on the loch on which they are released, particularly if the landscape allows some shifting of home range boundaries. Release site fidelity may be different on rivers, where there would be no natural boundary to curtail post-release exploration.

Longer-term maintenance of established territories will likely depend on the defendability of individual territories. However, because beaver densities remained low at the end of the trial, it is not possible to predict how (if at all) increasing population pressure would impact home range size. In the Biesbosch, animals released in subsequent years tended to occupy smaller, poorer quality territories, than those released initially (Campbell *et al.* 2005). Beaver territories are marked by scent mounds (Müller-Schwarze and Sun 2003) and are defended by regularly patrolling borders (Herr and Rosell 2004). In the beaver population in Norway, that is presumed to have reached carrying capacity, incursions by neighbours are thought to be minimal (territories of neighbours overlapped by only about 2%, Herr and Rosell 2004). At Knapdale, scent marking activity is not yet well developed, which probably suggests that territorial defence is not well developed (although we do not know to what extent beavers regularly patrol their territory, see section 5.3), and, in any case, the natural separation of lochs means that there are essentially no neighbours. We do not know whether beavers (whether additional translocated individuals or wild-born dispersers) would eventually establish home ranges on the streams between lochs.

As populations grow in number, they can either increase in distribution or increase in density (or both), but because there was essentially no increase in population size over the five years of the trial, we are unable to describe how beavers might spread in the landscape at Knapdale (for example, if supplementation occurred in the future). Elsewhere, during the colonisation process following reintroduction, beavers occupied distant sites before settling close to occupied sites, resulting in an initial range expansion with a lag in density increase (Hartman 1995, Fustec *et al.* 2001, John *et al.* 2010). The dispersal of sub-adults from the occupied area could contribute to this process. Unfortunately, of the five or more probable dispersers (three translocated, and at least one wild-born) recorded during the trial, we are unable to report whether any of these individuals survived, and, if so, where (or more importantly, how far away) they settled.

Most field signs (predominantly cutting, felling or gnawing trees or branches, presumably whilst foraging or obtaining materials for construction, or both) were located within 20 m of the waters' edge, and it is likely to be the case elsewhere in Scotland (98% field signs in the Tay catchments were located within 10 m of the waters' edge, Campbell *et al.* 2012). However, although there was very low intensity use further from the waters' edge, field signs were located up to 50 m[29] away from the waters' edge, and thus some level (probably only occasional) of beaver habitat use up to 50 or more metres from the waters' edge should be expected elsewhere (with a view to management and mitigation of undesirable impacts, should they occur). No beaver impacts on the Tay catchment were recorded beyond 20 m from the water's edge, however, surveys carried out from canoe may have missed occasional impacts further from the water. However, there was no evidence of a progressive increase in the distance of field signs from the water's edge over the duration of the trial, suggesting that activity further from the water was occasional, and did not indicate a need to forage further from the water due to resource depletion nearer the waters' edge. Spread of beaver habitat use (and thus impact) away from aquatic habitats is likely to be very limited, either at Knapdale or elsewhere in Scotland, and this is supported by the woodland monitoring that showed increased use of un-preferred resources nearer the water over time, rather than use of preferred resources at increasing distances from the water (see Iason *et al.* 2014.). There were no apparent seasonal patterns in use of habitat or space.

All beaver pairs built lodges (some more than one); only three of the four pairs built dams, and damming activity was not extensive (although the impact of the Dubh Loch dam was dramatic). Although there is an extensive literature describing dam building by beavers, it is not always predictable where or in what physical conditions beavers will build dams (Hartman and Törnlöv 2006). Dam building by beavers in the Tay catchment was minimal (only three of an estimated 38-39 occupied territories had dams, Campbell *et al.* 2012) and reintroduced beavers in the Morava River basin in the Czech Republic did not build dams at all (here water levels are stable and the river channel is too wide to dam, John *et al.* 2010). Canal building activity at Knapdale was sometimes extensive (e.g. on Un-named Loch (North) in Year 4 of the trial) but was variable among beaver families/lochs and among years. The factors influencing canal building activity were not clear (since there was no consistent or clear association with year/weather or with family/loch) but may simply reflect individual beaver behaviour and/or *ad hoc* home range 'improvement' activities. Canal building activity can modify habitats (and can have positive impacts on riparian biodiversity in wetland habitats, Anderson *et al.* 2014), but, on the basis of current information, it is not possible to predict when or where, or to what extent, beavers will build canals either at Knapdale, or elsewhere. On the whole, construction activities by beavers at Knapdale appeared to be 'normal' (and habitat use, in general, appeared to be in broadly in accordance with other European studies). We still do not have the understanding required to enable us to predict when, or where, beavers will construct dams elsewhere, but this was not a specified aim of the trial. Furthermore, undesirable impacts of beaver construction activities can usually be managed and mitigated. Even if dams are built, the use of flow-control devices may reduce their impact (Lisle 2003, and Campbell *et al.* 2012, for example,

[29] 50 m was the limit within which field signs were grouped in the GIS analysis.

suggest that lodges could be protected from erosion in an attempt to reduce the need for beavers to fell large trees for repair).

During the trial, sub-adults did leave their family groups, and there was evidence of disrupting pair bonds (for reasons unknown). The adult males paired with new female partners. We do not know the fate of the sub-adult dispersers but their low numbers (and the extended time period over which they left) make it unlikely that they would have met. At Knapdale, it is difficult to see how the number of families can increase via sub-adult dispersal (and subsequent forming of new families) until the reproductive success of the existing translocated families improves substantially. However, although we do not know how many animals were released on the Tay or when, there is evidence that new pairings have established in the wild (Campbell-Palmer *et al*., 2015). Given the success of beaver reintroductions elsewhere in Europe, it is probably reasonable to assume that beaver populations elsewhere in Scotland would grow and eventually form new families. However, as suggested in Section 3, we would recommend that any new beaver release is monitored to ensure that beavers establish and reproduce successfully. Data presented in this section demonstrate that beavers at Knapdale have established successfully, but reproductive success (in terms of producing young that survive to maturity) is less clear (see Section 3).

5. BEHAVIOUR OF TRANSLOCATED BEAVERS AT KNAPDALE

5.1 Aims

The original ecological monitoring protocols (see Campbell *et al.* 2010) specified that we would provide data on nightly movements of beavers. However, the discontinuation of VHF telemetry in the first year of the trial (see section 3.2) meant that this was not possible. Behavioural observations were also discontinued in the early stages of the trial because they were time consuming and observers felt that beavers were disturbed by their presence (which may have presented a welfare issue, but also meant that the data obtained did not provide a realistic representation of beaver movements). In Year 2, in an attempt to investigate alternative affordable replacements to the discontinued radiotelemetry, SBT proposed a trial to assess the feasibility of using inexpensive GPS transmitters (i-gotU tags) sold commercially as 'route trackers', to monitor animal movements. In consultation with SBT and SNH, the decision was made to adopt the use of i-gotU tags to obtain further information on beaver behaviour and movements at Knapdale. GPS telemetry is potentially able to provide a very detailed series of locations for beavers remotely and thus without the difficulties associated with observing beavers directly or with triangulation in VHF telemetry, and without significantly increasing the workload of the field team. Tag deployment can be combined to some extent with annual trapping of animals to minimise workload for SBT, and the level of animal handling required. Given the short deployments possible with these tags (maximum 10 days), the data obtained provides a short but detailed insight into beaver behaviour at Knapdale[30]. Whilst not of high priority, we used this novel method to compare nightly movements and activity patterns with comparable behavioural data from Norway, and thus to assess whether the translocated beaver population is behaving as would be expected (with a view to assessing how well the population has settled at Knapdale, and how the animals responded to the translocation process).

The use of GPS tags meant that the opportunity existed for additional lightweight devices to be deployed on beavers. Time-depth recorders (TDRs) are very small, lightweight devices (31 mm length, 8 mm diameter, weighs 2.7 g in air and 1 g in water) that are capable of recording depth and temperature at 1 second intervals (for approximately 6 days), thus providing detailed dive profiles, and, potentially, information on how beavers use the underwater environment. Our original aim, in the opportunistic use of these devices, was to investigate the extent to which beavers foraged in the aquatic habitat at Knapdale - a question that cannot be answered using field signs[31] or GPS data[32]. However, poor deployment success (see below), and the resultant small sample size, meant that we were unable to draw inferences about beaver behaviour across individuals. However, we did record > 400 dives, from which we were able to describe, in some detail, the characteristics of beaver dives. This aspect of the monitoring work was considered to provide 'non-essential' data on beaver diving behaviour that was tangential to the main aims of the ecological monitoring work, but capitalised on the opportunity to obtain unique data that has not previously been recorded for European beavers. With the aims of the trial in mind, and in line with the use of GPS tracking of a sub-set of animals to assess the behaviour of translocated beavers, we present a summary of the dive data here and compare it with comparable dive data currently being collected from wild beavers in Norway.

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[30] Precision is not sufficient for habitat analysis (e.g. to distinguish between use of loch bank and use of the water near the edge of the loch).

[31] Field signs are not usually detected in the water, although macrophyte 'mats' are sometimes observed, as well as evidence of feeding on aquatic plants at the shoreline or in the material covering lodges

[32] In addition to difficulties associated with imprecision when animals are near the waters' edge (see footnote 18), detecting aquatic habitat use from GPS data is also complicated by the fact that a fix will only be obtained if a beaver in the water is at the surface, but not all 'surfacing events' will be recorded due to the 15 minute fix interval.

5.2 Methods

5.2.1 Appropriateness of the methods

The use of TDRs on shallow diving species is well-established, and it has been demonstrated that dives as shallow as 20 cm, and as short as 2 seconds, can be precisely measured (see Hays *et al.* 2007). i-gotU GPS tags have been used as an animal tracking device on other species (e.g. hares, Reid and Harrison 2010), and have been used increasingly in recent years on seabirds (e.g. Chivers *et al.* 2013, Soanes *et al.* 2013, Soanes *et al.* 2014). However, it is a relatively novel method, and there is little published information on the quality or the accuracy of the data obtained from these devices. Before we deployed the devices on beavers, we assessed the accuracy and the potential usefulness of the method (given the aims of the deployments as detailed above).

Two potential problems with GPS data from beavers at Knapdale are i. 'fixes' (locations) not being obtained because the animal is underwater or in thick vegetation, and ii. inaccurate locations (that may be due to the device but are also likely to be compounded by the thick vegetation and extensive water at Knapdale). The implications of the first are that details of movement patterns may be lost (which is probably not crucial), or, more importantly, that biases arise because, for instance, animal locations are never recorded in a particular habitat (e.g. closed canopy woodland). The likely extent of problems due to missed fixes can be assessed by quantifying the proportion of missed locations in the data (based on the set fix interval rate) and, in the event that some habitat types appear not to be used, by independent verification using other methods (e.g. field sign data). The implications of inaccurate locations are obvious, insofar as both habitat use and movement patterns can clearly be grossly misrepresented if either accuracy or precision is low.

The precision (the extent of scatter of recorded locations around the actual location) of the tags was tested by placing test transmitters at eight geo-referenced locations, and setting the tags to record at 15 minute intervals over approximately 12 hours (n = 43 – 49 readings). Linear errors (distance between the estimated location and the actual location) were measured in ArcGIS (version 9.0, www.esri.com) for each GPS location recorded and summarised per test. Combining all eight tests, produced median errors of 5-19 m, and maximum errors of 23-75 m, which we considered to be adequate for the purpose of measuring the nightly distances moved by beavers. Precision was not sufficient for finer-scale analyses, such as habitat use (but that was not the primary aim).

i-gotU tags were deployed by SBT on two animals in February/March 2011 (Frank and Frid, the male and female from Loch Linne) for 9 and 8 nights, respectively. Tags were successfully retained on the animals for this period of time and were removed without damage to the beaver's skin. Fixes were missed in both deployments, but >90% successive fixes were achieved within 30 minutes or less (given a programmed inter-fix interval of 15 minutes and 5 minutes, respectively). Comparison of GPS data from these two individuals with observations recorded in the first year of the trial, and field sign data from Loch Linne, demonstrated that whilst there were differences in the spatial patterns in these different data types, GPS locations were recorded across the entire home range of these beavers, and reflected fairly well the areas used as indicated by field signs; intensely used areas (e.g. the area around the lodge) were clearly highlighted. GPS locations were not obtained from inside the lodge, but that was considered to be beneficial because it meant that GPS data could be used to estimate activity periods and emergence times. Overall, the data obtained from i-Got-U tags were deemed to be suitable for our purposes.

Animal deployments

Animals were trapped as described in section 3.1. i-gotU GT-120 GPS tags (weight 20 g, MobileAction Technology, www.i-gotu.com) and CEFAS G5 TDRs (CEFAS Technology Ltd., http://www.cefastechnology.co.uk) were glued to the animals' lower back following protocols outlined in Campbell-Palmer and Rosell (2013).

The original aim was to GPS-tag all adults over two years, with half the animals tagged in early summer and half in late autumn[33] (ensuring that there was even coverage of males and females in both seasons), each individual tracked for approximately two weeks. Ideally, all adults would be tracked in both seasons and the feasibility of this was to be reviewed as the project progresses. It was agreed that the other sub-adults or non-breeding adults would be tracked opportunistically if the opportunity arose.

In all cases, GPS tags were set to record over 24 hours, with 15 minute inter-fix interval; times referred to in the text are British Summer Time (BST) for April – October, Greenwich Mean Time (GMT) for November – March. For all deployments, actual inter-fix intervals, total number of fixes, and total number of nights covered, are given in Annex 1.

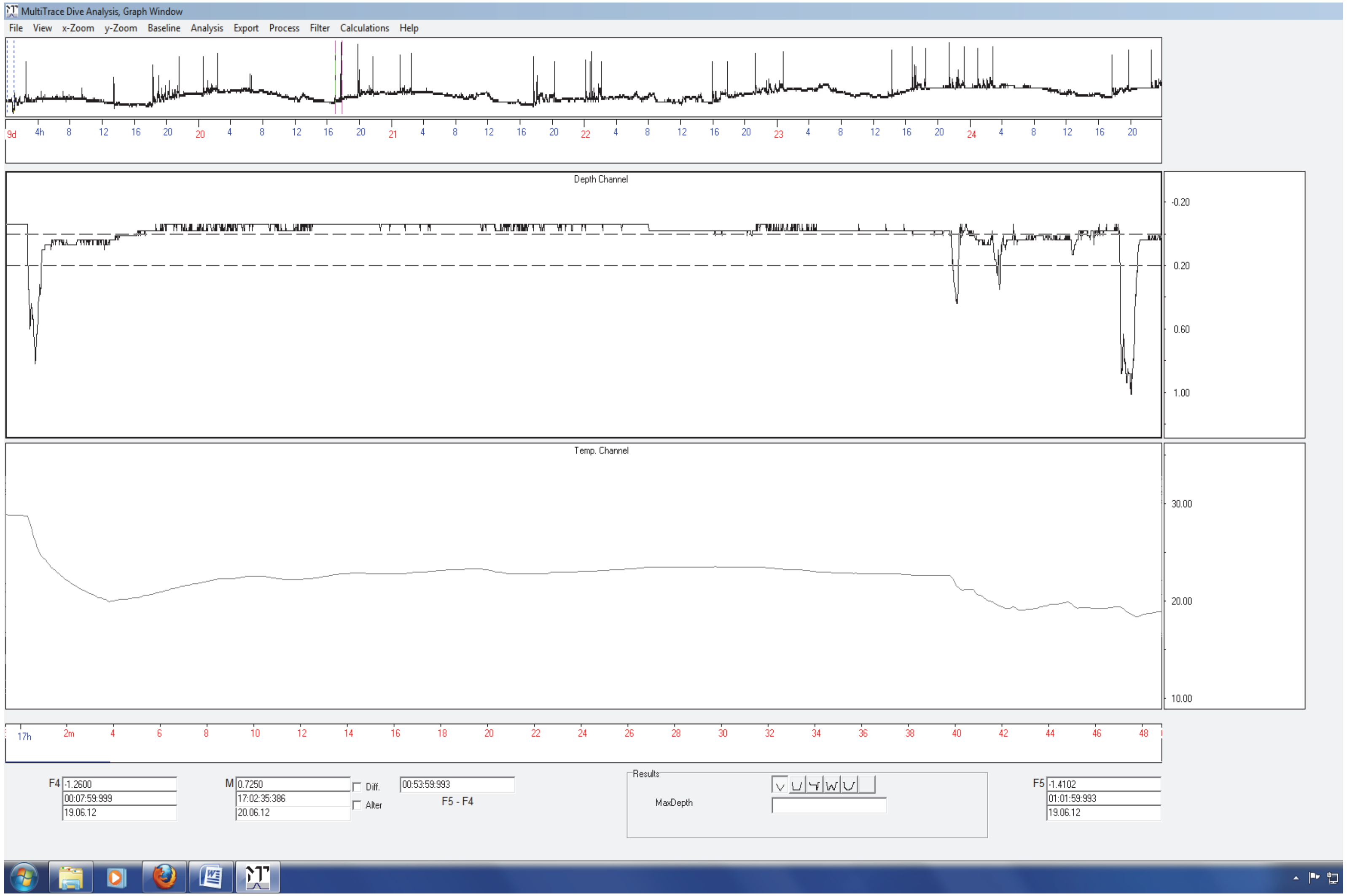
Because GPS was not priority monitoring, tagging was carried out as and when it fitted into SBT's existing field work schedule, and when it could be coordinated with annual trapping of animals. Eighteen GPS tags were deployed (including two in the initial trial), with at least one attempted deployment on each of the adult beavers, with the exception of two adults on Dubh Loch (Bjornar and Katrina) where it is difficult to trap (Table 13). Thirteen TDRs were deployed between June 2012 and October 2013 (Table 13).

The times of emergence from, and return to, the lodge were defined simply as the time of the first fix recorded each evening, and the time of the last fix recorded each morning, respectively. The length of nightly movement paths were measured in ArcGIS (version 9.0, www.esri.com). Sunrise and sunset times were from www.timeanddate.com.

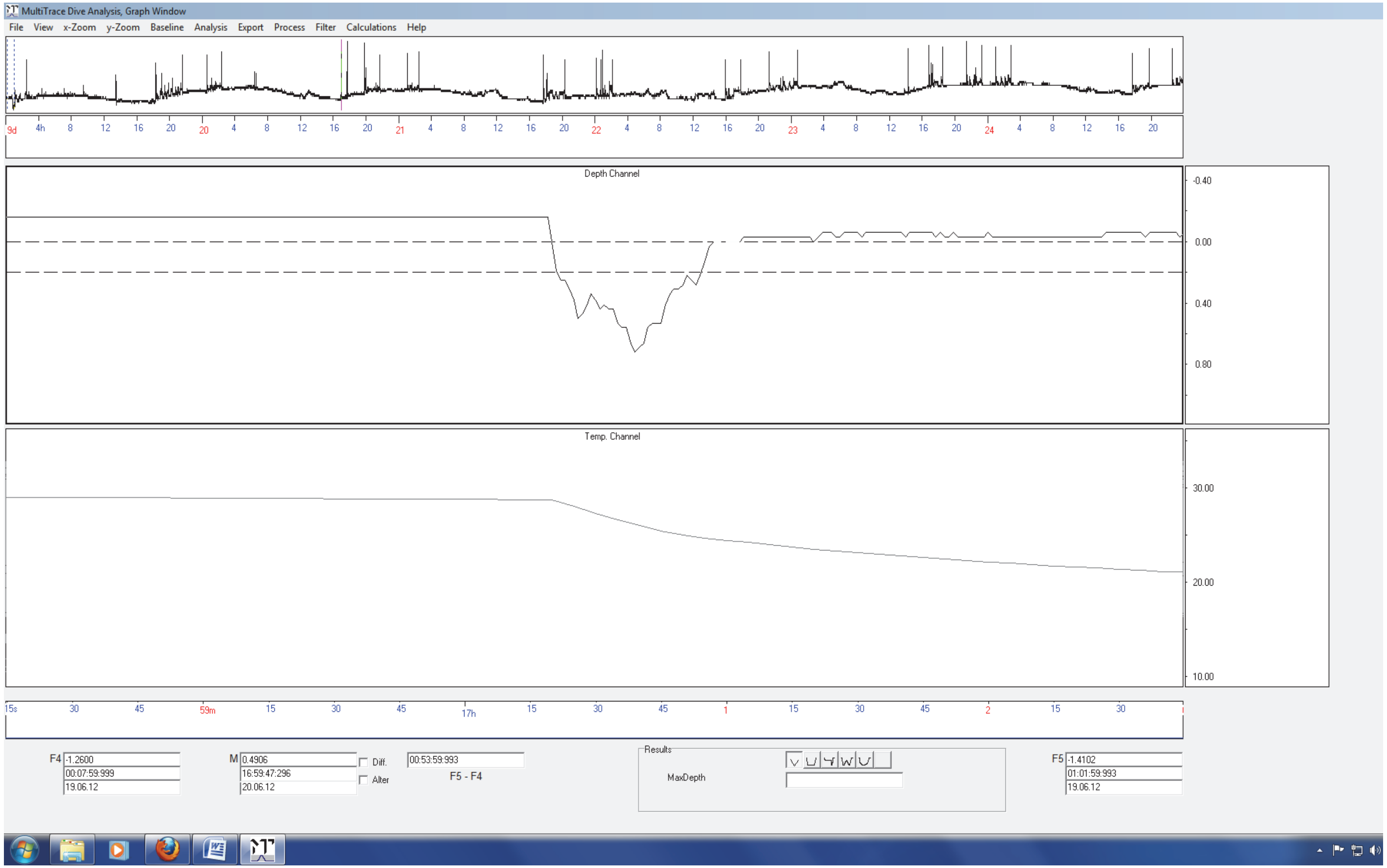
TDRs were set to record depth at 1-s intervals and temperature at 5-s intervals, over a period of 5–6 days (the total period being limited by battery life). We used MULTITRACE (Jensen Software Systems, http://www.jensen-software.com) to extract dive parameters, with a dive threshold of 0.4 m to exclude surface swimming and fluctuations in the water's surface due to wave action (precision of TDRs = 0.05 m, Hays *et al.* 2007). All dives were viewed, and the surface baseline corrected manually for each dive, before accepting parameter values. For each dive, we recorded dive depth (m) and dive duration (s).

Figure 24 illustrates the type of data obtained from the TDRs.

[33] Although the ideal situation would have been to track animals over winter, the animal welfare implications of trapping animals in winter, and the difficulties posed to fieldworkers, meant that a more feasible solution was to limit 'cold season' tracking to late autumn.


MultiTrace Dive Analysis, Graph Window
File View x-Zoom y-Zoom Baseline Analysis Export Process Filter Calculations Help
Depth Channel
Temp. Channel
-0.20
0.20
0.60
1.00
30.00
20.00
10.00
F4 -1.2600
00:07:59:999
19.06.12
M 0.7250
17:02:35:386
20.06.12
Diff.
Alter
00:53:59:993
F5 - F4
Results
MaxDepth
F5 -1.4102
01:01:59:993
19.06.12

a)



b)

Figure 24. Screen shots illustrating TDR data viewed in MtDive[34]. The top window shows the entire 6 day dataset (depth data). The two larger windows show the depth data (middle window) and the temperature data (bottom window) zoomed in to show a series of four dives over approximately 48 minutes (a) and a detailed dive profile within a four minute series of data (b). Dives are defined, in this case, as depths of greater than 0.2 m (indicated by the two dashed lines that mark 0 depth and 0.2 m depth respectively).

[34] A bespoke software program developed for analysis of TDR data by Jochim Lage, Jensen Software Systems.

5.3 Results and Discussion

5.3.1 Success of GPS and datalogger deployments

Successful retrieval of i-gotU tags and TDRs was low, and further problems were experienced with damage to i-gotU tags, which led to problems with data retrieval. Although similar problems were experienced with some of the TDRs, we were able to send these tags to the laboratory at CEFAS for data retrieval[35]. Thirteen of 18 i-gotU tags were retrieved, seven of those were obviously (beaver) damaged (resulting in either complete failure to retrieve the data or truncated datasets[36]) and a further two tags contained only limited data (Table 13). In total, nine GPS datasets were obtained from five individuals, but only three individuals (5 datasets) were successfully tracked over more than one night (Table 16).

Although preliminary i-gotU tags deployments were promising, loss rates and damage rates were too high (see Table 13) to justify continued tagging and so GPS tagging was discontinued after October 2013. Nevertheless, the data already obtained provides useful information on movements and activity patterns of a subset of animals and is presented below.

Of the 13 TDRs deployed, four were lost (probably 'groomed' off by other family members, as the tags were attached to the animals' back) and two malfunctioned during data download Table 14). Of the seven datasets analysed, one contained no dives and another showed considerable fluctuations in depth data[37] meaning that dives were difficult to define precisely. Data from the latter dataset are presented here but should be considered to include only a sample of dives actually made, and to represent only approximate measurements of dive parameters.

[35] The lack of product support for i-gotU tags is a disadvantage of the method.
[36] We assume that the tag stopped recording at the time that the tag was damaged.
[37]Possibly because the tag was approaching the end of its battery life.

Table 13. Deployment of i-gotU tags and time-depth recorders (TDRs) on translocated beavers at Knapdale, 2011-2013. Available datasets highlighted in grey.

Animal	Loch	Date of deployment	i-Got-U	TDR	Tag retrieval success
Frank	Loch Linne	22/02/11	✓		GPS data available
Frid	Loch Linne	02/03/11	✓		GPS data available
Eoghann	Lochan Buic	24/10/11	✓		i-Got-U tag lost
Trude	Lochan Buic	25/10/11	✓		GPS data available
Frank	Loch Linne	19/06/12	✓	✓	i-gotU tags damaged, limited GPS data[1]; TDR lost
Frid	Loch Linne	18/06/12	✓	✓	i-gotU tags damaged, limited GPS data[1]; TDR data available
Millie	Dubh Loch	03/07/12	✓	✓	i-gotU tags damaged, no data retrieved; TDR data available
Millie	Dubh Loch	23/10/12	✓	✓	Limited GPS data[1]; TDR data downloaded incorrectly
Christian	Un-named Loch (North)	21/11/12	✓	✓	i-gotU tags damaged, limited GPS data[1]; TDR data available
Frank	Loch Linne	29/11/12	✓	✓	Limited GPS data[1]; TDR data downloaded incorrectly
Frid	Loch Linne	29/11/12	✓	✓	GPS and TDR data available
Elaine	Un-named Loch (North)	03/12/12	✓	✓	i-gotU tags and TDR lost
Christian	Un-named Loch (North)	01/05/13	✓	✓	i-gotU tags and TDR lost
Christian	Un-named Loch (North)	26/06/13	✓	✓	i-gotU tags and TDR lost
Millie	Dubh Loch	30/07/13	✓		i-gotU tags damaged, no data retrieved
Trude	Lochan Buic	31/07/13	✓	✓	i-gotU tags damaged, no data retrieved; TDR data available
Christian	Un-named Loch (North)	10/09/13	✓	✓	i-gotU tags damaged, no data retrieved; TDR data available
Frank	Loch Linne	08/10/13	✓	✓	i-gotU tags lost; TDR data available

[1] see Table 16.

Table 14. Successful TDR deployments on translocated beavers at Knapdale, 2011-2013.

Animal	Loch	Date of deployment	Tag no.	Total dives recorded
Frid	Loch Linne	18/06/12	8230	35
Millie	Dubh Loch	03/07/12	8226	272
Christian	Un-named Loch (North)	21/11/12	8232	0
Frid	Loch Linne	29/11/12	8224	130
Trude	Lochan Buic	31/07/13	8232_2	115
Christian	Un-named Loch (North)	10/09/13	8232_3	119[1]
Frank	Loch Linne	08/10/13	8226_2	85

[1] This is a sample of dives performed by this animal (see text).

Activity patterns of beavers

Table 15 summarises individual beaver activity patterns, in terms of time of emergence from the lodge, time of return to the lodge and the time spent active and out of the lodge. With the exception of one individual (Frid) in June, emergence times appeared to be relatively consistent among individuals (medians per individual occurring between approximately 1900 hours and 2200 hours). Time of return to the lodge appeared to be slightly more variable (medians per individual occurring between approximately 0500 hours and 1000 hours, excluding Frid in June). Neither emergence time nor return to lodge time appeared to be closely related to sunset or sunrise times. Frid returned to the lodge earlier in June (0212 hours, when sunrise time was 0430 hours), which was probably related to the fact that she had young kits in the lodge at the time rather than sunrise time *per se*; however, at the same time of year, Frid also emerged from the lodge early (1740 hours) although sunset time was late (2200 hours). Frid was active for 452 minutes in June, Frank was also only active for an average of 510 minutes in June – both values were comparable to activity period durations reported in Sharpe and Rosell (2003) for beavers in Norway in spring and summer, but were the shortest activity durations recorded at Knapdale. Activity periods recorded in autumn and winter in Knapdale appeared to be substantially longer (up to almost 2 hours longer) than summary values reported in Sharpe and Rosell (2003) for beavers in Norway, but comparable to those reported for translocated beavers in the Biesbosch (Nolet and Rosell 1994). The maximum mean activity period recorded by Sharpe and Rosell (2003) in Norway was 584 minutes (9.7 hours), but these authors did not include animals in autumn when foraging and food caching, as well as 'pre-winter' construction activity, might be expected to increase in preparation for winter. Nolet and Rosell (1994) reported activity periods of up to 12 hours in winter[38], and found that during ice-free conditions in winter, beavers were more active (rested less) than during spring or summer. Activity periods of translocated beavers in Knapdale were between 530 and 701 minutes (8.8 – 11.7 hours) in autumn/winter.

Table 15. Activity patterns of four beavers at Knapdale (on eight separate occasions) as inferred from GPS data. Times are given in decimal hours (BST in June and Oct deployments, GMT in November and February); activity period is in minutes[39].

Animal[1]	**No. nights[2]**	**Emergence time Median (IQR)**	**Return time Median (IQR)**	**Activity period Mean ± SD**
Frank (Jun)	3	20.27 (19.69-20.63)	05.47 (04.52-07.90)	510.94 ± 65.25
Frid (Jun)	1	17.68 (17.28-18.08)	02.21 (02.11-02.30)	452.27
Trude (Oct)	9	19.31 (18.93-19.40)	06.76 (06.52-06.86)	680.11 ± 50.65
Millie (Oct)	1	20.04 (19.91-20.17)	08.07 (07.06-09.08)	616.13
Frank (Nov)	1	21.25 (21.15-21.35)	09.63 (08.49-10.76)	617.67
Frid (Nov)	6	22.10 (21.71-22.32)	10.02 (09.48-10.42)	701.01 ± 30.65
Frank (Feb)	7	21.68 (21.02-22.25)	06.78 (06.62-06.80)	530.50 ± 53.52
Frid (Feb)	6	19.87 (19.63-19.94)	06.88 (06.35-06.96)	645.88 ± 51.70

[1] Christian was not included because only one full night was covered, during which < 10 locations were obtained – it is not clear whether this was a short active period, or poor ability of the GPS to obtain locations. If these data are reliable, this animal was active the previous daytime morning until approx. 12 am, but only active for 47 minutes during the 'whole' night he was tracked.
[2] This is number of full nights to allow calculation of length of active period. Note that single nights include emergence/return times for the previous and following nights and thus have more than one emergence/return time.

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[38] We infer activity periods, in this case, on the basis of resting periods (Tr) reported in Nolet and Rosell (1994) and assuming that activity = 24 – Tr.
[39] Because fixes were only recorded every 15 minutes, emergence and return times recorded by i-gotU tags could be up to 15 minutes later (or earlier, respectively) than the actual emergence/return time of the beaver; thus, activity periods may be under- or over- estimated by up to 30 minutes (taking into account actual inter-fix intervals achieved, see Annex 1).

Nightly movements

The four beavers successfully tracked moved an average of 2,406 m per night (± 918 SD, n = 34 nights in total, Table 16). This is comparable to the distances moved by female beavers in Norway (2,572±1204 m) reported by Herr and Rosell (2004), although somewhat less than the movements reported for males (3,756±2247 m), and less than more recent measurements of nightly distance moved by beavers in Norway (c. 4 km for both females and males, range 3,241 – 6,891 m, Echeverria 2014). In Biesbosch, beavers moved an average of 5 km per night in winter, but within territories of 5 – 10 km (considerably longer than the home ranges occupied by beavers at Knapdale of between 1.8 and 4.7 km). The longest nightly movement recorded at Knapdale (> 4 km, see Table 16) was made by Millie, who inhabits the largest loch (Loch Coille-Bharr[40], with a perimeter of 4.3 km). However, it is also interesting that beavers occupying one of the smaller home ranges at Knapdale (Lochan Buic) appeared to make similar length nightly movements as did the beavers occupying the larger home ranges on Loch Linne and Dubh Loch/Loch Coille-Bharr (Table 16, Table 12). Unfortunately, we were unable to obtain reliable GPS data from the beavers on Creagmhor Loch/Un-named Loch (North). Beavers in Norway occupied territories of c. 4 km (Echeverria 2014).

It is important to remember that these data are only short-term data on a subset of animals - for example, there was only one night of data for Millie, so it was not possible to determine whether she travelled a long distance (around the entire perimeter of Loch Coille-Bharr) every night. Nightly movements revealed that beavers at Knapdale did not always cover their entire territory, or patrol the entire boundary of their home range, every night (see Fig. 25). In contrast, Nolet and Rosell (1994) suggested that beavers in Biesbosch in the third or fourth year post-release, patrolled their territories daily (although this assumption was on the basis of a 1:1 relationship between distance moved and territory size, rather than mapped movements matched with territory boundaries).

Examples of nightly movement paths are shown in Figure 25.

Table 16. Nightly movements of four beavers at Knapdale (on eight separate occasions) at Knapdale as inferred from GPS data. Distances moved are mean distance moved per night ± standard deviation (n = no. nights).

Animal[1]	**Loch**	**No. nights[2]**	**Total distance moved per night (m)**
Frank (Jun)	Loch Linne	3	2059±366
Frid (Jun)	Loch Linne	1	1770
Trude (Oct)	Lochan Buic	9	2331±663
Millie (Oct)	Dubh Loch	1	4492
Frank (Nov)	Loch Linne	1	1562
Frid (Nov)	Loch Linne	6	2654±497
Frank (Feb)	Loch Linne	7	1922±464
Frid (Feb)	Loch Linne	6	2460±723

[1] Christian was not included because only one full night was covered, during which < 10 locations were obtained – it is not clear whether this represents limited movement on that night, or poor ability of the GPS to obtain locations.
[2] This is number of full nights to allow calculation of length of nightly movements.

[40] Millie is part of the Dubh Loch family and although field signs suggest that this family predominantly use the smaller Dubh Loch, both field sign data and Millie's movements show that they also use most of the perimeter of the larger Loch Coille-Bharr.

Figure 25. Examples of nightly movement paths of beavers at Knapdale, as inferred from GPS locations recorded at approximately 15 minute intervals (see Annex 2), for a) Frank in February 2011, b) Frid in March 2011, c) Frid in March 2011, d) Millie in October 2012, and e) Trude in October 2011. b) and c) illustrate variation among nights for a single individual; d) and e) illustrate differences in movement distances on lochs of different sizes (note the different scales). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

5.4 Dive behaviour

The following summaries exclude data from Christian. Average mean dive duration was 25.0 s, average mean dive depth was 0.8 m and average maximum dive duration 60.5 s (n = 5 datasets from 4 individuals, Table 17). Average maximum dive depth was 1.6 m, and the overall maximum dive depth recorded was 2.4 m (Table 17). Mean dive duration and depth were comparable with mean dive parameters recorded for beavers in Norway, although the maximum dive durations recorded at Knapdale, of approximately one minute, were considerably shorter than the maximum dive duration of almost 5 minutes recorded in Norway (P. Graf and F. Rosell, unpub. data). Excluding Frid in June - who dived very little, perhaps because she was lactating - Knapdale beavers performed, on average, between 15 and 45 dives per day – unfortunately, comparable data on daily diving rates from Norway were not available. It is likely that beavers at Knapdale do dive more often, and can dive much deeper than reported here, because Christian made over 50 dives per day and appeared to be diving up to 3.5 m. Data obtained from Christian did not allow precise parameter estimates. Shallow dives recorded at Knapdale are probably a reflection of habitat differences rather than physiological differences in the animals themselves. Many species make shallower dives than they are physiological capable of since dive depth is a function of water depth and the depth at which prey/forage is located. Further, dive duration is usually correlated with dive depth, and thus shallower dives in shallow aquatic habitats would be expected to be of shorter duration than deeper dives by the same animal. Some of the larger lochs at Knapdale are deep: maximum depths of Loch Linne and Loch Coille-Bharr are 27 and 28 m, respectively[41], so dive depth at Knapdale is not constrained by loch depth. However, some of the smaller, and particularly productive lochs (e.g. Dubh Loch) are < 5 m deep (maximum depths of the other beaver-occupied lochs at Knapdale are between 5 and 15 m)[36], and evidence from macrophyte monitoring suggests that beavers on Loch Linne/Loch Fidhle were foraging on aquatic plants at a depth of 1.5 – 2.5 m (Willby *et al.* 2014), which is in accordance with maximum dive depths recorded. Presumably aquatic foraging by beavers takes place around the shallower edges of the loch where stands of aquatic and semi-aquatic macrophytes occur. The nightly movements shown in Figure 25 suggest that this is the case, but imprecision in GPS locations mean that it is difficult to distinguish between aquatic and terrestrial habitats, where locations occur near the waters' edge.

Although we were only able to record dive behaviour for a subset of individuals, and over short periods of time (3-6 days), we did detect considerable variation among individuals in both duration and depths of dives (see Table 17), suggesting that beavers at Knapdale exhibit a range of behaviours, as might be expected, in accordance with local habitat and seasonal needs.

[41] From Willby *et al.* (2014) based on modelled maxima as given in the GB Lakes Inventory, field survey estimates, or (for Loch Linne and Loch Coille-Bharr) from bathymetric mapping in 2012 commissioned by SNH.

Table 17. Summary of dive parameters for five beavers at Knapdale fitted with TDRs

Animal (month) _ Loch	Dive duration (s) mean, range	Dive depth (m) mean, range	No. dives/day mean, range, n days
Frid (June) _ Loch Linne	21.7, 10.6 – 49.3	0.6, 0.4 – 1.0	6.2, 4 – 8[1], 5
Millie (July) _ Dubh Loch	20.8, 5.0 – 77.2	0.9, 0.4 – 1.9	45.3, 21 – 59, 6
Frid (Nov) _ Loch Linne	34.3, 14.8 – 58.0	1.4, 0.4 – 2.4	22.4, 17 – 27, 5
Trude (July) _ Lochan Buic	22.0, 5.0 – 51.0	0.7, 0.4 – 1.5	22.0, 16 – 27, 5
Christian (Sept) _ Creagmhor Loch/Un-named Loch (North)	40.2, 8.0 – 97.0[2]	1.2, 0.4 – 3.5[2]	≥55, 3[2]
Frank (Oct) _ Loch Linne	26.1, 5.2 – 66.9	0.5, 0.4 – 1.1	15, 3 – 49, 5

[1] Frid was probably suckling young kits during this deployment
[2] This is a sample of dives performed by this animal, and parameters are approximations (see text).

5.5 Limitations and concluding remarks

In summary, although the data were limited (and comparative data not completely comparable), there is nothing to suggest that beavers at Knapdale were behaving very differently (in terms of their activity patterns and nightly movements) than beavers in Norway, although they were perhaps active for longer in autumn. Data from the Biesbosch (see Nolet and Rosell 1994) suggest that beavers may normally be active for longer in winter and early spring (November to March in their study), but, because the Biesbosch population was also a translocated population, it is not clear whether this reflects a seasonal difference, or a translocation effect (and comparisons are undoubtedly influenced by site-specific differences, particularly as relates to food availability). Further data to refine activity period estimates at Knapdale year-round would be ideal, as would further comparative data from Norway. However, in the absence of additional behavioural or biological areas of concern, it is probably of low importance.

The relatively short nightly distances moved by beavers at Knapdale are probably at least partly explained by the relatively small areas occupied, and may suggest that territorial activity is not yet well developed at Knapdale (perhaps due to the low densities present and the distances between occupied lochs). The relatively low level of scent marking recorded during field sign surveys provides support for the latter. However, neither the length, nor the pattern, of nightly movements currently warrants concern. Similarly, average dive parameters matched those recorded in Norway well, and whilst differences in extreme behaviours may be detected when further comparative data are available from Norway, it is more likely that these will be related to habitat differences rather than physiological or behavioural differences in the beavers themselves.

In future, it might be insightful to investigate the energetic implications of inhabiting a large range with patchy resources (e.g. Loch Coille-Bharr) as compared with a smaller one with abundant resources (e.g. Lochan Buic and the small 'ford' pond to the north of it, see Fig. 12); however, there is currently no evidence to suggest that the Dubh Loch family (which use Loch Coille-Bharr) are faring any worse than the Buic family in terms of either body condition (see Goodman 2014.) or reproductive success.

The short-term deployments possible with these devices meant that this part of the study was not designed to assess behaviour over the duration of the trial. Poor retrieval rates of devices also meant that we were unable to compare behaviour across beaver families occupying different lochs. Differences in diving behaviour among lochs comprising different aquatic habitats might, for example, help explain differences in beaver impact on aquatic vegetation (see Willby *et al.* 2014), or perhaps provide insight as to how beavers respond to depletion of favoured aquatic plant species, although inferences in either case would also be limited by small sample size (due to the limited number of beavers included in the trial).

However, this part of the study was opportunistic, insofar as it was not part of the original monitoring protocols, and these ecological questions were not within our remit as stated in Campbell *et al.* (2009). We were able to obtain detailed behavioural information from a subset of individuals that allowed a broad comparison with similar studies of beavers in the source population in Norway, and this allowed us to infer that there was no evidence that translocated beavers at Knapdale were behaving ‘abnormally’. On the basis of these somewhat limited findings, there is currently no reason to suggest that other individual beavers would not adapt similarly well to release either at Knapdale or elsewhere in Scotland. However, with animal welfare considerations in mind (see Harrington *et al.* 2013), we would always advocate some level of monitoring for any future translocation.

GPS tags and dataloggers are both useful devices for the provision of behavioural and ecological data that would otherwise be unobtainable. However, further use of GPS tags or other types of dataloggers on beavers at Knapdale, or elsewhere, if deemed necessary or useful for future monitoring or research, would require improvement of attachment methods and protection of the devices themselves during deployment (e.g. protection from other beavers biting the devices).

6. DID THE BEAVER RELEASE HAVE A NEGATIVE IMPACT ON OTTERS AT KNAPDALE?

6.1 Aims

One of the qualifying features of the Taynish-Knapdale Woods Special Area of Conservation (SAC) is the European otter (*Lutra lutra*) (which is also a UK BAP priority species and a European Protected Species). To demonstrate that the trial reintroduction of beavers into the SAC would not negatively impact on this particular qualifying feature, otter presence in the area was monitored over the duration of the trial. Two other riparian mammals - the American mink (*Neovison vison*) and the water vole (*Arvicola amphibius*) were also included in these surveys, as the former, at least, can be readily surveyed using the same methods as for the otter, and both occur in the same riparian habitats. Water voles are a UK BAP priority species and, if information on its occurrence could be collected at the same time, this was considered to be beneficial, as the current distribution of water voles in Scotland is still incompletely known. The American mink is a non-native invasive species, currently subject to local control measures.

Given the important ecological role that beavers play in influencing the hydrology of their habitat, and experience from elsewhere in their European range, negative impacts from beavers on any of these other species were considered unlikely.

6.2 Methods

Survey methods were based on Strachan (2007) and were undertaken by SNH. Surveys were carried out within the release area and, for comparison, in a separate and independent control area. The control area was selected to be of similar habitat to the release area but located far enough outside the release area to minimise the chance of a single otter territory overlapping both the release area and the control area. The area of Forestry Commission land surrounding Loch Glashan to the north-east of the Crinan canal was considered suitable for this purpose. Otter, mink and water vole field signs were recorded at all sites (details below). Further additional data on the presence of mink were provided by SBT from their mink control activities; SBT also provided incidental species data recorded on an *ad hoc* basis during camera trapping and other activities (including visitor sightings).

Twenty 100 m linear sites (10 in the release area, all on catchments used by beavers but not necessarily within the area currently occupied by beavers (see Fig. 26) and 10 in the control area) were surveyed annually in autumn (September – November[42]) between 2009 and 2013. Survey sites were selected amongst three broad habitat types (inland watercourse, freshwater loch outflow, coastal watercourse outflow/shoreline), with the additional specification that the two national otter survey sites within the release area – unnamed burn near Gariob Cottage, OS grid ref. NR781891 and the burn near Loch Barnluasgan, OS grid ref. NR789910 – were included amongst the ten sites to allow the use of survey data from earlier national otter surveys. Most sites were associated with bridges or obvious physical features such as loch outflows, and the same sites were surveyed each year. A full list of survey sites is provided in Table 18, and photographs are included in Harrington *et al.* 2012 and Harrington *et al.* 2013.

Sites were surveyed by searching the entire length of the 100 m site and recording the following field signs: sightings (actual animals seen), total number of otter spraints, number of otter resting places, presence of tracks/runs etc., total number of mink scats found, presence of mink tracks, other evidence of mink (including local reports), total number of water vole latrines, presence of water vole burrows and feeding signs. At most sites, it was possible to conduct the survey by walking within the watercourse channel and recording any

[42] Exceptionally December at some sites in one year

field signs observed from there. In very narrow watercourses, both banks could be inspected simultaneously, whereas at others it was necessary to survey each bank separately and/or complete part of the survey from the bank. Two of the larger watercourses (sites 3 and 16) were surveyed along one bank only. The length of each survey section was estimated by counting paces as the survey progressed, and the distance from the start to the first evidence of otter was recorded.

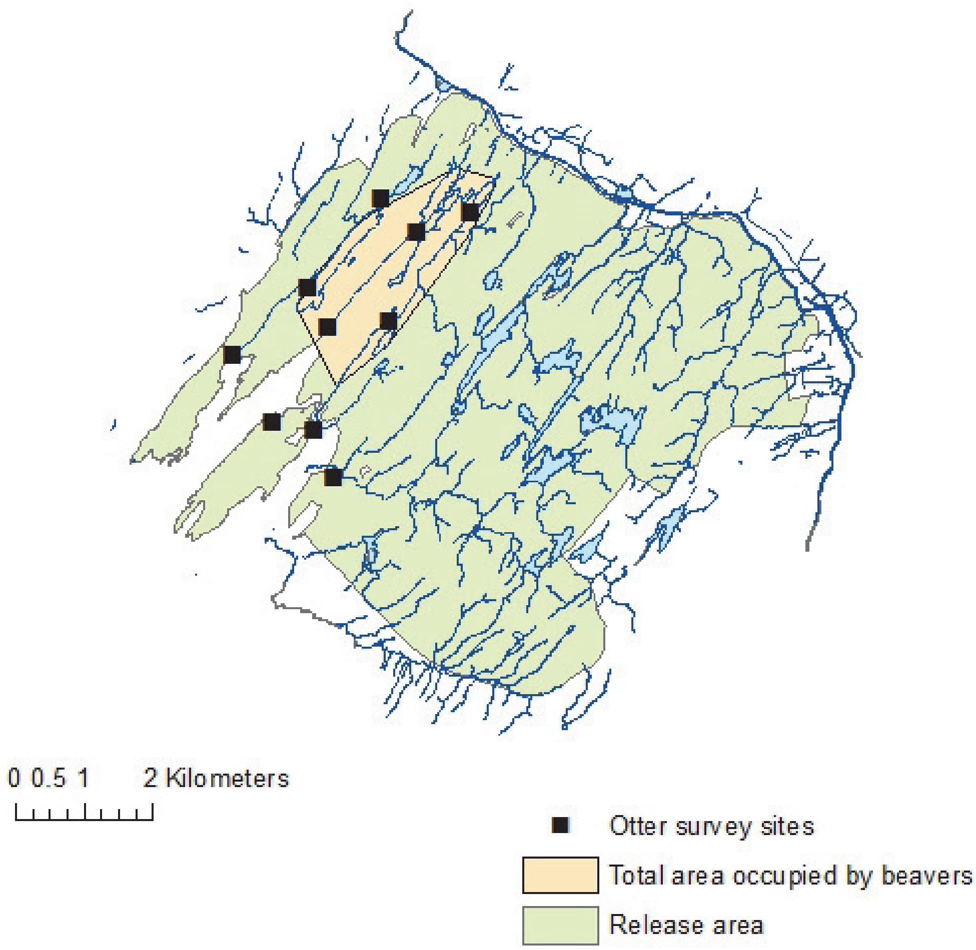


Figure 26. Otter survey sites within the release area, Knapdale, Argyll. The same sites were surveyed each year. 10 additional 'control' sites were surveyed outside the release area (locations in Table 18). Fresh water features are reproduced from the Ordnance Survey Great Britain MasterMap Topographic Area data © Crown Copyright and database rights 2015 Ordnance Survey 100017908.

Table 18. Location of all survey sites inside and outside the trial area. National survey sites are highlighted in bold. Sites 1-10 are control sites, sites 11-20 are within the trial area.

Site no.	X	Y	Description	Habitat type
1	188600	690900	100m downstream d/s of track	Inland
2	**194500**	**692400**	**100m d/s of road bridge**	**Inland**
3	191200	694800	100m d/s of track	Inland
4	191200	690200	100m u/s of entrance to un-named pond/lochan	Inland
5	**191700**	**689200**	**100m u/s of road bridge**	**Coast**
6	**192600**	**691500**	**100m d/s of road bridge**	**Coast**
7	191700	686600	100m south of landward end of pier	Coast
8	192000	692700	100m d/s of dam	Freshwater loch
9	193300	695800	100m d/s of fish ladder	Freshwater loch
10	195300	697000	100m d/s of dam	Freshwater loch
11	**178900**	**691000**	**Burn near L. Barnluasgan - d/s from road**	**Inland**
12	176700	688700	coastal burn u/s from shore	Coast
13	177800	689700	outflow from L. Coille-Bharr	Freshwater loch
14	**178100**	**689100**	**d/s from bridge - By Gariob cottage**	**Inland**
15	179400	690500	outflow from L. Linne	Freshwater loch
16	177300	687700	100m d/s of road bridge by L. Craiglin	Coast
17	177900	687600	up un-named coastal burn from shore	Coast
18	180200	690800	outflow from L. Creagmhor[43]	Freshwater loch
19	179000	689200	d/s confluence of 2 un-named burns, by ford	Inland
20	178200	686900	d/s confluence of Barnagad Burn & Alltan Ghabhar	Inland

Spraint surveys are not suitable for assessing habitat use by otters (because marking behaviour may not be associated with preferred habitats or habitats frequently used) but are useful for detecting broad changes in otter presence, distribution and relative abundance. Note that individual survey sites were not independent (although survey areas were) insofar as they might be occupied by the same otter, and thus site occupancy does not relate to number of otters.

Ten mink rafts were monitored by SBT at monthly intervals for management purposes (to inform any mink removal work required); these also provided potentially useful data on the presence and relative abundance of mink in the area.

Statistical analyses were carried out in R (version 3.0.2, R Core Team 2013).

6.3 Results

6.3.1 Otters

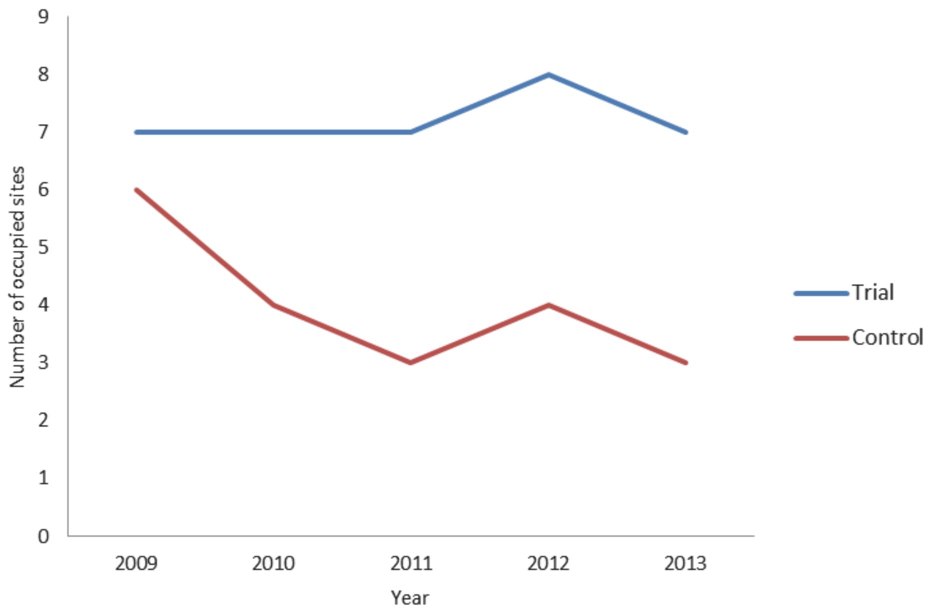
Evidence of otter activity (mostly spraints or footprints/otter paths) was recorded at between seven or eight survey sites (80%) annually in the trial area, and between three and six survey sites (60%) in the control area. This is slightly lower than the overall mean number of positive sites recorded across the SNH Argyll & Stirling Area during the 2003/04 national survey (89.13%). It is perhaps noteworthy that weather conditions (particularly high water levels) and delays in the timing of the survey (meaning that the surveys were carried out after autumnal leaf-fall) in the first three survey years meant that otter (and mink) presence may have been underestimated, but that in 2012, the survey was carried out earlier in the year (end of September) and during particularly dry conditions, which may have improved

[43] For practical reasons this site replaced the original site at the outflow of Loch McKay

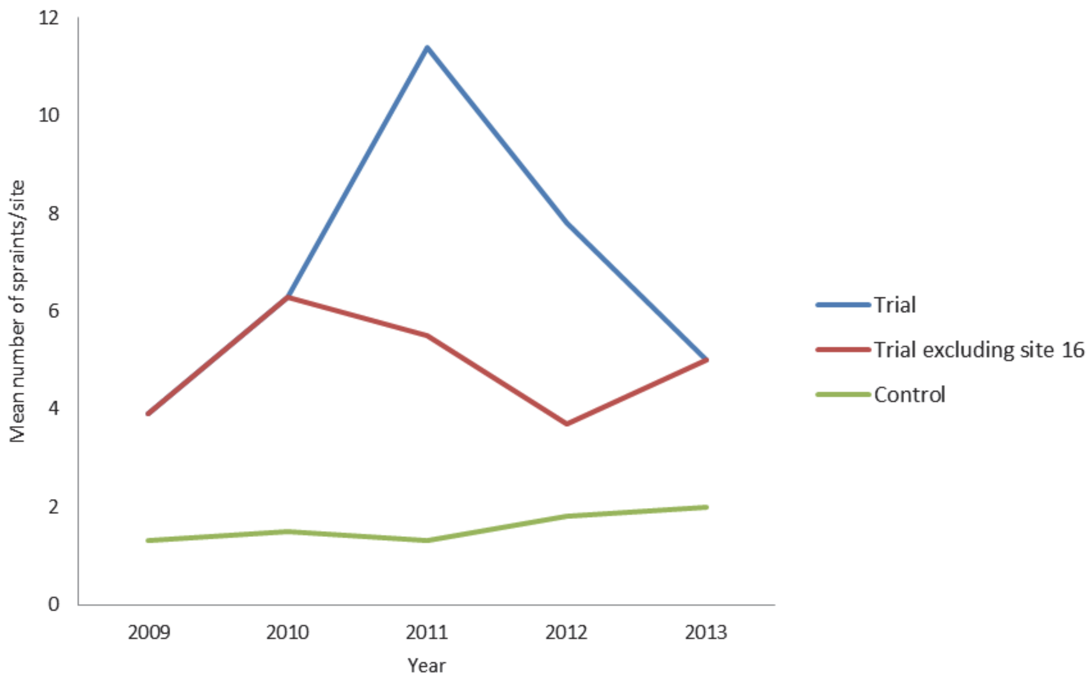
detectability. In 2013, survey conditions were variable with some sites visited either soon after heavy rain or, in some cases, during it. Water levels were very high at some sites (e.g. Sites 4 and 10), but low or “average” at others.

Nevertheless, whilst variable weather conditions might have influenced annual variation, and comparisons with the earlier national survey, they will not have influenced the relative difference between the trial and control area (because surveys of both were carried out at the same time of year). Otter occupancy (proportion of positive survey sites, i.e. those where signs of otters were detected) was significantly higher in the trial area than the control area (ANOVA using arcsine transformed data: Area, $F_{1,6} = 45.4$, $p<0.001$), but there was no evidence of a change over time between the two areas (Interaction term, Year*Area, $F_{1,6} = 4.9$, $p = 0.07$; Fig. 27a), suggesting that any differences between the trial and control area were pre-existing, and that beavers have not had any effect on otter presence in the trial area.

In all years, the mean *quantity* of spraint found at positive survey sites within the release area was substantially greater than at positive sites in the control area (ANOVA: Area, $F_{1,6} = 33.7$, $p=0.001$, excluding Site 16, see below), perhaps suggesting a higher level of overall otter activity within the release area, Fig. 27b). Many of the control area sites were at higher altitude than those in the trial area and were located within intensively managed commercial conifer plantations interspersed with areas of clear-fell and rough acid grassland. Within the trial area there is also a considerable proportion of commercial conifer forest, but there is a greater variety of woodland types and some areas of more fertile wet grassland. The complex sheltered coastline near to the trial area (see comment on Site 16 below) is also particularly favourable otter habitat and is considered likely to contribute to the higher overall levels of otter activity in this area. It is possible, therefore, that the whole forested control area around Loch Glashan represented a sub-optimal habitat for otters when compared with the beaver trial area to the south-west. There was no evidence of any change over time in the mean quantity of spraints found (Interaction term, Year*Area, $F_{1,6} = 0.3$, $p = 0.62$) suggesting, as above, that area differences were pre-existing, and not related to the release of beavers. Analysis of the mean quantity of spraint found per year is crude, and does not take account of variation among sites, however, although the difference in otter sprainting activity between areas is of some interest, number of spraints does not relate directly to either number of otters, or their habitat preferences (Yoxon and Yoxon 2014, and references therein), and so further more detailed analysis was not warranted.



a)



b)

Figure 27. Otter survey results, Knapdale, Argyll, 2009-2013, showing a) the number of occupied survey sites (i.e. those in which otter signs were detected) out of a total of 10 sites surveyed in both trial and control areas, and b) the mean number of spraints per survey site (for all sites where spraint was found). Site 16 is a coastal site at which particularly higher numbers of spraint are found.

Site 16 (a coastal watercourse site in the trial area) consistently had the highest spraint count (and abundant other field signs) – the entire length of this survey site is located between the freshwater Loch Craiglin and the nearby rocky coast, and forms an important thoroughfare for otters moving between freshwater and coastal habitats. In 2011, an adult female and a well-grown cub were sighted at this site, confirming that the site was also used for breeding. However, the spraint count at this site was lower in 2013 than in 2012 and 2011. In 2013, the north bank of the watercourse opposite the downstream end of the transect (below the culvert) was completely re-profiled to make way for a new access track. The area was formerly a boulder-dominated slope dropping down to the edge of the sea loch providing excellent holt and lie-up habitat. It is unclear whether this work and the associated disturbance influenced the level of otter activity at the site.

At sites 2, 5, 6, 11 and 14 other comparable survey data are available, either from earlier national otter surveys undertaken by the Vincent Wildlife Trust, or from SNH commissioned surveys in 2003/4 and 2011/12 for site condition monitoring purposes. These data are presented in Table 19. There are no obvious trends at sites 2, 11 or 14. At sites 5 and 6 the spraint counts in the three VWT surveys are higher than in the past five years, but it is questionable whether this difference signifies anything. At site 5 the 100m section was surveyed upstream of the road, due to difficulties with access in the other direction. The equivalent VWT surveys are thought to have taken place downstream of the road, so the sites are not directly comparable. There is also some uncertainty over the precise lengths of the VWT surveys.

Table 19. Comparison of spraint counts at those survey sites in the trial and control areas with a history dating back to the first national otter survey of Scotland in 1977-79

Site name (number) ***(VWT site number)***	**Survey Year (organiser)**									
	1977-79 (VWT)	**1984-85 (VWT)**	**1991-1994 (VWT)**	**2003-04 (SNH)***	**2011-12 (SNH)***	**2009 (SNH)****	**2010 (SNH)****	**2011 (SNH)****	**2012 (SNH)****	**2013 (SNH)****
A83 at Ardcastle (2) *(VWT 998)*	0	1	2	-	-	0	0	0	0	3
A83 at East Kames (5) *(VWT 942)*	4	5	4	-	-	2	0	1	2	1
A83 at Lochgair (6) *(VWT 999)*	4	6	5	-	-	0	0	2	1	0
Barnluasgan (11) *(VWT 859)*	8	10	14	1	0	8	12	8	6	3
Gariob (14) *(VWT 866)*	1	9	5	3	3	3	9	9	6	4

* SNH site condition monitoring data
** SNH Scottish Beaver Trial monitoring data

SBT report observing otters swimming around the lodges on Loch Linne, Dubh Loch and Lochan Buic (total sightings = 4 in Year 2, 2 in Year 3, 1 in Year 4). Otters have been captured by camera traps at beaver foraging trails and canals on Un-named Loch (North) and Dubh Loch, around the lodge on Lochan Buic, and on Loch Coille-Bharr (total camera captures = 7[44]). Otter tracks have been recorded on mink rafts on ten occasions (2 in year 2, 5 in year 3, 2 in Year 4, and 1 in Year 5). Only one direct interaction between beavers and otters has been recorded, during which two beavers were seen swimming towards an otter, the beavers splashed and then swam away – there was no other evidence of aggression or of close physical contact.

6.3.2 Mink

In Year 1, mink signs were recorded at one of the survey sites in the control area, and a further three sites had 'possible' mink presence (one in the release area and two in the control area). In Year 2, mink were confirmed at one site, and possibly present at one other (both in the control area). In Year 3, there were unconfirmed mink signs at three sites, and possible scats at two sites in Year 4. No mink scats were detected in Year 5.

SBT recorded mink tracks on rafts on 12 occasions in Year 2 and one occasion in Year 3; two mink were shot as part of control operations for this non-native species in Year 2. No mink signs were recorded in Year 3 but in Year 4 tracks were recorded on one raft at Coille-Bharr (outside the normal raft checking period), one mink scat was recorded at Coille-Bharr and a mink was caught on a camera trap at Dubh Loch (these records might all be from one mink). Mink were captured twice on a camera trap on a beaver forage trail at Loch Coille-Bharr in Year 5; no other mink signs were recorded in Year 5.

6.3.3 Water voles

No evidence of water voles was found during the trial, but this is not surprising given the late autumn/winter survey dates and the heavily-shaded habitat at many of the locations. No other signs of water vole have been recorded at Knapdale before or during the trial, a single sighting of a water vole was recorded on Loch Linne in August 2012.

6.4 Limitations and concluding remarks

There is a limit to the conclusions that can be drawn from data such as these, when considering species interactions. One issue is that the data presented here are naïve estimates of otter occupancy, i.e. they take no account of differences in detectability among sites or years. At least two sites in the trial area were consistently problematic in terms of survey, attributed largely to the complex terrain and dense vegetation which made access difficult in places and may have limited detectability. At one of these sites, otter presence was never confirmed, although the habitat is quite suitable. Detectability was therefore likely to have been an issue at this site and perhaps elsewhere where suitable habitat was present but otter signs were absent or very sparse and/or difficult to find. It was not possible to estimate detectability, which is predicted to vary between sites (for the reasons given above) and perhaps also between years. This is because only one visit was made to each site in each year and the available resources did not permit multiple visits.

A second issue is the small number of sites covered in these surveys, which means that only the most extreme effects were most likely to be detected (i.e. the disappearance of otter sign from all, or all but one, site, in one area, while they remain highly abundant in the other area)[45]. However, because we did not expect beaver presence to have a negative impact on

[44] Camera traps were only used extensively from Year 3.
[45] Power analyses showed that the effect sizes that could be detected at the end of the trial with more than 80% power, given that all coastal sites in the trial and in the control area were always occupied, were: 1) there are no non-coastal sites occupied in the trial area, but there are approximately 60% or more non-coastal sites occupied in the control area, or *vice versa*), or 2) there are approximately 10% of non-coastal sites (i.e. one site) occupied in the trial area, but all non-coastal sites in the control area are occupied, or *vice versa*.

otters, this slightly simplistic approach was considered to be appropriate. It is possible that more subtle effects occurred (and were undetected), but any such effects are more likely to have been positive, for example, use of beaver ponds by otters. We were unable to include this level of monitoring/investigation in the trial monitoring protocols due to resource limitations, but beaver-otter interactions could be further assessed post-trial. Overall, we considered the approach taken to be appropriate for the trial, given the resources available.

In conclusion, that there was no apparent evidence of an effect of beavers on otter presence was not surprising. Indeed, given the important ecological role that beavers play in influencing the hydrology of their habitat and experience from elsewhere in their European range, negative impacts from beavers on any of these other riparian mammals were considered unlikely. These surveys were not designed to provide high levels of statistical power to detect small changes in spraint density (which in any case is not related clearly to otter density or habitat use) but rather to detect a disappearance of otters (caused either directly by beavers, or indirectly by some other activity associated with the trial) – there was no evidence of any such change.

Mink abundance in the area appeared to be relatively low. Although it is possible that beaver activity may influence local mink activity (mink are known to use beaver lodges as den sites, and beaver ponds for foraging, elsewhere in Europe and in North America [as are otters], e.g. Knudsen 1962; Sidorovich 2011; see also Rosell *et al.* 2005), control methods for this non-native species are well established and were already in place at Knapdale.

It is likely that the nature of the survey sites and the timing of the survey were not suitable for providing supplementary data on water vole presence within the release area (however, this was not the main aim of the survey).

7. CONCLUSIONS AND RECOMMENDATIONS

7.1 Summary of main findings

Addressing the success and failure criteria of the trial, we draw the following general tentative conclusions:

1. Post-release survival of translocated animals was probably similar to that of successful reintroduction programmes elsewhere (considering reintroductions across taxa, as reviewed in e.g. Harrington *et al.* 2013). Certainly the relatively high rates of loss in the first few months post-release, that tended to stabilise over time, is a common pattern in reintroductions. This conclusion should, however, be taken with some caution as sample size was small, and confidence intervals for Kaplan Meier survival estimates were, as a result, very wide. The important 'unknown', in this respect, is the fate of missing translocated animals, but this is also a common problem in many reintroductions.
2. Although a stable core population was achieved within the time frame of the trial, there was no evidence of an increasing core population.
3. Although mortality levels of established adults were very low, mortality of wild-born kits (some years) was very high. Population viability analysis suggested that, if kit mortality levels remained as high as experienced during the trial, this would preclude establishment of a self-sustaining population. However, the small number of beavers (necessarily) included in the trial, mean that this result may reflect chance events and may not be generally applicable, and therefore should not be considered to indicate meeting the failure criteria for the trial.
4. Considering other riparian mammals present at the release site, there was no evidence of significant and unsustainable damage. Further, based on what is known of beaver-otter interactions elsewhere, any impacts of beaver presence on otters are more likely to be positive. We were unable to assess potential impacts on water voles.

Our findings with respect to the study of the ecology and biology of the European beaver at Knapdale were broadly as might have been expected from comparable studies in Norway (the source of the released beavers) and from the literature on reintroduced beavers in mainland Europe. Established home ranges were relatively small, especially for the pairs on the smaller lochs, but were not exceptionally small for European beavers. Detailed behavioural information from a subset of beavers (one year or more post-release) provided no evidence that translocated beavers were behaving 'abnormally' in any way; which might happen if animals were negatively affected by the translocation process, and/or failed to adapt to their new environment.

7.2 Outlook for Knapdale

The beavers that currently exist at Knapdale are unlikely to form a self-sustaining population (but this was not the intention of the trial). As a management option, it is clear that supplementation would be required if a self-sustaining population at Knapdale was desired. The difficulty lies in predicting how the population would grow even with supplementation. Currently, the demographic data collected during the trial are outside the range of values considered in the beaver population model by Rushton *et al.* (2002) to predict population growth at Knapdale prior to the trial. In this sense, rather than being able to refine the model at the end of the trial, the outcome has been to introduce even greater uncertainty. The uncertainty in parameter estimation (predominantly kit survival) is a direct result of small sample size – i.e. low kit survival may be associated with the particular three females that produced kits at Knapdale, with Knapdale itself (although there is nothing in the adult behaviour that would suggest that Knapdale is not suitable), or may be due to chance events. Low kit survival at Knapdale is of potential concern and we suggest that any supplementation at Knapdale in the future should be monitored to assess on-going reproductive success. We are not suggesting that further releases should not take place, but we do recommend that an adaptive management approach is adopted that includes assessment of kit production, litter size and kit survival, and re-assessment of likely population viability.

Because there was no increase in the number of families over the duration of the trial, we are unable to describe how beavers might spread in the landscape at Knapdale. Information from the literature on other beaver reintroductions, and natural recolonisations, suggests that beavers usually undergo an expansion in range before increasing in density, and so we would expect that, if numbers increased sufficiently, beavers would eventually occupy additional lochs in the area but would, at least initially, remain at relatively low density. Habitat use is likely to remain within 20 m of the water's edge. Construction activity will probably continue to vary among pairs, lochs and years and will likely be unpredictable (but could be managed insofar as dams can be removed if desired).

7.3 Relevance to potential beaver releases elsewhere in Scotland

The overall success in establishing translocated beavers at Knapdale, and the apparent suitability for beavers of quite different habitats and landscapes in the Tay river catchment (revealed by the spread of escaped or illegally released beavers there) suggests that European beavers will settle successfully elsewhere in Scottish riparian habitats. In loch systems elsewhere in Scotland, releasing beavers as pairs on separate lochs appears to be a good approach. Settlement patterns on riverine systems may be different.

As for supplementation at Knapdale, we strongly recommend that reproductive success (particularly kit survival) is monitored in any future releases. It is unlikely that high kit mortality rates will prove to be a generality in Scotland, but if 100% losses were experienced with a larger sample of animals over more than one year, we would urge that the cause be investigated. In any case, any release should include some level of monitoring, as well as continual re-assessment of progress and required management. Monitoring would not, however, need to be as intense as for the trial at Knapdale and could probably be limited to annual population counts and lodge watches, although field sign surveys (perhaps annual or bi-annual) at the boundaries of the release area would also be useful to assess population spread.

Wherever beavers are released, habitat use would likely be restricted predominantly to within 20 m of the waters' edge, although occasional use up to 50 m or more from the waters' edge should be expected depending on the surrounding land use. Construction activity is unpredictable, but experience in Europe suggests that it is manageable (i.e. dams can be removed, or their impacts mitigated).

The potential spread of beavers through Scotland will be explored further and reported on by Steve Rushton and a team based at Newcastle University, using information obtained from the trial at Knapdale and the existing beaver population on the Tay.

One possible reason for the apparent difference in reproductive success in Knapdale compared with that on the Tay is the different provenance of each population (Norway and Bavaria, respectively). There has been considerable debate concerning the 'correct' provenance for release in Scotland (see e.g. Halley 2011, Rosell *et al.* 2012, Senn *et al. 2014*) but discussion of that is beyond the scope of this report, or may be linked to the length of time since the populations were established. However, the possibility that beavers of

Bavarian origin have greater reproductive success than those of Norwegian origin is highly relevant to demographic considerations and warrants further attention.

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ANNEX 1: FIELD SIGN SURVEY DATA

Table A1.1. Number of beaver field signs recorded per season, Year 3 – 5, Knapdale, Argyll. Note that the number of field signs is approximately equivalent to the number of 10 m sections of loch/river bank in which signs were recorded (except that signs of different feature – see Table 11 – were recorded separately, so each 10 m section of loch/river bank could be counted more than once).

Family	Year	Summer	Autumn	Winter	Spring	Total/yr
Linne	3	69	66	91	77	303
	4	121	181	137	101	540
	5	82	58	122	78	340
Dubh Loch	3	62	61	79	76	278
	4	79	82	102	40	303
	5	52	31	34	21	138
Buic	3	56	39	37	29	161
	4	47	26	55	44	172
	5	52	35	41	25	153
Creagmhor	3	57	46	50	49	202
	4	32	57	66	48	203
	5	41	19	52	39	151

ANNEX 2: POST-RELEASE MOVEMENTS OUTWITH THE TRIAL AREA

Three individuals left the release area within the first month post-release: Andreas Bjorn, Gunn Rita and their daughter (Mary Lou). Andreas Bjorn left the release area within a few weeks of release and was located approximately 10 km north of the release area at Kilmartin Fish Farm in August 2009 (where he was recaptured and returned to the release site, although later removed from the programme, see Table 1). Gunn Rita disappeared in the second week post release, her female kit disappeared in mid-July. The kit was initially tracked via RF telemetry to the Crinan Canal but then disappeared. Beaver activity was noted on the River Add, approximately 3 km north of the trial area in October 2009 (Figure A2.1), but previously occupied burrows appeared to have been abandoned following flooding of the river in early winter 2009 – although further field signs were recorded at the same location in March 2010, none was reported to be fresh. A small beaver (of unknown identity) was sighted (and old field signs recorded) on Crinan Canal in April 2010 less than a kilometre from the release area. It was not possible to confirm whether these field signs and observations were of Gunn Rita, her young kit (Mary Lou) or both.

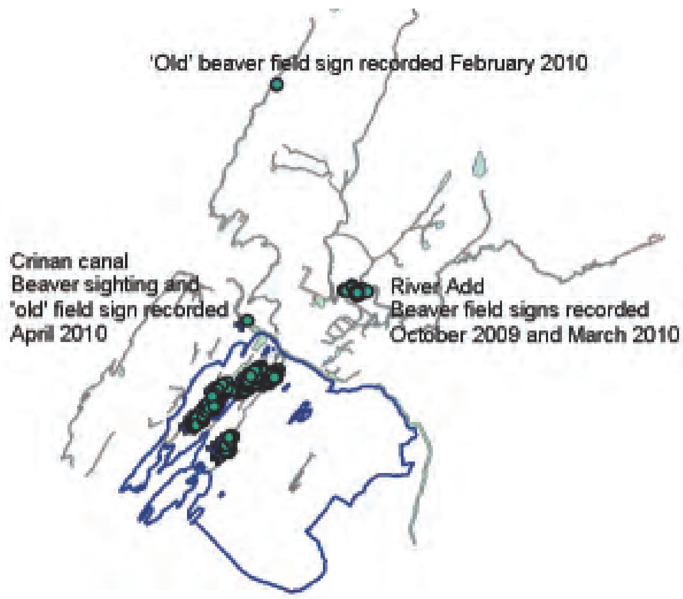

Figure A2.1. Field signs and observations (green dots) of beavers recorded outside the release area during the first year of the trial, 2009-2010. The blue line shows the boundary of the Knapdale release area.

ANNEX 3: QUALITY OF GPS DATA

Table A3.1 summarises the quality of the data obtained (in terms of the number of locations recorded, and the actual inter-fix intervals achieved[46]). Data quality was generally high: although success at achieving inter-fix intervals ≤ 15 minutes ranged between 30 and 60%, for all datasets at least 80% of inter-fix intervals were ≤ 30 mins (and for all but two low sample size datasets, 90% or more were ≤ 30 mins). Data from Millie on Dubh Loch also suggests that the higher vegetative cover at this loch was not problematic in terms of obtaining locations (although further analyses on the relative precision of GPS locations in different habitats have yet to be done).

Table A3.1. Quality of GPS data obtained from nine successful deployments on beavers at Knapdale. Inter-fix intervals are described as the proportion of intervals that are less than, or equal to, a specified time (excluding daytime periods when the animal was clearly in the lodge). Note that the tag deployed on Frid in 2011 was set to record at approximately five minute intervals (all others were set to record at 15 minute intervals).

Animal	**Total no. locations (no. nights)**	**Inter-fix intervals**		
		≤ 15 mins	**≤ 20 mins**	**≤ 30 mins**
Frank_2011	264 (9)	0.40	0.85	0.94
Frid_2011	571 (8)	0.27 ≤ 5 mins	0.80 ≤ 10 mins	0.97 ≤ 30 mins
Trude	390 (11)	0.55	0.85	0.90
Frank_June2012	158 (4.5)	0.39	0.87	0.92
Frid_June2012[1]	37 (2)	0.29	0.74	0.86[2]
Millie	72 (<2)	0.61	0.89	0.93
Christian	22 (<2)	0.45	0.80	0.80[2]
Frank_Nov2012	72 (<2)	0.44	0.92	0.93
Frid_Nov2012	314 (7)	0.54	0.88	0.94

[1] One large 3 hour inter-fix interval between 21.24 and 00.25 suggests that the animal was probably inactive during this period.
[2] Low sample size.

[46] A GPS tag may fail to obtain a location when the animal is underwater or in thick vegetation – when this occurs the tag will continue to attempt to obtain a location until it is successful, thus some inter-fix intervals will be longer than 15 minutes, and the proportion of inter-fix intervals that exceeds 15 minutes (and the actual duration of the inter-fix intervals) provides an indication of the ability of the tag to record the beavers movements precisely. (Accuracy of the locations obtained is a different issue that can only be assessed using stationary tests).

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