SCOTTISH BEAVERS

Beavers in Knapdale

Final report from the Scottish Beavers Reinforcement Project

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The Scottish Beavers Reinforcement Project was led by Scottish Beavers, a partnership between the Royal Zoological Society of Scotland (RZSS) and the Scottish Wildlife Trust created to continue the work of the Scottish Beaver Trial. It took place on land managed by Forestry and Land Scotland (previously Forestry Commission Scotland) and was licensed by NatureScot (previously Scottish Natural Heritage), which also coordinated the monitoring requirements at the site.

RZSS
THE WILDLIFE CONSERVATION CHARITY

Scottish Wildlife Trust

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Introduction: Bringing back beavers

The resurgence of the Eurasian beaver (*Castor fiber*) is one of Europe's great environmental success stories. Hunted to the brink of extinction, they are now present on many European waterways. As well as providing a vital source of water and services to many of Europe's citizens, major river systems such as the Rhine, the Rhône and the Danube are now home to the world's second largest rodent once again.

Beavers have arrived at this point through a combination of natural and assisted recolonisation, and with them comes change. This is a species with an awe-inspiring ability to modify its riparian environment: a true ecosystem engineer. As a result, beavers have a positive effect on the distribution and abundance of a wide range of other species, as well as on waterflow.

While the return of beavers has been enthusiastically followed by large sections of the public, this species' ability to influence the habitat around them has also brought them into conflict with humans. The resurgence of beavers therefore brings with it a necessary process of adaptation in a landscape that has changed since they were hunted to near-extinction. Humans and beavers must learn to live together once again; we need to develop a variety of management measures that allow us to benefit from the positive effects of their return, while mitigating any issues they may cause.

Beavers were lost from mainland Britain in the 16th century. Returning the species to the British landscape was therefore only ever going to be possible with human assistance. It was the legal and moral imperative provided by the EU Habitats Directive that saw the planned return of beavers to Scotland in the first decade of the 21st century and the subsequent creation of the Scottish Beaver Trial.

This historic project in Knapdale Forest (Figure 1), West Argyll, ran from 2009 to 2014, delivered by a partnership between the Royal Zoological Society of Scotland (RZSS), the Scottish Wildlife Trust and Forestry and Land Scotland (FLS). The Trial was an independently monitored scientific study of the ecology and biology of beavers in the Scottish ecosystem, and assessed the effects of beaver activities on the natural and socio-economic environment. It generated information to inform potential further releases at other sites with different habitat characteristics, determined the potential of beaver tourism, and explored educational opportunities arising from bringing back this charismatic species.

The outcomes of the Scottish Beaver Trial were documented in a technical report (Jones and Campbell-Palmer 2014) and will not be extensively detailed here. Instead, this publication focuses on the continuation of this story in Knapdale in the form of the Scottish Beaver Reinforcement Project. The project team hope that it will help to further inform future species reintroduction projects in Scotland and beyond.

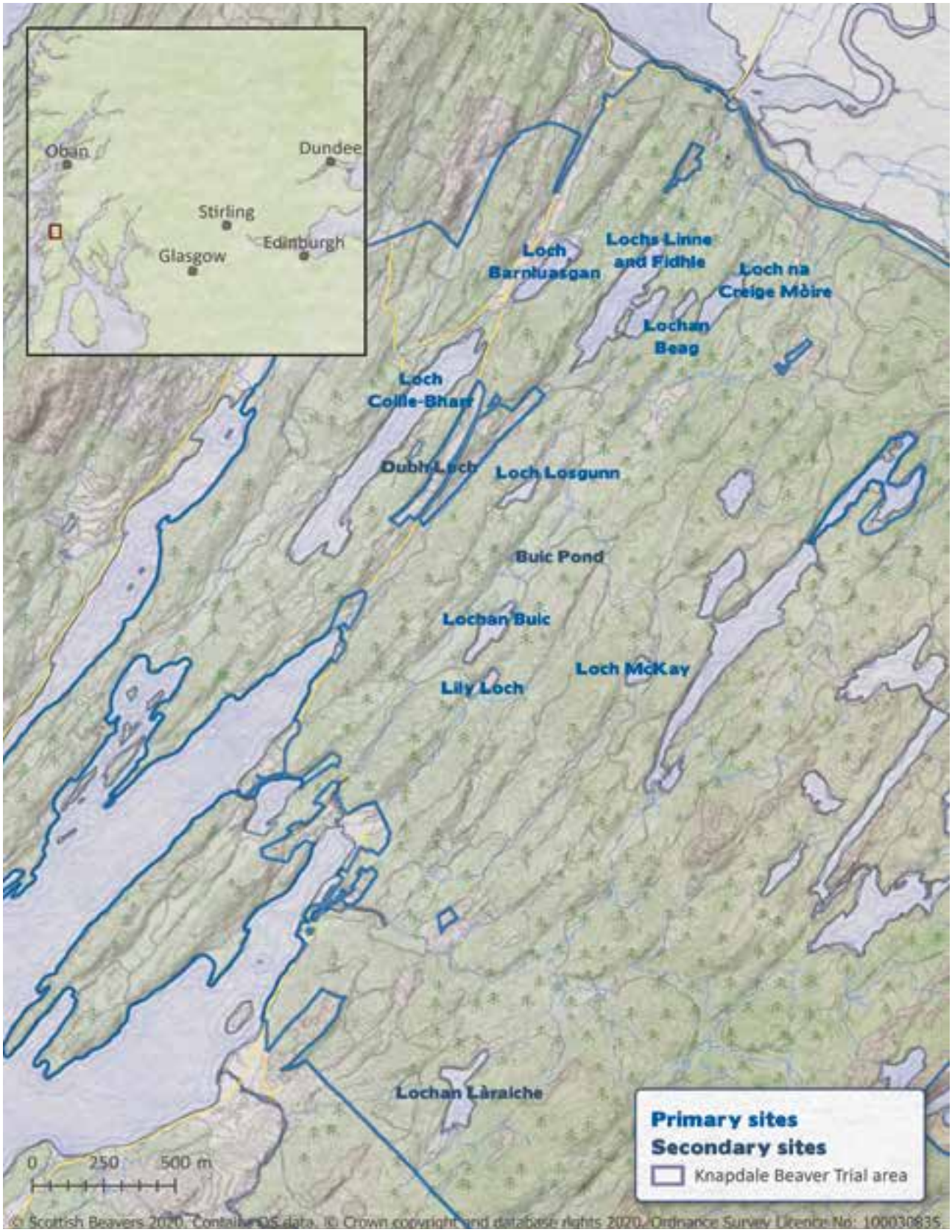
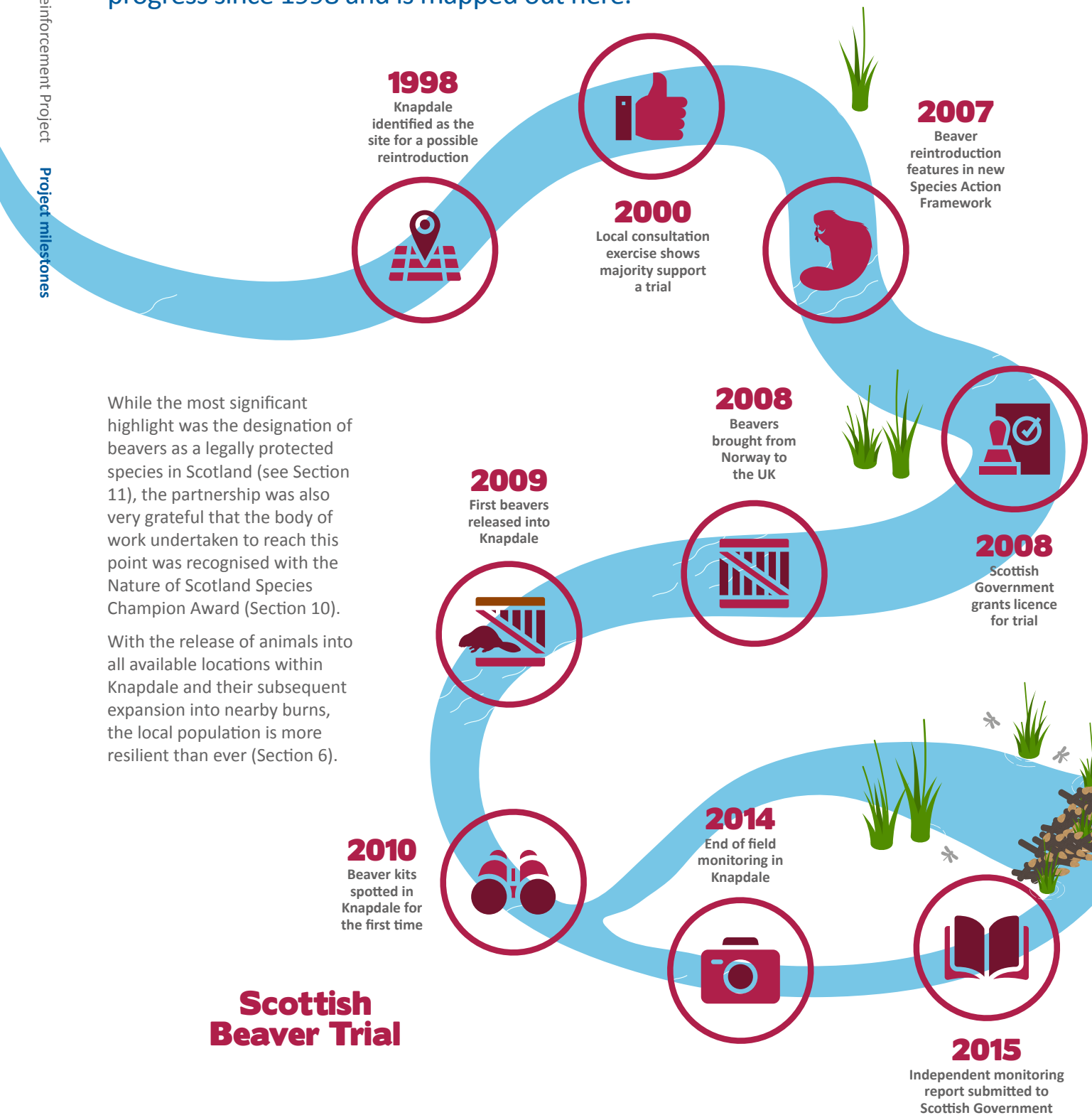


Figure 1: Knapdale Forest, showing the location of lochs assessed as being suitable for primary locations for beaver releases, and secondary lochs which also have the potential to host beavers.

Project milestones

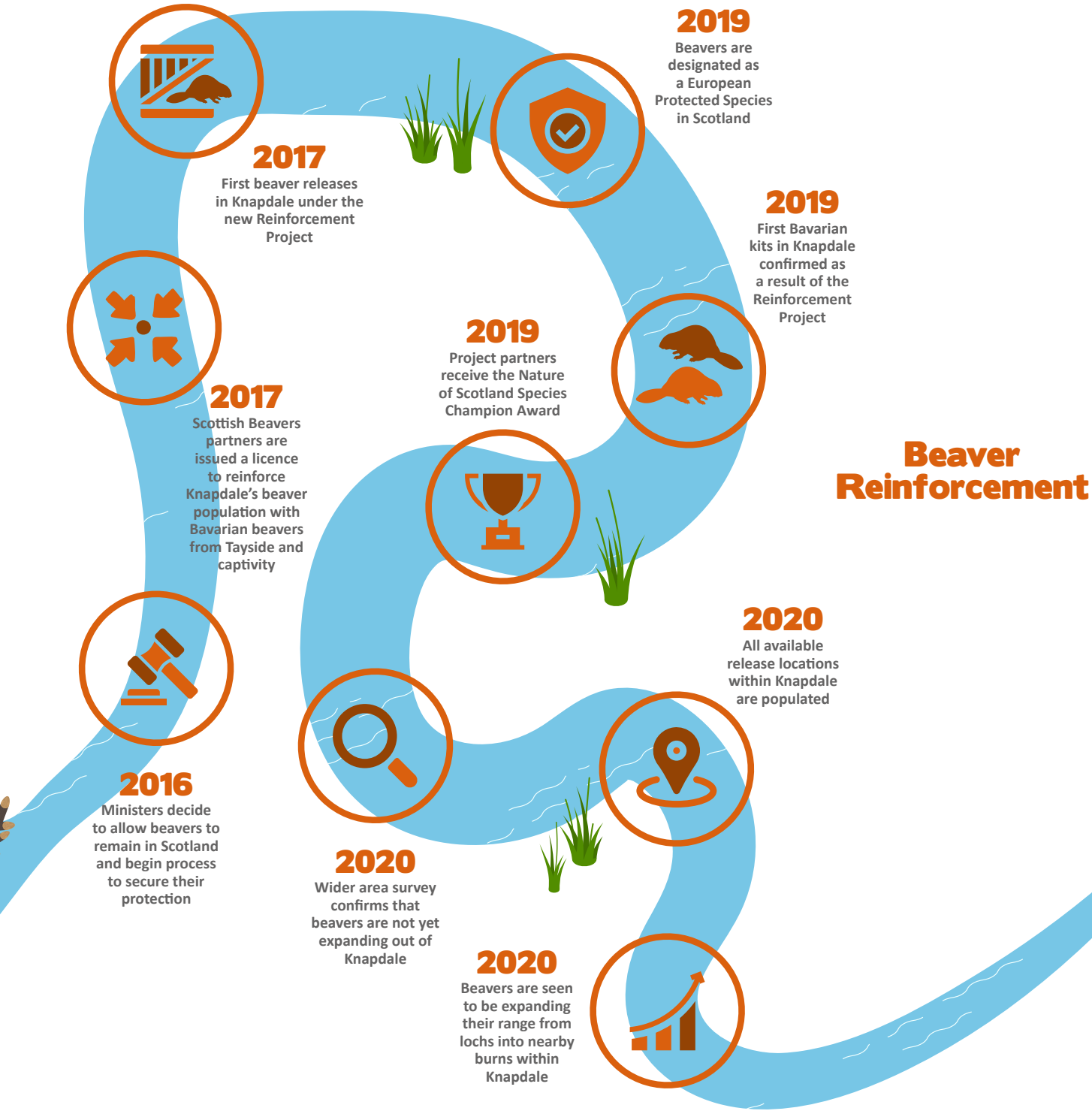
Releasing beavers into Knapdale has involved stakeholders from Scotland to Norway and beyond, resulting in the historic reintroduction of this enigmatic mammal to the country. This considerable achievement has been a work in progress since 1998 and is mapped out here.



While the most significant highlight was the designation of beavers as a legally protected species in Scotland (see Section 11), the partnership was also very grateful that the body of work undertaken to reach this point was recognised with the Nature of Scotland Species Champion Award (Section 10).

With the release of animals into all available locations within Knapdale and their subsequent expansion into nearby burns, the local population is more resilient than ever (Section 6).

Beaver Reinforcement



2016
Ministers decide to allow beavers to remain in Scotland and begin process to secure their protection

2017
Scottish Beavers partners are issued a licence to reinforce Knapdale's beaver population with Bavarian beavers from Tayside and captivity

2017
First beaver releases in Knapdale under the new Reinforcement Project

2019
Project partners receive the Nature of Scotland Species Champion Award

2019
Beavers are designated as a European Protected Species in Scotland

2019
First Bavarian kits in Knapdale confirmed as a result of the Reinforcement Project

2020
All available release locations within Knapdale are populated

2020
Wider area survey confirms that beavers are not yet expanding out of Knapdale

2020
Beavers are seen to be expanding their range from lochs into nearby burns within Knapdale

“There are few species that have such a significant and largely positive influence on the health and function of our ecosystems. The importance of beavers to Scotland’s biodiversity is huge.”

Roseanna Cunningham
Cabinet Secretary for Environment, Climate Change and Land Reform

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Section 1: The reason to reinforce

Between May 2009 and June 2010, 16 beavers were released into Knapdale Forest as part of the Scottish Beaver Trial, the first licensed reintroduction of a mammal to the UK. One of the largest field trials in Europe, it heralded the return of the species to Scotland after over 400 years of absence.

The Trial ended in 2014, with nine animals known to be present, and the following year the results were submitted to the Scottish Government in the *Beavers in Scotland* report produced by NatureScot (then Scottish Natural Heritage) (Scottish Natural Heritage 2015).

In 2016, Scottish Ministers took the landmark decision to allow beavers to remain, and to work towards securing European Protected Species status for the species in Scotland.

The beavers released into Knapdale as part of the Trial were never intended as a founder population that would distribute more widely across Scotland. Rather, they were introduced to assess the feasibility of reintroducing beavers more widely to Scotland. In fact, Knapdale Forest was selected as the site for the Trial not only because of the suitability of habitat it could offer beavers, but also due to its geomorphology, which was predicted to act as a natural barrier to prevent beavers dispersing from the area.

However, following the Trial and the successful establishment of beavers in Knapdale, it was felt that the population should be given the chance to remain and indeed thrive. With just nine individuals, all descended from the same population in Norway, there was a very real chance that Knapdale's beaver population could disappear over time, an outcome that the partner organisations wished to prevent. To halt this possible loss, RZSS and the Scottish Wildlife Trust reunited to form Scottish Beavers. The strategy of this partnership was to reinforce the Knapdale population by increasing both the number of beavers and the genetic diversity present by introducing beavers from additional source populations.

Due to the unofficial release of beavers descended from Central European populations (likely Bavaria in Germany) (McEwing *et al.* 2015; Campbell-Palmer *et al.* 2020) into Tayside and Beauly in Scotland, and other Bavarian-origin animals present in captive collections (Wildwood Trust, Kent and Derek Gow Consultancy, Devon), there were suitable sources of beavers already in the UK that could be used for the reinforcement. This allowed the introduction of novel genetic diversity while negating any need for extensive quarantine measures.

Licence application

A licence application was once again made to NatureScot, this time through the newly established Scottish Code for Conservation Translocations (National Species Reintroduction Forum 2014), with the following aim:

"To support the Cabinet Secretary for Environment, Climate Change and Land Reform's decision to allow beavers to remain in Scotland and expand naturally from two beaver policy areas (Knapdale and Tayside). The reinforcement will help increase the population of beavers in Knapdale and contribute towards the establishment and expansion of a sustainable population."* (Scottish Beavers 2017)

The goal of the three-year project (2017–2020) was:

To release beavers into the majority of suitable release points within Knapdale with a view to having the following during the three-year period:

1. At least one Norwegian-cross-Bavarian pairing that successfully breed.
2. An additional two pairs establish and breed as a direct result of the reinforcement.
3. The overall population equate to a minimum of five breeding pairs/family groups.

The translocation licence application was also made on the basis that beavers had been accepted in the local Knapdale area. There have been socio-economic benefits apparent within the local communities of Cairnbaan and Lochgilphead, and the loss of this species, which had been present for seven years at this point, would be detrimental to the local economy. Finally, beavers had already transformed some parts of the habitat within Knapdale, providing new areas of wetland. These new areas were benefiting a wide variety of other native species which would be lost should the beaver population be extirpated (made locally extinct).

The rationale for the reinforcement was robust: the animals were already present in the area; there was scientific evidence for the benefits of beavers to the environment and their effects at Knapdale in particular (Scottish Natural Heritage 2015); and by the time of application, beavers had been accepted as a native species by the Scottish Government.

*Policy areas refers to the Scottish Government decision to allow beavers to remain in Knapdale and Tayside.

In September 2017, NatureScot issued the Scottish Beavers partnership with a licence (number 103135). It allowed for the release of up to 28 beavers over three years into Knapdale Forest, with nine licence conditions including: the requirement for an annual licence return; that monitoring activities were agreed via a new Monitoring, Research and Management Coordination Group led by NatureScot; and that permission was required from the landowner, Forestry and Land Scotland (FLS, then Forestry Commission Scotland), for any releases.

Pre-release assessment of beavers in Knapdale

Before releasing new beavers into Knapdale, it was necessary to establish how many beavers remained in the area and where they were located. A survey was completed in 2016, prior to the reinforcement licence application, showing there were now a minimum of eight animals remaining at the Trial site including two or three breeding pairs. While the population appeared to be reproducing, there was still a high likelihood of eventual extirpation given the small population size and associated vulnerability.

The survey established that three lochs were occupied: Lochan Buic, Loch Coille-Bharr and Loch Losgunn. A number of the lochs previously occupied by beavers during the Trial looked to be vacant, having no sign of recent activity (Lochs Linne and Fidhle, the Dubh Loch, Lily Loch and Loch na Creige Mòire/Lochan Beag).

Minimising the risk of welfare impacts resulting from territorial disputes between resident beavers and newly released animals was an important consideration. Thus, a further survey was undertaken in September 2017, prior to any new releases, to ensure no animals were released into recently occupied lochs. This survey identified a minimum of ten individuals, all located within the same lochs as the survey a year earlier – two further adults were identified within the Coille-Bharr family (Figure 2). This information informed the selection of locations for the first releases of the reinforcement.

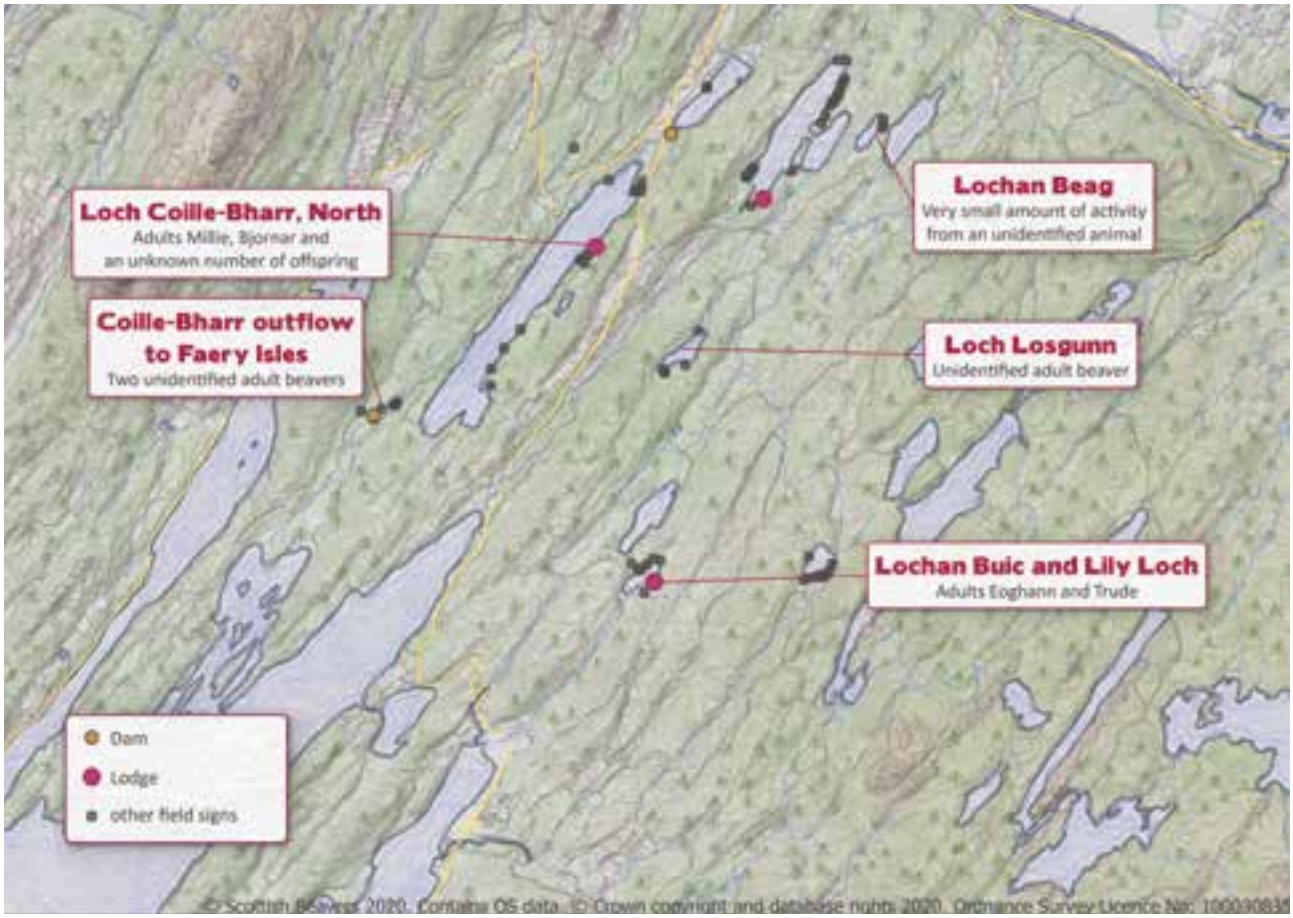
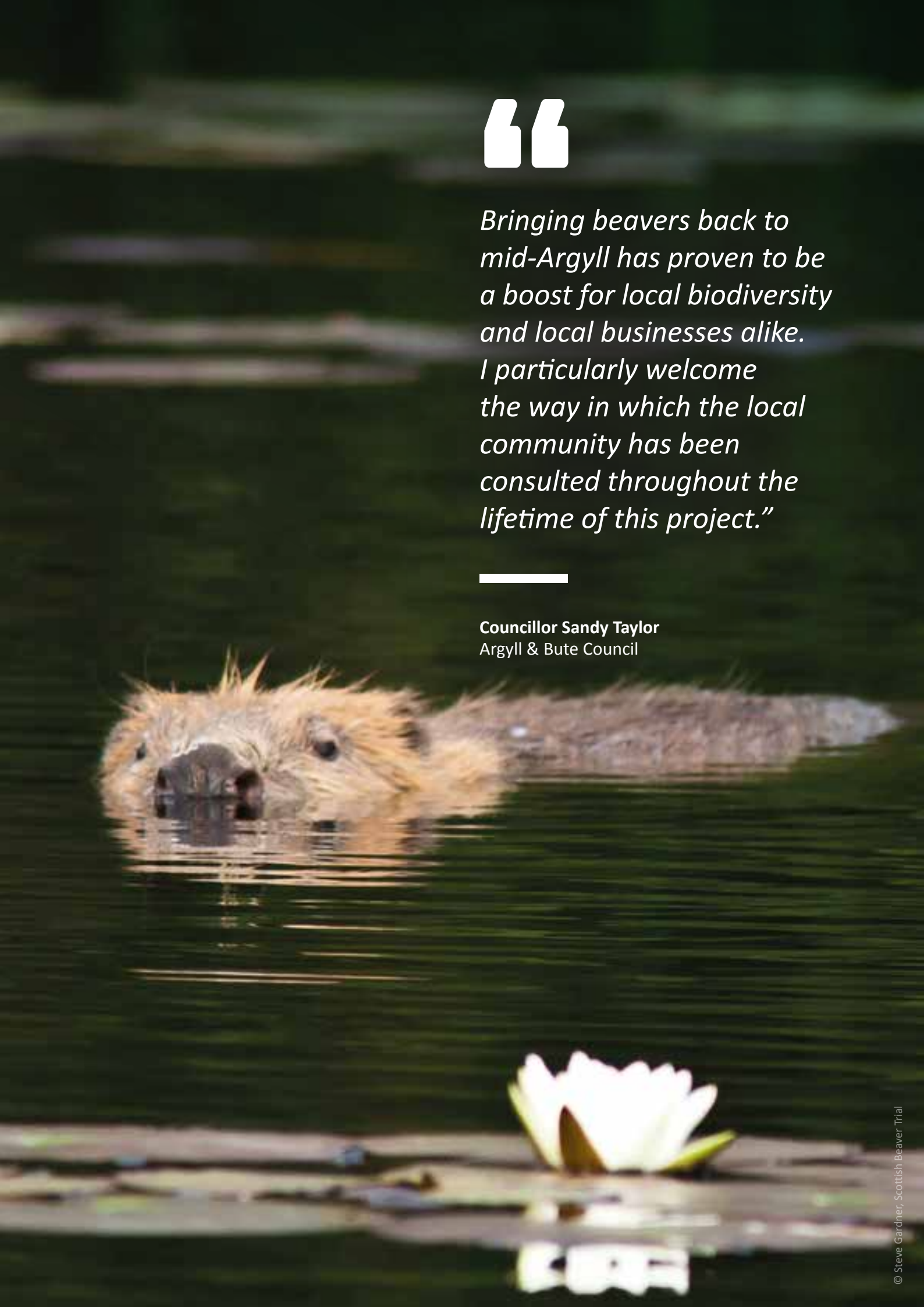


Figure 2: Results of the 2017 survey showing locations of beavers known to be present in Knapdale prior to any reinforcement releases.



Bringing beavers back to mid-Argyll has proven to be a boost for local biodiversity and local businesses alike. I particularly welcome the way in which the local community has been consulted throughout the lifetime of this project."

Councillor Sandy Taylor
Argyll & Bute Council

© Steve Gardner, Scottish Beaver Trial

Section 2: People and partnerships

Partnership working has been a key strength throughout the story of beavers in Knapdale. The Scottish Beavers delivery partners, the Scottish Wildlife Trust and RZSS, worked closely with Forestry and Land Scotland as landowners and NatureScot as licensing body and lead for designated feature monitoring at the site.

The project has always benefited from local support from volunteers and neighbours; during the reinforcement a successful partnership was formed with the Heart of Argyll Wildlife Organisation (HAWO), with their team providing valuable field support and monitoring of camera traps between field surveys when project staff were not present in Knapdale.

The project partners met regularly to plan operations and communications. Quarterly liaison meetings were held with FLS and NatureScot, in conjunction with Monitoring, Research and Management Coordination Group meetings. In addition, FLS provided support during surveys and facilitated local storage of equipment.

Community spirit

The Scottish Beaver Trial partners undertook extensive public consultation before the release of any animals into Knapdale, and this was repeated at the end of the Trial in 2014. Local support for wild beavers living in Mid-Argyll increased from 73% in 2007 to 84% in 2014, with 11% opposed. Further, of the 139 local residents who responded to the Trial survey, 53% indicated that their views on beavers had changed for the better over the course of the five-year trial period.

In 2017, neighbouring landowners and local households (5,000 people in postcodes PA29, PA30 and PA31) were invited to attend a stakeholder engagement event that was held on two consecutive days in August. A total of 61 people attended this event, with 67% of attendees in favour of the reinforcement plans and 10% unsure; the remaining participants provided no response (Figure 3).

Throughout the Reinforcement Project, the team held an annual community event either in Tayvallich Village Hall or at the Cairnbaan Hotel to provide updates on progress to local stakeholders. The final event in October 2020 was held online due to Covid-19 restrictions, but was still advertised extensively locally and was attended by 50 people.

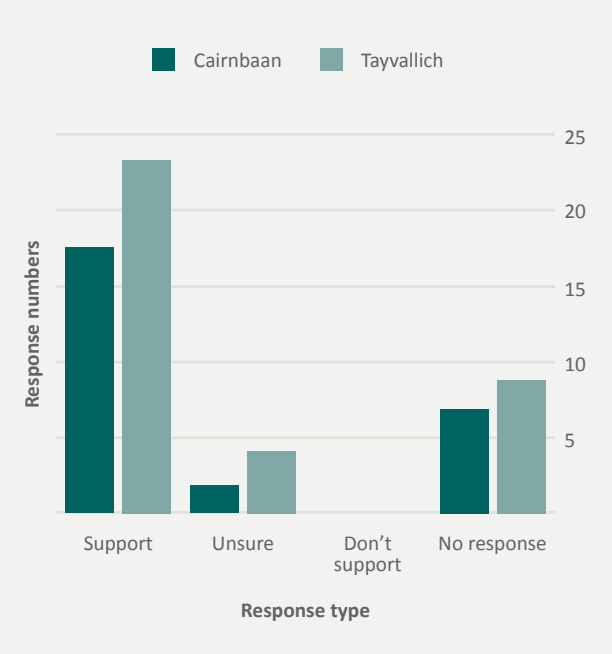


Figure 3: Responses to the question "Do you support beavers in Knapdale?" given by attendees of community engagement events held in the Knapdale area on 22nd and 23rd August 2017.

Beavers are not subtle. The signs they leave behind, combined with camera trap footage and visual sightings, allowed us to monitor the Knapdale population during the reinforcement. Our data paint a picture of a slowly growing population of beavers, transforming their surroundings to the benefit of wider biodiversity."

Dr Helen Taylor
RZSS

© Allard Martinius

Section 3: Monitoring during the reinforcement

The Scottish Beavers Reinforcement Project had two major focuses – releasing new beavers into Knapdale Forest (see Section 4) and monitoring the entire beaver population present in Knapdale. This included beavers from the original Trial and their descendants, plus new beavers released into the area and any offspring they might have in the life of the Reinforcement Project.

The monitoring programme for the Scottish Beavers Reinforcement Project was based on methods employed during the original Trial, but in a scaled-back form. During the Trial, an enormous amount of data on the beavers' habits and their effects on the local landscape were collected. While necessary, this was a very resource-heavy exercise that involved dedicated project staff living locally for the duration of the Trial, and it was agreed that this level of resource was neither available nor required for the Reinforcement Project.

Once the *Beavers in Scotland* report was submitted to the Scottish Government and the decision was made that beavers could remain in Scotland, the need for the intensive monitoring employed in the Trial passed. The Reinforcement Project aimed to strike a balance between collecting enough information on the welfare and whereabouts of individual beavers, especially shortly after release, and allocating limited resources effectively.

Translocation is stressful for animals, and an element of post-release mortality is inherent in any translocation. It was important to ensure sufficient data were collected during the reinforcement to allow the team to learn from their translocation strategies and adapt accordingly. Ultimately, however, the beavers released for the reinforcement were treated as wild animals, and, as such, any post-release intervention was minimised. The pre-release health screening protocols were kept consistent with the Trial to ensure public health concerns were met (see Section 9).

Questions to address

The key questions to answer during the Reinforcement Project were:

1. Where are beavers active within Knapdale?
2. Which lochs/territories are potentially available for releases?
3. How are the individuals released as part of the Reinforcement Project faring in their new environment?
4. How many births and deaths can be confirmed in the population?
5. Are selected designated features being effectively protected from potential impacts of the increased population of beavers?

With these questions in mind, and using the Trial licence conditions and monitoring methods as key references, the vast majority of monitoring in Knapdale during the Reinforcement Project was based on six-monthly field signs surveys, and camera trapping, with an intensive trapping and sampling effort in September 2019. Additional post-release monitoring was conducted for translocated animals. Table 1 gives details of the monitoring undertaken during this project and compares it with that from the Trial.

It was important to have a plan in place for what would happen if an animal translocated to Knapdale was not faring well immediately following release, or if an animal dispersed and caused issues for a landowner. In either case, recapture and removal of the animal might have been necessary, and a decision-tree was designed to establish when this might be required (see Appendix 3). In the end, this level of intervention was not required during the Reinforcement Project.

As individual beavers were not under constant surveillance, accurately ascertaining the fate of all individuals is challenging. It has been very possible (and likely) that some animals present in Knapdale remain undetected and, in addition, that ear tags fitted to beavers prior to release were lost, making the identification of individuals difficult. Thus, numbers of individuals estimated in the six-monthly surveys are always given as minimum figures. The search area is limited to the project area, linked waterways and the Crinan Canal, leaving extensive areas of dense forest to act as potential refuges.

It should be noted that the differences of approach and intensiveness of monitoring between the Trial and the Reinforcement Project mean that data for these two projects are not directly comparable, thus any comparisons made in this report are purely illustrative.

Table 1: Details of methods employed in the Scottish Beaver Trial (2009–2014) and the Scottish Beavers Reinforcement Project (2017–2020), illustrating similarities and differences between the two.

Monitoring method/feature	Scottish Beaver Trial	Scottish Beavers
Live trapping of beavers	The aim was to trap every animal at least once per year, ideally through spring to autumn, and more frequently if necessary, for deployment of GPS tags or veterinary intervention	September 2019 to conduct census and collect genetic samples
Direct observations to account for individuals	One observation per animal per month	Opportunistically as part of field signs survey every six months (March and September). Camera traps employed at a much-increased rate between surveys.
Kit monitoring	Fortnightly per family (loch) mid-July–September	Opportunistically as part of field signs survey every six months (March and September). Camera traps employed at a much-increased rate between surveys.
Mortality monitoring	As reported/discovered	As reported/discovered
Post-release monitoring	Twice every 24 hours for 10 days post-release, reduced to every other day, then every third day over the first month	Once 24 hours post release. Six-week post-release monitoring plan with camera traps, and a field signs survey in week two.
Field signs survey	Every 3 months. (Spring: March–May; Summer: June–August; Autumn: September–November; Winter: December–February)	Every six months: March and September
Lichen assemblage checks	Monitor during observations and field signs surveys	FLS: Visual check monthly when it coincides with recreation inspections
Diver breeding loch checks	If divers are present, checks for beavers must be carried out without any disturbance to breeding birds	Annually in March for presence check. April–July monitoring for dams, and, if so, monitor changes in water levels.
Land use impacts	As notified by FLS	As required as part of FLS general operations assessments
Public health	Quarterly Public Health water sampling. Monthly water data collection including: stageboards, rain gauges, water loggers, chemistry sampling.	Standalone notification steps agreed with public health and SG chief vets
Mink activity	Monthly mink raft checks	As necessary
Scheduled monuments	Every three months as per field signs survey – escalate any activity within buffer immediately	Every six months (March and September) as part of field signs survey. Any dam/lodge/digging within buffer to be escalated immediately.

Beavers are the ultimate 'ecosystem engineers', specialists in creating mosaics of wetland and woodland habitats. No other vertebrate species, apart from us, can change its environment so much through engineering activities."

Dr Martin Gaywood
NatureScot

© Scottish Beaver Trial

Section 4: Releasing new beavers into Knapdale

The licence for the Scottish Beavers Reinforcement Project gave permission to release up to 28 beavers into Knapdale Forest to increase genetic diversity within the population and the size of the population. Beavers released as part of the Trial were of Norwegian provenance, so all individuals chosen for release into Knapdale between 2017 and 2020 were of Bavarian origin, it having previously been demonstrated that Bavarian beavers contain some different genetic material to Norwegian beavers (Senn *et al*. 2014).

The main source of beavers for the Scottish Beavers Reinforcement Project was the Tayside beaver population, which originated from an unauthorised release around 2006 and is known from previous genetic work to be made up almost exclusively of Bavarian beavers with, potentially, a small number of Lithuanian/Polish-origin animals (McEwing *et al.* 2015; Campbell-Palmer *et al.* 2020). As some of these beavers are, unfortunately, causing conflict with landowners in Tayside, translocating these beavers into Knapdale was a good opportunity to help mitigate human–wildlife conflict while simultaneously boosting numbers and genetic diversity in the Knapdale population. The costs incurred for the trapping of these animals were met by NatureScot.

In addition, a small number of beavers translocated during the Reinforcement Project came from captive stock held at Wildwood Trust in Kent and Derek Gow Consultancy in Devon, as well as the unauthorised population of beavers on the River Beauly near Inverness. All of these sources are also Bavarian beavers.

Translocation procedure

Beavers were trapped, translocated and released in either early spring or early autumn to avoid disruption during the kit dependency period and to give beavers the opportunity to settle in and build up their food stocks ahead of winter.

All beavers destined for Knapdale were given an individual identification number, with SBB as the prefix (e.g. SBB01 etc.). All beavers received a full health screening by the vet team at RZSS Edinburgh Zoo (see Section 9), with the exception of three animals that were translocated and health-screened at Five Sisters Zoo in West Calder (SBB19, SBB20 and SBB21).

Blood samples for use in a genetic assessment of the population (see Section 8) were taken from all beavers during health screening. These blood samples were also used to genetically confirm that all individuals were European (*Castor fiber*) rather than North American (*C.canadensis*) beavers prior to release.

Beavers were released as single adults, pairs or family groups and, in two cases, single kits, into lochs that were known to be vacant from pre-release field signs surveys. In some cases (SBB01, SBB05, SBB08, SBB09, SBB10, SBB11, SBB12 and SBB13), animals were provided with an artificial lodge to serve as a temporary shelter and encourage them to stay at their release site. All of these animals (except SBB05) were also given supplementary food (apples and sweet potatoes) up to six weeks post-release. In one case where a kit was being released alone (SBB08), electric fencing was put in place to try and dissuade the kit from dispersing while the team waited for other adult members of its family to be caught and released in the same location. This intensive approach was only adopted for animals considered a great dispersal risk (e.g. lone kits awaiting family members: SBB08 and SBB11) or where there were concerns regarding their feeding habits while being held in the veterinary facility at Edinburgh Zoo (e.g. SBB01). Note that SBB09, SBB10, SBB12 and SBB13 only had access to a lodge and food because they were released at the same site as SBB08.

Following release, the relevant loch was checked after 24 hours and then monitored for six weeks using camera traps, with a field signs survey 14 days post-release, to attempt to establish the fate of the released beavers.

In total, 21 beavers were translocated and released into Knapdale during the duration of the project (see Appendix 1). Although the project licence allowed for additional releases, by March 2020 it was clear that all suitable release sites in Knapdale were occupied by established beavers from either the Trial or the reinforcement. As such, it was decided that no further releases were to be made into the area.

“As managers of Scotland’s national forests and land, we were pleased to host the ground-breaking Scottish Beaver Trial and the Reinforcement Project and, in doing so, help pave the way for the protection of the species in Scotland.”

Philippa McKee
Forestry and Land Scotland

© Philip Price, Loch Visions

Section 5: Expansion of beaver range within Knapdale

The six-monthly field signs surveys combined with camera trapping work conducted during the Reinforcement Project allowed for changes in the distribution and activity of beavers in the Knapdale area to be recorded over the three-year duration of the project. These data, coupled with findings from the intensive capture and sampling effort conducted in September 2019, aided the identification, where possible, of individual beavers and helped to establish breeding success.

The Knapdale project area includes nine lochs assessed as being suitable as primary locations for beaver releases (Figure 1), with other lochs also having potential to host beavers. Additionally, there are many burns and outflows that run into and out of these lochs that could support the expansion of the Knapdale beaver population, but it was decided these would not be used as release sites during the Reinforcement Project.

When the project began in 2017, only four of the nine suitable lochs showed recent signs of beaver occupation (Figure 2). The main stronghold for Knapdale's beavers was the three-loch system consisting of Loch Barnluasgan, Loch Coille-Bharr and the Dubh Loch, all of which were being occupied by a single family. In addition to this family, an established pair were occupying Lily Loch and Lochan Buic, and activity was recorded on Loch Losgunn from an unknown adult which seemingly disappeared early in the Reinforcement Project. Beavers had also expanded their range into the Loch Coille-Bharr outflow, running south from the loch to the sea through the area known as the Faery Isles. In total, there were thought to be three pairs/family groups present prior to any releases under the Reinforcement Project.

Observations during the Reinforcement Project

Despite the unknown fate of some of the beavers released into Knapdale over the course of the project (see Section 6), at least three pairs are known to have become established as a direct result of the reinforcement:

a) SBB01 and SBB05 occupying Loch McKay;

b) SBB13 and a male, most likely SBB07, occupying Lochs Linne and Fidhle;

c) SBB15 and SBB17 occupying Loch Losgunn.

The pair occupying Loch McKay were released from captive collections and are known to have produced kits. The other two pairs are from wild animals translocated from Tayside, with the pair occupying Lochs Linne and Fidhle known to have produced kits. The establishment of these new pairs led to all suitable lochs in Knapdale becoming occupied by established pairs or families of beavers (Figure 4).

It is worth noting that Knapdale's lochs were considered to be approaching capacity not because each loch hosted one pair/family of beavers, but because some pairs/families were occupying multiple lochs (Figure 4). Of the five known pairs and families identified by the end of the project, three were occupying multiple lochs.

By the end of the project in 2020, the original Norwegian family that occupied Loch Barnluasgan, Loch Coille-Bharr and Dubh Loch appeared to have split into two families. Both families appeared to occupy Loch Coille-Bharr, and both spent time in the beaver-created wetland around the Dubh Loch, but neither appeared to be using Loch Barnluasgan. The other original Norwegian pair using Lily Loch and Lochan Buic were observed to continue to occupy both of these, rotating activity between the two lochs.

Finally, at least some of the animals released onto Lochan Beag were observed moving between Loch na Creige Mòire, Lochan Beag, Loch Fidhle and Loch Linne on a regular basis. This is despite the topographical challenges of moving from the two upper lochs (na Creige Mòire and Beag) to the lower two (Fidhle and Linne), which involves traversing a near-vertical slope with a waterfall. These animals have also been known to use the outflows of Loch Linne and Loch Fidhle over the course of the Reinforcement Project.

Additional release strategies

As the lochs in Knapdale became occupied, two releases were made at more marginal, secondary release sites. The first saw the release of animals onto Lochan Làraiche, a site that was thought to be suitable for beavers but was not a priority site due to its slightly higher elevation and lack of connectivity with other waterways in the area. Four beavers (SBB16, SBB19, SBB20 and SBB22) were released onto Lochan Làraiche in September and

October 2019 (Table A1), but none of these beavers remained on the loch. One (SBB20) was later found deceased at the end of the Làraiche outflow (see Section 9), while the fate of the other three remains unknown.

The second release of this kind was made to assess whether established beavers which occupied more than one loch did so out of opportunism or requirement for resources. As mentioned above, one of the original Trial pairs occupied both Lily Loch and Lochan Buic, moving between the two on a relatively regular basis. In September 2019, it was observed that this pair was, for the time, only active on Lily Loch, with almost no activity observed on Lochan Buic. Thus, two new animals from Tayside (SBB18 and SBB21) were released onto Lochan Buic. Camera trap footage showed that these animals initially remained on the loch, but then disappeared. The fate of these two individuals remains unknown – and, sometime after their disappearance, the original pair resumed activity on Lochan Buic.

Dispersal into new waterways

At least some of the animals released onto Lochan Làraiche and Lochan Buic during the reinforcement appeared to have survived and spread into other waterways in Knapdale. In the final survey of the reinforcement in September 2020, new activity was recorded at the end of Barnagad Burn, on Buic pond and the Buic outflow (Figure 4).

In the same survey, evidence that beavers were moving from burn to burn via the saltwater inlet of Loch Sween was also discovered, with small saplings felled on the Faery Isles and on the peninsula between the Faery Isles and Achnamara (Figure 4). This promising discovery suggests that young adult beavers will be able to disperse away from their family groups and into neighbouring stream systems.

Overall, the number and spread of beavers, as well as the amount of beaver activity in Knapdale, has increased dramatically as a result of the reinforcement efforts.

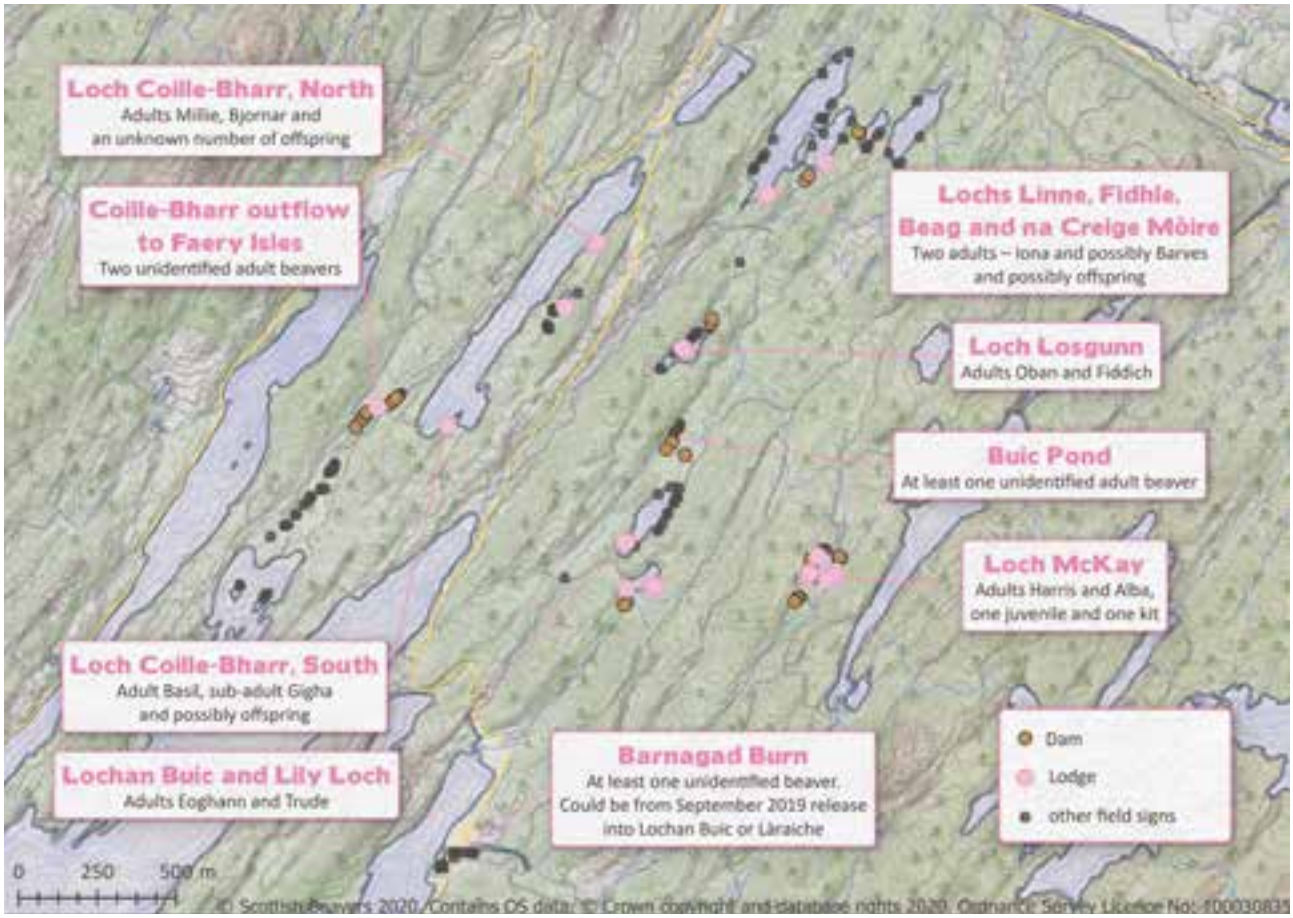


Figure 4: Known distribution of beavers in Knapdale Forest as of September 2020, the last field signs survey of the Reinforcement Project.

The Reinforcement Project has created real conservation benefits for beavers in Scotland, both through removing animals from high-conflict areas in Tayside, and by helping the original Knapdale population to become more diverse."

Gill Dowse
Scottish Wildlife Trust

© Steve Gardner, Scottish Beaver Trial

Section 6: Post-release survival and kit survival

As described above (Section 4), post-release survival and kit births and survival were monitored via a combination of field signs surveys, direct observations and camera trapping. This allowed an estimate to be made of the survival rates during the Reinforcement Project, which could be compared to those during the Trial – but, as stated in Section 3, these figures were collected using different monitoring regimes, so any direct comparison should be treated with caution.

Table 2 demonstrates the higher percentage of confirmed adult and sub-adult fatalities from animals released as part of the Trial and animals released during the Reinforcement Project.

The high mortality of kits released during the reinforcement is of note; three of the four kits released were confirmed deceased, and the fate of the other is unknown. The release of a lone kit (SBB08) during the reinforcement arose as the result of three animals from one family being trapped in Tayside at different times. The mother of this kit and a sibling kit were released 12 days later (SBB09, SBB10). SBB08 was found dead two days later c.4km away, near the Faery Isles, with stress being cited as a factor in the post-mortem. This death was in spite of this kit being provided with an artificial lodge and supplementary food, and the use of electric fencing to try to dissuade dispersal. It is likely that this kit dispersed before its family members were available for release. Another kit (SBB11) released alone from a different family was also found dead shortly after release. Again, this death was in spite of the provision of an artificial lodge and supplementary food.

Table 2: Comparison of fatalities of animals released during the Scottish Beaver Trial and the reinforcement. As monitoring was much more intensive during the Trial, the numbers are indicative rather than directly comparable. During the Trial, kit fatalities were also recorded, but are excluded here as not released animals. One of these deaths occurred after the Trial had finished.

Release Project	Last known age class	Total released	Confirmed deceased	% confirmed fatalities
Scottish Beaver Trial 2009–2014	**All animals**	16	5	31%
	Adult/ sub-adult	16	5	31%
	Kits	0	0	0%
Scottish Beavers Reinforcement 2017–2020	**All animals**	21	5	24%
	Adult/ sub-adult	17	2	12%
	Kits	4	3	75%

These lone kit releases went ahead to give the animals the best chance of survival, the alternatives being that they were shot in Tayside or held at Edinburgh Zoo quarantine facilities for a protracted length of time. However, as a result of the deaths of SBB08 and SBB11, the project team adopted the approach not to release kits unless accompanied by adult family members for the remainder of the project. Both these examples clearly illustrate the very real challenges of wild-to-wild translocations, where release strategy becomes tightly linked to conditions at the trap site.

The third kit to be confirmed deceased was either SBB10 or SBB12. This individual is known only from a skull discovered during the March 2019 survey. Genetic testing indicated the animal was of Bavarian origin, but it is not possible to tell which of the two kits the skull belonged to. The fact that the skull was found high up on an exposed bank suggests this animal was predated.

Fourteen kits were recorded during the Trial between 2009 and 2014, and 16 kits were detected as being born during the reinforcement period between 2017 and 2020. Figure 5 provides the status for these kits and those released from Tayside (four individuals), with the majority of animals unknown.

A large number of animals released currently have an unknown status (Figure 6). Animals were only marked as 'present' where a positive identification of a specific individual had been confirmed, through the presence of ear tags or other markings; often, unidentified animals would be spotted on camera traps. These animals could only be included in the population estimate if they were obviously distinguishable from other beavers (due to scarring, markings etc.). For instance, evidence indicates that animals using the Loch Coille-Bharr outflow to the Faery Isles were not being seen elsewhere (Figure 4), but the identity of these individuals was unknown. This results in the minimum population figure for Knapdale (14 adults, a juvenile and a kit) being higher than the number of identified individuals known to be present (13).

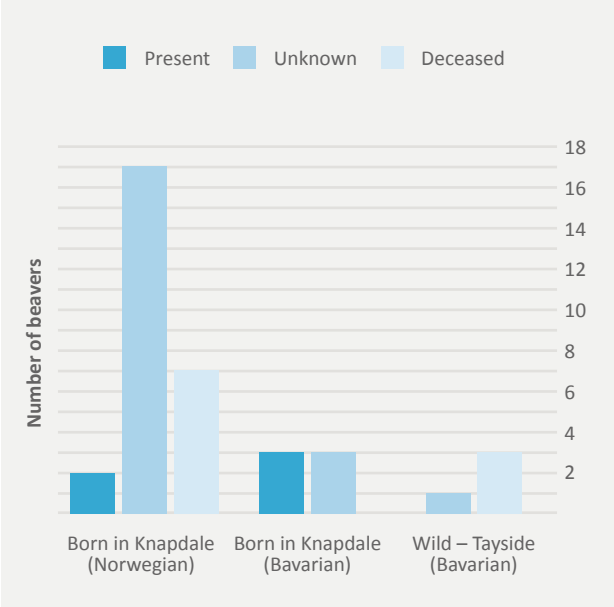


Figure 5: The number of kits born in Knapdale (of Norwegian origin and Bavarian origin) and the number of kits translocated from Tayside (all of Bavarian origin), broken down by their survival status as of September 2020.

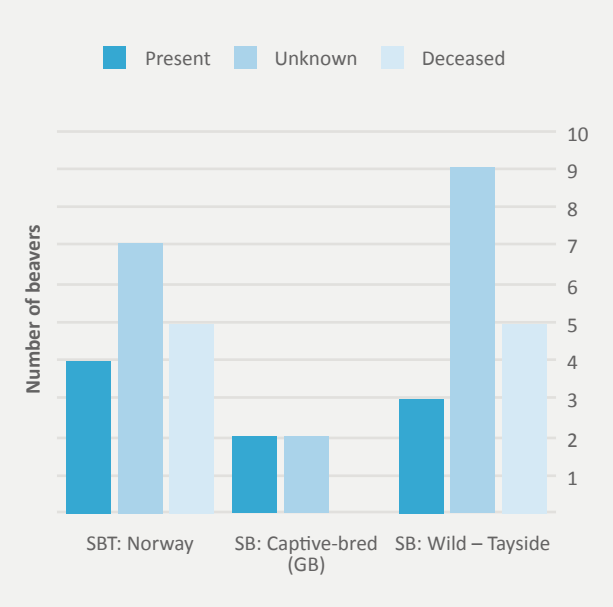


Figure 6: The total number of beavers translocated to Knapdale during the Scottish Beaver Trial (from Norway) and during the Scottish Beaver Reinforcement Project (from captivity and from Tayside), broken down by their survival status as of September 2020. As monitoring was much more intensive during the Trial, the numbers are indicative rather than directly comparable. Animals listed as "unknown" may still be present in Knapdale, but undetected, or they may be deceased or dispersed, but undetected.

Are survival rates as expected?

While the death of any of the released beavers was saddening and disappointing to the project team, such mortality needs to be seen in context of the similar reintroductions in Europe. First-year mortality rates in translocated beavers have been reported as 14% in Poland (Zurowski and Kasperczyk 1988), 17% in Germany (Heidecke 1986) and 36% in the Netherlands (Nolet *et al.* 1997). The rates of 31% for the Trial and 24% for the reinforcement are for the whole project periods (five and three years respectively) and not just the first year, so these figures sit within the known range.

Accurate figures on survival rates are difficult to obtain for kits. Unless they are trapped, tested, microchipped and tagged, it is impossible to know the gender of kits, and extremely difficult to subsequently identify individuals through observations or camera trapping, unless they show clear scars or markings.

Are the beavers with unknown status still alive in Knapdale?

Knapdale has proven to be a positive landscape for beavers, but the topography of the area and the physiology of beavers has made the monitoring of the animals difficult. Experience during the Trial with a range of monitoring methods including radio and satellite telemetry and GPS tags indicated these tools did not supply sufficiently detailed information for animal management within this setting.

So, where are all the 'unknown' beavers? With the dense forest and complex topography of Knapdale, there are many areas where animals could remain undetected for some considerable time. Assumptions should not be made about losses of animals because they are not seen on camera traps or in observation sessions, especially given the time between biannual surveys within the reinforcement. Field signs surveys detect areas of activity and active territories, but not numbers of individuals resident or transient at a site.

Population figures estimated during the Scottish Beavers Reinforcement Project quote only the minimum figures per survey, where there is confirmation of individuals, but that doesn't necessarily mean the unconfirmed animals have died or dispersed out of the area. A clear example of this was seen with one of the original Norwegian founder beavers, M10I16. This animal was last seen in 2014 (during the Trial) at Lochan Beag, but was found dead on the coast opposite Scotnish Farm in May 2018. M10I16 could have been resident in the Loch Coille-Bharr outflow to the Faery Isles, where identification of animals has been very difficult, but could equally have been active elsewhere (Loch Losgunn or another unknown territory) in the intervening time. Clearly, there is ample opportunity for beavers to live in Knapdale undetected.

Knapdale and Tayside beavers are the founders of further Scottish populations. Their anticipated meeting and eventual integration as they colonise new water courses will be a watershed moment, enabling greater genetic diversity and healthier populations in the future."

Dr Róisín Campbell-Palmer
Independent beaver ecologist

© Steve Gardner, Scottish Beaver Trial

Section 7: Extended area survey beyond Knapdale

As the Tayside population of beavers spreads west across Scotland, there is a possibility that, if beavers were to disperse out of Knapdale, the two populations could naturally meet and mix. As previously stated, one of the reasons that Knapdale was selected as the site for the Trial was that the landscape and the Crinan Canal would act as a barrier to beaver dispersal into the River Add catchment and beyond. However, early in the Trial, a family of two adults and a juvenile dispersed across the Crinan Canal, proving that it is not a completely impenetrable barrier.

Given the Scottish Government's stance on beavers having to disperse naturally if they are to expand beyond their current range, dispersal from the original Trial area is significant for the long-term population existence and expansion of Knapdale beavers. In addition to supporting the continued existence of beavers in Knapdale, determining whether individuals were dispersing north from Knapdale also adds to the national picture of beavers in Scotland and was considered useful to help influence future advocacy strategies.

In February 2020, Scottish Beavers commissioned Dr Róisín Campbell-Palmer and Kelsey Wilson to

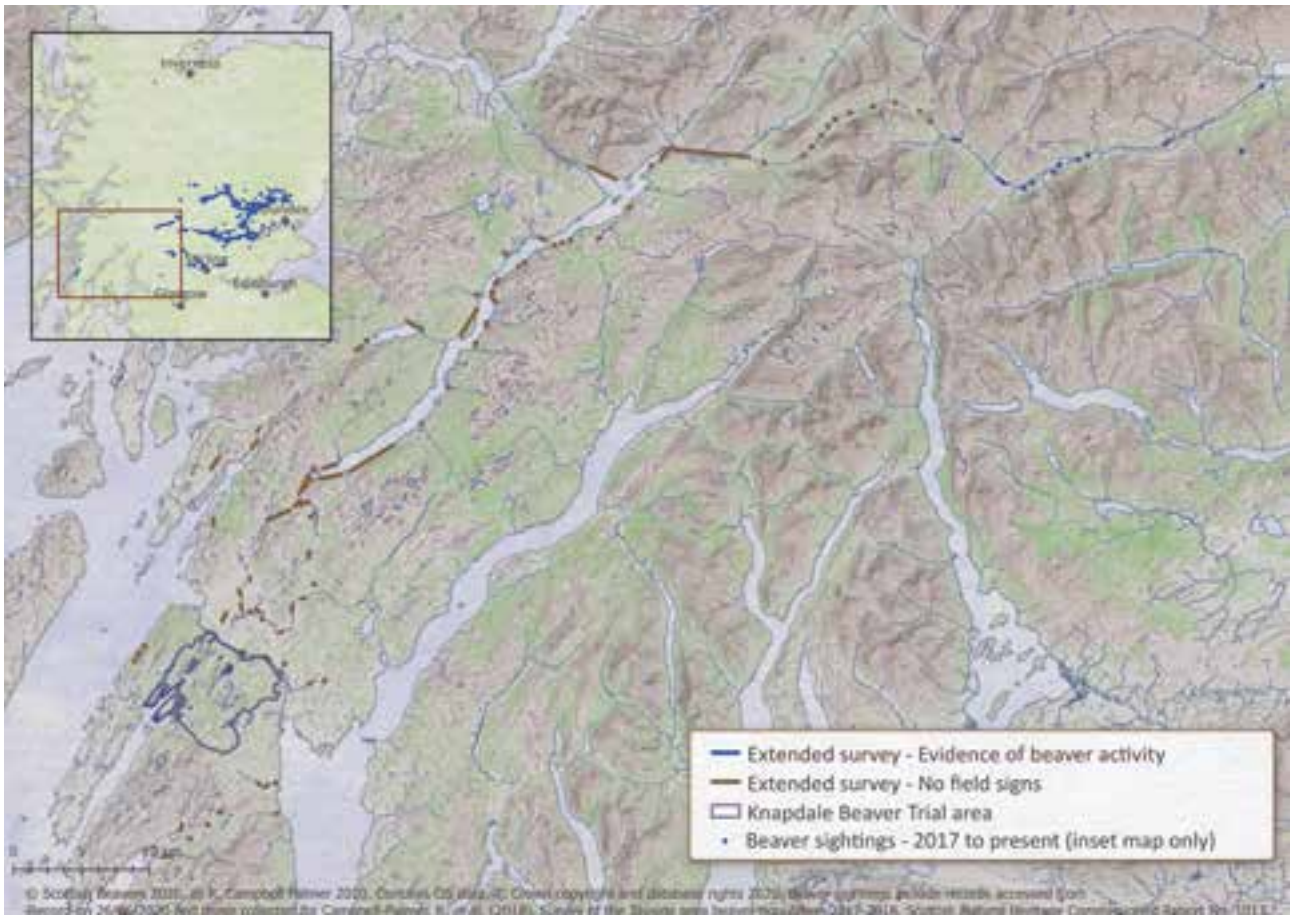


Figure 7: Map indicating areas covered by the extended area survey. Survey locations were selected on habitat suitability and accessibility for beavers and surveyors. The focus was on routes out of Knapdale and nearest wild population of beavers from Tayside. Sightings and national survey data included on the inset map are for context of current beaver extent nationally.

conduct a survey looking specifically for evidence of beaver expansion out of Knapdale.

The aims of this survey, which took a team of two people seven days, were:

- To use the methodology employed in the national survey for beavers in 2017/18 (Campbell-Palmer *et al*. 2018) to: 1) survey and record any beaver field signs outside of the Knapdale project area, including Loch Awe and associated tributaries, and significant watercourses immediately neighbouring Knapdale; and 2) determine the nearest active territories where beavers are most likely to be dispersing from the Tayside population.
- To assess and record suitable habitat for beavers in the extended survey area.
- To trap beavers, if significant evidence of their presence was discovered during the survey, for blood sampling to identify genetic origin.

Beavers have not yet expanded out of Knapdale

No field signs were detected within the extended Knapdale area or Loch Awe. The report therefore concluded that: "it can be assumed that Knapdale is a closed landscape for beavers and therefore no beaver trapping was undertaken" (Campbell-Palmer and Wilson 2020) (Figure 7).

The report also concluded that although suitable habitat is available between the Tayside and Knapdale populations, this is not currently being used by beavers. Although Knapdale isn't a completely closed population, there is an apparent failure to colonise outside of the project area after several years. "Without this and further translocation ideally to neighbouring suitable habitat, it seems the only realistic means by which the Knapdale and Tayside populations will join in this region is if growing Tayside population pressure results in colonisation from the north."

We need to plan for the future of beavers in Scotland, not just for tomorrow but for 100 years' time. This means ensuring that beaver populations start out with high levels of genetic diversity, giving them the best chance to adapt to any future challenges."

Dr Helen Senn
RZSS

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Section 8: The genetics of beavers in Knapdale

Genetic diversity is important for the ability of a population or species to adapt to novel environmental challenges, such as disease events and climate change (Reed and Frankham 2003). Populations and species that have experienced drastic declines in population size often have very low genetic diversity, which makes them vulnerable to such environmental shifts.

Norwegian beavers are known to have very low genetic diversity as a result of being hunted to very low numbers by the latter half of the 19th century (Collett 1897). As all beavers introduced to Knapdale during the Trial came from Norway and only nine were known to remain at the end of the Trial (including a pair consisting of a father and daughter), there were concerns about the long-term genetic viability of the Knapdale beaver population.

One of the major aims of the Scottish Beavers Reinforcement Project was to boost the genetic diversity in the Knapdale beavers by introducing animals of a different genetic background to the Norwegian-origin animals that were already present. All animals in Tayside (and those sourced from captivity) are thought to be of Bavarian descent, with potentially a small number of Lithuanian/Polish-descent animals (McEwing *et al.* 2015; Campbell-Palmer *et al.* 2020), and these animals are known to be somewhat genetically different from Norwegian beavers (Senn *et al.* 2014). Thus, introducing these animals to Knapdale should introduce new genetic variants and increase genetic diversity. To assess whether this strategy has been effective, it was important to measure genetic diversity in the Knapdale population before and after the reinforcement.

Collecting and analysing genetic data

Blood samples were taken from all beavers released into Knapdale for both the Trial and the reinforcement. Additionally, the field team undertook a major trapping effort in September 2019, allowing for blood samples to be taken from additional animals that had been born in Knapdale, both from Norwegian and Bavarian-stock parents.

The RZSS WildGenes conservation genetics team used ddRAD (Peterson *et al.* 2012) to genotype 19 Norwegian-origin Knapdale individuals (both introduced and Knapdale-born) and 21 Bavarian-origin Knapdale individuals (both introduced and Knapdale-born) at 2,031 Single Nucleotide Polymorphism (SNP) markers, using an SNP calling pipeline implemented in the program Stacks2 (Rochette *et al.* 2019) (see Appendix 2 for full methods). This data set included all individuals that had been released into Knapdale for which the team had good enough quality samples and data, and that might have contributed genetically to the population (i.e. any individuals that did not perish immediately after release).

Genetic diversity was estimated in the Knapdale population before and after reinforcement with individuals of Bavarian ancestry. There are numerous ways to measure genetic diversity. Here we present observed heterozygosity, allelic richness and number of fixed loci. Relatively high heterozygosity and allelic richness, and relatively low numbers of fixed loci, are indicative of a more genetically robust population. Estimates of average inbreeding coefficients (Fhat3) for the population are also presented,

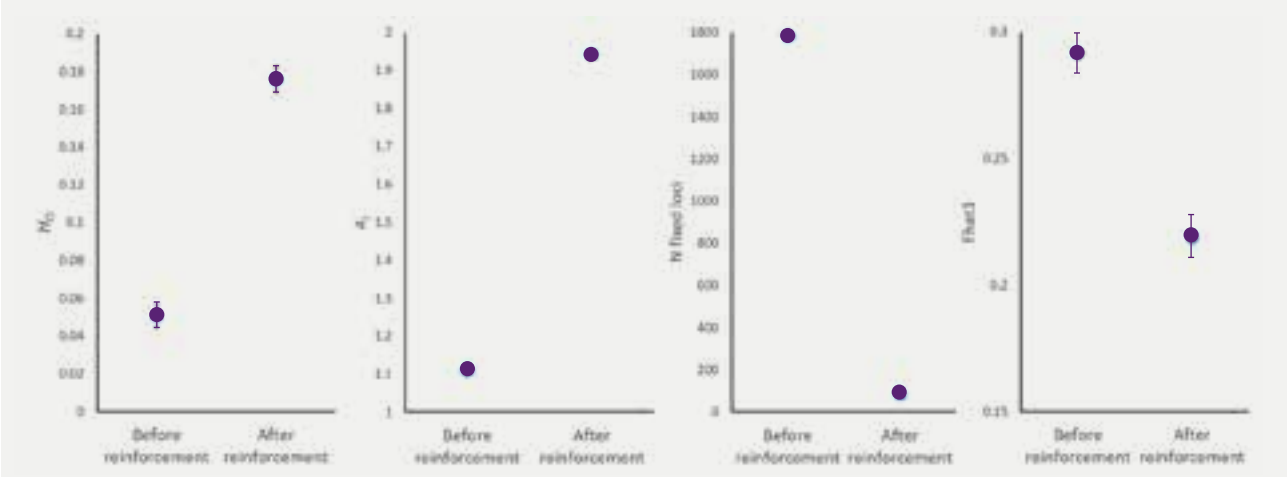

Figure 8: Genetic diversity in the Knapdale beaver population has increased significantly following reinforcement from Tayside with beavers of a different genetic stock. There is significantly greater heterozygosity (H_O) and allelic richness (A_r) in the population, far fewer fixed loci, and significantly less inbreeding (Fhat3) on average. Error bars represent 95% confidence interval.

as these are an indicator of the amount of mating that is occurring between relatives (inbreeding). As inbreeding can lead to a variety of fitness issues, it is desirable to keep inbreeding coefficients as low as possible.

The data show that reinforcement efforts in Knapdale have significantly increased genetic diversity in the population (Figure 8), but no breeding events between Norwegian-origin and Bavarian-origin animals were detected (Figure 9). With no evidence of genetic material being exchanged between Norwegian and Bavarian beavers, the data show two genetically separate populations. The hope is that in subsequent years, as kits from each group mature and disperse into Knapdale, mixing between Norwegian and Bavarian beavers will occur, resulting in a more connected and mixed population.

Knapdale beaver families

While establishing the full identity of all beavers in Knapdale and their relationships to one another is not possible with the data available, a combination of genetic and observational data was used to improve understanding of the largest beaver family present at the time in Knapdale: the Loch Coille-Bharr family group.

This family is of interest for two reasons: 1) it is one of the original Norwegian-origin families and the most successful family in Knapdale to date in terms of reproduction; 2) the mother of this family disappeared during the Trial and was replaced by her daughter, which formed a pair with her father, which has persisted ever since. All offspring from this father–daughter pairing will be very inbred, and this may present challenges for the family in future (see Appendix 2, Figure A2).

Fortunately, the genetic data suggest that other animals which have been introduced to Knapdale as pairs are not closely related, and there is no evidence of other father–daughter pairings or similar (data not shown).

A full scientific publication on the population genetics of beavers in Knapdale, Tayside, Norway and Bavaria, based on nuclear and mitochondrial DNA, will be published in 2021.

Is the inbreeding observed in Knapdale of concern?

In general, wildlife management programmes try to avoid inbreeding, as it acts to erode genetic diversity and can result in inbreeding depression (a reduction in the fitness of the offspring of related individuals versus those of unrelated individuals) (Allendorf *et al.* 2013, p.521).

It is often assumed that rodents are less vulnerable to inbreeding depression due to rapid reproduction and population growth rates (Mills and Smouse 1994), but empirical evidence contradicts this. Inbreeding has been shown to decrease litter size, offspring survival and mass in mice, and decrease survival of mice reintroduced to the wild (Jimenez *et al.* 1994; Lacy *et al.* 1996); decrease survival of offspring in marmots (Olson *et al*. 2012); decrease litter size across 25 generations of long-haired rats (Lacy and Horner 1997); and increase likelihood of death via coronavirus in naked mole-rats (despite regular inbreeding in this species) (Ross-Gillespie *et al.* 2007).

The evidence regarding inbreeding depression in beavers is mixed and inconclusive, as there have been no detailed studies on inbreeding depression in either the European or the North American species. Increased reproductive success in admixed vs non-admixed groups of beavers in Russia, and high incidence of jaw and dental abnormalities in beavers in Russia and the Elbe population, have all been cited as evidence of inbreeding depression in beavers (Halley 2011). However, it has also been argued that the positive population growth and lack of morphological abnormalities seen in non-admixed Scandinavian beavers is evidence of a lack of inbreeding depression, and that abnormalities in Russia and the Elbe could be caused by other environmental factors such as pollutants in the water (Rosell *et al.* 2012).

To our knowledge, no study has yet pieced together the genetic and fitness data required for a robust evaluation of inbreeding depression in any beaver population, and thus it is impossible to say with any certainty what the ramifications for inbreeding in Knapdale's beavers might be.

Ultimately, European beavers show relatively low genetic variation across the board, particularly the Norwegian population used in the initial reintroduction to Knapdale (Senn *et al.* 2014). Crucially, all European beavers have very low diversity at immune loci (Ellegren *et al.* 1993), which renders them potentially vulnerable to disease outbreaks. The Reinforcement Project has made successful steps towards increasing diversity in Knapdale beavers, but a lack of evidence for inbreeding depression in the species up to this point does not negate this phenomenon, and further genetic management of the Knapdale (and indeed the entire UK) beaver population may be needed in future.

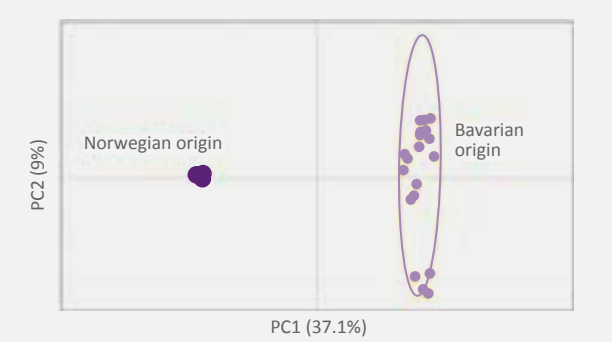

Figure 9: Principal component analysis (PCA) based on genotype data for Knapdale beavers and showing principal components 1 and 2 which, between them, explain 46% of the variance in the dataset. Each point on the PCA is an individual. Individuals closer together on the PCA are more genetically similar, while those further apart are more genetically different. Norwegian origin beavers clearly cluster together on one side, and Bavarian origin beavers on the other. There is more genetic variation in Bavarian beavers than Norwegian beavers in general, hence the looser clustering of Bavarian origin animals. As there are two clear clusters and no intermediate individuals, the data demonstrate a clearly structured population with no mixing between Norwegian and Bavarian stock animals as yet.

Much valuable information has been gained and published over the last 11 years to assure stakeholders and the public that the Eurasian beaver is thriving in Scotland and so far without evidence of any significant disease risks to wildlife, domestic animals or humans."

Dr Simon Girling
RZSS

© Russell Savory

Section 9: Health screening and post-mortems

As in the Trial, health screening of beavers prior to release for the reinforcement, and conducting post-mortems of any beaver carcasses recovered during the Reinforcement Project, was conducted by the veterinary team at RZSS Edinburgh Zoo. Health screening is important to prevent transmission of harmful pathogens from one population to another and to ensure animals are being released in good health to maximise their chance of survival on release.

Physical examination and diagnostic imaging

Twenty-one beavers were physically examined prior to translocation to Knapdale: 18 were examined at Edinburgh Zoo, and three (SBB19, SBB20 and SBB21) at Five Sisters Zoo, following the Edinburgh Zoo veterinary team's protocols. This examination includes listening to the individual's lungs and heart, feeling their abdomen for swelling or abnormalities, and assessment of their teeth, eyes and coat. No beaver demonstrated any significant abnormal clinical signs. All beavers were fitted with a microchip/transponder under the skin between their shoulder blades so as to permanently individually identify each beaver. Ear tags were placed in both ears so as to allow the possibility of remote identification. Body measurements, including weights, were taken and recorded, and body condition scores were considered to be optimal for the species (2.5–3 out of 5) (Girling 2013). Gender was identified through castoreum examination (Rosell and Sun 1999).

Four beavers (SBB01, SBB03, SBB04 and SBB05) underwent radiography, and also had ultrasound examinations under general anaesthesia to assess for *Echinococcus multilocularis* (*Em*). All four animals were negative for evidence of this parasite. In addition, broncho-alveolar fluid (BALF) lavage including acid-fast staining for mycobacteria in the lungs was carried out in the same four beavers under general anaesthesia, with negative results. After this, an exemption for testing Tayside beavers for *Em* and mycobacteria before being translocated to Knapdale was granted by the Scottish Government and so no further beavers underwent radiography, ultrasound or BALF examination.

Faecal examination

All 21 beavers were tested for known pathogenic gastrointestinal bacteria including *Salmonella*, *Campylobacter* and *Yersinia* spp., and all tested negative. In addition, all 21 beavers were tested for intestinal parasites including nematodes, cestodes, trematodes, *Eimeria*, *Giardia* and *Cryptosporidium* spp., and all were negative for detectable intestinal parasites with the exception of four beavers that tested positive for the beaver-specific intestinal fluke, *Stichorchis subtrequetrus* (Campbell-Palmer *et al.* 2013). Four beavers' faecal samples were tested by acid-fast staining for evidence of mycobacteria and were negative. Following these negative results, the Scottish Government granted an exemption on mycobacteria tests.

Urine testing

Urine samples were obtained for eight beavers and tested by quantitative polymerase chain reaction (qPCR) for *Leptospira* spp. bacteria as per Girling *et al.* (2019), and all were found to be negative. This testing was for a veterinary research project and thus was conducted opportunistically and not for all beavers.

Blood sample evaluation

Blood samples were taken from all 21 beavers, and haematology and biochemical parameters were found to be within normal published parameters (Girling *et al.* 2015).

Fifteen beavers were sampled for *Leptospira* spp. bacteria microscopic agglutination testing by the Animal and Plant Health Agency, Weybridge as per Girling *et al*. (2019), and all were found to have zero titres for *Leptospira* spp. pools 1–6. Again, the *Leptospira* spp. testing was for a veterinary research project and thus was conducted opportunistically and not for all beavers.

Post-mortem testing

Four beavers released into Knapdale over the course of the translocation were found dead after release and underwent a full post-mortem. Additionally, a beaver released as part of the original Trial was found dead during the Reinforcement Project and thus also underwent a full post-mortem.

The first beaver (SBB06) was found on 20 April 2018, around one week after release and approximately 9km from the release site (4km by freshwater and 5km by saltwater by the suspected route).

The beaver was an adult male, still in good body condition (3 out of 5 and with a bodyweight of 19.65kg, which was 1.25kg heavier than its release weight). Post-mortem results indicated septicaemia with pancreatitis and peritonitis associated with *E. coli* and *Kocuria kristinae* bacteria. *E. coli* is considered ubiquitous, but *K. kristinae* has been linked in humans to acute cholecystitis, septicaemia, and bacterial endocarditis as an opportunistic infection (Napolitani *et al.* 2019). Pre-release blood results from this individual (taken on 12 April the day before release) showed no evidence of pancreatitis or other organ-related damage, and no evidence of septicaemia. Microbiology prior to release did not isolate *Kocuria kristinae* or any other pathogenic bacteria. Weight gain in this individual in the week it was in Knapdale suggested the animal was feeding post-release and was confirmed by a full stomach and small intestines. The pathophysiological processes that occurred in this case are difficult to interpret but suggest a peracute septicaemia, probably associated with a pancreatitis caused by *Kocuria kristinae*. From previous knowledge of related historical cases, many of these similar cases appear to be triggered by a period of immunosuppression/ maladaption, which may have been triggered by the animal's self-migration from its release site over 9km to the area where it was ultimately found. This migration could have led to a physiological increased susceptibility to opportunistic emerging pathogens.

The second beaver (SBB08 – a female kit) was found on 1 October 2018 in the Faery Isles inlet of Loch Sween. The third beaver (SBB11 – a male kit) was found on 6 October 2018 at Tayvallich. Unfortunately, in both these cases, gross post-mortem and full microbial and histopathological examination was unremarkable, with no clear cause of death. In addition, no evidence of parasitism or trauma were identified in either case.

The fourth beaver (SBB20) was found on 21 October 2019 (released into Knapdale on 2 October 2019) on the shoreline at Kilmichael of Inverlussa, approx. 1.75km from the release site on Lochan Làraiche. This individual had moderate predation of the carcass, which limited interpretation of the post-mortem. The beaver was in good body condition with subcutaneous fat depositions over the chest and abdomen, with a full stomach and intestines. Evidence suggested that blunt trauma of an unknown source may have contributed to the animal's death. It is worth noting that the most likely dispersal route for this animal (the Lochan Làraiche outflow) involves numerous waterfalls, and it is possible that a fall on one of these could have resulted in the trauma seen in this autopsy.

The beaver originating from the Trial (M10I16) was presented for post-mortem in November 2018, having been found dead in the Scotnish Loch outflow. The body was poorly preserved due to decomposition, and freezing artefacts hampered histopathological investigation. No significant microbial or parasitic pathogens, or evidence of trauma, were identified at gross post-mortem to explain the death. S*tichorchis subtrequetrus*, the intestinal fluke of beavers, was identified in low numbers in the caecum, with no evidence of associated pathological changes.

Summary

Pre- and post-release testing of beavers translocated from Tayside to Knapdale did not reveal any evidence of previously reported beaver pathogens such as *Giardia, Salmonella* or *Leptospira* spp. infection. Body condition of beavers screened appeared good in all cases, and along with additional testing indicated that these beavers were coping well with their Scottish habitat.

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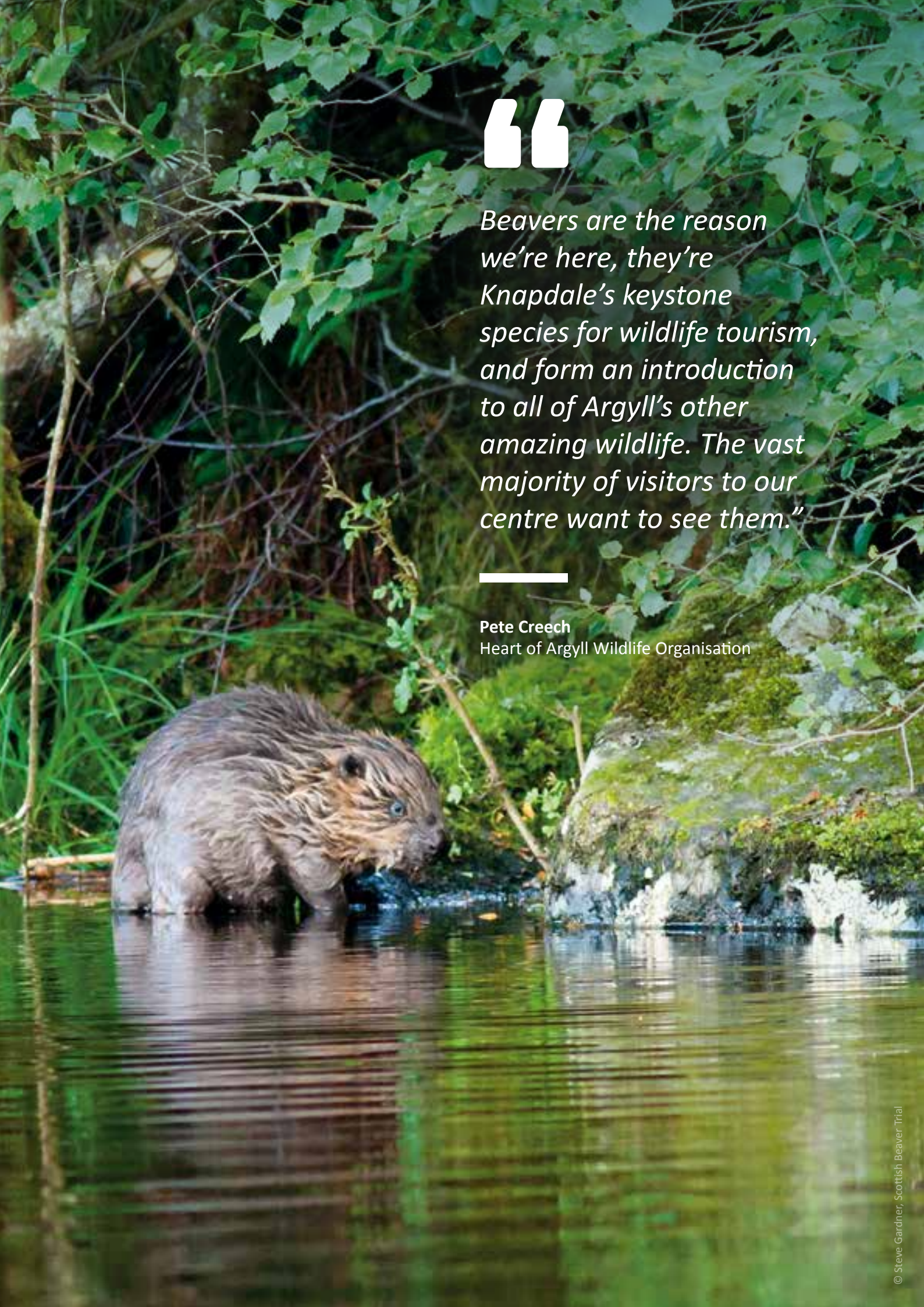

Beavers are the reason we're here, they're Knapdale's keystone species for wildlife tourism, and form an introduction to all of Argyll's other amazing wildlife. The vast majority of visitors to our centre want to see them."

Pete Creech
Heart of Argyll Wildlife Organisation

© Steve Gardner, Scottish Beaver Trial

Section 10: Scottish Beavers in the media

The reintroduction of a charismatic species like beavers was always going to generate a high level of media and public interest. Collaboratively produced press releases were distributed to media contacts, blog articles were published on the partners' websites, and regular updates were posted on the partners' social media channels. This resulted in stories from the project being picked up by the media on a regular basis.

Media coverage

Since 2017, 786 pieces in the Scottish and UK media have referred to the Scottish Beaver Trial or Scottish Beavers. Collectively these have had a reach of 84 million people. Articles have been published in national newspapers including the *Guardian*, *Daily Mail*, *Times*, *Scotsman* and *Herald*.

Interviews have been broadcast on BBC Radio Four, BBC Breakfast, Reporting Scotland, Radio Scotland Out of Doors, and many more. Media highlights during the Reinforcement Project include:

2017

The Scottish Beavers partners led calls for European Protected Species status to be given to beavers in Scotland. Significant advocacy included a joint letter from key figures in Scotland's environment movement supporting this aim, published in the *Guardian*.

2018

Knapdale's beavers were featured on the BBC's Grand Tour of Scotland's Lochs.

2019

The designation of beavers as a European Protected Species (see Section 11) garnered a lot of media coverage, and Scottish Beavers hosted Cabinet Secretary for Environment, Climate Change and Land Reform, Roseanna Cunningham, in Knapdale to celebrate.

The partners were thrilled to be recognised for over a decade of work bringing beavers back to Scotland and pushing for their protection when they won the Nature of Scotland Species Champion Award.

2020

The work of Scottish Beavers was featured on BBC Scotland's Inside the Zoo series.

Protected status is an important milestone for the return of beavers to Scotland's lochs and rivers. It follows decades of work by countless organisations and individuals to demonstrate the positive impacts that beavers can have."

Jo Pike
Scottish Wildlife Trust

© Heart of Argyll Wildlife Organisation

Section 11: Legal protection of beavers in Scotland

On 1 May 2019, the Scottish Government granted European Protected Species (EPS) status to Eurasian beavers in Scotland, making it illegal to disturb, capture or kill a wild beaver, or damage a breeding site or resting place of a wild beaver, except under licence. This landmark event came as a direct result of the Scottish Beaver Trial and subsequent *Beavers in Scotland* report (Scottish Natural Heritage 2015) and is thanks to decades of dedicated work by many people in a number of conservation organisations.

The Scottish Beavers partners engaged with a broad range of stakeholders with interests including conservation, farming, fisheries and forestry through the Scottish Beaver Forum to ensure a positive future for beavers nationally. Legal protection marked the beginning of a management framework in Tayside, where licences are required for landowners to manage beavers where they are causing significant damage, especially to Prime Agricultural Land.

The Scottish Beavers partners hosted a high-profile event to celebrate the milestone of EPS status, attended by Scottish ministers, researchers, conservationists and advocates who have been involved throughout the reintroduction process.

While securing EPS status is significant for beavers nationally, this new legislation has not significantly affected Knapdale's beavers. As landowners, FLS have been supportive and indeed pivotal in efforts to reintroduce beavers to Knapdale since the beginning. They have become accustomed to managing the impacts of beavers when required.


© Pete Haskell

Guardian


Historic day for Scotland as beavers get protected status


BBC News

Times


Beavers get protection — and a plea


Beavers given added protection against lethal control measures

ITV News

“Beavers create substantial benefits for both wildlife and people, and their return to Scotland demonstrates a progressive approach to managing our landscapes and biodiversity.”

Sarah Robinson
Scottish Wildlife Trust

© Steve Gardner, Scottish Beavers

Section 12: Did the Scottish Beavers Project reach its goals?

The Reinforcement Project has undoubtedly improved the resilience of the Knapdale beaver population. The number of confirmed animals in the area is higher than at the project outset, with actual numbers likely to be greater still. Beavers are more widespread, and breeding throughout the catchment has increased, as has genetic diversity in the population. Three of the four project goals have been met, with one on its way to being met in the near future (Figure 11).

The key aim of releasing beavers into the majority of suitable release points within Knapdale was shown to be met in the March 2020 survey, with animals seen to be expanding into burns, and activity in new areas being picked up in the September 2020 survey.

Two pairs were observed to have established and bred as a result of the Reinforcement Project (one on Loch McKay; the other on Lochs Linne and Fidhle), and five breeding pairs or family groups were confirmed (on Loch McKay; Lochs Linne/Fidhle/na Creige Mòire and Lochan Beag; Loch Coille-Bharr (two families); and Lochs Lily/Buic), with a further pair confirmed but not observed to be breeding (Loch Losgunn). It is possible that further breeding animals could have established in the Coille-Bharr outflow to the Faery Isles.

While mixing of animals between Norwegian and Bavarian-origin families was not detected during the lifespan of the project, Bavarian-origin animals were confirmed to be breeding in Knapdale. The higher density of animals within the catchment increases the likelihood that dispersing offspring from families with different genetic backgrounds will encounter each other and form a pair. In addition, one group of animals was observed to be consistently moving between Loch na Creige Mòire/Lochan Beag and Lochs Linne/Fidhle, demonstrating that animals will move between catchments, again increasing the likelihood that juveniles with different genetic backgrounds will meet.

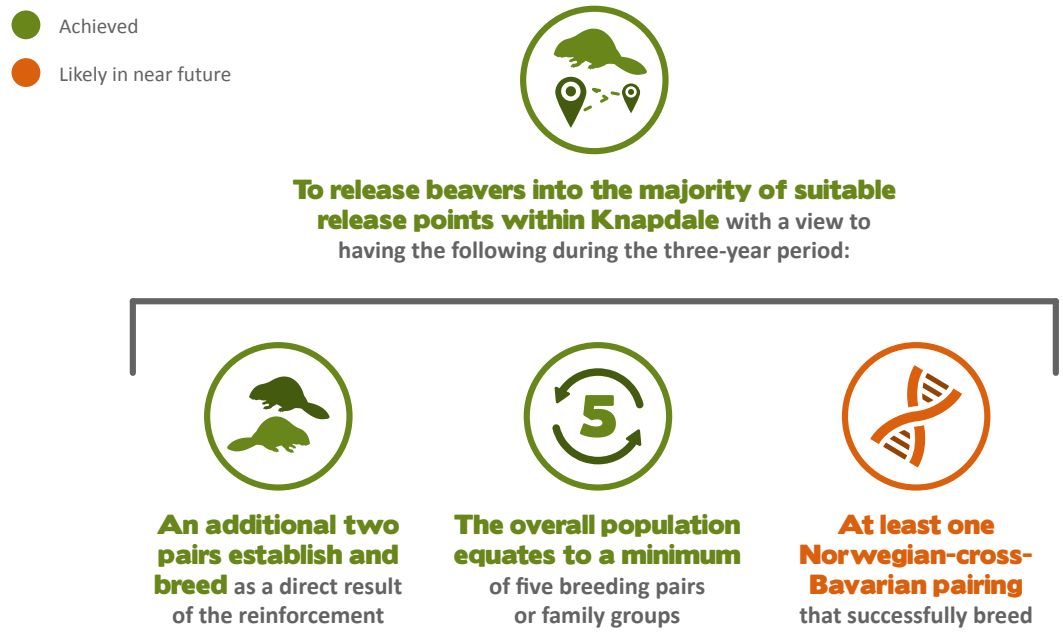

Figure 11: Goals of the Scottish Beavers Reinforcement Project as described at the outset of the project.

One of the boldest and most visionary conservation actions in a generation. C'mon the Beavers!"

Simon Jones
Scottish Beaver Trial (former)

© Steve Gardiner, Scottish Beavers

Section 13: The future of beavers in Scotland

The Knapdale beaver population is a clear illustration that in the right location, and with all the necessary permissions and consultation in place, beavers can flourish without negatively affecting their human neighbours. Not only that, but these ecosystem engineers will transform the landscape they inhabit in a way that is hugely beneficial to other native species, while bringing economic benefits to the area in the form of wildlife tourism.

The partners' hope is that the Scottish Beavers project can act as a template for efforts to reintroduce beavers responsibly in other areas of Scotland and more widely, securing the future of this impressive mammal while ensuring best practice for conservation translocation projects. Here, the Scottish Beavers partners offer some recommendations and insight gained over the course of the Scottish Beavers Reinforcement Project.

Recommendations for Knapdale

The Scottish Beavers partners have worked with beavers in Knapdale for over 10 years, first as part of the Trial and latterly for the reinforcement. As for any well-managed reintroduction, both the Trial and the reinforcement were relatively intensive processes. As a result, the Knapdale site is now at capacity in terms of all suitable habitat being occupied by beavers; and numerous beaver families are established, breeding and modifying their surroundings.

However, the future of beavers in Knapdale is by no means certain; the population is still in a relatively early stage of establishment, and the next decade will be an important test of whether the Knapdale beavers can become a self-sustaining population.

The following recommendations are designed to ensure the best chance of survival for the Knapdale beaver population:

1. Knapdale beavers should now be treated as a wild population. While FLS may elect to continue some degree of monitoring of these animals, interference and disturbance of the animals themselves should be kept to an absolute minimum.
2. Given the information gathered in the most recent survey, the team recommends that if FLS does elect to continue with some kind of monitoring, these efforts should focus on using camera traps to attempt to identify the beavers active on the Buic Pond, and at the end of Barnagad Burn.
3. A more intensive follow-up survey in 10 years' time (i.e. 2030) would be useful to ascertain whether the Knapdale beaver population has become sustainable. If this survey included trapping and genetic sampling, it would allow assessment of the size and genetic composition of the Knapdale beaver population at that point, and where it sits in relation to other beaver populations in Scotland and internationally.
4. If a future survey (such as that mentioned in recommendation 3) suggests that Knapdale remains a closed population with no migration in or out, genetic diversity will naturally erode over time. If this erosion continues then, eventually, further translocations may be necessary to guard against any negative effects of low genetic diversity. Given these circumstances, moving new animals into Knapdale or swapping some Knapdale beavers out for others with different genetic heritage could be considered.
5. Ultimately, it would be better for the long-term sustainability of the Knapdale population to naturally join with other beaver populations in Scotland. This could be encouraged through strategic releases on the edge of range into Loch Awe or the surrounding area, mitigating the need for future translocations into Knapdale.

Recommendations for beavers in Scotland

Although beavers are now recognised as a native species and protected by law, the Scottish Government's position at the time of writing is that there will be no translocations of beavers in Scotland outside their current range for the foreseeable future. This stance is driven by human–wildlife conflict in Tayside caused by the unauthorised release of beavers into the Tay catchment, an area with a very high percentage of Prime Agricultural Land. The Tayside situation underlines how critical it is for wildlife reintroductions to be conducted responsibly under licence, in suitable areas, and with appropriate consultation of all stakeholders.

Arguably, beavers cannot flourish in Scotland without being introduced into other areas. These areas should be far better suited to the co-existence of beavers and humans than Tayside, and have better opportunities for natural expansion than Knapdale. Currently, beavers caught in Tayside are translocated away from conflict areas to new reintroduction projects in England. This is fragmenting and depleting the Scottish population of beavers, and likely reducing genetic diversity. In the long term, Scotland requires a bigger-picture vision for beavers.

The following recommendations are to promote a thriving population of Scottish beavers:

1. Licensing requirements for proposed translocations of beavers in Scotland should be proportionate to the location. For example, translocation on the edge of the existing range of beavers should not require the same degree of licensing process undertaken for either of the Knapdale projects.
2. Introductions to other suitable sites in Scotland should be permitted to support the management framework and relocation of beavers from areas of high conflict. This would reduce pressure in areas of conflict, establish new beaver populations and their associated biodiversity benefits across a wider range of suitable sites, and build a more robust population of beavers in Scotland that is less vulnerable to localised population losses.
3. The Scottish Beaver Forum is a key discussion forum for beaver management that gives a voice to all stakeholders. This forum should continue openly and honestly discussing the conservation and management of beavers in Scotland, promoting the benefits of this species and seeking solutions to mitigate human–beaver conflict when it arises.
4. The total founder base for beavers in Scotland is still narrow and should be augmented when future releases are made possible. This may require further reintroductions from Europe.
5. The effective management of beavers at a national level demands a conservation action plan. This strategy should look beyond the current restrictions on beaver translocations and plan for a variety of scenarios that could promote the long-term persistence, population growth and range expansion of beavers in Scotland in a framework that maximises the benefits and minimises conflict.

Recommendations for beaver translocations

Beavers are not just back in Scotland – at the time of writing, beaver reintroductions are taking place in various locations in England, and there are discussions regarding beaver reintroductions to Wales. The hope is that the information presented here and in the *Beavers in Scotland* report will be valuable to other organisations working on beaver translocations in Britain. We note that, under the management framework in Scotland, translocation and lethal control are equal in terms of licensing: landowners considering trapping are already experiencing or expecting significant impact from beavers on Prime Agricultural Land. Thus, it is likely that any beaver being translocated out of Tayside to another project will be at risk of lethal control if capture and translocation is not successful. This situation puts added pressures on translocations that recipients of beavers should be aware of. We also note that beaver translocations have been positioned by some advocates as a preferable choice to lethal control in terms of animal welfare. However, translocations also carry appreciable welfare risks to the individuals being moved, and these risks should be accounted for when planning a translocation.

The past 10 years of beaver reintroduction work in Scotland have been a learning curve; as a result of the challenges and setbacks the team has faced, we make the following recommendations and observations:

1. We strongly recommend against releasing lone kits, or any number of kits without at least one adult family member. Our experience suggests that releasing kits without adults is most likely to lead to dispersal, stress and eventual death of the kits concerned.
2. When planning a translocation, if relying on beavers being trapped in conflict areas, be aware that it is challenging (often impossible) to plan or predict what animals might be in the area, how many of them will be trapped and what order they will be trapped in. Thus, while you might have planned to release a family, you might, for example, receive two individuals from different sites, or two individuals from the same site which might be a pair or might equally be mother and almost adult son/father and almost adult daughter. Further to this, unless genetic samples are gathered for these individuals prior to release, it will not be possible to ascertain these relationships and there will be a degree of uncertainty regarding the make-up and relatedness of the new population.
3. Despite our best efforts to predict the best habitat for beavers, they do not always remain in their release site and have often dispersed and seemingly chosen to live on stream systems and in ponds which would never have been selected as release sites.

4. Related to 2 and 3 above, consider whether additional strategies such as assisted releases involving artificial lodges or supplementary feeding should be employed and what the criteria are for doing so.

5. Post-release welfare is an important consideration in any translocation. The degree of post-release monitoring of beavers required will vary from project to project depending on the nature of the translocation (i.e. edge of range within same catchment vs move to a new area where beavers have been absent for hundreds of years). At the very least, organisations taking part in a translocation should be prepared to do basic visual checks for dead or injured animals in the week immediately following release. Depending on the project and the participants' preference/ resources, post-release monitoring can be scaled up to include checks for beaver activity (feeding signs and construction etc.) and camera trap monitoring. A plan for what intervention (if any) is to be carried out in the event of poor welfare outcomes being detected should be in place for all releases (see Appendix 3 for an example of how to do this).

6. Health-screening Eurasian beavers prior to any translocation (regardless of whether it is within catchment or further) is recommended on welfare and animal health grounds. This can be done in the field at the point of capture and will require a vet to be present. As a minimum, this will comprise:

    - a physical examination by a veterinary surgeon for evidence of injuries and disease
    - a blood sample to assess basic organ function and metabolites, and red and white blood-cell parameters to assess for evidence of anaemia or infectious disease
    - a faecal sample and in-field screening for reported beaver pathogens such as endoparasites (examination for *Giardia* and *Cryptosporidium* spp., coccidia and the presence of worm eggs/larvae)

    The Animal Health and Welfare (Scotland) Act 2006 (as amended) states that any animal released into the wild that has previously been held under human control (including trapping for translocation) has to be medically fit to release. The vet must assess whether this is the case, and, if the animal is judged unfit for release, the vet will need to assess whether the animal needs to be euthanased (which can be conducted by the vet without a NatureScot licence) or taken into captivity for treatment and release at a later date.

    Ideally, test results for *Salmonella* spp. would be available before an animal is released into its new home. However, *Salmonella* test results will take at least 1–3 days to become available, there are few holding facilities for beavers in Scotland, there is a welfare cost to holding beavers for any length of time and, of 105 beavers tested, none have tested positive for *Salmonella* spp. Given the above, we suggest that *Salmonella* testing be conducted prior to release where possible, but is not needed in all cases.

    No evidence of *Echinococcus multilocularis*, or *Mycobacterium bovis* has so far been identified in beavers in Scotland, suggesting that testing Scottish beavers for these pathogens is not currently necessary although data will continue to be collected by organisations such as the RZSS to keep adding to our full understanding of their potential disease risk.

7. It is essential to plan for the long term. If a release is to be conducted in a Trial style (i.e. no dispersal or connectivity with other populations due to a fenced area or natural barriers), ensure there is a plan for what to do if the beavers in the trial reproduce successfully and the population starts to grow. Where will juveniles disperse? How will genetic diversity and connectivity with other beaver populations in Britain be maintained? While beaver populations remain small, closed and fragmented, a degree of metapopulation management and human-mediated movement via additional translocations between sites will be necessary to ensure long-term persistence.

8. For the reintroduction of beavers into the UK to be a continued success, collaboration across borders would be extremely valuable. A database of beavers captured, translocated and released across the UK will aid future management and research, and feed into conservation strategies for beavers across the UK. Obliging licensed releases to submit genetic samples of released individuals to curated Biobank facilities would create an unrivalled asset, facilitating genetic and beaver health work required in the future.

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Appendices

Appendices included with this report:

- Appendix 1: Beaver release log
- Appendix 2: Detailed genetic methods and additional genetics results
- Appendix 3: Beaver release flow chart

Supplementary information available on request by emailing **enquiries@scottishwildlifetrust.org.uk**

- Scottish Beavers Licence application form
- Appendices to licence application
- Licence from NatureScot

Appendix 1

Beaver release log

Release project	Beaver ID	Source	Sex	Age at release	Release date	Release site	Status September 2020
SBT	M08K15 Frid	Norway	F	Adult	May 2009	Loch Linne/Fidhle	Deceased
SBT	M08K16 Frank	Norway	M	Adult	May 2009	Loch Linne/Fidhle	Unknown
SBT	M08K17 "Biffa's Brother"	Norway	M	Adult	May 2009	Loch Linne/Fidhle	Deceased
SBT	M08K18 Biffa	Norway	M	Sub-adult	May 2009	Loch Linne/Fidhle	Unknown
SBT	M08K06 Katrina	Norway	F	Adult	May 2009	Loch Coille-Bharr	Unknown
SBT	M08K05 Bjornar	Norway	M	Adult	May 2009	Loch Coille-Bharr	Present
SBT	M08K07 Marlene	Norway	F	Sub-adult	May 2009	Loch Coille-Bharr	Unknown
SBT	M08K08 Millie	Norway	F	Adult	May 2009	Loch Coille-Bharr	Present
SBT	M08K25 Andreas Bjorn	Norway	M	Adult	May 2009	Loch na Creige Mòire	Deceased
SBT	M08K26 Gunn Rita	Norway	F	Adult	May 2009	Loch na Creige Mòire	Unknown
SBT	M08K27 Mary Lou	Norway	F	Sub-adult	May 2009	Loch na Creige Mòire	Unknown
SBT	M08K24 Trude	Norway	F	Sub-adult	May 2010	Lily Loch	Present
SBT	M08K36 Tallak	Norway	M	Adult	May 2010	Lily Loch	Deceased
SBT	M10D09 Eoghann	Norway	M	Adult	June 2010	Loch na Creige Mòire	Present
SBT	M10D10 Elaine	Norway	F	Adult	June 2010	Loch na Creige Mòire	Unknown
SBT	M10I16 Christian	Norway	M	Adult	September 2010	Loch Buic	Deceased
SB	SBB01 Alba	Captive – DGC	F	Adult	October 2017	Loch McKay	Present
SB	SBB03 Wendy	Captive – WT	F	Adult	October 2017	Loch Linne	Unknown
SB	SBB04 Michael	Captive – WT	M	Adult	October 2017	Loch Linne	Unknown
SB	SBB05 Harris	Captive – WT	M	Adult	March 2018	Loch McKay	Present
SB	SBB06 Charlie	Wild – Beauly	M	Adult	April 2018	Loch na Creige Mòire	Deceased
SB	SBB07 Barves	Wild – Beauly	M	Adult	July 2018	Lochan Beag	Unknown*
SB	SBB08 Brogan	Wild – Tayside	F	Kit	September 2018	Lochan Beag	Deceased
SB	SBB09 Skye	Wild – Tayside	F	Adult	September 2018	Lochan Beag	Unknown
SB	SBB10 Arran	Wild – Tayside	M	Kit	September 2018	Lochan Beag	Unknown
SB	SBB12 Fergus	Wild – Tayside	M	Kit	September 2018	Lochan Beag	Unknown
SB	SBB11 Barra	Wild – Tayside	M	Kit	September 2018	Lochan Buic/Buic Pond	Deceased
SB	SBB13 Iona	Wild – Tayside	F	Adult	October 2018	Lochan Beag	Present
SB	SBB14 Murrin	Wild – Tayside	F	Adult	October 2018	Loch Linne	Unknown
SB	SBB15 Fiddich	Wild – Beauly**	F	Sub-adult	August 2019	Loch Losgunn	Present
SB	SBB17 Oban	Wild – Tayside	M	Adult	August 2019	Loch Losgunn	Present
SB	SBB16 Fricka	Wild – Tayside	F	Adult	September 2019	Lochan Làraiche	Unknown
SB	SBB18 Oronsay	Wild – Tayside	F	Sub-adult	September 2019	Lochan Buic	Unknown
SB	SBB21 Colonsay	Wild – Tayside	M	Adult	September 2019	Lochan Buic	Unknown
SB	SBB19 Delfin	Wild – Tayside	F	Adult	September 2019	Lochan Làraiche	Unknown
SB	SBB20 Islay	Wild – Tayside	F	Sub-adult	September 2019	Lochan Làraiche	Deceased
SB	SBB22 Monadh	Wild – Tayside	F	Adult	October 2019	Lochan Làraiche	Unknown

*SBB07 Barves' location is technically unknown, but he is suspected to be resident on the Linne/Fidhle/Beag/na Creige Mòire system in a pair with SBB13 Iona. In Source, DGC = Derek Gow Consultancy, and WT = Wildwood Trust.

** SBB15 Fiddich was originally trapped in Beauly and transferred to the RZSS Highland Wildlife Park in October 2018 to overwinter, as she was too small to release alone.

Appendix 2

Detailed genetic methods and additional genetics results

Beaver DNA extractions

DNA extractions were performed with one of four sampling kits (depending on sample type): Qiagen DNeasy, Qiagen DNA Investigator, Fujifilm Blood, Fujifilm tissue sampling kits. Many of the beaver samples were concentrated from multiple extractions using an Eppendorf Concentrator Plus.

ddRAD library preparation

DNA quality was assessed via agarose gel electrophoresis on a 1% gel, and only non-degraded DNA (as judged by a tight high molecular weight band against a lambda standard) was selected for the library preparation stage. DNA was quantified using a Qubit Broad Range dsDNA Assay (Thermofisher Scientific) according to the manufacturer's instructions and normalised to approximately 7 ng/µl. Many samples were concentrated using an Eppendorf Concentrator Plus to achieve this.

A double digest RAD (ddRAD) library was constructed according to Bourgeois *et al.* 2018. Individual genomic DNAs were restriction-digested by SbfI and SphI, and then Illumina-specific sequencing adaptors (P1 and P2) were ligated to fragment ends. The pooled samples were size-selected (400–700bp fragments) by gel electrophoresis, PCR-amplified (15 cycles) and the resultant amplicons (ddRAD library) were purified and quantified. Combinatorial inline barcodes (5 or 7 bases long) included in the P1 and P2 adaptors allowed each sample replicate to be identified post-sequencing. ddRAD library preparation and sequencing were carried out across two sequencing libraries. Libraries were sequenced on a 150bp paired-end run on a single lane of an Illumina HiSeq 4000 by Novogene.

Reference data were generated previously. To ensure quality control between libraries, within-library and between-library positive controls were included. Library preparation for ddRAD was as described above, except that each sample was subjected to the procedure twice, each with a different combination of barcodes. During the bioinformatic procedure, all reads for a single sample were combined.

ddRAD bioinformatic procedures

ddRAD sequencing data were analysed to identify SNPs and apply quality control measures to generate a robust data set for subsequent population genetic analyses. SNPs can be identified from ddRAD sequencing data either with (reference-based) or without (*de novo*) a reference genome. SNPs identified through reference-based analyses are typically more robust than those identified by *de novo* methods and are therefore preferable when possible. Studies have shown that SNP identification using genomes of closely related species is highly robust (Galla *et al*. 2020). Therefore, the recently generated North American beaver genome (Lok *et al.* 2017) was used to identify SNPs. SNP identification was carried out using STACKS v2.52 for both methods (Figure A1). During and following SNP identification, quality control was carried out to exclude any SNPs or samples which were deemed low-quality, and therefore their data were potentially erroneous (Figure A1).

Figure A1: Details of SNP calling and filtering pipeline for ddRAD data

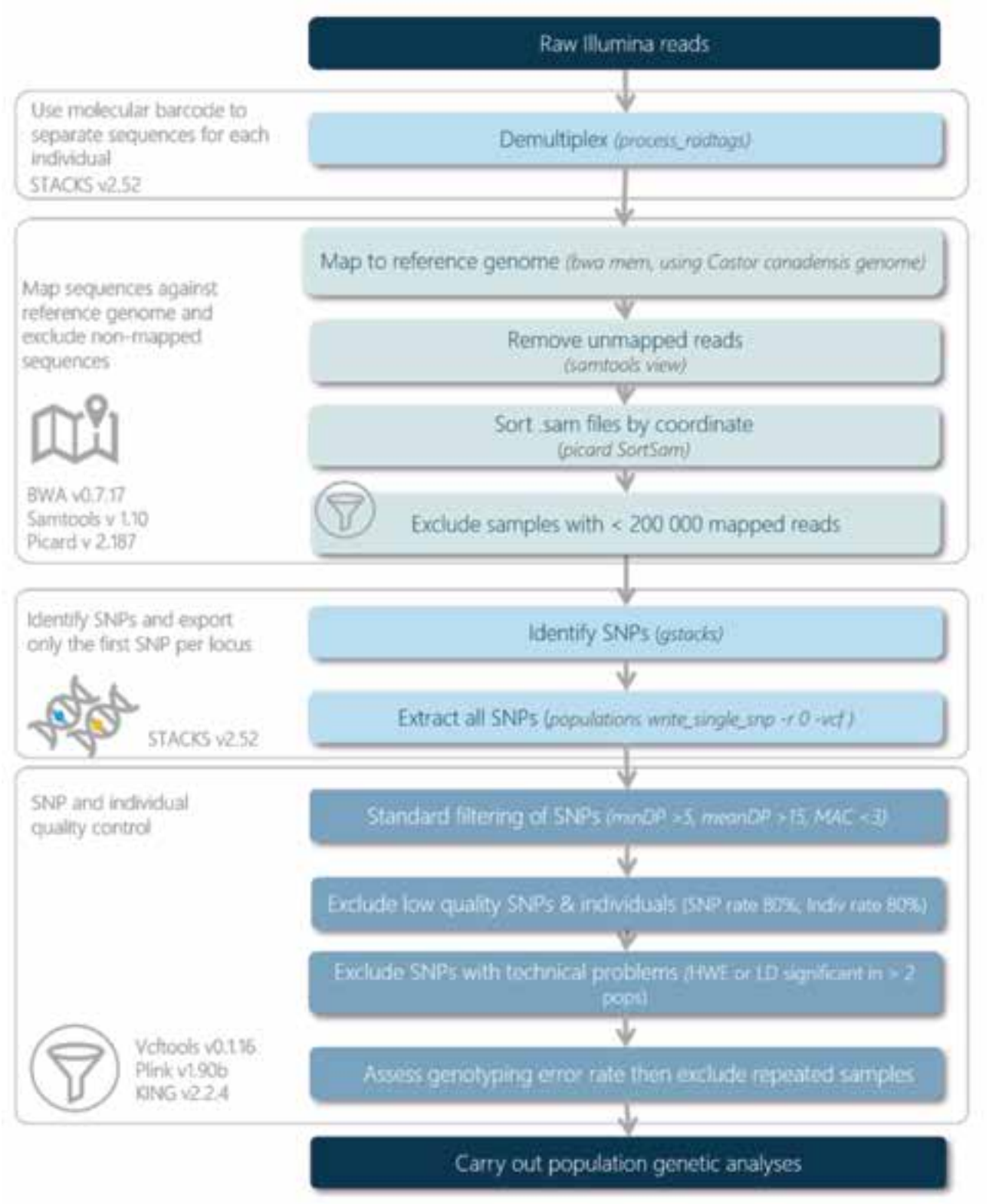
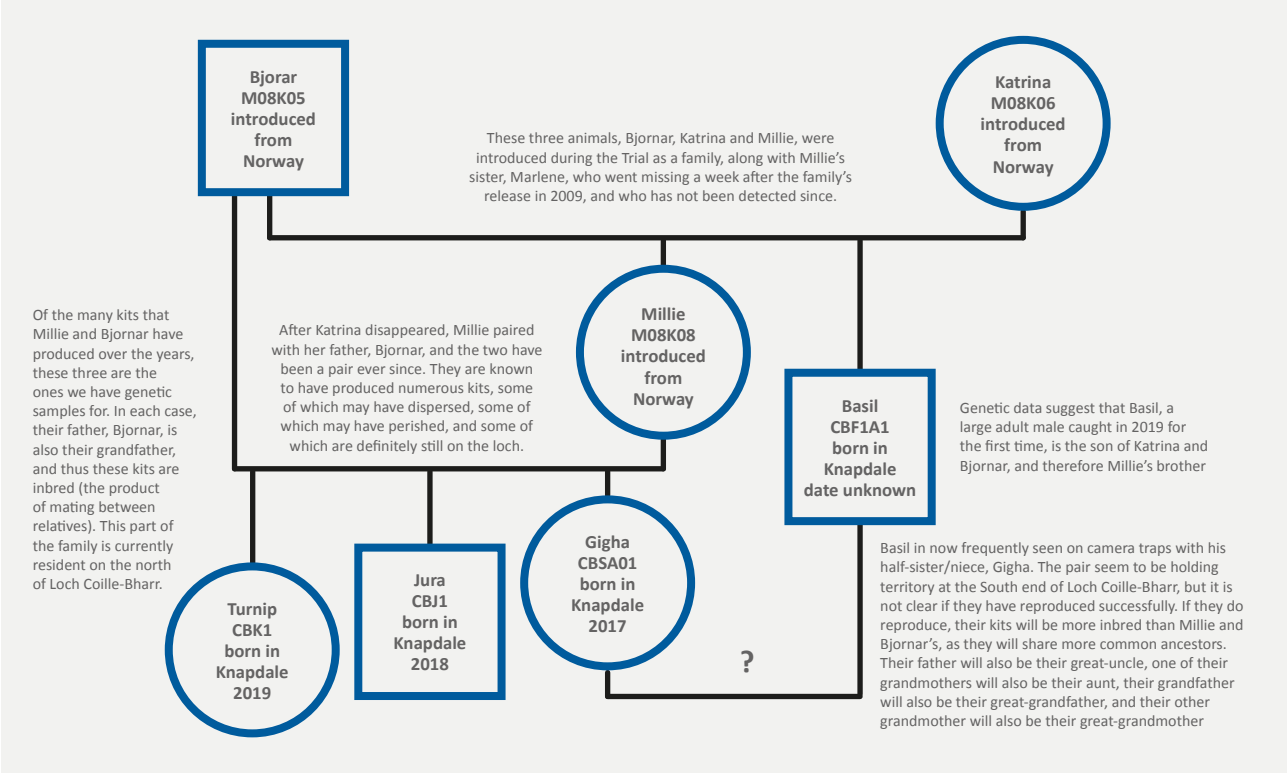


Figure A2 : Beaver pedigree



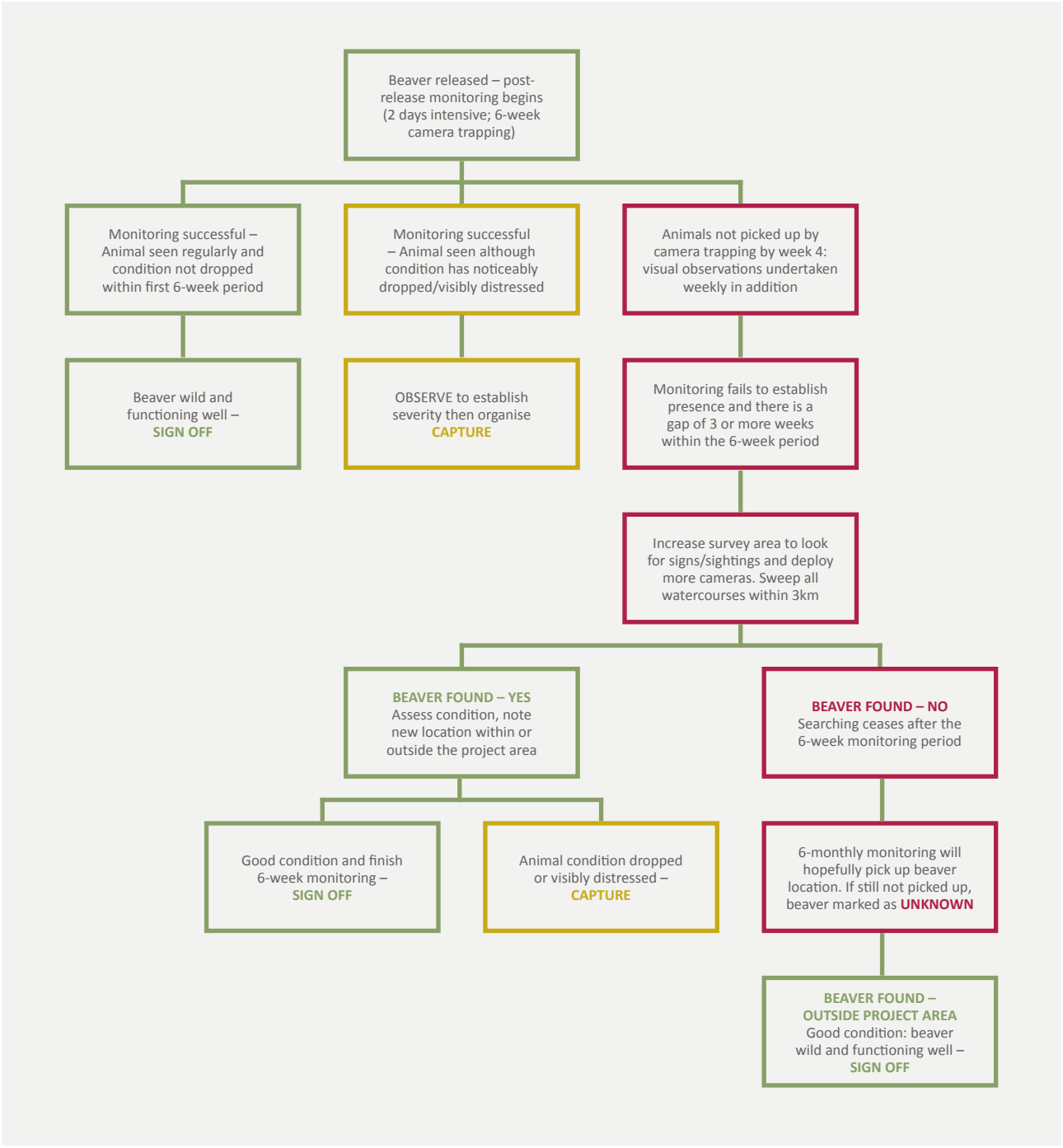
A pedigree (family tree) for the genetically sampled beavers residing on Loch Coille-Bharr during the Reinforcement Project. Squares are males, circles are females, horizontal lines join pairs, with vertical lines leading to the offspring of those pairs. As can be seen, the Loch Coille-Bharr beaver family are inbred, with a father–daughter pairing and a potential half–sister half–brother/uncle–niece pairing.

Appendix 3

Beaver release flow chart

If beaver show any of the following, then capture will apply:

- Obvious serious injury (e.g. loss of limb, large cut)
- Abnormal behaviour (e.g. head tilt)
- Body score of less than 1.5



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