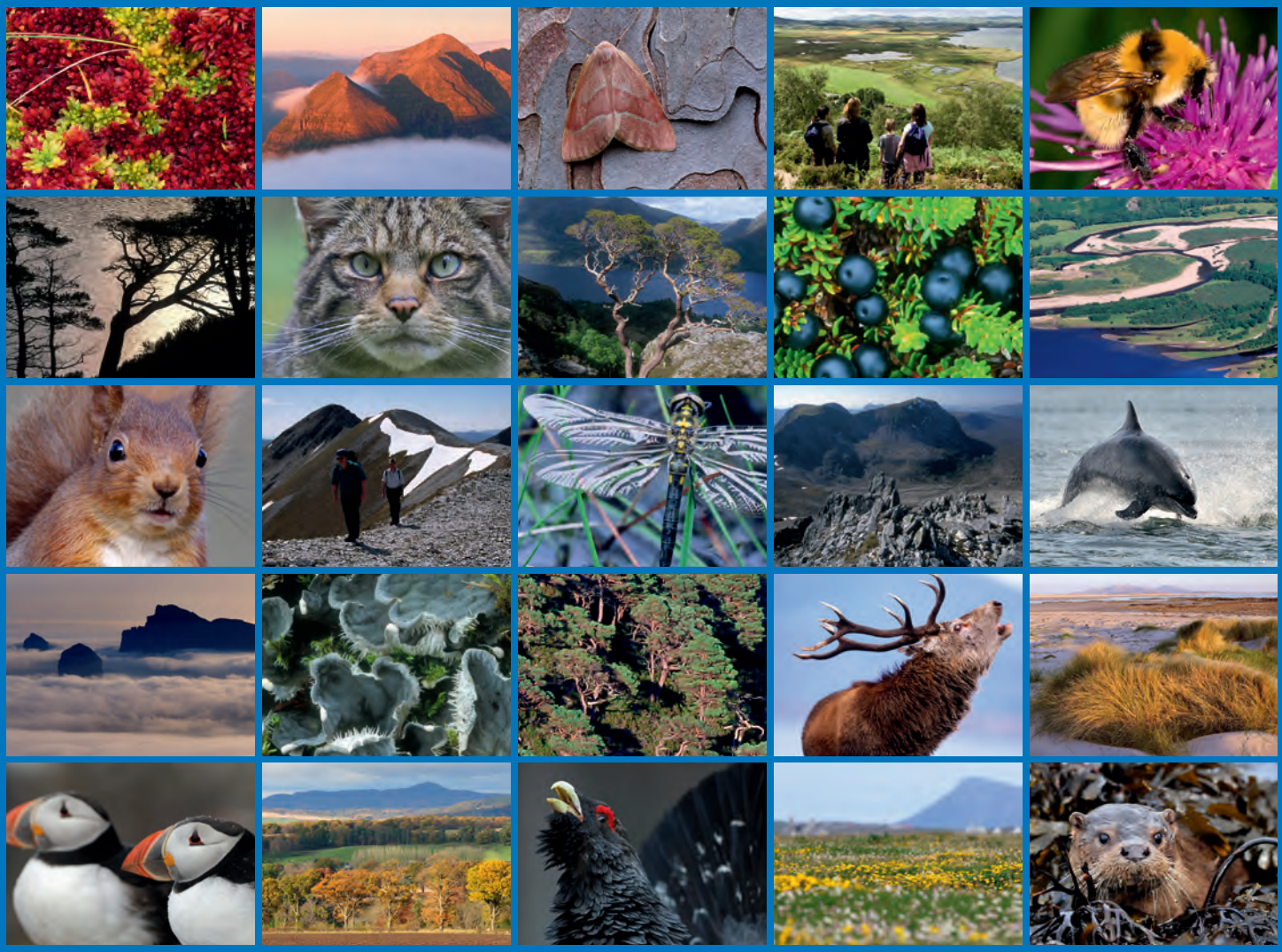
Scottish Natural Heritage
Commissioned Report No. 682

Genetic assessment of free-living beavers in and around the River Tay catchment, east Scotland



Scottish Natural Heritage
Dualchas Nàdair na h-Alba
All of nature for all of Scotland
Nàdar air fad airson Alba air fad

COMMISSIONED REPORT

Commissioned Report No. 682

Genetic assessment of free-living beavers in and around the River Tay catchment, east Scotland

For further information on this report please contact:

James Scott
Scottish Natural Heritage
Great Glen House
INVERNESS
IV3 8NW
Telephone: 01463 725363
E-mail: james.scott@snh.gov.uk

This report should be quoted as:

McEwing, R. Senn, H. & Campbell-Palmer, R. 2015. Genetic assessment of free-living beavers in and around the River Tay catchment, east Scotland. *Scottish Natural Heritage Commissioned Report No. 682.*

COMMISSIONED REPORT

Summary

Genetic assessment of free-living beavers in and around the River Tay catchment, east Scotland

Commissioned Report No. 682
Project No: 13810
Contractor: Royal Zoological Society of Scotland
Year of publication: 2015

Keywords

Beavers; Tayside; Tay; genetics; Eurasian.

Background

There is an estimated minimum of 38 active beaver groups identified within the River Tayside catchment, in east Scotland (Campbell *et al*., 2012). These beavers are of unknown species and geographical provenance, and there is therefore a requirement to provide basic information on this 'population' so that information can be provided to aid the upcoming Scottish Government decision on beaver reintroduction and to advise any relevant management plans regarding their future. The findings from the Scottish Beaver Trial (SBT), along with information gathered through the Tayside Beaver Study Group (TBSG), and experiences from European counterparts living with beavers, will all be considered by the Scottish Government to determine not only the future of the SBT and Tayside beaver populations, but also the future of beaver reintroduction to Scotland.

RZSS has developed a suite of genetic markers to be used for identifying individuals for beaver reintroduction and post-release monitoring, as advised by the IUCN Reintroduction Guidelines (IUCN 2013). RZSS was asked to utilise these new genetic tools to investigate the identity and origins of the beavers now resident on the River Tay catchment.

This report highlights the findings of the genetic analysis from blood samples collected from live-trapped individuals and tissue samples from collected cadavers of beavers living within the River Tay catchment. More detailed descriptions of the genetic markers, methodology and analytical techniques implemented here can be found in Senn *et al*. (2013, 2014) and McEwing *et al*. (2014).

Main findings

- Twenty-five Tayside beaver samples were analysed. All individuals were genetically determined to be the Eurasian beaver species (*Castor fiber*).
- All beaver samples were genetically tested to ascertain the origin of their source population; all had a German (most likely Bavarian) provenance.
- The beaver samples were consistent with the Tayside population originating from three distinct lineages of *C. fiber* from Germany.
- If treated as a single biological population, a high degree of genetic diversity (measured as allelic richness and expected heterozygosity) was evident in comparison to other

sampled beaver populations across the Eurasian range. Such an observation is expected, given the likely admixed population origin (Bavarian) of the beavers on the Tay catchment.

- Evaluating the relatedness among the twenty-five samples indicated the likelihood of there being approximately three parent / offspring relationships; eleven full sibling relationships; ten half sibling relationships and twenty-two first cousins relationships.
- From a genetic perspective, as many of the beavers within the Tayside catchment are closely related the degree of inbreeding in the future could be a cause for concern, particularly if dispersal becomes limited.
- The extent to which the beavers in the River Tay catchment are acting as a biological (freely breeding) population is yet to be determined. This requires consideration when assessing levels of genetic diversity, relatedness and therefore their genetic health. The genetic data provided here should be considered a baseline measure of genetic health and we advise future replicated studies to monitor genetic health effectively over suitable time scales i.e. in one generation.

For further information on this project contact:
James Scott, Scottish Natural Heritage, Great Glen House, Inverness, IV3 8NW.
Tel: 01463 725363 or james.scott@snh.gov.uk
For further information on the SNH Research & Technical Support Programme contact:
Knowledge & Information Unit, Scottish Natural Heritage, Great Glen House, Inverness, IV3 8NW.
Tel: 01463 725000 or research@snh.gov.uk

Table of Contents **Page**

Acknowledgements

This project is supported through a partnership of Scottish Natural Heritage and the Royal Zoological Society of Scotland. We would like to thank Neil Mitchell and Helen Dickinson for all their assistance in the field and the RZSS veterinary team for sample collection. We are most grateful to all those who provided permission for beaver monitoring and trapping on their land, assistance in the field at numerous sites and to those who reported and collected animals for post-mortem screening. Thanks also to Rob Ogden and Iain Bainbridge for comments on earlier drafts of this report.

1. BACKGROUND TO THE PROJECT

1.1 Beavers in Scotland

There are various sources of information regarding the historical existence of beavers in Britain, including palaeontological, archaeological (gnawed timber and bones) and historical records (carvings, place names and written records) (Conroy *et al*., 1998; Coles, 2006). Bone fragments, typically skull fragments, have been found across Scotland and historical written texts catalogue the demise of the beaver (Conroy *et al*., 1998). The Eurasian beaver (*Castor fiber*) most likely colonised England and then Scotland via the land bridge from continental Europe as suitable habitat became available, and this population was later isolated from continental Europe when the land bridge was inundated (Yalden, 1991).

Beavers were thought to be generally extinct in Britain by the 1600s, although there is some evidence of small pockets of animals surviving later in parts of Wales and Scotland (Coles, 2006). Their disappearance was driven by unsustainable hunting for their pelt, castoreum and meat. Beavers (including the North American beaver, *C. canadensis*) have since been introduced at various times and places within Britain, including on the Isle of Bute, although most of these introductions were short-lived and not viewed as serious attempts to restore beaver populations. Effectively, beavers have been absent from Scotland and the rest of Britain for around 400 years, other than in zoological and private collections.

The European Union's Habitats Directive requests that member states investigate the desirability of reintroducing certain former indigenous species, and in 1995 Scottish Natural Heritage begin a number of studies to examine the feasibility of reintroducing the Eurasian beaver to Scotland (e.g. Conroy & Kitchener, 1996). As a consequence of these feasibility studies and some concerns raised in public consultations, a trial reintroduction of a limited number of Norwegian beavers was proposed and licensed in 2008. Contemporaneously, reports of the presence of free-living beavers around the River Tay catchment began to be noted from 2006, presumably escapees from private collections or unlicensed reintroduction attempts using captive-bred or imported wild-caught beavers from continental Europe. In 2012 it was estimated that around 38 active beaver groups were present in and around the Tay catchment (Campbell *et al*., 2012).

This project was commissioned in an attempt to provide additional information about the beavers in and around the Tay catchment by utilising genetic techniques which were being developed specifically for post-release monitoring purposes for any future licensed reintroduction (Senn *et al*., 2013, 2014; McEwing *et al*., 2014).

1.1 Genetic techniques for wildlife monitoring

Genetic techniques can augment direct survey and field observation studies of wildlife, offering an insight into ecological parameters that are difficult or impossible to determine by other methods. Upon collection of a suitable biological sample originating from an individual, genetic profiling of that sample can be used as a means of collecting standard ecological data, and can determine: the species or subspecies, the sex, individuality, paternity and relatedness to other beavers. In addition, analysis of sufficient quality genetic data can also be used to compare and contrast different populations of the same species and in this way identify an individual's population of origin and any potential risk of evolutionary or adaptive constraints that a population may be facing.

Beavers have been the focus of many academic research projects, principally focusing on the geographical structuring or phylogeography across their range (e.g. Durka *et al*., 2005). However until recently, only a limited number of genetic markers have been developed and are utilised for beaver population genetics. Utilising a limited number of genetic markers can result in a lack of power for resolving population parameters and difficulties in utilising

genetic data effectively to elucidate ecological parameters. To aid any post-monitoring release of a licenced reintroduction to Scotland, additional genetic markers have now been developed (see below).

1.2 Objectives

- To attempt to gather a representative sample.
- To determine beaver species present.
- To examine population of origin.
- To assess diversity.
- To estimate level of familiar relatedness.

2. COLLECTION OF BIOLOGICAL SAMPLES FOR ANALYSIS

The quality (undamaged) and quantity (total yield) of DNA in a given sample is directly associated with the quality (amount / freshness / preservation method) of the biological sample collected. Blood and tissue samples offer the highest quality and quantity of DNA and are therefore amenable to the most detailed genetic interrogation and thus produce the maximum amount of data. However, invasively sampling wild animals for DNA studies can be difficult to undertake logistically, often requiring licences, and potentially resulting in negative welfare or behaviour associations, which even if only short-lived, are undesirable. At the other end of the spectrum non-invasive sampling of animals, for example from faecal or hair collection from the field, provides low yields, often of damaged DNA, which does, however, still allow a limited genetic analysis without the trauma of restraining or interfering with the animal under study.

The genetic source sample type required is therefore dependent on the amount of genetic information required to address questions concerning the individual animals or population under study. For this project, where a large amount of genetic data was sought for interrogation, only good quality source samples would be sufficient for analysis.

2.1 Samples used in this study

Samples of tissue and / or blood were supplied from specimens of beaver cadavers, and from blood sampling live-trapped beavers under anaesthesia as part of a health assessment study commissioned by SNH through the TBSG, to evaluate the health of free-living beavers within the River Tay catchment. Findings from this work are reported separately (Campbell-Palmer *et al*., 2014). Table 1 shows the samples used in this study and Figure 1 shows the distribution of sampling locations across the River Tay catchment.

Table 1. List of tissue and blood samples available for genetic screening.

ID	Sample	Sex	Age
TB01	blood sample via live trapping	M	Sub-adult
TB02	blood sample via live trapping	M	Sub-adult
TB03	blood sample via live trapping	M	Adult
TB04	blood sample via live trapping	F	Sub-adult
TB05	blood sample via live trapping	F	Sub-adult
TB06	blood sample via live trapping	M	Sub-adult
TB07	blood sample via live trapping	M	Adult
TB08	Tissue from post mortem	M	Sub-adult
TB11	Tissue from post mortem	M	Sub-adult
TB12	Tissue from post mortem	M	Adult
TB13	blood sample via live trapping	M	Kit
TB14	blood sample via live trapping	F	Adult non-breeding
TB15	blood sample via live trapping	F	Kit
TB16	Tissue from post mortem		
TB17	Tissue from post mortem	M	Kit
TB18	blood sample via live trapping	M	Sub-adult
TB19	blood sample via live trapping	F	Adult non-breeding
TB20	blood sample via live trapping	F	kit
TB21	Tissue from post mortem	F	kit
TB22	Tissue from post mortem	M	Adult
TB23	Tissue from post mortem	F	Adult
TB24	Tissue from post mortem	?	fetus BEV383
TB25	Tissue from post mortem	?	fetus BEV383

3. THE SPECIES OF FREE-LIVING BEAVER IN SCOTLAND

3.1 Species of the *Castor* genus

The genus *Castor* has two distinct, extant species, *C. fiber* (Eurasian beaver) and *C. canadensis* (North American beaver), which diverged approximately 7.5 million years ago, after beavers colonised North America from Eurasia (Horn *et al*. 2011). However, since then they have not displayed naturally overlapping distributions. This long separation has resulted in probable reproductive incompatibility between the species with no live hybrid offspring being reported from captive breeding attempts (Kuehn *et al*., 2000) and with a different chromosome number being present (Lavrov & Orlov, 1973). Both species suffered significant population declines, the extirpation of populations and almost became extinct, predominantly as a result of unsustainable trapping for fur (Halley & Rosell, 2002). Eventual reduction in the fur trade, protection strategies and proactive translocations, saw the recovery of both species through active restoration and natural population spread. The restoration of the Eurasian beaver from near extinction at the end of the 19th century is often viewed as a conservation success (Nolet & Rosell, 1998).

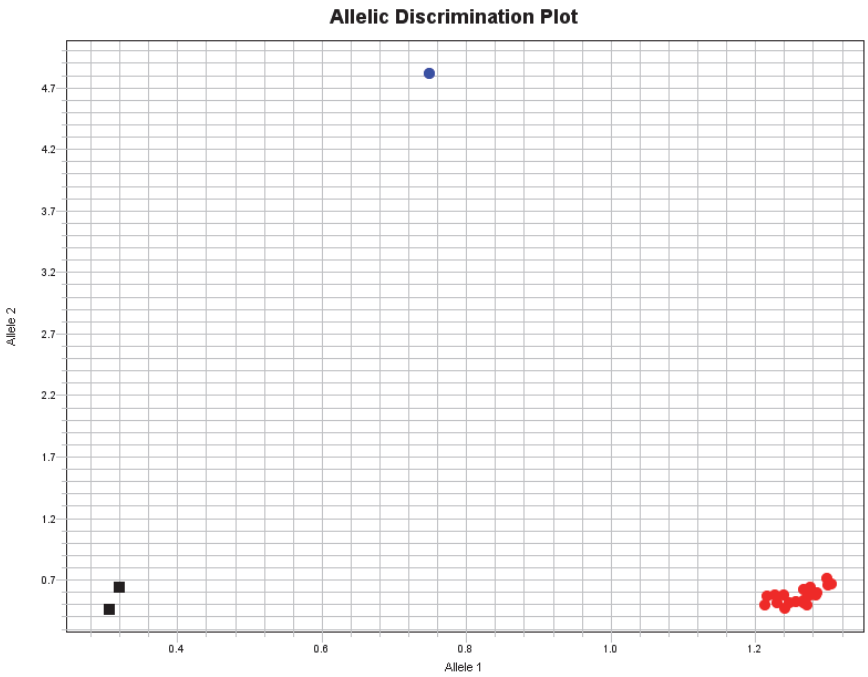
Despite *C. canadensis* having no natural dispersal capability to Eurasia, significant numbers of the species have been introduced to various parts of Europe (Dewas *et al*., 2012; Parker *et al*., 2012). Prior to the two beaver species being recognised as distinct, North American beavers, being more freely available than Eurasian beavers, were imported to establish harvestable populations for the fur trade in Finland (Lahti & Helminen, 1974). They have also been held in captivity as part of zoological or private collections, many of which have experienced escapes at some point in their history. Smaller population of North American beavers originating from captive escapes are now evident in parts of Germany, Luxemburg and Belgium (Dewas *et al*., 2012). Invasive populations of *C. canadensis* could be negatively impacting the recovery of *C. fiber* in some of its previous distribution, and represent a serious animal management issue (Parker *et al*., 2012). *C. fiber* and *C. canadensis* are morphologically, behaviourally and ecologically very similar. Current accepted methods for discrimination between species rely on the analysis of DNA sequence data which is time-consuming and expensive, or the examination of anal gland secretions by experienced field workers (Sun & Rosell, 1999). A rapid and inexpensive DNA technique for identifying the species of *Castor* was recently described in McEwing *et al*. (2014). This is the technique which was utilised for the twenty-five beaver samples collected for this study.

3.2 Genetic assessment of species of free living beavers in Scotland

All twenty-five samples of beaver collected from the River Tay catchment were tested genetically to establish their species. Genetic differences between both species where identified by Horn *et al*. (2001) and two of these genetic differences were targeted for species identification (see McEwing *et al*., 2014).

The 16S rRNA mitochondrial gene is a coding gene and two nucleotide base positions were found to be fixed for different nucleotide bases between the two species. Two KASP™ probes were designed around the nucleotide differences, resulting in the incorporation of a differently coloured fluorophore at each base during a PCR process. *C. fiber* has a 'C' nucleotide at position 1971 of that gene and *C. canadensis* a 'T'. For the second position 2473, *C. fiber* has an 'A' while *canadensis* has a 'G'. The results of the genetic screening of the beaver sample (Figure 2) identified all beavers as *C. fiber*.

SNP position 1971



SNP position 2473

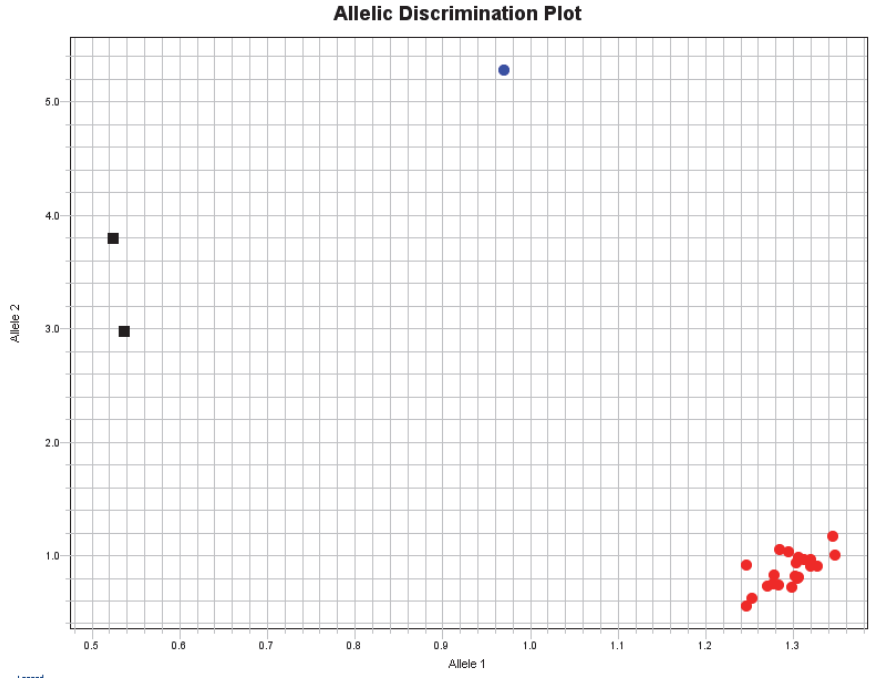


Figure 2. Identification of the River Tay catchment beaver samples using allelic discrimination at markers 1971 (top) and 2473 (bottom) on the 16s rRNA mitochondrial gene following McEwing et al. (2014). Each dot represents a single beaver. For both tests, the red dot cluster represents 25 unknown beaver samples as well as a control for C. fiber, the blue dot is a control for C. canadensis. Black squares represent negative controls.

4. POPULATION GENETIC ASSESSMENT OF FREE-LIVING BEAVERS IN SCOTLAND

As highlighted in the introduction, population genetic studies of *C. fiber* have been hampered by a low number of informative genetic markers with which to base evolutionary or ecological inference. Senn *et al*. (2013) developed a new suite of Single Nucleotide Polymorphism (SNP) genetic markers for *C. fiber* and utilised these markers for investigating *C. fiber* across its current range (Senn *et al*., 2014). By applying these new markers to the beaver samples from the River Tay catchment, similar data could be collected and compared with the Eurasian population data.

4.1 Background – the genetic tools previoulsy developed for assessing *C. fiber*

A subset of 275 nuclear SNP markers identified by Senn *et al*. (2013) were screened for the River Tay catchment beavers using an Illumina Beadxpress™ assay. For more detailed description of methods and further analysis in a European context please see Senn *et al.* (2013 and 2014). Genotype data for all samples are available from the SNH project manager or directly from the authors.

5. ASSESSING THE GEOGRAPHICAL PROVENANCE OF FREE-LIVING BEAVERS IN SCOTLAND

By utilising a suite of genetic SNP markers (Senn *et al*., 2013), Senn *et al*. (2014) were able to show genetic differences between geographically disparate beaver populations across Eurasia. By comparing the data from the River Tay catchment samples with the complete dataset of Eurasian beavers utilised in Senn *et al*. (2014) it was possible to assign the beavers to a source population with a high degree of confidence (Figure 3).

All samples of *C. fiber* collected from the River Tay catchment were assigned to, and originate from, a source population from Germany (p>0.99) and were most likely from the Bavaria region. Furthermore, three different genetic lineages were evident from the data. As a comparison, eight samples from the licensed beaver trial in Mid-Argyll were all assigned to a source population in Norway which is consistent with their actual provenance, as agreed under the licence conditions.

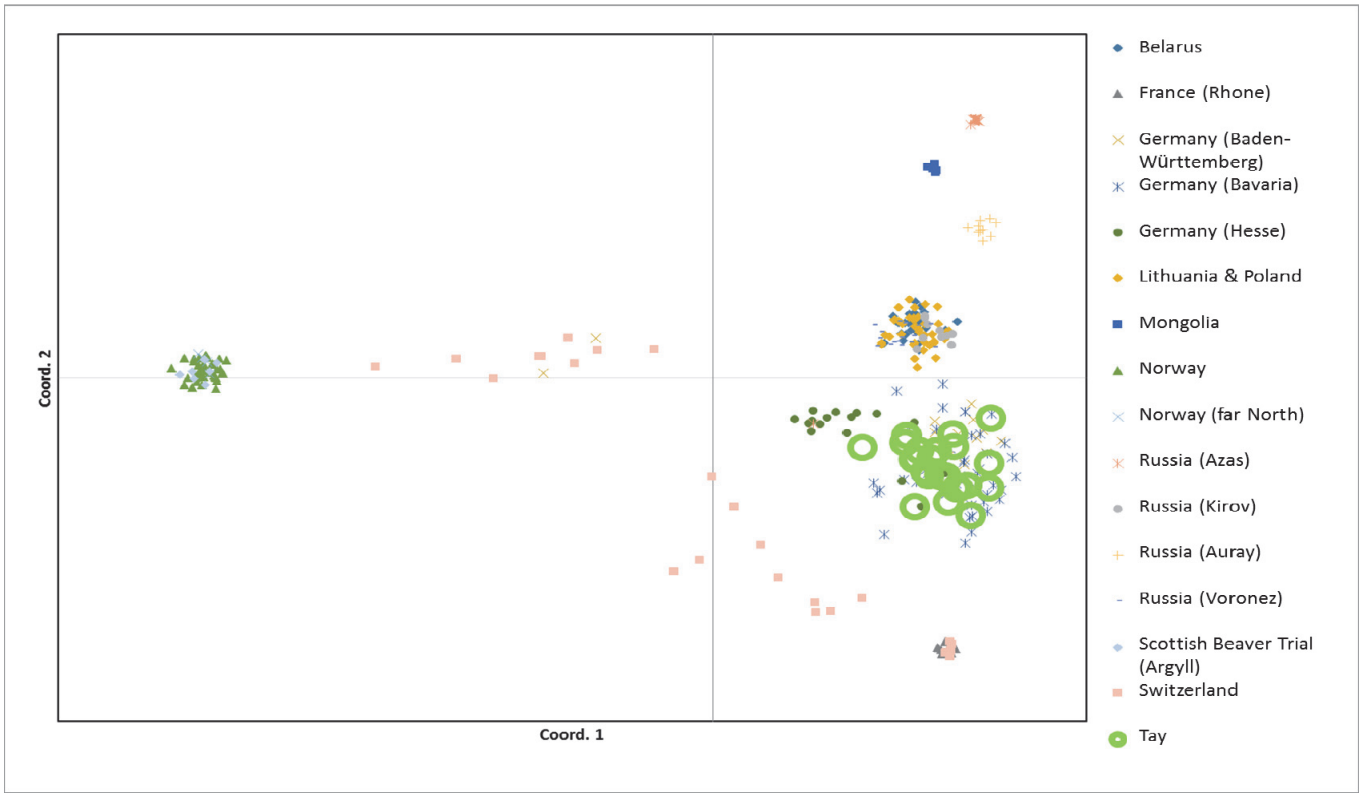


Figure 3. Identifying the geographical origin of beavers on the River Tay catchment, east Scotland. Each point on the graph represents an individual beaver and the proximity of points to each other represents how closely related they are. Here the Tayside beaver data (green circles) are plotted against the reference data from Senn et al. 2014. The Tayside beavers group with the beavers from Bavaria and Baden- Württemberg (Germany) on the right-hand side of the graph whereas the beavers from the Scottish Beaver Trial (Argyll) clearly group with beavers sampled from Norway on the far left of the graph as would be predicted by their origin (Norway).

6. ASSESSING THE GENETIC VARIABILITY OF FREE-LIVING BEAVERS IN SCOTLAND

In order to assess the genetic diversity (essentially the future capacity to adapt) of the beavers sampled here we first needed to assume that the beavers have formed a natural population where they are able to migrate and breed freely, and that the sample size can adequately reflect the genetic diversity within the population. This assumption allows us to provide an estimate of the genetic variability in the River Tay catchment and compare it across other populations in the *C. fiber* range.

Genetic variability was assessed using two measures: the first is a measure of the expected heterozygosity (i.e. the expected probability that an individual will be a heterozygote at a particular genetic locus or set of loci); and secondly, a measure of allelic richness (the number of different alleles per locus averaged across the population). Both of these measures were also used for an assessment of genetic diversity across the range *for C. fiber* (Senn *et al*., 2014) allowing a direct comparison between different populations. Figure 4 shows the genetic diversity as measured across some Eurasian populations and the River Tay catchment.

The measures of genetic diversity in the River Tay 'population' are consistent with healthy beaver populations across the Eurasian range. Although the current population centred on the River Tay catchment is estimated to consist of ~38 active groups (Campbell *et al*., 2012), it is suspected that this 'population' was established by a limited number of founders, and so genetic diversity could be compromised as a result of limited founding diversity and subsequent genetic drift. However, the founding population's source (Germany) has the highest recorded genetic diversity so far measured, a likely consequence of an admixed descent, and therefore genetic diversity in the River Tay catchment beaver 'population' is consistent with the highest levels of genetic diversity in populations across Eurasia.

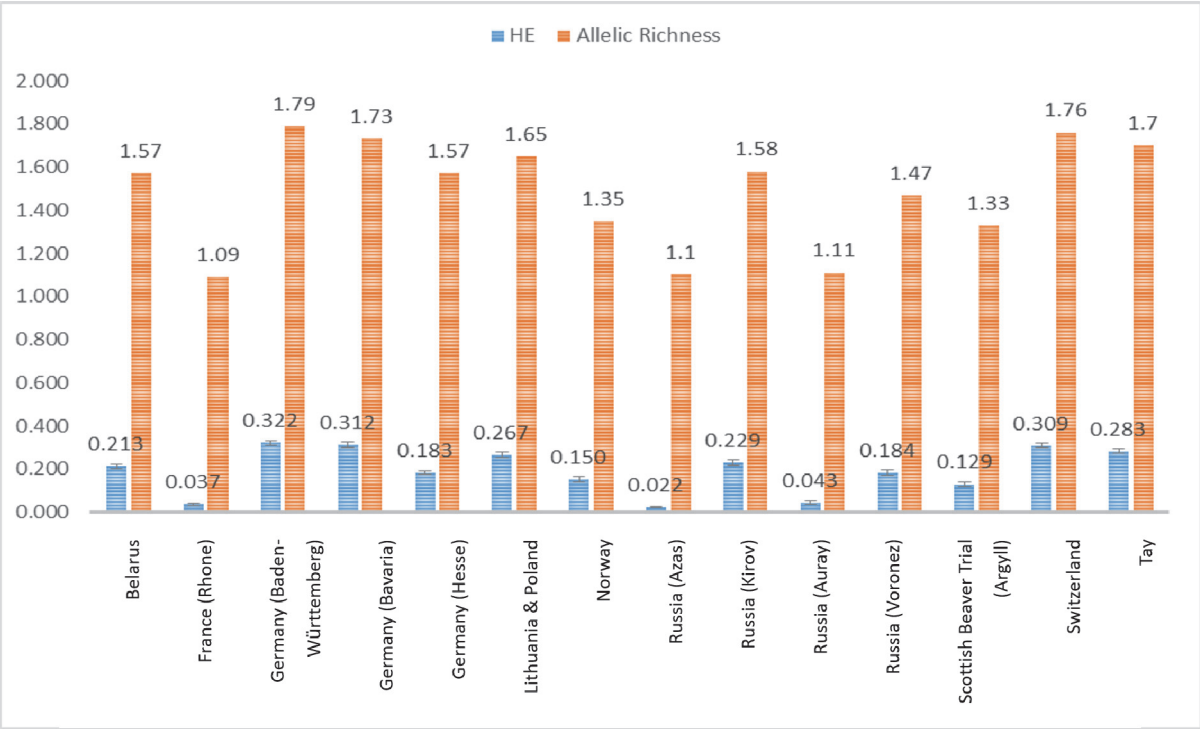


Figure 4. Genetic diversity measures of beavers from across the Eurasian range. Heterozygosity (HE) and allelic richness are inversely correlated with inbreeding. Therefore high relative measures are approximate indicators of genetic health.

7. ASSESSING THE RELATEDNESS AMONGST INDIVIDUALS OF FREE-LIVING BEAVERS IN SCOTLAND

Genetic diversity is not the only measure of the genetic health of a population. The relatedness of individuals within any population is also a key metric to their future health. Inbreeding, resulting from the mating of related individuals generally has a negative effect on population health, because it is likely to increase the level of genetic disease. Inbreeding events are unavoidable in naturally recolonising species, because small numbers of individuals moving out to establish new colonies will have limited access to new unrelated mates. However, subsequent colonisation events by other individuals can quickly reduce the effect of inbreeding.

For beavers within Scotland, living in a 'closed' population without expectation of augmentation, the effects of inbreeding are arguably more important than those of lowered genetic diversity per say. An overly inbred population could result in maladapted individuals and could negatively affect any future official beaver reintroduction. Active management is normally undertaken in any reintroduction program to ensure that inbreeding is discouraged.

Calculating the relatedness amongst individuals becomes more straightforward with an increase in the number of genetic markers used. On average, a parent and offspring will share approximately 50% (0.5) of their genetic component, similarly siblings share on average 0.5 of their genetic component, half siblings half of that value (0.25) and 1st cousins half again (0.125).

By utilising the SNP dataset for the beaver samples and comparing their genotypes in a pairwise fashion we can get an estimate of mean relatedness. Table 2 highlights the closer relatedness pairings (cousin and above) from the pairwise comparisons. The data from three of the samples available, TB23, TB24 and TB25 (representing a known mother and 2 of her offspring respectively) demonstrates the approach.

Table 2. Mean molecular relatedness amongst Tay catchment beaver samples, listing all pairwise relationships above approximately 1st cousin level. In real life the molecular relatedness values returned from genetic estimates are not distributed into discrete categories (there is variance surrounding them). Therefore it is not possible to categorically define relationships based on this data, however the relationships in the table below clearly conform to a high degree of familial relatedness.

INDV1	INDV2	Mean molecular relatedness	Known relationship
TB11	TB21	0.5740	
TB23	TB25	0.5454	parent-offspring
TB23	TB24	0.4934	parent-offspring
TB04	TB12	0.4537	
TB08	TB11	0.4464	
TB01	TB02	0.4012	
TB24	TB25	0.3832	full-sibling
TB02	TB08	0.3432	
TB02	TB04	0.3043	
TB03	TB24	0.2966	
TB01	TB03	0.2777	
TB14	TB25	0.2660	
TB03	TB20	0.2567	
TB03	TB04	0.2504	

TB04	TB14	0.2474
TB14	TB24	0.2423
TB02	TB03	0.2386
TB04	TB24	0.2184
TB01	TB20	0.2139
TB12	TB17	0.2004
TB04	TB23	0.1942
TB12	TB14	0.1927
TB01	TB16	0.1917
TB02	TB22	0.1890
TB16	TB23	0.1874
TB03	TB17	0.1858
TB14	TB19	0.1773
TB14	TB15	0.1758
TB06	TB22	0.1752
TB01	TB14	0.1735
TB15	TB24	0.1730
TB14	TB23	0.1591
TB04	TB20	0.1548
TB01	TB15	0.1526
TB15	TB20	0.1495
TB12	TB24	0.1492
TB02	TB24	0.1476
TB04	TB17	0.1468
TB20	TB24	0.1442
TB06	TB07	0.1365
TB04	TB25	0.1349
TB02	TB23	0.1329
TB16	TB25	0.1281
TB18	TB24	0.1273
TB01	TB04	0.1267

8. CONCLUSIONS

This study achieved a representative sample from the current Tayside beaver distribution, determining that Eurasian beavers of Bavarian origin were present. All beaver samples were genetically tested to ascertain the origin of their source population; all had a German (most likely Bavarian) provenance and originating from three distinct lineages. If treated as a single biological population, a high degree of genetic diversity (measured as allelic richness and expected heterozygosity) was evident in comparison to other sampled beaver populations across the Eurasian range. Such an observation is expected, given the likely admixed population origin (Bavarian) of the beavers on the Tay catchment.

This study demonstrates just how useful genetic information can be for monitoring and assessing individuals, populations and species of interest. The reintroduction of certain species into their former native range, although facilitated by European legislation, and generally supported by the public, can often be contentious. While it is a straightforward process to extirpate populations or species in a very short period of time, it is not so straightforward to redress that situation, in a stable way, in a similar timescale. Many animal reintroductions for conservation purposes fail, perhaps not immediately but over an observable timescale (Fischer & Lindenmayer, 2000). Based upon best practice from previous reintroduction projects from all taxa and around the world, the IUCN has established a set of guidelines that if followed will ensure the best possible chance of a successful reintroduction (IUCN, 1998; 2013).

The full background to the establishment of beavers within the River Tay catchment has not been documented though is often openly discussed. While the “how” and “why” is beyond the remit of this study, it does highlight the subsequent need to identify additional funding in order to clarify the origin, genetic and health status of this population. With an estimated population of ~38 active groups by 2012 (Campbell *et al*., 2012), the actual number of escaped / released individuals is unknown. It is therefore difficult to assess other population demographic data such as mortality and survival rates, which are needed to draw more definite conclusions on long-term viability and success. All the beavers sampled here originated from Germany, representing three distinct lineages, and are, from a genetic diversity perspective good candidates for a reintroduction, although genetics is not the only criterion for selection of founders.

The decision on the future of these animals has yet to be made by the Scottish Government, who will ultimately direct any future management strategies. From a genetic perspective, as many of the beavers within the Tayside catchment are closely related the degree of inbreeding in the future could be a cause for concern, particularly if dispersal becomes limited. The genetic data provided here should be considered a baseline measure of genetic health and we advise future replicated studies to monitor genetic health effectively over appropriate time scales i.e. in one generation.

9. REFERENCES

Campbell, R, Harrington, A., Ross, A. & Harrington, L. 2012. Distribution, population assessment and activities of beavers in Tayside. *Scottish Natural Heritage Commissioned Research Report No. 540.*

Coles, B. 2006. *Beavers in Britain's Past*. Oxbow Books, UK.

Conroy, J. & Kitchener, A. 1996. The Eurasian beaver (*Castor fiber*) in Scotland: a review of the literature and historical evidence*. Scottish Natural Heritage Review No. 49.*

Conroy, J.W.H., Kitchener, A.C. & Gibson, J.A. 1998. The history of the beaver in Scotland and its future reintroduction. *In*: Lambert, R.A. (Ed.), *Species history in Scotland: introductions and extinctions since the ice age*. Scottish Cultural Press, Aberdeen, pp.107-129.

Dewas, M., Herr, J., Schley, L., Angst, C., Manet, B., Landry, P. & Catusse, M. 2012. Recovery and status of native and introduced beavers *Castor fiber* and *Castor canadensis* in France and neighbouring countries. *Mammal Review*, **42**, 144-165.

Fischer, J. & Lindenmayer, D. 2000. An assessment of the published results of animal relocations. *Biological Conservation*, **96**, 1-11.

Horn, S., Durka, W., Wolf, R., Ermala, A., Stubbe, A., Stubbe, M. & Hotreiter, M. 2011. Mitochondrial genomes reveal slow rates of molecular evolution and the timing of speciation in beavers (*Castor*), one of the largest rodent species. *PLoS ONE* 6(1):e14622.doi:10.371/journal.pone.0014622.

IUCN 1998. *IUCN/SSC Guidelines for Re-Introductions*. IUCN Species Survival Commission, Gland, Switzerland.

IUCN/SSC 2013. *Guidelines for Reintroductions and Other Conservation Translocations*. Version 1.0 IUCN Species Survival Commission, Gland, Switzerland. viiii +57pp.

Kuehn, R., Schwab, G., Schröder, W. & Rottmann, O. 2000. Differentiation of *Castor fiber* and *Castor canadensis* by non-invasive molecular methods. *Zoo Biology*, **19**, 511-515.

Lahti, S. & Helminen, M. 1974. The beaver *Castor fiber* (L.) and *C. canadensis* (Kuhl) in Finland. *Acta Theriologica*, **19**, 177-189.

Lavrov, L.S. & Orlov, V.N. 1973. Karyotypes and taxonomy of modern beavers (Castor, castoridae, Mammalia). *Zoologicheskii-Zhurnal*, **52**, 734-742.

McEwing, R., Frosch, C., Rosell, F. & Campbell-Palmer, R. 2014. A DNA assay for rapid discrimination between beaver species as a tool for alien species management. *European Journal for Wildlife Research*, doi:10.1007/s10344-010344-014-0803-6.

Nolet, B. & Rosell, F. 1998. Comeback of the beaver *Castor fiber*: An overview of old and new conservation problems. *Biological Conservation*, **83**, 165-173.

Parker, H., Nummi, P., Hartman, G. & Rosell, F. 2012. Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and plan for eradication. *Wildlife Biology*, **18**, 354-365.

Rosell, F., Parker, H. & Steifetten, Ø. 2006. Use of dawn and dusk sight observations to determine colony size and family composition in Eurasian beaver *Castor fiber. Acta Theriologica,* **51**, 107-112.

Strachan, R.S. & Moorhouse, T.P. 2006. *The Water Vole Conservation Handbook.* Wildlife Conservation Research Unit & The Environment Agency.

Senn, H., Ogden, R., Cezard, T., Gharbi, K., Iqbal, Z. 2013. Reference-free SNP discovery for the Eurasian beaver from restriction site-associated DNA paired-end data. *Molecular Ecology*, **22**, 3141-3150.

Senn, H., Ogden, R., Frosch, C., Syrůčková, A., Campbell-Palmer, R., Munclinger, P., Durka, W., Kraus, R.H.S., Savejev, A.P., Nowak, C., Stubbe, A., Stubbe, M., Michaux, J., Lavrov, V., Samiya, R., Ulevicius, A., & Rosell, F. 2014. Nuclear and mitochondrial genetic structure in the Eurasian beaver (*Castor fiber*) – implications for future reintroductions. *Evolutionary Applications,* 7, 645-662.

Sun, L. & Rosell, F. 1999. Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *C. fiber*. *Wildlife Biology*, **5**, 119-123.

Yalden, D.W. 1991. History of the Fauna pp 7-18 in *The Handbook of British Mammals* Corbet, G.B. & Harris, S. (eds.) pp 7-18. Blackwell Scientific Publications, Oxford.

ANNEX 1: DISTRIBUTION OF BEAVER SAMPLES IN THE STUDY

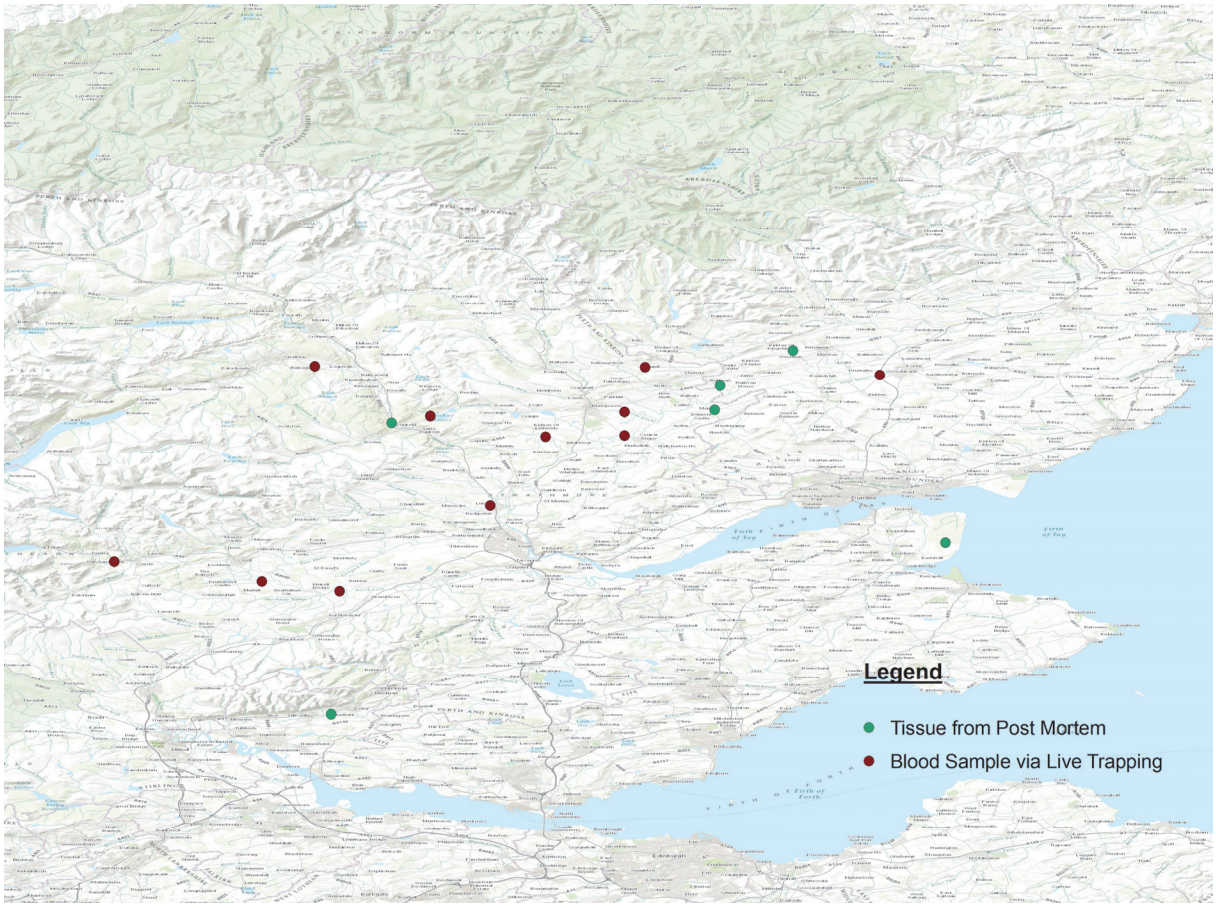


Figure 5. Distribution of beaver samples in the study (tissue and blood samples). NB. Two additional samples outside of the map range not marked.

www.snh.gov.uk

ISBN: 978-1-78391-078-6

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

You can download a copy of this publication from the SNH website.

recycle

Scottish Natural Heritage
Dualchas Nàdair na h-Alba
All of nature for all of Scotland
Nàdar air fad airson Alba air fad