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Beaver genetic surveillance in Britain

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ABSTRACT

Founder genetic composition can affect reintroduction success, especially as the number of animals released tends to be small and therefore less genetically diverse than their source populations. Numerous translocations and reinforcements of beavers, *Castor fiber*, have occurred with little regard to geographic and/or genetic origin. Beaver reintroduction to Britain has been haphazard and currently disjointed populations of varying status exist – from sanctioned wild releases, unlicensed populations and naturalistic enclosed projects. This study investigated the genetic composition of two originally unofficially released beaver populations in Britain - Tayside, east Scotland, and River Otter, Devon, to provide data to support decision on their future management. From both wild populations ($n = 34_{Tayside}$, $n = 9_{Devon}$) all were confirmed as Eurasian beaver. The vast majority, origin was likely assignable to Germany and the mixed founder population of Bavaria. Eighty-two percent of the Tayside individuals examined at 275 loci were at least as closely related as first cousins, with pairwise estimates of relatedness at 26 loci indicated that the Devon beavers were more closely related on average. So far there is no evidence to suggest that beavers are failing to adapt to the British environment despite their reduced genetic founder based, however attention to genetic augmentation and longer-term management of genetic diversity should be factored into comprehensive restoration plans for the species across Britain. Many recent reintroductions are relying on serial founder events from an already limited founder base and that is counter to best practice in reintroduction planning.

1. Introduction

Reintroductions, translocations and reinforcements are biodiversity and population conservation tools. Although successful projects are well documented, many conservation reintroductions have failed (defined as lack of self-sustaining population establishment and/or failure to meet conservation objectives) for a variety of reasons (Griffith et al., 1989;

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Fischer and Lindenmayer, 2000; Seddon et al., 2007; Jule et al., 2008; Germano and Bishop, 2009; Robert, 2009). Species reintroductions have also occurred through unofficial releases or escapes from captive collections (e.g. wild boar, *Sus scrofa*, in England, Wilson, 2003; Eurasian beaver in Belgium, Verbeylen, 2003). However, founder populations are often small and genetically isolated, which can significantly influence their long-term viability (Miller et al., 2009), as genetic diversity is lost through inbreeding, resulting in decreased population fitness and adaptation ability (Frankham et al., 2002). Small population sizes can result in reduced fitness due to inbreeding effects and loss of adaptive potential (e.g. response to changes in habitat, climatic, disease and competition), and so ultimately greater extinction risk (Lande and Shannon, 1996). Inbreeding and loss of genetic diversity leading to a loss of adaptive potential have all been suggested as possible factors in reintroduction failures (Marshall and Spalton, 2000; Kephart, 2004; Vilas et al., 2006; Weeks et al., 2011). In any reintroduction or reinforcement, various and sometimes conflicting considerations will impact on founder stock selection including availability of source animals, genetic criteria, as well as political and socio-economic factors (Miller et al., 1999). In unplanned or unauthorised reintroductions, or those founded through escapes, baseline data (on the animals involved or ecological baselines on which they may impact) are lacking and so can present significant issues when attempting to assess either the suitability of founders or their environmental impacts.

Founder stock genetic composition can have a significant impact on reintroduction success, especially as they tend to be less genetically diverse than source populations (Williams et al., 2000). Founder composition will affect demographic parameters such as population growth, rates of inbreeding and loss of genetic diversity, which in turn can influence the long-term fitness and viability of a population (Frankham et al., 2002; Jamieson et al., 2007; Miller et al., 2009). Maintaining genetic diversity is an important management objective of any reintroduction programme (IUCN/SSC, 2013)and pre-release genetic screening to ensure high genetic diversity is a vital part of this (Senn et al., 2014; El Alqamy et al., 2011).

As a result of the fur trade, Eurasian beavers were hunted to the verge of extinction by the end of the 19th. A handful of relict populations in fragmented refugia, thought to number ~1200 individuals survived (Nolet and Rosell, 1998). Since the 1900s, beaver numbers have recovered throughout much of their former European range as a result of a combination of legal protection, hunting regulation, proactive reintroductions/translocations and natural recolonisations. Genetic analysis of mitochondrial DNA and MHC DRB gene sequences demonstrates low diversity within these refugia populations, though distinctions between them exist (Babik et al., 2005; Ducroz et al., 2005; Durka et al., 2005). The Eurasian beaver, *Castor fiber*, has been widely translocated throughout Europe with little regard of genetic origin (Nolet and Rosell, 1998; Halley and Rosell, 2002; Halley et al., 2012). In Britain, they became generally extinct around the 12th century in England and Wales, and by the 16th century in Scotland (Conroy et al., 1998; Coles, 2006). Radiocarbon-dating of a beaver gnawed stick indicates beaver surviving within the Tyne River, north England, until the 14th century (Manning et al., 2014).

The sourcing of beavers for restoration to Britain has been debated academically (Halley, 2011; Rosell et al., 2012; Senn et al., 2014). Skull and mandible morphology comparisons from British beaver fossils determined overall they were most similar (though not identical) to Telemark, Elbe and Rhône populations (Kitchener and Lynch, 2000). Genetic investigations since have demonstrated that British beavers were part of a broad 'west' clade (Marr et al., 2018), congruent with this morphological variation. A government sanctioned, scientific trial reintroduction investigated the feasibility of bringing beavers back Scotland using wild Norwegian animals, as a precautionary approach (Scottish Beaver Trial, Jones and Campbell-Palmer, 2014; Gaywood, 2018). Outside of this official trial, a significant population (~114 active territories, Campbell-Palmer et al., 2018) of wild-living beavers also exist throughout the River Tay catchment ('Tayside beavers'), Perthshire, east Scotland. The Eurasian beaver has become a 'European Protected Species' in Scotland since the May 1, 2019. Following a successful public campaign, an unofficial group of beaver on the River Otter, in Devon, England, were permitted to remain after meeting strict health screening requirements. The statutory body, Natural England (NE), issued a licence for a five-year trial period to study these animals and their impacts, c. Future decisions on the wider reintroduction of beavers to England and Wales are pending.

Both the Tayside and Devon populations are composed of either accidental escapees or illegal releases, and were initially of unknown species (i.e., Eurasian or North American beaver, *C. canadensis*), origin, genetic and health status. The North American beaver has been introduced to parts of Europe through both official releases and accidental escapes from captive collections (Dewas et al., 2012; Parker et al., 2012). Both extant beaver species were classed as one species until relatively recent genetic analysis distinguished them on basis of chromosome number differences (48 pairs in Eurasian, 40 in North American, Lavrov and Orlov, 1973). Due to the physiological, ecological and behavioural similarity between Eurasian and North American beavers, it is important to clarify which species is present. Given the near identical ecological niches occupied by these species, regional extirpation and even eventual extinction is possible, therefore there is a pressing need to ensure the non-native North American beaver is not introduced. Any confirmed North American beaver or individuals presenting significant health risks should be removed from the wild.

The Tayside and River Otter populations have been established outside of statutory procedures therefore outwith IUCN translocation guidelines, with no baseline data collected on the released individuals. The aim of this study was to validate the species (i.e., Eurasian or North American beaver), investigate Eurasian population origin and make some basic inferences on levels of genetic diversity.

2. Methods

2.1. Study areas

The River Otter catchment covers 250 km^2 predominantly in East Devon, England rising in the Blackdown Hills and flowing ca. 65 km south before discharging into the English Channel near Budleigh Salterton. The area is divided into nine sub-catchments with the main tributaries being the River Tale, River Love and River Wolf. It is mostly rural catchment, with small, dispersed settlements, and more intensive agricultural practices dominating the southern end. Half of the catchment is improved grassland, with 28% arable and horticulture, and 5% urban and suburban. Beavers of unknown origins have been present from 2008 (Brazier et al., 2020).

The River Tay catchment is over 5000 km^2 (main River Tay ~193 km long), rising at Ben Lui, in Argyll, west Scotland, flowing into the North Sea at the Firth of Tay, Dundee, east Scotland (SEPA, 2010). It has several major tributaries, in which beavers have become established - notably the rivers Almond, Earn, Isla, and Tummel. The main land-use in the lowland part of the catchment area is intensive agriculture. Although unverified (TBSG, 2015), beavers are thought to have been present in this area for at least 15 years.

Five individuals (confirmed to be living in two family units) were live trapped by APHA staff along the River Otter, Devon in February and March 2015. These animals were housed at captive facilities at Derek Gow Consultancy, Devon. Under licence issued by NE, they were re-released once health screening confirmed that they were healthy. A further four individuals were sampled, consisting of two additionally released to augment the population, and another two present in the population in January 2016. Genetic samples were obtained during health screening procedures.

2.2. Animal handling and sample collection

A live-trapping programme was carried out across the Tayside catchment from October 2012 until April 2014. All beaver handling, including transportation and re-release occurred under licence issued by Scottish Natural Heritage. Live trapping of River Otter beavers occurred through APHA and/or under ROBT project licence issued by NE. The primary purpose of both these trapping programmes were to collect a range of biological samples for veterinary screening (see Campbell-Palmer et al., 2018). This government-required screening provided opportunistic sampling collection for genetic analysis, the main aim of which was to determine beaver species present, and their origin. Trapped individuals were examined by experienced beaver handlers and veterinary staff from the Royal Zoological Society of Scotland (RZSS). Gaseous anaesthesia using isoflurane in 100% oxygen was used to induce and maintain anaesthesia. All examinations and sample collection occurred under general anaesthesia. In addition, cadavers (or parts thereof) of any lethally controlled or road kill beavers were also examined.

2.3. Genetic screening

In total genetic analysis was conducted for 43 animals, 34 from Tayside (Scotland) and 9 from Devon (England). DNA was extracted from all live trapped beavers (EDTA blood samples) and cadavers (or parts thereof via muscle sample) using a DNeasy®Blood& Tissue kit (QIAGEN, Valencia, CA, USA). Since the analyses happened at over a period spanning a number of years (2013–2016), genetic analysis methods were altered somewhat over the course of the study due to financial constraints and/or the evolution of genetic technology.

A number of separate analyses were performed on the samples:

1) Species ID

This was performed on all 39 samples: In order to confirm the beaver were *Castor fiber*, genetic differences at two Single Nucleotide Polymorphisms (SNPs) loci of the 16S rRNA mitochondrial coding gene that exhibit fixed differences between Eurasian and North American beaver were used (McEwing et al., 2014). SNP genotypes were resolved using KASP™ probes (LGC Genomics Ltd, UK) run on a Step-One RT-PCR machine (McEwing et al., 2014).

2) Analysis with 275 nuclear SNPs

Performed on 22 out of 34 of the Tayside beavers. These were genotyped at 275 nuclear SNP markers identified by Senn et al. (2013) to assess genetic diversity, estimate molecular relatedness and conduct an origin population assignment analysis. These loci were screened using an Illumina Beadxpress™ assay according to standard conditions.

3) Analysis with a reduced subset of 26 nuclear SNPs

A further 12 Tayside and 9 sampled from Devon were genotyped at a subset of 26 loci, previously identified as variable in Central European and Norwegian populations (Senn et al., 2014). Assays were run using the KASP™ genotyping chemistry, according to manufacturer instructions. This panel of markers can also be used for conducting individual identification and

parentage assignments, although with more limited power than first anticipated in described (Senn et al., 2014). The 26 loci are a subset of the 275 loci and thus all samples have been analysed at a common panel of 26 loci.

2.3.1. Statistical analysis

Individual genetic variability was assessed as a measure of the expected heterozygosity (i.e. the expected probability that an individual in a population will be a heterozygote at a particular genetic locus or set of loci), and as a measure of allelic richness (the number of different alleles per locus averaged across the population and standardised by sample size). Both measures were also used for assessing levels of genetic diversity across the species range for Eurasian beavers (Senn et al., 2014), allowing a direct comparison between the different origin populations. Reference samples from a published dataset of 306 beavers from 13 populations across Eurasia described and mapped in Senn et al. (2014) were used in origin population assignment and to benchmark genetic diversity and relatedness. Genetic diversity estimates of individual relatedness were only generated in the samples for which we had 275 markers due to issues of power. The presence of ascertainment bias is well documented in SNP markers and small panels are therefore inadequate to draw detailed inferences of familial relatedness as local inbreeding can impact adversely on power.

Population assignment was conducted using the software GeneClass2 (Piry et al., 2004) in 275 and 26 loci datasets using the 'assign/exclude population as origin of individuals' option (Piry et al., 2004). The threshold value was set to $p = 0.05$. The probability of an individual being assigned to all possible reference populations was calculated using the (Rannala & Mountain method. 1997) and the 1st and 2nd rank assignment examined. Bayesian assignment was also performed in STRUCTURE 2.3.4 (Pritchard et al., 2000; Falush et al., 2007), for the 26-loci dataset. The model was run using a burn-in of 50,000 and a run of 1 million Markov chain Monte Carlo steps, under the standard model of admixed ancestry (with the parameter alpha inferred from the data, using a uniform prior) and the model of correlated allele frequency ($\lambda = 1$). Three independent replicates of $K = 1–8$ were conducted. K, ultimately a subjective measure, was determined by eye (see Appendix 1).

To look at broad genetic structure in the data, principle component analysis (PCA) was implemented in the adegent package in the software R 3.1.3 (R Core Team, 2015).

Estimates of average population-level relatedness was generated in the software CoAncestry (Wang, 2011). For these analyses allele frequencies were estimated directly from the genotype data and genotype error rate was set to zero. Estimates of pairwise relatedness were then generated between all combinations of individuals using the Wang estimator. Average population-wide measures were then calculated in the same software.

Other population genetic summary statistics were generated using the software GenAlEx (Peakall and Smouse, 2006).

3. Results

All samples ($N = 34_{Tayside}$, $N = 9_{Devon}$), were confirmed as being from Eurasian beavers using the mtDNA test.

All Tayside animals, apart from one, were assigned with a 60–100% (depending on marker set used) probability to the reference population from Germany (Bavaria) (Table 1). The exception (TB29) genotyped at 26 loci, was assigned to the Lithuania/Poland population with a score of 69.5% (Table 1).

For the Devon animals, assignment was conducted twice, once against all reference data and once against all reference data and the Tayside data, since the release in Devon happened subsequent to the establishment of the population on Tayside. During the first assignment, all but three Devon individuals assigned with highest probability to reference samples held for Germany (Bavaria) populations. The assignment probabilities were in the range (57–98%). The remaining three animal was assigned with highest probability (54–81%) to the German (Baden-Württemberg) dataset (Table 1). When assignment was conducted again, including the Tayside population in the reference dataset, there were four animals which assigned with highest probability to Tay (D1, D6, D7, D9) with a 41%, 98%, 66% and 63% assignment probability. The second ranking population was the first ranking population given under the first assignment scenario (see Table 1).

These results were also broadly supported through PCA of the 275- and 26-loci datasets, with all samples (except TB29) clustering within a Germany (Bavaria/Baden-Württemberg) population cluster (Fig. 1, for PCA of the whole dataset at 26 loci). Examination of the data using STRUCTURE at cluster deemed to most parsimoniously capture the data structure ($K = 4$-$K = 6$) revealed that Devon and Tayside samples formed mixed origin clusters with similar composition profile to the Germany (Bavaria/Baden-Württemberg) populations (Supplementary Material Fig. 1).

The genetic diversity of the Tayside population (HE 0.28; allelic richness 1.70; 275 loci) is comparable to the mostly likely source population of Bavarian selected from among the datasets (HE 0.31; 1.73). Comparative figures for populations across Europe can be found in Table.3 of Senn et al. (2014). Similar estimates of genetic diversity are not presented for the Devon population due to the low number of samples.

Among the 22 individuals from Tayside genotyped for 275 SNP loci, data from three known relationships (mother and 2 foetuses) was used as a benchmark for relatedness. This determined that the majority of individuals (81.8%, $N = 22$) were at least as closely related as first cousins (defined as coefficient of relatedness >0.125, Wright, 1922). At this level of relatedness there were three separate family clusters (Fig. 2), one extended family of 18 animals, a group of three animals all related to each other at approximately first cousin level, and a singleton (TB13) that was relatively unrelated to any other animals sampled. Mean and variance of pairwise relatedness (Wang estimator) between all individuals in the sample populations

Table 1
First and second rank GeneClass2 assignment and associated probabilities for each individual Tayside and Devon beaver screened against a reference data set of either all 275 SNP loci or the reduced 26 SNP loci panel (Senn et al., 2014).

Beaver	Rank 1	Score	Rank 2	Score	Loci
TB01	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB02	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB03	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB04	Germany (Bavaria)	81.3	Germany (Baden-Württemberg)	18.7	275
TB05	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB06	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB07	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB08	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB09	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB10	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB11	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB12	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB13	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB14	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB15	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB16	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB17	Germany (Bavaria)	99.7	Germany (Baden-Württemberg)	0.3	275
TB18	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB19	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB20	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB21	Germany (Bavaria)	100	Germany (Baden-Württemberg)	<0.01	275
TB22	Germany (Bavaria)	98.9	Germany (Baden-Württemberg)	1.1	275
TB23	Germany (Bavaria)	76.5	Germany (Baden-Württemberg)	20.2	26
TB24	Germany (Bavaria)	68.4	Germany (Baden-Württemberg)	20.9	26
TB25	Germany (Bavaria)	60.8	Germany (Baden-Württemberg)	29.1	26
TB26	Germany (Bavaria)	70.4	Germany (Baden-Württemberg)	25.7	26
TB27	Germany (Bavaria)	92.3	Germany (Baden-Württemberg)	7.2	26
TB28	Germany (Bavaria)	78.2	Germany (Baden-Württemberg)	9.2	26
TB29	Lithuania/Poland	69.5	Germany (Bavaria)	15.5	26
TB30	Germany (Bavaria)	92.3	Germany (Baden-Württemberg)	7.2	26
TB31	Germany (Bavaria)	96.6	Germany (Baden-Württemberg)	2.1	26
TB32	Germany (Bavaria)	72	Germany (Hesse)	24.5	26
TB33	Germany (Bavaria)	96.4	Germany (Baden-Württemberg)	2.2	26
TB34	Germany (Bavaria)	77.7	Germany (Baden-Württemberg)	21.9	26
D1	Germany (Baden-Württemberg)	54.7	Germany (Bavaria)	34.1	26
D2	Germany (Bavaria)	87.7	(Baden-Württemberg)	11.378	26
D3	Germany (Baden-Württemberg)	65.9	Germany (Bavaria)	34.0	26
D4	Germany (Bavaria)	57.8	Germany (Baden-Württemberg)	41.9	26
D5	(Baden-Württemberg)	81.8	Germany (Bavaria)	18.1	26
D6	Germany (Bavaria)	80.6	Germany (Baden-Württemberg)	18.0	26
D7	Germany (Bavaria)	57.8	Germany (Baden-Württemberg)	41.9	26
D8	Germany (Bavaria)	98.6	Germany (Baden-Württemberg)	0.8	26
D9	Germany (Bavaria)	70.9	Germany (Baden-Württemberg)	22.4	26

indicates that relatedness within Tayside beavers is significantly higher than between animals from Tayside and Bavaria or relatedness within the Bavarian source population ($N_{Tayside} = 22$, $N_{Bavaria} = 49$, number of loci = 275, Fig. 3A).

Obtaining accurate measures of molecular relatedness is not possible with a dataset of 26 loci, however mean and variance of pairwise relatedness (Wang estimator) between all individuals in the sample populations indicates that relatedness is higher on average than within Tayside and Devon than within Germany (Bavaria) and between all combinations of those populations ($N_{Tayside} = 34$, $N_{Bavarian} = 49$, $N_{Devon} = 9$, number of loci = 26, Fig. 3B). Comparisons are only given to the Germany (Bavaria) population as this is the most commonly assigned to source population (see Table 1).

4. Discussion

This study has highlighted a suite of important factors to consider when assessing the suitability of individuals to form a founding population. Genetic analysis confirmed all sampled animals were Eurasian beavers. The North American beaver is identified as a different species. It can readily adapt to European habitats and directly compete with Eurasian beavers. The two species are very difficult to distinguish in the field without closer investigation (Rosell and Sun, 1999), but are genetically distinct (Lavrov and Orlov, 1973; McEwing et al., 2014) therefore it was crucial to establish that North American beavers have not been introduced. Examining the population of reintroduced Eurasian beavers from a biological perspective, genetic analysis suggests individuals within both populations are closely related, though Devon beavers are significantly more related. This may have important repercussions for the long-term viability of populations founded only from this stock. There was no evidence (body condition and pathology) that these beavers are failing to adapt to the British environment or

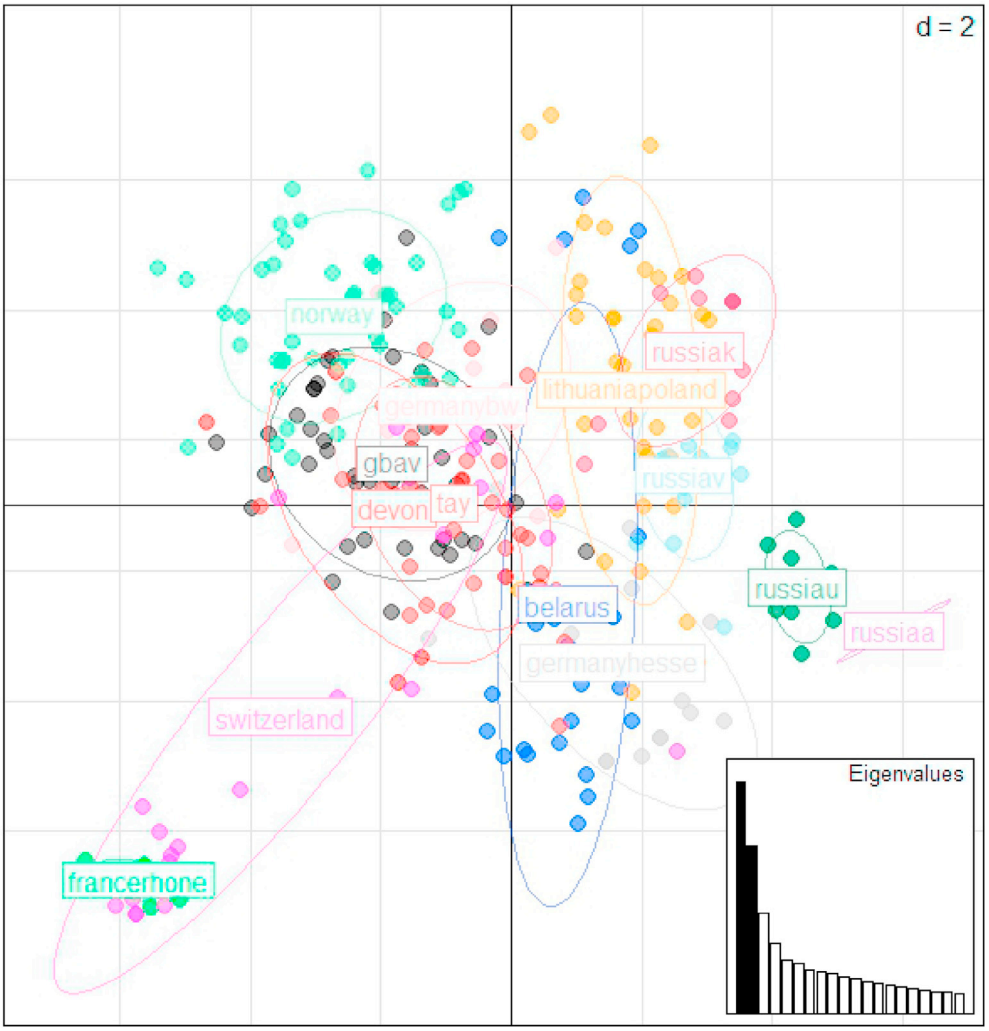

Fig. 1. Identifying the genetic origin of 34 beavers on the River Tay catchment, east Scotland and River Otter, Devon, England. Each point on the graph represents an individual beaver and the proximity of points to each other represents how genetically similar are. Tayside beaver data (brown circles) and Devon beavers (red circles) are plotted against the reference data from Senn et al. (2014). The Tayside and Devon beavers group with the beavers from Bavaria and Baden-Württemberg (Germany). Data presented here is for 26 loci. Analysis at the subset of data with 275 loci results in tighter population clusters (see Senn et al., 2014) but the general groupings remain the same. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

experiencing compromised welfare. Both populations are displaying evidence of growth and increased distribution (Campbell-Palmer et al., 2018; Brazier et al., 2020).

With any reintroduction, consideration should be given to whether the conservation objective is to prioritise the need to replicate what was formally present, or restore a population with a broad adaptive potential to current and future environments (Broadhurst et al., 2008; Sgro et al., 2011). The analysis of genetic diversity, population structure and measures of relatedness are all essential tools for appropriate assessment of wild (e.g. Senn et al., 2010) and captive (Ogden et al., 2007) populations. This is particularly those destined for species reintroduction projects (e.g. Ogden et al., 2005) and have undergone significant population reductions (e.g. El Alqamy et al., 2011). The Eurasian beaver has recovered based on an estimated eight relic populations of 30–300 individuals each, that underwent genetic bottlenecks and have since established to >1 million individuals (Halley et al., 2020). It may be assumed that genetic diversity and inbreeding are not significant in the restoration of this species (though refer to the latest concerns in Finland, Iso-Touru et al., 2020). However, current existing single source populations are underpinned by low levels of genetic diversity (Babik et al., 2005; Durka et al., 2005; Senn et al., 2014) and many successful reintroductions in central Europe are the result of deliberate mixed releases or mixing following natural expansion (Frosch et al. (2014), the latter is of course not possible on an island.

Population structure and assignment analysis suggests that both these beaver populations are highly likely to originate from a mixed sourced reintroduced population (as the majority of the samples assigned with the greatest probability >90%

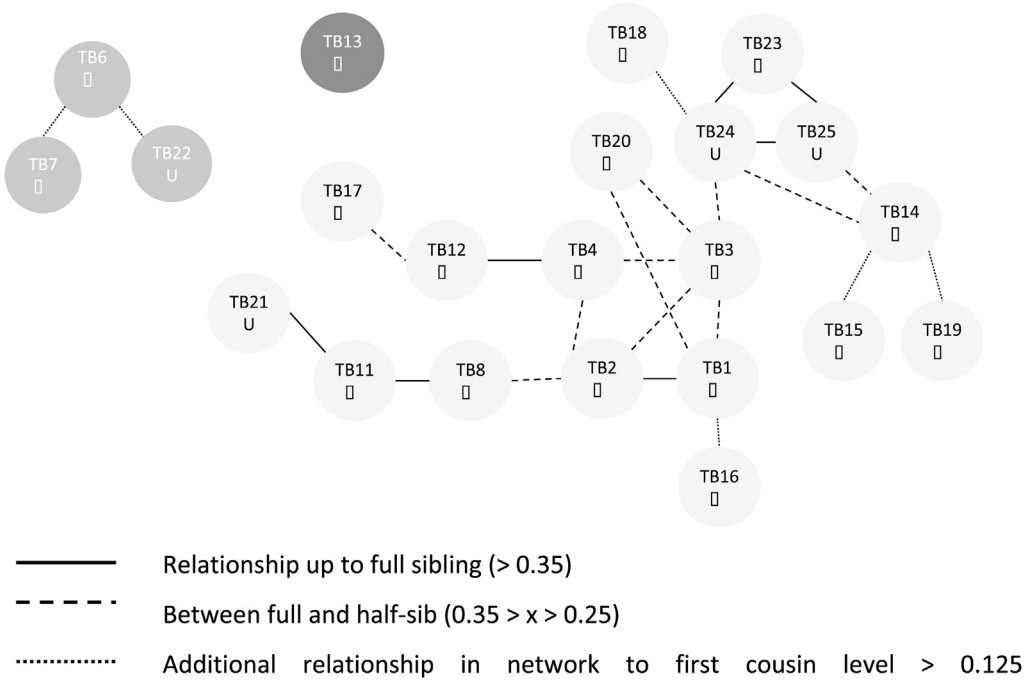

Fig. 2. Mean molecular relatedness amongst Tayside beavers sampled and genotyped at 275 loci (Wang estimator). Three separate clusters are evident, one extended family of 18 animals, a group of three animals all related to each other at approximately first cousin level, and a singleton (TB13) that was relatively unrelated to any other animals sampled.

using the higher resolution methodology to Bavaria). Of course, the ability to assign is only as good as the reference data in questions and all the possible sources of the beavers are not represented despite the fairly extensive reference data available. However, the assignment method GenClass2 has been shown to be a highly sensitive tool to assign individuals back to origin population even when these have been separated only by a few generations of breeding (e.g. see Bylemans et al. (2016) for assignment of fish farm escapees). High assignment probabilities (Table 1) indicate therefore that at least, for many individuals, the true population of origin is known. The founding population in Bavaria, has a high level of genetic diversity, a likely consequence of an admixed descent. Reproductive rates in beavers may exhibit inbreeding depression effects, with increased fecundity often citied in mixed refugia populations (Saveljev and Milishnikov, 2002; Halley, 2011), though further investigation and comparable methods are required to confirm this. Levels of relatedness were higher between all Tayside and Devon individuals than for wild Bavarian beavers, though there is no evidence of reduced fecundity and both populations are actively breeding and increasing in distribution. Although there are an estimated ~114 active territories in Tayside (Campbell-Palmer et al., 2018), the genetic results clearly indicate that of the 22 individuals screened using the high-density genetic methodology, these could be considered as belonging to one of three family groups. This suggests that a small number of individuals were part of the release and/or that they were already closely related at the point of release, both highly likely if they were from a captive source. It also suggests that there would be scope for elevation of the genetic diversity and reduction of the level of inbreeding through improved management in the future, similarly this has concluded by recent Finish study (Höglund et al., 2002). Genetic management could include conservation translocations under a meta-population management plan. There may be a case for reinforcing genetic diversity with Elbe fur-trade refugia beavers, as the 'missing' western clade from current British populations, as original Bavarian stock included Rhône and Telemark, along with eastern clade ancestry. More insidious effects on the success of reintroductions which have been shown to be associated with a low heterozygosity due to inbreeding include reduced reproductive success in some species (Höglund et al., 2002). To date, this has not been seen in the wild populations of Eurasian beavers in Britain, although ongoing monitoring is warranted. Active management is normally undertaken in any reintroduction programme to ensure that inbreeding is mitigated for.

The Tayside beavers could provide a reasonable source of founding individuals for any future reintroduction of this species, though genetic management to encourage diversity is recommended. Caution about sourcing from the current Devon population is recommended. This is a much smaller population, originating from a significantly closely related number of animals. Though small numbers (5) of additional, non-related beavers have been released under licence to increase the genetic diversity of the River Otter population, there is no evidence of breeding between these recently released individuals with original animals and/or their descendants.

Although outside the remit of this study, if the decision was made to reinforce or reintroduce beavers to other parts of Scotland or Britain, then the suitability of Tayside beavers from a purely genetic stance would need to be carefully managed.

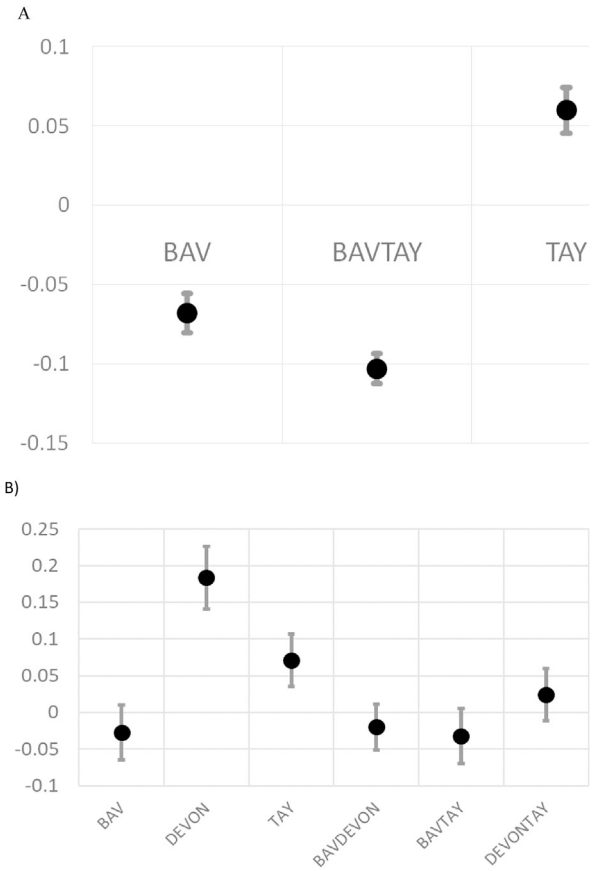

Fig. 3. Mean and variance of pairwise relatedness (Wang estimator) between *Castor fiber* individuals sampled from Tayside, Devon and Germany (Bavaria) populations. A) at 275 loci relatedness within Tayside (TAY) beavers is much higher than between animals from Tayside and Bavaria (BAVTAY) or within the Bavarian (BAV) source population ($N_{Tayside} = 22$, $N_{Bavarian} = 49$). B) The pattern is repeated at 26 loci but with higher levels of variance. At this panel of 26 loci, a comparison can also be made with the Devon samples which show the highest levels of mean pairwise relatedness ($N_{Tayside} = 34$, $N_{Bavarian} = 49$, $N_{Devon} = 9$). Comparisons are only given to the Germany (Bavaria) population as this is the most commonly assigned to source population (see Table 1).

Repeatedly removing small groups of animals from one part of Britain (without further enriching of genetic material) to seed new releases in another may reduce genetic diversity in the source population, likely resulting in suboptimal genetic diversity in the founder populations. This will not generate any additional genetic diversity within Britain and potentially lead to increased localised inbreeding. The issuing of 39 lethal control licences as part of SNH Beaver Mitigation Scheme, across prime agricultural areas in Tayside, has seen at least 87 individuals shot in the first year (SNH, 2020), with clear evidence of additional dispatch outside this official process. However, the intention is that more opportunities for translocation will be identified. Decisions on beaver management have involved a wide range of stakeholder groups, and have to take into account many complex biological and socio-economic considerations. Increasing the use of translocation in the future will better enable the preservation of genetic diversity which might be otherwise lost through lethal control. A full metapopulation management strategy in the context of a National Species Action Plan is needed to ensure it reaches and retains Favourable Conservation Status. A more detailed genetic analysis of released beaver populations in Scotland (Knapdale/Tayside) and England is currently underway in support of this.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of NatureScot or Natural England.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01275.

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