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MOLECULAR ECOLOGY

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Journal:	*Molecular Ecology*
Manuscript ID:	MEC-14-1017.R2
Manuscript Type:	Original Article
Date Submitted by the Author:	27-Jan-2015
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Keywords:	Conservation Genetics, Wildlife Management, Invasive Species, Mammals, Predator Prey Interactions

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An invasive non-native mammal population conserves genetic diversity lost from its native range

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Abstract

Invasive, non-native species are one of the major causes of global biodiversity loss. Although they are, by definition, successful in their non-native range, their populations generally show major reductions in their genetic diversity during the demographic bottleneck they experience during colonization. By investigating the mitochondrial genetic diversity of an invasive non-native species, the stoat *Mustela erminea,* in New Zealand and comparing it to diversity in the species' native range in Great Britain, we reveal the opposite effect. We demonstrate that New Zealand stoat population contains four mitochondrial haplotypes that have not been found in the native range. Stoats in Britain rely heavily on introduced rabbits *Oryctolagus cuniculus* as their primary prey, and were introduced to New Zealand in a misguided attempt at biological control of rabbits, which had also been introduced there. While invasive stoats have since decimated the New Zealand avifauna, native stoat populations were themselves decimated by the introduction to Britain of Myxoma virus as a control measure for rabbits. We highlight the irony that while introduced species (rabbits) and subsequent biocontrol (myxomatosis) have caused population crashes of native stoats, invasive stoats in New Zealand, which were also introduced for biological control, now contain more genetic haplotypes than their most likely native source.

Key Words: *Mustela erminea*, stoat, bottleneck, myxomatosis, epizootic, genetic variation

Running title: An invasive ark for genetic diversity

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44 **Introduction**

45

46 The number of individuals within a population substantially influences the
47 amount of genetic variation maintained over time, with rapid reductions in
48 population size significantly lowering genetic diversity (Nei et al. 1975, Lynch &
49 Gabriel 1990, Lande 1998). Examining contemporary patterns of genetic
50 diversity may therefore allow us to infer the historical sizes of populations, and
51 the processes that caused historical demographic bottlenecks (Avise 2004,
52 Frankham et al. 2010, Allendorf et al. 2012). Introduced populations provide an
53 unplanned opportunity to investigate the genetic consequences of population
54 bottlenecks, with a general prediction of reduced genetic diversity compared to
55 their source population, due to their small founding sizes. For most introduced
56 populations this is the observed pattern, though higher numbers of individuals
57 introduced, more introduction events, and more source populations may buffer
58 against such genetic losses (Dlugosch & Parker 2008).

59

60 In 1884, stoats (*Mustela erminea*) were introduced to New Zealand from Britain
61 for the purposes of invasive rabbit (*Oryctolagus cuniculus)* control (Thompson
62 1922). Over the following 20–30 years they arrived in large numbers on a series
63 of shipments, organized both by the New Zealand government and private
64 associations (King & Murphy 2005). In the first two years of introduction, at
65 least 224 stoats were released in New Zealand (King 1984), and in 1885 around
66 3,000 stoats and weasels (*Mustela nivalis*) were sent from Lincolnshire alone
67 (King & Moors 1979). Determining the exact number of stoats that were
68 successfully liberated in New Zealand is impossible from historical records, as
69 shipments often did not separate weasels from stoats in tallies, and the records
70 of most liberations have been lost; however the total number of stoats liberated
71 is likely to have been several thousand. The bulk of known shipments were to
72 New Zealand's South Island where rabbits were particularly numerous
73 (Thompson 1922, King 1984). Stoats were liberated in sufficient numbers and in
74 so many places that they had spread throughout both main islands of New
75 Zealand by the end of the nineteenth century (King & Murphy 2005).

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77 As part of an investigation of the colonization history of New Zealand, we
78 examined patterns of the distribution of genetic variation of stoats in New
79 Zealand and compared this with Great Britain. This comparison has the potential
80 to elucidate the relative demographic histories of each population subsequent to
81 their separation. Because the size of the British stoat population has fluctuated
82 significantly subsequent to the separation of the two populations in response to
83 fluctuating rabbit numbers – with a known severe demographic bottleneck in the
84 1950s due to myxomatosis (King & Powell 2007), these specific variations were
85 accounted for in our analysis.

86

87 **Methods**

88

89 **Sample collection and DNA extraction**

90 Spatially representative stoat samples were collected as part of pest control
91 operations from 16 locations throughout New Zealand (DRYAD:
92 doi:10.5061/dryad.h77tb). Five individual stoats were sampled from each
93 location yielding a total of 80 stoats sampled. Tissue samples were taken from
94 each individual and DNA was isolated using a Bio-Rad AquaPure Genomic Tissue
95 Kit (Cat# 732-6343) following the manufacturer's protocol.

96

97 **PCR and sequencing**

98 As mitochondrial DNA (mtDNA) is a particularly sensitive indicator of population
99 bottlenecks for the maternal lineage (Avise 2004), the hypervariable region 1
100 (HVR1) of the mitochondrial control region was chosen for this study. This was
101 amplified with the primers DS1 and MER-R (Kurose *et al.* 1999). PCR
102 amplifications were performed in 25μl reactions containing 1μl of DNA extract,
103 GeneAmp 1x PCR Gold buffer (15mM Tris-HCl, 50mM KCl, pH 8.0), 2.5mM MgCl2,
104 200 μM each dNTP, 0.5μl of 10μM each primer and 0.3μl of AmpliTaq Gold DNA
105 Polymerase (Applied Biosystems). Amplification was carried out in a GeneAmp
106 PCR System 9700 thermocycler (Applied Biosystems) under the following
107 conditions: 95 ^{o}C 7 min, followed by 35 cycles of 94 ^{o}C 1min, 55 ^{o}C 1 min, 72 ^{o}C 2
108 min, and a final extension at 72 ^{o}C 10min. PCR Products to be sequenced were

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109 purified using a High Pure PCR Product Purification Kit (Roche Diagnostics).
110 Purified products were then sequenced on an automated Applied Biosystems
111 Model 310 sequencer (Applied Biosystems, Inc).
112
113 **Haplotype networks**
114 Sequences were aligned in Geneious 7.1.5 (Biomatters) using geneious global
115 multi-alignment assuming 93% similarity. A maximum parsimony network was
116 then created of these New Zealand control region haplotypes, along with 186
117 haplotypes from stoats from across Eurasia collected and sequenced by
118 Martínková and colleagues (2007) using the software TCS (Clement et al. 2000).
119 The level of difference in haplotype composition between populations was tested
120 for using Fisher's exact test. The detection threshold for haplotype frequency
121 was determined using the equation $(1-f)^n = \alpha$ where f = true frequency in the
122 population, n = number of samples and α = alpha level.
123
124 **Genetic drift simulations**
125 Two sets of Wright-Fisher genetic drift simulations were then run in the
126 software R to investigate the effect of the two demographic bottlenecks (1.
127 arrival of stoats in New Zealand, 2. myxomatosis in Britain) on mitochondrial
128 haplotype frequencies. The R code for these simulations can be obtained at
129 (DRYAD doi:10.5061/dryad.h77tb). Simulations were set to run from the year
130 1883 (before the introduction of stoats to New Zealand in 1884) until 2000. All
131 simulations were repeated with 1,000 iterations, and population numbers are for
132 female stoats only to represent the sampling of the maternally inherited mtDNA
133 haplotypes.
134
135 The first simulations were performed to investigate if the population bottleneck
136 caused by the introduction of stoats to New Zealand, and subsequent expansion
137 of the New Zealand population, could have led to a significant change in allele
138 frequency. From a British population of 300,000 (King & Powell 2007) with the
139 current New Zealand haplotype proportions, two simulations were run – one
140 with a founding population of 100 females, and one with 500 females. The
141 known number of stoats released in New Zealand was 224 in the first two years

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142 (King 1984), and the large number of unrecorded releases subsequent to this
143 mean the true total is likely to be far greater (King & Powell 2007); therefore the
144 first simulation is for a very conservative (small) bottleneck scenario, and the
145 second a more realistic one (though still conservative). The simulated
146 population then grew, doubling every year until it reached 100,000, at which
147 point it fluctuated around this value with a normal distribution N(100,000,
148 10,000). This value of 100,000 stoats in New Zealand was derived from a pre-
149 breeding population estimate of 200,000 (King and Powell 2007).
150
151 The second set of simulations was performed to investigate how severe the
152 demographic bottleneck needed to be for the British stoat population to show
153 the observed haplotype proportions (if a genetic bottleneck was responsible for
154 the difference in haplotype frequencies). As the first simulation indicated that
155 the New Zealand stoat population bottleneck is unlikely to have changed the
156 haplotype proportions greatly (see Results), these were used as the initial
157 starting values for the British stoat population. The pre-bottleneck population
158 (1883–1952) was defined as normally distributed N(300,000, 3,000). The
159 minimum population size was then varied (100, 500, 1,000) with durations from
160 1–3 years. The population size was then modelled to be normally distributed
161 N(20,000, 5,000) for the subsequent 10 years, and this was followed by an
162 increase to a normal distribution N(100,000, 10,000). The values for the
163 population sizes were derived from an assumption that the current British stoat
164 population is roughly equal to the New Zealand population: this is a conservative
165 estimate as current estimates have it as larger (King and Powell 2007). The
166 relative sizes of the population over time were estimated from the trapping
167 records (Tapper unpublished in King and Powell 2007), assuming that these can
168 be extrapolated to the population as a whole.
169

170 Results

171
172 Five haplotypes were found from 80 New Zealand stoats (GenBank Accession #
173 KP307771-KP307775), alignment: (DRYAD doi:10.5061/dryad.h77tb).. The

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174 most common haplotype (NZ_hap_1) is identical to the single haplotype
175 observed in all British stoats, and the other four haplotypes were most closely
176 related to the British haplotype (differing from it by only one base pair), and
177 more distantly related to the mainland European and Irish haplotypes (Figure 1).
178 The range of haplotypes was significantly higher in the South Island of New
179 Zealand, with haplotypes 2–4 only recorded here (Figure 1).
180
181 With only one haplotype detected in the British stoat population, the total
182 proportion of all haplotypes other than this haplotype must be <5.12% with 95%
183 confidence, and <7.76% with 99% confidence, given the level of sampling. Given
184 this detection threshold, both haplotypes 2 and 3 should have each been
185 detected in Britain – if the haplotype frequencies were the same in the New
186 Zealand and British populations, and it is extremely likely that at least one of the
187 combinations of haplotypes 2–5 would to be detected. New Zealand as a whole is
188 highly significantly more diverse than Britain ($p < 0.001$), with stoats on the
189 South Island being significantly more genetically diverse than those on the North
190 Island ($p < 0.001$).
191
192 The simulation of the New Zealand stoat population haplotype fluctuations
193 illustrates that large increases in the proportions of rare alleles are unlikely
194 (figure 2). In some simulations rare alleles (4 and 5) did however go extinct in
195 New Zealand due to genetic drift (figure 2). From these simulations, over 95% of
196 genetic drift was observed in the first six years when population sizes were small
197 (up to 3,200). Subsequent to this, the haplotype proportions remained
198 reasonably constant (figure 2).
199
200 For the simulation of the British stoat population, the size and variability of the
201 populations outside of the acute bottleneck phase had minimal effect on levels of
202 genetic drift; the only important variables that determined the level of drift were
203 the minimum population size (N_{min}) and the duration of this bottleneck – as
204 expected from random genetic drift. The sudden increase in genetic drift caused
205 by the bottleneck associated with myxomatosis can be seen in figure 3. In order
206 to obtain results which reflected the decrease in frequency of haplotypes 2–5

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207 below the detection threshold, an extremely severe bottleneck well below 1% of
208 the original population (with an $N_{e(f)}$ of less than 100) for several years was
209 required (Figure 4). This detection threshold is the probability of detecting at
210 lease one of these four alleles which were not detected in Britain given the
211 sampling effort (57 samples), when randomly sampling a population with the
212 final allele frequencies derived from each bottleneck simulation.
213

214 **Discussion**

215

216 Our results show that the introduced invasive stoat population of New Zealand is
217 significantly more diverse than native stoats in Britain, based on mitochondrial
218 DNA control region sequence data. There are five possible mechanisms that
219 could produce this observed pattern: 1) multiple source populations for New
220 Zealand stoats, 2) insufficient sampling of British stoat genetic diversity, 3)
221 genetic drift following foundation causing an increase in previously rare alleles
222 in the New Zealand population, 4) in-situ mutation in the New Zealand stoat
223 population, and 5) a significant genetic bottleneck for British stoat populations in
224 the 20th Century. Our results support the 5th scenario, for reasons outlined
225 below
226

227 The available data do not support the establishment of genotypes in New
228 Zealand from outside of Britain, as the New Zealand haplotypes are most similar
229 to the single British haplotype, which differs from all haplotypes detected in
230 mainland Europe by at least two substitutions. This supports the belief that the
231 New Zealand stoat population was founded entirely from one or more British
232 sources - as historical records imply (King & Powell 2007). Sampling in Britain
233 was widespread, therefore it seems unlikely that unsampled spatial structure is
234 responsible for the lack of diversity observed within the British stoat population.
235

236 Using the simulation of genetic drift for the introduction to New Zealand we
237 demonstrate that the significant increase in rare alleles required for the
238 observed pattern is unlikely to occur. While rare alleles can surf the expansion

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239 fronts of introduced populations, rapidly expanding in frequency (Excoffier and
240 Ray 2008) it remains improbable that four rare haplotypes were all
241 independently significantly amplified in frequency. Similarly, the probability of
242 four independent mutations arising and independently surfing to high frequency
243 is unlikely, though we cannot rule either of these scenarios out completely due to
244 the many unknown parameters of the population expansion and mutation rate.
245
246 Our data is most consistent with a scenario where British stoats went through a
247 very significant genetic bottleneck after the introduction of stoats to New
248 Zealand, resulting in the loss of mitochondrial diversity in the population. Given
249 that trapping records show a very significant demographic bottleneck in British
250 stoats due to myxomatosis in the 1950s (Jefferies & Pendlebury 1968; King &
251 Powell 2007), this event is the most likely cause for this hypothesized genetic
252 bottleneck for British stoats.
253
254 European rabbits are not native to Britain, having been introduced around 2,000
255 years ago – though they did not become naturalized in the wild until around the
256 mid 12th century (Lever 2009). When the myxoma virus arrived in Britain, the
257 UK government supported its spread as a biological control agent for this
258 agricultural pest (Bartrip 2008). The rapid spread and severity of the
259 myxomatosis epizootic detrimentally affected a number of native predator
260 species in Britain, particularly the stoat (Sumpton & Flowerdew 1985). Native
261 British stoats had become particularly specialized and reliant upon the
262 introduced rabbits (McDonald et al. 2000, McDonald 2002), with rabbits forming
263 over 80% of their diet before the myxomatosis epizootic (Southern 1956). From
264 1953 to 1955 myxomatosis arrived in Britain, causing over 99% of the rabbit
265 population to die (Sumpton & Flowerdew 1985). This loss of prey had a drastic
266 effect on the British stoat population. Poor breeding success for stoats was
267 found immediately after myxomatosis (Lockley 1956). Young stoats died of
268 starvation (Haslam 1955), and fewer pregnant or nursing females were observed
269 than in previous years (Hervey 1955). Significant changes in diet and behaviour
270 were noted, with an increased reliance on invertebrates, birds and rodents, often
271 including prey items not usually eaten by stoats (Cobnut 1955, Brown 1955, Day

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272 1968). These changes in diet did not prevent a dramatic population crash: the
273 average number of stoats caught annually decreased by 84% for the ten years
274 following the myxomatosis outbreak across records kept by game estates
275 (Jefferies & Pendlebury 1968; King & Powell 2007). On some of these game
276 estates, there were no stoats caught during a full calendar year despite continued
277 effort and high and increasing tallies of weasels (*Mustela nivalis*) (King & Moors
278 1979, King & Powell 2007). Over the whole of Britain, stoats remained scarce
279 with the demographic bottleneck lasting 10–15 years.
280
281 The New Zealand and British stoat populations had different demographic
282 histories around the time of their respective population bottlenecks, which are
283 likely to have affected the severity of the genetic bottlenecks experienced. The
284 New Zealand population rapidly expanded after the initial releases (King &
285 Murphy 2005), which would minimize the loss of genetic diversity; while in
286 Britain the severe demographic bottleneck lasted for several generations and
287 recovery was slow: a scenario particularly likely to result in the loss of genetic
288 diversity (Allendorf et al. 2012). If this demographic bottleneck is responsible
289 for the observed difference in haplotype diversity between New Zealand and
290 British stoat populations, our simulations indicate that the British stoat
291 population bottleneck must have collapsed to an effective female population size
292 across Britain of less than a few hundred for several years to account for the
293 present lack of diversity. Due to the simplifying assumptions of the simulations
294 we do not try to interpret this in terms of actual stoat numbers; we simply
295 highlight that the demographic bottleneck must have been extremely severe to
296 cause the implied loss of diversity.
297
298 Historical DNA has been obtained from museum specimens of stoats
299 (Martínková & Searle 2006), and further investigation of historical samples may
300 better elucidate the former mitochondrial diversity of British stoats. Using
301 modern methods for capturing ancient DNA (e.g. Bahcall 2013) it should also be
302 possible to obtain nuclear DNA from these historical samples, to examine if
303 nuclear diversity has also been lost from Britain, but potentially retained in New
304 Zealand stoats.

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305

306 Introduced populations generally lose genetic variation relative to their source
307 populations (Dlugosch & Parker 2008). Of the genetic studies of introduced
308 populations reviewed by Dlugosch & Parker (2008), only 6/76 had increased
309 (>10%) allelic diversity in the introduced population, and in each of these
310 studies there was either a significant sampling bias towards the introduced
311 population, or there were multiple introductions from multiple source
312 populations, which has allowed an accumulation of this widely sampled variation
313 (e.g. Ellstrand & Shierenbeck 2000, Genton et al. 2005, Kolbe et al. 2008,
314 Kennington et al. 2012). Our results suggest that introduced populations can act
315 as an 'ark for genetic diversity' lost from their native populations. This result has
316 similarities to those of Martínková et al. 2014, who found that introduced voles
317 (*Microtus arvalis*) in the Orkney Islands retained ancestral mitochondrial
318 diversity that had been lost from mainland Europe in the 5000 years since their
319 introduction to these islands. Red squirrels (*Sciurus vulgaris*) in Ireland, which
320 are admixed between native and introduced squirrels from Britain, have also
321 retained genetic diversity lost from Britain (Finnegan et al. 2008). Genetic
322 analyses have also shown that supposedly extinct sub-species have survived in
323 introduced populations, with invasive tammar wallabies (*Macropus eugenii*) in
324 New Zealand shown to be a supposedly extinct subspecies from South Australia
325 (Taylor & Cooper 1999). Reintroducing species to parts of their native range
326 where they have been extirpated is now common conservation measure (Ewen
327 et al. 2012). Throughout Europe and in the UK in particular, once common birds
328 such as the grey partridge (*Perdix perdix*), and the cirl bunting (*Emberiza cirlus*),
329 which have introduced populations elsewhere, have been declining dramatically
330 due to changed farming practices (Gregory et al. 2007). As we move toward
331 conserving genetic biodiversity, the genetic diversity conserved in introduced
332 populations may also be considered valuable and therefore worthy of
333 reintroduction.

334

335 An important aspect of these results is that we interpreted them in light of a
336 known demographic history for both populations, and the interpretation would
337 potentially be different if we did not have this prior information. Many studies

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338 infer demographic and colonization history based on contemporary patterns in
339 genetic diversity, such as studies of glacial refugia in Europe (e.g. Hewitt 1999,
340 2000). If our results were obtained from populations where the history of each
341 population was unknown, the interpretation could be that the more diverse
342 population (New Zealand) was a source population or refugium, and the British
343 population was an expansion/introduction from New Zealand. Because of this,
344 care is needed in interfering historical processes from contemporary genetic
345 variation, as it may be difficult to distinguish between a source population losing
346 variation, and an expansion/introduction scenario.
347

348 **Acknowledgements**

349

350 We thank the editor Rob Colautti and two anonymous reviewers for their
351 constructive comments which greatly improved the manuscript. We thank
352 Natália Martínková and Jeremy Searle, for their assistance and for the use of their
353 data. Also thanks to James Russell for his comments. We thank Oliver Hannaford
354 for his assistance in programming the simulations. We thank New Zealand's
355 Ministry of Business, Innovation and Employment (Science and Innovation
356 Group) for funding to the Invasive Mammal Impacts Programme (contract
357 C09X0909) and core funding to Crown Research Institutes. We also thank
358 Carolyn King, Landcare Research and the New Zealand Department of
359 Conservation for their help in obtaining samples.
360

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459 wallabies (Macropus eugenii) as an extinct taxon. Animal Conservation, **2**, 41-49
460 Thompson GM (1922) The Naturalisation of Animals and Plants in New Zealand. .

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461 Cambridge.

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464 **Data Accessibility**

465 All data and simulations have been uploaded to dryad (doi:10.5061/dryad.h77tb) and

466 genbank (GenBank Accession # KP307771-KP307775) for publication.

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494 **Figure legends:**

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496 **Figure 1 Distribution and haplotype network of mitochondrial control**
497 **region haplotypes sampled from across New Zealand and Britain, including**
498 **samples from mainland Europe and Ireland. The size of each circle**
499 **represents the sample size from each location.**

500

501 **Figure 2 Average proportions and 95% confidence limits of alleles 1 – 5 in**
502 **two simulated bottleneck scenarios for the New Zealand population**
503 **assuming the present day sampled proportions of haplotypes were present**
504 **in 1883. From top to bottom: haplotype 1 (black), haplotype 2 – (red),**
505 **haplotype 3 (green), haplotype 4 & 5 (blue). Confidence limits show that**
506 **95% of all simulations had haplotype frequences within this range.**

507

508 **Figure 3** Average proportions and 95% confidence limits of alleles 1 – 5 in the
509 simulated mysomatosis bottleneck scenario for the British stoat population, assuming
510 the present day sampled New Zealand proportions of haplotypes were present in
511 Britain in 1883. Minimum population size = 100 Females for three years. From top to
512 bottom: haplotype 1 (black), haplotype 2 – (red), haplotype 3 (green), haplotype 4 & 5
513 (blue). Confidence limits show that 95% of all simulations had haplotype frequences
514 within this range.

515

516 **Figure 4 Final haplotype percentages with 95% condidence intervals for**
517 **the combined haplotypes 2 – 5 under varying bottleneck scenarios for the**
518 **British stoat population: (N(min) = 100, 500, 1000), bottleneck duration =**
519 **(1,2,3 years). Detection thresholds given the sampling in Britain are shown**
520 **as dotted and dashed lines.**

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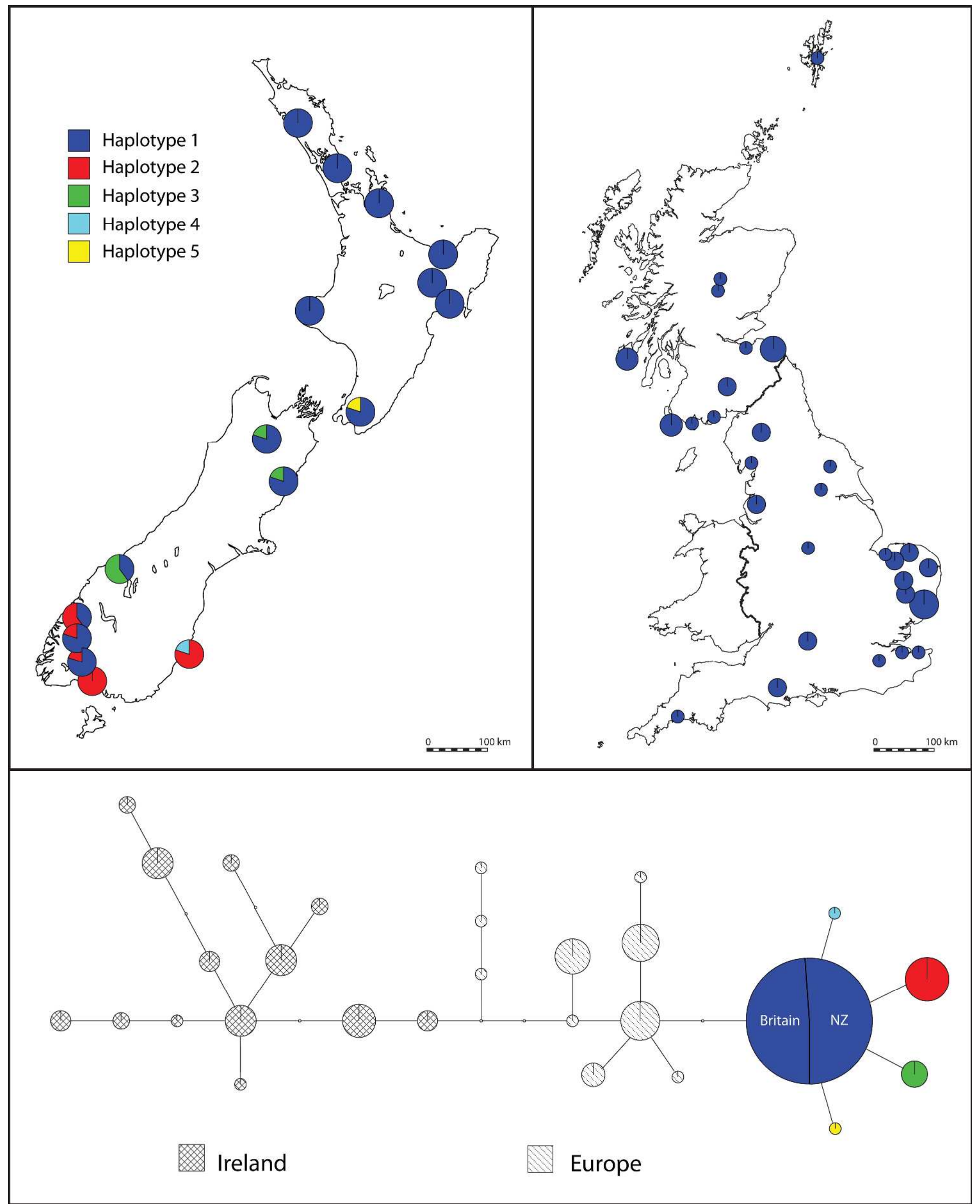
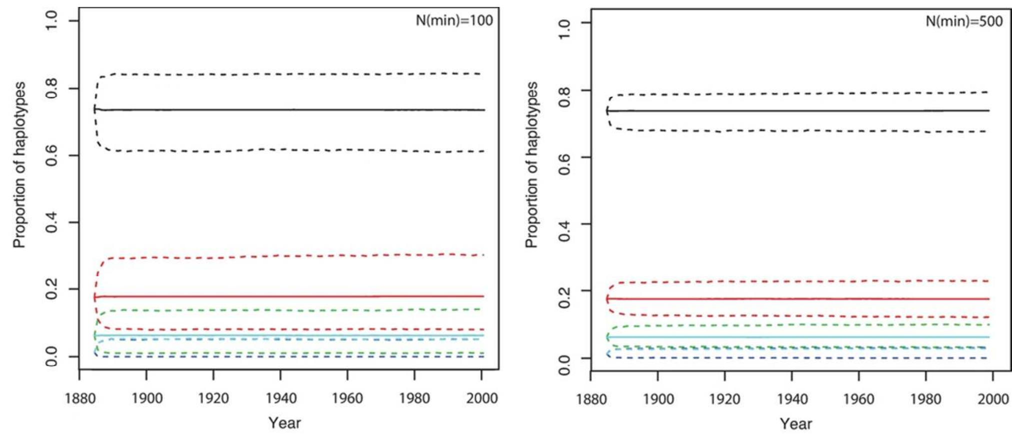


Distribution and haplotype network of mitochondrial control region haplotypes sampled from across New Zealand and Britain, including samples from mainland Europe and Ireland. The size of each circle represents the sample size from each location.
397x495mm (300 x 300 DPI)



Average proportions and 95% confidence limits of alleles 1 – 5 in two simulated bottleneck scenarios for the New Zealand population assuming the present day sampled proportions of alleles were present in 1883. From top to bottom: haplotype 1 (black), haplotype 2 – (red), haplotype 3 (green), haplotype 4 & 5 (blue). Confidence limits show that 95% of all simulations had haplotype frequences within this range.
85x38mm (300 x 300 DPI)

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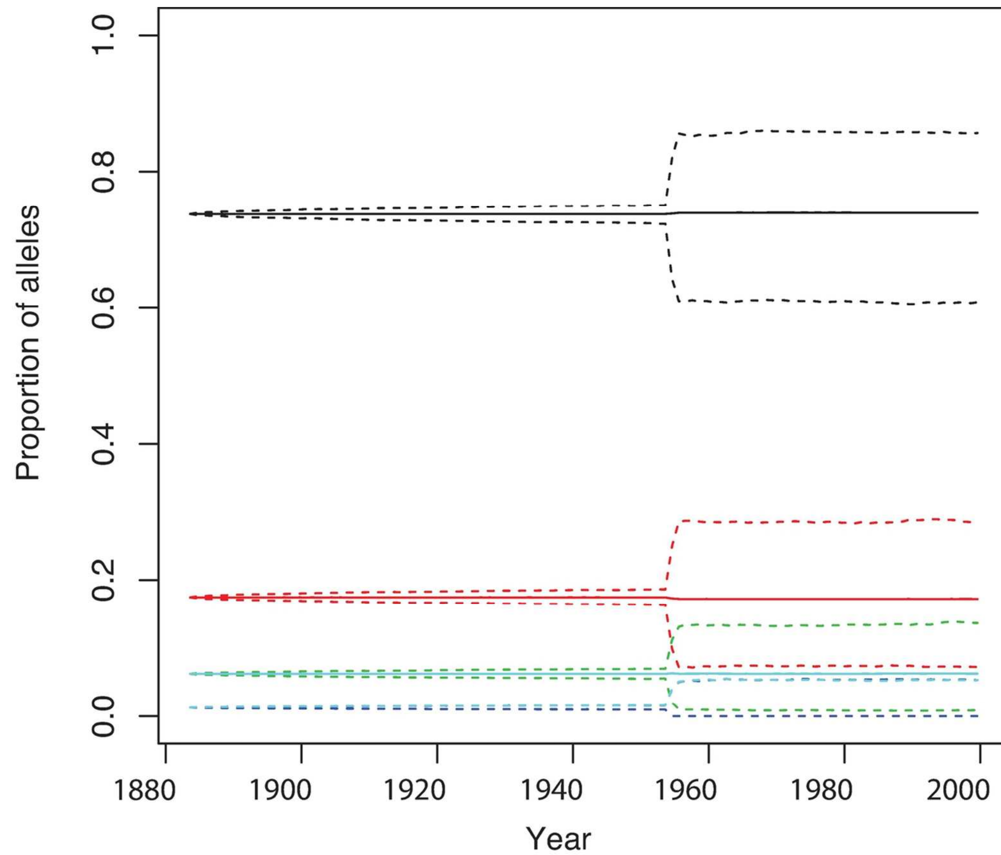
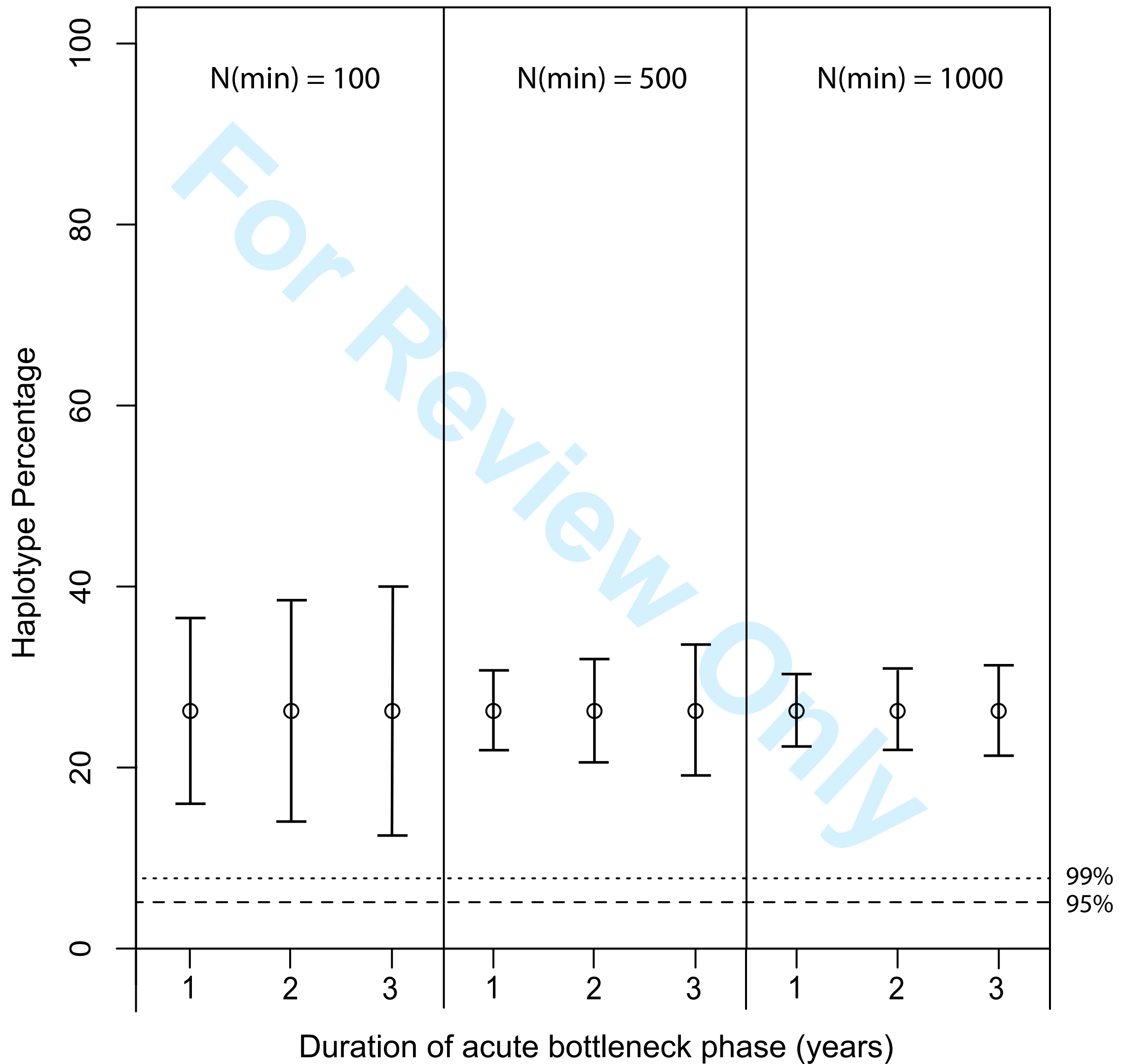


Figure 3 Average proportions and 95% confidence limits of alleles 1 – 5 in the simulated mysomatosis bottleneck scenario for the British stoat population, assuming the present day sampled New Zealand proportions of haplotypes were present in Britain in 1883. Minimum population size = 100 Females for three years. From top to bottom: haplotype 1 (black), haplotype 2 – (red), haplotype 3 (green), haplotype 4 & 5 (blue). Confidence limits show that 95% of all simulations had haplotype frequences within this range.
120x108mm (300 x 300 DPI)



N(min) = 100
N(min) = 500
N(min) = 1000
Haplotype Percentage
0
20
40
60
80
100
1
2
3
1
2
3
1
2
3
99%
95%
Duration of acute bottleneck phase (years)
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