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RESEARCH ARTICLE

Molecular comparison of historical and contemporary pine marten (*Martes martes*) populations in the British Isles: evidence of differing origins and fates, and implications for conservation management

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Abstract We investigated the origins and persistence of European pine marten (*Martes martes*) populations across the British Isles by identifying mitochondrial DNA (mtDNA) sequences from contemporary populations (sampled since 1981) and comparing these with those of older 'historical' museum specimens (pre-1981) originally collected from the same geographic areas. Excluding Scotland, where the haplotype composition of populations appears to be unchanged, haplotypes found in contemporary and historical marten populations elsewhere differed both temporally and geographically. While these data suggest that the contemporary Irish population is descended from a relict population that passed through an early to mid 1900s bottleneck, the historical and contemporary English and Welsh populations differ in their abundance of specific mtDNA control region haplotypes. These data appear to suggest that particular haplotypes may have been lost from England and Wales at some point in the early to mid 1900s, but further nuclear DNA work is required to determine whether this shift has occurred by rapid genetic drift in the mtDNA control region or whether relict populations have been replaced by pine martens from elsewhere. If the reported shifts in mtDNA haplotypes reflect population extirpation events, historical pine marten populations of England and Wales would appear to have become extinct in the twentieth century (in Wales after 1950 and in England after 1924). Additionally, the recent occurrence of haplotypes originating from continental Europe, and of *M. americana*, suggest that relict populations of England and Wales have been replaced by, or hybridised with, occasional released, escaped and/or translocated animals. The implications of these results for pine marten conservation, and particularly reintroduction, are discussed.

Keywords Marten · *Martes* · Haplotype · Extinction · Reintroduction

Introduction

The European pine marten (*Martes martes*) is a medium-sized arboreal mustelid that is found in low densities throughout most of Western Europe where it is indigenous (Helldin 1998; Mitchell-Jones et al. 1999), and primarily associated with mature deciduous and coniferous forests (Domingo-Roura 2002). During the last century populations have declined over much of their former range because of habitat alterations, fragmentation and historical persecution (Langley and Yalden 1977; Mitchell-Jones et al. 1999; Bright 2000), with some populations contracting markedly (Langley and Yalden 1977). In Britain and Ireland populations dwindled to a distributional nadir in the early and mid 1900s respectively (Langley and Yalden 1977). Following a reduction in persecution and tightening of legislation (e.g. Wildlife and Countryside Act 1981, Legislation.gov.uk 2010), populations in some parts

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of their British Isles range have recovered (Ireland, O'Mahony et al. 2006 and O'Sullivan 1983; Scotland, Balharry et al. 1996), mirroring population-scale recoveries in other parts of Europe (e.g. Bulgaria, Spiridonov and Spassov 1998), but in contrast pine marten populations in England and Wales have failed to increase naturally (Birks and Messenger 2010). This has lead to the species' inclusion in the UKBAP (United Kingdom Biodiversity Action Plan) list of priority species in 2007 (http://www.ukbap.org.uk/NewPriorityList.aspx) and the subsequent development of a strategy for pine marten recovery (Jordan 2011). The origin of these contemporary animals has been debated (e.g. Bright et al. 2000; Birks and Messenger 2000), but determining this and their current status are essential to informing decisions about the conservation management of these vulnerable populations.

Determining the geographical origin of invasive species is increasingly important as their ecological and economic impact is better understood (e.g. Pitra et al. 2005), but information on the origin of specific populations of native species, particularly where there is a suspicion that these may have been introduced, can also be of great conservation value. Although some authors point to a continuous stream of pine marten evidence from particular areas of England and Wales as possibly indicating the long-term persistence of populations (e.g. Birks and Messenger 2010), others have suggested that random escapes, releases or translocations could account for their current presence (e.g. Yalden 1999) at least in some areas (Strachan et al. 1996). Determining which of these hypotheses is correct is particularly important as reintroduction programmes become an increasingly common method of addressing biodiversity loss (Hayward and Somers 2009). Indeed, previous plans to reintroduce the pine marten to England in the late 1990s (Bright and Smithson 1997, Bright et al. 2000) were opposed on the grounds that existing populations may contain relict types arguably of special conservation value and potentially vulnerable to genetic dilution (Birks and Messenger 2000), but to date no evidence of such relict types has been provided.

The use of molecular markers is generally necessary for identifying relict types, because in most cases morphological characters do not exhibit sufficient intraspecific variation to characterize populations (e.g. Rozhnov et al. 2010). Mitochondrial DNA (mtDNA) is a useful genetic marker because of relatively high levels of variation within and between populations. The current distribution of *M. martes* haplotypes is well known across much of the range (Denmark, Pertoldi et al. 2008a; England, Kyle et al. 2003; Russia, Rozhnov et al. 2010; Europe, Davison et al. 2001) and populations are significantly differentiated by the mtDNA control region haplotype (Davison et al. 2001; Kyle et al. 2003; Pertoldi et al. 2008b) despite the fact that pine marten populations across Europe diverged from a common European refugium following a recent glaciation (Davison et al. 2001). Such geographic patterns of maternally inherited mitochondrial haplotypes are common in mustelids (e.g. wolverine, *Gulo gulo*, Walker et al. 2001), and would be particularly expected in species such as the pine marten where females are philopatric (Mitchell-Jones et al. 1999). As such, determining an individual animal's mitochondrial haplotype can give an indication of its likely origin, information which is particularly important for the development of sound conservation management strategies.

In this paper we assess the genetic structure of contemporary pine marten populations (since 1981) across the British Isles using mitochondrial haplotype variation in the control region. The haplotype compositions of contemporary populations are compared with those of historical populations from the same geographic areas, samples of which were collected from museum specimens (pre-1981) with known provenance. These data allow us to determine whether contemporary populations are likely to be descended directly from historical populations or whether they may be the result of escapes, covert releases or translocations from elsewhere. Such information is invaluable in deciding the appropriate conservation action for pine martens in England and Wales, particularly in determining whether reintroduction can be considered and, if so, whence founder stock should be sourced.

Methods and materials

Specimens and sampling

For convenience, we refer to samples collected before the Wildlife and Countryside Act (1981) as having been taken from 'historical' populations, and those collected in and since 1981 as from 'contemporary' populations. On average 29 ± 16.37 years (mean ± SD) separated samples collected from the same country from these two main periods (England 40 years, Ireland 14, Scotland 16, Wales 46). The historical period was further sub-divided into periods of potential relevance to pine marten populations in the British Isles: Victorian/pre-war, <1914; Wars and intervening period 1914–1945; Post war/pre-legislation 1946–1980).

Samples of pine marten scats, hairs and bodies were collected from contemporary populations. Scats were collected on a series of organised pine marten scat surveys (e.g. Messenger et al. 2010), and by volunteer surveyors elsewhere who collected and posted faecal material. Scats were collected using fresh disposable wooden spatulas and placed into small labelled zip-lock bags, with great care being taken to avoid cross-contamination. Hairs were collected in Ireland from baited hair-tubes (see Mullins et al. 2010 for methods), and genetic material was also collected from occasional road casualties.

Samples from historical populations (1865–1977) were collected by locating specimens housed in museums and private collections. Pine marten skins, skulls and full mount specimens of known provenance and known dates of collection were sampled. To sample skulls (including those in mounted specimens), a clean curette was inserted into the nasal cavity of the skull and 10–20 mg of bone material was carefully dislodged (see Wisely et al. 2004). Fragments were collected onto sterile aluminium foil and poured directly into a secure sterile container. In each case, one side of the nasal cavity was left intact. Skins and mounted specimens without a skull were sampled by plucking hair with sterilised pliers. Hairs were taken from below the tail-base region to avoid causing accidental aesthetic damage to the specimen. Most samples were collected directly by NRJ, PT and JM, but some specimens were kindly sampled by museum staff. In such cases, detailed instructions and equipment were provided and a minimum of 8 hairs were requested from each specimen. Samples were also collected from specimens held in captivity in Zoological gardens or by private collectors. Additional existing haplotype data were gleaned from published work, and sources are cited where appropriate.

DNA analysis

DNA was extracted from scats and hair samples as described previously (O'Reilly et al. 2008; Mullins et al. 2010) and from bone and tissue samples using the ZR Genomic DNA extraction kit (Zymo Research Corporation 17062 Murphy Ave. Irvine, CA 92614, U.S.A. Cat. No. D3050) according to the manufacturer's instructions. The presence of pine marten DNA was determined using the pine marten specific qPCR assay as described previously with the PM3 Taqman™-MGB probe (Mullins et al. 2010). The qPCR assay was also used to quantify the DNA to identify samples suitable for DNA sequencing. Extraction of DNA from museum samples was carried out in a separate room with separate reagents and equipment. A 315 bp fragment of the mitochondrial control region was PCR amplified using primers LMS3 (5′ TCC CTA AGA CTC AAG GAA GA 3′) (Statham 2005) and PM-Rev (5′ GGC CCG GAG CGA GAA G 3′) (O'Reilly et al. 2008). The 10 μl PCR reaction contained 5 μl GoTaq® Hot Start Green Master mix (Promega Corporation 2800 Woods Hollow Road, Madison, WI 53711, USA, Cat. No. M5123) 200 nM each primer and 2–10 ng DNA. The thermal cycling protocol was 94 °C initial denaturation for 2 min, followed by 50 cycles of 94 °C for 20 s, 57 °C for 30 s and 72 °C for 30 s with a final extension for 10 min at 72 °C. PCR products were purified for sequencing using a ZYMO DNA Clean and Concentrate-5™ (D4004). The PCR products were sequenced on both strands using the Applied Biosystems BigDye® v3.1 cycle sequencing kit used according to the manufacturer's instructions. The sequencing reaction was analysed using the ABI 310 Genetic Analyser. DNA sequences were analysed using the Lasergene software package (DNASTAR Inc. 3801 Regent Street, Madison, WI 53705 USA).

Comparing the likely haplotype composition of historical and contemporary populations

To investigate and compare the likely prevalence of haplotypes in historical and contemporary populations respectively, we varied the proportion of animals in a hypothetical population that exhibited a particular haplotype, and calculated the probability of randomly obtaining the actual haplotype results data we obtained from empirical data for each population under these hypothetical circumstances. To calculate this probability, we derived and used the formula: $P = (t!/(n! \times (t - n!))) \times H^n \times (1 - H)^{(t-n)}$, where H is the theoretical proportion of the population that is the predominant historical haplotype, n is the number of samples collected of the predominant historical haplotype, and t is the total number of samples analysed from the population. Historical and contemporary populations were treated separately in the above calculations, and their likely haplotype compositions compared. In the event that non-native haplotypes were discovered in contemporary populations, these results were compared with the known current distribution of *M. martes* haplotypes across Europe (Davison et al. 2001) to establish their probable origin.

Statistical analyses

Statistical tests were carried out in 'R' (R Development Core Team 2008). To maximise the chances of independence, and to ensure that we have the best estimates of population haplotype composition, analyses do not include samples from known littermates. To avoid pseudoreplication, samples collected within 50 km of another sample of the same haplotype were excluded from analyses if it was possible that they could have been from the same individual (i.e. if one or both samples were not carcasses or if samples were collected <10 years apart).

Results

157 pine marten samples from the British Isles were collected from museums and the field and subjected to DNA analysis (Appendix Table 1). The qPCR assay was used to confirm species and to identify samples for haplotype determination. Samples with a qPCR Ct value <30 cycles were chosen for further analysis. Using this criterion, we were able to determine the haplotype of 133 of these samples. Forty-five of these samples were from pre-1981 specimens and 81 were from specimens collected subsequently (it was not possible to determine the dates of collection for 7 samples). The distribution of these samples are shown temporally (Fig. 1) and geographically (Fig. 2).

England

All samples ($n = 6$) from historical populations were identified as originating from haplotype i individuals, suggesting that haplotype i was the predominant or exclusive native pine marten haplotype of England. This haplotype was last detected in England from a specimen collected in 1924. In contrast, none of the samples ($n = 11$) retrieved from the contemporary English population (all collected since 1990) came from haplotype i individuals. Most of these (8 of 11) were haplotype a, one from Southern England was identified as haplotype g and two from Northern England showed evidence of introgression with *M. americana* (Kyle et al. 2003; Davison et al. 2001).

Comparing the proportion of animals of haplotype i and other haplotypes (pooled) in the historical versus contemporary pine marten populations of England confirms that the haplotype composition of historical and recent populations differ significantly (Binomial test of proportions: $\chi^2 = 12.9032$, d.f. = 1, $p < 0.001$; 95 % CI = 0.871 − 1). This result holds even when we remove instances where evidence exists of deliberate translocation (e.g. a carcass in full winter coat found in a Worcestershire woodland in summer, Forrest et al. 2002) or accidental escape (a road casualty found <5 km from a known collection in Hampshire, Birks et al. 2005) ($\chi^2 = 11.123$, d.f. = 1, $p < 0.001$; 95 % CI = 0.861 − 1).

Wales

In Wales, as in England, all samples ($n = 7$) from historical populations were identified as originating from haplotype i individuals. This haplotype was last detected in Wales from a specimen collected in 1950. Only two genetic samples have been collected from Wales since then and both were from haplotype a individuals collected in 1996 and 2007. Bearing in mind the small sample size presented here, these data suggest that, as in England, the haplotype composition of historical and recent populations of Wales differ significantly (Binomial test of proportions: $\chi^2 = 4.1441$, d.f. = 1, $p = 0.04178$).

Fig. 1 The occurrence of different haplotypes in pine marten ▶ specimens from the British Isles (by country) over four key periods. Haplotypes from each country are plotted separately against the year of collection, and years are clumped into periods defined by their relevance to pine marten conservation. Numbers in superscript are sample sizes >1 for particular years. The annotation 'ND' denotes specimens where haplotypes were not determined

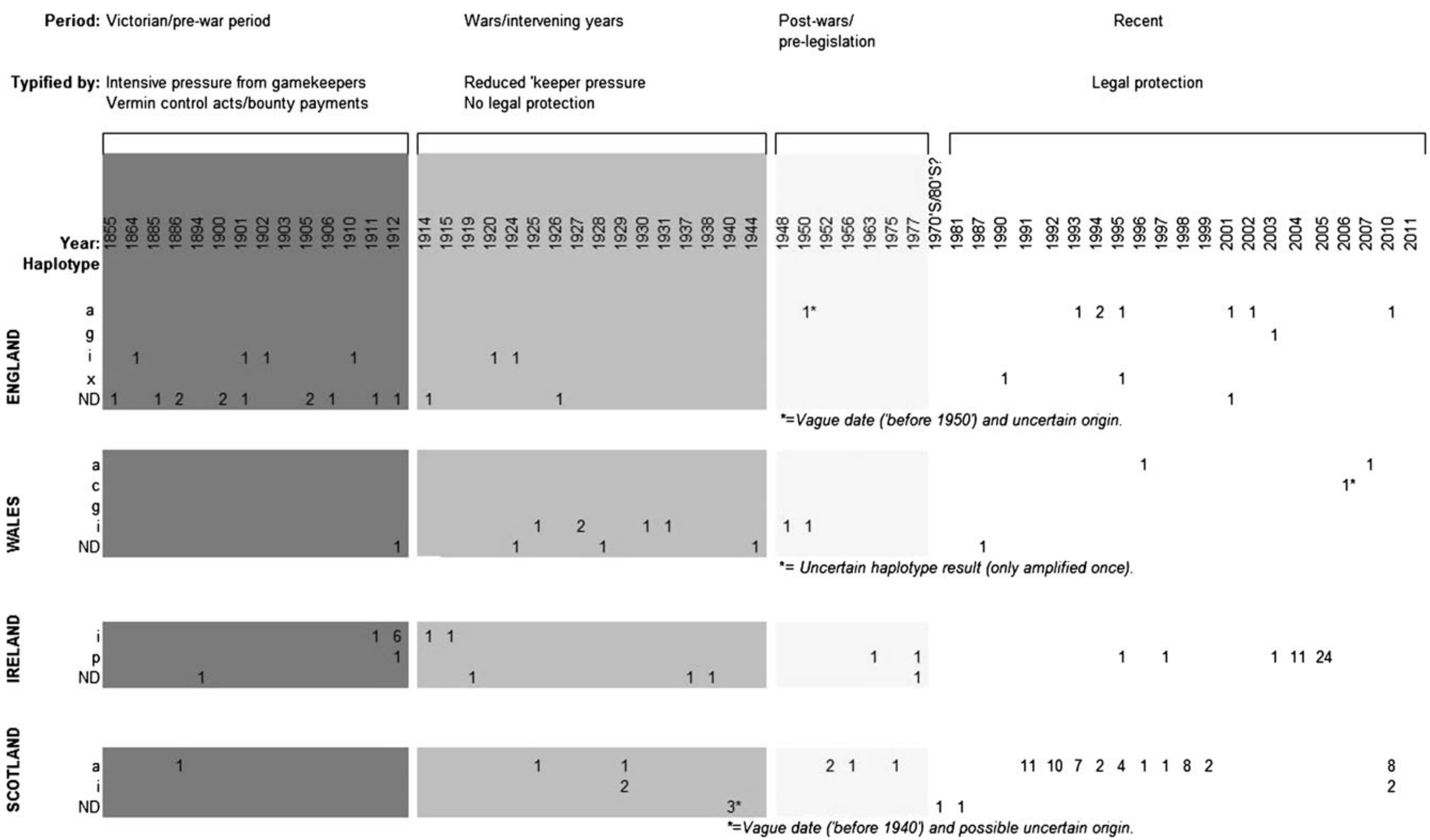
England and Wales combined

Since the genetic data described above suggest that historical populations of England and Wales were of similar composition (predominantly, or perhaps exclusively, haplotype i), and as there are no major geographical barriers between the two countries, meaning that for conservation purposes they could be managed as the same population in the future, we combined data for England and Wales. These combined data suggest that the haplotype composition of historical and recent populations of England and Wales differ significantly (Binomial test of proportions: $\chi^2 = 22.154$, d.f. = 1, $p < 0.00001$; 95 % CI = 0.923 − 1). Again, this result holds when three samples from England were removed from the analysis because persuasive evidence of deliberate translocation or accidental escape was available ($\chi^2 = 20.141$, df = 1, $p < 0.001$; 95 % CI = 0.916 − 1).

The probabilities of obtaining the actual haplotype results identified, given different hypothetical population structures for England and Wales, were calculated and are shown in Fig. 3a. Extrapolating from these curves, we can estimate that it is likely ($p > 0.95$) that the proportion of the contemporary population (post-1981) of England and Wales that is haplotype i is <0.00426. In practical terms this means that it is unlikely that more than one haplotype i animal would be found in a population of 235 animals. This contrasts markedly with estimates from data collected pre-1981 where we estimate that the proportion of the historical population that was haplotype i was >0.99607, meaning that one would expect that at least 234 out of 235 animals would be haplotype i.

Scotland

Both historical and contemporary pine marten populations in Scotland appear to have contained both haplotype a and haplotype i individuals, with haplotype a predominating in



Period: Victorian/pre-war period — **Typified by:** Intensive pressure from gamekeepers; Vermin control acts/bounty payments

	Year: Haplotype	1855	1864	1885	1886	1894	1900	1901	1902	1903	1905	1906	1910	1911	1912
ENGLAND	a														
	g														
	i		1					1	1				1		
	x														
	ND	1		1	2		2	1			2	1		1	1
WALES	a														
	c														
	g														
	i														
	ND														1
IRELAND	i													1	6
	p														1
	ND					1									
SCOTLAND	a				1										
	i														
	ND														

Period: Wars/intervening years — **Typified by:** Reduced 'keeper pressure; No legal protection

	Year: Haplotype	1914	1915	1919	1920	1924	1925	1926	1927	1928	1929	1930	1931	1937	1938	1940	1944
ENGLAND	a																
	g																
	i				1	1											
	x																
	ND	1						1									
WALES	a																
	c																
	g																
	i						1		2			1	1				
	ND					1				1							1
IRELAND	i	1	1														
	p																
	ND			1										1	1		
SCOTLAND	a						1				1						
	i										2						
	ND															3*	

Period: Post-wars/pre-legislation

	Year: Haplotype	1948	1950	1952	1956	1963	1975	1977	1970'S/80'S?
ENGLAND	a		1*						
	g								
	i								
	x								
	ND								
WALES	a								
	c								
	g								
	i	1	1						
	ND								
IRELAND	i								
	p					1		1	
	ND							1	
SCOTLAND	a			2	1		1		
	i								
	ND								1

Period: Recent — **Typified by:** Legal protection

	Year: Haplotype	1981	1987	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2001	2002	2003	2004	2005	2006	2007	2010	2011
ENGLAND	a						1	2	1					1	1						1	
	g															1						
	i																					
	x			1					1													
	ND													1								
WALES	a									1										1		
	c																		1*			
	g																					
	i																					
	ND		1																			
IRELAND	i																					
	p								1		1					1	11	24				
	ND																					
SCOTLAND	a				11	10	7	2	4	1	1	8	2								8	
	i																				2	
	ND	1																				

ENGLAND: *=Vague date ('before 1950') and uncertain origin.

WALES: *= Uncertain haplotype result (only amplified once).

SCOTLAND: *=Vague date ('before 1940') and possible uncertain origin.

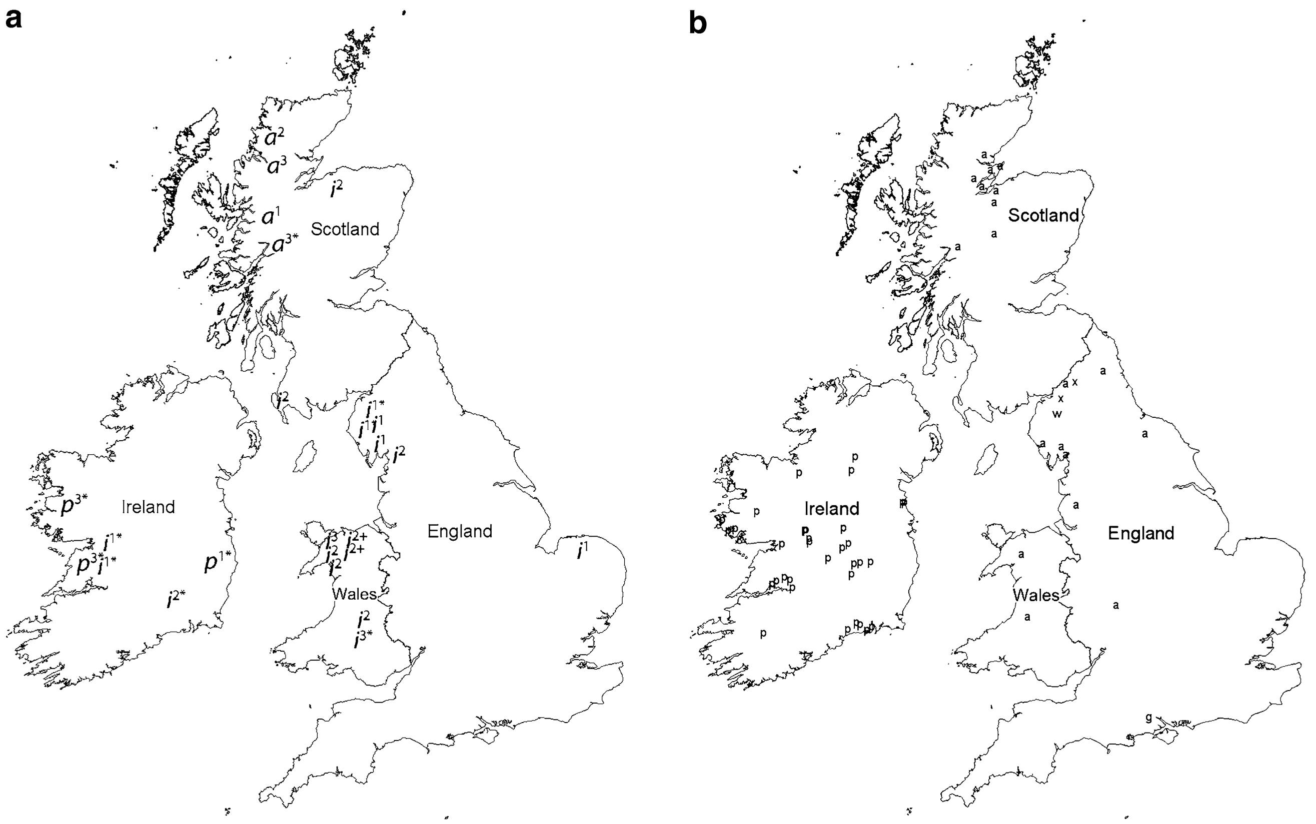


Fig. 2 The distribution of *Martes martes* mitochondrial haplotypes collected in the British Isles from historical (pre-1981; Fig. 2a) and contemporary (1981 onwards; Fig. 2b) populations. Each sample's location is demarked by its haplotype letter, with the historical period of collection shown as a superscript (1 = Victorian/pre-war, <1914; 2 = wars and intervening period 1914–1945; 3 = post war/pre-legislation 1946–1980). Locations accurate to region only are shown by *

both periods. Our sample of historical populations contained 20 % haplotype i individuals (2/10) compared with 7.69 % in our sample of recent populations (1/13). Although lower, the proportion of haplotype i individuals found in recent populations is not significantly different from that of historical populations (Binomial test of proportions: $\chi^2 = 0.0597$, d.f. = 1, $p = 0.807$). The probability of obtaining the actual haplotype results we have identified, given different hypothetical population structures for Scotland, were calculated and are shown in Fig. 3b.

Ireland

The contemporary pine marten population of Ireland appears to consist entirely of haplotype p individuals ($n = 38$), whereas the historical population appears to have been predominantly haplotype i (9/10), as in England and Wales. This shift appears to have occurred around the early 1900s, when haplotypes i and p apparently coexisted. The last specimen of haplotype i in Ireland was collected in Kilkenny in 1915; the first haplotype p specimen was found in 1912 in Wicklow. Due to the similarities of haplotypes p and i (Davison et al. 2001), and the suspected contraction of populations at around the same time, it is suggested that haplotype p evolved directly from haplotype i, possibly in Ireland, and haplotype i was then lost from the population during a genetic bottleneck caused by population contraction.

Captive specimens

The genetic composition of the captive population of pine martens in England, Scotland and Wales is shown in Appendix Table 2. Sixteen samples were collected from captive specimens, for all but one of which we were able to determine the mitochondrial haplotype. The majority (86.7 %) of specimens were of known native British haplotypes (all haplotype a); the remainder were haplotypes previously identified in continental Europe.

Discussion

The genetic structure of historical and contemporary pine marten populations across the British Isles were compared

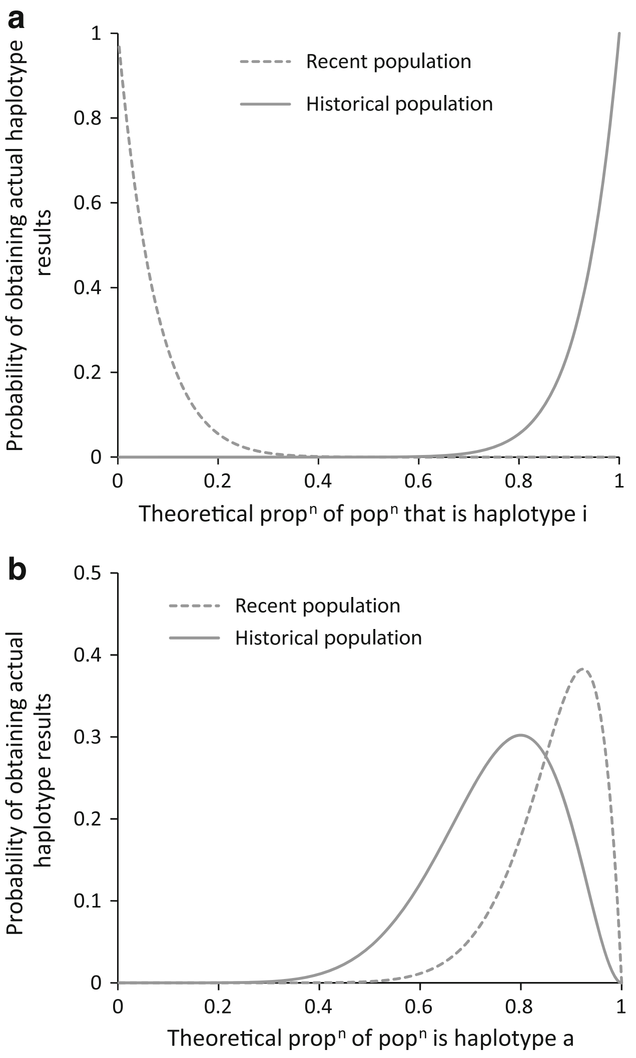


Fig. 3 The probability of obtaining our empirical haplotype results given different hypothetical population structures for **a** England and Wales combined and **b** Scotland

in order to inform future conservation management policies for the species in these regions. While the mtDNA results presented in this paper indicate that contemporary Scottish and Irish pine marten populations are directly descended from historical populations from the same regions, contemporary populations in England and Wales appear to consist primarily, if not exclusively, of individuals or their descendents originating from elsewhere that have now apparently replaced, or at least hybridised with, the original relict haplotype i.

It is suspected that pine martens were introduced into Ireland up to 1000 years ago, for their fur (Yalden 1999) or as pets (Searle 2008), and the earliest archaeological evidence of pine martens in Ireland dates from the Bronze Age (Woodman et al. 1997). Historical populations in Ireland apparently consisted entirely of haplotype i individuals; that the same haplotype composition has been found in historical populations of England and Wales but not Scotland suggests that the original Irish stock was possibly derived from southern Britain. The original haplotype i population appears to have been replaced by a population now consisting entirely of individuals of a closely-related haplotype (p). This ‘switch’ appears to have occurred around 1915, from when the last evidence of haplotype i pertains. As this broadly coincides with a reported decline in the mid-1900s (Fairley 2001; O’Sullivan 1983), this may suggest a population bottleneck potentially involving differential survival of haplotype p individuals. However, as mtDNA is not under strong selection it is likely that any bottleneck might have resulted in a merely stochastic decline of haplotype i individuals through genetic drift in this small population.

In Scotland, it was previously thought that both contemporary and historical populations consisted entirely of haplotype a individuals (Davison et al. 2001), but the data presented in this paper show this not to be the case. Our data provide the first evidence that historical and contemporary Scottish populations contain both haplotype a and haplotype i individuals, but as yet the extent and/or prevalence of haplotype i is not known for contemporary populations due to a limited geographical coverage of specimens obtained. Given the potential conservation value of haplotype i individuals—particularly as a potential source population for any future reintroduction to England and/or Wales—it is recommended that subsequent pine marten surveys of Scotland include a genetic haplotyping component.

Although previous genetic work (Kyle et al. 2003) and an uninterrupted chain of sightings and other evidence from some areas (Birks and Messenger 2010) suggested that some indigenous pine martens might still exist in England and Wales, data presented here suggest that this may no longer be the case. In contrast to the situation in Scotland, the contemporary pine marten populations of southern Britain have not recovered from historical declines (e.g. Strachan et al. 1996) and appear to be genetically distinct from historical populations from the same regions. While all (13) DNA samples retrieved from historical populations (1864–1950) were derived from individuals of haplotype i, none of the 14 samples collected since 1990 were of this type. Instead, the majority of recent samples collected from across England and Wales were from haplotype a individuals, which is the predominant haplotype found in the present-day population of Scotland. Interestingly, Kyle et al. (2003) obtained samples from English pine marten population(s) between 1990 and 1995 and concluded that native haplotypes persisted in England and Wales, as samples were of the same haplotype as were found in Scotland. However, the data presented here suggest that this was not in fact the case, and that the population had already undergone significant change from what might be considered the 'original' relict type.

There are two main hypotheses that could explain how this shift in population-scale haplotype composition might have occurred in southern Britain. First, it is possible that haplotype a individuals were always present alongside haplotype i in England and Wales, but that they were not detected in the historical sample. Although such an effect could theoretically have occurred if haplotype a individuals were difficult to detect in the historical sample, the data presented here suggest that this is unlikely, and the observation that haplotype a was 'easily' detected both in the historical samples elsewhere and in the contemporary population of England and Wales serves to illustrate this. However, it should be noted that following the main nineteenth century decline there were thought to be five distinct surviving populations (Strachan et al. 1996), all of which would appear to have shifted from predominantly haplotype i to predominantly haplotype a. Although such an effect might feasibly have occurred in a single population passing through a bottleneck, such results are extremely unlikely to have occurred independently in all of these separate populations, unless haplotype i populations were more susceptible to extinction. There is no reason to suspect that individuals of different haplotypes may be more susceptible to extinction, nor is this possibility supported by the evidence presented here, as haplotype i was most prevalent in the historical samples of England and Wales, and both haplotype i and haplotype a individuals survived a contraction in Scotland simultaneously to that further south.

In considering this first potential explanation however it is also important to discuss the limitations of mtDNA analysis. As mitochondria are maternally inherited, mtDNA data can only present a partial picture of the population genetics of a species, and even then the picture may potentially only reflect more ancient processes. It is important to realise that haplotype data tells us little about the potential that there has been much hybridisation (historical or otherwise) between type a animals and indigenous type i animals. Evidence of such a process would not show up in maternally inherited haplotypes, but contemporary populations of non-relict types could still contain significant nuclear genetic material from relict types. Therefore any site-specific adaptations may potentially have been maintained within contemporary populations. As such, we can only tentatively suggest that relict populations may have been extirpated and replaced by immigrants from elsewhere. It is also possible that data presented here could reflect rapid genetic drift for mtDNA following a population bottleneck that might not have affected functional nDNA variations quite so drastically. Indeed, female philopatry contributes to the discrete geographical patterns of haplotype distribution seen in *Martes*, and other mustelids (e.g. wolverine, Walker et al. 2001) but long-distance male-biased dispersal in the pine marten (Macdonald and Barrett 1993) could potentially contribute to gene flow between disjunct populations. Although combining the data presented here with most recent population estimates (Harris et al. 1995) suggest that haplotype i may now be functionally extinct in England and Wales, it is important to realise that these populations may nonetheless still contain important DNA from relict populations.

Alternatively, it is possible that an historical population consisting entirely of haplotype i individuals has been replaced over the past 150 years, mainly by haplotype a animals from elsewhere with little to no hybridisation with relict types. Nuclear DNA analyses are required to confirm or refute this hypothesis, but if this has occurred, these individuals could have arrived either as a result of escapes and/or deliberately released animals, or by natural migration south from Scotland. In northern areas of England it is perhaps possible that martens may have naturally repopulated from a southern Scottish source population primarily made up of individuals that were reintroduced into Galloway forest in the 1980s (Shaw and Livingstone 1992). Such recolonisation is not inconceivable for a species known to cover large distances (Macdonald and Barrett 1993). Indeed the 2001 haplotype a scat found in south Cumbria was approximately 160 km by the most direct route overland to the closest known population of martens. In addition, the 2010 (haplotype a) scat found on top of a pine marten den box in Northumberland was only approximately 70 km direct from the site of a known release of pine martens by the Scottish Society for the Prevention of Cruelty to Animals (SSPCA) in south east Scotland (C. Seddon, personal communication). In contrast to these cases, records from North Wales and central and southern England are very unlikely to be the result of natural dispersal from Scotland. In addition to the vast distances involved, the urban conurbations of northern England are also likely to represent a significant barrier to dispersal and recolonisation from the North, as they have proved to be for European polecats (*Mustela putorius*) attempting to move in the opposite direction (Birks 2008).

Given the haplotype differences described here between contemporary and historical populations, it is also important to consider whether pine martens currently found in England and Wales might be there as the result of recent anthropogenic processes. Mustelids have in the past been deliberately translocated by humans for food and clothing (Griffiths 1991, 1993; Mithen 1994), but the motives for doing so may have shifted recently, as European planning laws now take into account the presence of priority conservation species as a consideration in development. For example, pine marten scats are suspected to have been 'planted' prior to an ecological survey in a Cumbrian wood that was being sold for development (Anon, personal communication), and the translocation of a dead pine marten to a Worcestershire woodland is at least suspected as the carcass was discovered in full winter coat in the height of summer (Forrest et al. 2002). In addition, unmonitored and undocumented translocations of pine martens are known to have taken place before martens were legally protected (e.g. in North Yorkshire, G. Woodroffe, personal communication, reported in Strachan et al. 1996), and have probably been conducted elsewhere in England too (Bright and Harris 1994; Yalden 1999). Given the extent of admixture in some of the populations of England and Wales, it seems probable that there have been multiple sources for introduction or restocking.

Overall, the evidence presented here shows that historical and contemporary populations of pine martens differ in the abundance of specific mtDNA control region haplotypes. These data appear to suggest that particular haplotypes may have been lost from England and Wales at some point in the early to mid 1900s, but further nDNA work is required to determine whether this shift has occurred by rapid genetic drift in the mtDNA control region or whether relict populations have been replaced by pine martens from elsewhere. In northern England it is possible that some recent records are the result of individuals dispersing from populations of animals translocated into southern Scotland from further north, but we also have direct evidence of escapes or deliberate translocations elsewhere in England and Wales. These results have important implications for the future approach to the conservation and population recovery of pine martens in England and Wales. In particular, when it was suggested previously that pine martens should be reintroduced to parts of England (Bright and Harris 1994; Bright et al. 2000), this proposal received stiff opposition on the grounds that potentially unique populations may be vulnerable to genetic dilution (Birks and Messenger 2000). As Jefferies and Mitchell-Jones (1993) pointed out, local genetic races are of particular scientific interest and conservation value and should be perpetuated if possible; but evidence presented here suggests that this is no longer a consideration, as the local genetic race of pine martens in England and Wales may have already been lost. Reintroduction is therefore now a possible route to restoring pine marten populations to England and Wales, should such a restoration be deemed necessary and desirable (Jordan 2011). According to IUCN guidelines, it is desirable that source animals come from wild populations, and that founder stock should be supplied from a population that is closely related genetically to the original native stock or sub-population (IUCN 1995). Analysis of zoo specimens held in England, Wales and Scotland showed an abundance of non-native types, making current captive populations unsuitable as potential sources of animals for any future reintroduction or release to England and Wales. In addition, many studies have shown that captive stock may not be a good source of animals for reintroduction (e.g. Araki et al. 2007, Montgomery et al. 2010; but see Herr et al. 2008) and so it is suggested that any future reintroduction of pine martens here considers the use of wild stock. Should a healthy population containing haplotype i individuals be discovered in Scotland then this may be the most appropriate source population, assuming it could sustain such harvesting and that conditions in the target release area are suitable for a new population to thrive (Jordan 2011). Alternatively, the contemporary population of haplotype p individuals in Ireland, directly descended as they possibly are from the original English and/or Welsh stock may also prove to be a suitable source population. However, in interpreting these results, particularly where conservation management decisions are concerned, it is important to realise the limitations of mtDNA studies such as this. Further work on nuclear DNA is required to determine the degree to which the genetic composition of historical populations may have changed as a result of genetic drift or more recent hybridisation.

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Appendix

See Tables 1 and 2

Table 1 Haplotypes, provenance and current locations for all pine marten material used in this study collected from (a) England, (b) Wales, (c) Scotland, (d) Ireland, and (e) unknown provenance

Haplotype	Reference	Specimen type	Specimen origin (vice county)	Grid ref.	Current location	Cat. No	Collection date	Sample type	Known sex
a									
I	n/a	Unknown	Kelling Heath (VC27 East Norfolk)	TG1141	Norwich Museum	1924.145.39.3	1864	Skin	
I	n/a	Unknown	Carnforth (VC60 West Lancashire)	SD4970	Natural History Museum London	1990.488	25/11/1924	Dried flesh	M
I	n/a	Mount (with skull)	Rusland (VC69 Westmorland)	SD3487	Haybridge Nature Reserve, Cumbria	n/a	13/05/1902	Hair	F
I	n/a	Skin, skull	Borrowdale (VC70 Cumberland)	NY2010	Tullie House Museum, Carlisle	37–1933	1901–1902 winter	Hair, maxillo-turbinary	
I	n/a	Dried skin, skull	(VC70 Cumberland)		Natural History Museum Dublin	1911.211.1	09/09/1910	Maxillo-turbinary	M
I	n/a	Unknown	(VC70 Cumberland)	NY30	Cliffe Castle Museum	CC9650 and CC1702	14/03/1920	Skin	M
W	Davison et al. (2001)	Unknown	(VC67 South Northumberland)		Unknown	Unknown	1990s		
X	Birks and Messenger (2010)	Skin	(VC67 South Northumberland)	NY68	Private collection	Unknown	1990	Hair	
A	Birks and Messenger (2010)	Skull	(VC62 North-east Yorkshire)	NZ50	National Museums of Scotland	Unknown	1993	Unknown	
A	Birks and Messenger (2010)	Skin, skull	(VC67 South Northumberland)	NZ09	Private collection	Unknown	1994	Unknown	
A	Kyle et al. (2003)	Mount (roadkill)	(VC59 South Lancashire)	SD51	Private collection	Unknown	1994	Hair	
A	Birks and Messenger (2010)	Skin, skull	(VC70 Cumberland)	NY58	Private collection	Unknown	1995	Unknown	
X	Kyle et al. (2003)	Carcass	(VC70 Cumberland)	NY46	Private collection	Unknown	1995	Unknown	
A	Birks and Messenger (2010)	Scat	(VC69 Westmorland)	SD48	Unknown	Unknown	2000	Scat	
A	Birks and Messenger (2010)	Carcass	Chaddesley Wood (VC37 Worcestershire)	SO97	The Vincent Wildlife Trust	Unknown	2002	Hair	
G	Birks and Messenger (2010)	Carcass (roadkill)	Dibden (VC11 South Hampshire)	SU40	Waterford Institute of Technology	Unknown	2003	Hair	
A	n/a	Scat	Kidland (VC68 North Northumberland)	NY10	Waterford Institute of Technology	Unknown	2010	Scat	F

Table 1 continued

Haplotype	Reference	Specimen type	Specimen origin (vice county)	Grid ref.	Current location	Cat. No	Collection date	Sample type	Known sex
A	n/a	Scat	Grizedale Forest (VC69)	SD39	Waterford Institute of Technology	Unknown	2011	Scat	
b									
I	n/a	Skull	Capel Curig (VC49 Caernarvonshire)	SH7258	National Museum of Wales, Cardiff	25.331	1925	Maxillo-turbinates	F
I	n/a	Skull	Llanbedr (VC48 Merionethshire)	SH5826	National Museum of Wales, Cardiff	27.121	1927	Maxillo-turbinates	F
I	n/a	Mount	(VC42 Breconshire)	SO0142	Leicester City Museum	Z82.1927.	03/1927	Hair	F
I	n/a	Skull	North Wales (unknown)		National Museum of Wales, Cardiff	30.206	1930	Maxillo-turbinates	M
I	n/a	Skull	North Wales (unknown)		National Museum of Wales, Cardiff	31.249	1931	Maxillo-turbinates	M
I	n/a	Unknown	Llyn Crafnant nr Trefriw (VC49 Caernarvonshire)	SH7461	National Museum of Wales, Cardiff	48.147	1/5/48	Hair	
I	n/a	Skin	unknown (VC42 Breconshire)		National Museum of Wales, Brecknockshire	50.445	21/11/1950	Skin/hair	
A	Birks and Messenger (2010)	Scat	Cardigan (VC46 Cardiganshire)	SN77	Waterford Institute of Technology		2007	Scat	
A	Davison et al. (2001)	Scat	Caernarvon (VC49 Caernarvonshire)	SH75	Unknown		1996	Scat	
c									
A	Richie (1920)	Mount	Kintail (VC97 West Inverness-shire)	NG91	National Museums of Scotland	n/a	1886	Hair	
A	n/a	Mount	Drumbeg, Lairg (VC108 West Sutherland)	NC13	National Museums of Scotland	1925.33	1925	Hair	M
I	n/a	Mount	House of Knock (VC74 Wigtownshire)	NX05?	National Museums of Scotland	1932.2	02/10/1929	Hair	M
I	n/a	Unknown	Rosebrae Quarry, Oakwood nr Elgin (VC95 Moray)	NJ1863	Elgin Museum	MX53	1929	Bone and hair	M
A	n/a	Skin, skull	(VC97 West Inverness-shire)	NN17	National Museum of Wales, Cardiff	52.102	1952	Hair	F
A	n/a	Mount	Arenakaig estate, Achnashellach (VC106 West Ross and Cromarty)		National Museums of Scotland	1956.58	06/08/1956	Hair	

Table 1 continued

Haplotype	Reference	Specimen type	Specimen origin (vice county)	Grid ref.	Current location	Cat. No	Collection date	Sample type	Known sex
A	n/a	Mount (with skull)	(VC97 West Inverness-shire)	NN17	Kendal Museum	1981.3	c.1975	Hair	
A	Davison et al. (2001)	Unknown	Chairlift Clinmore (unknown)		National Museums of Scotland	95/8/105	07/06/1995	Liver	
A	Davison et al. (2001)	Unknown	Aviemore police station (VC96 East Inverness-shire)	NH81	National Museums of Scotland	95/8/103		Liver	
A	Davison et al. (2001)	Suspected roadkill	A9 Daviot Hill (VC96 East Inverness-shire)	NH73	National Museums of Scotland	95/8/104		Liver	
A	Davison et al. (2001)	Unknown	Benderloch, Oban (VC98 Argyllshire)	NM9036	Unknown			Tongue	F
A	Davison et al. (2001)	Unknown	Barcaldine, Oban (VC98 Argyllshire)	NM9641	Unknown			Tongue	M
A	Davison et al. (2001)	Unknown	Oban (VC98 Argyllshire)	NM9038	Unknown			Tongue	F
A	Davison et al. (2001)	Unknown	Benderloch, Oban (VC98 Argyllshire)	NM9139	Unknown			Ear, skin, hair	
A	Davison et al. (2001)	Roadkill	A9 nr Layby, Ardullie roundabout (VC106 East Ross and Cromarty)	NH5862	Disposed of.	DB02	12/04/1993	Roadkill	M
A	Davison et al. (2001)	Roadkill	A830 Fort William/ Mallaig road (VC97 West Inverness-shire)	NN0876	Disposed of.	DB05	30/05/1993	Roadkill	F
A	Davison et al. (2001)	Roadkill	Munlochy, Black Isle (VC106 East Ross and Cromarty)	NH6453	Disposed of.	DB01	08/01/1993	Roadkill	F
A	Davison et al. (2001)	Roadkill	North side of Dornoch Firth (VC107 East Sutherland)	NH7690	National Museums of Scotland	DB03	05/05/1993	Roadkill	M
A	n/a	Mount	Black Isle (VC106 East Ross and Cromarty)	NH65	Tullie House Museum, Carlisle		1993	Hair	
A	Davison et al. (2001)	Suspected roadkill	A9, opp. Crubenmore junct. (VC96 East Inverness-shire)	NN6791	Unknown		08/07/1994	Unknown	
A	Davison et al. (2001)	Suspected roadkill	A9, Daviot Brae (VC96 East Inverness-shire)	NH73	Unknown		16/07/1994	Unknown	

Table 1 continued

Haplotype	Reference	Specimen type	Specimen origin (vice county)	Grid ref.	Current location	Cat. No	Collection date	Sample type	Known sex
A	n/a	Roadkill	A382 Black Isle (VC106 East Ross and Cromarty)	NH7867	The Vincent Wildlife Trust	n/a	16/12/1999		
A	Davison et al. (2001)	Unknown	Barcaldine, Oban (VC98 Argyllshire)	NM9641	Unknown			Tongue	M
A	Davison et al. (2001)	Unknown	Oban (VC98 Argyllshire)	NM9038	Unknown			Tongue	F
A	Davison et al. (2001)	Unknown	Benderloch, Oban (VC98 Argyllshire)	NM9139	Unknown			Ear, skin, hair	
A	n/a	Scat	unknown origin (unknown)		Released by SSPCA nr. Peebles	n/a	2009	Scat	
A	n/a	Scat	unknown origin (unknown)		Released by SSPCA nr. Peebles	n/a	2009	Scat	
I	n/a	Scat	Isle of Eriska, nr. Oban (VC98 Argyllshire)	NM9043	Released by SSPCA nr. Peebles	n/a	2010	2 scats	
A	n/a	Scat	Nevis Range (VC97 West Inverness-shire)	NN1777	Waterford Institute of Technology	n/a	2010	6 scats	
A	n/a	Roadkill	A82 Inverness to Drumnadrochit (VC96 East Inverness-shire)	NH5836	The Vincent Wildlife Trust	n/a	Unknown	Bone	
A	n/a	Mount	unknown origin (unknown)		National Museums of Scotland	1940.7.25	Unknown	Hair	
A	n/a	Mount	unknown origin (unknown)		National Museums of Scotland	1940.7.x	Unknown	Hair	
A	n/a	Mount	unknown origin (unknown)		National Museums of Scotland	1940.7.23	Unknown	Hair	
d									
I	n/a	Skin, skull	Kilkenny (VCH11 Co. Kilkenny)		Natural History Museum Dublin	1911.296.1	Unknown	Hair, bone	M
I	n/a	Skin	Loughrea (VCH15 South-east Galway)		Natural History Museum Dublin	1912.359.1	25/5/1912	Hair, skin	F
I	n/a	Unknown	Loughrea (VCH15 South-east Galway)		Natural History Museum Dublin	1912.361.1	27/8/1912	Hair	M
I	n/a	Skin, skull	Loughrea (VCH15 South-east Galway)		Natural History Museum Dublin	1912.362.1	30/8/1912	Hair, skin, bone	F
I	n/a	Skin, skull	Loughrea (VCH15 South-east Galway)		Natural History Museum Dublin	1912.360.1	6/8/1912	Hair, skin, bone	M

Table 1 continued

Haplotype	Reference	Specimen type	Specimen origin (vice county)	Grid ref.	Current location	Cat. No	Collection date	Sample type	Known sex
I	n/a	Skin, skull	Gort (VCH15 South-east Galway)		Natural History Museum Dublin	1912.358.1	6/6/1912	Hair, skin, bone	F
P	n/a	Skin, skull	(VCH20 Co. Wicklow)		Natural History Museum Dublin	1912.287.1	2/6/1912	Hair, skin, bone	F
I	n/a	Skin, skull	Cappagh (VCH6 Co. Waterford)		Natural History Museum Dublin	1914.216.1		Hair, skin, bone	F
I	n/a	Skin, skull	Thomastown (VCH11 Co. Kilkenny)		Natural History Museum Dublin	1919.4.1	7/7/1915	Hair, skin, bone	F
P	n/a	Dried skin and skull	Near Partry (VCH27 West Mayo)		Natural History Museum Dublin	1977.106.1	20/7/1977	Hair	M
P	n/a	Dried skin and skull	unknown origin (unknown)		Natural History Museum Dublin	2006.6.4		Maxillo-turbinary	
P	n/a	Mount	Ballyvaughan, nr Corkscrew Hill (VCH9 Co. Clare)		Natural History Museum Dublin	2010.13.1	c.1963		
P	n/a	Whole, frozen animal	Tullamore (unknown)		Natural History Museum Dublin	2010.14.1	01/07/05	Hair	
P	Lynch, 2005	Roadkill	(VCH16 West Galway)	L6456	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH16 West Galway)	L6945	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH16 West Galway)	L7945	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH27 West Mayo)	M0872	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH4 Mid Cork)	R1603	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH9 Co. Clare)	R3269	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH9 Co. Clare)	R3675	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH15 South-east Galway)	M4124	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH9 Co. Clare)	R5178	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH9 Co. Clare)	R5478	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH9 Co. Clare)	R5566	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH28 Co. Sligo)	G6723	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH17 North-east Galway)	M7545	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH15 South-east Galway)	M8029	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH18 Offaly)	N0708	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH23 Westmeath)	N2748	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH18 Offaly)	N2922	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH14 Laois)	S4187	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH14 Laois)	S4297	Unknown	n/a	c.2005	Unknown	

Table 1 continued

Haplotype	Reference	Specimen type	Specimen origin (vice county)	Grid ref.	Current location	Cat. No	Collection date	Sample type	Known sex
P	Lynch, 2005	Roadkill	(VCH14 Laois)	S4999	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH19 Co. Kildare)	N6501	Unknown	n/a	c.2005	Unknown	
P	Lynch, 2005	Roadkill	(VCH31 Co. Louth)	O0983	Unknown	n/a	c.2005	Unknown	
P	Davison et al. (2001)	Unknown	(VCH14 Laois)		Unknown	Mama9	Unknown	Unknown	
P	Davison et al. (2001)	Unknown	(VCH9 Co. Clare)		Unknown	Mama38	Unknown	Skin + hair	
P	Davison et al. (2001)	Unknown	Tourmakeady, Lough Mask (VCH27 West Mayo)	M1069	Unknown	Mama39	Unknown	Tongue	M
P	Davison et al. (2001)	Unknown	Tourmakeady, Lough Mask (VCH27 West Mayo)	M1069	Unknown	Mama40	Unknown	Tongue	F
P	Davison et al. (2001)	Unknown	Ballygriffy, Ennis (VCH9 Co. Clare)	R3182	Unknown	Mama41	Unknown	Ear skin + hair	
P	Davison et al. (2001)	Unknown	Killeagh (VCH5 East Cork)	×07	Unknown	Mama63	Unknown	Skin	
P	Davison et al. (2001)	Unknown	Lismore (VCH6 Co. Waterford)	S00	Unknown	Mama64	Unknown	Muscle	M
P	Davison et al. (2001)	Unknown	unknown origin (unknown)		National Museums of Scotland	Mama146 and R202/98	Unknown	Muscle	
P	Davison et al. (2001)	Unknown	unknown origin (unknown)		National Museums of Scotland	Mama147 and R203/98	Unknown	Muscle	
P	Statham (2005)	Roadkill	Kilclooney, Mahon Bridge (VCH6 Co. Waterford)	S3410	Waterford Institute of Technology	MM01	01/06/1997	Tissue	M
P	Statham (2005)	Roadkill	The Curragh (VCH19 Co. Kildare)	N7812	Waterford Institute of Technology	MM02		Tissue	M
P	Statham (2005)	Roadkill	unknown origin (unknown)		Waterford Institute of Technology	MM03		Tissue	M
P	Statham (2005)	Roadkill	Unknown (VCH14 Laois)		Waterford Institute of Technology	MM04		Tissue	F
P	Statham (2005)	Roadkill	Westmeath (VCH23 Westmeath)		Waterford Institute of Technology			Tissue	
P	Statham (2005)	Roadkill	Kilmeaden/Portlaw Rd (VCH6 Co. Waterford)	S4913	Waterford Institute of Technology	MM06	14/12/2003	Tissue	M

Table 1 continued

Haplotype	Reference	Specimen type	Specimen origin (vice county)	Grid ref.	Current location	Cat. No	Collection date	Sample type	Known sex
P	Statham (2005)	Roadkill	Ballyfin (VCH14 Laois)	N3800	Waterford Institute of Technology	MM07		Tissue	F
P	Statham (2005)	Roadkill	Athy (VCH19 Co. Kildare)	S6495	Waterford Institute of Technology	MM08		Tissue	F
P	Statham (2005)	Roadkill	Athy (VCH19 Co. Kildare)	S6295	Waterford Institute of Technology	MM09		Tissue	M
P	Statham (2005)	Roadkill	unknown origin (unknown)		Waterford Institute of Technology			Tissue	
P	Statham (2005)	Roadkill	Cahir (VCH7 South Tipperary)	S0324	Waterford Institute of Technology	MM11		Tissue	M
P	Statham (2005)	Roadkill	Durrow (VCH14 Laois)	S3976	Waterford Institute of Technology	MM12		Tissue	M
P	Statham (2005)	Roadkill	Crom (VCH33 Fermanagh)	H3724	Waterford Institute of Technology	MM13	02/04/2004	Tissue	F
P	Statham (2005)	Roadkill	Tramore Rd (VCH6 Co. Waterford)	S6007	Waterford Institute of Technology	MM15	16/06/2004	Tissue	M
P	Statham (2005)	Roadkill	Enniskillen/Belfast Rd (VCH33 Fermanagh)	H4245	Waterford Institute of Technology	MM16	24/06/2004	Hair	M
P	Statham (2005)	Roadkill	Dunmore Rd (VCH6 Co. Waterford)	S6409	Waterford Institute of Technology	MM18	19/06/2005	Tissue	M
P	Statham (2005)	Hair trap, scat survey	Portlaw (VCH6 Co. Waterford)	S4614	Waterford Institute of Technology		2004	4 hair, 4 scat	
e									
I	n/a	Skin, skull	unspecified, suspected Cumbria (unknown)		Tullie House Museum, Carlisle	95–1969.1	c.19C	Hair, maxillo-turbinary	
I	n/a	Unknown	unspecified, suspected England (unknown)		National Museums and Galleries on Merseyside	D.126		Unknown	
A	n/a	Mount (with skull)	unspecified, suspected Cumberland (unknown)		Manchester Museum	A.1445–1	<1950	Hair, maxillo-turbinary	

Table 2 Haplotypes and current locations for all known captive pine martens in England, Scotland and Wales

Collection and location	Haplotype	Animal ID	Sex	Sample type
British Wildlife Centre	A	Buttons	F	Scat
–VC17 (Surrey)	A	Bonnie	F	Scat
	A	Clyde	M	Scat
	G	Hamish	M	Scat
New Forest Otter, Owl and Wildlife Park	A	Rory	M	Scat
–VC11 (South Hampshire)	A	Mrs P	F	Scat
	A	Psipsina	F	Scat
Chestnut Centre Conservation Park	B	Pob	M	Scat
–VC57 (Derbyshire)				
Private (Martin Noble)	A	Mortimer	M	Scat
–VC11 (South Hampshire)	A	Merlin	M	Scat
	A	Pixie	F	Scat
Wildwood Trust, Herne Bay	A	Yorkie or Pandora		Scat
–VC15 (East Kent)	A	Wispa		Scat
Highland Wildlife Park, Kingussie	A	Heather	F	Scat
–VC96 (East Inverness-shire)	A	Maurice	M	Scat
Private (Huw Denman)	ND	Poppy	F	Scat
–VC44 (Carmarthenshire)				

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