Population genetics of the hazel dormouse, *Muscardinus avellanarius*, in South-West England

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Executive Summary

- The hazel dormouse is a European protected species that is vulnerable to habitat loss and fragmentation.
- Molecular ecology analyses can be used to describe and compare the population genetics of a species across the landscape and inform conservation management.
- Here, genetic samples were collected from hazel dormice across South West England and analysed, using genetic microsatellite markers.
- The central-periphery hypothesis states that populations found at the species' edge-of-range will have reduced abundances and increased isolation, compared to populations within the range core, due to sub-optimal resources and/or ecological conditions.
- Populations which are smaller and/or more isolated are likely to have a lower genetic diversity, due to the random evolutionary process genetic drift. Additionally, there is likely to be higher genetic differentiation amongst such populations, due to relatively restricted dispersal between them.
- Therefore, it was predicted that populations further west, in Cornwall, would exhibit lower genetic diversity and higher genetic differentiation amongst them, compared to those further East in Devon. This is due to the former being located towards the tip of a peninsula, and at the edge of range for this species, whilst Devon is considered within the core range of dormice.
- The results demonstrated highly structured genetic populations across the study site, which concurs with expectations for a species with poor dispersal ability and habitat specialism, and elucidates their vulnerability to habitat fragmentation.
- The population genetic patterns across the study area concurred with the prediction. However, further study is needed to ascertain the exact mechanisms responsible for the observed patterns.
- Higher genetic differentiation, such as seen in Cornwall, indicates populations that are genetically distinct and therefore may be important for evolutionary adaptation. As such, maintaining these populations and their genetic composition should be considered an important objective. Any loss of Cornish populations should be monitored and mitigated, as it may indicate a range contraction. Additionally, Devon populations, with a higher genetic diversity should be continued to be monitored and protected.

Abstract
Here, I report the findings of a project that comprises one of the first studies pertaining to hazel dormouse molecular ecology. The project significantly contributed to my PhD in Biological Sciences, which was completed in October 2012 at the University of Exeter, Cornwall Campus.

I investigated the population genetics of hazel dormice at the regional scale, across the core and periphery of their range within the south-west UK. Microsatellites, highly variable genetic markers, were utilised in order to genotype DNA sampled from hair-root cells from wild dormice. A wide range of analyses were employed in order to describe and quantify genetic differentiation, diversity, and inbreeding amongst hazel dormouse populations, as well as describe population structuring and isolation by distance patterns across the study area. The findings provide important insights into the patterns of dormouse population genetics at a regional scale, which have the potential to guide conservation actions for this species.

The central-periphery hypothesis states that populations found at the edge-of-range of a species will have reduced abundances and increased isolation, compared to populations within the range core, due to sub-optimal resources and/or ecological conditions (Diniz-Filho *et al*. 2009). Therefore, I predicted that the peripheral populations, furthest west in my study area (i.e. Cornwall), would demonstrate lower genetic diversity and higher genetic differentiation compared to core populations further east (i.e. Devon). This can be explained due to smaller, more isolated populations being subjected to increased genetic drift and reduced gene flow between populations.

The results clearly reveal significant genetic differentiation across all levels of population structure and variation in genetic diversity between regions. I find a powerful signal of reduction in genetic diversity, and an increase in differentiation between core and peripheral populations. I consider rival hypotheses for the mechanisms driving this population genetic pattern, and place the results in the context of conservation strategies for UK dormice. The implications of our findings are two-fold: first, if limited national funds for dormouse conservation must be allocated to populations of highest genetic diversity, priority should be given to maintaining core populations, such as those in Devon; second, if the preservation of genetic diversity across the species is considered of importance, the more isolated and differentiated populations, such as those in Cornwall, should be conserved.

Additionally, the project involved a large number of volunteers in order to collect sufficient genetic samples across the study area. A range of events were also conducted, in order to engage the wider public and promote the conservation of the dormouse in the South-West, UK and beyond, through involving the local community.

Introduction

The hazel dormouse is listed on Appendix III of the Bern Convention and Annex IV of the EU Habitats and Species Directive. In 1996 it was listed as lowest risk/near threatened on the IUCN Red List, however this has now been changed to of least concern (Amori *et al*. 2008). This reflects the species' relatively common distribution across its range. However, conservation concern remains for hazel dormice in the north-westerly parts of its range, such as in the UK, Netherlands, Sweden, Germany and Denmark, where populations are declining. Therefore the hazel dormouse is included in several national Red Lists (Amori *et al*. 2008, Juškaitis 2008). Within Britain, it is reported to have become extinct in approximately 50% of its range in the last 100 years, and a national decline of 19% from 1991 to 2000, and therefore is a Biodiversity Action Plan species (Bright *et al*. 2006).

Due to the dormouse's arboreal nature, poor dispersal ability, habitat specialism and low population densities and reproductive potential, it is vulnerable to habitat loss, degradation and fragmentation (Bright & Morris 1996). Such threats may occur due to human development and land-use change from urbanisation, roads, agriculture and forestry (i.e. conversion of ancient woodland to conifer plantations) (Amori *et al*. 2008, Bright *et al*. 1994, Juškaitis 2008). The change in management practices of woodlands, leading to less sympathetic regimes, has also likely affected dormouse populations (Bright & Morris 1989). Examples include clear-felling, the decrease of coppicing practices and general neglect that leads to heavy shading and loss of the understory (Bright & Morris 1989, Bright & Morris 1993).

In order to facilitate conservation management of this species, it is therefore of importance to gain a full understanding of the effects of habitat and landscape variables on dormouse ecology. This study aims to contribute towards addressing this need by investigating the population genetic structure among dormice in a fragmented landscape.

Increased habitat fragmentation and degradation will lead to smaller, more isolated populations. Subsequently, such populations will suffer from a reduction in genetic diversity, through an evolutionary process called genetic drift (Frankham 1996). A lower genetic diversity may lessen the ability of a population to adapt to new pressures such as environmental change, of particular importance to dormice due to their hibernation behaviour and specialist habitat requirements. Combined with the increased likelihood of small populations becoming extinct due to stochastic events and inbreeding, this is of great conservation concern. Additionally, there will be increased genetic differentiation amongst isolated populations. Genetic differentiation is of interest to conservationists, as it may indicate populations that are genetically distinct and thus potentially evolutionary significant, with important genetic adaptations.

I aimed to investigate the genetic diversity and differentiation amongst hazel dormouse populations at the regional scale in the south-west UK, which comprises a strong-hold area of dormice, in Devon, and edge-of-range populations in Cornwall. The central-periphery hypothesis predicts that

peripheral populations will have reduced abundances and increased isolation, compared to populations within the range core, due to sub-optimal resources and/or ecological conditions and increased isolation (Diniz-Filho *et al*. 2009). Therefore, I hypothesised that populations at the edge-of-range will demonstrate lower genetic diversity and higher genetic differentiation compared to those found in the core range.

It was anticipated that the results will inform habitat management and other conservation practices for this species, by assisting in refining conservation priorities, such as being able to identify particular subpopulations that have critically low genetic diversity. The identification of distinct genetic populations will also suggest how to protect these to maintain genetic integrity.

GLOSSARY

Admixture: The interbreeding between two populations.
Alleles: a particular version of a gene or microsatellite. For the latter, this is dictated by the number of repeats that a microsatellite has. An individual has two alleles for each gene or microsatellite, one inherited from its mother and one from its father.
Allelic richness: The number of different alleles within a population.
Frequency of private alleles: The number of unique alleles found in the focal population only, and not in any other population sampled.
Gene flow: Transfer of alleles between populations, due to dispersal that is then followed by successful reproduction by the immigrant. Barriers to gene flow will result in genetic differentiation amongst populations.
Genetic differentiation (F_{ST}): a measure of genetic differentiation amongst populations. Where there are barriers to gene flow within a population, individuals either side of the barrier will become increasingly genetically distinct. The more impermeable to gene flow, the more pronounced genetic differentiation.
Genetic diversity: variation in the genetic composition. There are a variety of measures used to describe genetic diversity within a population, including allelic richness and frequency of private alleles.
Genetic drift: An evolutionary process describing the random change in the frequency of alleles within a population. In small populations genetic drift results in the loss of many alleles, leading to a reduction in genetic diversity.
Genetic structure: Pattern in the genetic composition amongst individuals. If there is panmixic random mating within a population there will be little or no structure. However, if there are restrictions to gene flow, structure will be detectable.
Genotype: The determined allele types for a gene or microsatellite for an individual.
Inbreeding (F_{IS}): Reproduction with close relatives, leading to a reduction in genetic diversity. May also result in reduction in fitness due to inbreeding depression.
Isolation by distance: Pattern of a clinal correlation between genetic distance and geographical distance between populations.
Microsatellites: Sections of DNA at a specific location (loci) along an individual's genome, that have repeat sequences of 2, 3 or 4 bases. The number of repeats is highly variable between individuals and it is this variability that can be used in genetic analyses to look at patterns of population structure and relatedness.

Methods

Sample collection

I established collaborations with a range of wildlife groups, NGOs and government organisations from across the study area. This allowed the identification of established National Dormouse Monitoring Program nest box schemes from which to acquire genetic samples. Additionally, nest boxes funded by this project contributed to several new dormouse monitoring schemes being set-up. Genetic samples were collected by myself and other licenced dormouse monitors. During standard monthly monitoring sessions, a small clump of hairs were plucked from the animal's hip area using tweezers, under licence issued by Natural England. Additional genetic samples were acquired from dead individuals stored at Paignton Zoo. Hair samples were stored at -20°C and tissue samples in ethanol and/or at -80°C.

I planned to collect approximately 200 genetic samples, however, due to additional funding being acquired for the project, along with a much more successful collection program than anticipated, I was able to collect over 600 samples. Once poor quality and repeat samples, and those from close relatives (which would bias population genetics analyses) were removed from the dataset, 237 individual samples remained for genetic analyses. These samples were distributed across 13 main populations, with a minimum of five individual samples and an additional 14 locations with four or less individuals. This distinction was necessary, as only populations with at least five samples were utilised in certain genetic analyses. Figure 1, indicates the location of sampled sites, as well as 20 sites surveyed for dormice by myself in 2008, using dormouse nest tubes, but where no dormice were detected in west Cornwall.

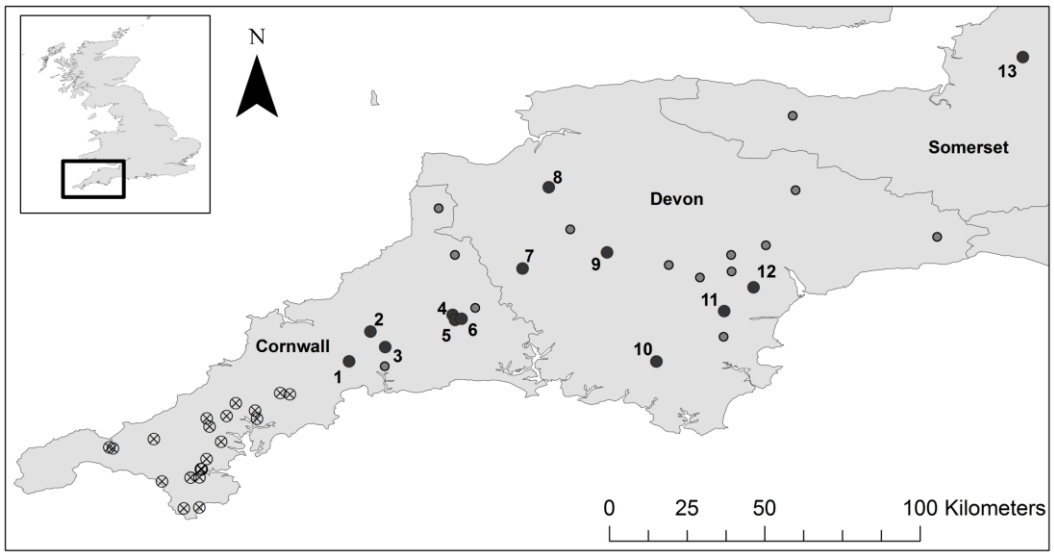

Figure 1. Study area of south west England peninsula: 13 populations (large, numbered black dots) in which we were able to sample n>5 dormouse individuals: 1-HelmanTor, 2-Penlan, 3-West Bodmin, 4-Middlewood, 5-Darley, 6-Stara, 7-Roadford, 8-North Devon, 9-Okehampton, 10-East Ivybridge, 11-Newton Abbott, 12- Haldon, 13- Cheddar; and 14 populations with n≤5 (small grey dots). Additionally, 20 sites surveyed for dormouse presence in 2008 throughout mid and west Cornwall, (but no dormice were detected) are indicated (crossed circles). The three counties, Cornwall, Devon and Somerset are also labelled. Inset map shows extent of entire survey area.

Laboratory work

I was successful in an application to attend the NERC-funded Biomolecular Analysis Facility at the University of Sheffield. This collaboration provided me with additional funds and training in molecular genetics lab work and analyses, including designing and developing genetic microsatellite markers for use in this study. Early on in the project, it became apparent that several of the published dormouse microsatellite markers, developed by Naim et al. 2009, included errors. Therefore, my developing new markers became paramount in ensuring I had sufficient markers for the successful implementation of this project. Ultimately a suite of 22 microsatellites were used for population genetic analysis.

DNA was extracted from the cells located at the root of the hair samples, the microsatellites of interest amplified using the polymerase chain reaction and then genotyped using an ABI 3730 48-well capillary DNA Analyser.

Analysis

Error checks were performed on the genotype data, such as comparing re-runs of the same samples to ensure results were consistent. The program ML-RELATE (Kalinowski *et al.* 2006) was utilised to identify samples from close-relatives, and the data from one of each relative these were subsequently removed, to avoid bias in the population genetics analyses.

Population genetic structuring was analysed using the program STRUCTURE v2.3.3 (Falush *et al*. 2003, Pritchard *et al*. 2000). STRUCTURE uses Bayesian clustering to assign individuals to populations based solely on genotype data only, with no *a priori* information on sample location. Since the true total number of populations (*K*), in the study area is unknown separate models are run for a range of hypothesised *K* values. Each *K* model is given an estimated log probability of data value, which indicates which value of *K* is most likely. For each *K* model every individual dormouse is given a membership coefficient (*Q*) for each population, which is a probabilistic value of the individual's ancestry for that population. Where individuals are admixed they may be assigned to two or more populations. The bar plots produced in STRUCTURE are also vital in the interpretation of the data, where *Q* for each individual for all populations is displayed, with each vertical bar corresponding to an individual and each population represented by a different colour.

I then tested the effect of region, and a continuous core-to-periphery longitudinal distribution, on: two parameters of genetic diversity (frequency of private alleles and allelic richness); genetic differentiation; isolation by distance and inbreeding. These analyses were conducted using a suite of population genetic programmes, including MICROSATELLITE ANALYSER v4.05 (Dieringer & Schlötterer 2003), GENEPOP v4.0.10 (Raymond & Rousset 1995, Rousset 2008), ADZE v1.0 (Szpiech *et al.* 2008), SPAGeDi v1.3 (Hardy & Vekemans 2002). Additional statistical analyses were conducted in R v2.14.1 (R Foundation for Statistical Computing 2011).

Results and Discussion

The results revealed moderate to very high genetic differentiation amongst the sampled populations within the study area. At the highest hierarchical level, the STRUCTURE results indicated that there were three populations (*K*), which corresponded to a) Devon and Somerset, b) East Cornwall and c) Mid Cornwall. Within each of these regions sub-structuring was identified by running further STRUCTURE analyses for each region separately. The number of *K* within each of these regions is best described as 7, 3 and 3 respectively, and these results also corresponded well with geographical location. The estimated membership coefficient (Q) for each individual, for the highest hierarchical level, as well as sub-structuring within these, is displayed as bar plots in figure 2. Bar plots for additional *K* models are shown for the sub-structured populations, to allow for comparisons between different possible models, as the interpretation of the number of *K* is not definitive in STRUCTURE analyses. This strong genetic structuring concurs with expectations, as the populations of species, such as the hazel dormouse, with low population densities and dispersal abilities are unlikely to have significant admixture and therefore will be relatively genetically distinct.

Considering regional patterns, there is strong, significant, evidence for reduced genetic diversity, increased differentiation and stronger isolation by distance at the western edge of the study area. The significantly lower allelic richness in the Mid Cornwall and East Cornwall regions compared to Devon/Somerset, but with no clinal effect of longitude (figure 3a), is likely due to limited dispersal between Cornwall and Devon/Somerset. Natural and man-made landscape barriers to dispersal reduce gene flow, leading to small, isolated, more differentiated populations that experience elevated genetic drift and lower genetic diversity (Goossens *et al*. 2005). In our study, the large river Tamar runs along the border between Cornwall and Devon and may create a dispersal barrier to dormice, especially in the south where it is at its widest. In the north this watercourse is narrower and likely to be more permeable to dormouse dispersal, where the tree canopy connects above the waterway, however, generally there is less woodland cover, with habitat being dominated by moorland (Bodmin Moor) in this part of the region.

Both region and longitude showed significant correlations with the frequency of private alleles (figure 3b). Therefore, in addition to the barrier effects of the river Tamar and Bodmin Moor, there is strong evidence for a decline in this measure of genetic diversity from the core to the periphery of the dormouse range sampled along the southwest England peninsula. This concurs with our expectations, based on the central-periphery hypothesis, as those populations which had the highest genetic differentiation and lowest genetic diversity were in Mid Cornwall, which is on the edge of the range for this species (as supported by the surveys which failed to detect hazel dormice in West Cornwall, figure 1). There was relatively lower population differentiation amongst Devon/Somerset

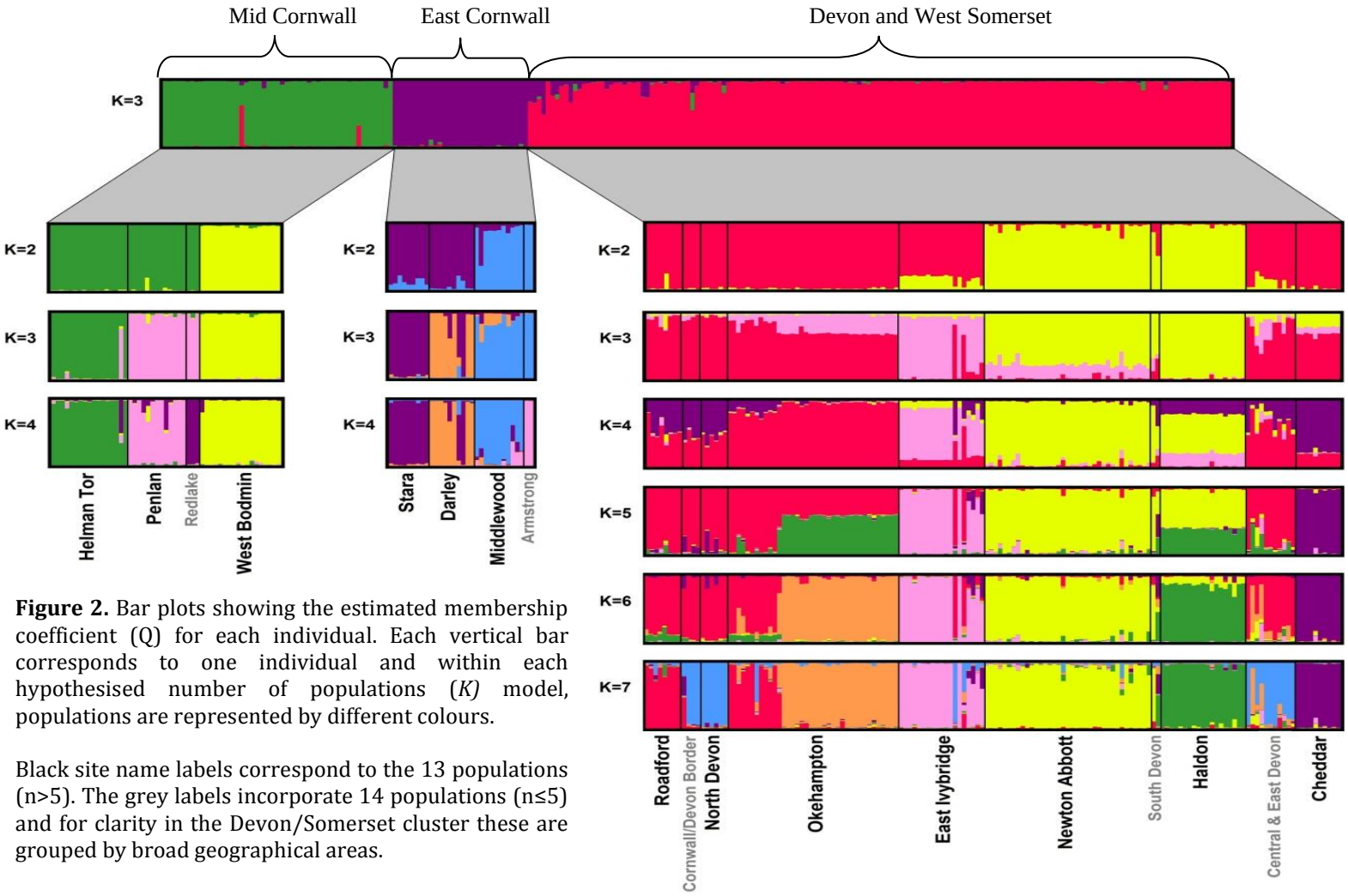

Figure 2. Bar plots showing the estimated membership coefficient (Q) for each individual. Each vertical bar corresponds to one individual and within each hypothesised number of populations (*K)* model, populations are represented by different colours.

Black site name labels correspond to the 13 populations (n>5). The grey labels incorporate 14 populations (n≤5) and for clarity in the Devon/Somerset cluster these are grouped by broad geographical areas.

populations compared to those within Mid Cornwall and there was a stronger isolation by distance pattern amongst the populations found within Cornwall, compared to populations from the centre of Devon (Figure 4). Peripheral populations are likely to be more isolated and patchily distributed, with reduced population sizes and more variable densities (Lawton 1993, Vucetich & Waite 2003). Such restricted gene flow between habitat patches, compared to within the core range where there may be a more continuous distribution, will lead to increased genetic differentiation (Keyghobadi *et al*. 2005, Slatkin 1987). Additionally, isolated, small populations are subject to elevated genetic drift, further contributing to genetic differentiation amongst peripheral populations, as well as reducing genetic diversity in comparison to larger populations (Frankham *et al*. 2002).

It is of concern that populations in Cornwall are less genetically diverse and as such, these populations may be at a higher risk of extinction. However, there was no significant effect of either region or longitude on the inbreeding coefficient, which suggests dormouse behaviour is facilitating the avoidance of inbreeding even in the least genetically diverse populations (figure 3c).

However, it should be noted that the edge-of-range patterns do not imply causation. Alternative mechanisms may be driving the variation in genetic diversity between populations. Contemporary explanations are confounded by historical variables, such as past barriers to gene flow, habitat configurations and climatic changes that have driven range expansions and contractions. As populations advanced westward they may have left a signature of decreasing genetic diversity. (Hampe & Petit 2005, Slatkin 1987).

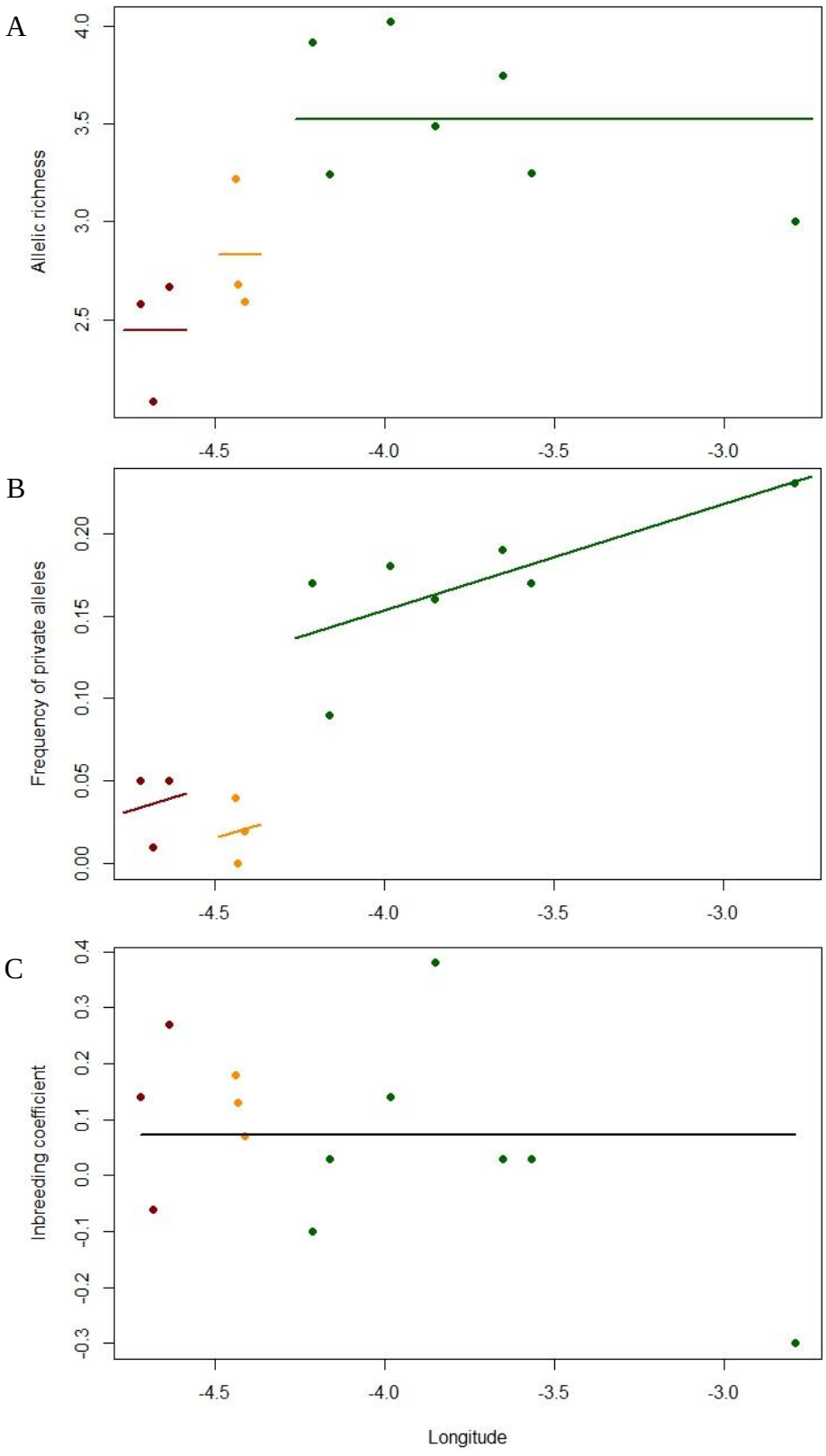

Figure 3. Plots showing the model outcomes of the effect of region and longitude on: a) allelic richness; b) frequency of private alleles; and c) inbreeding coefficient. Longitude is plotted against the population genetic parameter, and regions are denoted by different colour points: red-Mid Cornwall, orange-East Cornwall and green-Devon/Somerset.

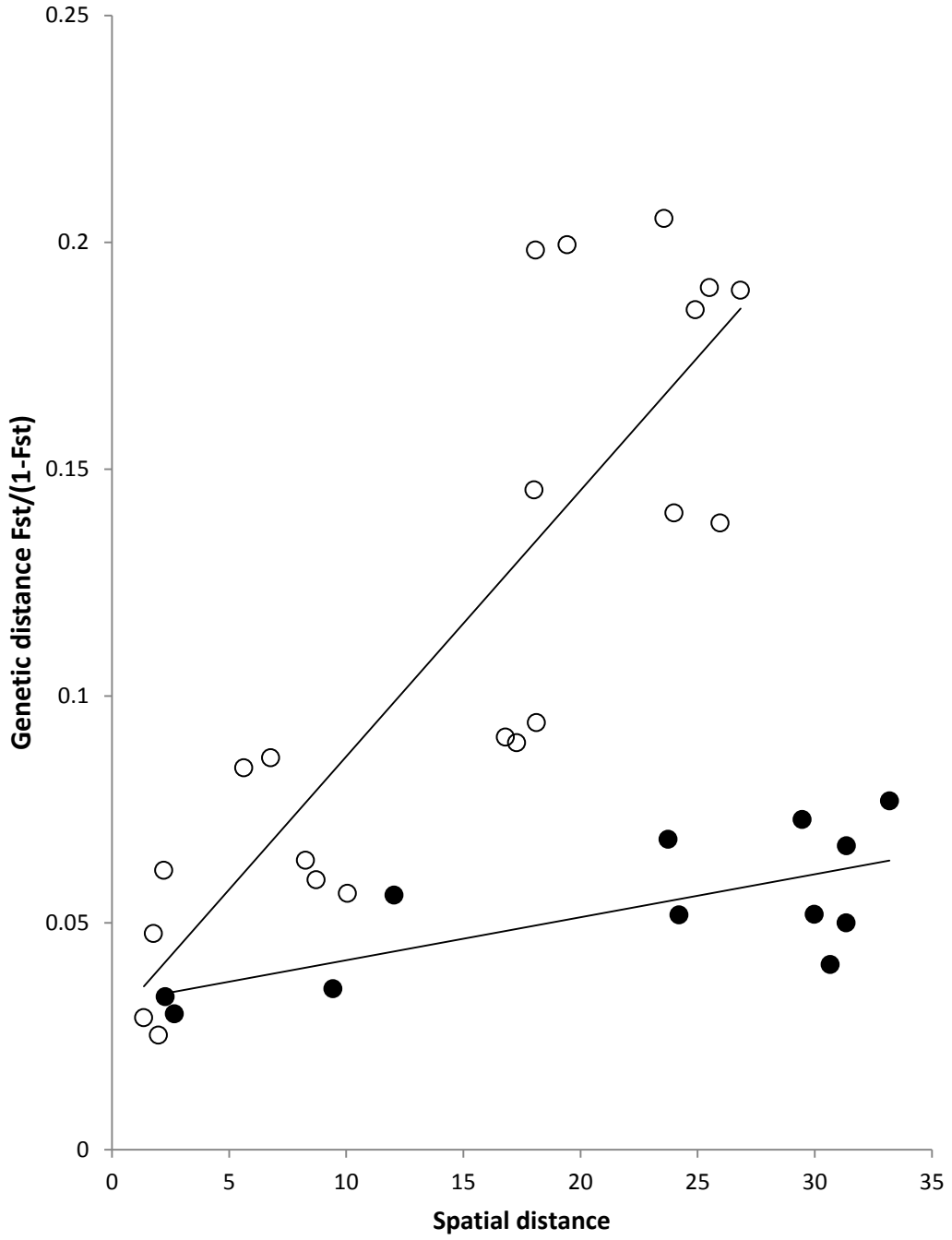

Figure 4. Comparison of the patterns of isolation by distance, showing a plot of spatial distance against genetic distance, in Cornwall (open circles) and Devon (solid circles), proxies for peripheral and core areas respectively.

Conclusion

The strong genetic differentiation and structuring I describe amongst populations at the landscape scale concurs with the premise that dormice are particularly vulnerable to habitat loss and fragmentation. Since dormice are habitat specialists, with low dispersal rates, reproductive potential and population densities (Bright 1993, Bright & Morris 1996), we expect this species to form small, isolated and genetically differentiated populations within their preferred habitat matrix. Such populations are vulnerable to increased genetic drift and inbreeding, leading to lower levels of genetic diversity, population fitness and adaptive potential, as well increased vulnerability to stochastic events. Such effects threaten population persistence, and therefore understanding their mechanistic basis is of utmost importance for conservation management.

The implications of the described regional genetic patterns for dormouse conservation require careful consideration. Peripheral populations that are genetically distinct may have local adaptations that are advantageous to the evolution of future populations (Lesica & Allendorf 1995). In the light that Cornish hazel dormouse populations are likely to be genetically distinct, it would be unadvisable to recommend landscape-scale management plans that connect Cornish and Devon populations, or to translocate animals from other locations into unoccupied Cornish woodlands. Such actions may prove to diminish the genetic distinctiveness of Cornish populations and lead to a loss of important adaptations that allow them to survive on the edge of this species range. Clearly this supposition warrants further investigation, however, in the meantime we recommend that conservation managers concentrate on the habitat management of Cornish woodlands that ensure the persistence of existing dormice populations across Cornwall. Further, we encourage active landscape-scale conservation amongst Cornish populations, through the connectivity of habitat patches, such as by improving hedgerows (Mortelliti et al. 2011). This should encourage recolonisation of woodland patches were dormice appear to have become extinct. Hostility of intervening habitat matrix is a predictor of species patch occupancy and therefore conservation management of this matrix is likely to increase dispersal between patches (Prugh et al. 2008). For example, especially in the light of continuing urbanisation, encouraging “wildlife-friendly” garden management may facilitate patch occupancy within the dormouse range. Continuing evidence that hazel dormice are not restricted to ancient woodland should also guide conservation efforts to include other habitats, such as coniferous forest and scrub (e.g. Chanin & Woods 2003, Eden & Eden, 1999), which even if sub-optimal, may improve the facilitation of dormouse distribution throughout the landscape. Continued monitoring of the populations in Cornwall is vital to detect any future contractions in population range here, especially in the light of continued anthropogenic threats.

Additionally, range contractions should be of concern for the entire UK population, as models predict a positive correlation between regional occupancy and local abundance (Lawton 1993, Zuckerberg *et al.* 2009) and the loss of peripheral populations may have a knock-on negative effect on core population abundance. Therefore there is a strong argument for the conservation of Cornish

dormouse populations. However, it is argued that as core populations are more stable and contain higher levels of genetic diversity it is more efficient to focus limited conservation resources, in such core areas (Petit *et al.* 1998). This standpoint advocates the argument for prioritising conservation of Devon populations. Therefore we also encourage the continuing protection of Devon dormouse populations, in order to maintain genetic diversity within the UK dormouse population as a whole.

Suggestions for further work

In order to tease apart the combination of historical and contemporary ecological mechanisms acting on the population genetics, wider sampling and further analyses are required, such as approximate Bayesian computation and coalescent modelling (Cornuet *et al.* 2008). In addition, the integration of phylogeographic information may allow us to distinguish between contemporary and historical influences and quantitative genetics may provide insights into adaptive processes (Eckert *et al.* 2008). To more vigorously test the periphery-core hypothesis, analyses such as ours are required across the entire range of dormice. Additional, more vigorous, landscape analyses may highlight the relative importance of natural and anthropogenic features which hinder dispersal. Such studies would require an increased continuous sampling scheme across the landscape (Manel *et al.* 2003).

Outputs

In addition to the findings outlined in this report, there is a variety of outputs which have been achieved due to this PTES funded project. These include:

- Chapters that comprise part of my PhD in Biological Sciences at the University of Exeter, Cornwall Campus. The completed thesis was approved by the University and an electronic copy submitted to the University's archive.
- Nest boxes that were established at several sites in the south-west UK have become successful NDMP schemes, with new records of dormice.
- The nest box installation facilitated the involvement of the general public in several events, run in partnership with organisations such as the Cornwall Mammal Group, Cornwall and Devon Dormouse Groups and the Exeter University's Ecological Society (Figure 5).
- The increased number of NDMP sites also complemented the Natural England training of new volunteers for licenced dormouse monitoring.
- A large number of previously licenced dormouse monitors assisted with the collection of genetic samples and therefore were able to become involved with a scientific project.
- The microsatellite genetic markers I developed have been added to the public access EMBL Nucleotide Sequence Database, and therefore are freely available for future researchers to use for hazel dormice and possibly other species in the same taxon.
- I presented a summary of the findings at the Population Genetics Conference Annual Meeting in Nottingham and at the Student Mammal Society Conference in Reading 2012, where at the latter I won first prize

for best talk. I also gave talks at the Molecular Ecology Group meeting at Sheffield University and Biology Department at the Cornwall Campus, Exeter University.

- During my PhD I gave several presentations to the general public on the work I was conducting on dormice for my PhD, in association with the Cornwall Mammal Group, Cornwall Wildllife Trust, Cornwall and Devon Dormouse Groups, and Friends of Kilminorth Woods.
- I am currently editing my PhD chapters, with the view of submitting them to peer-reviewed scientific journals. I will of course keep PTES informed of the all progress associated with this and acknowledge the Trust fully.

Figure 5. Volunteers helping to install dormouse nest boxes at Cabilla Cornwall Wildlife Trust Reserve.

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