Biodiversity and Conservation
https://doi.org/10.1007/s10531-025-03134-6

ORIGINAL RESEARCH

Conservation of an isolated and genetically unique population: red squirrels on the Isle of Wight

Alyson E.V. Buchanan[1] · **Demetra Andreou**[1] · **Kathy H. Hodder**[1] · **Melissa A. Toups**[1,3] · **Phillipa K. Gillingham**[1] · **Marin Cvitanović**[1] · **Helen Butler**[2] · **Emilie A. Hardouin**[1]

Received: 8 January 2025 / Revised: 13 May 2025 / Accepted: 1 August 2025

Abstract

Island populations face a higher extinction risk than mainland ones due to their smaller population sizes, limited genetic diversity, and increased vulnerability to environmental changes and stochastic events. The Isle of Wight red squirrel population is culturally and economically significant, being the largest remaining population in Southern England and genetically distinct from European populations. We used a multidisciplinary approach to assess the population's long-term viability, evaluating habitat and food resources, analysing microsatellite genetic data, and using life history data to model population viability. Results indicated that natural food resources, supplemented by additional feeding, could sustain and support population growth. Microsatellite data identified two genetic clusters in the east and west of the island. Although F_{ST} values were non-significant, indicating gene flow between subpopulations, elevated F_{IS} values suggest localised mating dynamics driven by limited dispersal and spatial structure rather than systemic inbreeding. Population viability analyses suggested that habitat fragmentation and localised inbreeding do not pose immediate threats. However, maintaining connectivity between subpopulations remains crucial to preserving genetic diversity and reducing future risks of genetic isolation or increased inbreeding. Under pessimistic scenarios with reduced survival rates and fewer litters, model predictions indicated population decline and increased extinction risks. Future research should incorporate fine-scale spatial genetic analyses using genome data to explore population structure, local adaptation, and differentiate local mating dynamics from population-wide inbreeding. While direct data on inbreeding, litter sizes, and survival rates are challenging to obtain, these insights are critical for understanding population dynamics and guiding conservation efforts.

Keywords Eurasian red squirrels · Rodentia · Microsatellites · Extinction risks · Small populations · Population structure

---

Communicated by Khor Waiho.

Extended author information available on the last page of the article

Introduction

Island populations face a heightened risk of extinction compared to those on the mainland (Frankham 1997; James et al. 2016). This vulnerability arises from a variety of threats (Frankham 2005; Losos and Ricklefs 2009; James et al. 2016). Many island populations exhibit lower levels of genetic variation compared to mainland populations, often due to founder effects and bottleneck events following colonisation, which makes them particularly susceptible to genetic drift (Nei et al. 1975; Frankham 1997; Habel and Zachos 2013). Additionally, habitat fragmentation, long-term isolation, and limited geographical area may further contribute to reduced genetic diversity, driving population fluctuations and repeated bottlenecks (Stuessy et al. 2014). These factors can significantly impact the overall health of populations, influencing their resilience to environmental changes and their ability to adapt (Frankham et al. 2010).

Reduced genetic variation has been found to compromise fitness, disease resistance, and adaptability to environmental changes in various species (Lacy 1997; Bernatchez 2016; Pröhl and Rodríguez 2023). For instance, in nine populations of deer mice, parasite load (nematode *Capillaria hepatica*) showed a negative relationship with genetic diversity (Meagher 1999). Tome's spiny rats (*Prochimys semispinosus*) were found to experience reduced genome-wide and major histocompatibility complex (MHC) diversity due to habitat fragmentation caused by anthropogenic disturbance, weakening the host's ability to adapt to parasites (Fleischer et al. 2024).

In the United Kingdom, red squirrel (*Sciurus vulgaris*) populations show lower diversity in immune response genes, including MHC, compared to their mainland European counterparts (Ballingall et al. 2016). This reduction in MHC diversity is part of a broader pattern of reduced genome-wide genetic variation, which has been shown to increase extinction risk and impair evolutionary potential (Ballingall et al. 2016; Ørsted et al. 2019). Low MHC diversity suggests an increased vulnerability to disease, limiting the red squirrels' capacity to respond to new pathogens or environmental changes (Ballingall et al. 2016).

Invasive grey squirrels (*Sciurus carolinensis*), introduced in 1876, have significantly contributed to the decline of native red squirrel populations through competition for food and habitat, pushing red squirrels into less favourable coniferous habitats in northern Britain (Kenward et al. 1998; Wauters et al. 2023). Grey squirrels also spread squirrelpox virus, which has further exacerbated red squirrel population declines and may have contributed to reduced genetic variation (Carroll et al. 2009; Ballingall et al. 2016). In response to these threats, red squirrels have been protected under the UK Wildlife & Countryside Act since 1981, with measures implemented to safeguard their habitats and prevent harm from competition and disease (HM Government 1981).

Today, red squirrel populations in the British Isles are largely confined to Scotland, Ireland, and parts of northern England, where they are less impacted by grey squirrels and ongoing management programmes exist to trap and remove grey squirrels (Lurz et al. 1995; Bosch and Lurz 2012). Populations in Wales and southern England are small and isolated (Dunn et al. 2021; Hardouin et al. 2021). Many British Isle populations show genetic ties to mainland European red squirrels due to past reintroduction programs (Hale et al. 2001; Ogden et al. 2006). In southern England, red squirrels are restricted to islands, including the Isle of Wight, as well as Brownsea and Furzey Islands in Poole Harbour (Fig. 1), where they are shielded from competition with grey squirrels. These small and isolated red squir-

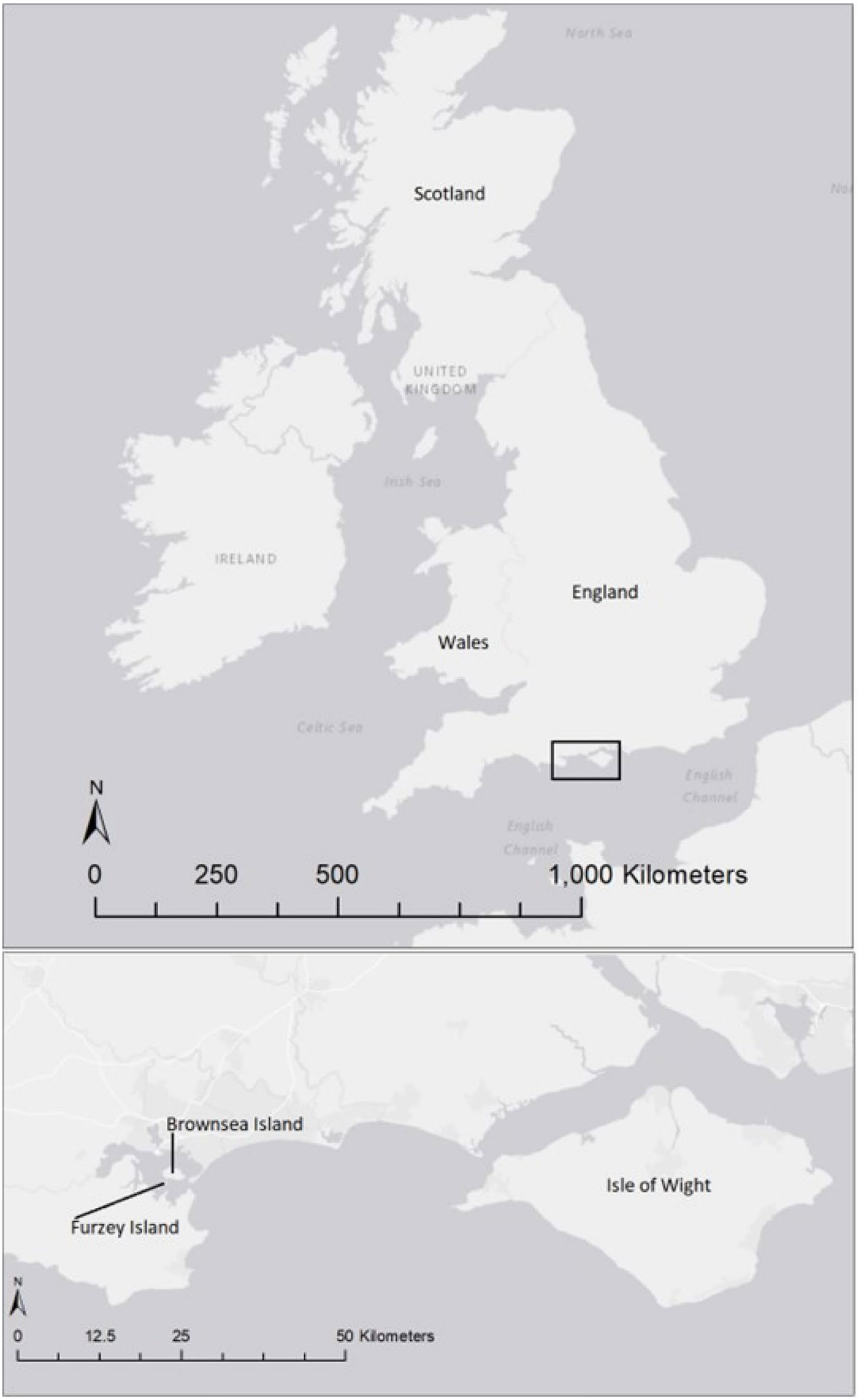

Fig. 1 Map of the Isle of Wight and Poole Harbour, including Brownsea and Furzey Islands, which host the only populations of red squirrels in southern England

rel populations harbour unique genetic lineages compared to populations across the UK and Europe, reinforcing the importance of their conservation (Hardouin et al. 2019).

Of these three islands, the Isle of Wight is home to the largest remaining red squirrel population in southern England, with an estimated 3,500 individuals (Butler 2022). The absence of grey squirrels on the Isle of Wight has allowed red squirrels to thrive in both deciduous and coniferous woodlands, with presumably higher densities in deciduous forests where more desirable food sources are available (Gurnell 1987; Bosch and Lurz 2012). As the largest population in southern England, the Isle of Wight's population is vital for safeguarding the species' genetic diversity and is a key focus for conservation efforts (Hardouin et al. 2021).

However, habitat fragmentation may be a significant threat to the long-term viability of the Isle of Wight population, as it limits gene flow and increases extinction risk (Delin and Andrén 1999; Reher et al. 2016). Previous genetic analyses suggest low genetic diversity on the Isle of Wight, with limited gene flow between the eastern and western parts of the island, likely due to fragmentation caused by rivers, roads, urban development, agricultural land, and the loss of hedgerow corridors (Hardouin et al. 2021; Butler 2022). Understanding how habitat fragmentation impacts gene flow is crucial for conservation, as it can influence reproductive success and overall population stability. Red squirrel reproduction is density-dependent and closely tied to food availability and habitat quality, highlighting the importance of these factors for population sustainability (Wauters and Lens 1995; Wauters et al. 2004).

Studies have shown that red squirrels typically breed for the first time at around one year of age, though this can vary depending on environmental conditions and resource availability (Wauters et al. 2004; Bosch and Lurz 2012). Variation in breeding age and litter size is influenced by food resources, habitat quality, and interactions with conspecifics. Increased litter numbers and earlier breeding have been associated with abundant food supplies and stable habitats, which support reproductive success (Wauters and Lens 1995; Wauters et al. 2004; Bosch and Lurz 2012). Additionally, supplementary feeding can support population stability by ensuring a consistent food supply, influencing habitat use patterns and supporting reproduction (Reher et al. 2016). However, while factors such as habitat quality and food availability have been individually studied, the combined effects of habitat fragmentation, genetic diversity, and supplementary feeding on the long-term viability of the Isle of Wight's red squirrel population have not yet been fully integrated into a single analysis.

This study aims to understand the potential threats to the Isle of Wight red squirrel population through a multidisciplinary approach. This will be achieved by (i) investigating population structure and potential inbreeding, (ii) assessing the carrying capacity of the island by quantifying the amount of suitable habitat as well as key food resources, (iii) evaluating the population's viability using a modelling approach, and (iv) examining the extent of supplementary feeding on the island through questionnaire-based interviews.

Materials and methods

Sample collections

In total, we collected 44 new *Sciurus vulgaris* hair or tissue samples to supplement previously unrepresented locations from Hardouin et al. (2021), especially in the central and western woodlands on the island. All samples were collected by the Wight Squirrel Project. Most samples were collected opportunistically, usually from roadkill (tissue samples), while others were collected using hair tube traps ($N = 8$), where opportunistic collection was not possible.

To assess potential biases in the opportunistic collection of red squirrel carcasses for genetic sampling, a negative binomial regression on the presence of squirrel carcasses relative to land cover types was performed. Carcass locations were mapped, and land cover types (e.g., urban, forest, agricultural) were classified based on a 3 km^2 grid. The sampling effort included various habitat types, ensuring coverage of key red squirrel habitats, such as forests. See supplementary materials for further methodological details (Supplementary material 1).

Microsatellite genotyping

We extracted DNA using the QIAGEN DNeasy® Tissue Kit (ear tissue) or QIAGEN QIAamp DNA Micro kit (hair samples) following the manufacturers' instructions. However, changes were made to the final elution step, where 25 µl Buffer AE was pipetted directly into the column, incubated at room temperature for one minute, and then centrifuged at 6000 x g (repeated for a second time with a total of 50 µl Buffer AE being eluted). Fifteen microsatellite markers were genotyped on 44 samples using the protocol from Hardouin et al. (2021). The 44 newly acquired samples were then combined with the existing 108 samples from Hardouin et al. (2021) for genetic analysis. Calibration between the two datasets was completed by genotyping six previously genotyped samples from Hardouin et al. (2021). Fragment analysis was outsourced to DBS-genomics. Allele calling was performed using Geneious Prime 2021.1.1 (Biomaters 2021). Genotyping is available in supplementary materials (Supplementary material 2).

Genetic analysis

Population structure was investigated using STRUCTURE (Pritchard et al. 2000) with a burn-in period of 250,000 simulations followed by a run length of 750,000 Markov chain Monte Carlo (MCMC) simulations and ten iterations for each K (number of clusters) with the admixture model. The most likely number of clusters (K) was determined using StructureSelector, which incorporates several methods for selecting K including Evanno's and Puechmaille's method (Li and Liu 2018). Run convergence was investigated using CLUMPP (Jakobsson and Rosenberg 2007; Li and Liu 2018). STRUCTURE was run on the full dataset to assess island-wide structure. Additional STRUCTURE analyses on subpopulations and a Discriminant Analysis of Principal Components (DAPC) were also performed and are presented in supplementary materials (Supplementary material 3).

Genetic diversity analyses were conducted using specialised R packages to gain insights into genetic variation and population structure. The Adegenet package was used for reading and manipulating genetic data and for implementing Monmonier's algorithm (Jombart 2008). The Hierfstat package facilitated the calculation of observed heterozygosity (H_o), expected heterozygosity (H_s), and the inbreeding coefficient (F_{IS}) (Goudet et al. 2022). The Boot package was utilised for bootstrapping confidence intervals for F_{IS} to improve the reliability of the estimates (Canty et al. 2024). Genetic diversity indexes, F_{IS}, F_{ST}, isolation by distance (IBD), and genetic boundaries were inferred using Adegenet, Hierfstat, and Boot (Jombart 2008; Goudet et al. 2022; Canty et al. 2024). Additionally, the Pegas package (Paradis 2010) was employed to test for departures from Hardy-Weinberg equilibrium.

Isle of Wight carrying capacity

Red squirrel primary habitat on the Isle of Wight was assessed in ArcGIS using Light Detection and Ranging (LiDAR) derived tree canopy polygon maps developed by Terra Sulis Research CIC (2023). LiDAR polygons were classified into habitat types (i.e., deciduous, coniferous, mixed) based on National Forest Inventory (NFI) maps (Forestry Commission 2020) and transect data collected by the Wight Squirrel Project, with Ordnance Survey Great Britain (OSGB) grid references (Emorgan_ANG 2019), used to correlate the transect data with the LiDAR polygons. Since 1999, Wight Squirrel Project transect data has been collected biannually, adhering to the data collection training and methods developed by the National Red Squirrel Monitoring Program (Red Squirrels Northern England).

LiDAR polygons were first overlaid with the NFI maps to classify the polygons according to NFI habitat types. There was a wider extent of forest polygons identified in the LiDAR-derived maps than in the NFI maps, with the LiDAR identifying forests in areas where the NFI layer suggested no forest was present. Therefore, for the LiDAR polygons that could not be classified using the NFI data, an OSGB grid map was overlaid to assign grid references to those polygons. These grid references were then matched with the transect data, allowing transect habitat type categories to be added to the polygon attribute table.

Only polygons that were greater than or equal to one hectare or combinations of polygons within 600 m of each other adding up to one hectare or greater, and not obstructed by barriers (roads and rivers), were used in the carrying capacity calculations. These conditions were established from the average woodland size requirements of one squirrel per hectare (Wauters et al. 1994; Bosch and Lurz 2012) and the maximum distance of 680 m red squirrels will travel in a day (Delin and Andrén 1999; Rodríguez and Andrén 1999). The remaining polygons were then combined to establish the total available habitat across the island. The metapopulation density was then calculated by dividing the estimated population size of 3,500 red squirrels (Butler 2022) by the available habitat.

The range in number of red squirrels the Isle of Wight woodland habitat could support was calculated by multiplying the amount of woodland habitat by known red squirrel density values (0.5–1.10 ha) (Bosch and Lurz 2012) associated with the types of habitats present on the Isle of Wight. Red squirrels need between 305 and 418 kJ of food daily (Bosch and Lurz 2012), which we used to determine their annual food requirements. We set minimum requirements at 111,325 kJ/year, average requirements at 131,948 kJ/year, and maximum requirements at 152,570 kJ/year (Table 1), calculated by multiplying the estimated daily energy requirements per squirrel (305–418 kJ/day) by 365 days. Food availability was

Table 1 Maximum number of red squirrels the Isle of Wight could support based on various scenarios of annual tree crop production

	2% Trees Producing Food		5% Trees Producing Food		10% Trees Producing Food	
	Min Food Avail. (kJ/ha)	Max Food Avail. (kJ/ha)	Min Food Avail. (kJ/ha)	Max Food Avail. (kJ/ha)	Min Food Avail. (kJ/ha)	Max Food Avail. (kJ/ha)
Min Food Req. (Squirrel/Year)	4571	6206	11428	15516	22857	31032
Avg. Food Req. (Squirrel/Year)	3857	5236	9642	13091	19284	26182
Max Food Req. (Squirrel/Year)	3336	4529	8339	11321	16678	22643

estimated based on a range of values collated from the literature by Bosch and Lurz (2012), where 13–27% of trees in European woodlands in any given year is expected to produce seed crops. To account for inter- and intraspecific competition for resources and interannual changes in tree crop productivity, the potential rates of woodland crops produced annually were decreased from 13 to 27% (Pesendorfer et al. 2020) to 2–25%. The lower percentages therefore simulated a loss of food from interspecific competition with other tree dwelling species (Bosch and Lurz 2012).

West and East carrying capacity & migration rates

East and west subpopulation sizes were calculated to allow estimation of migration rates between the two subpopulations. Subpopulation sizes were calculated in ArcMap 10.8.2 by first applying the Monmonier algorithm results (Fig. 2a) as a barrier between the west and east to divide the mapped LiDAR (Fig. 2b). The area of the divided habitats (hectares) was then multiplied by the estimated current metapopulation density (0.6 squirrels/ha), which was calculated from an estimated population size of 3,500 red squirrels (Butler 2022) distributed across 5,812 hectares of available woodland habitat. This provided an estimate of the east and west subpopulation sizes. NeEstimator V2.1 was used to calculate the effective population sizes (N_e) for the east and west subpopulations separately (Do et al. 2014). Migration rates (m) were calculated using N_e and microsatellite derived F_{ST} values in the following calculations: (i) $N_m = (1 - F_{ST})/4F_{ST}$ (ii) $m = N_m/N_e$ (Wilson and Rannala 2003; Cheng et al. 2020; Lin et al. 2023).

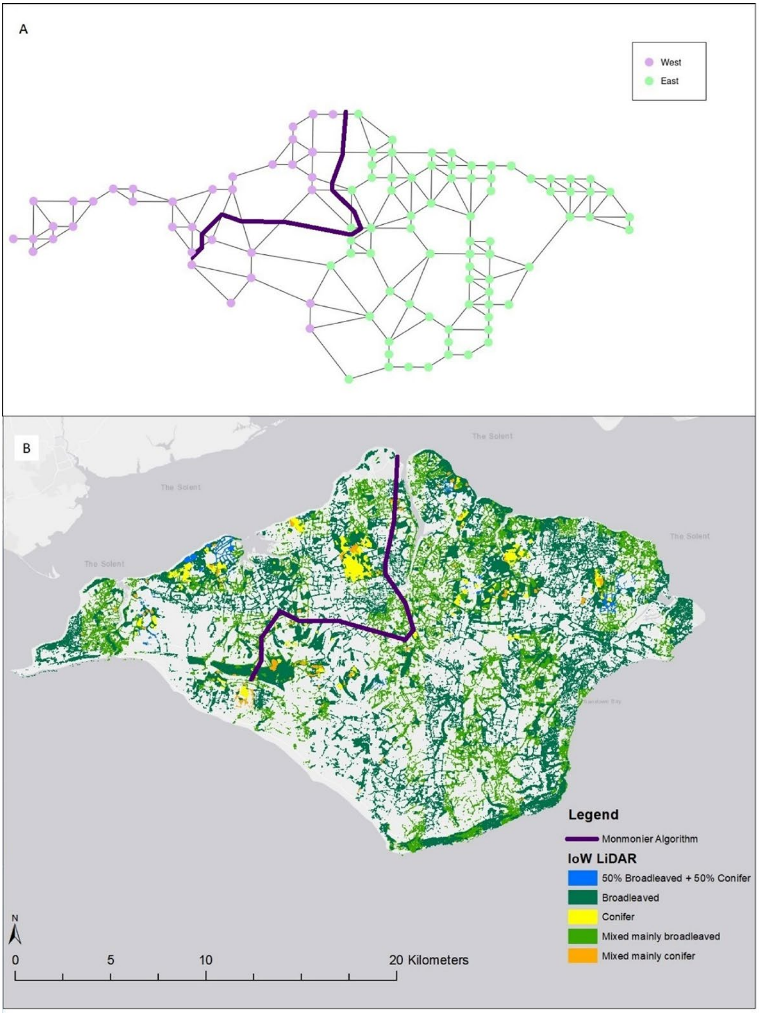

Fig. 2 **a** Spatial distribution of genetic barriers between red squirrel samples on the Isle of Wight, as inferred by the Monmonier algorithm. Each circle represents the geographic location of an individual red squirrel, with the resulting genetic barrier represented by the thick dark purple line. Squirrel samples are colour-coded according to their genetic cluster: light purple indicates individuals from the western genetic cluster, and green represents individuals from the eastern genetic cluster. These colours reflect the spatial distribution of genetic variation, with individuals from different geographic regions showing some degree of genetic separation corresponding to the east–west divide. **b** The genetic barrier (dark purple line) inferred by the Monmonier algorithm overlaid on a LiDAR-derived woodland classification map of the Isle of Wight. The LiDAR data shows canopy cover and classifies woodland types (e.g., broadleaf, conifer). The purple line illustrates where gene flow is potentially restricted and marks the boundary where habitat polygons were divided to estimate carrying capacities and subpopulation sizes for the east and west red squirrel subpopulations

Population viability

The population viability for the entire Isle of Wight metapopulation was analysed using Vortex (Lacy and Pollak 2023). Red squirrel reproduction is density dependent (Wauters and Lens 1995; Wauters et al. 2004), and many of the demographic parameters required for the population viability modelling are unknown for the Isle of Wight red squirrels. Therefore, different scenarios were modelled based on a previous analysis of red squirrels (Rézouki et al. 2014), with adjustments made from additional literature findings as follows:

All scenarios incorporated allele frequencies from 15 microsatellite loci as the genetic input. Each scenario was run using 1,000 iterations over both 20-year and 50-year time spans, representing 10 and 25 generations of red squirrels respectively (Mace and Lande 1991; Rézouki et al. 2014). For the metapopulation, the Isle of Wight was treated as a single population model. The minimum carrying capacity assumed the metapopulation had reached its maximum, while the maximum carrying capacity was calculated based on habitat-specific density ranges. A density of 1.1 squirrels per hectare was used for this calculation, as this value aligns with the highest densities observed in other studies conducted in similar woodland habitat types (Bosch and Lurz 2012), across the 5,812 hectares of woodland. Juvenile survival rates were set at 15% and 25% in pessimistic and optimistic scenarios respectively, while adult survival rates were set at 77% in pessimistic and 96% in optimistic, based on minimum and maximum values from Bosch and Lurz (2012). A mean litter size of three with a maximum of six was used in the pessimistic scenario (Rézouki et al. 2014), while the optimistic scenario used a mean litter size of four with a maximum of seven (Bosch and Lurz 2012) (Table 2).

Additionally, population viability analyses were performed as a two-population model for the west and east subpopulations, while incorporating migration, dispersal survival, carrying capacity, and subpopulation size estimates (Lacy and Pollak 2023). Dispersal survival rates were set at 50% for the pessimistic scenario and 70% for the optimistic scenario, based on literature (Larsen and Boutin 1994; Haughland and Larsen 2004).

Supplementary feeding survey

A survey was conducted to investigate the extent of supplementary feeding on the Isle of Wight, with the aim of understanding both the quantity and quality of food provided to red squirrels. First, by estimating how much additional food is being supplied to the population, we can better assess the island's ecological carrying capacity and the squirrels' potential population viability. Supplementary feeding may enhance survival and reproductive success, particularly during periods of natural food scarcity, thereby contributing to population growth (Butler 2022). Second, the survey helped identify the types of food provided and feeding frequency, which is essential for evaluating potential health risks. Some commonly offered foods, such as peanuts, have been associated with nutritional deficiencies and metabolic bone disease in red squirrels.

The digital survey was developed in Jisc, an online survey development program and approved by the Bournemouth University ethics committee. The survey began with participant information and consent requirements, then proceeded to our questions (see Supplementary materials 4 to view survey). The survey was shared with members of the public from November 30th, 2023, through July 31 st, 2024. The survey link was distributed to island residents via Wight Squirrel project email listings, handed out at island public events and festivals, or posted at public buildings such as libraries.

Results

Population genetic differentiation

Of the 44 new Isle of Wight red squirrel samples genotyped, 36 yielded at least 70% genotypic data and were included in the analysis. The hair samples were initially tested but consistently failed to meet this threshold due to poor amplification and were excluded from downstream analyses. These 36 samples were combined with the 108 from Hardouin et al. (2021), resulting in a total of 144 individuals used in the study.

The best supported population structure model was found to be K = 2, as determined using the Evanno method, indicating the presence of two genetic clusters on the Isle of Wight (Fig. 3). This result was investigated further due to the known bias of STRUCTURE toward K = 2 (Janes et al. 2017). K = 3 and K = 4 were also explored but the same main two clusters were found (Supplementary material 3). STRUCTURE analysis was also performed on the two clusters independently, but no more substructuring was found (Supplementary material 3). A DAPC was also conducted to further investigate the population structure and again two clusters were found (Supplementary material 3). The geographical distribution of the two genetic populations correspond to the west and east Isle of Wight subpopulations, with some allele mixing (Fig. 4), further supporting the presence of two red squirrel subpopulations on the island. The observed heterozygosity (H_o) for the Isle of Wight was 0.34 (SD = 0.21) and the expected heterozygosity (H_e) was 0.43 (SD = 0.22). When divided into two subpopulations, the west subpopulation had the same H_o and H_e values as the entire Isle of Wight metapopulation, $H_o = 0.34$ (SD = 0.21) and $H_e = 0.43$ (SD = 0.22). In contrast, the east subpopulation had a slightly higher H_o of 0.35 (SD = 0.21) and a lower H_e of 0.40 (SD = 0.25). The inbreeding coefficient (F_{IS}) for the entire Isle of Wight metapopulation was 0.22 (95% CI: 0.12–0.33). For the west subpopulation F_{IS} was 0.27 (95% CI: 0.10–0.46), while the east subpopulation F_{IS} value was 0.18 (95% CI: 0.07–0.33).

A Mantel test revealed a significant positive correlation (0.203, $p = 0.001$) between geographical and genetic distance matrices, indicating that individuals located closer together tend to be more genetically similar. The F_{ST} value between the west and east subpopulations was 0.055 ($p = 0.103$), indicating no significant genetic differentiation. Although the STRUCTURE analysis indicated the presence of two genetic subpopulations, the lack of significant differentiation in the F_{ST} analysis suggests that these subpopulations may still be genetically similar, with shared gene flow or limited barriers to gene exchange. Results from the Monmonier algorithm (Fig. 2a) suggest the presence of physical barriers interfering with genetic mixing. This could imply that while there is genetic substructure, the differentiation between these subpopulations is not strong enough to be detected with the F_{ST} analysis alone.

Table 2 20-year projections of optimistic and pessimistic population viability modelling scenarios, including growth rate, probability of extinction, and expected heterozygosity. Standard deviation is reported in parentheses after the mean (SD)

Age at first litter	% Juvenile survival	% Adult survival	Mean offspring	Max offspring	% Survival of dispersers	Number of Litters	% Breeding females at low density	Growth rate	Probability of extinction	Expected heterozygosity
Isle of Wight as 1 Population										
1 year	15	77	3	6	-	1	35	−0.27 (0.17)	0.01	0.43 (0.03)
							50	−0.26 (0.15)	0.01	0.44 (0.03)
						2	35	−0.06 (0.10)	0.00	0.47 (0.01)
							50	−0.04 (0.08)	0.00	0.47 (0.01)
	25	96	4	7	-	1	35	0.02 (0.13)	0.00	0.47 (0.00)
							50	0.07 (0.10)	0.00	0.47 (0.00)
						2	35	0.02 (0.10)	0.00	0.47 (0.00)
							50	0.32 (0.08)	0.00	0.47 (0.00)
2 years	15	77	3	6	-	1	35	−0.32 (0.22)	0.20	0.40 (0.05)
							50	−0.32 (0.21)	0.16	0.41 (0.04)
						2	35	−0.14 (0.12)	0.00	0.47 (0.01)
							50	−0.13 (0.11)	0.00	0.47 (0.01)
	25	96	4	7	-	1	35	−0.01 (0.17)	0.00	0.47 (0.00)
							50	0.01 (0.13)	0.00	0.47 (0.00)
						2	35	0.08 (0.13)	0.00	0.47 (0.00)
							50	0.18 (0.11)	0.00	0.47 (0.00)
West and East Isle of Wight Subpopulations										
1 year	15	77	3	6	50	1	35	−0.30 (0.18)	0.11	0.45 (0.04)
							50	−0.29 (0.17)	0.06	0.46 (0.00)
						2	35	−0.08 (0.10)	0.00	0.51 (0.01)
							50	−0.06 (0.08)	0.00	0.51 (0.01)
	25	96	4	7	70	1	35	0.01 (0.13)	0.00	0.50 (0.01)
							50	0.06 (0.09)	0.00	0.50 (0.00)
						2	35	0.17 (0.09)	0.00	0.50 (0.01)
							50	0.31 (0.07)	0.00	0.50 (0.00)

Table 2 (continued)

Age at first litter	% Juvenile survival	% Adult survival	Mean offspring	Max offspring	% Survival of dispersers	Number of Litters	% Breeding females at low density	Growth rate	Probability of extinction	Expected heterozygosity
2 years	15	77	3	6	50	1	35	−0.36 (0.23)	0.54	0.40 (0.06)
							50	−0.35 (0.22)	0.50	0.41 (0.06)
						2	35	−0.17 (0.12)	0.00	0.51 (0.01)
							50	−0.16 (0.11)	0.00	0.51 (0.01)
	25	96	4	7	70	1	35	−0.02 (0.17)	0.00	0.50 (0.01)
							50	0.00 (0.13)	0.00	0.50 (0.01)
						2	35	0.07 (0.12)	0.00	0.50 (0.00)
							50	0.16 (0.10)	0.00	0.50 (0.00)

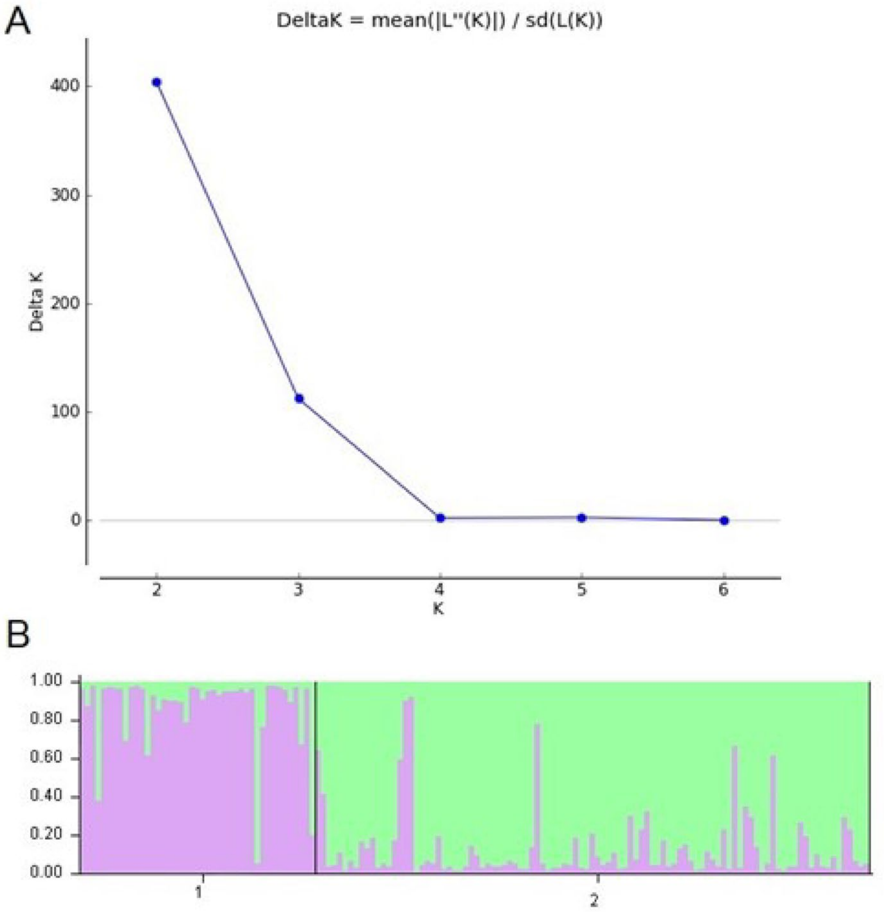

Fig. 3 Genetic structure of red squirrels on the Isle of Wight. **A** shows the Delta K plot, identifying K = 2 as the most likely number of genetic clusters using the Evanno method. **B** presents the STRUCTURE bar plot for K = 2, with each vertical bar representing an individual squirrel grouped by sampling location. Colours indicate the proportion of each individual's genome assigned to each cluster: purple for Cluster 1 (western Isle of Wight) and green for Cluster 2 (eastern Isle of Wight)

Isle of Wight carrying capacity

The total area of primary woodland habitat on the Isle of Wight is estimated to be 5,812 hectares (ha) (Fig. 2b). The carrying capacity of this woodland habitat, defined as the maximum sustainable population based on habitat availability, is projected to be between 2,906 and 6,394 squirrels (Table 3). These estimates are based on habitat modelling and do not incorporate seed crop availability. The current metapopulation density of red squirrels, calculated by dividing the estimated population size (3,500 squirrels) by the available woodland habitat (5,812 hectares), is approximately 0.6 squirrels per hectare.

To further assess the sustainability of this population, we estimated carrying capacity based on annual seed crop availability, using energetic requirements of red squirrels and

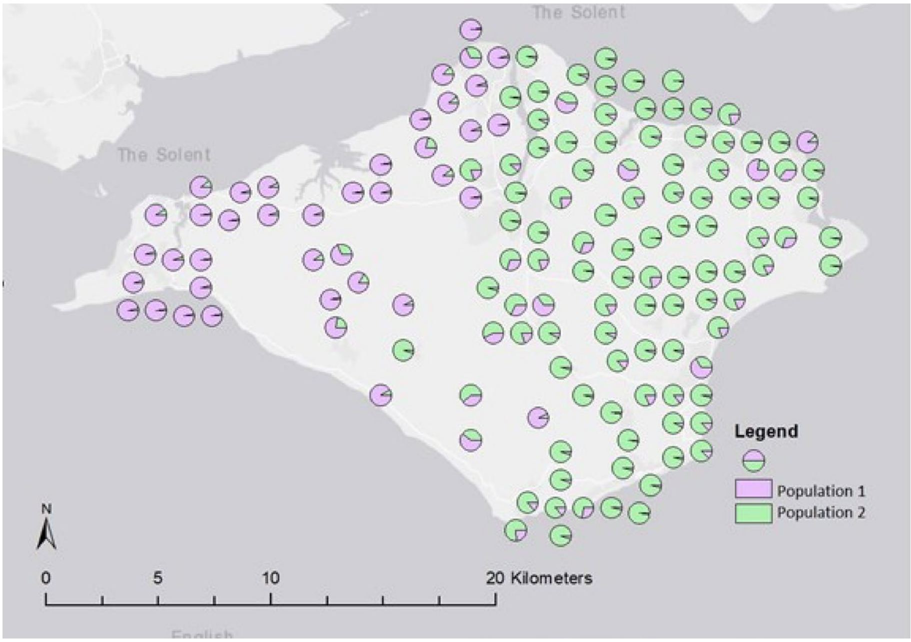

Fig. 4 Geographical distribution of the two genetic populations inferred from STRUCTURE results on the Isle of Wight

Table 3 Carrying capacity of the 5812 hectares of woodland habitat based on a range of red squirrel population densities

Population Density (squirrels/ha)	Carrying Capacity
0.5	2906
0.6	3500
0.7	4068
0.8	4650
0.9	5231
1.0	5812
1.1	6394

tree productivity. Estimated energetic needs ranged from 111,325 to 152,570 kJ per squirrel per year, depending on minimum, average, or maximum consumption rates (Table 1). If red squirrels could access seed crops from just 2% of trees on the Isle of Wight in any given year, our estimates suggest sufficient food would be available to sustain 3,336–4,571 individuals. In scenarios where squirrels could access seed crops from 5% of trees, this rises to 8,339 to 11,428 individuals. These calculations assume that a small fraction of trees produce viable seed crops each year and that squirrels can effectively forage within that range. Therefore, annual seed crop production appears to be adequate to support the current populations (estimated at 3,500 individuals) and may even allow for future growth.

West and east carrying capacity & net migration rates

The west contains 2,058 hectares of primary woodland habitat, supporting an estimated population size of 1,239 individuals and an effective population size (N_e) of 99.2. The net migration rate in this region is 4.37%. These values are influenced by spatial genetic structure identified through the Monmonier algorithm, which identified genetic barriers that may restrict gene flow and help delineate this subpopulation.

In contrast, the east encompasses a larger habitat area of 3,754 hectares and supports an estimated population of 2,260 individuals. Despite its larger size, the eastern subpopulation has a lower N_e of 70.9 and a higher net migration rate of 6.12% (Table 4).

Carrying capacity estimates based on varying population densities (Table 4) suggest that the west could support up to 2,264 individuals at a density of 1.1 squirrels/ha, while the east could sustain approximately 4,129 individuals under the same density assumption.

Population viability

In 20-year projections, the deterministic model considered the Isle of Wight red squirrel populations either as a single metapopulation or as two distinct subpopulations (west and east). Under optimistic survival and reproductive parameters, with juvenile survival at 25% and adult survival at 96%, the populations exhibited population growth. In contrast, the pessimistic scenario with juvenile survival at 15% and adult survival at 77% showed a decline in population. The population decline increased the probability of extinction only when females produced just one litter annually. This threshold applied regardless of whether individuals began breeding at one or two years of age, and the pattern remained consistent across both the metapopulation and subpopulation scenarios.

However, higher survival rates did not always guarantee population growth for the metapopulation or subpopulation scenarios. When breeding was delayed until two years of age and females produced only one litter per year instead of two, the population declined, even with a juvenile survival rate maintained at 25%. In this scenario, only 35% of breeding females were reproducing, which contributed to the population declines. Population growth occurred when the number of litters produced was increased to two annually (Table 2). Conversely, scenarios where breeding started at one year of age, with lower overall survival but an increase in the number of litters from one to two annually and 50% of females reproducing, led towards population stability (Table 2).

In 50-year projections, population declines were consistently observed across pessimistic scenarios, leading to an increased risk of extinction. Extending projections to 50 years showed that demographic trends remained consistent over time, with scenarios of reduced survival experiencing higher extinction probabilities and a decline in heterozygosity. Simulations indicated that heterozygosity could range from 0.53 to 0.62 over 20 years in low-

Table 4 Carrying capacity of the west and east Isle of Wight subpopulations' woodland habitats at two different population densities (0.6 and 1.1 squirrels per hectare), alongside population size, effective population size, and net migration rates

Subpopulation	Primary woodland habitat (ha)	Population size (*n*)	Effective population size (Ne)	Net migration rate (m)	Carrying capacity at 0.6 density	Carrying capacity at 1.1 density
West	2058	1239	99.2	0.04	1239	2264
East	3754	2260	70.9	0.06	2260	4129

survival conditions, while scenarios with higher survival and migration ranged from 0.62 to 0.70 (Table 2).

Supplementary feeding survey

75 survey responses were collected from across the Isle of Wight (Fig. 5). The majority of respondents (89.3%) placed feeders outside for wildlife, and 84.1% of these individuals provided food year-round. Among those feeding wildlife, 81.7% reported intentionally feeding red squirrels. Of these, 71.8% had read the Wight Squirrel Project's feeding guide, and 68.1% reported efforts to follow it. Hazelnuts, sunflower seeds, and peanuts were the most commonly provided foods (Fig. 6).

Discussion

We present a multidisciplinary study to understand the potential threats to the endangered red squirrel population on the Isle of Wight. Our results confirm population fragmentation on the island, with limited migration between the eastern and western regions, as well as low genetic diversity overall. Interestingly, our findings also suggest that the red squirrel population on the Isle of Wight is not at carrying capacity, particularly since supplementary feeding is widespread. Population viability analysis highlights the critical importance of juvenile and adult survival for population growth.

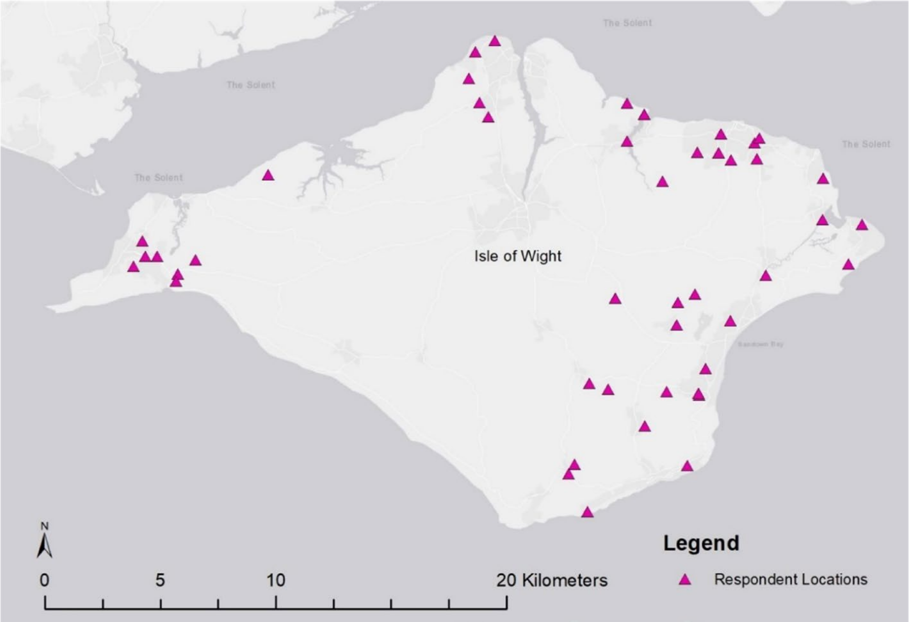

Fig. 5 Locations of survey respondents across the Isle of Wight

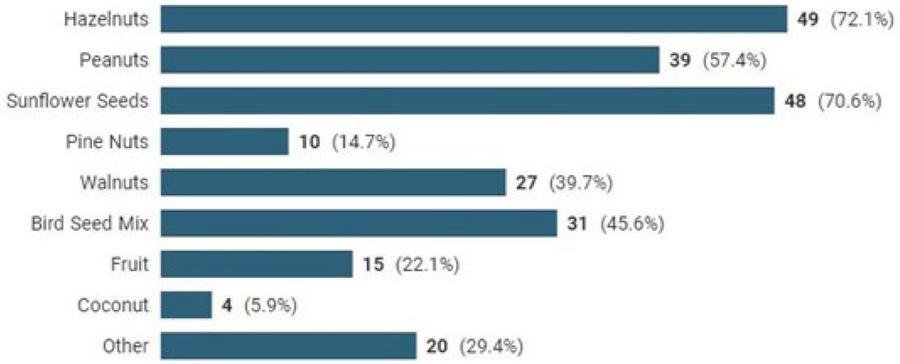

Fig. 6 Percentage of respondents providing various food types to wildlife on the Isle of Wight

Genetic diversity and population structure

Genetic diversity among the Isle of Wight red squirrel population is low, consistent with findings in other UK populations (Ogden et al. 2006; Hardouin et al. 2021). Observed heterozygosity (H_o) for the Isle of Wight population ranges from 0.34 to 0.35 and expected heterozygosity (H_e) from 0.40 to 0.43, comparable to mainland UK populations where H_o ranges from 0.25 to 0.39, with H_e values close to 0.43 (Ogden et al. 2006). European populations, such as those in Savoie and Parc de Sceaux, France, exhibit slightly higher genetic diversity, with H_o values reaching 0.47 (Rézouki et al. 2014). In contrast, two populations in Germany show much higher genetic diversity, with H_o values of 0.68 and 0.69 (Hardouin et al. 2021). While the Isle of Wight population shows similar levels of genetic diversity to other UK populations, it still represents reduced diversity compared to many continental European populations. This relatively constrained genetic variation, combined with the island's geographical isolation, (Frankham 1997) may increase long-term risks by limiting adaptability and increasing susceptibility to disease (Frankham 2005). Restricted gene flow between the western and eastern subpopulations further compounds this isolation, emphasising the importance of connectivity to mitigate genetic risks (Frankham et al. 2010).

The inbreeding coefficients (F_{IS}) for the western ($F_{IS} = 0.27$) and eastern ($F_{IS} = 0.18$) subpopulations suggest some reduction in observed heterozygosity relative to expectations under Hardy-Weinberg equilibrium. These values are comparable to those reported in other red squirrel populations in the UK (Ogden et al. 2006) and parts of continental Europe (Hardouin et al. 2021), reflecting patterns typical of small or isolated populations. Notably, some loci in our dataset (e.g., Rsm3, Scv13, Scv23) are nearly fixed, likely contributing to lower H_o and subsequently elevated F_{IS} estimates. The associated confidence intervals, which include values near zero, indicate that the observed F_{IS} values may not reflect true population-wide inbreeding but rather localised mating patterns (Szulkin et al. 2009; Hagell et al. 2013).

The results suggest that the apparent inbreeding is more likely due to mating among close relatives within smaller, localised areas of the population rather than systemic inbreeding across the entire population. This pattern aligns with the dispersal ecology of red squirrels, where individuals often settle and mate near their natal areas (Wauters et al. 1994).

Such behaviour can lead to localised genetic variation and increases in inbreeding coefficients, particularly when overall genetic diversity is low, as observed in the Isle of Wight population.

This phenomenon aligns with the concept of isolation by distance, first described by (Wright 1943), where limited dispersal and spatial structure result in increasing genetic relatedness among nearby individuals. As a result, genetic differentiation occurs as a function of geographic distance, which can resemble patterns of inbreeding but arises primarily due to geographic constraints rather than a systemic breakdown in genetic health (Slatkin 1993). Recent studies have demonstrated the pervasiveness of isolation by distance across species and landscapes, emphasising its importance in shaping spatial genetic structure (Meirmans 2012; Bradburd et al. 2013).

Consequently, the limited genetic variation in the Isle of Wight population exacerbates these patterns, as neighbours are more likely to be genetically related, further driving localised increases in inbreeding coefficients. Future studies incorporating fine-scale spatial genetic analysis and red squirrel sex data (not available for this study) could help disentangle the effects of local dispersal from population-wide inbreeding (Hardouin et al. 2021). While the non-significant F_{ST} values suggest some level of gene flow between the eastern and western subpopulations, the observed F_{IS} values may still reflect localised mating dynamics driven by limited dispersal and spatial structure. Such analyses could confirm whether these patterns result from true inbreeding or are primarily shaped by the population's ecological and spatial constraints. Notably, there is currently no evidence of inbreeding depression within the population (Butler 2022). Nonetheless, maintaining connectivity between the subpopulations remains essential as a precautionary measure to preserve genetic diversity and mitigate the risk of future genetic isolation or increased inbreeding (Frankham et al. 2010).

Habitat suitability, carrying capacity, & food availability

Our analysis of woodland area, population size, effective population size, and migration rates between the subpopulations provides key insights into their ecological dynamics. While the eastern subpopulation benefits from a larger habitat area and overall population size, both subpopulations exhibit low effective sizes, indicating potential genetic concerns (Frankham et al. 2010). Both subpopulations have positive net migration rates (0.06 in the east and 0.04 in the west), indicating that there is movement of individuals in both directions. However, the higher net migration rate in the east suggests a greater inflow of individuals into the western subpopulation compared to the outflow from the west, which helps support genetic diversity and stability in the west (Hagell et al. 2013). Conversely, the east's higher net migration rate could indicate that more individuals are leaving the eastern subpopulation, potentially limiting its population size and contributing to reduced genetic diversity over time (Slatkin 1993).

Our carrying capacity analysis further emphasises that both subpopulations could support larger densities. The observed population densities of approximately 0.6 squirrels per hectare across the Isle of Wight's woodland habitat remains well below its estimated carrying capacity, which could range from 0.5 to 1.1 squirrels per hectare. This suggests that factors such as limited migration, localised dispersal patterns, and suboptimal survival rates may be constraining population growth. Strategies to improve survival rates, such as reducing roadkill and mitigating other anthropogenic threats, could help both subpopulations increase toward their habitat's carrying capacity (Shuttleworth et al. 2015). Improving habitat provision and ensuring matrix permeability are essential for facilitating gene flow, which can bolster population stability and growth (Slade et al. 2020).These strategies could include establishing wildlife corridors or buffer zones to connect fragmented habitats.

By comparison, a small urban park in Paris, France, such as the Parc de Sceaux, which spans 72 hectares and supports a red squirrel population of 100–120 individuals and maintains high genetic diversity and stability despite limited habitat. The population density in the park ranges from 0.139 individuals per hectare in the mature woodlands to 0.167 individuals per hectare in the younger woodlots, which are likely of lower quality for both habitat and food. This lower density in the younger woodlots may reflect the suboptimal conditions for red squirrels in these areas. Nevertheless, the overall stability of the population is likely supported by higher migration rates from surrounding areas (Rézouki et al. 2014), underscoring the importance of even modest levels of gene flow in maintaining genetic health (Frankham et al. 2010). However, unlike the Parc de Sceaux, the Isle of Wight lacks external source populations, making internal connectivity between its subpopulations critical for mitigating isolation effects and maintaining genetic diversity.

To enhance genetic stability and population resilience over time, targeted management should focus on improving survival rates, facilitating migration between subpopulations, and enhancing habitat connectivity. Strategies that emphasise habitat preservation and informed supplementary feeding practices may be essential to support the Isle of Wight red squirrels, given its isolated nature.

Population viability and conservation implications

In terms of demographic factors, the number of litters produced each year emerged as a critical determinant of population growth, underscoring how reproductive output can provide resilience against potential population declines. Similar trends in resource-limited habitats demonstrate that low survival rates and reproductive challenges can restrict population growth, underscoring the importance of reproductive output for resilience (Rodrigues et al. 2010). Producing only one litter per year was associated with declining growth rates in pessimistic scenarios, raising the likelihood of extinction, especially under lower juvenile (15%) and adult survival rates (77%). Evidence from other populations experiencing environmental pressures, such as poor seed production or energy demands, highlights how low survival rates can limit population persistence (Rodrigues et al. 2010). In contrast, populations producing two litters per year, which is the more typical reproductive pattern for red squirrels, demonstrated greater resilience. Higher reproductive output provided a buffer against challenging conditions, even in scenarios with reduced survival rates.

Isle of Wight red squirrels typically begin breeding at one year old, producing two litters per year with an average of three offspring per litter (Butler 2022), suggesting high reproductive potential. This average litter size is an important factor in population resilience (Fagan et al. 2001; Risch et al. 2007). Although our model does not isolate specific effects of survival rates or litter size, shifts in these parameters influence population projections. In some multi-litter species, climate change has extended the breeding season, allowing for more or better-spaced litters (Møller et al. 2010). Similar changes in red squirrels could result from altered environmental conditions and food availability, which are critical for reproductive success.

Warmer springs could lead to earlier or more abundant food resources, improving female condition and increasing the number or size of litters (Møller et al. 2010). Conversely, food scarcity, especially in winter or early spring, may reduce maternal condition, lowering reproductive output and juvenile survival (Butler 2022). Additionally, climate-driven mismatches between food peaks and reproductive timing could hinder recruitment, ultimately affecting population stability (Fagan et al. 2001; Møller et al. 2010).

Food availability before and during breeding is particularly influential. For example, Selonen et al. (2016) found that early spring temperatures and late winter precipitation were linked to earlier reproduction and larger litters in European red squirrels, likely due to increased availability of buds and shoots. On the Isle of Wight, warmer springs could enhance food access and reproductive output (Wauters and Lens 1995; Haughland and Larsen 2004). However, despite both natural and supplementary food sources, the population remains below carrying capacity. This suggests survival constraints or other limiting factors (Rodrigues et al. 2010; Reilly and Lawton 2024).

Fifty-year projections indicated that trends of population growth or decline were likely to persist over time, highlighting the critical importance of survival rates and reproductive success for long-term viability. Studies of populations persisting under marginal conditions further underscore how low survival rates and reproductive output can limit long-term viability, particularly in resource-limited and extreme habitats (Rodrigues et al. 2010). Modelling the population as a metapopulation rather than as distinct subpopulations did not alter growth trends, reinforcing factors critical to stability include adult and juvenile survival, litter numbers, and breeding age. As observed in other species (Pröhl and Rodríguez 2023), populations with higher reproductive output are generally more resilient, particularly when food resources are ample (Reher et al. 2016). However, in extreme habitats with cold winters and poor resource availability, reproductive success may be insufficient to compensate for survival challenges, leading to reduced population resilience (Rodrigues et al. 2010).

Research on urban red squirrels shows that supplementary feeding practices in semi-urban environments, such as those in Hamburg (Germany), can improve individual body condition and reduce food stress during periods of natural scarcity (Reher et al. 2016). While this does not directly increase reproductive success, improved body mass is associated with better survival and reproductive outcomes (Reher et al. 2016). On the Isle of Wight, supplementary feeding appears to support the population during food shortages (Butler 2022), and our survey suggests a substantial portion of individuals may rely on human-provided food during such times. This provisioning may buffer the population against resource fluctuations and effectively increase the island's carrying capacity. However, residents frequently offer peanuts, despite their association with nutritional deficiencies and metabolic bone disease in red squirrels (Shuttleworth 2000; Bosch and Lurz 2012), highlighting the risks of inappropriate feeding. These findings underscore the importance of targeted public education campaigns that encourage safe, nutritionally appropriate feeding practices to maximise benefits without compromising squirrel health. Long-term modelling shows that trends in population growth or decline are likely to persist, emphasising the key roles of adult and juvenile survival, litter size, and age at first breeding in long-term viability (Rodrigues et al. 2010; Pröhl and Rodríguez 2023; Reher et al. 2016).

Additionally, supplementary feeding can alter squirrel behaviour, leading to increased road crossings and higher vehicle-related mortality (Reher et al. 2016). Urban and suburban areas also expose squirrels to other dangers, such as predation by domestic pets, drowning, trapping, and traffic accidents (Shuttleworth et al. 2015). Implementing safe travel corridors and enhancing habitat connectivity are essential to reduce these risks, enabling safer movement and mitigating the impacts of urbanisation on squirrel populations (Bosch and Lurz 2012).

Conclusion

Although detailed reproductive data for red squirrels on the Isle of Wight remains limited, this study provides important insights into their population dynamics and conservation outlook. Genetic analyses highlight low diversity and some degree of substructure, particularly between eastern and western regions, likely shaped by partial barriers to dispersal. Habitat-based carrying capacity estimates suggest the island can support a substantial metapopulation, and population viability modelling under both optimistic and pessimistic scenarios indicates long-term persistence is feasible. While supplementary feeding is widespread and may help buffer the population during periods of low natural food availability, our estimates also suggest that annual seed crop production is generally sufficient to support current population levels. This highlights the importance of ensuring that supplementary feeding practices do not introduce unintended health risks. Promoting safe, nutritionally appropriate feeding through public education could enhance population health while minimising harm. Future research on local movement, breeding patterns, and seasonal resource use would help refine conservation efforts, particularly in maintaining connectivity and managing habitat to support long-term resilience.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-025-03134-6.

Acknowledgements We would like to extend our sincere thanks to BU, WightFibre and the Isle of Wight National Landscape for their invaluable support of this research. We would also like to thank the Wight Squirrel Project and all the dedicated volunteers who assisted with sample collection. Additionally, we are grateful to Magdalena Barrow for her expert assistance in the laboratory. Finally, we would like to thank the two anonymous reviewers for their constructive comments and suggestions, which greatly improved this manuscript.

Author contributions Alyson E.V. Buchanan: Methodology, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Reviewing & Editing, Visualisation. Demetra Andreou: Writing – Reviewing & Editing, Supervision. Kathy H. Hodder: Writing – Reviewing & Editing, Supervision. Melissa A. Toups: Writing – Reviewing & Editing, Supervision. Phillipa K. Gillingham: Writing – Reviewing & Editing, Supervision. Marin Cvitanović: Formal analysis, Writing – Reviewing & Editing. Helen Butler: Conceptualisation, Resources, Writing – Reviewing & Editing, Supervision. Emilie A. Hardouin: Conceptualisation, Writing – Reviewing & Editing, Supervision, Funding acquisition

Funding This work was part of a PhD project match-funded by Bournemouth University, WightFibre and the Isle of Wight National Landscape.

Data Availability Microsatellite genotype data is provided as supplementary material in STRUCTURE format (Supplementary material 2).

Declarations

Conflict of interest The authors declare they have no conflict of interest.

References

Ballingall KT, McIntyre A, Lin Z et al (2016) Limited diversity associated with duplicated class II MHC-DRB genes in the red squirrel population in the United Kingdom compared with continental Europe. Conserv Genet 17:1171–1182. https://doi.org/10.1007/s10592-016-0852-3

Bernatchez L (2016) On the maintenance of genetic variation and adaptation to environmental change: considerations from population genomics in fishes. J Fish Biol 89:2519–2556. https://doi.org/10.1111/jfb.13145

Biomatters (2021) Geneious Prime. Retrieved from https://www.geneious.com

Bosch S, Lurz PWW (2012) The Eurasian red squirrel: *Sciurus vulgaris*, 1st edn. Westarp Wissenschaften, Hohenwarsleben

Bradburd GS, Ralph PL, Coop GM (2013) Disentangling the effects of geographic and ecological isolation on genetic differentiation. Evolution 67:3258–3273. https://doi.org/10.1111/evo.12193

Butler H (2022) Red squirrels on the Isle of Wight. Red squirrel conservation on the Isle of Wight. 1991–2020. Available at: https://www.wightsquirrels.co.uk/pdf/Red%20Squirrels%20on%20the%20Isle%20of%20Wight%20LowRez.pdf

Canty A, Ripley B, Brazzale AR (2024) Boot: bootstrap functions (Originally by Angelo canty for S). Contributed Packages, CRAN

Carroll B, Russell P, Gurnell J et al (2009) Epidemics of squirrelpox virus disease in red squirrels (*Sciurus vulgaris*): temporal and serological findings. Epidemiol Infect 137:257–265. https://doi.org/10.1017/S0950268808000836

Cheng J, Kao H, Dong S (2020) Population genetic structure and gene flow of rare and endangered *Tetraena mongolica* maxim. revealed by reduced representation sequencing. BMC Plant Biol. https://doi.org/10.1186/s12870-020-02594-y

Delin AE, Andrén H (1999) Effects of habitat fragmentation on Eurasian red squirrel (*Sciurus vulgaris*) in a forest landscape. Landsc Ecol 14:67–72. https://doi.org/10.1023/A:1008040001801

Do C, Waples RS, Peel D et al (2014) Neestimator v2: re-implementation of software for the estimation of contemporary effective population size (*Ne*) from genetic data. Mol Ecol Resour 14:209–214. https://doi.org/10.1111/1755-0998.12157

Dunn M, Marzano M, Forster J (2021) The red zone: attitudes towards squirrels and their management where it matters most. Biol Conserv 253:108869. https://doi.org/10.1016/j.biocon.2020.108869

Emorgan_ANG (2019) OSGB_Grid_1km. ArcGIS online

Environment and Climate Change Canada (2020) Recovery Strategy for the Vancouver Island Marmot (*Marmota vancouverensis*) in Canada. Species at Risk Act Recovery Strategy Series 2 parts

Fagan M, Prendergast, et al (2001) Characterizing population vulnerability for 758 species. Ecol Lett 4:132–138. https://doi.org/10.1046/j.1461-0248.2001.00206.x

Fleischer R, Eibner GJ, Schwensow NI et al (2024) Immunogenetic-pathogen networks shrink in Tome's spiny rat, a generalist rodent inhabiting disturbed landscapes. Commun Biol 7:169. https://doi.org/10.1038/s42003-024-05870-x

Forestry Commission (2020) National Forest Inventory Woodland GB 2020. *mapping.geodata forestry*, 2020 Ordnanace Survey 100021242

Frankham R (1997) Do island populations have less genetic variation than mainland populations? Heredity (Edinb) 78:311–327. https://doi.org/10.1038/hdy.1997.46

Frankham R (2005) Genetics and extinction. Biol Conserv 126:131–140. https://doi.org/10.1016/j.biocon.2005.05.002

Frankham R, Ballou JD, Briscoe DA, McInnes KH (2010) Introduction to conservation genetics, 2nd edn. Cambridge University Press, Cambridge

Goudet J, Jombart T, Kamvar ZN et al (2022) hierfstat: Estimation and Tests of Hierarchical F-Statistics. CRAN: Contributed Packages 0.5–11

Gurnell J (1987) The natural history of squirrels. Christopher Helm, London

Habel JC, Zachos FE (2013) Past population history versus recent population decline – founder effects in island species and their genetic signatures. J Biogeogr 40:206–207. https://doi.org/10.1111/jbi.12017

Hagell S, Whipple AV, Chambers CL (2013) Population genetic patterns among social groups of the endangered central American spider monkey (*Ateles geoffroyi*) in a human-dominated landscape. Ecol Evol 3:1388–1399. https://doi.org/10.1002/ece3.547

Hale ML, Lurz PWW, Shirley MDF et al (2001) Impact of landscape management on the genetic structure of red squirrel populations. Science 293:2246–2248. https://doi.org/10.1126/science.1062574

Hardouin EA, Baltazar-Soares M, Schilling A et al (2019) Conservation of genetic uniqueness in remaining populations of red squirrels (*Sciurus vulgaris* L.) in the south of England. Ecol Evol 9:6547–6558. https://doi.org/10.1002/ece3.5233

Hardouin EA, Butler H, Cvitanović M et al (2021) Wildlife conservation in a fragmented landscape: the Eurasian red squirrel on the Isle of Wight. Conserv Genet 22:571–583. https://doi.org/10.1007/s10592-021-01380-z

Haughland DL, Larsen KW (2004) Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. J Mammal 85:225–236. https://doi.org/10.1644/BWG-113

HM Government (1981) Wildlife and Countryside Act 1981. Available at: Legislation.gov.uk

Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806. https://doi.org/10.1093/bioinformatics/btm233

James JE, Lanfear R, Eyre-Walker A (2016) Molecular evolutionary consequences of island colonization. Genome Biol Evol 8:1876–1888. https://doi.org/10.1093/gbe/evw120

Janes JK, Miller JM, Dupuis JR et al (2017) The $K=2$ conundrum. Mol Ecol 26:3594–3602. https://doi.org/10.1111/mec.14187

Jombart T (2008) *adegenet*: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Kenward RE, Hodder KH, Rose RJ et al (1998) Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. J Zool 244:7–21. https://doi.org/10.1111/j.1469-7998.1998.tb00002.x

Lacy RC (1997) Importance of genetic variation to the viability of mammalian populations. J Mammal 78:320–335. https://doi.org/10.2307/1382885

Lacy RC, Pollak JP (2023) Vortex: a stochastic simulation of the extinction process. Version 10.7.0. Chicago Zoological Society, Brookfield, Illinois, USA.

Larsen KW, Boutin S (1994) Movement, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75:214–223. https://doi.org/10.2307/1939395

Li Y, Liu J (2018) Structureselector: a web-based software to select and visualize the optimal number of clusters using multiple methods. Mol Ecol Resour 18:176–177. https://doi.org/10.1111/1755-0998.12719

Lin T, Yang J, Yu Z et al (2023) Genetic diversity and population structure of *Mastacembelus armatus* in the river systems of Southern China revealed by microsatellites. SN Appl Sci. https://doi.org/10.1007/s42452-023-05534-1

Losos JB, Ricklefs RE (2009) Adaptation and diversification on islands. Nature 457:830–836. https://doi.org/10.1038/nature07893

Lurz PWW, Garson PJ, Rushton SP (1995) The ecology of squirrels in spruce dominated plantations: implications for forest management. Ecol Manage 79:79–90. https://doi.org/10.1016/0378-1127(95)03617-2

Mace GM, Lande R (1991) Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. Conserv Biol 5:148–157. https://doi.org/10.1111/j.1523-1739.1991.tb00119.x

Meagher S (1999) Genetic diversity and *Capillaria hepatica* (nematoda) prevalence in Michigan deer mouse populations. Evolution 53:1318–1324. https://doi.org/10.1111/j.1558-5646.1999.tb04547.x

Meirmans PG (2012) The trouble with isolation by distance. Mol Ecol 21:2839–2846. https://doi.org/10.1111/j.1365-294X.2012.05578.x

Møller AP, Flensted-Jensen E, Klarborg K et al (2010) Climate change affects the duration of the reproductive season in birds. J Anim Ecol 79:777–784. https://doi.org/10.1111/j.1365-2656.2010.01677.x

Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. Evol (N Y) 29:1. https://doi.org/10.2307/2407137

Ogden R, Shuttleworth C, McEwing R, Cesarini S (2006) Genetic management of the red squirrel, *Sciurus vulgaris*: a practical approach to regional conservation. Conserv Genet 6:511–525. https://doi.org/10.1007/s10592-005-9006-8

Ørsted M, Hoffmann AA, Sverrisdóttir E et al (2019) Genomic variation predicts adaptive evolutionary responses better than population bottleneck history. PLoS Genet 15:e1008205. https://doi.org/10.1371/journal.pgen.1008205

Paradis E (2010) Pegas: an R package for population genetics with an integrated–modular approach. Bioinformatics 26:419–420. https://doi.org/10.1093/bioinformatics/btp696

Pesendorfer MB, Bogdziewicz M, Szymkowiak J et al (2020) Investigating the relationship between climate, stand age, and temporal trends in masting behavior of European forest trees. Glob Chang Biol 26:1654–1667. https://doi.org/10.1111/gcb.14945

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959. https://doi.org/10.1093/genetics/155.2.945

Pröhl H, Rodríguez A (2023) Importance of genetic–fitness correlations for the conservation of amphibians. Animals 13:3564. https://doi.org/10.3390/ani13223564

Red Squirrels Northern England Spring Monitoring Programme In: Northumberland Wildlife Trust. https://rsne.org/spring-monitoring-programme/

Reher S, Dausmann KH, Warnecke L, Turner JM (2016) Food availability affects habitat use of Eurasian red squirrels (*Sciurus vulgaris*) in a semi-urban environment. J Mammal 97:1543–1554. https://doi.org/10.1093/jmammal/gyw105

Reilly E, Lawton C (2024) Assessing the effects of habitat loss and deterioration on a red squirrel translocation site: insights for future conservation management. Ecol Evol 14:e70482. https://doi.org/10.1002/ece3.70482

Rézouki C, Dozières A, Le Cœur C et al (2014) A viable population of the European red squirrel in an urban park. PLoS One 9:e105111. https://doi.org/10.1371/journal.pone.0105111

Risch TS, Michener GR, Dobson FS (2007) Variation in litter size: a test of hypotheses in richardson’s ground squirrels. Ecology 88:306–314. https://doi.org/10.1890/06-0249

Rodrigues D, Wauters LA, Romeo C et al (2010) Living on the edge: can Eurasian red squirrels (*Sciurus vulgaris*) persist in extreme high-elevation habitats?? Arct Antarct Alp Res 42:106–112. https://doi.org/10.1657/1938-4246-42.1.106

Rodríguez A, Andrén H (1999) A comparison of Eurasian red squirrel distribution in different fragmented landscapes. J Appl Ecol 36:649–662. https://doi.org/10.1046/j.1365-2664.1999.00426.x

Selonen V, Wistbacka R, Korpimäki E (2016) Food abundance and weather modify reproduction of two arboreal squirrel species. J Mammal 97:1376–1384. https://doi.org/10.1093/jmammal/gyw096

Shuttleworth CM (2000) The foraging behaviour and diet of red squirrels *Sciurus vulgaris* receiving supplemental feeding. Wildl Biol 6:149–156. https://doi.org/10.2981/wlb.2000.010

Shuttleworth CM, Signorile AL, Everest DJ, Lurz PWW (2015) Assessing causes and significance of red squirrel (*Sciurus vulgaris*) mortality during regional population restoration: an applied conservation perspective. Hystrix Ital J Mammal 26:69–75. https://doi.org/10.4404/hystrix-26.2-11166

Slade A, White A, Kortland K, Lurz PW (2020) An assessment of long-term forest management policy options for red squirrel conservation in Scotland. Hystrix Ital J Mammal 31:137–147. https://doi.org/10.4404/hystrix-00351-2020

Slatkin M (1993) Isolation by distance in equilibrium and non-equilibrium populations. Evol (N Y) 47:264–279. https://doi.org/10.2307/2410134

Stuessy TF, Takayama K, López-Sepúlveda P, Crawford DJ (2014) Interpretation of patterns of genetic variation in endemic plant species of oceanic islands. Bot J Linn Soc 174:276–288. https://doi.org/10.1111/boj.12088

Szulkin M, Zelazowski P, Nicholson G, Sheldon BC (2009) Inbreeding avoidance under different null models of random mating in the great tit. J Anim Ecol 78:778–788. https://doi.org/10.1111/j.1365-2656.2009.01544.x

Terra Sulis Research CIC (2023) LiDAR tree canopy map of England. https://terrasulis.org/

Wauters LA, Lens L (1995) Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. Ecology 76:2460–2469. https://doi.org/10.2307/2265820

Wauters L, Casale P, Dhondt AA, Dhondt AA (1994) Space use and dispersal of red squirrels in fragmented habitats. Oikos 69:140. https://doi.org/10.2307/3545294

Wauters LA, Matthysen E, Adriaensen F, Tosi G (2004) Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. J Anim Ecol 73:11–25. https://doi.org/10.1111/j.1365-2656.2004.00792.x

Wauters LA, Lurz PWW, Santicchia F et al (2023) Interactions between native and invasive species: a systematic review of the red squirrel-gray squirrel paradigm. Front Ecol Evol. https://doi.org/10.3389/fevo.2023.1083008

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191. https://doi.org/10.1093/genetics/163.3.1177

Wright S (1943) Isolation by distance. Genetics 28:114–138

Authors and Affiliations

Alyson E.V. Buchanan[1] · **Demetra Andreou**[1] · **Kathy H. Hodder**[1] · **Melissa A. Toups**[1,3] · **Phillipa K. Gillingham**[1] · **Marin Cvitanović**[1] · **Helen Butler**[2] · **Emilie A. Hardouin**[1]

✉ Alyson E.V. Buchanan
abuchanan@bournemouth.ac.uk

[1] Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Christchurch House, Talbot Campus, Poole, Dorset BH12 5BB, UK

[2] Wight Squirrel Project, Isle of Wight, UK

[3] Department of Biology, University of Louisiana at Lafayette, Louisiana, Lafayette 70503, USA