

Effects of food availability on the trophic niche of the hazel dormouse *Muscardinus avellanarius*

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ABSTRACT

The scale at which variations in food availability affect the foraging habits of individual animals can determine how the distribution of food resources affects populations. For species of conservation concern, these factors can have important implications for the management of habitats, as spatial and temporal variations in resource availability influence the trophic ecology of both individuals and populations. The hazel dormouse *Muscardinus avellanarius* is a species with seasonal dietary shifts and limited ranging, and whose populations in Great Britain are exhibiting marked decline, despite conservation measures. We compared resource availability and variation in dormouse traits with their trophic characteristics, determined by stable isotope analysis of dormouse hair and of their putative food items.

The trophic levels of individual dormice were associated with the abundance of invertebrates in the surrounding habitat and in the woodland as a whole. Assessment of dormouse dietary composition suggests that the proportions of invertebrates and of tree seeds and flowers in dormouse diets are affected by the abundance of food plants in the local habitat. This suggests that dormice can exploit both invertebrates and plants in proportion to their availability, and are variable in their predatory habits, in response to both the availability of invertebrates and plants.

Dormouse populations exhibit a broader trophic niche in autumn than in spring, most likely a consequence of their consumption of foods derived from a wider variety of tree and shrub species. We found no relationship between isotope signatures or food availability and the body mass or torpor of individuals, or the status of populations. This may be because, on the sites we studied, dormice could adapt to different food availabilities without discernible individual and population effects.

Dormice are opportunistic feeders, rather than specialists, making use of abundant food resources at a local scale. Habitat conservation for dormice, therefore, could benefit from establishing and maintaining habitats that increase the overall abundance and uniform distribution of both flower and fruit-bearing shrubs and trees and invertebrate populations, at a fine spatial scale.

1. Introduction

The availability of sufficient food resources, distributed in a way that allows efficient exploitation during foraging, is a key attribute of a species' habitat requirements (Polis et al., 1997). Understanding of diet and habitat use can therefore enable more effective conservation measures to be implemented, through improved provision of these

resources (Lyngdoh et al., 2014; Newsome et al., 2010; Newsome et al., 2015). Diet composition of individuals, both within and between populations, can vary spatially, e.g. between habitat types or microclimates (Anderson et al., 2009; Mustamäki et al., 2013). Diet composition can also vary among demographic groups, e.g. between age classes (Blanco-Fontao et al., 2013; Inger et al., 2006), and between time-frames, e.g. between seasons (Codron et al., 2011, 2013; Jaeger

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et al., 2010). There is therefore a need to understand how diet varies, as diet composition is dynamic and depends on the intrinsic characteristics of the animal as well as extrinsic variation in the environment (Ben-David and Flaherty, 2012; Newsome et al., 2010).

Seasonal shifts in resource use are relatively common in temperate environments, due to seasonal variation in the abundance of plants and invertebrates (Inger and Bearhop, 2008). The consistency of a population's trophic niche through time and across space can determine the adaptability of animals to the availability of seasonal resources (Inger et al., 2006; Phillips and Eldridge, 2006). In turn, the likely effects of changes in resource availability can be predicted when the effects of habitat on diet composition are understood (Cucherousset et al., 2011; van der Putten et al., 2004). Finally, the scale at which variation in food availability impacts the diet of a species will reflect its requirements for the spatial distribution of that resource (Vander Zanden et al., 2000).

The availability of food sources and the feeding habits of individuals can have ramifications for their condition, breeding and survival (Anderson et al., 2009; Cucherousset et al., 2011; Vander Zanden et al., 2014). If these differences in resource availability or feeding strategy affect many individuals in a population, they can, in turn, impact population rates of recruitment, dispersal and abundance (Ben-David and Flaherty, 2012). Furthermore, between-species interactions such as predation and competition also determine the feeding habits of a population (Miranda et al., 2014). Therefore, an understanding of the trophic habits of individuals and populations can provide insight into interactions with its habitats and thus the relative value of particular habitat conservation measures.

Stable isotope analysis (SIA) has been employed widely in the characterisation of animal diets, movement and foraging ecology, and provides a means of quantifying and comparing the trophic characteristics of individuals and populations (Crawford et al., 2008; Kelly, 2000). SIA methods exploit the fact that ratios of heavy to light stable isotopes in a consumer's tissues reflect those in their diet, and so can provide a powerful means of characterising diet composition and variation (De Niro and Epstein, 1978; Inger and Bearhop, 2008). SIA can additionally capture an animal's general trophic characteristics, such as the trophic level at which it feeds, by quantifying the differences between nitrogen isotopic signatures and those of the surrounding habitat (McCutchan et al., 2003; Post, 2002).

While sometimes cruder in its dietary detail than other methods, such as faecal or gut analysis, which might identify specific foods, niche characterisation through stable isotopes can be less susceptible to some of the biases present in these methods, such as the differences in digestibility of food sources in faecal analysis (Hobson and Clark, 1992). SIA can also provide a fuller representation of general feeding behaviour, as tissues can be sampled, the turnover of which reflects varying timeframes of dietary intake, enabling a broader perspective than the 'snapshots' provided by stomach or faecal analysis (Araújo et al., 2007). This has enabled quantification of trophic niches across whole populations of animals (Fink et al., 2012; Newsome et al., 2012). Metrics developed by Layman et al. (2007, 2012) can help identify a population's isotopic position, niche size, and the distribution of individual stable isotope signatures within a population. These metrics can then be compared between populations in different seasons and between habitat and resource settings, in order to determine the relationships between populations and their habitats across time (Crawford et al., 2008; Inger and Bearhop, 2008).

In this study, we aim to examine trophic variability in the hazel dormouse *Muscardinus avellanarius*, among individuals and populations, and relate this to resource availability, individual characteristics and population status. Such an understanding both adds to wider knowledge of the trophic responses of species of conservation concern to different habitats, and the scale at which this has individual and population effects, and might guide specific habitat management recommendations for this protected species. Thus the impacts of variations in resource availability are particularly useful in aiding species of

conservation concern. The hazel dormouse is a small arboreal rodent that, although currently widespread across much of Europe, is rapidly declining in parts of its range (Hutterer et al., 2016; Goodwin et al., 2017). In the UK, recent analysis of a national citizen-science monitoring scheme, the National Dormouse Monitoring Programme, revealed population declines of 72% (95% confidence intervals 62–79%) from 1993 to 2014 (Goodwin et al., 2017). Population declines and range contraction merit an IUCN Red List categorisation of dormice in the UK as 'Vulnerable' (possibly 'Endangered'; Goodwin et al., 2017), and the species is protected under Annex IV of the EU Habitats Directive (1992). It is important, therefore, to gain a further understanding of the species' ecology in areas where populations are in decline.

The status of hazel dormouse populations is partly determined by quality and configuration of their habitat (Goodwin et al., 2018; Mortelliti et al., 2014; Sozio et al., 2016). While it has been shown that some habitats are related to both increased abundance and breeding of dormice, other habitat types have been linked only to increases in abundance or breeding. Such variation will be partly attributable to the requirements for, and value of, different food resources at different points of the season (Anderson et al., 2009; Inger et al., 2006). Hazel dormice feed on a succession of plant and invertebrate food resources through from spring until autumn; the period in which they are active (Juškaitis, 2007; Richards et al., 1984). The identity of tree and invertebrate species selected by dormice has been shown to vary between different habitats (Juškaitis and Baltrūnaitė, 2013; Richards et al., 1984; Sara and Sara, 2007), suggesting that, rather than being specialist feeders, dormice are reasonably adaptable in their selection of food items (Juškaitis, 2007). It has also been suggested that dormice feed at different trophic levels depending on seasonal phenological change and the abundance of alternate resources (Eden and Eden, 2001; Juškaitis, 2007). Invertebrate consumption may be highest in spring when plant food is less abundant (Chanin et al., 2015), after which dormice may progress to eating soft and then hard tree mast as it becomes available (Juškaitis and Baltrūnaitė, 2013; Richards et al., 1984).

In this study, we examined relationships between the diets of hazel dormouse individuals and populations and their demographic characteristics and habitat. We investigated the effects of seasonal local resource availability on the trophic signatures of individuals within woodlands, and the effect of site-level food availability on the trophic characteristics of populations. Since dormice feed on a succession of the available foods in woodlands, we expect there to be seasonal shifts in diet, and differences in the consumption of both plant and invertebrate foods based on their availability. We also investigated whether food availability at the local scale (surrounding a nest box) affected an individual's trophic position and at the site scale affected a population's trophic characteristics.

We then assessed whether there was any relationship between habitat or trophic signature and individual condition (body weight and state of torpor) or population status (indices of abundance, breeding and trend in abundance over a period of at least five years). The variability in availability and nutritional profiles of different foods between seasons and sites, can have consequences for the accumulation of fat reserves and this in turn will affect the state of torpor of an animal and the foraging strategy employed (Juškaitis, 2005). It was hypothesised that dormice with access to increased plant foods in autumn were more likely to be heavier, and therefore more likely to be in state of torpor as they have accumulated enough fat reserves and no longer need to continue foraging. If different responses are employed more commonly across individuals of one site than another, and as weight has been linked to hibernation mortality and breeding (Juškaitis, 1999; Csorba, 2003), we might expect the increased availability of food to result in higher abundance of dormice, amounts of breeding and more positive trajectories of populations at different sites. We also assessed whether there were particular trophic signatures of dormice associated with better individual and population status.

We also conducted a dietary assessment of the dormouse population

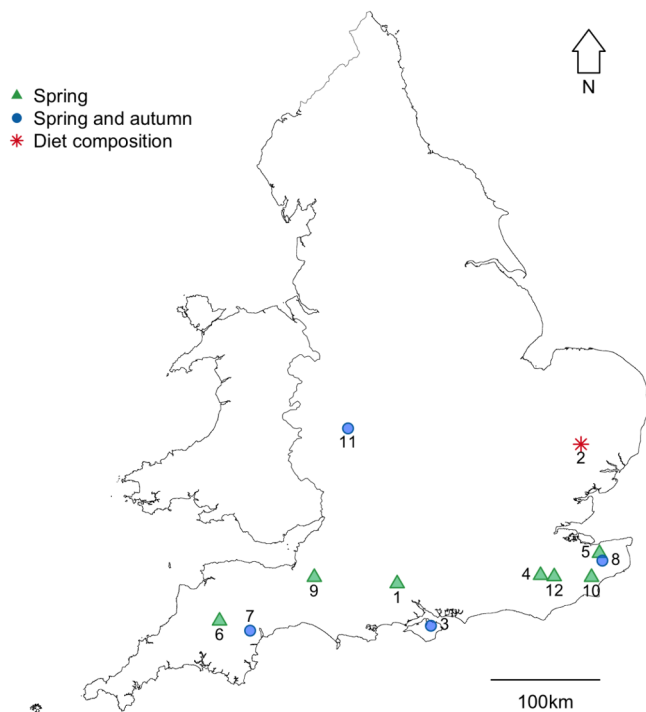


Fig. 1. Locations of the 12 sites in the UK where dormice were sampled for stable isotope analysis of their diets. Sites are labeled with their numbered ID (see Table 1). The seven sites with enough samples in spring 2015 are shown as triangles and four sites adequately sampled in both spring and autumn 2015 are circles. Bradfield Woods, for which adequate samples were collected in spring and autumn, and for which diet composition was assessed through stable isotope mixing model analysis, is marked as an asterisk.

of one high-quality woodland habitat across two seasons, estimating the proportional contribution of each putative food group. Through this assessment of the trophic responses of dormice to their habitat, we aim to gain a better understanding of the effects of food resource configuration within woodlands. Such knowledge will inform the conservation of dormice through more effective habitat management.

2. Methods

2.1. Sample collection and processing

We sampled dormice at 20 study sites located across the south and Midlands of England, in a range of habitat types, from hazel coppice to mixed conifer and broadleaf forest. Dormice were surveyed using nestboxes in the late spring (May or June) and autumn (September) of 2015. Of these 20 sites in spring, adequate samples ($n > 4$) were obtained on 12 sites (Four sites from 17th to 27th May 2015; and eight sites from 15th to 30th June 2015), and five of these sites also had enough samples collected in autumn (16th to 25th September 2015) for additional analysis of summer diet (Fig. 1; Table 1). Sites where more than four dormice were sampled were included in analyses of individual dormouse signatures, whereas analysis of the isotopic characteristics of populations required more than ten samples. Individual trophic analysis required complete information on all dormouse characteristics and local food availability, and not all samples could be included in this analysis; therefore the sample sizes for population and individual analyses differ (Table 1).

We sampled dormouse hair for stable isotope analysis of Carbon and Nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), as the metabolically inert keratinous tissue of hair provides a broad overview of dietary information from the point at which it was grown (Martinez del Rio et al., 2009). Variation among dietary items in the relative abundance of stable isotopes of C and N can

be marked and is conserved up the food chain, hence these two isotopes are often employed in dietary studies (Kelly, 2000). Late spring and autumn sampling periods were chosen, as most studies of the moult of hazel dormice identify a moulting period in spring and a second in late summer (Lozan, 1970; Homolka, 1978; Juškaitis and Büchner, 2013). Samples collected in May or June will therefore likely have grown over spring and reflect spring diet, whereas hair sampled in autumn will comprise hair grown in the summer and reflect summer diet. Hair samples were plucked using tweezers from the upper left hind leg of animals weighing > 10 g, as juvenile dormice over this weight will be feeding independently. The animal's sex, age class (adult or juvenile), weight, and state of torpor (active or torpid) were recorded before they were returned to their nest box.

In order to test for consistency within individuals, duplicate hair samples (2 separate plucked samples from the same area) were analysed where possible (there were 52 occasions when two samples were taken from dormice in the same sampling event). The repeatability of these duplicate samples was investigated using linear mixed effects models in the R package rptR (Stoffel et al., 2017). These analyse the proportions of variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ that are attributable to the identity of the individual from which the sample was taken. 95% confidence intervals are generated through bootstrapping the data and running the model 1000 times.

In order to assess the relationship of the trophic characteristics of a population to its status, time-independent, site-level indices of dormouse abundance, breeding and trend on sites were calculated over a period of monitoring of at least 5 years from 1993 to 2017. Following Goodwin et al (2017), indices were derived through fitting models to counts of dormice and to breeding events, with explanatory terms for year and site, and an offset for number of boxes used, to control for survey effort.

2.2. Food availability

In order to ascertain the local availability of potential plant and invertebrate foods, surveys were undertaken along four 50 m transects of width 2 m at north, south, east and west directions from each nest box in which a dormouse had been sampled, on the same day as dormouse surveys on each site. This transect distance was chosen as it approximates the average maximum nightly distances travelled from a nest site by hazel dormice (Bright and Morris, 1992; Goodwin et al., 2018; Juškaitis, 1997). All individual trees and plants over 1 m in height found within the transect strip were recorded. Food source samples, specific parts of plant species that had been identified as being potentially important in dormouse diet in the literature were also collected (Appendix A; Bright and Morris, 1993; Juškaitis, 2007; Juškaitis et al., 2016; Juškaitis and Baltrūnaitė, 2013; Richards et al., 1984; Sara and Sara, 2007).

As hair will have been grown over the several months prior to sampling (hair samples taken in late spring most likely represent early spring diet and autumn hair samples represent late summer diet), there is a potential mismatch between the availability of foods when hair is grown and when food samples were collected. Within a single woodland, however, there are variations in light and warmth which means that plants of the same species come into flower and fruit at different times in different areas (Chazdon and Percy, 1991; Chen et al., 1999). Large variation in phenophase (of over at least one month) within British woodlands was found among different tree species, especially in warmer years such as 2015 (Cole and Sheldon, 2017; Met Office, 2020). As a result, flowers and fruits, which were available at the time of hair growth, are likely also to have been available within the woodland when samples were collected.

The proportion of the plants recorded in the surrounding area that were dormouse food plants was used as a measure of the availability of plant food, i.e. the number of stems of food plants as a proportion of the total number of stems of plants. While abundance of food plants

Table 1

Numbers of hazel dormice sampled on twelve woodlands in England in two seasons. Seven sites have adequate samples available for spring only and five sites have samples available for spring and summer isotopic analysis. Three sites (2, 3 and 7) are used in the within-site comparative analysis of population trophic niche in spring and summer using SIBER Bayesian ellipse estimation. Mixing model analysis of dietary composition was conducted for site 2, as well as isotopic analysis for spring and summer.

Site ID	UK region	National grid reference	County	Number of dormice sampled			
				Spring		Summer	
				Individual	Population	Individual	Population
1	South-West	SU23	Wiltshire	5	–	–	–
2*	East	TL96	Suffolk	10	10	18	24
3	South-East	SZ59	Isle of Wight	5	15	4	17
4	South-East	TQ64	Kent	10	12	–	–
5	South-East	TR16	Kent	5	–	–	–
6	South-West	SX69	Devon	12	12	–	–
7	South-West	SX99	Devon	16	17	12	12
8	South-East	TR15	Kent	10	10	7	–
9	South-West	ST53	Somerset	7	11	–	–
10	South-East	TR03	Kent	7	–	–	–
11	West-Midlands	SO87	Worcestershire	4	–	10	12
12	South-East	TQ74	Kent	8	–	–	–
Total	England			99	87	51	65

(number of stems) appears to be the more direct measure of food availability, we aimed to quantify the relative availability of food plants within the area surrounding the nest box, and thus used a proportional measure, reducing the confounding influence of plant density. For instance, by a simple count of stem number, large stems will be under-recorded compared to extent of spatial coverage in the canopy, and small stems will appear more abundant compared to spatial coverage. However, the proportion of food plants correlates strongly with their total number (Spearman's Rank correlation test $R_s = 0.82$, $p < 0.001$), and is therefore still related to the density of stems. Simpson's diversity index of vegetation in the area surrounding the nest box was also calculated (Simpson, 1949).

Invertebrate samples were collected by standardised tree beating (hitting the nearest accessible five branches each five times, while holding a 1.5 m² collecting sheet under each branch) at five points around each occupied nest box: one sample adjacent to the nest box and one at the end of each of the four survey transects. Samples were frozen at -80 °C before invertebrates were identified to Order and counted. Invertebrate counts used in analysis were the numbers of herbivorous and omnivorous invertebrates (at the Order level) found in the habitat surrounding each dormouse's nest box. Accordingly, the Simpson's diversity index of invertebrate Orders in the area surrounding the nest box was calculated (Simpson, 1949). An index of total food availability was also calculated as the sum of the scaled proportions of food and invertebrate abundances (scaling subtracted the mean of the sample and divided by the sample standard deviation).

To facilitate comparison of dormouse stable isotope signatures among sites, we established a common baseline for each site of isotope signatures of plants. Baseline isotope values were needed for each site so that the offset of dormouse isotopes (and thus their local trophic level) could be estimated (Post, 2002). Flowers were used as baseline samples for sites, as these have been found to be the main dormouse food source in spring (Juškaitis and Baltrūnaitė, 2013) and were present on all sites. Species included were: blackberry *Rubus fruticosus*, black bryony *Tamus communis*, dogwood *Cornus sanguinea*, gorse *Ulex europaeus*, hawthorn *Crataegus monogyna*, honeysuckle *Lonicera periclymenum*, rowan *Sorbus aucuparia* and wayfaring tree *Viburnum lantana*. At all sites, 5–15 flower samples (mean 7.7 ± 0.7 SE) were analysed. In total, 104 flower baseline samples were analysed: as we aimed accurately to quantify representative values of source groupings, 12 samples were outside the expected range of plant isotopic values, or further than 2.5 standard deviations away from the sample mean (all other samples were clustered around the mean) and so considered to be

anomalous or the result of analytical machine error and excluded (Kohn, 2010).

2.3. Stable isotope analysis

Prior to analysis, plant and invertebrate samples were processed by drying the samples for 24 h in a freeze-drier and homogenising with a mortar and pestle. Then ~ 1 mg of dried and homogenised plant or invertebrate sample was weighed into tin capsules. Between 0.4 and 0.8 mg of dormouse hair samples were weighed directly into tin capsules.

The masses of the stable isotopes of carbon and nitrogen were quantified using elemental analysis, isotope ratio mass spectrometry using a Sercon 2020 isotope ratio mass spectrometer at Elementex (Gunnislake, Cornwall, UK) and University of Exeter laboratories. Stable isotope ratios were expressed as δ values in ‰, the ratio of heavy to light isotope relative to the isotopic ratios of an international standard for each element: the Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$. Samples were scale-corrected for both elements using standards USGS40 and USGS41 (Glutamic acid). Estimated precision was $\pm 0.1\%$ based on these standards and a laboratory QC material (bovine liver standard) run within sample batches.

2.4. Stable isotope dietary composition in Bradfield Woods

In addition to comparison among sites, we reconstructed diet composition of dormice at a single site (Bradfield Woods) in Suffolk. For this site, stable isotope analysis of all potential food sources collected from the area around an occupied nest box was conducted to reliably quantify the variation among sources (Phillips, 2012). For parts of flowers (anthers, stems, petals) and fruits (stones, seeds, outer flesh), each constituent part was analysed separately and, if shown to be similar, were grouped thereafter. We then grouped species-level food sources into six food groups to capture variation that was both isotopically and biologically meaningful (Phillips and Gregg, 2001). The six food groups were: hazel, honeysuckle (Juškaitis et al., 2016; Juškaitis and Baltrūnaitė, 2013; Richards et al., 1984); Lepidoptera (the main invertebrate food source proposed by other studies; (Chanin et al., 2015; Juškaitis et al., 2016); Omnivorous invertebrate Orders (representing other potential invertebrate food sources; Juškaitis (2007); Richards et al. (1984)); shrubs (flowers, vegetative parts and early berries and catkins in spring and seeds, nuts, berries and late flowers in

autumn) and trees (oak and willow flowers in spring and acorns and ash seeds in autumn). These were broad groupings as there were large overlaps between species within food groups and our hypotheses were focused on the general foraging niche of dormice in different seasons (Appendix A) (Phillips and Gregg, 2001, 2003; Phillips et al., 2005).

2.5. Statistical analysis

R version 3.4.2 (R Core Team 2017) was used for all analyses.

Before any statistical analysis, dormouse $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were adjusted in relation to the isotopic baseline for each site in order to allow comparison of values between sites. This was done by first subtracting the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic baselines for each site from the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic baselines for all sites. For each element, this generated the distance of the isotopic baseline of each site from the mean of all sites. This distance was then subtracted from the value for each dormouse on that site to give adjusted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, scaling dormouse isotopic signatures by their relative position from the isotopic baseline of their woodland site (Post, 2002).

2.5.1. Individual trophic analysis

In order to ensure robust characterisation of the isotopic values of dormice on particular sites, only those sites with samples from at least five dormice were used in isotopic analysis of individuals.

To analyse among-individual variation in the baseline-adjusted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of dormice, linear mixed effect models with a Gaussian error structure and a random effect for site were used. Models included a fixed effect for season. Explanatory dormouse variables were state of torpor, weight, age class and sex, and food availability variables were the proportion of food plants in the surrounding woodland and Simpson's diversity index of vegetation, the invertebrate abundance count and the Simpson's diversity index of invertebrate Orders.

As all analyses sought to determine the main determinants of individual or population isotopic variation, an information theoretic approach and multi-model averaging was used. Model selection involved a ranked comparison of the Akaike Information Criterion corrected for small sample sizes (AICc), for all subsets of the full model, and model averaging over the top model set (Lindberg et al., 2015; Whittingham et al., 2006) using the MuMIn package (Barton, 2016). All models included in the top model set were within 2 ΔAICc of the top model (Burnham and Anderson, 2002). Conditional model averaging was performed as the hypotheses regarding resource availability were specific (Grueber et al., 2011). See Appendix B, Table B1 for top model sets. For population trophic analysis, where models had a small number of explanatory variables, backwards stepwise selection was also performed for validation. Correlations between explanatory variables were investigated using Spearman's Rank correlation tests prior to individual-level analyses, to ensure no variables were correlated above 0.5 r_s . Results are expressed as effect sizes and 95% confidence limits, and relative importance (RI), the proportion of top model sets which included the explanatory variable.

In order to examine whether dormouse traits (sex, weight and age class) and environmental variables (availability and diversity of plant and invertebrate food and total food availability) were predictors of whether an animal was in torpor, a generalised linear mixed model with a binomial error structure and a logit link function was used. To examine the effect of the same explanatory variables on the mass of animals, a linear mixed effect model with a Gaussian error structure was used. Weights of animals were log-transformed to normalise their distribution. Model coefficients were exponentiated in both cases to give predictions on the response scale.

2.5.2. Dormouse diet composition in Bradfield woods

Bayesian stable isotope mixing models (BSIMMs) were used to assess the contributions of the six food groups to dormouse diets, using the R package SIMMR at a population and individual level (Parnell

et al., 2010). The enrichment of heavy isotopes arising from the ingestion and transfer of carbon and nitrogen to consumer (dormouse) hair was accounted for by calculating Trophic Discrimination Factors (TDFs) through the R package SIDER (Healy et al., 2018), which uses phylogenetic, diet-type and habitat information to estimate TDFs and can improve the fit of Bayesian stable isotope mixing models (Swan et al., 2020). TDFs were 3.49 (± 1.54 SD) for $\delta^{15}\text{N}$ and 2.67 (± 1.91 SD) for $\delta^{13}\text{C}$.

The estimated proportions of food sources for each individual derived from stable isotope analyses were then compared to food availability (proportion of food plants and invertebrate abundance) using Spearman's rank correlation test. The relationship between the likelihood of torpor and estimated mean dietary proportions for each dormouse was investigated using a generalised linear model with a binomial error structure and a logit link function. The effect of the same dietary proportions on the weight of dormice was investigated using a linear regression model with Gaussian error structure.

2.5.3. Population trophic analysis

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and 5 ellipse-based metrics were used to characterise the isotopic space (isospace) occupied by sampled dormouse populations in spring and autumn (Layman et al., 2007, 2012). This was done using the R package SIBER (Jackson et al., 2011) for all site visits that had over 10 individual dormouse isotope signatures (11 visits to 8 different sites; Table 1). Population isotopic ellipse-based metrics used were: Standard Ellipse Area corrected for small sample sizes (SEAc); Range of carbon values ($\delta^{13}\text{C}$ range); Range of nitrogen values ($\delta^{15}\text{N}$ range); Nearest-neighbor distance (NND); and mean distance to centroid (CD) (Layman et al., 2007, 2012). The effects of site and season on the isospace metrics ($n = 11$) were investigated with linear regression models. For spring samples, the effects of the mean proportion of food plants and mean invertebrate abundance around nest boxes on the isospace metrics of dormouse populations ($n = 7$) were investigated in separate linear regression models with Gaussian error structures. Bonferroni correction was used to correct for multiple hypothesis testing, as the effects of the availability of plants and invertebrates were investigated in separate models. Some isospace metrics (SEAc, $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range) were log-transformed to normalise their distribution.

For sites that were visited in both spring and autumn and on which more than ten dormice were sampled in each visit, comparisons could be made between the niche space occupied in spring and summer within sites (Table 1). Means and credible intervals of Standard Ellipse Areas were calculated via Bayesian methods (Jackson et al., 2011). Differences between Bayesian estimates of SEAc for the two different seasons on each site was calculated via the mean ($\pm 95\%$ CLs) difference between 1000 draws from posterior estimates of SEAc in each season (Jackson et al., 2011). Overlaps between the ellipses in each season on each site was calculated in a similar way, by estimating the overlap between the 2 ellipses in 1000 draws from posterior estimates. This was then converted to the mean ($\pm 95\%$ CLs) percentage overlap of 1000 draws from posterior estimates of ellipses in each season (Jackson et al., 2011).

The relationship between dormouse population status at each site (Abundance, Breeding and Trend indices) and each measure of that populations' isotopic niche (mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, SEAc, $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, CD and NND) was investigated in single explanatory variable analysis, and Bonferroni corrected.

3. Results

3.1. Individual trophic characteristics

Separate samples from the same individual dormice ($n = 52$) were more similar than those from other dormice on the same site, and thus measures taken from the same dormouse were considered repeatable.

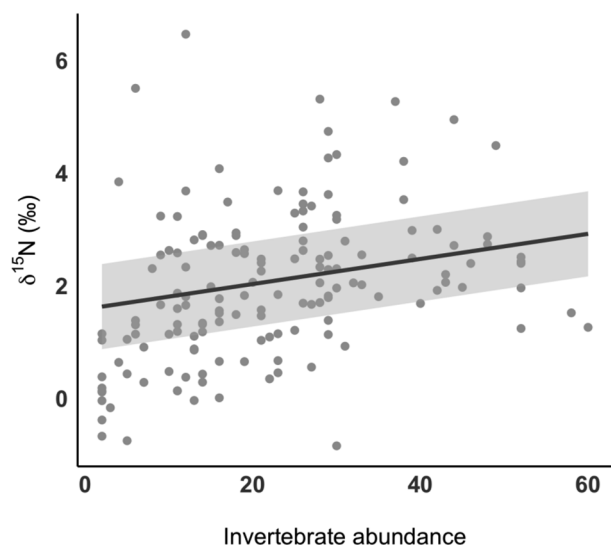


Fig. 2. Relationship between $\delta^{15}\text{N}$ of hazel dormouse hair samples and the abundance of invertebrates sampled at 5 points surrounding the dormouse nest box (one point 5 m from the nest box; 4 points 50 m from nest box), as determined by linear mixed effect model, with the shaded area denoting standard error of effect size. $\delta^{15}\text{N}$ signatures were standardized among sites by subtracting the site baseline from dormouse signatures.

Measures taken at the same time from the same dormouse showed high repeatability as assessed through linear mixed effects models: baseline-adjusted $\delta^{15}\text{N}$ values had a repeatability of 0.91 (0.84, 0.94 95% CLs), and $\delta^{13}\text{C}$ values had a repeatability of 0.87 (0.78, 0.92 95% CLs). The mean difference between $\delta^{15}\text{N}$ of duplicate samples from the same individual was 0.42 (± 0.05 SE), compared to a difference of 1.02 (± 0.14 SE) between individuals on the same site. The mean difference between $\delta^{13}\text{C}$ of duplicate samples from the same individual was 0.26 (± 0.08 SE), compared to a difference of 0.62 (± 0.06 SE) between individuals on the same site.

Isotope values from 150 dormice from 12 sites were analysed (99 dormice in spring and 51 in summer). Dormice with more invertebrates in the area surrounding their nest box had higher $\delta^{15}\text{N}$ signatures (an increase of 2.23 parts per mil for every 100 invertebrates (95% CLs: 0.44, 4.01); $\text{RI} = 1$; Fig. 2) and lower $\delta^{13}\text{C}$ values (a decrease of -1.55 (95% CLs: -2.73 , -0.36) for every 100 invertebrates; $\text{RI} = 1$). Dormice with a higher Simpson's diversity of vegetation in the surrounding areas also had higher $\delta^{15}\text{N}$ signatures (Effect size = 2.54 (95% CLs: 0.34, 4.73); $\text{RI} = 1$). The proportion of food plants and the diversity of invertebrate Orders in the habitat surrounding the nest box, however, had no significant effects on the isotopic signatures of dormice. There were no significant differences between the $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values of dormice with respect to sex, age class, weight, state of torpor or season.

The availability of food plants and invertebrate foods in the local area were not related to each other (Spearman's rank correlation test $R_s = 0.08$, $p = 0.57$), and therefore responses to differences in the abundances of these food types are likely to be distinct processes.

Adult dormice were more likely to be active in autumn ($n = 132$, odds ratio = 43 (4.12, 448.81 95% CLs); $\text{RI} = 1$) and, within season, were less likely to be active when they weighed more ($n = 132$, odds ratio = 0.78 (0.61, 0.97 95% CLs); $\text{RI} = 1$). There were no significant effects of sex or food availability on the state of torpor. Adult dormice were significantly heavier in autumn ($n = 132$, 17% heavier (12%, 23%); $\text{RI} = 1$) and males were significantly heavier than females ($n = 132$, 9% heavier (5%, 14%); $\text{RI} = 1$). There were no significant effects of invertebrate abundance, proportional food plant abundance or the total amount of food resources within the area surrounding a nest box on a dormouse's weight.

3.2. Diet composition

For Bradfield Woods in Suffolk, the isotope signatures of 10 dormice, 97 plant and 51 invertebrate samples were analysed for spring, and 24 dormice, 154 plant and 53 invertebrate samples for autumn. This represented an average of 6.4 (± 0.6 SE) invertebrate and 14.6 (± 1.6 SE) plant samples for each nest box in which dormice were captured and sampled.

Tree flowers contributed more to dormouse diet in spring than other food groups, making up an estimated 34% of dormouse diets (10%, 55%; Fig. 3). Tree seeds were also important in summer diet, contributing 25% of the diet (11%, 39%), as were honeysuckle flowers and berries, which formed 22% of the diet (8%, 37%; Fig. 3). The differences in these two groups between the two seasons were the most pronounced: 77% of the distribution of estimates of tree flower consumption in spring were larger than those in autumn for tree seeds; and 71% of the distribution of estimates of honeysuckle consumption in autumn were larger than those in spring.

The estimated contributions of each food group to the diets of dormice across both seasons were related to food availability in the area around the nest box occupied by the individual. The mean estimated proportion of honeysuckle in the diet was positively related to the proportional availability of food-plants in the surrounding habitat ($r_s = 0.47$, $p = 0.006$). The contributions of Lepidoptera and of omnivorous invertebrates to dormouse diets were both significantly negatively related to the proportion of food-plants in the surrounding area ($r_s = -0.44$, $p = 0.011$; $r_s = -0.48$, $p = 0.005$, respectively).

The weight and probability of torpor of individual dormice were not significantly related to their diet composition.

3.3. Population trophic characteristics

After correction for multiple hypothesis testing, the mean $\delta^{15}\text{N}$ values of dormice in spring were higher on sites with greater abundances of invertebrates (Effect size = 4.77 parts per mil for every 100 invertebrates (0.72, 8.81 95% CLs); $\text{RI} = 0.54$; Table A2). However, the mean $\delta^{13}\text{C}$ values of dormouse populations in spring were not related to measures of food availability.

The sizes of dormouse isotopic trophic niches (SEAc), were significantly greater in autumn than in spring (2.56 times larger (1.20, 5.44 95% CLs); $\text{RI} = 1$; Fig. 4A). This difference appeared to be most attributable to the increased ranges in $\delta^{13}\text{C}$ values, which were also greater in summer (2.84 times larger (2.25, 3.71 95% CLs); $\text{RI} = 1$; Fig. 4B). There were no differences in any of the other Layman's metrics (SEAc, C range, N range, NND, CD) between sites, or in relation to mean proportion of food plants or mean numbers of invertebrates in spring (Table A2).

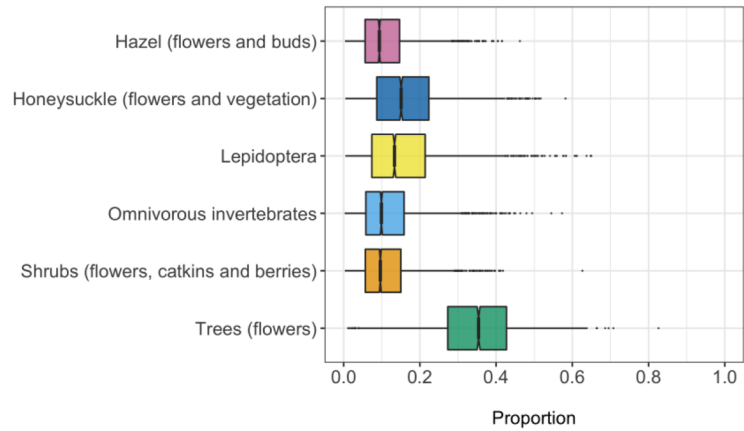
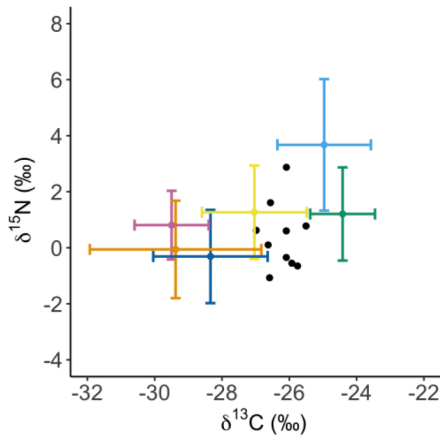
For three sites that were visited in both spring and autumn (and on which more than 10 dormice were sampled in each visit; Sites 2, 3 and 7; Table 1), Bayesian estimates of trophic niche area (SEAc) were larger in autumn than in spring on two of the three sites (Fig. 5). The mean differences in the estimates of SEAc in spring and autumn were 5.0 (1.3, 10.2 95% CLs; 99% of probability distribution comparisons were larger in autumn than in spring) and 1.6 (0.3, 3.6 95% CLs; 99% of comparisons were larger) respectively on these sites. The third site had a non-significant size difference of 0.7 (-0.4 , 1.7 95% CLs).

After correction for multiple hypothesis testing, no measures of population status (Abundance, Breeding and Trend indices) on sites were related to any measures of isotopic niche (mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ or LMs; Table A3).

4. Discussion

Stable isotope analyses of dormouse tissue and of their putative food sources indicate that foods from trees were important in dormouse diets in both spring (flowers) and autumn (seeds). This finding emphasises

Spring



Summer

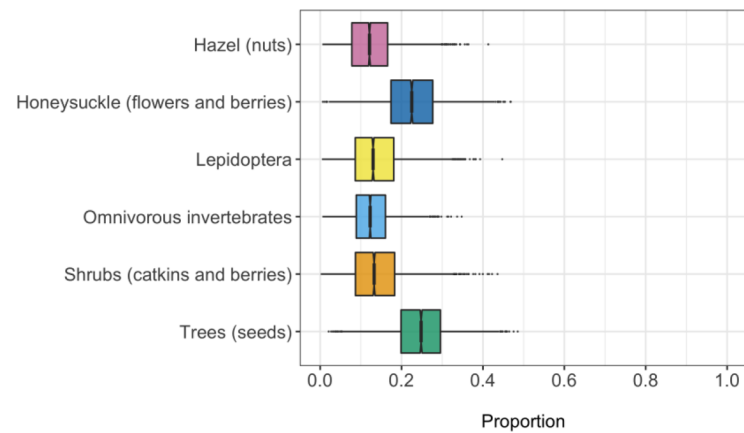
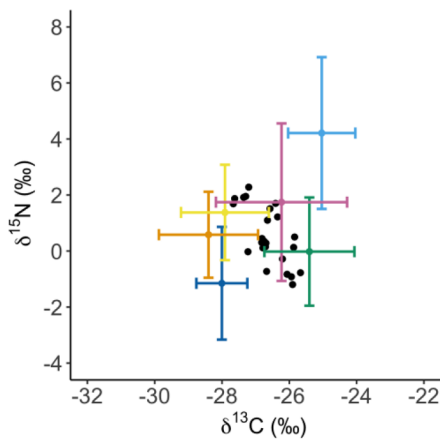


Fig. 3. Stable isotope ratios of dormice and their potential food groups and estimates of the proportional contributions of potential food groups to the diets of dormice living in Bradfield Woods, Suffolk, England. Dormice are shown as black dots. Food groups are shown as mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ \pm standard deviation error bars. Proportional contributions to diets are calculated using Bayesian mixing models in SIMMR. Trophic discrimination factors have been applied to adjust food group isotopic positions upwards for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

the importance of large trees that produce a significant number of flowers in spring and mast in autumn. It also suggests that tree seeds (particularly from ash and oak) may play a larger role in dormouse diet composition than has previously been assumed (Ancillotto et al., 2014; Juškaitis, 2007). Honeysuckle was an important food source, reflecting its abundance in the woodland. Hazel did not appear to be an important food source in late summer, though this reflects the fact that the

sampled hair was grown over the summer, before hazelnuts had ripened.

All three analyses (individual, population, mixing model) provide evidence that dormice are opportunistic feeders, feeding on foods that are more readily available within their immediate vicinity of the resting site at which they were sampled. Invertebrate abundance at different spatial scales was important in determining trophic level ($\delta^{15}\text{N}$) of

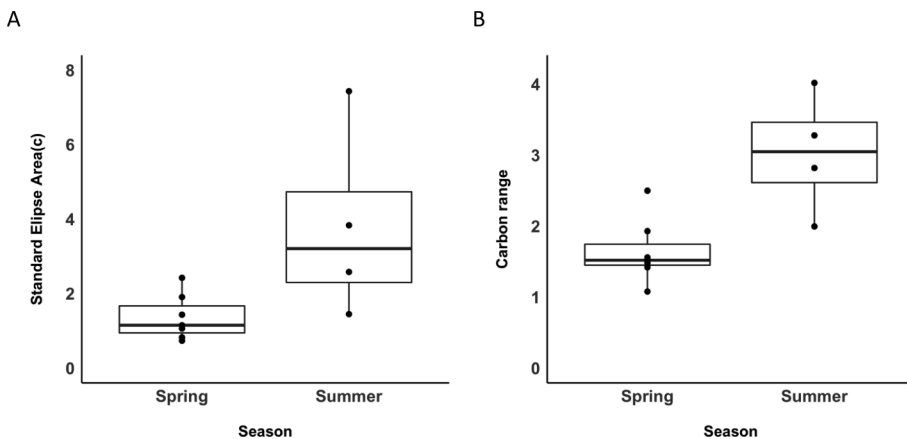


Fig. 4. Isotopic trophic niche areas (A) and Carbon ranges (B) of dormouse populations in English woodlands in spring and summer. Trophic niche areas are Bayesian estimates of the Standard Ellipse Area corrected for small sample sizes and Carbon range is the range of $\delta^{13}\text{C}$ values of individual dormice isotopic signatures, following Layman et al. (2007, 2012). Boxplots show the median (central line) and the 25th and 75th percentiles (box). Points showing the values for single sites are included.

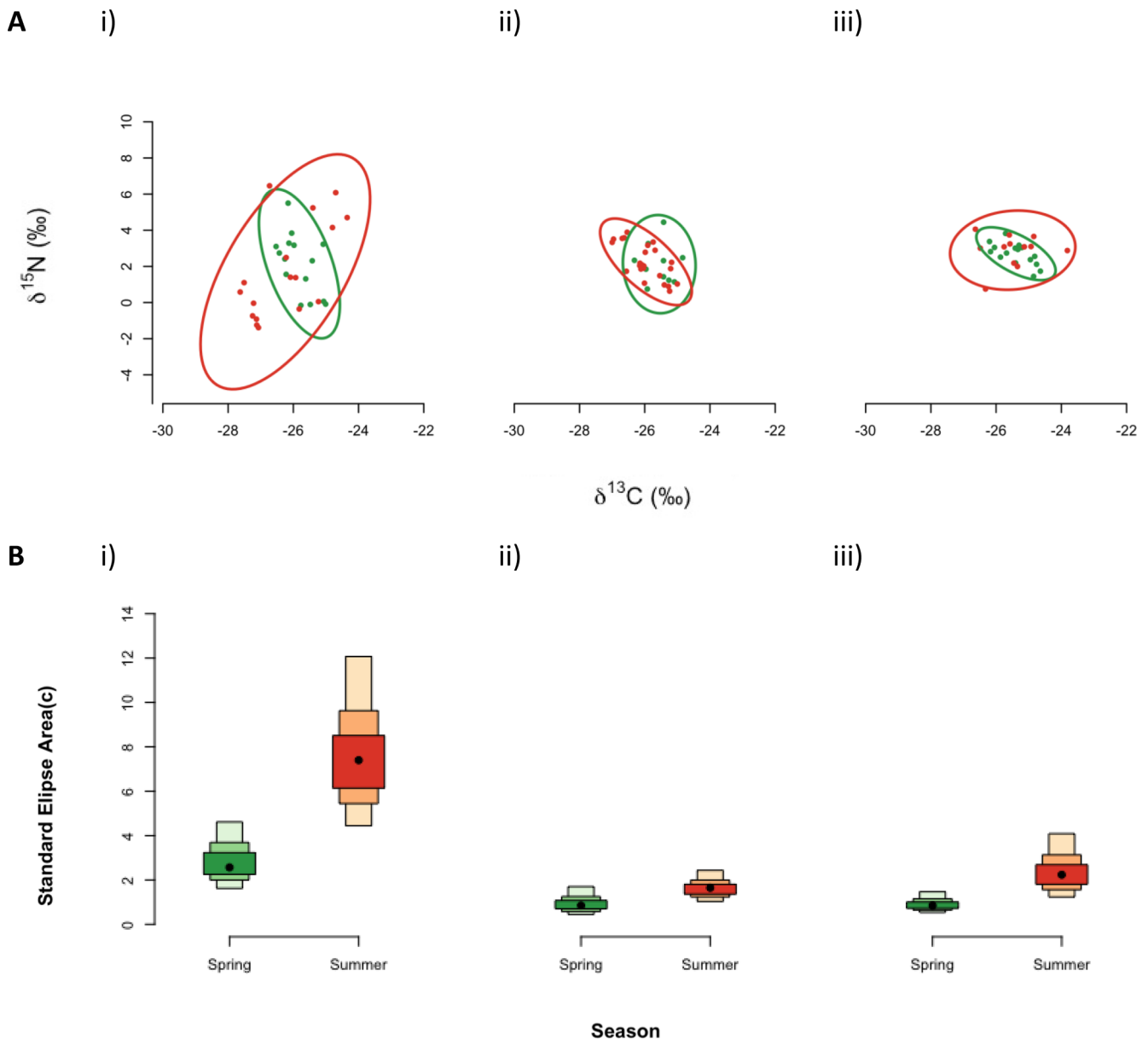


Fig. 5. The isotopic niche spaces occupied by dormouse populations in spring and summer in three English woodlands: (i) Site 3 (ii) Site 2 (iii) Site 7 (Table 1). Isotope ratios of dormouse hair and their isotopic niche spaces are shown in (A) and Bayesian posterior estimates of the Standard Ellipse Area corrected for sample size (SEAc) in (B). Isotope values are adjusted by site isotopic baselines.

dormice, and invertebrates may play a more important part in dormouse diet than other studies have found (Juškaitis, 2007). Slightly more counterintuitively, the $\delta^{13}\text{C}$ values of dormice were negatively related to the abundance of invertebrates. This could be because dormice rely more heavily on food sources from trees (which have higher $\delta^{13}\text{C}$ values; see Fig. 3) when there are fewer invertebrates available in spring. Diet reconstruction also shows that dormice appear to increase their consumption of invertebrates in response to the reduced availability of plant foods, as increased proportion of omnivorous invertebrates and Lepidoptera in the diet of individuals was related to reduced availability of food plants. Both these findings suggest that dormice are facultative predators, and can feed at different trophic levels in response to varying availability of both plant and animal food resources.

The relationship between higher $\delta^{15}\text{N}$ values and increased diversity of vegetation might appear counterintuitive, as one might expect higher proportions of vegetation to be eaten when more plant species are available. On the other hand, diverse vegetation communities are

inevitably composed of some species that do not bear large quantities of flowers or fruit. This finding therefore could bolster evidence of the adaptable feeding behaviour of the dormouse, as populations might require a dominance of fruiting and flowering species in woodland habitat, and feed more on invertebrates when these are scarce.

These findings illustrate that dormice are adaptable feeders, utilising food resources that are locally abundant (Juškaitis, 2007; Juškaitis et al., 2016). This counters previous suggestions that dormice have very specific feeding habits (Morris, 2003; Richards et al., 1984). Within generalist species, local adaptations to resource availability are important for determining trophic ecology (Ben-David et al. 1997; Camus and Arancibia, 2013; Layman and Allgeier, 2012). Understanding that this response can occur at such a small scale, in this case within a 50 m radius of the occupied nest box, suggests that dormice adapt to their local resource conditions and do not travel further from the nest site to acquire the resources that comprise the bulk of their dietary intake (Vander Zanden et al., 2000).

While we found relationships between food availability and

dormouse isotopic signatures, we found no relation between isotopic signature or differences between food availability on the condition of individuals. This could be due to the fact that the dormouse's flexible feeding strategy means they acquire adequate nutrition from whatever food is available with no measurable impact on an individual's body condition (Juškaitis, 2007; Juškaitis et al., 2016). However, physiological consequences of diet may be subtle and act over longer timeframes, especially compared to demographic and seasonal parameters.

The size of a population's trophic niche was greater when sampled in autumn, corresponding with findings at single sites that dormice have a varied diet of both invertebrate and plant foods over the summer and early autumn (Bright and Morris, 1993; Richards et al., 1984). The greater range of $\delta^{13}\text{C}$ values in summer diet indicates this larger niche is driven by consumption of a greater diversity of plant foods. This effect may be particularly pronounced on the sites we studied, as greater seasonal diet variability in better quality habitat has been found with other species (Blanco-Fontao et al., 2013). This is in accordance with other studies that have observed dormice tending to eat a great proportion and range of plant matter in late summer and autumn (Bright and Morris, 1993; Juškaitis et al., 2016; Richards et al., 1984).

Despite these relationships between food availability and population trophic niche, we did not find any differences in population attributes in relation to population isotopic characteristics. It is possible that the subtle effects of habitat were too small to be detected within our sample. An alternative explanation however is that food resources are not a limiting factor within our study sites, which have relatively high-density dormouse populations and a high number of food plants. Following others (Lobo and Millar, 2011; Shaner et al., 2013), we suggest that further studies identifying physiological mechanisms by which diet can have population-level consequences would be of real value here. Other environmental factors, such as climate or landscape, might therefore affect population dynamics on these sites to a greater extent (Goodwin et al., 2018). Additionally, it would be beneficial to look at other differences between sites, for instance predator abundances and nest site prevalence, to investigate whether these might relate to population declines.

The connections we found between food availability and trophic position, and the consistency of this finding in individual and population level analyses and mixing models, highlights that stable isotope analysis can provide broad insights into dormouse feeding ecology (Araújo et al., 2007). That said, in woodland settings, where putative food groups overlap in their isotopic signatures, and where dormice appear to have generalist diets, the degree of taxonomic resolution provided by isotopic methods is clearly not as fine as might be provided by other methods, such as molecular analysis of faeces (Inger and Bearhop, 2008). The strength of the isotopic approach is that it can represent diet composition in terms of the major items ingested over longer timeframes and is less sensitive to short-term dietary changes (Richards et al., 1984). We found that for a surprisingly generalist species, however, isotopes cannot disentangle fine-scale variation within shrub, tree and invertebrate groups used in mixing models, and cannot build a detailed picture of the likelihood of specific plant and invertebrate foods being consumed (Araújo et al., 2007).

There are some caveats to the results of this study, particularly to do with the sampling of sources for the mixing model. By using the dietary information contained in hair tissue, we include a level of temporal uncertainty associated with the growing period. We aimed to control for this uncertainty by standardising our sampling procedure and selecting sampling periods within two timeframes during which hair moult and growth is documented (Homolka, 1978; Juškaitis and Büchner, 2013; Lozan, 1970). There is still some disagreement, however, in the timing of moult in dormice, which can be influenced by climate and habitat (Juškaitis and Büchner, 2013). We found consistency, however, between samples from the same individual, indicating that hair is growing generally in the same area at the same time. While many studies do not present values for the consistency of

samples representing the same dietary time periods, the differences between individuals' isotopic values we found are smaller than, or similar to, other studies looking at within-individual differences (Kim et al., 2012; Grecian et al., 2015). The repeatability values we found are also higher than for temporal analysis within individuals, providing further evidence that the dormouse hair samples are from similar time frames (Hjernquist et al., 2009; Larson et al., 2013; Zango et al., 2019). Similarly, variations in phenological timings of individual plants within a woodland (Cole and Sheldon, 2017) means it is likely we were able to collect samples of plants which were available when dormouse hair was grown. While there is still some chance that some plant phenophases will have ended, or invertebrate communities changed, before collection began, the broad source groupings in mixing models mean these specific differences are unlikely to change the relative abundance of resources between local areas in the woodland. For individual and population trophic analyses, this is unlikely to have had a large effect as, individual plants were recorded as food plants even if their flowering or fruiting time had ended, and invertebrate abundance is broadly indexed.

This consistency between samples, with the broad timeframes covered by our sampling periods, mean conclusions about feeding cannot be more temporally specific, and some more detailed temporal differences in trophic ecology may be masked. Our food sampling was subject to several, likely minor, practical constraints: we were only able to collect plant and invertebrate samples in the daytime and up to human head height, we were unable to include aphids, an invertebrate group reportedly consumed by dormice (Juškaitis, 2007), as they were generally < 3 mm; and finally, we were unable to sample bird's eggs, which have been found to be consumed by dormice. Additionally, tree beating may not be able to fully capture numbers of some taxa, e.g. flying insects, but has proven able to capture a range of species. Given the grouping of food species into broad groups; the requirement of an index of invertebrate abundance rather than an absolute count; the equivalence of sampling across sites; and the small size and low biomass of aphids (Juškaitis et al., 2016; Juškaitis and Baltrūnaitė, 2013; Sara and Sara, 2007) we consider these sampling omissions unlikely to have substantially altered our conclusions.

By analysing landscape-scale count data, the status of dormouse populations has been shown to be more favourable (in terms of abundance, breeding and population trends), in woodlands whose management is favourable to particular plant and tree species (Goodwin et al., 2018a). Here we have confirmed the importance of certain food sources to dormice, honeysuckle in particular, but have provided additional evidence of the importance of trees throughout the year, arising from their extensive flowering in spring and seed production in autumn. This highlights the importance of large masting trees in the habitat of dormice, as well as shrubby habitats, which have been demonstrated to be beneficial on a population level (Goodwin et al., 2018a). In addition, we show that dormice readily exploit invertebrates where these are available, or when preferred food plants are scarce. Our dietary analyses, therefore demonstrate the means by which dormice might benefit from woodland management plans which take into account that they: (i) consume a variety of plant foods in the autumn, (ii), exploit invertebrate foods, (iii) consume a high proportion of food from trees in spring and summer and (iv) are affected by small-scale differences in food availability. Resulting management actions could include establishing and maintaining habitats along rides and in glades with a high diversity of plant species and high abundances of invertebrates; preserving large trees with an abundance of flowers; and ensuring these habitats occur throughout the woodland.

Author contributions

The manuscript was conceived and guided by CG, RM, DH and SB. The fieldwork was planned and conducted by CG and PC, with input from GS. Data were analysed by CG, with advice from GS. The

manuscript was written by CG and reviewed and revised by RM, DH, PC and GS.

CRedit authorship contribution statement

Cecily E.D. Goodwin: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing - original draft, Writing - review & editing. **George J.F. Swan:** Formal analysis, Writing - review & editing. **David J. Hodgson:** Supervision, Writing - review & editing. **Sallie Bailey:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing - review & editing. **Paul Chanin:** Investigation, Methodology, Writing - review & editing. **Robbie A. McDonald:** Conceptualization, Funding acquisition, Project administration, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. The food source groups, constituent samples and sample sizes used in dietary assessment of dormice in Bradfield Woods.

Source groups	Constituent samples					
	<i>Spring</i>	(<i>n</i>)	<i>Total n</i>	<i>Autumn</i>	(<i>n</i>)	<i>Total n</i>
Hazel	Hazel leaf buds	21	21	Hazel nut	20	20
Honeysuckle	Honeysuckle flower	15	20	Honeysuckle flower	8	25
	Honeysuckle leaf	5		Honeysuckle berry	17	
Shrubs	Birch catkin	10	33	Birch catkin	5	85
	Bramble flower	15		Bramble berry	19	
	Hawthorn berry	8		Hawthorn berry	45	
				Sloe berry	4	
Trees	Oak flower	15	23	Rose hip	12	
	Willow flower	8		Acorn	20	24
Lepidoptera	Larvae	7	9	Ash seed	4	
	Adults	2		Larvae	6	6
Omnivorous	Hemiptera	2	42	Hemiptera	3	47
Invertebrates	Coleoptera	13		Coleoptera	19	
	Araneae	24		Araneae	20	
	Dermaptera	2		Dermaptera	5	
	Ephemeroptera	1				

Appendix B. Analytical tables

See Tables B1–B3.

Table B1

Top model sets ($\Delta AICc < 2$) for all model selection analyses included in the results.

Formula	df	LogLik	AICc	$\Delta AICc$	Weight
Individual trophic analysis: $\delta^{15}N$ signature of dormice					
Invert_abund + Plant_diversity	5	-234.2	478.9	0	0.04
Invert_abund + Plant_diversity + Weight	6	-233.5	479.6	0.7	0.03
Invert_abund + Plant_diversity + Prp_food_plants	6	-233.5	479.6	0.7	0.03
Invert_abund + Plant_diversity + Weight + Prp_food_plants	7	-232.5	479.9	1.0	0.02
Invert_abund + Plant_diversity + Sex	6	-233.8	480.1	1.2	0.02
Invert_abund + Plant_diversity + Season	6	-234.1	480.7	1.8	0.02
Invert_abund + Plant_diversity + Activity	6	-234.1	480.7	1.8	0.02
Invert_abund + Plant_diversity + Prp_food_plants + Sex	7	-233.0	480.8	1.9	0.01
Individual trophic analysis: $\delta^{13}C$ signature of dormice					
Invert_abund + Season	5	-149.6	309.6	0	0.02
Invert_abund + Season + Age_class	6	-148.6	309.8	0.2	0.02
Invert_abund + Season + Activity	6	-148.7	309.9	0.3	0.02
Invert_abund + Season + Sex	6	-148.7	309.9	0.4	0.01
Invert_abund	4	-150.9	310.1	0.5	0.01

(continued on next page)

Table B1 (continued)

Formula	df	LogLik	AICc	ΔAICc	Weight
Invert_abund + Season + Age_class + Activity	7	-147.7	310.2	0.7	0.01
Invert_abund + Season + Activity + Sex	7	-147.7	310.3	0.7	0.01
Invert_abund + Sex	5	-150	310.4	0.8	0.01
Invert_abund + Season + Age_class + Sex	7	-147.8	310.4	0.9	0.01
Invert_abund + Season + Invert_diversity	6	-149	310.5	0.9	0.01
Invert_abund + Invert_diversity	5	-150.1	310.6	1.0	0.01
Invert_abund + Season + Age_class + Activity + Sex	8	-146.9	310.8	1.3	0.01
Invert_abund + Prp_food_plants	5	-150.2	310.9	1.3	0.01
Invert_abund + Season + Activity + Invert_diversity	7	-148.1	310.9	1.3	0.01
Invert_abund + Season + Invert_diversity + sex	7	-148.1	310.9	1.3	0.01
Invert_abund + Invert_diversity + sex	6	-149.2	310.9	1.4	0.01
Invert_abund + Invert_diversity + Prp_food_plants	6	-149.2	310.9	1.4	0.01
Invert_abund + Season + Weight	6	-149.2	311	1.4	0.01
Invert_abund + Season + Invert_diversity + Age_class	7	-148.1	311	1.4	0.01
Invert_abund + Sex + Prp_food_plants	6	-149.3	311.2	1.6	0.01
Invert_abund + Plant_diversity	6	-149.3	311.2	1.6	0.01
Invert_abund + Sex + Invert_diversity + Prp_food_plants	7	-148.2	311.2	1.6	0.01
Invert_abund + Season + Activity + Sex + Invert_diversity	8	-147.1	311.3	1.7	0.01
Invert_abund + Season + Prp_food_plants	6	-149.4	311.3	1.7	0.01
Invert_abund + Season + Age_class + Prp_food_plants	7	-148.3	311.3	1.8	0.01
Invert_abund + Age_class	5	-150.5	311.4	1.8	0.01
Invert_abund + Weight	5	-150.5	311.4	1.8	0.01
Invert_abund + Season + Age_class + Activity + Invert_diversity	8	-147.2	311.4	1.9	0.01
Invert_abund + Season + Age_class + Plant_diversity	7	-148.3	311.5	1.9	0.01
Invert_abund + Season + Activity + Plant_diversity	7	-148.4	311.5	1.9	0.01
Invert_abund + Season + Activity + Weight	7	-148.4	311.6	2.0	0.01
Dormouse activity state (Active Torpid)					
Season	4	-65.3	138.9	0	0.05
Season + δ ¹⁵ N	5	-64.6	139.7	0.8	0.03
Season + δ ¹⁵ N + δ ¹³ C	6	-63.7	140.1	1.2	0.03
Season + Sex	5	-64.9	140.2	1.3	0.02
Season + δ ¹³ C	5	-65	140.4	1.5	0.02
Season + Plant_diversity	5	-65	140.4	1.5	0.02
Dormouse body weight					
Season + Sex + δ ¹⁵ N	6	90.9	-169.2	0	0.07
Season + Sex + δ ¹⁵ N + Plant_diversity	7	91.9	-168.9	0.3	0.06
Season + Sex + Plant_diversity	6	90.6	-168.6	0.6	0.05
Season + Sex	5	89.2	-168	1.2	0.04
Season + Sex + δ ¹⁵ N + Invert_abund	7	91.2	-167.4	1.8	0.03
Season + Sex + δ ¹⁵ N	7	91.2	-167.4	1.8	0.03
Season + Sex + Total_food	7	91.2	-167.4	1.8	0.03
Season + Sex + Plant_diversity + Total_food	6	90	-167.3	1.9	0.03
Season + Sex + Plant_diversity + Invert_abund	7	91.1	-167.2	2.0	0.03
Population trophic analysis: SEAc					
Season	3	-7.6	24.5	0	0.82
Population trophic analysis: Range in δ¹³C					
Season	3	-0.3	9.9	0	0.95

Table B2

The p-values of the tests of the relationships between food availability and mean dormouse isotopic niche characteristics. As two tests were performed on each metric, the critical p-value was 0.025.

	Mean prop. food plant cover	Mean invertebrate abundance
Mean δ ¹³ C	0.12	0.49
Mean δ ¹⁵ N	0.28	0.02*
SEAc	0.08	0.69
δ ¹⁵ N range	0.08	0.52
δ ¹³ C range	0.55	0.19
NND	0.05	0.85
CD	0.13	0.28

Table B3

The p-values of the tests of the relationships between the dormouse isotopic niche characteristics of different populations and the Abundance, Breeding and Trend indices of that population. As a model of each metric was run separately for each population index (7 models), the critical p-value was 0.00625.

	Mean $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SEAc	$\delta^{15}\text{N}$ range	$\delta^{13}\text{C}$ range	NND	CD
Abundance index	0.85	0.97	0.19	0.26	0.15	0.17	0.33
Breeding index	0.62	0.29	0.48	0.83	0.02	0.30	0.95
Trend index	0.80	0.21	0.55	0.58	0.71	0.64	0.51

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