

Research article

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Unravelling the seasonal dietary dynamics of the endangered garden dormouse (*Eliomys quercinus*) in Flanders, Belgium

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Abstract. The garden dormouse (*Eliomys quercinus*) faces significant population declines across Europe, prompting urgent conservation measures. A critical aspect of these efforts is understanding the species' dietary composition and preferences within specific areas and how this changes throughout the year. We compared garden dormouse diets between two habitats in West Flanders, Belgium with faecal analysis from May to October, covering almost their entire active phase. Our findings revealed a diverse diet of both plant and animal matter, with notable variations between habitats and seasons. Blackberries and other fruits, leaves, and to a lesser extent flowers, were the predominant plant-based food sources in both study areas, with seasonal fluctuations indicating a dietary shift throughout the dormouse's active period. Spring diets consisted primarily of young leaves and flowers, changing to increased fruit consumption in summer. Beetles emerged as a main animal food source throughout the entire active period. Snails were prominently eaten in the woody area, while millipedes prevailed in the diet in the dune environment, both more in spring than later in the active season. These insights highlight the importance of maintaining diverse fruit sources and preserving beetle, snail, and millipede populations for garden dormouse conservation. This study provides valuable insights into dormouse dietary preferences and thus contributes to targeted conservation strategies being essential for the survival of the dormouse.

Keywords. Garden dormouse, *Eliomys quercinus*, diet, faecal analysis, seasonal variation.

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Introduction

The garden dormouse (*Eliomys quercinus*) is categorized as 'Near-Threatened' in both the European and Global Red List (Bertolino *et al.* 2008; EEA 2023). This species has declined dramatically over the past thirty years, surpassing that of any other rodent in Europe. Its geographical range has shrunk significantly by 50% since 1978 and by another third since 2008 (Temple & Terry 2007; Bertolino

2017). While dormice are common and widely distributed in South-western Europe (Portugal, Spain, France and Italy), North-western, Central and Eastern Europe have witnessed a sharp decline (Germany, Belgium, Ukraine, Czech Republic, Romania, and Croatia) or even total disappearance (Lithuania, Latvia, Estonia, Poland, Finland, and Slovakia), emphasizing the urgent need for targeted conservation efforts in these specific areas (Bertolino *et al.* 2008; Cortens & Verbeylen 2009; Meinig & Büchner 2012; Bertolino 2017; Bennett & Richard 2021; Verbeylen 2022; Pilāts *et al.* 2023; Büchner *et al.* 2023; Cichocki *et al.* 2024).

One possible contributing factor to the decreasing populations in these areas is the diminishing of suitable habitats where open spaces with shrubby vegetation have been replaced by dense woody areas or by intensified agriculture (Bertolino 2017; Bennett & Richard 2021). This diminishment of suitable habitats coincides with a decrease in food sources, which inevitably affects garden dormouse populations (Bertolino 2017; Bennett & Richard 2021). In order to protect and maintain the existing dormouse populations, highly detailed and localized conservation strategies need to be developed (Amori *et al.* 1995; Meinig & Büchner 2012; Bertolino 2017; Mori *et al.* 2020). One critical aspect for the development of these plans is a more detailed understanding of the diet composition and thus, preferred food sources of dormice within the specific areas where they occur and how this varies throughout the year (Kuipers *et al.* 2012; Litvatis 2000; Büchner *et al.* 2022; Llobat & Marín-García 2022).

The garden dormouse is an omnivorous species with a preference for arthropods (Kuipers *et al.* 2012). Nevertheless, the proportion of different food items in their diet has been found to vary seasonally and focussing an investigation on only a few months may lead to biased conclusions. One of the initial studies exploring the seasonal variation in the garden dormouse's diet was conducted by Gil-Delgado *et al.* (2010) in Mediterranean Spain, where the garden dormouse is common. Applying these findings to other regions with different environmental conditions proves challenging. Only a few studies have been conducted outside the Mediterranean regions, but they either had a low sample size, or lasted just a few months, neglecting any seasonal variation (Holišova 1968; Kahmann *et al.* 1972; Palacios 1975; Gigirey & Rey 1999; Bekkers & Van Turnhout 2010; Kuipers *et al.* 2012).

The current study focuses on the garden dormouse's diet throughout its active period in West Flanders, Belgium, using faecal analysis. The garden dormouse is classified as 'endangered' in Flanders, and the province of West Flanders wants to protect its remaining garden dormouse populations, ensuring that they can remain at a sustainable level (Dochy 2013). A detailed insight into their diet is currently lacking, which is needed to improve the conservation management in this region (Dochy 2013). The current study was conducted in two different areas – an inland nature reserve and a coastal area – about 50 kilometres apart, from May to October, which captures almost the entire regional active period of dormice (Cortens & Verbeylen 2009; Verbeylen 2022). This setup allows us to compare seasonal diet preferences between two distinct environments, being characterized by different vegetation and soil types.

Given that the garden dormouse is omnivorous, we anticipated detecting both plant and animal matter in its diet. Nevertheless, the frequency of specific food items is expected to vary seasonally, dependent on their availability. We hypothesized that green plant material and flowers would be more prevalent in the diet during the spring and summer months, while fruits and seeds would feature more prominently in summer and autumn. Due to their preference for arthropods, we also expected finding a higher occurrence of arthropod parts in the diet of dormice throughout all seasons. Lastly, we expected to detect differences in diet composition between the two study sites, primarily owing to variations in food availability within these locations.

Material and methods

Study area

The study was conducted in two different areas: a woody and a dune area. The woody area (Leiekant-'t Schrijverke; 50.810935 N, 3.224964 E; see the analysis script, the R-markdown file, in the supplementary information) is a nature reserve located in Kortrijk next to the river 'Leie'. It has a wide variety of vegetation types, including sparse pasture, thicket vegetation and brushwood. The dune area (Doornpanne; 51.122352 N, 2.664685 E) is located in Koksijde at the west coast of Belgium. This part of the Doornpanne consists mainly of dunes with calcareous dune grassland, shrub vegetation, poplar forest and thorny thicket vegetation.

Nest boxes are present in both areas (11 in the woody and 15 in the dune area, installed in 2010 and 2015, respectively), which the garden dormice use for hibernation, and as maternity nests and as resting places during daytime (Cortens & Verbeylen 2009). The design of these nest boxes, with the entrance facing the tree, was developed by British researchers Morris *et al.* (1990) for hazel dormice, and afterwards adapted and installed for different dormouse species throughout Europe.

Faecal sampling & analysis

At both sites, faecal samples were collected at the end of each month from May to October 2022. Each time, the same nest boxes were checked and as many faeces as possible were collected and placed in the freezer (-22 °C) at the end of the day. To ensure only fresh faecal samples were collected each month and to avoid contamination with older faeces, the nest boxes were thoroughly cleaned in April and after each monthly sampling.

The faecal samples were analysed following Kuipers *et al.* (2012) two weeks after the last collection period in October. Each faecal dropping was placed in a separate test tube to which boiled lukewarm water was added to soften them. The test tubes were then gently shaken and set aside for a couple of minutes, allowing the debris to settle at the bottom. The fluid at the top was removed and the faecal sample was placed inside a petri dish. The samples were then analysed using a stereo microscope (6–50 ×) and tweezers. The different food remains were categorized based on the comparative collection of Kuipers *et al.* (2012), which was supplemented by faecal samples from a previous, unpublished, study and additional collections of arthropods. The latter were sampled in both areas from August until September using pitfalls (28 plastic cups with a height of 10 cm and a diameter of 7.5 cm) and the arthropods were used for additional comparisons. The final reference collection was then cross-referenced using field guides and the advice of different taxonomic experts. The food remains of plant origin were grouped into the following categories: green plant parts (leaves), stamen (flowers), fruit pulp/peels (fruits), blackberry seeds (blackberries) and other seeds (Fig. 1A). For food remains of animal origin, the categories were: Hemiptera, Diptera, Dermaptera, Hymenoptera, Coleoptera, Gastropoda, Diplopoda, Orthoptera, Isopoda, Araneae, Opiliones, Pseudoscorpiones, Aves, Mammalia and hairs (Fig. 1B; R-markdown file in supplementary information for more details). Lastly, an 'undetermined' category was included for the animal items that were not identifiable. Mosses were frequently found as well, but were not considered as food for the dormice, since mosses and feathers are primarily used as nesting materials. Feathers were only considered as a food remnant if they were abundantly present in the faecal sample.

Statistical analysis

A total of 671 faecal samples were collected ($N_{\text{Dune area}} = 261$, $N_{\text{Woody area}} = 411$) from 21 nest boxes ($N_{\text{Dune area}} = 10$, $N_{\text{Woody area}} = 11$) in May-October 2022. For each separate faecal sample, presence (1) and absence (0) for each of the 21 categories of food remains was recorded.

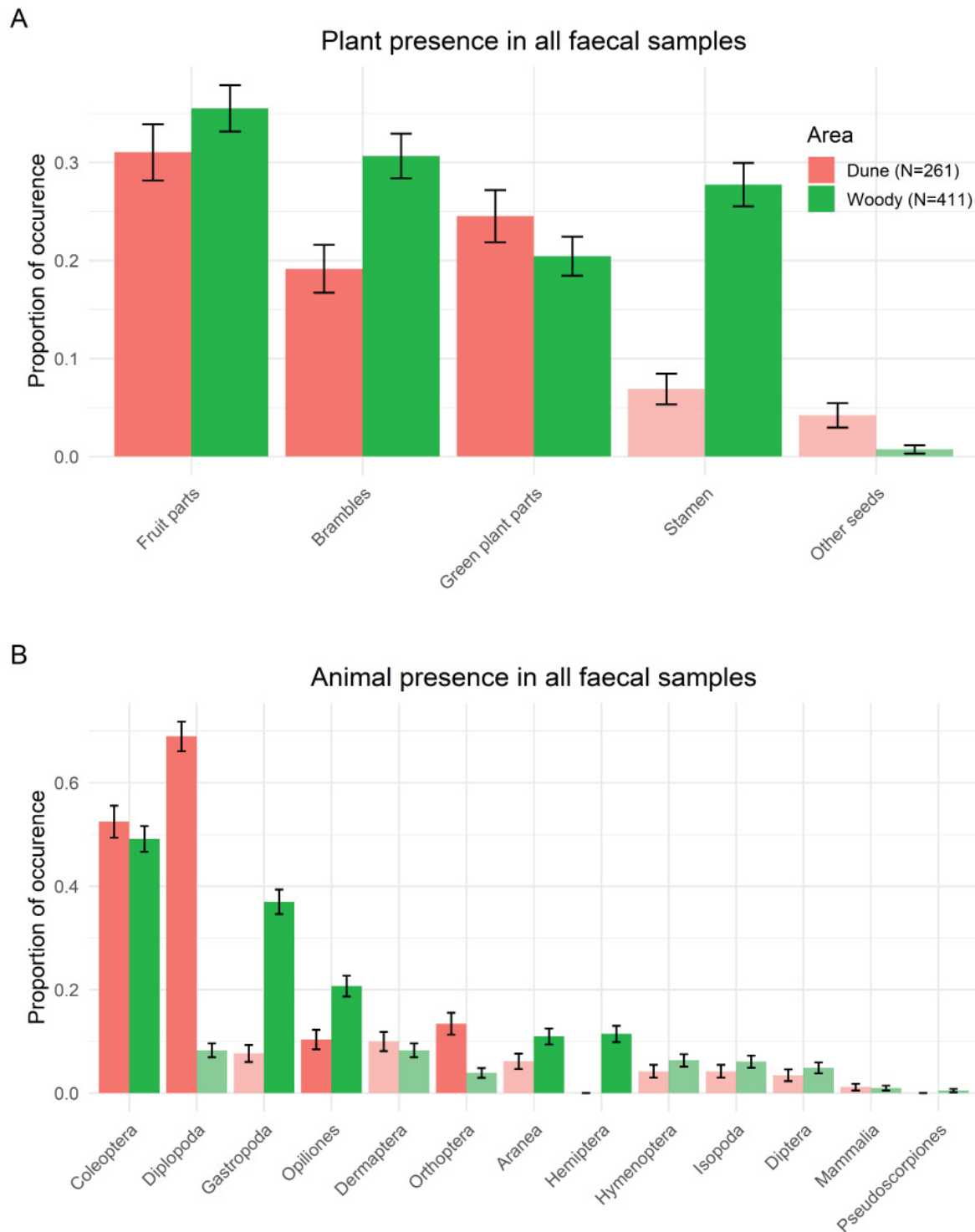


Figure 1 – Proportion of occurrence of the different (A) plant- and (B) animal-based food categories in all analysed faecal droppings collected in the woody (green) and dune (red) area. Proportions were calculated as the sum of all faecal samples containing a specific food category divided by the total number of analysed faecal samples; \pm standard error. Food categories where the occurrence was lower than 10% were made transparent.

The prevalence of all categories of food remains (total occurrence/number of analysed faecal samples) during the whole study period is shown in Fig. 1 (see R-markdown in supplementary information for more details). We excluded categories of food remains that occurred less than 10% in both areas from further analysis (Fig. 1), as well as the categories ‘undetermined’ and ‘hairs’ which were both found in more than 95% of the faecal samples in both areas (see table in R-markdown file in the supplementary information). Lastly, we also excluded Hemiptera from further analysis since they were never found in faecal pellets in the dune area, and led to issues regarding model convergence during the first steps of the analysis.

We then constructed a dataset in which we calculated the percentage of occurrence of each category of food remains for each collection period and nest box (number of faecal samples in which the category occurred/total number of faecal samples analysed from the nest box in that month; see supplementary information). In this dataset, each nest box was considered as a single data point per month. In October, there were only data from three nest boxes (i.e., datapoints). We therefore decided to group data from September and October together in further analysis (see R-markdown in supplementary information).

We ran a separate generalized linear mixed model with a binomial error distribution, for each category of food remains (green plant parts, fruit pulp/peels, blackberry seeds, stamen, Coleoptera, Gastropoda, Diplopoda, Orthoptera, Opiliones and Araneae). In each model, we included sampling month (categorical), area (dune/woody) and an interaction between them as fixed effects, allowing us to test if the proportion of a specific category of food remains varied over the different months and between the two areas. Nest box, nested as variable within each sampling area, was included as a random effect. The proportions of different food items were weighed by the total number of faecal samples that were analysed from the nest box in that particular month.

All statistical analyses were conducted with R software 4.2.1 (R Core Team 2016) with the R package lme4 (version 1.1-35.1; Bates *et al.* 2015). Post hoc tests were performed using the lsmeans package (version 2.30-0; Lenth 2016), and the DHARMA package (version 0.4.6; Hartig 2022) was used to test the model assumptions. Only the model with Araneae showed zero-inflatedness. A new model was constructed with the glmmTMB package (version 1.1.8; Brooks *et al.* 2017) to account for this. All the codes, statistical analyses, results, data visualisation and data preparation are summarized in the R-markdown file in the supplementary information.

Results

Proportion of occurrence of all categories of food remains

Fruit pulp/peels were the most common category of plant origin, found in $33.78\% \pm 1.82\%$ (proportion \pm SE) of all analysed faecal samples (dune area (D): $31.03\% \pm 2.86\%$; woody area (W): $35.52\% \pm 2.36\%$; Fig. 1A). The second most common food item were blackberry seeds (all samples (A): $26.19\% \pm 1.70\%$; D: $19.16\% \pm 2.44\%$; W: $30.66\% \pm 2.27\%$), followed by parts of green plants (A: $22.02\% \pm 1.60\%$; D: $24.52\% \pm 2.66\%$; W: $20.44\% \pm 1.99\%$). Second to last were stamen, which were more frequently present in faecal pellets in the woody area than in the dune area (A: $19.64\% \pm 1.53\%$; D: $6.90\% \pm 1.57\%$; W: $27.74\% \pm 2.21\%$). Undetermined seeds were rare as food remains in both areas (A: $2.08\% \pm 0.55\%$; D: $4.21\% \pm 1.24\%$; W: $0.73\% \pm 0.42\%$; Fig. 1A).

Coleoptera (beetles) were the most common category of animal origin in faecal pellets (A: $50.45\% \pm 1.93\%$; D: $52.49\% \pm 3.09\%$; W: $49.15\% \pm 2.47\%$; Fig. 1B). Diplopoda (millipedes) were the second most prominent category of animal food remains (A: $31.85\% \pm 1.80\%$) overall. However, the occurrence of this category differed between the two areas and was more prominent in the dunes (D: $68.97\% \pm 2.86\%$) than in the woody area (W: $8.27\% \pm 1.36\%$). The opposite effect was found for Gastropoda (snails), the

third most frequent category in faecal pellets (A: $25.60\% \pm 1.68\%$; D: $7.66\% \pm 1.65\%$; W: $36.98\% \pm 2.38\%$). Opiliones (harvestmen) were the fourth most common category as food remains (A: $16.67\% \pm 1.44\%$; D: $10.34\% \pm 1.89\%$; W: $20.68\% \pm 2.00\%$), followed by Araneae (spiders; A: $9.08\% \pm 1.11\%$; D: $6.13\% \pm 1.48\%$; W: $10.95\% \pm 1.54\%$). Dermaptera (earwigs) occurred in less than 10% of the faecal samples in both areas (A: $8.93\% \pm 1.10\%$; D: $9.96\% \pm 1.85\%$; W: $8.27\% \pm 1.36\%$) and were therefore excluded from further analysis. Orthoptera, on the other hand, had a lower overall presence in all faecal samples compared to the previous category (A: $7.59\% \pm 1.02\%$), but were kept in the analysis because their presence was higher than 10% in the dunes (D: $13.41\% \pm 2.11\%$; W: $3.89\% \pm 0.95\%$; Fig. 1B). The last seven categories, Aves (A: $7.89\% \pm 1.04\%$; D: $4.21\% \pm 1.24\%$; W: 10.21 ± 1.49), Hemiptera (A: $6.99\% \pm 0.98\%$; D: 0.00% ; W: $11.44\% \pm 1.57\%$), Hymenoptera (A: $5.51\% \pm 0.88\%$; D: $4.21\% \pm 1.24\%$; W: $6.33\% \pm 1.20\%$), Isopoda (A: $5.36\% \pm 0.88\%$; D: $4.21\% \pm 1.24\%$; W: $6.08\% \pm 1.18\%$), Diptera (A: $4.32\% \pm 0.78\%$; D: $3.45\% \pm 1.13\%$; W: $4.87\% \pm 1.06\%$), Mammalia (A: $1.04\% \pm 0.39\%$; D: $1.15\% \pm 0.66\%$; W: $0.97\% \pm 0.48\%$) and Pseudoscorpiones (A: $0.30\% \pm 0.21\%$; D: 0.00% ; W: $0.49\% \pm 0.34\%$) were rare and therefore not used for further analysis (Fig. 1B). Lastly, undetermined animal parts were present in almost all samples (D: $100\% \pm 0.00\%$; W: $0.98\% \pm 0.01\%$). These parts were often extremely small, making it impossible to determine their taxonomic origin.

Monthly variation in diet composition

Plant materials

The proportion of garden dormouse faeces with green plant parts was relatively high in May in both areas, but decreased throughout the following months (Fig. 2A). Only in July, green plant material was significantly more frequent in faecal pellets in the dunes than in the woody area (Supplementary Figure 1B). The decrease of this diet component in the woody area occurred more rapidly at the beginning of the year, with proportions in May being significantly higher than in all other months (Supplementary Figure 1D). For the dune area, this decrease was more gradual and frequencies of green plant material were only significantly lower in the last three months (August, September and October) as compared to May (Supplementary Figure 1C). The opposite pattern can be observed for the fruit parts, with proportions increasing from less than 10% in May to more than 60% in September–October in both areas (Fig. 2B). While there were no significant differences in the proportion of fruits in the faeces between the two areas over the different months (Supplementary Figure 2B), there were differences in the timing of this increasing trend. In the dune area, the proportion of faeces with fruit parts increased significantly from May to July after which it remained relatively constant (Supplementary Figure 2C). For the woody area, this proportion remained low and constant until July, after which it increased significantly in August and remained constant until the end of the active season (Supplementary Figure 2D).

The graph with the proportion of faeces with blackberry seeds had a parabolic shape, with a peak in the middle of the active period of the garden dormouse (Fig. 2C). This parabolic trend, however, was only significant for the woody area, where the proportions increased significantly from May to July, remained constant from July to August and then decreased significantly in the last months (Supplementary Figure 3D). There were no statistically significant differences ($p > 0.05$) in the proportion of blackberry seeds among the different months within the dune area (Supplementary Figure 3C), nor between the two study areas (Supplementary Figure 3B). The proportion of flowers in the diet (faeces with stamen) differed significantly between the two areas (Fig. 2D), especially in May and July (Supplementary Figure 4B). Indeed, in the woody area this proportion was high in May and decreased significantly until July after which it remained constant (Supplementary Figure 4D), while in the dune area, the proportion of flowers remained relatively low during the entire study period (Supplementary Figure 4C).

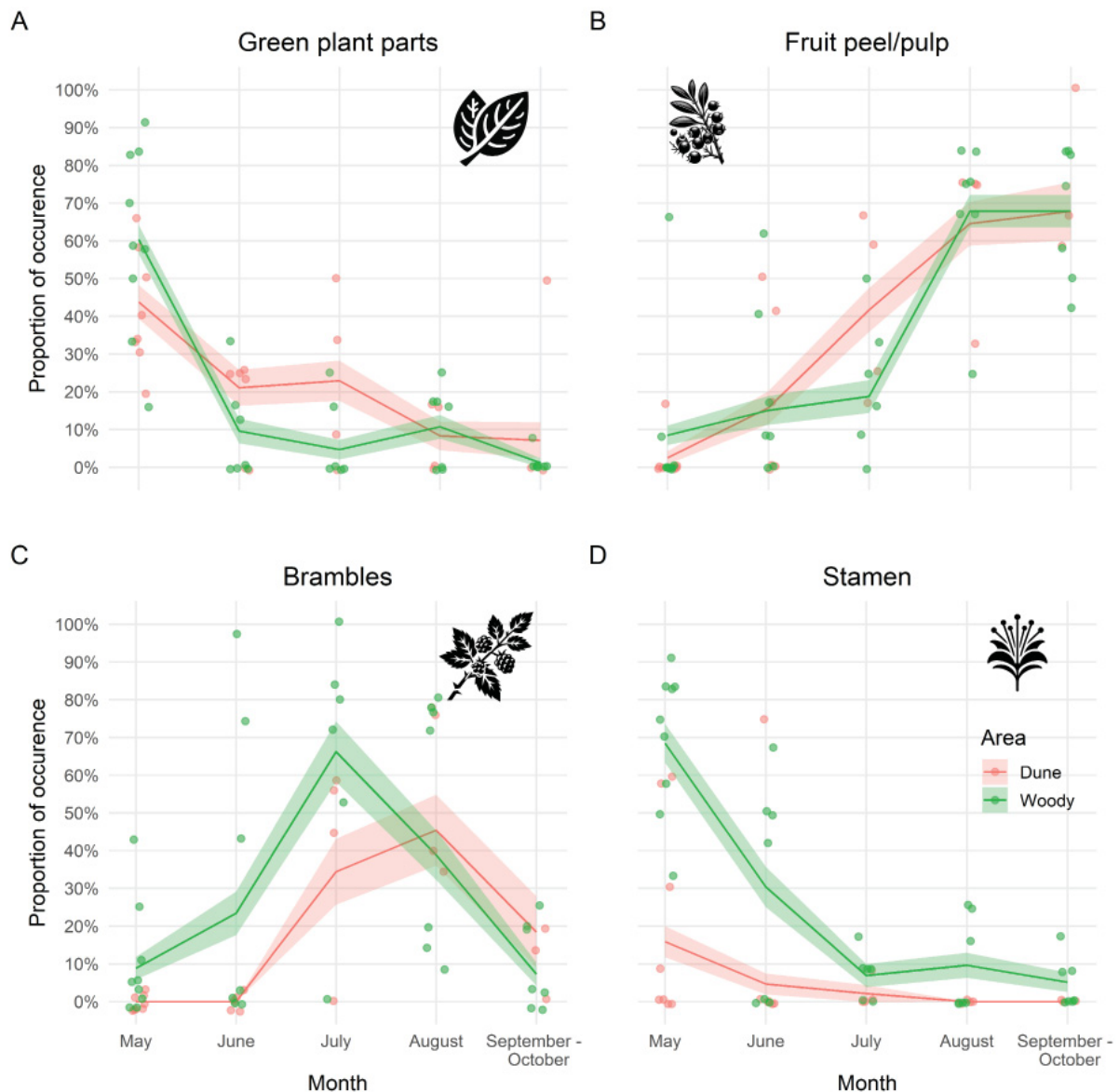


Figure 2 – Temporal variation of the proportion of the different main plant-based food categories in all analysed faecal droppings collected in the woody (green) and dune (red) area. Proportions were calculated as the number of faecal samples containing the specific food category divided by the total amount of analysed faecal samples per nest box in each month. The lines represent the mean percentage per sampling period (\pm standard error) and the dots are the estimated proportions per nest box.

Animal materials

The proportion of faeces with Coleoptera remains was consistently high throughout the whole active period of the garden dormouse in both areas (Fig. 3A; Supplementary Figure 5). The frequency of Gastropoda remains within faeces was significantly higher in the woody area than the dune area (Fig. 3B) from May to August (Supplementary Figure 6B), but not in September-October. This can be explained by the fact that in the woody area this proportion decreased significantly in August compared to the previous three months, when it had been relatively stable, and was zero in September and October (Supplementary Figure 6D). In the dune area, the presence of gastropod remains in the faeces was low

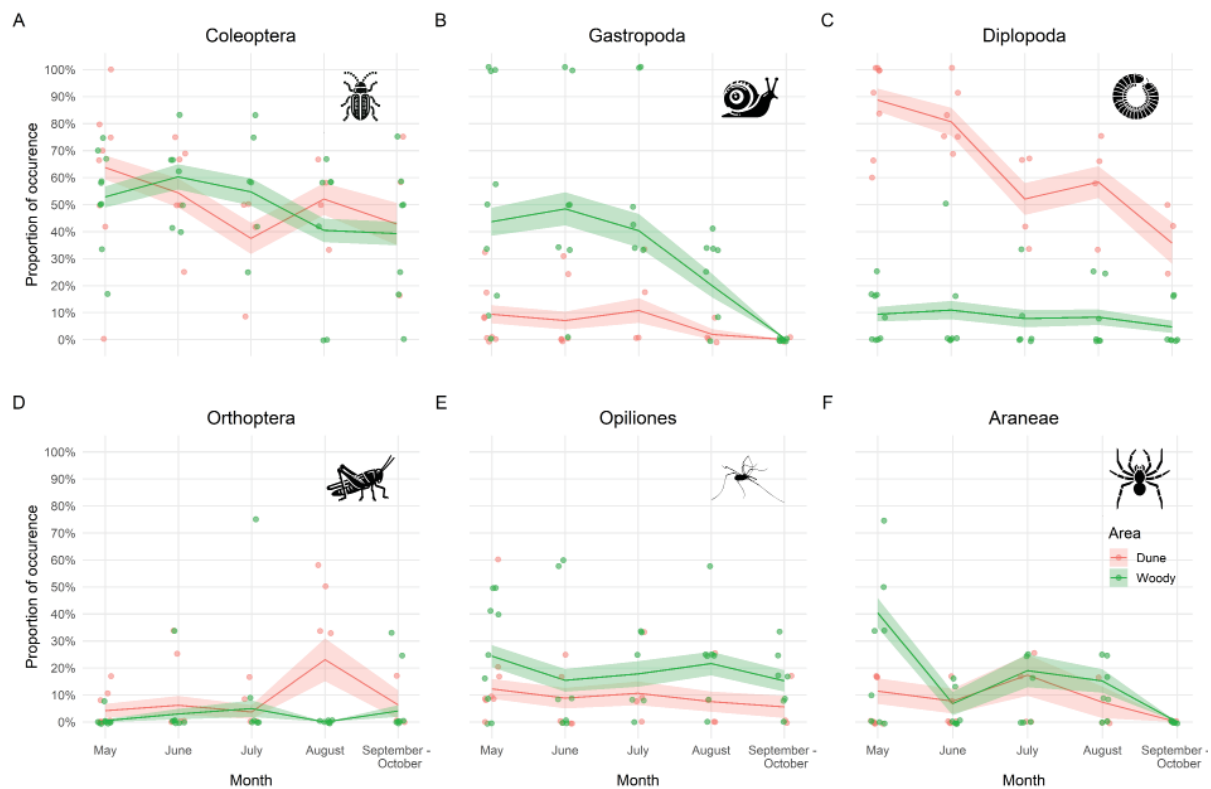


Figure 3 – Temporal variation of the proportion of the different main animal-based food categories in all analysed faecal droppings collected in the woody (green) and dune (red) area. Proportions were calculated as the number of faecal samples containing the specific food category divided by the total amount of analysed faecal samples per nest box in each month. The lines represent the mean percentage per sampling period (\pm standard error) and the dots are the estimated proportions per nest box.

throughout the different months (Supplementary Figure 6C). For Diplopoda, the opposite pattern could be observed. Diplopoda remains were present in a significantly higher proportion of faeces in the dune than in the woody area throughout the whole active period (Fig. 3C; Supplementary Figure 7B). In the woody area, faeces proportions with Diplopoda remains remained consistently low throughout the year (Supplementary Figure 7D) whereas in the dune area, the proportion decreased gradually, and the only significant drop was found between May and September-October (Supplementary Figure 7C).

The presence of Orthoptera remains in the faecal samples was consistently low in both areas throughout the study period (Fig. 3D; Supplementary Figure 8), with one exception, a significantly higher proportion for the dune area in August as compared to the previous months (Supplementary Figure 8C). Opiliones remains made consistently up a low proportion of faeces in both areas and did not vary through time (Fig. 3E, Supplementary Figure 9). The same pattern could be found for Araneae (Fig. 3F; Supplementary Figure 10) except for May. During that month, the proportion of Araneae remains in the faeces was significantly higher in the woody area, after which it significantly dropped (Supplementary Figure 10B, D).

Discussion

In this study, we compared the dietary patterns of garden dormice between two distinct habitats within West Flanders, Belgium, being characterized by differing vegetation and soil types (an inland forest

and a coastal dune landscape). The analysis relied on the examination of faecal droppings which were collected monthly from May to October from different nest boxes, encompassing almost the entire active phase of this species, as they typically hibernate from late September-November to mid-April-mid-May in Flanders (Cortens & Verbeylen 2009; Verbeylen 2022). As anticipated due to the species' omnivorous nature, our findings revealed that the garden dormice in our study areas consumed a combination of plant and animal matter (Table 1). However, the relative proportions of these dietary components varied between the two habitats and seasonally.

Plant materials

Blackberries and other fruits, leaves, and to a lesser extent, flowers were the predominant dietary components identified in the faecal samples in both study areas. However, their proportional representation was notably lower as compared to the studies conducted in the Netherlands and Slovakia (Holišova 1968; Kuipers *et al.* 2012). For the fruits, this difference can probably be explained by differences in the sampling period. Our study period spanning from May to October, revealed a remarkable seasonal variance in fruit consumption, which was around 10% of faeces with fruit remains in spring and then increased significantly during the summer to more than 60% in both habitats. Kuipers *et al.* (2012), on the other hand, collected their samples from the end of June to the middle of November, the period in which fruit remains were also highly prevalent in the faecal pellets in our study. The summer period in our study, where we found high proportions of fruit parts in the diet, coincides with the availability and ripening of berries of the most common berry-bearing shrub species in the dune area (*Hippophae rhamnoides* and *Crataegus monogyna*) and the woody area (*Sambucus nigra*, *Crataegus monogyna* and *Prunus spinosa*). These fruits have a high content of water, carbohydrates and antioxidants (Atkinson & Atkinson 2002; Ruiz-Rodríguez *et al.* 2014; Ciesarová *et al.* 2020), which is vital for fat accumulation for hibernation, increasing the garden dormice's chance for survival (Ambid *et al.* 1990; Giroud *et al.* 2023).

Regarding leaves, however, the same explanation cannot be applied, since the proportion of this food item in the diet declined during the year. This suggests that leaves are replaced by fruits in the diet of dormice in our study areas, and the replacement becomes more prevalent during summer with the decreasing nutritional value of aging leaves. Younger leaves are easy to digest and are richer in nitrogen and water, making them a better source for both hydration and nutrients than older leaves (Mattson 1980; Hörtensteiner & Feller 2002). The discrepancy in the proportions of leaves in our study compared to the results from the Netherlands (Kuipers *et al.* 2012) and Slovakia (Holišova 1968) might be attributed to the reduced availability of suitable young leaves in our study sites, given the limited size of the woody area (6.76 ha) and sparse tree cover in the dune area.

The proportion of blackberry seeds was similar to results from the Netherlands (Table 1). We also noticed that the proportions peaked in July and August in both study areas, which coincides with the ripening period of blackberries from July to September (Finn & Clark 2012). Lastly, a significantly higher proportion of flowers was observed in the woody area during spring (May and June) than in the dune area, where flower remains were almost completely absent in the faeces throughout the whole study period. This pattern can be explained by an increased floral presence in woody regions during spring.

Altogether, our findings indicate a shift in the plant components of the diet of the garden dormouse throughout its active period. In spring, the diet is primarily comprised of green, young leaves and flowers (predominantly in the woody area). These become gradually replaced by blackberries at the onset of summer, and are later supplemented by various other fruits until hibernation. This sequential dietary changes mirrors the availability of these plant food sources, and support the opportunistic feeding behaviour of the garden dormouse.

TABLE 1

Updated overview table from (Kuipers *et al.* 2012) on the occurrence of the various main food categories of the garden dormouse in percentage, comparing the findings of the current with previous published dietary studies.

Region	This study	Belgium	the Netherlands	the Netherlands	Kuipers <i>et al.</i> (2012)	Slovakia	North-West Spain	Formentera, Spain	South Spain
Method		Faeces	Faeces	Faeces	Faeces	Stomach	Stomach	Stomach	Stomach
Number of Samples	671	671	40	139	10	20	40	27	27
Sampling period	Spring – Autumn	Spring	Spring	Summer – Autumn	Summer – Autumn	Summer – Autumn	Spring	Autumn	Autumn
Animals									
Millipedes	32% (D: 69%; W: 8%)	66%	70%	60%	65%	18%	11%	11%	11%
Centipedes	–	–	–	–	–	28%	11%	48%	48%
Beetles	50% (D: 52%; W: 49%)	7%	35%	20%	35%	90%	53%	–	–
Hymenopterans	6% (D: 4%; W: 6%)	6%	11%	10%	10%	100%	–	–	–
Earthworms	–	–	22%	10%	10%	26%	–	–	–
Snails	26% (D: 8%; W: 37%)	–	–	–	–	20%	60%	26%	26%
Grasshoppers and crickets	8% (D: 13%; W: 4%)	–	7%	–	–	55%	93%	11%	11%
Spiders	24% (D: 17%; W: 28%)	1%	–	–	–	20%	68%	–	–
Lizards	–	–	3%	6%	1%	–	–	–	–
Mammals	1% (D: 1%; W: 1%)	1%	–	–	–	–	–	–	–
Birds	8% (D: 4%; W: 10%)	–	–	–	–	–	–	–	–
Plants									
Nuts and seeds	–	–	–	–	–	15%	–	7%	7%
Blackberries, and raspberries	26% (D: 19%; W: 31%)	–	22%	–	–	60%	–	26%	26%
Juniper berries	–	–	–	–	–	–	–	11%	11%
Green plant parts	22% (D: 25%; W: 20%)	35%	66%	50%	–	–	–	–	–
Fruit pulp/peels	34% (D: 31%; W: 36%)	–	76%	–	–	–	–	–	–
Flowers (stamen)	20% (D: 7%; W: 28%)	9%	1%	–	–	–	–	–	–

Animal materials

The consistent presence of beetles in approximately 50% of the faecal samples throughout the entire active period in both habitats suggests that they are a vital food source for garden dormice. Beetles are rich in proteins and other essential nutrients (Kim *et al.* 2019) and will therefore contribute substantially to the garden dormouse's nutritional needs for growth, reproduction and overall health. In addition to beetles, we found that snails and millipedes were important animal food sources as well, although their prevalence differed between the two study areas. Snails were significantly more frequent in the diet of garden dormice residing in woody areas, while millipedes were more prevalent in the dune environment. A possible explanation for the snails is that their density (and thus availability) is higher in woody areas, since they favour moist and shaded environments to minimize moisture loss (Rosin *et al.* 2017; Wehner *et al.* 2019). However, it is not clear whether this is also the case for our study sites. Although millipedes typically favour similar ecological conditions (Kime & Golovatch 2000; David 2009; David & Handa 2010), they occurred more frequently in the diet of the of garden dormice residing in the dune area. One potential explanation is that the densities, and availability, of millipedes are lower than expected in the wooded area, though the underlying reasons remain unclear. Ecosystem acidification, which is partly attributed to increased nitrogen depositions, is known to adversely affect the exoskeletons of millipedes (Vogels *et al.* 2023). This effect may be more pronounced in forest areas compared to dune areas, as the annual nitrogen deposition at our forest study site is nearly twice as high as that at our dune study site (Vlaamse Milieumaatschappij 2024). This effect, however, would need to be a recent phenomenon since Kime (2004) found a higher number of millipede species in the sandy loam region than in the maritime (dune) area in Flanders. An alternative explanation could be that the garden dormouse prefers to forage on snails over millipedes and will only feed on the latter when snails are less abundant. However, this contrasts with the findings of Kuipers *et al.* (2012) where millipedes showed a significantly higher proportion in the diet than snails. A more comprehensive investigation focusing on the densities of these animal groups in both environments is needed to identify the underlying factors. This would also require sampling these invertebrates in higher parts of the vegetation (shrubs and trees).

Interestingly, both snails and millipedes were more prominently present in the diet during spring, after which their proportions diminished toward the end of the active period. Both millipedes and snails contain significantly higher concentrations of calcium than other invertebrates. They are an important source of calcium for songbirds (Graveland *et al.* 1994; Bureš & Weidinger 2003) and, based on our results, potentially for garden dormice as well. This could be especially relevant in spring, when a higher intake of calcium is needed due to the onset of the reproduction period, which starts in May-June in Flanders (Cortens & Verbeylen 2009). It is thus plausible that garden dormice actively seek these food items during this crucial reproductive phase. The latter explanation is not unlikely given that garden dormice were shown to exhibit scavenge and predatory behaviours (Díaz-Ruiz *et al.* 2017). The proportion of spiders (Opiliones and Araneae) and grasshoppers in the diet remained around 20% throughout the year in both study areas suggesting that they are a stable and relative important food source throughout the year.

In summary, our study highlights the importance of two primary animal food sources for garden dormice in Flanders. Beetles emerged as the prevalent food source in both woody and dune environments throughout the entire active period. Snails and millipedes constituted the second most frequent animal food source in woody and dune areas, respectively, with their presence declining throughout the year, indicating a seasonal preference for these food items, particularly during spring.

Conservation implications

The garden dormouse populations across Europe have experienced substantial declines in recent decades (Bertolino 2017). Ongoing conservation efforts are directed toward revitalizing and safeguarding these

remaining populations and their habitats. However, safeguarding habitats requires a broader approach ensuring both ample connectivity between them and the availability of appropriate food sources (Amori *et al.* 1995; Meinig & Büchner 2012; Bertolino 2017; Mori *et al.* 2020; Verbeylen 2022). A comprehensive understanding of their dietary preferences is crucial for effective conservation strategies of the dormouse. One way to study this is to investigate the proportion of different food categories present in their faecal droppings, providing insights into their dietary habits and preferences. However, it is important to note that the number of faecal droppings containing certain food items does not necessarily equate to the volume of those items consumed, which is impossible to quantify using faecal droppings alone. Therefore, interpretations of dietary preferences may vary depending on whether volume-based calculations are considered. Furthermore, dietary studies based solely on morphological analysis, such as the current study, have additional limitations. While morphological approaches offer valuable insights into food category presence, they tend to underestimate the importance of plants with higher digestibility or faster decomposition rates and lack the resolution to identify certain food items at finer taxonomic levels, inevitably leaving some materials unclassified. Although more costly, the application of DNA sequencing techniques, such as high-throughput metabarcoding, would greatly improve accuracy and taxonomic detail, offering a more comprehensive understanding of species' feeding ecology (Iwanowicz *et al.* 2016; Gabrielson *et al.* 2024) and we recommend applying this approach to future studies on diet preference of dormice. Despite its limitations, our methodology can serve as a valuable proxy for assessing dietary preferences, and offers insights into the relative importance of different food categories in the garden dormouse's diet in Flanders.

Our study confirmed the omnivorous diet of the garden dormouse, which consists of both plant and animal materials (Büchner *et al.* 2022). In our study, the plant-based component of their diet predominantly comprised leaves and flowers in spring, which were then replaced by fruits later in the year. Conservation initiatives should, therefore, prioritize the availability of adequate and diverse tree and shrub species within dormice habitats, to provide a continuous succession of blossoms and fruits throughout the active season. This availability of fruit-bearing plant species is also necessary outside of the period examined by the current study, as garden dormice can also be active late in the season (November–December) and now and then even in winter (Cortens & Verbeylen 2009). Climate change, leading to warmer, wetter, and more variable winters, and therefore a faster depletion of fat reserves, will make access to food in winter even more important. Regarding animal-based dietary components, our findings emphasized the importance of beetles as the primary and consistent food source throughout the year. Snails prevailed as the second most frequent animal-based food source in woody areas, whereas millipedes were equally important in the dune environment. Conservation strategies should prioritize the maintenance of viable beetle, snail, or millipede populations within these habitats. The two latter are calcium-rich invertebrates as they use calcium as structural elements in their exoskeletons. Nitrogen-deposition driven soil acidification poses a threat to these invertebrates, as their calcium-bearing exoskeletons will dissolve at low pH (Vogels *et al.* 2023), which will, in turn, jeopardize garden dormouse populations feeding on these invertebrates. Monitoring and mitigating soil acidification should thus also be considered for conservation of the remaining garden dormouse populations.

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Data accessibility

The data and the corresponding R-markdown file will be archived online on figshare, a public and digital repository https://figshare.com/articles/online_resource/Eikelmuis_analyse/24968985?file=43971183

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