The hazel dormouse *Muscardinus avellanarius* prefers more often forest edges before and after hibernation

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Different habitat types of the hazel dormouse: hedgerow, forest edge and structured forest (photographs by Dalida Dutoit).

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Abstract

Biodiversity loss is a worldwide crisis that has been worsening over the last century. To preserve species from extinction, conservation plans can be implemented. For that matter, knowledge about species is necessary. However, there are many knowledge gaps amongst many taxa. This study focuses on the hazel dormouse *Muscardinus avellanarius*, an endangered rodent present in Switzerland, particularly sensitive to habitat degradation and destruction. It deals with the different habitat types that the hazel dormouse can occupy throughout the year. The goal is to understand the dynamic of the species' occupancy and to uncover where the species occurs most before and after hibernation, given that there might be a difference in the habitat preference between fall and spring. To research that, 150 footprint tunnels were used in the Val-de-Ruz (canton of Neuchâtel) and Gantrisch (canton of Bern) regions in Switzerland. They were placed in hedgerows, forest edges and structured forests. Every week, the 30 transects, composed of 25 footprint tunnels for each habitat type category in each region, were checked for two months before and after the hibernation of the hazel dormouse. Detection/non-detection data was recorded thanks to the identification of the footprints. Occupancy models were fitted to account for imperfect detection. The habitat type impacts significantly the occupancy of the hazel dormouse: the species seems to prefer forest edges to hedgerows or structured forests. The interaction between the habitat type and the season also has a significant influence on its occupancy: forest edges occupancy decreases between fall and spring. However, in hedgerows and structured forests, occupancy is indicated to be low and constant between seasons. The slope is the only topographical variable to significantly influence occupancy, with a steeper slope decreasing hazel dormouse occupancy. Thanks to the survey conducted in three different habitat types, this study could demonstrate that the hazel dormouse is not as associated with hedgerows as the literature suggests. Forest habitats are more preferred by the hazel dormouse, whether it is before or after hibernation.

Keywords

Hazel dormouse, footprint tunnels, habitat type preference, occupancy models, R-package 'unmarked', species conservation.

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1. Introduction

1.1. Biodiversity and species conservation

Since the year 1500, 30% of species worldwide (with a level of uncertainty of 16-50%) have faced the threat of extinction or have been extinct (Isbell et al., 2023). Since the industrial revolution, circa 200 years ago, humans induced a severe species loss (Ceballos et al., 2015). By 2100, 37% of species (with a level of uncertainty of 20-50%) could go extinct if the biodiversity loss trends do not change (Isbell et al., 2023). The biodiversity loss rate is so high that experts call it a potential sixth mass extinction (Ceballos et al., 2015), highlighting the emergency to slow down this crisis (IPBES, 2019).

There are several drivers to the decline in biodiversity considered worldwide (IPBES, 2019; Isbell et al., 2023). Mainly land- and sea use change (also known as habitat loss and degradation) and over- or direct exploitation of species, but also climate change, pollution and invasive alien species threaten biodiversity in terrestrial and aquatic ecosystems (IPBES, 2019; Westveer et al., 2022). The more biodiversity gets lost, the more ecosystem functions will be negatively impacted (Isbell et al., 2023). Ecosystem functions are considered as sources of services and goods. These are necessary and profitable for humans (De Groot, 1992). They stem from ecosystem structures and natural processes, which themselves result from reactions and exchanges between biotic and abiotic elements of ecosystems. There are four generalized ecosystem functions: they regard the regulation of ecological processes, the habitats for shelter and reproduction, the production of biomass, and the information for human health and reference (for evolutionary questions) (De Groot et al., 2002). Ecosystem functions depend on biodiversity, and both are declining. Some services and goods from nature are irreplaceable (IPBES, 2019). Restoring the environment and preserving biodiversity, despite being complex, is the only way to stabilize humans' relationship to nature (De Groot, 1992). Biodiversity loss stands as a threat to humans because their quality of life depends on the ecosystem functions that biodiversity supports (De Groot et al., 2002; Isbell et al., 2023; Marselle et al., 2021). For example, the loss of biodiversity in agroecosystems threatens food security for humans. Thus, maintaining high biodiversity levels and ecosystem quality is fundamental for all living species on Earth (IPBES, 2019).

Regions in the world are not affected the same by the drivers of species decline (IPBES, 2019). Latin America and the Caribbean are the regions with the highest population change rate between 1970 and 2018, which represents a decrease of 94%. Following comes Africa with 66%, and Asia and the Pacific with 55% of population decline. North America has seen a decrease by 20%, and Europe and Central Asia by 18% (WWF, 2022). Globally, population sizes declined by 69% in average between 1970 and 2018. These percentages come from the Living Planet Index, which is based on the number of known species and the populations' size changing over time (WWF, 2022). These geographical trends cannot be directly compared one to another, as the regions do not have the same data available to evaluate the index. Furthermore, regions have not been impacted by the threats for the same amount of time, and they did not have the same biodiversity to start with. However, these percentages show that everywhere in the world, biodiversity and populations are decreasing (Westveer et al., 2022).

As biodiversity loss gets more serious over time, it is crucial to act against it and increase the implementation of conservation actions to protect species and ecosystems from extinction or disturbance. If more conservation efforts and investments are implemented soon, 25% instead of 37% of species could go extinct by 2100 (Isbell et al., 2023). For 30 years, plans to reduce biodiversity loss have been carried out, but declines in biodiversity have still been reported (WWF, 2022). Biodiversity conservation and species conservation correspond to strategies to postpone or ideally stop biodiversity loss and species extinction (IPBES, 2019; Isbell et al., 2023; Tälle et al., 2023). Between action plans for species, ecological restoration, ecotourism, and the creation of national parks, many conservation approaches exist (Rands et al., 2010). The necessity for those plans is reinforced as even more species, still unknown to human knowledge, might be at threat. In fact, knowledge gaps stand as obstacles in the fight against biodiversity loss (IPBES, 2019). Filling them is a challenge for the conservation of species and biodiversity (Rands et al., 2010). For well-known species and groups, there is enough knowledge to implement conservation actions for them. However, for some underdescribed species groups, knowledge is too scarce to do so (IPBES, 2019). In consequence, some other species can embody a whole group of species or environmental factors and act as representative of that group. This can be helpful regarding conservation assessments or action plans (Caro & O'Doherty, 1999). Higher-taxon approaches, or umbrella, keystone, flagship and indicator species can fill that role in vertebrate species (Tälle et al., 2023; Zhang et al., 2020). The protection of one landscape, ecosystem or group of species, can benefit several taxa and natural entities, when following some criteria (Tälle et al., 2023). The surrogate species aimed at in conservation plans should have taxonomic, functional, or ecological similarities with the species meant to "co-preserve". Furthermore, higher-taxon approaches are more helpful regarding monitoring surveys, and plans at regional or landscape scale represent a worthwhile trade-off between effective implementation and successful plans (Tälle et al., 2023).

Mammal species are well described, and it is the second group with the highest extinction percentage (almost 2% of extinct mammals in 2018) after amphibians and before birds. The survival of mammal species has been declining since 1980 according to the Red List index (IPBES, 2019). Species in general do not face the same extinction risk. For instance, there is a clear distinction between large and small mammals. The higher extinction risk of large mammals is not based on the vulnerability that a slow life history brings (Fisher & Owens, 2004). It relies more significantly on both intrinsic ecological traits (biology and life-history) and environmental factors (geographic ranges and human impacts), whereas the extinction risk of smaller species seems to depend solely on environmental factors. Thus, larger species brave a more severe decline predisposition (Cardillo et al., 2005).

Another difference between small and large mammals is the number of studies carried out for each category: studies on small mammals are less numerous than those on larger mammals. This is problematic, as population monitoring and knowledge are necessary to assess conservation statuses (Capt, 2022). One species particularly affected by this issue is the hazel dormouse *Muscardinus avellanarius*. In Switzerland, there is a lack of population knowledge regarding this species (Capt, 2022; Haag, 2014). Even if knowledge on the species has been deepened in the last 30 years in the United Kingdom, it remains less developed in other countries or regions (Haag, 2014). Nonetheless, the number of studies on this species

continues to increase over time and across different regions, shedding light on various aspects of its ecology. This study aims to contribute to that body of knowledge.

1.2. *Muscardinus avellanarius*

The hazel dormouse *Muscardinus avellanarius*, also called the common dormouse, is a small mammal that belongs to the Glirid family. It is a small, copper-colored and arborical rodent (Figure 1), who lives on trees and scrub branches in woodlands, hedgerows and woody areas. Woody areas with shrubs that are at least 20 hectares large are excellent habitats for the hazel dormouse. Vegetation is very important for that species because it lives and feeds on it. The hazel dormouse diet consists in insects, flowers (pollen and nectar), nuts, seeds and berries. It can live on many species of trees and bushes like hazels, oaks, honeysuckles, brambles, sycamore maples, ash, viburnum, yews, hornbeams, brooms, swallows, birches, sweet chestnuts, blackthorns, hawthorns, conifers, and ivies (Bright et al., 2006). The hazel dormouse can distance itself up to 70 meters away from its nest, moving through the vegetation according to the food availability, which varies from a season to another (Bright et al., 2006). Moreover, the hazel dormouse can travel 1700 meters for seasonal migration (Holzgang et al., 2001). So, around mid-September, young individuals migrate to new territories to raise their offspring (Haag, 2014).

Figure 1: Hazel dormouse (Vassen, 2019).

Regarding the habitat types of the hazel dormouse, hedgerows seem to be a qualitative habitat (Capt, 2022; Dondina et al., 2016; Wolton, 2009). They consist of a tree or shrub line that is more than 20 meters long and less than five meters thick (Wolton, 2009). Hedgerows are man-made structures created when trees, bushes and understory vegetation are aligned into rows. This results in a linear network with an ecological value, as well as a managing one (Baudry et al., 2000). Forest edges are another habitat occupied by the hazel dormouse (Čanády, 2015; Capt, 2022; Goodwin, Hodgson, et al., 2018), and they represent the border of a forest with another kind of land (Bright et al., 2006). Forest edges are an ecotone habitat (Capt, 2022) resulting from natural or human fragmentation (Vu Ho et al., 2023). They are considered to be an excellent habitat for the hazel dormouse, as a great amount of sunlight reaches the habitat's interior part (Bright et al., 2006). The undergrowth of structured forest parts can also be a habitat for the hazel dormouse (Capt, 2022; Sozio et al., 2016). The forest structure refers to its layout or how the forest is assembled. This assemblage counts the spatial distribution of the vegetation (like the geometry of the understory or the canopy), the soil characteristics, the species composition and distribution, and the age of vegetation (Seidler, 2017). Thus, it is suggested that a structured forest has a certain richness in different vertical vegetation structures.

As the hazel dormouse needs a combination of plant species in its habitat to match its diet needs, it is considered as a specialist species for habitat and food (Bright & Morris, 1996; Morris, 2003). It is in consequence sensitive to habitat changes (Bright & Morris, 1996; Dondina et al., 2018; Sozio et al., 2016) and mostly threatened by habitat-linked threats (Bright et al., 2006). The hazel dormouse is also an indicator species (Bright & Morris, 1996; Fischer & Graf, 2023; Morris, 2003): as it needs habitats with a high diversity of plant species, it indicates

such rich woody habitats in a landscape. Moreover, the focus on hazel dormice also highlighted the importance of hedgerows as habitats for many taxa (Morris, 2003). The hazel dormouse is a flagship species as well: it designates biodiverse and well-connected habitat sites in the landscape, which are beneficial for numerous other animal species (Haag, 2014; Morris, 2003). Thus, the conservation of the hazel dormouse benefits the species itself, along with other taxa and different habitats (Morris, 2003).

During its whole lifespan, the hazel dormouse spends some time a day in a state of torpor. This consists in not moving anymore and laying on the ground, inactive and cold (Bright et al., 2006). This state saves up energy during cold times and is similar to hibernation (Woodland Trust, n.d.) but delays the reproduction (Bright et al., 2006).

The hazel dormouse hibernates during the months from October until March/April (Bright et al., 2006) or May (Bright & Morris, 1996). The hazel dormouse starts to hibernate to save energy when there is not much food available and when it starts to freeze. Smaller individuals can start it later, continuing to eat until later in fall (Bright et al., 2006). Results from Gubert et al. (2023) also suggested that the individuals of the species can start hibernation at different times. The hazel dormouse spends winter alone (Bright et al., 2006). It weaves a small and tight nest under dead leaves (near coppice stools or hedges), logs, or mosses (Bright et al., 2006; Gubert, 2022). The hazel dormouse plans to hibernate where it is humid and continuously cool. During that time, its metabolism is slowed down so that fat reserves last until spring (Bright et al., 2006). Winter mortality is high in the hazel dormouse: in Juškaitis' study (1999), 56% of adults died over winter, 55% and 70% (depending on the population) of early litter juveniles died, and 78% and 84% (depending on the population) of the late litter juveniles died, without any significant difference between sexes. Moreover, warmer winters induce a more rapid burnt of fat reserves, which can be fatal for smaller individuals (Bright & Morris, 1996; Juškaitis, 1999). Colder winters are in fact associated with a higher hazel dormouse abundance (Goodwin, Suggitt, et al., 2018).

Since 1982 in Switzerland, the hazel dormouse has been under protection of the federal convention of the 19th of September 1979 about wildlife and natural environments conservation[1]. Conserving the hazel dormouse is necessary and useful, because it is endangered, foremost because of the threats on its habitats. It is classified as vulnerable according to the Red List for Switzerland (Capt, 2022), so it needs protection or preservation to not go extinct in the future. According to Bright et al. (2006), the hazel dormouse is directly threatened by habitat degradation, fragmentation, and inappropriate habitat management (i.e., when there is no maintenance of a human-influenced habitat over time). Habitat quality matters for the species. As a matter of fact, when tree canopies are dense (because trees compete for the light), less food is available for the hazel dormouse in the understory, which makes the habitat less suitable. Similarly, if humans do not manage the coppice well, it becomes too dark, and the understory has less food for the hazel dormouse. Decreasing the diversity of vegetation (and in consequence food) where the hazel dormouse lives deteriorates its habitat and its corridors. It can cause fragmentation of woodlands, which can isolate populations (Bright et al., 2006) and make them suffer from loss of gene flow due to inbreeding

[1] RO 0.455, https://fedlex.data.admin.ch/eli/cc/1982/802_802_802

(Bani et al., 2017). In that case, hazel dormouse populations are easily subject to local extinction (Bright et al., 2006). Another direct threat to the species is the loss of habitat, or habitat destruction, which happens when humans transform woodlands into farmlands, roads and urban areas (Bright et al., 2006). Climate and weather can both affect directly and indirectly the hazel dormouse negatively (Capt, 2022), as they can decrease the breeding success and survival (Bright et al., 2006; Combe et al., 2023). In fact, three consequent years with unsuitable conditions can lead to local extinction (Bright et al., 2006). Other species stand as well as indirect threats. The squirrel represents a competition for food, and the deer damages bushes where the hazel dormouse eats (Bright et al., 2006). Furthermore, the landscape structure indirectly influences the population genetics: if it is continuous, the hazel dormouse can benefit from it (Bani et al., 2017). So, the threats regarding the hazel dormouse concern generally its habitat and how the populations are shaped. There is no serious disease or pathogen threatening the hazel dormouse (Bright et al., 2006). The predators of the hazel dormouse, which are owls, domestic cats, badgers (Woodland Trust, n.d.), corvids, squirrels (Wolton, 2009), birds and foxes (Gubert, 2022) do not stand as threats to the species (Bright et al., 2006), except during hibernation, when there is only little snow on the ground (Juškaitis, 1999).

To relief the weight of the existing threats on the hazel dormouse, conservation plans can represent solutions. Conserving the hazel dormouse can be practical because it is a charismatic species (Morris, 2003). As it is easier to receive the public's support if it has sympathy for the species in question in the conservation action plan, it is judicious to work on the hazel dormouse.

Not much was observed about the hazel dormouse' occupational habits of different habitat types during the months before and after hibernation. More is known about the plants preferred by the species (Bright et al., 2006; Dondina et al., 2016; Goodwin, Suggitt, et al., 2018; Juškaitis, 2008; Mortensen et al., 2022; Wolton, 2009), and the hibernation itself of the species (Bright et al., 2006; Gubert, 2022; Juškaitis, 1999). This study is concerned with the hazel dormouse's dynamic habitat choice, which may change between seasons. Other literature rather deals with a fixed and "defined" relationship between the hazel dormouse and its habitat preferences (Goodwin, Suggitt, et al., 2018; Mortensen et al., 2022). Moreover, this study covers the months usually not included in other studies. The latter rather monitored the hazel dormouse during the months of April/May to October (Bullion et al., 2018; Juškaitis, 2008; Vaudroz et al., 2023).

The gap in the knowledge of hazel dormouse population in Switzerland (Capt, 2022; Haag, 2014) and in the species' dynamic ecology, as well as the high winter mortality of the species (Juškaitis, 1999) and the habitat-directed threats on it (Bright et al., 2006) represent all motivations to research what needs to be protected before and after hibernation for the hazel dormouse. Furthermore, there seem to be no study, at least in Switzerland, that researched the occupancy of the hazel dormouse in three different habitat types simultaneously. Knowing more about these subjects would benefit the conservation of the species.

1.3. Goals of the study

Detailed knowledge on hazel dormouse populations is essential for the implementation of conservation plans (Haag, 2014). In consequence, the general objective of this master thesis is to understand what habitat sites the hazel dormouse occupies around hibernation times in two different Swiss regions to protect and conserve it in the months preceding, during, and following hibernation. It is interesting to know what differs in the habitat-occupational habits of the species before and after hibernation. If the hazel dormouse occupies the sites in a different manner between different seasons, this will matter for the conservation, as the different sites will not necessarily be protected, promoted, or conserved at the same moments in the year. Knowing where the species is present is useful to act in its favor, as it is complex to protect or promote populations of a species if too little is known about their occurrences (Bullion et al., 2018). Conserving the hazel dormouse can protect it from threats and extinction. It can also help conserve other species, or some landscapes and habitats where the hazel dormouse occurs (Morris, 2003).

One goal of this study is to compare the occupied locations by the hazel dormouse before and after hibernation, in other words to explore the habitat types where it occurs in fall and in spring. Another goal of this study is to understand the activity dynamic of the species. The point here is to observe which habitat types are occupied during fall, which ones are occupied during spring, and thus understand if there is a seasonal difference in occupancy. For this aspect, this study also aims at estimating at which moment all hazel dormice are inactive before hibernation, and when they become active again after hibernation. Both goals can be assessed at the population level.

1.4. Research question and hypothesis

This master thesis' research question is the following: How does the habitat occupancy of the hazel dormouse differ before and after hibernation, and what affects that occupancy? This question can be divided into two sub-questions. Does occupancy change between habitat types and seasons? Here, occupancy can be analyzed within one or both seasons. And does occupancy change within one habitat type between seasons? Here, occupancy is studied in one habitat type between two seasons. The factors used to discuss those questions are different habitat types, temperature (important for the dynamic analysis), and topographical aspects (elevation, exposition, slope and hillshade). Elevation was found to affect hazel dormouse occupancy, as a proxy for temperature (Melcore et al., 2020), but topographical factors are less explored environmental variables in hazel dormouse research. This study aims to go further in the relationship between topography and hazel dormouse presence to specify its habitat more precisely.

Three different habitats of the hazel dormouse were monitored for this study: the hedgerow, the forest edge and the structured forest. This aims at providing insights on whether there are any observed changes in the habitat occupancy of the hazel dormouse, either during the fall and spring seasons or between them. In this work, the "occupancy" of habitat is studied, rather than the "use". The occupancy relies on the fact that a species is continuously present in an area over a certain amount of time, whereas the use means that a species is present in an area at one or several moments over a certain amount of time (Mackenzie, 2005b). The goal of this

study is to analyze the species' occupational state in different habitat types over two halves seasons.

We hypothesize that the hazel dormouse occupies the same sites before and after hibernation, because when a habitat is of quality for the species, it should not go elsewhere. As the hazel dormouse is a specialist (Bright & Morris, 1996; Morris, 2003), if a habitat type suits the hazel dormouse species enough for it to use that habitat, the species should not change its home range, and occupy the habitat as long as it is still suitable. Some variations in the habitat type occupancy can however be expected, as the species can move away from its nest (Bright et al., 2006) and migrate seasonally (Haag, 2014; Holzgang et al., 2001).

2. Methods

2.1. Experimental device

As mentioned in different sources, the footprint tunnel methodology is the most practical method to monitor the hazel dormouse (Al-Fulaij et al., 2018; Bullion et al., 2018, 2021; Melcore et al., 2020). For this study, 150 footprint tunnels (Figure 2), lent by the Minimus Verein[2], were used to obtain detection/non-detection data on the hazel dormouse. These tunnels are squared (circa 10x10cm) and 40 centimeters long. They are composed of synthetically laminated cardboard. Inside of a tunnel comes a rectangular piece made from the same material (Figure 3), which can slip out of or in the tunnel. On this piece, one or two pieces of printing paper are attached thanks to paper clips (in red on Figure 3). At one or two places on that inside piece, one or two pieces of sticky tape are sticked to put non-harmful ink, constituting of paraffin oil and graphite, on it (A. Dürst, personal communication, March 20, 2024). The aim of those tunnels is to let small mammals cross them and leave their footprint traces on the paper, without any bait to attract them (Bullion et al., 2018; Hitchcock, 2019).

Figure 2: Footprint tunnel with informative label.

The footprint tunnel methodology is reported to be the most effective methodological approach to monitor the hazel dormouse (Bullion et al., 2021; Melcore et al., 2020). It has multiple advantages: it is easy to recognize the species' triangular footprints (Al-Fulaij et al., 2018; Hitchcock, 2019), it is a cheap methodology (Al-Fulaij et al., 2018; Melcore et al., 2020) as well as non-invasive (Bullion et al., 2018), and one does not need a license to implement it (Al-Fulaij et al., 2018).

Two types of inside parts were used for potential further research on the methodology (Figure 3). The footprint tunnels with two pieces of paper and one piece of sticky tape in the middle were coded as "A" (Figure 3a and 3c). The footprint tunnels with one piece of paper in the middle and two pieces of sticky tape at both ends were coded as "B" (Figure 3b and 3d). These different kinds of footprint tunnels were randomly attributed to the sites and transects. No

[2] Swiss association for studies on the Glirid family: https://www.verein-minimus.ch/

influence on the results regarding the hazel dormouse occupancy was expected from this difference. However, the kind of footprint tunnel was still considered as a covariate for hazel dormouse detection.

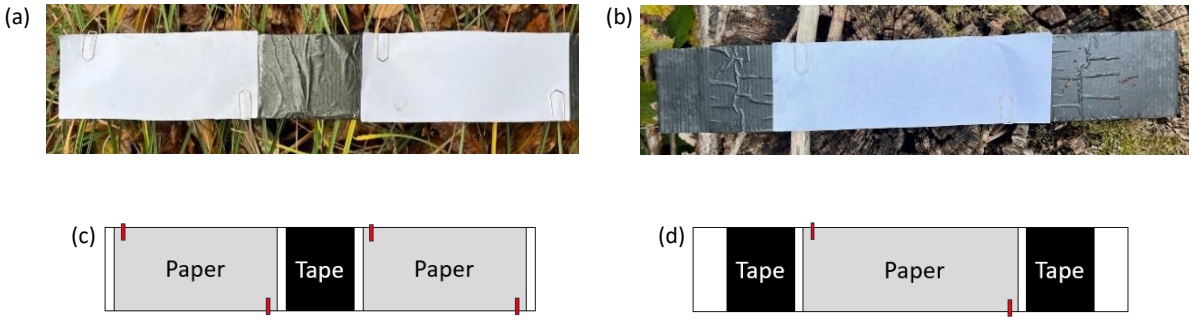

Figure 3: Inside parts of the footprint tunnels, (a) first type "A" and (b) second type "B". Schema of the inside part, (c) first type, (d) second type. In red are the paper clips. On the sticky tapes comes the ink.

2.2. Transects and habitat sites description

Half of the footprint tunnels (n = 75) were placed in the Val-de-Ruz, canton of Neuchâtel, (Table A1b[3]) because of previous evidence of the hazel dormouse a year before the study (Vaudroz et al., 2023). The other half of the footprint tunnels (n = 75) were placed in the Gantrisch region, canton of Bern, (Table A1a), for the same reason. Adrian Dietrich (from UNA, Bern[4]) shared evidence data of the hazel dormouse from the precedent year of the study. Two regions were (partially) used as research areas to gather more data than only one research area would bring.

30 transects of 100 meters were selected for the whole study. In each transect, one footprint tunnel was placed every 25 meters (5 footprint tunnels for 100 meters). 15 transects were in the Val-de-Ruz, and 15 others were in the Gantrisch (transects centroids in Table A1). There were three categories of habitat in which the footprint tunnels were positioned: hedgerows, forest edges, and structured forests. Five transects belonged to each category in each region. So, there were 75 footprint tunnels in the Val-de-Ruz, 25 in hedgerows, 25 in forest edges, 25 in structured forests, and the same amount of footprint tunnels were present in each category in the Gantrisch.

Hedgerows, forest edges and parts of structured forests were investigated because they are known habitats of the hazel dormouse (Bright et al., 2006) and all occur in the Val-de-Ruz and in the Gantrisch. In all three kinds of habitat, the presence of vertical structure richness in vegetation was important, as the hazel dormouse needs to move on enough trees and shrubs in the understory (Bright et al., 2006). Every area chosen for the transects followed four criteria. Firstly, the hedgerow transects had to be connected to forests, as connectivity contributes to a better habitat for the hazel dormouse (Bright et al., 2006; Mortensen et al., 2022). Secondly, the canopy percentage in the forest edge and structured forest transects had

[3] "A" stands for "Appendix".
[4] UNA - Atelier für Naturschutz und Umweltfragen: https://www.unabern.ch/

to be under 50% (A. Dietrich, personal communication, August 22, 2023) so that enough light could get to the understory which is a rich food source for the hazel dormouse (Bright et al., 2006; Bright & Morris, 1990; Ramakers et al., 2014). Thirdly, the forested areas connected to the hedgerows, and the ones counting the forest edges and structured forest parts needed to be at least 20 hectares large to be of good quality for the hazel dormouse (Bright et al., 2006). Lastly, the major stage of development of the trees had to be medium to ensure the presence of enough medium height vegetation in the transects, which is useful for the movements of the hazel dormouse (Bright et al., 2006). This last criterium was only addressed for forest edges and structured forests.

The transects were chosen on QGIS (QGIS.org., 2024) using 1:25000 maps of Switzerland and different sources for environmental data (see footnotes). The four criteria were evaluated on QGIS. To assess the connectivity and calculate the 20 hectares, hedges near forests (< 20 ha) were investigated and the forest surfaces were measured on the 1:25000 map on QGIS. For the canopy coverage and the vegetation development stage, some layers given by the canton of Bern[5,6] regarding the canopy degree and the stage of development of the vegetation were used. For the canton of Neuchâtel, no such data was available. So, LIDAR data of the canton of Neuchâtel[7,8] was helpful to see where the most medium vegetation was present.

To select official hedgerows for the project, a shapefile on the use of agricultural land[9,10] from the website geodienste.ch[11] was downloaded and used. “Official” means that the owners of those hedgerows are responsible to manage them. This aspect is beneficial for the study, as cutting the hedges provides appropriate nest sites for the hazel dormouse (Wolton, 2009). The forest edges and structured forest parts were of interest for selection when they were near the “official” hedgerows seen on the QGIS software layer. Three criteria were then checked for these two habitat types: a canopy cover below 50%, their belonging to a 20 hectares large forest, and the major presence of medium-developed vegetation. Regarding the structured forest habitat, the criterium of medium vegetation development was crucial to be looking at the right places for the implementation of the methodology. We think that this habitat type is the one where the understory might be in general less developed (in comparison to forest edges or hedgerows).

This study tried as much as possible to target places where the hazel dormouse had been detected the year before (known thanks to C. Vaudroz and A. Dietrich’s data), or several years before (known thanks to InfoSpecies’ data[12]). Other footprint tunnels were placed at sites with no past hazel dormouse evidence but were put there to expand population knowledge.

[5] Geoportal des Kantons Bern / Géoportail du canton de Berne
[6] Access under: https://www.agi.dij.be.ch/de/start/geoportal/geodaten/geodaten-zum-download/bezug-von-geoprodukten-nach-regionen.html?zoning=WALDINFO
[7] Données cartographiques du SITN © [2023] / Service de la Géomatique et du Registre Foncier
[8] Access under: https://sitn.ne.ch/lidar/
[9] Données cartographiques du SITN © [2023] / Service de la Géomatique et du Registre Foncier
[10] Geoportal des Kantons Bern / Géoportail du canton de Berne
[11] Access under: https://www.geodienste.ch/services/lwb_nutzungsflaechen
[12] Access under: https://www.infospecies.ch/fr/donnees/demande-donn%C3%A9es.html

After choosing the transects online, each transect was visited physically to check its suitability for the study. This means that the quality of each habitat type and the length of each transect were controlled. The length of the habitat areas had to be at least 100 meters. For the quality, enough vertical variations in vegetation had to be present effectively. Afterwards, every owner of every land planned to have footprint tunnels in was asked for the permission to do so. The names of the landowners were retrieved from the cadastral plan from both cantons[13,14] and the contact information (phone numbers or addresses) was found on Search.ch[15] or by word of mouth.

2.3. Data collection

The 16th and 17th of October 2023, all footprint tunnels were placed in the Val-de-Ruz and in the Gantrisch, respectively. At each site where a footprint tunnel was placed, the following data was noted down: the identification number of the tunnel (Bullion et al., 2018), the coordinates of the site, the type of footprint tunnel (A or B), the location of the tunnel (on a branch or on the ground), and the plant species on which the tunnel was placed. The footprint tunnels were attached with cable ties to random horizontal branches at approximatively 1-1,5 meters from the ground (Bullion et al., 2018; Melcore et al., 2020). For each transect, one footprint tunnel was put on the ground, at the bottom of coppice or attached to a stump. As this study focuses on the hibernation of the hazel dormouse, it was strategic to place some footprint tunnels on the ground as the hazel dormouse goes to the ground to nest for winter before hibernation and moves from its winter nest on the ground to the branches to create a new spring nest (Juškaitis, 2008).

The 23rd and 24th of October 2023, during the first control visits, the plant species on which the footprint tunnels were placed were identified thanks to Plantnet[16] and the work of Lüder and Terrisse (2020). The 27 different plant species on which the footprint tunnels were placed are the following: 3 dog roses (*Rosa canina*), 59 common hazels (*Corylus avellana*), 2 alpine currants (*Ribes alpinum*), 4 common spindles (*Euonymus europaeus*), 6 blackthorns (*Prunus spinosa*), 4 European ash trees (*Fraxinus excelsior*), 2 common hawthorns (*Crataegus monogyna*), 4 European alders (*Alnus glutinosa*), 1 common nettle (*Urtica dioica*), 26 European beeches (*Fagus sylvatica*), 3 elders (*Sambucus nigra*), 2 common dogwoods (*Cornus sanguinea*), 5 stumps, 3 European fly honeysuckle trees (*Lonicera xylosteum*), 1 field maple (*Acer campestre*), 1 European silver fir (*Abies alba*), 2 white willows (*Salix alba*), 2 sycamore maples (*Acer pseudoplatanus*), 1 European crab apple (*Malus sylvestris*), 1 wayfaring tree (*Viburnum lantana*), 1 grey alder (*Alnus incana*), 1 raspberry plant (*Rubus idaeus*), 6 European blackberry plants (*Rubus fruticosus aggregate*), 5 European spruces (*Picea abies*), 1 small-

[13] For the canton of Bern: https://www.map.apps.be.ch/pub/synserver?query1=egrid&keyvalue1=CH455046373571&keyname1=EGRID&project=a42pub_oereb_oeffen_FR&language=fr&userprofile=geo&client=core

[14] For the canton of Neuchâtel: https://sitn.ne.ch/theme/main?lang=fr&map_x=2550050&map_y=1205000&map_zoom=1&baselayer_ref=blank&tree_groups=gp_points_interets%2Cgp_photos_360%2Cgp_main%2Cgp_base_layers&tree_group_layers_gp_photos_360=&tree_group_layers_gp_main=&tree_enable_3-plan_cadastral=true

[15] Access under: https://search.ch/

[16] Plantnet is an application that allows one to identify different plant species thanks to pictures: https://plantnet.org/

leaved lime (*Tilia cordata*), 3 goat willows (*Salix caprea*), and 1 rowan (*Sorbus subg. Sorbus*). This data was useful for the occupancy models.

The data collection started before the beginning of hibernation, the 16th of October 2023, which is close to the theoretical time when the species goes into hibernation (Bright et al., 2006). The last control in fall was the 5th of December 2023, when no footprints of the species were detected anymore. Two control visits with no traces of footprints and a mean temperature of circa 0°C in the research area meant that the hazel dormice were hibernating. Only one week with zero footprints was kept in the data recordings. The presence of the species was inspected for a second time from the 3rd of March 2024, which is close to the theoretical end of hibernation, to assure that the study could capture the first activity trace of the hazel dormouse (Bright et al., 2006). The first footprints of the species were found the 18th of March 2024. The last control in spring was the 22nd of April 2024, so that there was the same amount of control visits (seven) for each seasonal research phase. According to Melcore et al. (2020), the footprint tunnels need to be checked every ten days. Rather than that, the controls were done more often (every six, seven or eight days) for logistic reasons. If needed, the paper was changed, and the ink recharged. The pieces of paper were changed when there were footprints on them or when the paper was damaged and not usable anymore. The identification of the hazel dormouse's footprints was based on the identification book of Swiss mammals by Marchesi et al. (2011). It describes and gives a scaled image of the front and hind foot shapes of the traces. Moreover, a second identification of the footprints was proceeded for better data accuracy, with the same process. A third-party opinion on the traces was a few times helpful to identify unclear footprints.

Environmental data was retrieved from the sources SWECO25[17] and MeteoSwiss[18]. The "alti3d" dataset (Swiss Federal Office of Topography [swisstopo], 2016) was used. It was downloaded from the raster database SWECO25 to get data for the elevation, exposure, hillshade and slope variables. The "raster" package (Hijmans, 2023) was helpful to retrieve this data. From MeteoSwiss, daily mean temperature data (two meters above ground) for the research period was retrieved from their IDAWEB data portal. Weekly means were calculated for each control visit with data from the precedent week. The meteorological measures came from the stations of Riggisberg (Gantrisch), Cernier and Chaumont (Val-de-Ruz). For the week between the 24th and the 30th of October 2023, data was missing for the Cernier station. In consequence, the data was replaced according to the following calculation: the average measured temperature difference between the two stations in the canton of Neuchâtel was taken and added to the temperature data (24th-30th of October) of the Chaumont station (consistently colder station).

2.4. Statistical analysis

The methodology of footprint tunnel for hazel dormouse surveying allows to get detection/non-detection data, or presence/likely-absence data, rather than presence/absence data (Bullion et al., 2018; Mackenzie, 2005a, 2005b). The latter would imply the certainty of species absence, which cannot be asserted in this study (Bailey & Adams, 2005; Mackenzie,

[17] https://zenodo.org/communities/sweco25/records?q=&l=list&p=1&s=10&sort=newest
[18] https://www.meteoswiss.admin.ch/#tab=forecast-map

2005b). The detection of a species counts as a presence, but the non-detection does not count as an absence (Mackenzie et al., 2002). So, imperfect detection needed to be accounted for in this research (Mackenzie, 2005b) to not assess incorrect ecological relationships (Fiske & Chandler, 2011). It would have been effective to combine the footprint tunnel method with another according to Bullion et al. (2018), but the efforts to implement marking-tracking methodology for this study were unfortunately not fulfilled.

The hazel dormouse detection/non-detection data noted for each site represented the response variable (Paniccia et al., 2018). The 150 sites were sampled seven times over a season and each measure was seasonally replicated (Kéry & Royle, 2021). In this study, the sites data were used as analytical unit (Capt, 2022; Dorazio et al., 2011) rather than the transects data, because the parameters (for detection and occupancy) were different from site to site and were not homogeneous throughout the transects. So, 150 dependent sites were considered for the statistical analyses. The recorded data was in the form of a detection history for each site (Mackenzie et al., 2002).

63 missing data were reported in the dataset (Table A5), due to issues that happened when an inside part of a tunnel slipped out of it, was lost, or if the tunnel was tilted. All scenarios prevented footprint recording. There were more missing data in fall than in spring, but in both seasonal surveys, they did not impact the analysis (full explanation in Appendix 8.1.3). There was little variability in the distribution of the missing data in fall (Figure A3a). They were equally distributed throughout the habitat types. Thus, the missing data seemed to not be attributed to a chronic error or problem. The missing data were less equally distributed in spring, but as the number of missing values was smaller in spring, no problem with missing data was considered (Figure A3b).

Multiple explanatory variables were taken for the model analyses: the region of research (Gantrisch, Val-de-Ruz), the season (fall, spring), the habitat type (hedgerow, forest edge and structured forest), as well as the following environmental variables: weekly mean temperature, elevation, exposition, hillshade and slope.

To explain habitat preferences of the hazel dormouse, occupancy models were used rather than generalized linear models. Occupancy models are useful to calculate occupancy probabilities when detectability is lower than 100% (Mackenzie et al., 2002). Furthermore, occupancy models were more adequate to use because they account for imperfect detection when assessing a species' occurrence (Mackenzie et al., 2002). Specially for this study, it was highly judicious to also consider detection in the models, because it might be that the hazel dormouse prefers a habitat in which it is less detectable. This can induce wrong estimation of parameters (Tyre et al., 2003; Yackulic et al., 2013).

An occupancy model can be understood as two regressions that describe the detection of a species, and the occupancy, i.e. the true occurrence of the species (Kéry & Kellner, 2024). Site characteristics can influence the detection and the occupancy, but survey characteristics can only impact the detection. These precisions make occupancy models stronger than other linear models to predict occurrence (Bailey & Adams, 2005). Multiple-species models and

multiple-season models can be fitted in that sense (Fiske & Chandler, 2011). In this study, one species' occupancy is at interest, during two sampling seasons.

Before fitting models, detection/non-detection data and missing data were explored using the "kableExtra" (Zhu, 2021) and "ggplot2" (Wickham, 2016) packages in R 4.3.3 (R Core Team, 2024). Then, statistical analyses were performed using the "unmarked" package (Fiske & Chandler, 2011; Kellner et al., 2023) for occupancy models. Before the analyses, correlation between covariates was detected and accounted for, and continuous variables were standardized to fit models (Wilkinson, n.d.).

Occupancy models need three datasets. One is a matrix (y) with the detection/non-detection data for each site. The data is put in a chronological order (the first sampling season, then the second etc.). Another dataset (siteCovs) includes columns with site-level covariates that do not change throughout time. The last one (obsCovs) has columns with observation-level covariates, which can change over time (Fiske & Chandler, 2011; Wilkinson, n.d.). If there is a missing data in the siteCovs, all data from the site with the missing data is omitted in the models. If missing data is in the obsCovs, only the specific occurrence (the missing data) is left out of the models (Fiske & Chandler, 2011). For the models to independently fit the seasonal data to different parameters, the detection/non-detection data is seasonally stacked. So, the seasons were represented as blocks in this study's dataset: the fall data was the above half, and the spring data was the bottom half. This ensured that the closure assumption of occupancy models was respected, i.e. that the state of presence/absence of the species in the research areas was stable during the survey periods (Kéry & Royle, 2021).

In occupancy models, detection and occupancy parameters are formulated. In this study, two models were fitted with the occu() function (Fiske & Chandler, 2011). Detection probabilities are accounted for in addition to the occupancy probabilities (Kéry & Kellner, 2024). The season and the region constituted the base in the detection covariates in both models. To both models, other variables were added to the detection, and they were kept if they had a significant effect on it. The following were tested: weekly main temperature, placement of the footprint tunnel, kind of footprint tunnel, and plant species on which the tunnel was placed.

In model 1, the interaction between the season and the habitat type, their main effects, and the random intercepts of sites and transects were considered as the basic occupancy covariates. The random effect of site was added to account for the hierarchical order of site brought by the seasons of survey. The random effect of transect was added to account for the interdependency between sites constituting the same transect. In model 2, there were the same covariates in the occupancy, except the main effect of the habitat type, which was removed to constraint the model to analyze the effect of habitat between the seasons. That way, the occupancy model could rather focus on how habitat types interact with seasons. Model 1 tested the interaction between habitat and season on occupancy, i.e. how occupancy changes between habitats and seasons. This abled to understand the habitat preference of the hazel dormouse and analyze whether it changes between seasons. Model 2 tested how occupancy within each habitat changes between seasons, i.e. whether the occupancy of a specific habitat changes between seasons. Other parameters (elevation, exposition, hillshade and slope), were subsequently added to the models, and they were kept if they brought

significant effects when added to the base models alone. In both occupancy models, the placement of the footprint tunnel and the kind of tunnel were retained for detection, but the variables of temperature and plant species were not. Regarding occupancy covariates, hillshade and slope were the only significant topographical effects when added alone to the base models. So, the other topographical variables were discarded.

The dynamic analysis of the hazel dormouse occupancy during the months preceding and following hibernation, so the interaction between season, habitat type and time (in week) was also of interest in this study. However, it was not added to the final models, because there was not enough data for the models to converge. Instead, descriptive analysis was used to interpret this aspect.

Predicted occupancy was plotted using either predictions retrieved from the models and the "ggplot" function (Wickham, 2016), or directly the "plotEffects" function. The final models were evaluated with three goodness-of-fit tests for occupancy models: the sum of squared errors (SSE), the Pearson's Chi-squared (Chisq), and the Freeman-Tukey Chi-squared (Wilkinson, n.d.).

3. Results

3.1. Footprint identification

171 hazel dormouse footprints were identified in total in this study (Table A2) in 51 of the 150 surveyed sites. ~71.9% of the footprints identified were from the Gantrisch region, and ~28.1% were from the Val-de-Ruz region (Table A2, Figure A5). These footprints are considered as presence signs of the species. The distribution of the data indicates that most sites (103 of 150) had zero signs of presence of the hazel dormouse over fall in both research regions (Figure A1a). In spring, it was the case with 20 more sites (Figure A1b).

Hazel dormouse signs were noted in all habitat types and in both regions. There is a variability in the data distribution, but more data was retrieved in the Gantrisch (Table A2), and more footprints were noted in forest edge habitats (Figure A5). Many sites and transects were not occupied by the hazel dormouse, during either fall or spring, or both (Figures A2.1 and A2.2). Supplementary observations regarding the number of footprints in relation to the connectivity between habitat types can be found in the Appendix 8.1.2 (Table A3).

3.2. Descriptive dynamic of occupancy between habitats

All hazel dormouse individuals were inactive by the 27th of November in the Val-de-Ruz, and by the 4th of December in the Gantrisch (Figure 4). In both regions, less activity was noted in spring than in fall. Furthermore, during active periods, there were always (except once) higher numbers of footprints recorded in the Gantrisch than in the Val-de-Ruz (Figure A4). Activity signs in spring were reported earlier in the Gantrisch, the 18th of March, than in the Val-de-Ruz, where footprints were found again from the 26th of March (Figure 4).

The dynamic aspect of hazel dormouse occupancy during fall and spring could not be fitted in a model. In consequence, a description of the dynamic habitat type choice was produced (Figure 4). In the Gantrisch, the main habitat of occupancy changed from forest edges in fall to structured forests in spring (Figure 4a). In the Val-de-Ruz, forest edges were constantly more

occupied by the hazel dormouse during both seasons, but structured forests were not occupied in spring (Figure 4b). In both regions, the descriptive dynamic of occupancy shows that the preference of habitat type does not seem to vary much throughout one season (Figure 4).

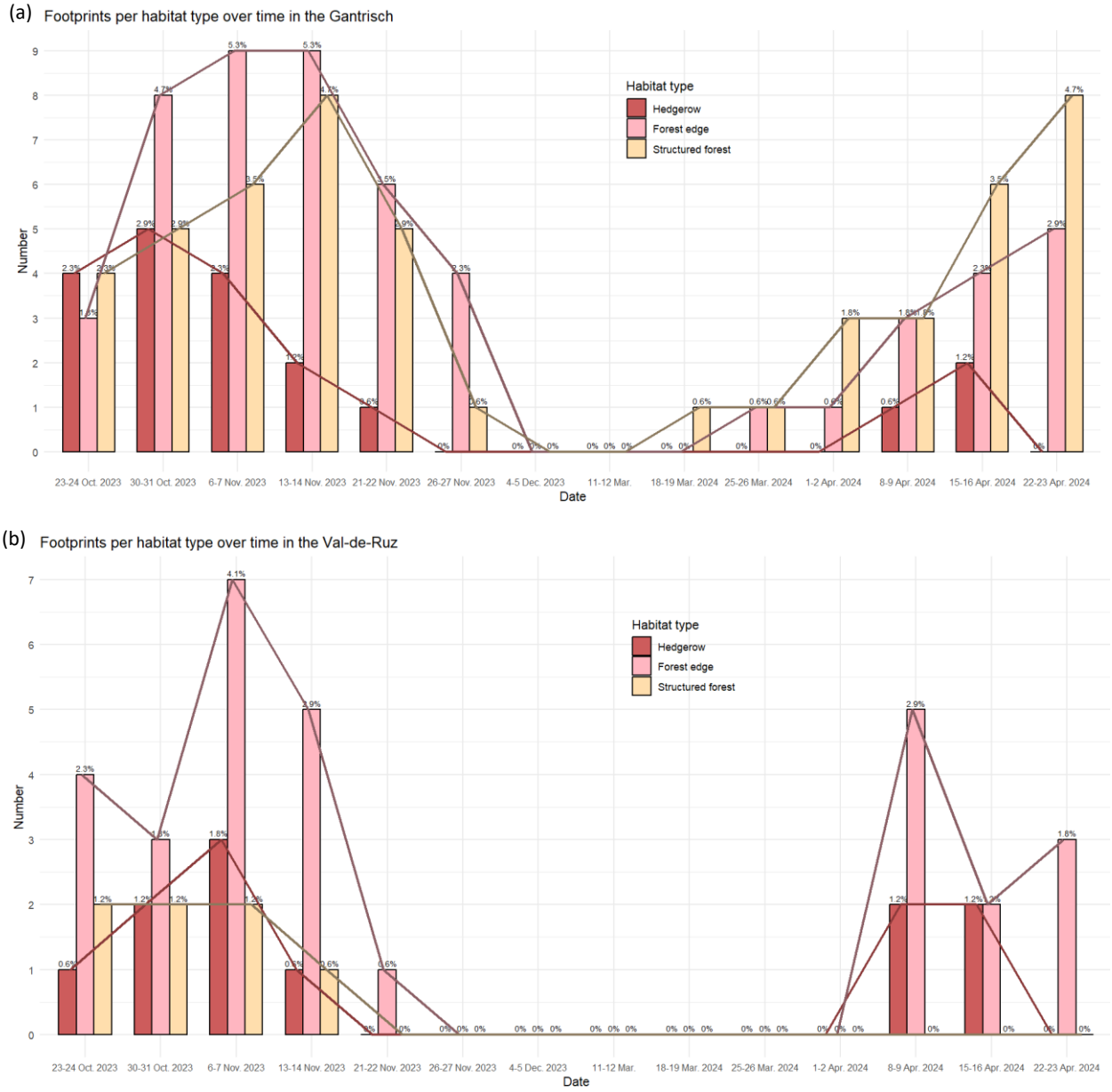

Figure 4: Number of footprints per week in fall and spring according to each habitat type in the (a) Gantrisch and (b) Val-de-Ruz. The percentages are an indication in relation to the total of footprints found in both research regions (171).

3.3. Modelled dynamic of occupancy between habitats

The model diagnostics were tested on both models. The evaluation of the model 1, where the main effects are included (habitat type preference between sites and seasons), returned values much larger than 0.05 (SSE: 0.145; Chisq: 0.130; freemanTukey: 0.429). The evaluation of the model 2, without the main effect of habitat type (habitat type occupancy only between seasons), also returned values much larger than 0.05 (SSE: 0.129; Chisq: 0.126; freemanTukey: 0.399). Both models are thus well-fitting models (Wilkinson, n.d.).

Detection does not change between the first and second model. The variables of season, region, footprint tunnel placement and footprint tunnel kind have all significant effects on detection in both models (Table A6).

Occupancy effects are different between the two models, except for the parameters that are the same in both, i.e. hillshade and slope. Hillshade has no significant influence on hazel dormouse occupancy, but the slope does (Tables 1 and 2).

In model 1 (habitat type preference compared between habitat types and seasons), the interaction between habitat type and season does not have a significant effect on hazel dormouse occupancy, nor does the main effect of season, but the main effect of habitat type does (Table 1).

In model 2 (habitat occupancy compared between seasons), the interaction between habitat type and season has a significant effect on the hazel dormouse occupancy (Table 2). There is no sole effect of habitat type analyzed, and season alone has no significant effect (Table 2).

Occupancy in forest edges seems to always be higher than in the other habitat types. Hedgerows are almost not occupied according to the models. Structured forests are seemingly only occupied a little. All trends decrease from fall to spring, with overall smaller occupancy in spring (Figure 5).

Occupancy in hedgerows and structured forests is indicated to be low and constant between seasons. Occupancy in forest edges seems to be lower in spring than in fall. It decreases by ~30%. Confidence intervals are the largest for the forest edge habitat, and the smallest for the hedgerow habitat type. In spring, confidence intervals are smaller than in fall (Figure 5).

Model 1 results: occupancy

Variable	Estimate	SE	z.value	p.value
seasonfall	0.853	0.869	0.981	0.3265
seasonspring	-0.642	0.882	-0.728	0.4666
habitat_typehr	-3.825	1.524	-2.509	0.0121
habitat_typesf	-2.887	1.394	-2.070	0.0384
scale(hillshade)	0.767	0.567	1.353	0.1760
scale(slope)	-1.367	0.622	-2.196	0.0281
seasonspring:habitat_typehr	-0.290	1.303	-0.223	0.8238
seasonspring:habitat_typesf	1.007	1.260	0.799	0.4241

Table 1: Model 1 results for occupancy covariates. 95% confidence interval. Significance was retained when p.value < 0.05.

Model 2 results: occupancy

Variable	Estimate	SE	z.value	p.value
seasonfall	0.853	0.869	0.981	0.3264
seasonspring	-0.642	0.882	-0.728	0.4667
scale(hillshade)	0.767	0.567	1.354	0.1759
scale(slope)	-1.367	0.622	-2.196	0.0281
seasonfall:habitat_typehr	-3.826	1.524	-2.510	0.0121
seasonspring:habitat_typehr	-4.116	1.568	-2.625	0.0087
seasonfall:habitat_typesf	-2.887	1.394	-2.071	0.0384
seasonspring:habitat_typesf	-1.880	1.286	-1.462	0.1437

Table 2: Model 2 results for occupancy covariates. 95% confidence interval. Significance was retained when p.value < 0.05.

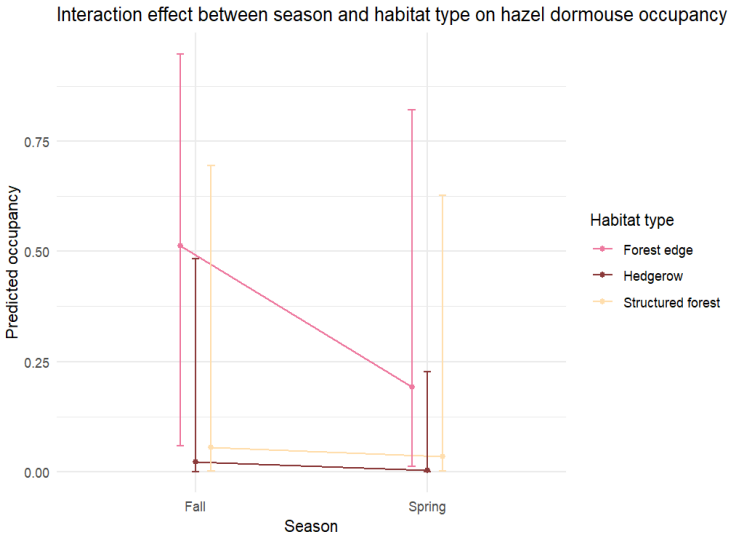

Figure 5: Occupancy of the hazel dormouse in fall and spring according to each habitat type in both research regions. The outputs of the models 1 and 2 show the same predicted occupancy for both models.

Both models indicate that the slope might be the only topographical variable to significantly influence hazel dormouse occupancy. The effect of the slope is the same between both models (Tables 1 and 2). The confidence interval is large, but a steep slope is associated with less occupancy by the hazel dormouse (Figure 6).

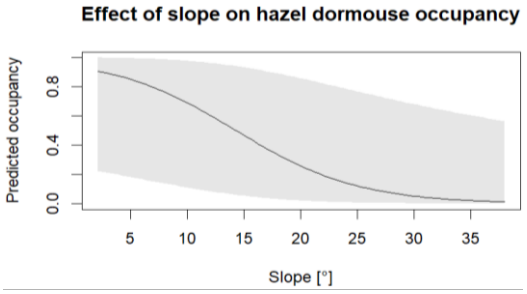

Figure 6: Relationship between the slope (in degrees) and the hazel dormouse occupancy.

4. Discussion

4.1. Detection problems and methodological approach

During the fieldwork periods, problems arose in the detection. The inner parts of the footprint tunnels slipped sometimes out of the tunnels. For the 28 times it happened (20 in fall and eight in spring), the inside part was placed back in the tunnels. From the third visit, the falling parts were attached with tape to the tunnels. Five inside parts went lost (one in fall, four in spring), and they were replaced the week after the loss. Sometimes, footprint tunnels were horizontally tilted to one side of the branch, even though they were solidly attached with cable ties. These problems possibly happened because of the wind, or because of certain animals moving the tunnels or the inside parts. One footprint tunnel placed on the ground was even destroyed, surely by an animal (Figure 7), and another was probably taken away by a flood during heavy rains. These detection problems made it impossible for the hazel dormice to walk on the paper and leave traces, resulting in missing data in the detection history. To ensure a more successful data collection, we recommend attaching the footprint tunnels very firmly to the branches, using multiple cable ties and/or sticky tape. Moreover, the inside parts can be inserted in a manner that they hardly slip away, which can be achieved by letting the paper clip stick out and block the inside part's horizontal movement.

Figure 7: Destroyed footprint tunnel.

In this study, the detection of the hazel dormouse was not perfect, as it was awaited. In fact, the hazel dormouse is difficult to monitor because it is mostly active during the night, and it has a low density (Melcore et al., 2020). It was also reported that it is difficult to find the direct presence of the species because of its many inactive periods (hibernation or state of torpor) and its small size (Al-Fulaij et al., 2018). Consequently, it is crucial to use the best method as possible to detect and monitor the hazel dormouse. Different studies demonstrated that the species is more frequently detected with footprint tunnels than with other methods like nesting boxes and nesting tubes (Bullion et al., 2021; Melcore et al., 2020). Thus, this method is considered to be the standard to monitor the hazel dormouse among other species (Melcore et al., 2020). Despite the imperfect detection in this study, the monitoring of the hazel dormouse with footprint tunnels was effective.

4.2. Descriptive dynamic of occupancy between habitats

During the seasons and between them, the choice of habitat type was constant. Forest edges were the most occupied, followed by structured forests, except in the spring in the Val-de-Ruz,

where no presence was detected there (Figure 4). There is a one-week gap between the two hibernation start dates of the two research regions (Figure 4). This gap can exist because of specific differences between hazel dormouse individuals (Bright et al., 2006; Gubert et al., 2023).

The hump-shaped frequentation of footprint tunnels during the fall season (Figure 4) can be explained by an adaptation phenomenon. The hazel dormice can take time to get used to the footprint tunnels, because they are not natural elements of their environment. This explains the increase of the footprint tunnel frequentation at the beginning of the monitoring (Haag, 2014; Nams & Gillis, 2003). The low but increasing number of footprints at the beginning of the survey might not be attributed to the fact that the hazel dormouse follows the maturity of its food (Bright et al., 2006; Haag, 2014). The frequentation of the tunnels might change according to the food presence near the tunnels. However, this is not likely the reason for the increase in tunnel frequentation, as the hazel dormouse had probably already reached its definitive hibernation location by mid-October (when the footprint tunnels were placed on the field). Furthermore, mid-September migration had already taken place (Haag, 2014), so the increase in footprints in fall is surely not attributed to migration. The decrease in footprints at the end of the fall monitoring can be explained by the beginning of hibernation. As not all individuals go into hibernation at the same time (Bright et al., 2006), the decrease in the frequentation is gradual.

The hibernation start time found in this study can be estimated to be late, in comparison to October, which is what the literature suggests (Bright et al., 2006). Nevertheless, Gubert et al. (2023) found that some hazel dormice can remain active until December. So, if compared to those observations, this present study's results might not be unusual. The time gap in both study's results can possibly be explained by climate change. As the hazel dormouse starts its hibernation with the first frosts (Bright et al., 2006) and climate change makes those frosts occur less (BAFU et al., 2020), hibernation can be postponed. The October 2023 month was warmer compared to other October months in Switzerland. The mean temperature of October 2023 in Switzerland was 3,1°C higher than between 1991 and 2020 (MétéoSuisse-Blog, 2023). The higher temperatures might have led to a later hibernation of the hazel dormouse. The first frost in Switzerland occurred around early December (MétéoSuisse-Blog, 2024), coinciding with the hazel dormouse's hibernation start.

Hibernation lasted until March, which is in theory not too early (Bright et al., 2006). If we understand it to be a little bit earlier than in theory, it can possibly be because of climate change. Higher temperatures can be an explanation to earlier hibernation emergence in the edible dormouse *Glis glis*, parent rodent of the hazel dormouse (Fietz et al., 2020). The same could be happening to the hazel dormouse. The 2023-2024 meteorological winter was one of the milder ones in Switzerland since 1864. This winter was 2,5° warmer than the norm between 1991 and 2020, except the 2019-2020 winter (MétéoSuisse-Blog, 2024). This might explain why individuals emerged already mid-March from hibernation (Figure 4).

Short-term weather variations have negative impacts on the populations of the hazel dormouse (Combe et al., 2023; Goodwin, Suggitt, et al., 2018). Milder temperatures during the winter can threaten the survival of hibernating mammals (Bright & Morris, 1996; Combe

et al., 2023). Higher ambient temperatures lead to higher metabolic rates in the species, which then burns fat reserves more quickly, possibly finishing them before the end of winter (Bright & Morris, 1996). This present study demonstrates that the warmer temperatures during the 2023-2024 fall and winter might have delayed and shortened hibernation of hazel dormice in Switzerland, and impact hazel dormouse survival.

4.3. Modelled dynamic of occupancy between habitats

No change in habitat type preference was noted between fall and spring. The hazel dormouse seems to prefer forest edges with a soft slope, before and after hibernation (Figures 5 and 6). These results support the hypothesis that if the hazel dormouse prefers a habitat type, it will continue to occupy it during both seasons of fall and spring. Occupancy did not change within hedgerows and structured forests between seasons, but it decreased by ~30% in forest edges between fall and spring. This is not understood as a decrease in preference for forest edges, but rather as a decrease in general occupancy.

The large confidence intervals of the effects of habitat type and slope indicate some variability in the predicted occupancy (Figures 5 and 6). So, variability in the habitat type preference can be suspected, as hypothesized. In spring, the confidence intervals for habitat type effects are smaller, which means that occupancy was more consistent across the habitat types in spring (Figure 5). Each effect should in consequence be interpreted with regards to its variability.

The predicted occupancy sunk after hibernation (Figure 5). More than 50% less footprints were recorded in spring (Table A2). Forest edges are less occupied in spring, but no other habitat type seems to have an increased occupancy in spring (Figure 5). So, hazel dormice might have not changed their habitat type preference: they either left the survey perimeter or died during the winter (Juškaitis, 1999). In fact, the decrease in occupancy between fall and spring could be explained by the hazel dormouse's high winter mortality (Juškaitis, 1999). The hazel dormouse nests in the surface layer of the soil, and this makes them vulnerable to predators, flooding, and stomping (Bright & Morris, 1996). Predatory presence in winter can be increased if there is no snow. In fact, not enough snow cover at the beginning of the winter can represent an unfavorable condition for the hazel dormouse's hibernation (Juškaitis, 1999). The decrease in occupancy is possibly not linked to individual differences. Thus, the idea that some hazel dormice would still be asleep by the time the survey ended is potentially incorrect. Monitoring the hazel dormouse in May is effective (Bright et al., 2006) and so, by the end of April (time of this study's survey ending), all individuals should have been awake.

The hazel dormouse's appreciation for forest edges was indicated in other surveys (Goodwin, Hodgson, et al., 2018; Ramakers et al., 2014), supporting this study's results. The hazel dormouse was also reviewed to be strongly associated with forests (Fedyń et al., 2021), and according to other literature, hedgerows seem to be habitats that the hazel dormouse appreciates as well. However, in this present study, hedgerows had the smallest occupancy probabilities in fall and spring (Figure 5). In Vaudroz et al. (2023), no hazel dormouse footprints were found in hedgerows in the Val-de-Ruz. This gap could be attributed to differences in the way the hazel dormouse occupies its habitats between different regions or countries. The present study and the one by Vaudroz et al. (2023) based their research on Swiss territory, whereas other studies took place in the United Kingdom or Northern Germany (Bright et al.,

2006; Ehlers, 2012; Gubert, 2022; Wolton, 2009). Furthermore, Vaudroz et al. (2023) explained the low preference for hedgerows in their study with a low plant species diversity in this habitat type. They also found that two dominant plant species in their monitored hedgerows were negatively associated with the hazel dormouse's presence. Bright et al. (2006) and Ehlers (2012) underlined the necessity of woody plant diversity for the species. However, elements like a diversity factor or the presence of certain plant species were not included in this study's transects selection, which might explain the poor presence of hazel dormouse in hedgerows. The monitored hedgerows might have had the wrong vegetation characteristics to be suitable for the hazel dormouse. The preference for forest edges could thus be explained by the presence of certain plant species in that habitat type (Bright et al., 2006; Mortensen et al., 2022; Scopes et al., 2024) or other factors regarding vegetation. The vegetation was not considered as a variable influencing occupancy in this study, as the link between plants, hazel dormouse presence and habitat suitability has been covered in multiple previous studies and literature (Bright et al., 2006; Dondina et al., 2016; Goodwin, Hodgson, et al., 2018; Goodwin, Suggitt, et al., 2018; Juškaitis, 2008; Mortensen et al., 2022; Vaudroz et al., 2023; Wolton, 2009). Rather, the "raw" habitat type categorization was used to predict occupancy. The little occupancy in hedgerows compared to the literature could also be assigned to the impossibility of conquering these habitats for the species. The already existing connectivity might then be not connective enough. Moreover, the hedgerows could be more useful for connecting habitat patches and dispersal (Dondina et al., 2018; Fedyń et al., 2021; Iannarilli et al., 2017), but less occupied as habitats themselves. In fact, Carroll (2013) analyzed that hedgerows can stand as habitat and linking pathway for the hazel dormouse.

The habitat type preference could be defined in a more complex manner than just with a "type". In this study, the habitat choice and its dynamic were in focus, so habitat types were used as broad categories to describe occupancy. However, those categories could be divided into sub-categories based on different important factors of the hazel dormouse ecology, such as vegetation structure, diversity, or plant species. For a deeper interest in the relationship between dynamic and occupancy, more behavioral and environmental processes of habitat selection could be considered (Gubert, 2022). Deepening the link between the hazel dormouse and its dynamic habitat choice would also be interesting to better encompass the needs of the hazel dormouse in terms of processes. The preference from an individual point of view could be examined, using tracking devices to survey hazel dormouse occupancy. This would allow a more precise understanding of the habitat choice dynamic developed in this study. The methodology of radio tracking has already been used on the hazel dormouse in regards to its habitat (Bright, 1998; Bright & Morris, 1990; Goodwin, Hodgson, et al., 2018; Gubert, 2022; Mortensen et al., 2022) and could be used to understand the dynamic habitat preference as a result of habitat selection processes (Gubert, 2022).

Environmental variables do not seem to influence hazel dormouse occupancy according to this study. The temperature, and the variable regarding the plant species on which footprint tunnels were placed were not added in the models, because the models could not converge. Even if elevation was found to impact hazel dormouse occupancy in the past (Melcore et al., 2020), it was not the case in this study. Maybe not enough different altitudes were surveyed to be able to predict hazel dormouse occupancy significantly with elevation. Exposition does

not seem to have a significant effect on occupancy, and the effect of hillshade becomes unsignificant when added with other variables to the base model (Tables 1 and 2). The slope is the only variable that has a significant effect on hazel dormouse occupancy, but its confidence interval is large (Figure 6). So, when accounting for the effect of slope on hazel dormouse, the variability in the occupancy probabilities should be considered.

4.4. Implications for conservation

The results support that hazel dormice in the Gantrisch and in the Val-de-Ruz prefer forest edges with a soft slope (Figures 5 and 6). However, it does not mean that the hazel dormouse only occupies this kind of habitat. As the descriptive data shows, hazel dormice were found in hedgerows and structured forest as well (Figures 4 and A5). There is a higher probability of finding the species in forest edges during fall and spring in both research regions, but the hazel dormouse can occur in other habitats too. In the Val-de-Ruz, the detection of hazel dormouse is lower (Table A6), meaning that there might be fewer hazel dormice in that region than in the Gantrisch.

This research highlighted a potential misconception of the hazel dormouse in Switzerland. In the literature, the species is often considered as a hedgerow species (A. Dietrich, personal communication, June 17, 2024). England has historically many hedges (Baudry et al., 2000), where hazel dormice can be present. In Switzerland, the hazel dormouse is also associated with hedgerows (Delarze et al., 2015), but this habitat type does not seem suitable enough for the species in this country (A. Dietrich, personal communication, June 17, 2024). Forest edges might be preferred by the species, at least in the Val-de-Ruz and parts of the Gantrisch. In a recent study conducted in southwest England, hazel dormice frequented more often scrubs than hedgerows, supporting the idea that accounting for scrub habitats, like forest edges, can add value to habitat restoration (Scopes et al., 2024). So, forest management in Switzerland needs to consider habitats in forests more to preserve the hazel dormouse.

New sites with hazel dormouse presence were discovered in this study (Table A4). Knowing sites where the hazel dormouse occurs in the Gantrisch and in the Val-de-Ruz can help municipalities or other corps to make woodland or forestry management plans friendlier to the species. Regarding the management of forest edges, owners do not necessarily have to manage them. However, cutting between 75% and 100% of the mature trees in the edges can help conserve the hazel dormouse, because it allows the understory to grow which is great for its habitat (Ramakers et al., 2014). Tree felling should be managed to not disturb the hazel dormouse's movements, and be aligned with woodland conservation purposes (Goodwin, Hodgson, et al., 2018).

The generality drawn by the results, i.e. that hazel dormice occupy forest edges the most in the Val-de-Ruz and in the Gantrisch, is to be taken carefully. Other habitats need to be managed in a friendly way, knowing that the hazel dormouse can occur there as well. To account for every hazel dormouse individual in a region, the region in its whole should be surveyed, but time, logistic and financial limitations complicate this kind of monitoring. If the hazel dormouse occupied different habitat types before and after hibernation, or if it were completely absent from some habitat types, the management planning would be easier to realize. However, the ecological complexity of a species is to be calculated with in natural

management plans. Moreover, whatever the nature of a management conservation action plan is, the seasonal decrease in occupancy and the variability in forest edge occupancy are to be remembered when creating conservation plans for the hazel dormouse.

5. Conclusion

The goal of the study was to understand the hazel dormouse's dynamic habitat type preferences to know when and where to focus conservation actions in two Swiss regions. The footprint tunnels were effective tools to research those preferences. Occupancy before and after hibernation was researched in different habitat types used by the species. In fall and in spring, the hazel dormouse seems to prefer forest edges than hedgerows or structured forests. A soft slope is also indicated to be a sign of higher occupancy probability. Occupancy can change within one habitat type between seasons, for instance in forest edges where a decrease was noted after hibernation. The dynamic aspect of occupancy could be statistically analyzed only between seasons, but not during seasons. This limitation hindered a deeper dynamic analysis of habitat occupancy. In the future, this topic can be further explored. It can be associated with a more complex categorization of habitat type, using more than just the type to describe a habitat.

Three habitat types of the hazel dormouse were surveyed simultaneously in this study, which was done for the first time in Switzerland. The advantage of comparing the occupancy between three habitat types is the following: if a survey only monitors one habitat type in a region, it will not indicate if there are any hazel dormice in other kinds of habitat. Surveying multiple habitats helps to assess the presence of a species in a region in a more complete way.

The results reveal that hazel dormice are present at various sites in the Gantrisch and in the Val-de-Ruz, and that their presence depends on a preference tendency. This knowledge is useful for conservation purposes, even if no data on density, abundance, or other parameters regarding the species and individuals were considered in the analyses (Chanin & Woods, 2003). As the hazel dormouse literature comes mainly from the UK (Haag, 2014), it was interesting and essential to analyze hazel dormice in their habitats in two Swiss regions. New habitat sites were noted, which also counts as useful population knowledge for hazel dormouse conservation plans. This study highlighted that the hazel dormouse is rather a forest edge species than a hedgerow species. This clarification in the habitat preference is an important result for forest management and species conservation.

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8. Appendix

8.1. Figures and tables

8.1.1. Transects centroids

Coordinates of the transect centroids

(a)

Transect ID	Coordinate x	Coordinate y
g_hr_1	2590979,890	1183770,758
g_hr_2	2597498,979	1184377,029
g_hr_3	2599588,938	1183971,415
g_hr_4	2593729,251	1185701,369
g_hr_5	2600618,587	1183315,293
g_fe_1	2591043,819	1183688,958
g_fe_2	2590606,694	1184086,822
g_fe_3	2590715,717	1184420,502
g_fe_4	2593809,890	1185810,945
g_fe_5	2600421,686	1183293,770
g_sf_1	2591042,617	1183649,587
g_sf_2	2597143,192	1184269,979
g_sf_3	2591064,676	1182753,438
g_sf_4	2601682,543	1186728,723
g_sf_5	2600033,034	1183182,372

(b)

Transect ID	Coordinate x	Coordinate y
vdr_hr_1	2557300,299	1206282,408
vdr_hr_2	2557566,361	1206550,373
vdr_hr_3	2555130,041	1206541,488
vdr_hr_4	2562415,906	1213503,263
vdr_hr_5	2562793,406	1208084,352
vdr_fe_1	2557280,871	1206178,906
vdr_fe_2	2557631,903	1206554,684
vdr_fe_3	2555626,499	1208340,157
vdr_fe_4	2562418,433	1213564,679
vdr_fe_5	2562838,765	1208193,518
vdr_sf_1	2557534,968	1206295,530
vdr_sf_2	2557861,192	1206537,576
vdr_sf_3	2555380,809	1208582,399
vdr_sf_4	2562445,648	1213578,386
vdr_sf_5	2562929,927	1208244,111

Table A1: Coordinates of the transects centroids in the (a) Gantrisch and (b) Val-de-Ruz.

8.1.2. Footprint identification

Number of hazel dormouse footprints identified

	Both regions	Gantrisch	Val-de-Ruz
Both seasons	171	123	48
Fall	118	84	34
Spring	53	39	14

Table A2: Number of footprint identifications found according to the regions and the different research periods.

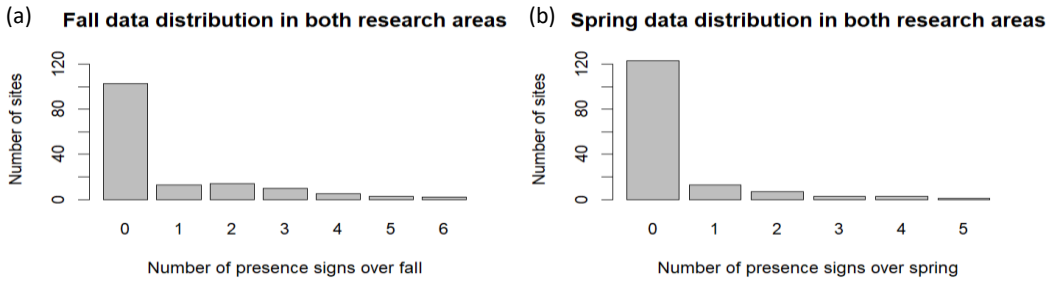

Figure A1: Bar plots illustrating how many presence signs the sites had for (a) fall and (b) spring in both research regions.

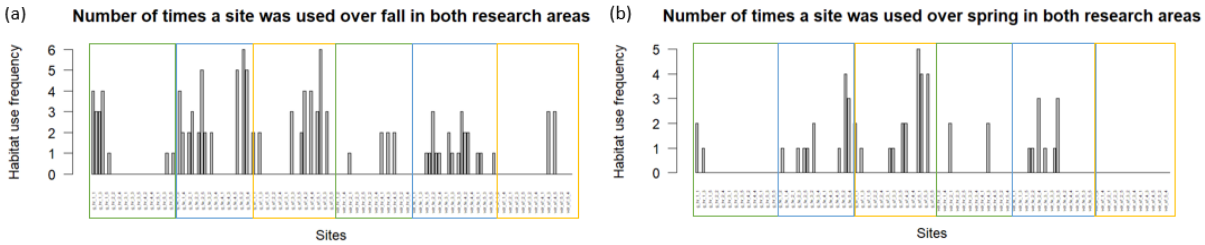

Figure A2.1: Bar plots illustrating the presence signs identified at the 150 sites where footprint tunnels were placed for (a) fall and (b) spring. Each bar represents a site on the x-axis. First comes the data from the Gantrisch and then, from the middle to the right comes the data from the Val-de-Ruz. The habitats are ordered in the following way: hedgerows (in green), forest edges (in blue) and finally structured forests (in yellow).

Three hedgerows, one forest edge and one structured forest had no hazel dormouse presence in the fall in the Gantrisch. In the fall in the Val-de-Ruz, three hedgerows and three structured forests were not occupied, whereas all monitored forest edges were occupied by the species. In spring, four hedgerows, one forest edge and one structured forest were not occupied in the Gantrisch. During the same season in the Val-de-Ruz, three hedgerows, and three forest edges had no presence signs. The biggest lack of presence noted for a habitat type category regards structured forests in spring in the Val-de-Ruz (Figures A2.1 and A2.2).

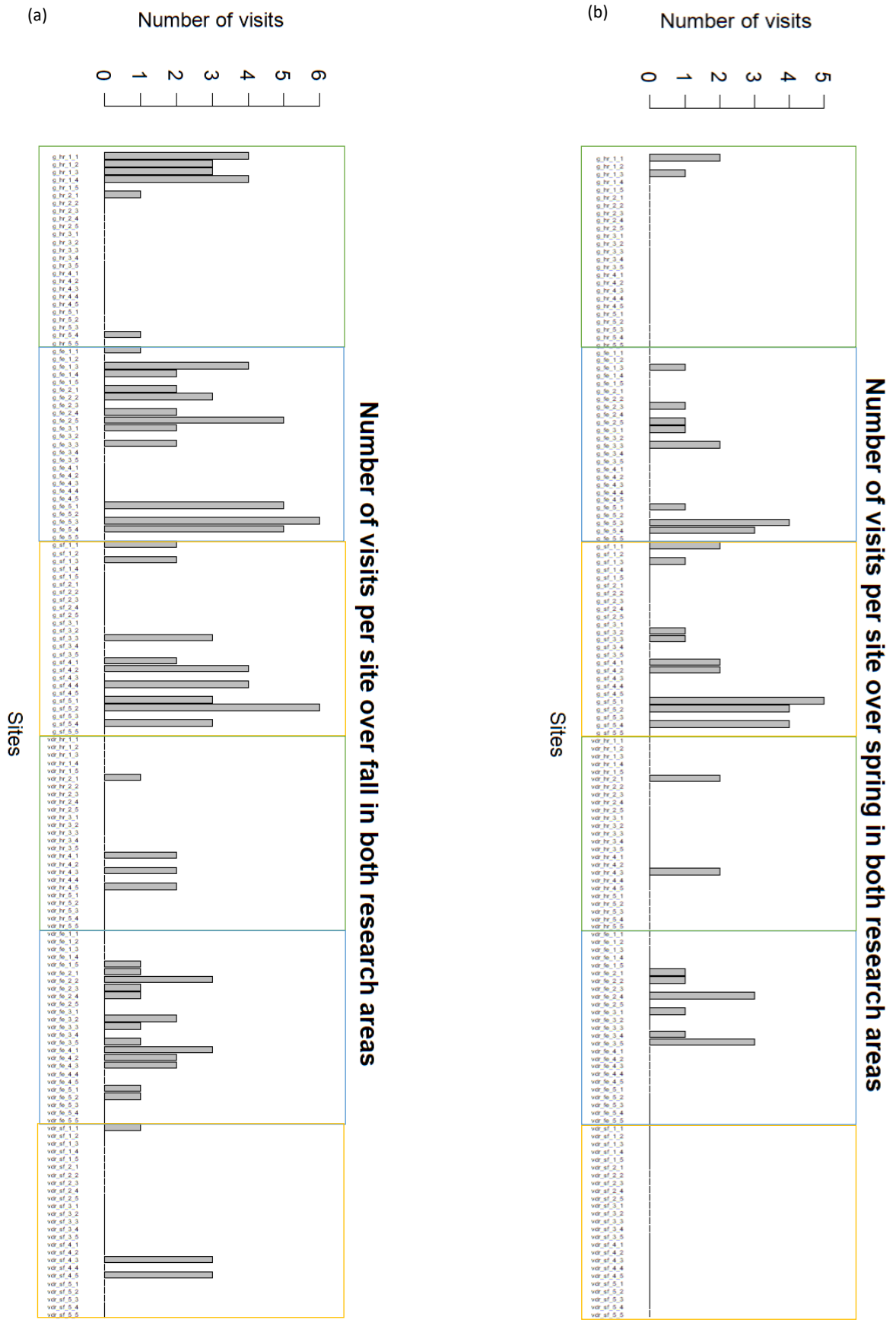

Figure A2.2: Bar plots illustrating the presence signs identified at the 150 sites where footprint tunnels were placed for (a) fall and (b) spring. Each bar represents a site on the x-axis. First comes the data from the Gantrisch and then, from the middle to the right comes the data from the Val-de-Ruz. The habitats are ordered in the following way: hedgerows (in green), forest edges (in blue) and finally structured forests (in yellow).

Number of footprints in relation to the connectivity between habitat types

	Both seasons	Fall	Spring
HR connected to FE	27	20	7
HR not connected to FE	0	0	0
SF connected to FE	39	24	15
SF not connected to FE	20	14	6

Table A3: Numbers of footprints in both research regions in monitored hedgerows (HR) and structured forests (SF) when those habitat types were directly connected to monitored forest edges (FE) or not.

When monitored hedgerows were directly connected to monitored forest edges, more footprints were found than in monitored hedgerows that were further away from monitored forest edges. In the latter, no footprints were found at all. When monitored structured forests were directly connected to monitored forest edges, more footprints were found than in monitored structured forests that were further away from monitored forest edges. More footprints were always found in structured forests than in hedgerows.

Coordinates of the sites with hazel dormouse presence

(a)

Region	Habitat type	Footprint tunnel identification	Coordinate x	Coordinate y
Gantrisch	Hedgerow	g_hr_1_1	2591039	1183780
Gantrisch	Hedgerow	g_hr_1_2	2591011	1183781
Gantrisch	Hedgerow	g_hr_1_3	2590982	1183774
Gantrisch	Hedgerow	g_hr_1_4	2590953	1183765
Gantrisch	Hedgerow	g_hr_5_4	2600622	1183335
Gantrisch	Forest edge	g_fe_1_1	2590995	1183676
Gantrisch	Forest edge	g_fe_1_3	2591036	1183685
Gantrisch	Forest edge	g_fe_1_4	2591068	1183694
Gantrisch	Forest edge	g_fe_2_1	2590569	1184056
Gantrisch	Forest edge	g_fe_2_2	2590573	1184057
Gantrisch	Forest edge	g_fe_2_3	2590601	1184088
Gantrisch	Forest edge	g_fe_2_4	2590630	1184106
Gantrisch	Forest edge	g_fe_2_5	2590646	1184116
Gantrisch	Forest edge	g_fe_3_1	2590757	1184453
Gantrisch	Forest edge	g_fe_3_3	2590710	1184425
Gantrisch	Forest edge	g_fe_5_1	2600469	1183276
Gantrisch	Forest edge	g_fe_5_3	2600421	1183297
Gantrisch	Forest edge	g_fe_5_4	2600393	1183303
Gantrisch	Structured forest	g_sf_1_1	2591000	1183623
Gantrisch	Structured forest	g_sf_1_3	2591030	1183646
Gantrisch	Structured forest	g_sf_1_4	2591065	1183663
Gantrisch	Structured forest	g_sf_3_2	2591064	1182723
Gantrisch	Structured forest	g_sf_3_3	2591071	1182744
Gantrisch	Structured forest	g_sf_4_1	2601655	1186706
Gantrisch	Structured forest	g_sf_4_2	2601680	1186708
Gantrisch	Structured forest	g_sf_4_4	2601702	1186747
Gantrisch	Structured forest	g_sf_5_1	2600014	1183181
Gantrisch	Structured forest	g_sf_5_2	2600040	1183168
Gantrisch	Structured forest	g_sf_5_4	2600022	1183201

(b)

Region	Habitat type	Footprint tunnel identification	Coordinate x	Coordinate y
Val-de-Ruz	Hedgerow	vdr_hr_2_1	2557603	1206524
Val-de-Ruz	Hedgerow	vdr_hr_4_1	2562429	1213456
Val-de-Ruz	Hedgerow	vdr_hr_4_3	2562411	1213502
Val-de-Ruz	Hedgerow	vdr_hr_4_5	2562405	1213551
Val-de-Ruz	Forest edge	vdr_fe_1_5	2557327	1206203
Val-de-Ruz	Forest edge	vdr_fe_2_1	2557609	1206508
Val-de-Ruz	Forest edge	vdr_fe_2_2	2557626	1206532
Val-de-Ruz	Forest edge	vdr_fe_2_4	2557639	1206583
Val-de-Ruz	Forest edge	vdr_fe_3_1	2555595	1208296
Val-de-Ruz	Forest edge	vdr_fe_3_2	2555610	1208324
Val-de-Ruz	Forest edge	vdr_fe_3_3	2555628	1208344
Val-de-Ruz	Forest edge	vdr_fe_3_4	2555650	1208364
Val-de-Ruz	Forest edge	vdr_fe_3_5	2555658	1208384
Val-de-Ruz	Forest edge	vdr_fe_4_1	2562379	1213578
Val-de-Ruz	Forest edge	vdr_fe_4_2	2562384	1213556
Val-de-Ruz	Forest edge	vdr_fe_4_3	2562409	1213555
Val-de-Ruz	Forest edge	vdr_fe_5_1	2562861	1208146
Val-de-Ruz	Forest edge	vdr_fe_5_2	2562845	1208167
Val-de-Ruz	Forest edge	vdr_fe_5_5	2562821	1208243
Val-de-Ruz	Structured forest	vdr_sf_1_1	2557493	1206268
Val-de-Ruz	Structured forest	vdr_sf_3_1	2555357	1208548
Val-de-Ruz	Structured forest	vdr_sf_4_3	2562468	1213575
Val-de-Ruz	Structured forest	vdr_sf_4_5	2562405	1213566

Table A4: Coordinates of the sites with hazel dormouse evidence in the (a) Gantrisch and (b) Val-de-Ruz.

8.1.3. Missing data

Number of missing data in the dataset

	Total	Last/First week	Presence	Rest
Both seasons	63	29	4	30
Fall	53	28	3	22
Spring	10	1	1	8

Table A5: Number of missing data in the whole dataset, categorized by seasons and characteristics of the missing data's sites.

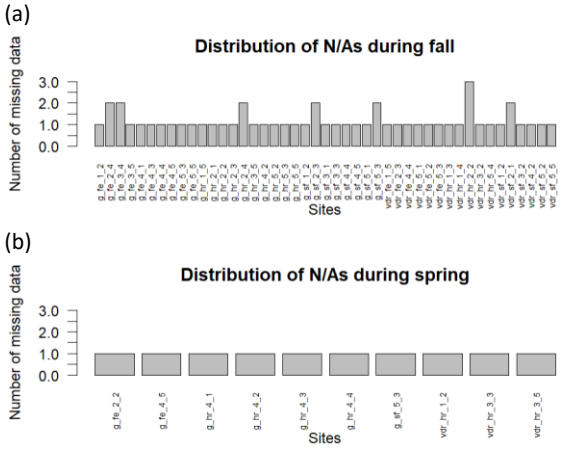

Figure A3: Bar plots illustrating at which sites the missing data were noted in both research regions in (a) fall and (b) spring.

63 missing data (N/As) were reported in the whole dataset. N/As were reported whenever the detection non-detection could not be recorded on the paper in a tunnel. N/As represent absences of data, either because the inside part of the tunnel slipped out of the tunnel, was lost or because the tunnel was tilted, and no footprints could be printed. In fall, 53 missing data were recorded (Table A5). 28 of these were noted the last week of data collection. Normally, they would be considered as absences/non-detection, i.e. "0s" at these sites, as the species must have been inactive. Thus, we believe that these 28 N/As do not interfere with the analysis. 22 other missing data were reported at sites where no sign of hazel dormouse presence was found during other controls. However, three of the 53 N/As were noted at sites where evidence of the hazel dormouse was recorded during other controls. In our opinion, these three N/As could be problematic, as there could have been a distinctive sign of detection or non-detection rather than a lack of data. However, these three N/As represent only 0.29% of the total fall data (1050). So, the three pieces of missing data are marginal. In spring, following the same logic as for the data retrieved in fall, the missing data did not impact the data analysis, as they almost all occurred at sites where no hazel dormouse footprints were noted during other controls (Table A5). Only one N/A was present where there could have been a distinct sign of hazel dormice. It represents only 0.1% of the total spring data (1050). So, during both seasons, we think that the missing data did not interfere with the data analysis.

Regarding the missing data in fall, there is little variability in the distribution of the missing data (Figure A3). The N/As were noted at 45 different sites, with only one presenting three absences of data, six presenting two, and 38 presenting only one. 28 sites with N/As were in the Gantrisch, for 17 in the Val-de-Ruz. 16 sites with N/As were in forest edges, 15 in hedgerows, and 14 in structured forests. So, the missing data were equally distributed throughout the habitat types. Thus, the missing data seemed to not be attributed to a chronic error or problem. The missing data in spring were distributed differently (Figure A3). Ten different sites had each one missing data, seven of them were in the Gantrisch, and three were in the Val-de-Ruz. Two sites with N/As were in forest edges, seven were in hedgerows and one was in a structured forest. The missing data were less equally distributed in spring, but as the number of missing values was smaller, no problem with N/As was considered.

8.1.4. Activity dynamic

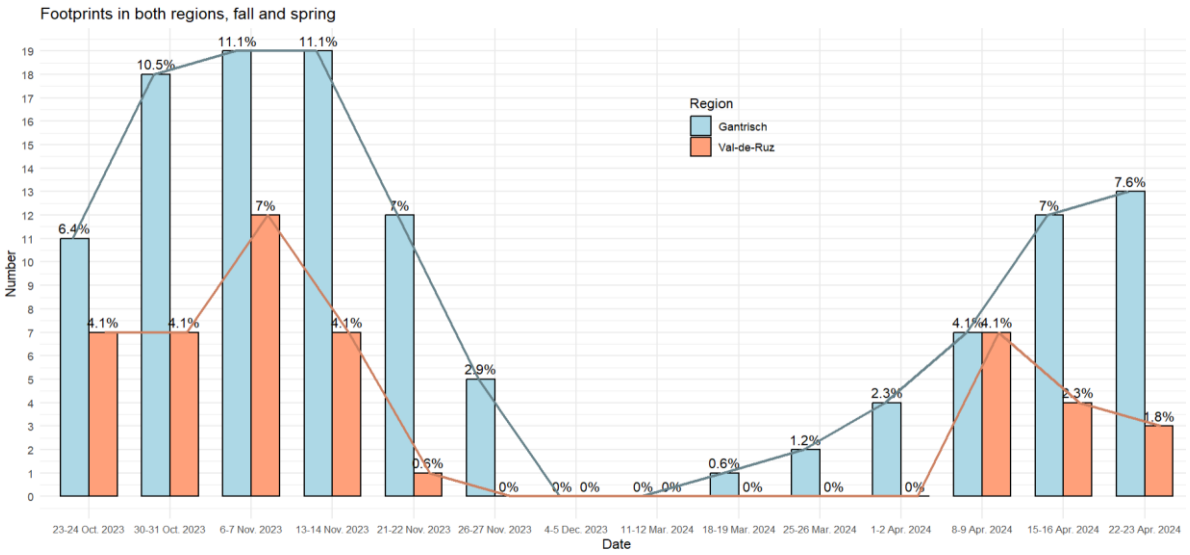

Figure A4: Activity dynamic of the hazel dormouse before and after hibernation, all habitat types combined, in both research regions. The percentages for each week are an indication in relation to the total of footprints found (171). This bar plot illustrates the count of footprints week after week, with a hibernation break from December to March.

8.1.5. Habitat type preference

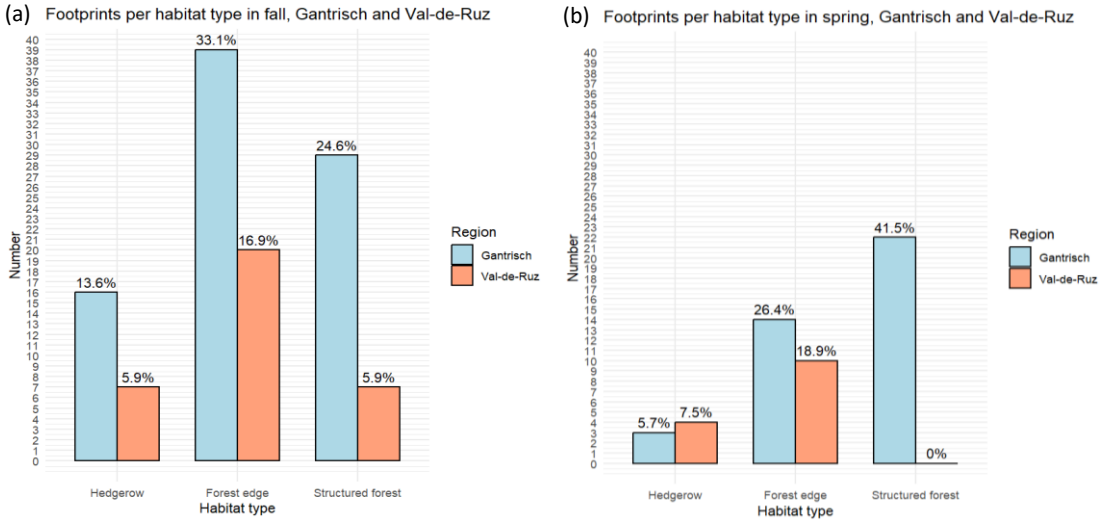

Figure A5: Number of footprints in the different habitat types in the two research regions during (a) fall and (b) spring. The percentages are an indication in relation to the total of footprints found in each season (118 in fall, 53 in spring).

Model 1 and 2 results: detection

Variable	Estimate	SE	z.value	p.value
seasonfall	-2.311	0.507	-4.561	5.10e-06
seasonspring	-3.036	0.526	-5.776	0.00e+00
regionvdr	-0.725	0.262	-2.770	5.60e-03
height_or_groundht	1.956	0.467	4.192	2.76e-05
ft_kindb	0.211	0.232	0.906	3.65e-01

Table A6: Model results for detection covariates. 95% confidence interval. Significance was retained when p.value < 0.05.