

Presumed seed specialists rely on fungi as their primary food source at the sub-Arctic treeline

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Abstract

Range boundaries limit local populations, which may experience pronounced fluctuations in resource availability, particularly at higher latitudes, often seen as resource pulses. In boreal forests, conifers undergo pulses of seed production followed by intervals of low seed production, profoundly affecting consumers dependent on these resources. Red squirrels (*Tamiasciurus hudsonicus*) are considered seed specialists across the boreal forest. We evaluated how annual changes in white spruce (*Picea glauca*) cone production at the sub-Arctic treeline near Churchill, MB, Canada, influenced squirrels' use of alternative food sources, predicting that low cone production would increase reliance on alternate foods. Cone crops varied from 2020–2023, with a mast year in 2022 of 471 cones per tree, approximately 70–80% lower than mast years elsewhere, and lower crops in other years (6–115 cones per tree). Furthermore, the number of filled seeds (containing an embryo) per cone was low, ranging from 0.6 ± 0.03 (mean $\pm$ SE) in 2022 to 3.6 ± 2.6 in 2023. Using stable isotope ratios of hair and Bayesian mixing models, we found that squirrels primarily consumed fungi (~70% of diet), even in mast years, with other food sources varying with cone production. The dominance of fungi in squirrel diet even in mast years, highlights the dietary plasticity of red squirrels beyond seed specialization challenging the seed specialization paradigm. Flexible foraging strategies likely allow populations to persist in resource-limited environments and may facilitate range expansion as climate change reshapes habitats.

Introduction

Species with extensive geographical distributions often have smaller, fragmented populations near their range limits, where habitats are harsher than at the core of their distributions (Gaston 2003, Lynch et al. 2014). Range boundaries can be shaped by physical barriers directly preventing species' dispersal (Gross & Price 2000) or gradients in climatic variables, which create physiological limits. In the northern hemisphere, it is commonly thought that northern range boundaries are frequently governed by abiotic factors like extreme climate, while biotic factors, such as competition, and food availability, impose additional constraints at southern range limits (Brown et al. 1995, Sirén & Morelli 2020). However, combinations of factors likely work in concert, limiting the expansion of species beyond their range. Compared to core environments, range boundary habitats often exhibit greater climatic variability (Rehm et al. 2015), which imposes physiological limits and impact population growth (Sexton et al. 2009). Although range boundary habitats can be expansive, they are often low quality or exist as fragmented patches of high-quality habitat. Climatic factors and the corresponding influences on habitat suitability, population density, and reproductive fitness strongly reinforce range limits and can be further exacerbated by inter and intraspecific interactions and resource availability. At northern range boundaries, extreme climates can reduce the availability and accessibility of food sources, particularly during winter. The variation in seasonal climates at higher latitudes dictates large annual and seasonal fluctuations in resource availability (Humphries et al. 2005), as shorter growing seasons and cooler seasonal temperatures restrict primary and secondary productivity (Gross & Price 2000, Callaghan et al. 2004). Species respond to fluctuations in food sources in multiple ways. Some species, such as the boreal woodland caribou (*Rangifer tarandus caribou*), migrate seasonally following food sources (Rettie

& Messier 2000, Ferguson & Elkie 2004). Other species, such as wolverines (*Gulo gulo*), may change activity patterns or cache food to buffer against fluctuating food availability in an overall low-productivity environment (van der Veen et al. 2020). When food is spatially and temporally variable, species may rely on pulses of food sources.

Pulsed resources are episodic events of superabundant resource production with long inter-pulse periods of normal or subnormal production. While resource pulses are short-lived, they drive the dynamics of many plant and animal communities. The bottom-up effect of pulsed resources can be seen at the level of the individual, the population, and indirectly at the community level (Yang et al. 2008, Yang et al. 2010). At the individual level, consumer diets shift in response to pulsed resources, which induces numerical responses in consumer populations. These responses then propagate across trophic levels as increased densities in consumers become secondary resource pulses for higher trophic levels (Yang et al. 2010).

The boreal forest, one of the world's largest terrestrial biomes, represents the northern range limit for many species (Kayes & Mallik 2020, Krebs et al. 2023). Conifers in the boreal forest experience periodic masting, with years of high seed production followed by long intervals of low or absent seed production (Kelly & Sork 2002, Lamontagne & Boutin 2007, Archibald et al. 2012). Mast years are often synchronous across large geographical areas (Lamontagne & Boutin 2007, Krebs et al. 2012) and overwhelm seed predators, enhancing seed survival and establishment (Kelly & Sork 2002). White spruce (*Picea glauca*) is the dominant tree species in dry habitats at the north limit of the boreal forest (Bonan and Shugart 1989) and exhibits periodic masting (Archibald et al. 2012, Krebs et al. 2012, Krebs et al. 2023) approximately every 3–5 years (Lamontagne & Boutin 2007). Many small mammals rely heavily on spruce seeds, but may switch to alternative food sources, such as fungi, which can be highly abundant but nutrient-poor, during non-mast years (Ostfeld & Keesing 2000, Fletcher et al. 2010).

The dietary strategies of species can be defined based on the breadth of their dietary niches. Facultative generalists typically have a very broad dietary niche compared to facultative specialists that exhibit a narrower dietary niche (Shipley et al. 2009, Pagani-Núñez et al. 2016). However, both groups exhibit behavioural plasticity. Facultative generalists optimize resources by switching to more abundant or accessible food sources, while facultative specialists can expand their diet when primary resources are scarce, enabling both groups to exploit fluctuating resources and maintain broad geographic distributions, making them more successful in habitats where food availability is low and heterogeneous (Shipley et al. 2009, Newbury & Hodges 2018, Szumski et al. 2023). In contrast, obligate generalists, though able to use diverse food sources, have limited specialization and may be less efficient in optimizing their diet in such environments, and obligate specialists are vulnerable due to their reliance on specific resources, which could be scarce (Shipley et al. 2009, Dehling et al. 2021). Due to the low predictability of food abundance, generalist species are common at northern range boundaries (Callaghan et al. 2004). Facultative specialists living in these habitats may exhibit behaviours more like facultative generalists when primary food sources are unpredictable and fluctuate dramatically. Individuals may also employ behavioural methods such as food hoarding and increasing litter and clutch

sizes to take advantage of years of superabundant food (Callaghan et al. 2004, Boutin et al. 2006, McAdam et al. 2019).

American red squirrels (*Tamiasciurus hudsonicus*) are primarily granivorous, specialising in conifer seeds across most of their distribution (Steele 1998, Boutin et al. 2006). In the northern parts of their range, red squirrels appear to feed almost exclusively on white spruce seeds (McAdam & Boutin 2003). While seeds constitute the majority of squirrel diet, red squirrels can opportunistically consume a large variety of foods including fungi (Layne 1954, Steele 1998, Fletcher et al. 2010), berries (Benhamou 1996, Currah et al. 2000), and animal prey, including songbird eggs (Bayne & Hobson 2002, Willson et al. 2003) and young lagomorphs (Layne 1954, Sullivan & Sullivan 1982, Peers et al. 2020). These alternative food sources, however, typically make up a small proportion of annual diet (Layne 1954), and are relied on only when spruce cone availability is low. Despite observations of consumption of alternative food sources, detailed quantifications of non-seed food sources are often lacking (Currah et al. 2000, Fletcher et al. 2010). Many life history parameters of red squirrels, including reproduction (Boutin et al. 2006, Lane et al. 2015), growth (McAdam & Boutin 2003), and overwinter survival (Steury & Murray 2003, LaMontagne et al. 2013), are intimately linked to spruce cone production (Humphries & Boutin 2000, McAdam & Boutin 2003, Réale et al. 2003, Boutin et al. 2006). Assuming seed productivity is consistent, seed availability can be estimated through spruce cone availability by counting the number of cones produced within the study area (Lamontagne & Boutin 2007, Kucheravy et al. 2021). However, the quality and quantity of seeds produced each year can also vary (Waldron 1965, Zasada 1988), further influencing overall food availability.

We reconstructed the diet of red squirrels living at their sub-Arctic range boundary using stable isotope analysis and explored how spruce cone production affected squirrel diet. We hypothesised that squirrels would adopt a highly supplemented diet in low cone years and predicted that 1) overall cone production would be low, 2) squirrels would frequently consume alternate food sources, depending on the yearly abundance of cones, and 3) their dietary niche would be broad. We further predicted that 4) fall diet would be broader than spring diet, as alternate food sources such as fungi and berries are more abundant in fall.

Methods

Study area

Our study area near Churchill, MB (58°45' N, 94°04' W) on the western edge of Hudson Bay, is on the transition between boreal forest and Arctic tundra. The forest is primarily composed of white spruce, black spruce (*Picea mariana*), and tamarack (*Larix laricina*) (Mamet & Kershaw 2011, Mamet & Kershaw 2013), and is heavily fragmented by patches of wetlands and open tundra (Harper et al. 2011, Harper et al. 2018). The forest has a low density of mature trees (~ 600 stems ha^{-1}) and a sparse canopy of ca. 25% (Lafleur 1999). The proximity of the sub-Arctic treeline to Hudson Bay, which is frozen eight months of the year, exposes the region to cool summer temperatures and extreme winters (Mamet & Kershaw

2011). In our study area, mean monthly temperatures ranged from -28.4 to -15.1 °C in winter (November–April) and 1.2 °C to 20.6 °C in summer (June–August) from 2019–2023 (Environment Canada).

Fieldwork was conducted in boreal woodland consisting of patchy forest, transitioning to a denser forest and ending in an open-canopy forest near a large fen (Fig. 1). We established sites at 250 m intervals along a 7 km transect running north to south, looking for signs of squirrel activity such as vocalisations, cone debris, and middens. Middens are large food caches containing hundreds to tens of thousands of cones (Haines et al. 2022, Wishart 2023), and are easily identified by the concentrated accumulation of cone debris, often reaching surface areas up to a few hundred m² (Steury & Murray 2003). Very few true middens, characterized by large fields of cone debris, were observed in our study area. Here, we define a ‘midden’ as any form of food cache, including true middens and burrows with cone debris that have the potential to contain cones. To account for juvenile dispersal and the possibility of squirrels taking over previously unoccupied sites, we checked all sites for signs of squirrel activity each year in early June.

Food availability

To assess annual spruce cone production, we conducted cone counts of individually marked trees each August (five trees per site; 9 sites in 2020, 26 sites in 2021–2023). Each tree was at least 5 m from the nearest sampled tree and had a minimum of 5 cm diameter at breast height (DBH), representing the approximate minimum age at which white spruce trees can bear cones (Lamontagne & Boutin 2007). At squirrel-occupied sites, we sampled the five closest trees to the midden. At unoccupied sites, we selected the five closest trees from a flagged reference point, following a bearing determined using a random number generator. Each August, we took 3–5 photographs of each tree on opposing sides. Using ImageJ image processing software, we counted the cones visible in each picture (Nygren et al. 2017). The photographs for each tree were matched to avoid double-counting cones. We calculated food availability at each site as the mean number of cones per tree (Kucheravy et al. 2021), multiplied by tree density to estimate cones per hectare. To calculate tree density at each site, we counted the number of white spruce trees (> 5 cm DBH) within four 15 m radius plots (two on each side of the flagged reference point) spaced 20 m apart. To estimate seed production, we used data from the control sites, which encompassed our sampling area, from Benjamin et al. (2024). We collected cones from the upper part of the crown using a pole pruner. The number of cones collected per tree depended on their availability but averaged 13 ± 1 cones. The cones were air-dried for at least 72 h prior to dissecting and removing the seeds. We placed the seeds in 95% ethanol to separate the filled seeds containing an embryo (sinking seeds) from empty seeds (Ho 1984, Sirois 2000).

To estimate availability of fungi, in 2022 we collected all epigeous fungal sporocarps within two randomly selected 15 m radius plots at each site. In 2023, we collected all epigeous fungi within four 1-m² quadrats placed 5 m from each site’s centre point in the four cardinal directions. At occupied sites, the midden served as the centre, and at unoccupied sites, we used the cone count centre point. All

samples were oven-dried for 48–72 hrs, and dry fungal biomass (kg ha^{-1}) was used to reflect fungus availability at each site (Derbridge & Koprowski 2019).

We monitored squirrel hoarding activity using motion-activated Browning trail cameras (model: Strike Force Extreme and Strike Force HD Pro X) installed at 17 occupied sites (one camera per site). We chose sites with previously observed middens and installed each camera facing the largest midden if a site had multiple middens. Cameras captured bursts of three photos when activated within a three-metre detection range, with a 0.5 second recovery between bursts. We recorded the date, time, location, and type of food items hoarded from August 1 to September 30, reflecting the typical harvest period for squirrels in central areas of the boreal forest (Fletcher et al. 2010, Archibald et al. 2013) and to account for the shorter growing seasons and earlier winters characteristic of the northern boreal treeline. Squirrels entering middens with food or crossing the camera's field of view carrying food, were classified as hoarding events. Observations may have underestimated activity if a midden had multiple entrances not covered by cameras.

Stable isotope sample collection and preparation

Red squirrel body hair moults in spring and fall, while tail hair moults only in the fall (Nelson 1945). We collected body hair (~ 3–4 clippings, ~ 0.5 cm behind the shoulder) and tail hair (~ 2–3 cm) each June, from a total of 103 squirrels (90 unique individuals, 9 recaptures, and 4 donated by local trappers) to compare seasonal diets. We captured squirrels using Tomahawk live traps (model #202). We recorded the sex and marked each squirrel with a Passive Integrated Transponder (PIT) tag injected under the skin for permanent identification and metal ear tags threaded with coloured pipe cleaners for visual identification

We collected samples of potential food sources from forested and forest-wetland regions within our study area in August 2021 (Table S1). Samples included white ($n = 9$) and black spruce seeds ($n = 9$), tamarack seeds ($n = 6$) and buds ($n = 15$), and the most common species of berries ($n = 97$), lichen ($n = 22$), and fungi ($n = 110$).

Hair samples were washed twice with mild, soapy water and rinsed thoroughly before drying in a drying oven for 48 hours. We removed seeds from spruce cones and dried the seeds, fungi, berry and lichen samples in a drying oven for a minimum of 48 hours, and ground all food samples to a powder using a mortar and pestle, washing the tools between samples with 70% ethanol. All samples were analyzed for carbon and nitrogen stable isotope ratios on a continuous-flow isotope ratio mass spectrometer (Delta V Advantage) coupled to a Costech 4010 Elemental Combustion system and a ConFlo IV universal interface.

Data analysis

We used stable isotope analysis to examine annual and seasonal variation in squirrel diets. The isotopic composition of a consumer's tissues reflects dietary sources, adjusted by trophic discrimination factors (TDFs) to account for isotopic shifts during assimilation (Phillips 2012, Parnell et al. 2013). We applied rodent-specific TDFs and standard deviations of $\Delta^{13}\text{C} = 3.3 \pm 2.2\text{‰}$ and $\Delta^{15}\text{N} = 1.9 \pm 0.2\text{‰}$ (Hobbie et al. 2017, Pauli et al. 2019) to source isotope values. Using a K nearest-neighbor (KNN) randomization test ($k = 15$) we classified 231 samples into five isotopically distinct food groups: berries (species $n = 7$), lichen ($n = 2$), conifer seeds and buds (not isotopically distinct: ANOVA: $\delta^{13}\text{C}$: $F_{3,35} = 0.65$, $p = 0.59$; $\delta^{15}\text{N}$: $F_{3,35} = 1.57$, $p = 0.38$), and fungi divided into two groups (genera $n = 5$) due to $\delta^{15}\text{N}$ variation across genera and habitats (forest vs forest-wetland) (Table S1, Figure S1).

We estimated the dietary contribution of each food group to squirrel diet using Bayesian isotopic mixing models with the MixSIAR and *rjags* packages (Parnell et al. 2013) in R. All models incorporated uniform prior distributions and concentration dependence using the mean elemental concentrations for each prey group. We used Markov-chain Monte Carlo (MCMC) methods to estimate the parameters of the mixing models and ran three parallel MCMC chains with a burn-in of 50,000 iterations. We generated posterior samples using 150,000 iterations of the models and a thinning rate of 50 and checked model convergence using the Gelman and Geweke diagnostic tests produced by MixSIAR (Geweke 1991, Jackson et al. 2011, Gelman et al. 2014).

Stable isotope ratios were also used to estimate dietary niche breadth, where narrower isotopic niches indicate more specialised diets (Bearhop et al. 2004, Jackson et al. 2011). For opportunistic species, niche breadth can shift seasonally and annually with food availability. Isotopic niche breadth was modelled using an ellipse-based approach with the Stable Isotope Bayesian Ellipses in R (SIBER) package in R. We compared isotopic signatures from body (spring diet) and tail (fall diet) hair samples. Previous studies suggest the fall moult occurs between late August and into September (Kranowski 1969) and the spring moult occurs between April and May (Layne 1954), although populations at higher latitudes can moult between March and June (Lepage & Parker 1988). However, we did not observe signs of moulting during our trapping efforts throughout June and into early July. We therefore assumed that all body hair collected in June was recently grown. We generated metrics for isotopic niche breadths using standard ellipse areas corrected for small sample size (SEA_c) and Bayesian Standard Ellipse Areas (SEA_b) (150,000 MCMC iterations, 95% credible interval). We compared seasonal and annual niche breadths using the credible intervals to estimating the probability (0–1) that one group's ellipses were smaller than another (Jackson et al. 2011). We also examined the dietary niche overlap between ellipses by calculating the proportion of ellipse overlap using 1,000 draws of the posterior estimates of each ellipse.

All statistical analyses were conducted in R (version 4.0.5). We used generalised linear mixed effects models (GLMM) to determine if mean cone production varied annually, using 'site ID' as a random effect. Since the cone count data was overdispersed, we used a negative binomial link function. For fungal biomass, we used a paired t-test to determine if dry fungal biomass varied from 2022 to 2023.

We examined annual variation in filled seed counts per cone using a linear model (LM) with cone production (total cones per tree) and seed production (total number of seeds per cone, comprising both filled and empty seeds) as additional explanatory variables. To examine the effect of cone abundance on hoarded food items, we used trail camera observations to determine the daily mean cone and fungi hoarded per camera. We used a GLMM for each food source with a Poisson link and accounted for spatial variation using 'site ID' as a random effect.

We tested for annual and seasonal variation in squirrel diet, using a multivariate analysis of variance (MANOVA) to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between years and body and tail hair. We further examined annual diet variations in MixSIAR, with 'year' (4 levels) as a fixed effect and 'site ID' (26 levels) as a random effect. Squirrels were only trapped at 26 of the 29 sites in our study area. We ran a second mixing model to estimate individual diets using 'squirrel ID' as a fixed effect. We incorporated the mean individual dietary proportions from MixSIAR into three beta regression models (berries, fungi, and lichen) with a canonical link function using the *betareg* package in R to determine if the consumption of alternate food sources fluctuated with cone abundance, using the mean cone abundance at the sites where the individuals were trapped. We used beta regression models since dietary proportions range from zero to one (McAulay et al. 2020). We paired all squirrel diets with cone production estimates from the previous fall, as tail hair reflects the previous fall's diet and body hair collected in summer reflects the spring diet when most food items such as fungi, cones, and berries were not yet available. Thus, squirrels likely relied on food cached the previous fall.

Results

Tree density across sites averaged $483.7 \text{ stems ha}^{-1}$ ($\pm 54.2 \text{ SE}$; range 56 to 579). From 2020 to 2023, annual spruce cone production varied significantly (Table S2), with the greatest number of cones per tree in the most recent year of 2022 (471.2 ± 33.1), low crops in 2021 (7.9 ± 0.8) and 2023 (6.2 ± 1.2), and a moderate cone year in 2020 (11.5 ± 6.0). The number of filled seeds per cone was low overall, but also varied annually (Table S2), with the greatest number of filled seeds per cone in 2023 (4.9 ± 1.6), the fewest number in the most recent year of 2022 (0.6 ± 0.0), and a low production of filled seeds in 2021 (2.4 ± 0.6). Fungus production across sites ranged from 0.0 to 8.5 kg ha^{-1} , with greater abundance in 2022 (3.5 ± 0.5) compared to 2023 (2.5 ± 0.6) ($t_{25} = 5.51$, $p = 0.014$). Variability of fungal abundance between sites was high but lower in 2022 (coefficient of variation = 67%) compared to 2023 (coefficient of variation = 114%).

Mean daily observations of spruce cone and fungus hoarding in August and September fluctuated annually in response to cone production (GLMM cones: $z_{1,46} = 9.1$, $p < 0.001$; fungi: $z_{1,46} = -2.3$ $p = 0.004$). Cone hoarding was highest in 2022 ($8.1 \pm 0.2 \text{ cones day}^{-1}$), lowest in 2021 (0.9 ± 0.3), and relatively low in 2020 (2.3 ± 0.3) and 2023 (1.4 ± 0.6). Fungus hoarding was highest in 2021 ($1.0 \pm 0.2 \text{ sporocarp day}^{-1}$), lowest in 2020 (0.1 ± 0.0) and 2022 (0.1 ± 0.0), and relatively low in 2023 (0.7 ± 0.1).

Male and female squirrels did not differ in $\delta^{13}\text{C}$ ($t = -0.44$, $df = 51.43$, $p = 0.661$) or $\delta^{15}\text{N}$ ($t = -0.97$, $df = 51.43$, $p = 0.543$) (Table S3 and Figure S1), and neither $\delta^{13}\text{C}$ nor $\delta^{15}\text{N}$ values varied seasonally (MANOVA $F_{1,87} = 2.9$, $p = 0.596$). The Bayesian ellipses were also similar in size (female $\text{SEA}_b = 3.7$; male $\text{SEA}_b = 3.2$) and the proportional overlap between male and female ellipses was also high (0.862), further suggesting a similar diet. However, $\delta^{15}\text{N}$ values varied annually within each season (spring: $F_{2,86} = 18.53$, $p < 0.001$; fall: $F_{2,86} = 14.19$, $p < 0.001$), but $\delta^{13}\text{C}$ did not (spring: $F_{2,86} = 1.72$, $p = 0.153$; fall: $F_{2,86} = 0.99$, $p = 0.135$). The areas of the Bayesian ellipses reflecting dietary niche breadths in fall ($\text{SEA}_b = 2.9$) and spring ($\text{SEA}_b = 3.3$ 2.8) were similar (Fig. 2), as the proportion of posterior draws where the ellipses were smaller in fall than spring was 0.514. The proportional overlap between spring and fall ellipses was 0.815, further suggesting a high degree of similarity between seasonal diets (Table S3). The areas of the ellipses were largest in 2022 (spring: $\text{SEA}_b = 2.5$; fall: $\text{SEA}_b = 2.7$), following a low crop in 2021, and the smallest in 2023 (spring: $\text{SEA}_b = 1.0$; fall: $\text{SEA}_b = 1.1$), following the mast year in 2022 (Fig. 2, Fig. 3). Similarly, the dietary niche breadth in 2023, following the mast year, was narrower than 2022 (reflecting a low crop in 2021) for both spring and fall (Table S3).

Squirrel diet consisted predominantly of fungi (Fig. 4) (> 57% in spring and > 62% in fall), with a small conifer cone contribution (~ 30% in spring and fall) (Table S4 and Figure S2). However, consumption of different food groups varied annually (Fig. 4). Filled seed production significantly affected the consumption of most alternate food sources (fungi: $z = -4.68$, $p < 0.001$, pseudo $r^2 = 0.661$; berry: $z = -4.22$, $p < 0.001$, pseudo $r^2 = 0.442$). However, lichen consumption was not affected by changes in cone production ($z = -1.31$, $p = 0.054$, pseudo $r^2 = 0.118$).

Discussion

This study demonstrated that red squirrels, often considered seed specialists, can exhibit a diet predominantly composed of fungi rather than seeds, which to our knowledge has not been found elsewhere. The sporadic and low cone production in our study area, along with a low number of filled seeds within cones, is reflected in this predominantly fungal diet. In interior boreal forest, many studies have recorded extensive white spruce cone production in mast years over thousands of cones per tree (Krebs et al. 2012, McAdam et al. 2019, Leeper & LaMontagne 2021, Krebs et al. 2023, Wishart 2023). While cone production quadrupled in our mast year (2022), the total number of cones per tree rarely exceeded 600 cones per tree, with a maximum of 1288 cones. Given the low tree density and small tree size in our study area compared to interior areas of squirrel habitat (Young et al. 2002, Sharma & Parton 2007, Boonstra et al. 2008), food availability per hectare remains limited. Although we experienced two years of low crops in our 4-year study period, low cone crops succeeding a mast year are not uncommon due to the immense energy requirements of a mast year (Krebs et al. 2012). The single masting event we observed, as well as the 2018 mast year from our study area (Kucheravy et al. 2021), did not achieve crop yields to the same extent as other studies (Table 2). Unfavourable environmental and climatic conditions at distributional edges can affect tree growth, resulting low cone production, and a reduction

or failure to produce viable seeds. In particular, the dynamics of tree populations at northern latitudinal limits can be linked to the limiting effect of low seasonal temperatures and short growing seasons on pollen and seed production and the subsequent germination and establishment of seeds and seedlings (Henttonen et al. 1986, Zasada 1988, Sirois 2000). In conifers, while long-term cone production is frequently linked to tree size, for species such as white spruce, climatic limitations in the past and current years rather than endogenous factors often dictate cone crop size (Messaoud et al. 2007, Krebs et al. 2012, LaMontagne 2020). Seasonal temperature changes in our study region typically exhibit a delay of approximately one month compared to boreal forest regions farther south of the northern treeline (Environment Canada data from Haines Junction Airport, Yukon, and Churchill Airport, Manitoba). Additionally, snow cover can persist for up to two months longer (Scott et al. 1993). The variable nature of the climate at the northern boreal forest treelines reduces the likelihood of having consecutively abundant years for spruce cones (Messaoud et al. 2007). Additionally, life history theory predicts individuals will prioritize limited energy budgets toward growth, survival, and reproduction to maximize fitness. In the harsh growing conditions presented at the northern treeline, trees may allocate energy toward growth instead of reproduction.

In addition to fluctuation in spruce cone production, the quality and quantity of seeds per cone can vary with cone size and year (Waldron 1965, Zasada 1988), potentially making cone numbers a poor predictor of food availability. Without the embryonic tissues, empty seeds have little nutritional value for granivores (Verdú & García-Fayos 1998). As the proportion of empty seeds increases within cones, the handling cost of finding highly nutritious seeds also increases (Verdú & García-Fayos 1998, 2001). In our study area, the percentage of filled seeds per cone fell from 8.5% (2021) to 1% in the mast year (2022). Such observations are lower than those observed in other white spruce forests. In northern Ontario, O'Connell (2005) reported that the percentage of filled seed per cone ranged from 26–42% in a non-mast year. Furthermore, in contrast to our observations, Waldron et al. (1965) noted an increase in filled seed in mast years compared to non-mast years, from 12–58% in southern Manitoba. Reduced pollination is commonly associated with empty seeds in conifers (O'Connell et al. 2006). In many spruce species, unpollinated ovules can develop into seed coats that contain degenerated gametophytes (Owens 1995). Factors such as small stand sizes, low tree density, and environmental stresses such as temperature, water availability, and nutrients, can restrict pollination, increase inbreeding, and raise seed abortion rates (Owens 1995, O'Connell et al. 2006, Benjamin et al. 2024). For plants residing at the northern limit of their distribution, shorter and cooler growing seasons can result in low seed quality and quantity (Zasada 1992, Lavoie & Payette 1994). Specifically, studies have suggested low seasonal temperatures during spring pollination can lead to seed abortion and cone damage (Zasada 1992, Owens 1995) and inhibit seed maturation (Sirois 2000). In white spruce, multi-year reproductive cycles increase susceptibility to such factors affecting seed production. In our study, while the number of filled seeds per cone was low, the total number of filled seeds per tree exceeded those in low cone crop years due to the abundance of cones. However, extracting filled seeds from many empty cones likely increases predator handling costs, influencing seed predator abundance and foraging efficiency (Perea et al. 2013). The low

seed quality in our study area may further explain why squirrels in this area predominantly consumed fungi.

In our study area, fungi appeared from late August to early September with an annual variation typical for boreal forest fungal crops (Luoma et al. 2003, Krebs et al. 2008). Mean dry biomass was comparable with other studies in coniferous forests, including interior boreal forest (2.5 kg ha^{-1}) (Krebs et al. 2008) and Douglas-fir forests in the Pacific Northwest ($2\text{--}5 \text{ kg ha}^{-1}$) (Luoma et al. 2003). Fungal reproduction can also experience widespread synchrony (Mehus 1986). Our estimates of spruce cone and fungal abundance could be biased by squirrels sampling and caching food prior to our surveys. Despite conducting surveys at consistent times annually, fluctuations in fungal emergence due to rainfall could mean peak abundance was missed.

At the northern treeline, red squirrels must constantly adjust to fluctuating seasonal temperatures and food availability. Optimal foraging theory states that species prioritize high-energy foods to maximize fitness (Stephens & Krebs 1986), exhibiting specialized diets when preferred resources are abundant and broader diets when resources are scarce. Our results support foraging theory, with a narrower dietary niche breadth following the mast year, although broader than expected if spruce seeds were the dominant food source, likely due to the low quality of seeds at the treeline. In non-mast years, dietary niche breadths generally expanded, with broadest niche observed during the low cone crop in 2021.

Fungi were the primary contributor to squirrel diet ($\sim 70\%$) across all seasons and years, although other food sources, including berries, were more prominent during the low cone crop year (2021 but reflected in the 2022 diet). Although not a major component, berries increased during low cone years. Like fungi, berries are typically abundant in late summer and early fall and can act as an important source of carbohydrates when spruce seeds are scarce (Stephens et al. 2019). Lichen was negligible and showed no variation with cone abundance, consistent with red squirrel's limited use of this resource (Currah et al. 2000, Dubay et al. 2008).

Red squirrels are also known nest predator of understory-nesting birds, such as passerines, in northern coniferous forests (Reitsma et al. 1990, Sieving & Willson 1998, Willson et al. 2003). However, passerines were excluded from our stable isotopes models because they arrive for the mating season in early June, after the spring moult has occurred. Snowshoe hares were also excluded as a potential food source since predation by red squirrels is rare and mainly involves young hares (< 2 weeks old) in spring and summer (O'Donoghue 1994). In more interior northern regions of red squirrel habitat, snowshoe hares typically have three litters (late May, late June - July after the spring molt, and early August before the fall moult) (O'Donoghue 1994, Oli et al. 2020). But delayed spring conditions in our study area shift reproduction into late August, overlapping with fall molt hair growth. However, during August and September, red squirrels are intensely focused on harvesting spruce cones and fungi, reducing their likelihood of consuming alternative food sources. Further, other studies reporting hare consumption by red squirrels have observed squirrels scavenging on hare carcasses in winter (Peers et al. 2020), which was not covered by the timeline of hair growth in our study.

We observed little seasonal variation in diet during our study period. In early summer, red squirrels will feed on spruce buds and new growth as their winter food caches become depleted, shifting to primary resources, such as spruce seeds and fungi, as they become more abundant in late summer and early fall (Ren et al. 2017). As spruce buds were isotopically similar to seeds, we were unable to differentiate between the two food items in spring diet. However, squirrels were observed eating spruce buds in early summer during our study. By late summer and fall, as primary resources become available, squirrels likely consume the same food items they are caching.

Throughout their distribution, red squirrels primarily consume conifer seeds and are considered conifer specialists (Smith 1968, Fletcher et al. 2010, McAdam et al. 2019, Wishart 2023). In northern interior areas of boreal forest, red squirrels rely exclusively on white spruce seeds (McAdam & Boutin 2003, Boutin et al. 2006) with individuals hoarding up to 20,000 cones for winter (Smith 1968, Hurly & Lourie 1997). While spruce cones may not be abundant at the treeline, our results suggest squirrels still prefer conifer seeds, with seed availability influencing the consumption of alternate foods like fungi and berries. Fungi are a known alternate food source for red squirrels, often comprising over half of squirrel's diet in low cone years (Steele 1998, Currah et al. 2000, Koprowski 2005, Teron & Hutchison 2013, Derbridge & Koprowski 2019, Pauli et al. 2019). Fungal hoarding by red squirrels fluctuated with cone production, peaking during the low cone crop year (2021) and declining in the mast year (2022). In the northern boreal forest, spruce cone hoarding can be highly variable, and red squirrels will switch from hoarding cones to fungi in years of low production, hanging mushrooms in trees to dry prior to caching (Currah et al. 2000, Krebs et al. 2008). Fletcher et al. (2010) noted that fungi comprised over 60% of observed caching events when spruce cone production was low, but only 1% of cached items during abundant cone years. The availability and minimal foraging effort needed make fungi a valuable secondary food source for squirrels, and squirrels play a key role in fungal spore dispersal (Krebs et al. 2008).

Conclusion

In summary, the production of white spruce cones varies greatly, and red squirrels have had to adjust their diet according to the availability of primary resources. Compared to similar studies conducted elsewhere in the northern boreal forest (LaMontagne et al. 2005, LaMontagne 2007, Lamontagne & Boutin 2007, Krebs et al. 2012, Wishart 2023), spruce cone production was generally lower at the sub-Arctic treeline. As a consequence, red squirrels living at the sub-Arctic edge of their range rely on fungi as their primary food source, even during mast years. While the caching and consumption of fungi by red squirrels is not a new phenomenon (Currah et al. 2000, Fletcher et al. 2010, Pauli et al. 2019), fungi have not previously been documented as the primary food source for red squirrels, which emphasizes how marginal treeline is for squirrels.

Climate change is altering vegetation patterns in the sub-Arctic and within the treeline, leading to increased tree density and recruitment (Payette et al. 2001, Mamet & Kershaw 2011, Mamet & Kershaw 2013). In recent decades, changes in masting dynamics have been largely attributed to climate change.

In the northern boreal forest, the intervals between mast years have shortened from 5–7 to 2–4 years since 2006 (Krebs et al. 2023). As a result, the restrictions placed on squirrels by limited food availability may lessen in the future, increasing the success of future populations and the likelihood of range expansion. However, given the low proportion of filled seed within cones, it is unclear if these shortened intervals between mast years represent increased seed availability. Understanding how factors operate within range boundaries to restrict a species' success and how species conform to these limitations can provide insight into adaptations along latitudinal gradients (Gaston 2009) and species' potential for future range expansion.

Declarations

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Conflicts of interest/competing interests

The authors declare they have no conflict of interest.

Ethics approval

All data and samples collected were in accordance with the ethical standards of the University of Manitoba (animal care protocol F20-010) and approved by Government of Manitoba Wildlife and Fisheries branch (Permit no: WB2433).

Consent to participate

Not applicable

Consent for publication

Availability of data and material

The datasets used for this study are available from the corresponding author upon request.

Code availability

The code used for this study is available from the corresponding author upon request.

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Tables

Table 1: Comparison of white spruce cone counts and the percentage of seeds that were filled seeds within spruce cones near Churchill, MB, Canada, from interior forests within red squirrel distribution.

Location	Total cones/tree	Years	Reference
Mast year			
Treeline	74 - 863	2022	this study
Treeline	0 - 407	2018	Kucheravy et al. 2021
Yukon	1,000 - 2,500	1993 - 2010	Krebs et al. 2012
Yukon	750 - 3,000	2005 - 2022	Krebs et al. 2023
Yukon	1,000 - 3,500	2008 - 2022	Wishart 2023
Michigan	2,400 - 2,700	2012 - 2017	Leeper & LaMontagne 2021
Non-mast year			
Treeline	0 - 123	2020 - 2023	this study
Treeline	0 - 93	2019	Kucheravy et al. 2021
Yukon	0 - 200	1993 - 2010	Krebs et al. 2012
Michigan	216	2012 - 2017	Leeper & LaMontagne 2021
Wisconsin	6 - 186	2012 - 2014	Corona et al. 2022
Filled seeds/cone (%)			
Mast year			
Treeline	1.2 ± 0.1	2022	this study
Southern Manitoba	58	1954 - 1963	Waldron 1965
Alaska	60.5	1957 - 1959	Zasada & Gregory 1969
Non-mast year			
Treeline	6.4 ± 1.4	2021 - 2023	this study
Southern Manitoba	12 - 48	1954 - 1963	Waldron 1965
Northern Quebec	66	2001 - 2004	Messaoud et al. 2007
Northern Ontario	26 - 42	1994	O'Connell 2006
Alaska	22 - 62	1954 - 1963	Zasada & Gregory 1969

Figures

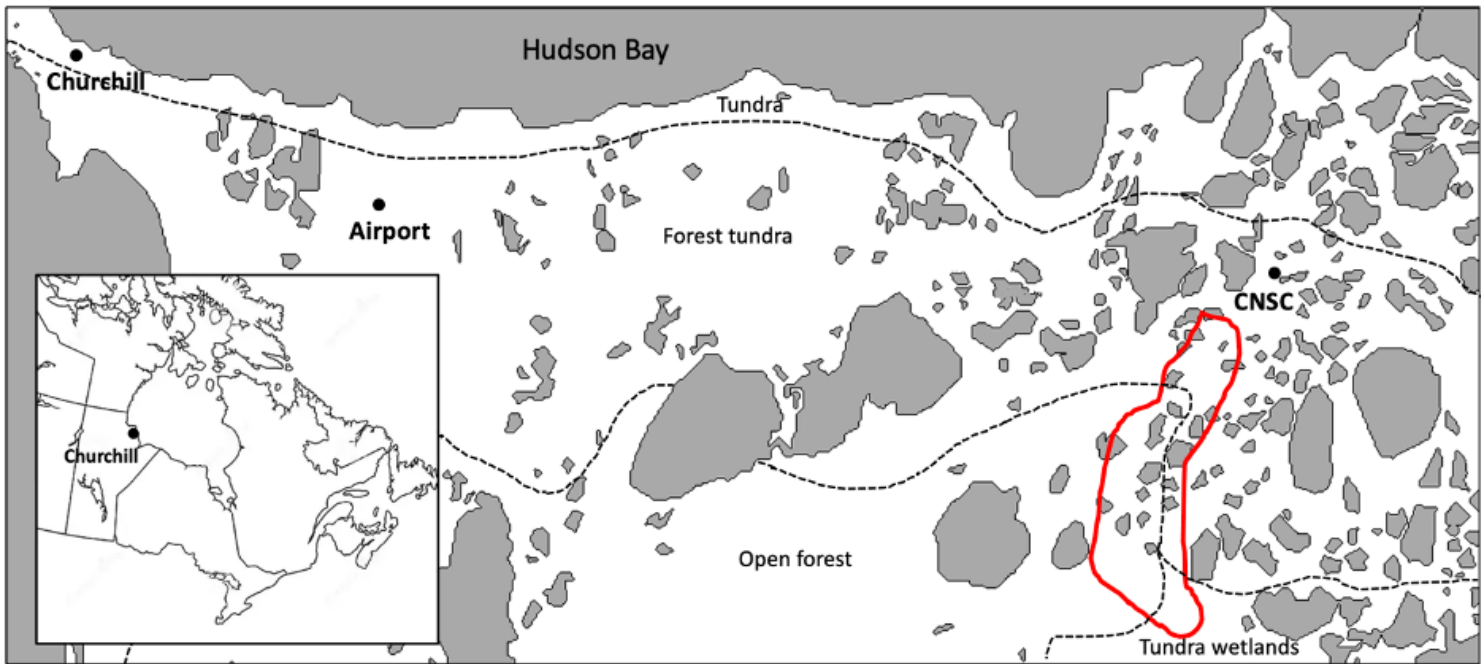


Figure 1

A map of the study area (outlined in red) located near Churchill, MB, Canada. Dashed lines delineate separate habitat types (Corkery et al. 2019).

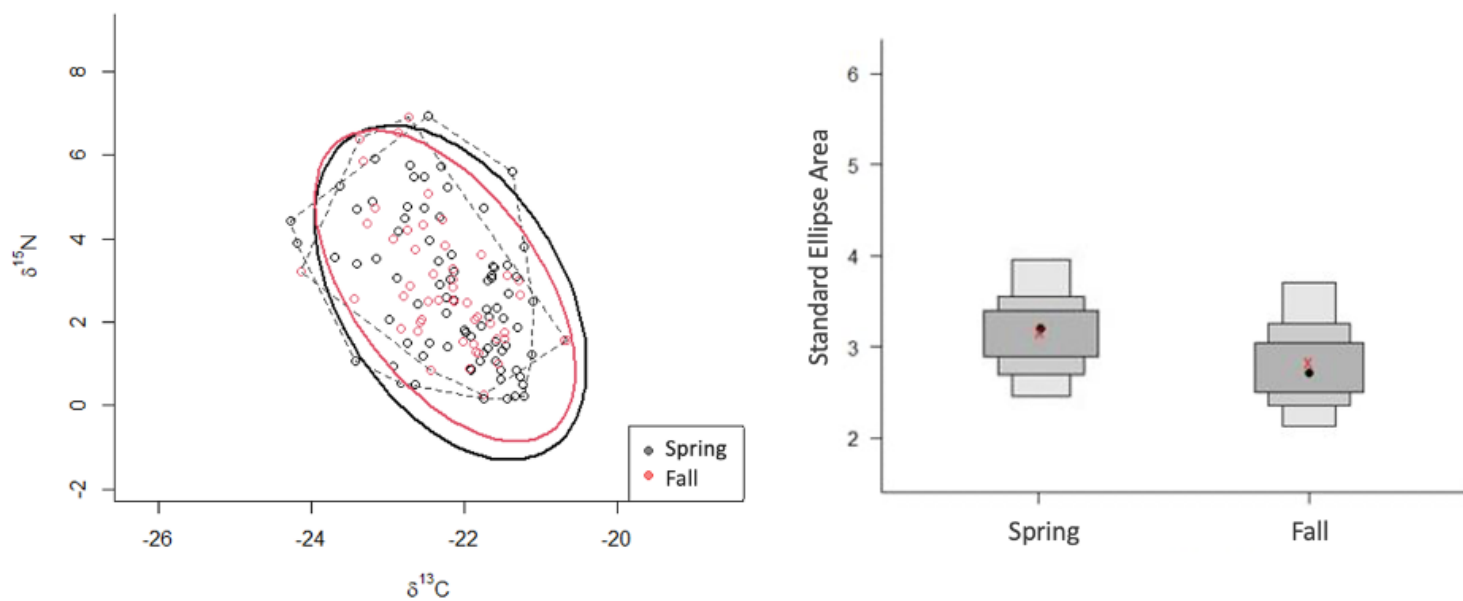


Figure 2

Comparison of seasonal dietary niches from 2020 – 2023 and the associated standard ellipse areas (SEA). Bayesian ellipses are generated using the SIBER package in R. The dotted lines indicate convex hulls and solid lines indicate standard ellipse areas. The black dots in the SEA represent the median, the red 'x' the mode, and the boxes indicate the 50, 75, and 95% credible intervals.

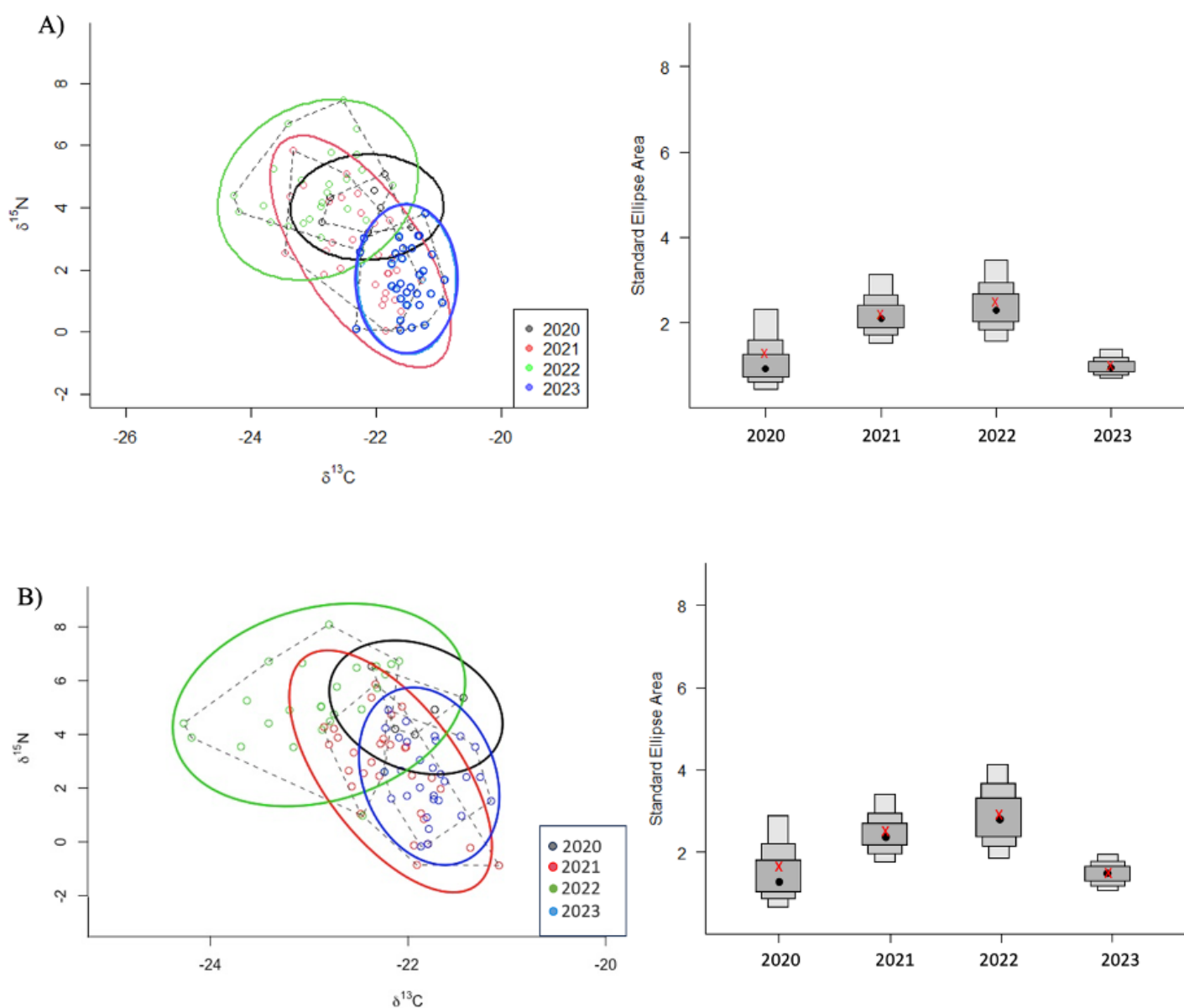


Figure 3

Comparison of A) spring and B) fall dietary niches from 2020 – 2023 and the associated standard ellipse areas (SEA). Bayesian ellipses were generated using the SIBER package in R. The dotted lines indicate convex hulls and solid lines indicate standard ellipse areas. The black dots in the SEA represent the median, the red 'x' the mode, and the boxes indicate the 50, 75, and 95% credible intervals.

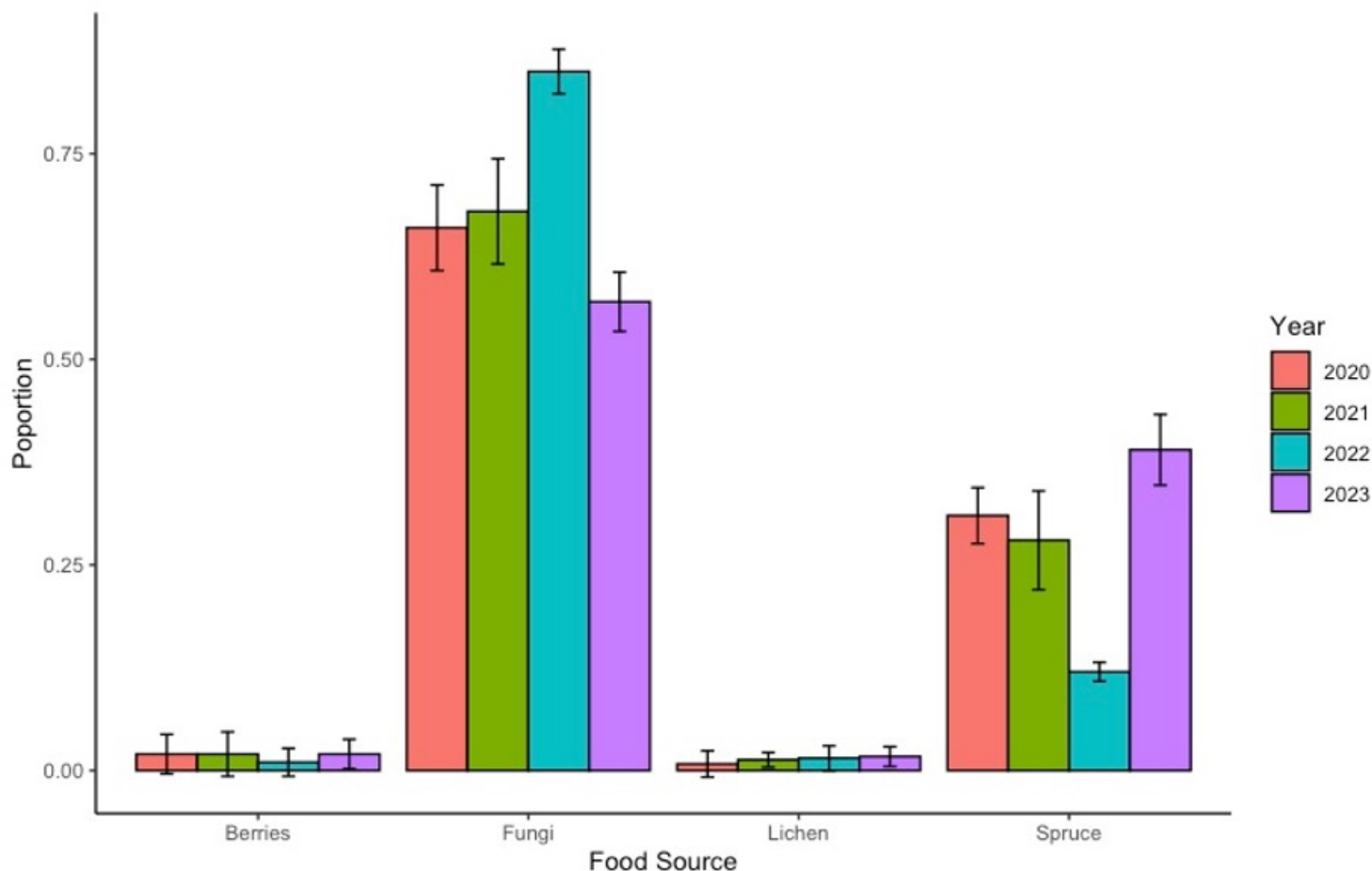


Figure 4

Comparison of the annual contributions of five food sources to spring squirrel diet from 2020 – 2023 (mean $\pm$ SD). Proportions were estimated from Bayesian mixing models using the MixSIAR package in R. Note: 2022 diet (blue) reflects the low cone crops in 2021, and 2023 diet (purple) reflects the 2022 mast year.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [OecologiaelectronicsupplementaryWindsor.docx](#)