Received: 30 January 2024 | Accepted: 5 June 2024

DOI: 10.1111/1365-2656.14148

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Resource availability alters breeding strategies in a small mammal community

Ryan B. Stephens[1,2] | Joshua S. Willems[2] | Mariko Yamasaki[3] | Christine A. Costello[3] | Rebecca J. Rowe[2]

[1]Department of Biological Sciences, East Tennessee State University, Johnson City, Tennessee, USA

[2]Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire, USA

[3]Forest Sciences Laboratory, USDA Forest Service Northern Research Station, Durham, New Hampshire, USA

Correspondence
Ryan B. Stephens
Email: stephensrb@etsu.edu

Funding information
USDA National Institute of Food and Agriculture McIntire-Stennis, Grant/Award Number: 1006881, 1016133 and 1026211; Research Joint Venture Agreement, Grant/Award Number: 19-JV-11242307-044

Handling Editor: Isabella Capellini

Abstract

1. Following a resource pulse, animals may finance reproduction by consuming concurrently available resources (income breeding) or by storing resources for future reproduction (capital breeding). Understanding how these reproductive strategies are used is important for determining the ecological mechanisms that structure timing of reproduction and that drive interannual population fluctuations in animals.
2. We gathered a reproductive dataset for five small mammal species over a 12-year period in Northeastern USA during which six masting events of American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) occurred. Masting created alternate years where seeds were either available late (masting year) or early (cached from the previous year) in the breeding season. The small mammal species differed in reliance on seeds and overwintering strategies. We quantified the diet using stable isotopes and recorded reproduction timing, proportion breeding and litter size in females and testes size in males.
3. Timing of seed availability minimally affected litter size but strongly affected proportion breeding and timing of reproduction. During masting years (late seed availability), a higher proportion of females reproduced, with breeding taking place later in the season (lactation timed with peak seed availability), although the delay was restricted in *Napaeozapus insignis*, an obligate hibernator. After a fall mast, cached seeds were used as capital in the following spring (early seed availability) to support a litter that, depending on the species, occurred 24–79 days sooner than a mast year. No late-season reproduction occurred in years with early seed availability except for *Myodes gapperi* which produced a second litter, likely financed by fungal consumption. Males also showed strong responses to seed availability, mirroring female reproduction with testes size staying constant in years with late seed availability and sharply decreasing over the breeding season in years with early seed availability.
4. Our results highlight that although photoperiod and temperature broadly set bounds of the breeding season in temperate environments, resource availability influences the reproductive strategies that species use, which in turn alters

reproductive timing and can drive large inter-annual population fluctuations. Differences in overwintering strategies and diet may further modulate reproductive timing and output relative to resource pulses.

KEYWORDS
capital breeding, income breeding, masting, reproduction, reproductive timing, resource pulse

1 | INTRODUCTION

Successful reproduction in animals is dependent on individuals obtaining sufficient nutrients and energy sources (Drent & Daan, 1980). Depending on the timing of resource availability, individuals may employ different strategies to obtain the resources needed to compensate for reproductive costs (Williams et al., 2017). Animals that finance reproduction with concurrently available resources are often referred to as income breeders whereas those that use stored resources, either as endogenous reserves or caches, are referred to as capital breeders (Jönsson, 1997; Stephens et al., 2009). Although income and capital breeding have traditionally been delimited as a dichotomy, it is now well recognized that these breeding strategies represent a continuum and may be plastic depending on conditions (Jönsson, 1997; Williams et al., 2017). Understanding how species finance reproduction and under what circumstances species switch between income and capital breeding strategies is important for determining the ecological mechanisms and life-history strategies that promote reproduction and recruitment.

To maximize recruitment, individuals often synchronize the most energy-intensive period of reproduction with peak resource availability (Visser & Both, 2005). In seasonal environments, breeding early in the season is often associated with higher reproductive fitness as recruits have more time to prepare for winter (Réale et al., 2003; Verhulst et al., 1995). However, when seasonal environments experience late-season pulses in resource availability, individuals may either delay reproduction until resources are available (income breeding) or store resources prior to the breeding season (capital breeding; Stephens et al., 2014; Thomas et al., 2001; Williams et al., 2017). In some instances, species may switch between strategies as resource availability fluctuates over the years. For example, in northern Canada, North American red squirrels (*Tamiasciurus hudsonicus*) transition between capital and income breeding strategies in order to match resource availability with lactation (Fletcher et al., 2013), the most energetically costly phase of reproduction in mammals (Stebbins, 1977). In years following masting of spruce trees (where large seed crops are released) red squirrels use horded seeds as capital to breed early in the season and in years when horded seeds are unavailable, squirrels delay reproduction to match concurrently available food sources including fresh spruce cones and fungi (Boutin et al., 2006; Fletcher et al., 2013). Masting is one of the most common resource pulses in boreal and temperate forests and can exert strong effects on small mammal (rodents and shrews) populations (Ostfeld & Keesing, 2000). However, most studies of masting relative to reproduction are single species assessments (particularly in Sciuridae and Gliridae—Bieber, 1998; Fletcher et al., 2013; Kager & Fietz, 2009; Tissier et al., 2020), making it unclear how masting events may influence reproductive strategies among small mammal species with different diets and autecologies. Further, most studies have focused on female reproduction relative to masting and few studies have explored if male allocation to reproduction is also influenced (but see Bieber, 1998).

In the northeastern USA, trees such as American beech (*Fagus grandifolia*) often mast every other fall, interspersed with years with very low seed production (Jakubas et al., 2005; Jensen et al., 2012). This creates alternate years where seeds are available to small mammals either late in the breeding season (during years with a fall mast) or early in the breeding season (from seeds cached during a previous fall mast). Here, we investigated how timing of seed availability influenced reproductive strategies (of males and females) in a small mammal community using a 12-year dataset where alternate-year masting events of American beech and eastern hemlock (*Tsuga canadensis*) produced 6 years each with late and early seed availability. We determined how the timing of seed availability influenced female reproductive activity (proportion breeding), output (litter size) and timing (pregnant and lactating), and male reproductive allocation (testes length). We focused on five species common in forests of the northeastern USA (Stephens, Hocking, et al., 2017), including the northern short-tailed shrew (*Blarina brevicauda*), southern red-backed vole (*Myodes gapperi*), woodland jumping mouse (*Napaeozapus insignis*), white-footed mouse (*Peromyscus leucopus*) and deer mouse (*P. maniculatus*). These species are all similar in body size (ca. 20 g) and thus have comparable energetic requirements and constraints. Although these species all cache and consume seeds (Martin, 1984; Moore et al., 2022), their main food items differ considerably with *B. brevicauda* primarily consuming arthropods, *M. gapperi* primarily consuming fungi and the mice primarily consuming seeds (Linzey & Linzey, 1973). We used stable isotope analysis of food sources and consumer tissues to link the timing of seed availability with seed consumption. All species are active throughout the year except *N. insignis* which hibernates during the winter (Whitaker & Wrigley, 1972).

We hypothesized that timing of seed availability would change both litter size, proportion of females breeding and reproductive strategies of small mammals but that differences in overwintering strategies and dietary specialization would modulate species-specific responses. Specifically, we predicted that individuals would

time reproduction to match seed availability such that reproduction would be later in masting years (income breeding) and earlier in years with cached seeds from the previous fall (capital breeding). We also predicted that litter size would be largest during mast years when resources should be most abundant compared to the following years when caches are limited (Michałand et al., 2016). We expected that the strength in reproductive timing and output patterns would vary by reliance on seeds with the weakest response in the insectivorous shrew and fungivorous vole and the strongest response in the granivorous mice. We also predicted that testes size in males would not change with seed availability because energy allocation to testes is relatively small (Kenagy & Trombulak, 1986), and food availability has little influence on gonad size in small mammals (Glass & Swerdloff, 1980). Thus, with a relatively low reproductive cost to testes, there is a benefit in maintaining reproductive structures throughout the breeding season (Bronson, 1985).

2 | MATERIALS AND METHODS

2.1 | Study system and seed availability

Our study was conducted at Bartlett Experimental Forest, within the White Mountain National Forest, New Hampshire USA (44°3′7.2″ N, −71°17′25.1″ W). This 2343-ha research area is dominated by American beech (hereafter—beech), eastern hemlock (hereafter—hemlock) and red maple (*Acer rubrum*) with lesser components of red spruce (*Picea rubens*), yellow birch (*Betula alleghaniensis*), sugar maple (*A. saccharum*), white ash (*Fraxinus americana*) and white birch (*B. papyrifera*). The climate is humid continental, with warm summers (mean July temperature, 19°C) and cold winters (mean January temperature, −9°C) with 127 cm of precipitation distributed evenly throughout the year (King et al., 2011; Richardson et al., 2007). We tracked seedfall using seed baskets at Bartlett Experimental Forest and nearby Hubbard Brook Experimental Forest (see Section 2.2). Additionally, from field sampling of small mammals (see Section 2.3), we quantified seed consumption using stable isotope analysis of dietary items and hair from live-trapped small mammals (see Section 2.5) and assessed reproductive activity from kill-trapped small mammals (see Section 2.6).

2.2 | Seedfall

Seeds are among the most important food sources available to small mammals in the study region (e.g. Stephens et al., 2019). To index seed production of the dominant tree species, we deployed 10 seed baskets at each of 12 mark-recapture grids distributed across dominant forest types at Bartlett Experimental Forest (Stephens, Remick, et al., 2017), for a total of 120 seed baskets. Baskets were constructed of sand bags suspended over wire frames and collected a 0.25 m^2 area (Hughes et al., 1987). We targeted beech and red maple trees, however, baskets also collected hemlock seeds, among other species. For each mark-recapture grid (8×8 station arrangement), we placed a seed basket at a randomly selected station from each column ($n=8$) that had a beech or red maple tree >10 cm at diameter at breast height (1.37 m). Additionally, we also placed a seed basket under the largest beech and red maple tree on each grid, resulting in a total of five seed baskets under both beech and red maple trees on each grid. Baskets were established in the summer of 2017 and were collected in the fall (late October/early November), spring (late May/early June) and summer (early July) of each year. After drying the basket contents, we removed and counted large seeds (e.g. beech and red maple) and noted whether they were viable or nonviable. We then sieved (2 mm) the remaining material to remove conifer needles and spread the contents across a grided sheet. We counted small seeds (e.g. hemlock) in at least 25% of the grid cells and scaled this to estimate the total seeds per basket.

Of the dominant tree species, beech and hemlock release seeds throughout the fall and early winter, whereas red maple produces seeds in the early summer. Fall seed production is known to be particularly important for driving rodent populations (Clotfelter et al., 2007; Tissier et al., 2020), and we thus focused on beech and hemlock seed production relative to small mammal reproduction. Annually, we indexed seed production of beech and hemlock as the sum of the fall and subsequent spring seed basket collections and calculated seed biomass per m^2 for viable seeds (mass of individual seeds based on Moore et al., 2022). Although beech seeds are a preferred food source, both beech and hemlock seeds are high in lipids and hemlock is collected and consumed when beech seeds are not available (Moore et al., 2022). Hemlock seeds have been largely overlooked as a food source for small mammals, but our data indicate that, at the landscape level, hemlock seed biomass can be similar to beech (Figure 1). Although we only had direct measurements of seed production at Bartlett Experimental Forest for half of our study duration (2017–2022), masting is synchronized across regions (Koenig & Knops, 1998; Piovesan & Adams, 2001) and beech seedfall data from Hubbard Brook Experimental Forest (about 40 km away) was highly correlated with Bartlett Experimental Forest ($R^2=0.92$; Figure S1), providing an index of seed production for the entire study duration (Figure 1).

Peak seedfall for beech nuts occurs between September and early October (Leak & Graber, 1993). Following a seedfall event, seeds are either consumed immediately or are cached and consumed through the spring and early summer of the following year (Stephens et al., 2019; Wolff, 1996). In northern temperate zones, small mammals primarily breed from spring through fall (McLean & Guralnick, 2021). As such, following a masting event in the fall, the breeding season could overlap with seed availability either that fall (hereafter—late seed availability) or the following spring (hereafter—early seed availability). During our study (2011–2022) seed production was high during odd years and extremely low during even years (note that although beech seedfall was low in 2021, hemlock seedfall was high; Figure 1). Thus, in the context of breeding small mammals, we assessed 6 years with late seed availability (odd years) and 6 years with early seed availability (even years).

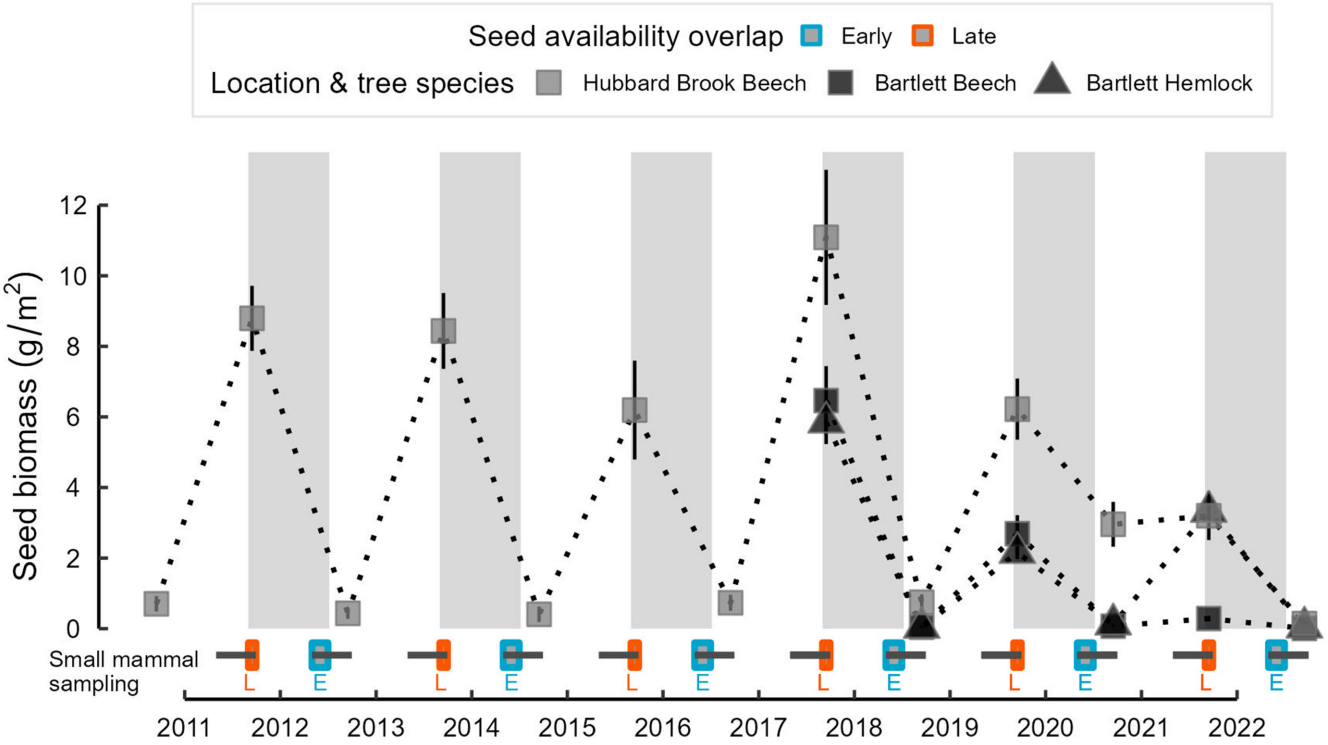

FIGURE 1 Seedfall biomass from 2010 through 2021 from Hubbard Brook and Bartlett Experimental Forests and its availability to small mammals during the breeding season. Shapes represent mean (±1 SE) beech and hemlock seed biomass, with lines connecting years. Vertical, grey-filled boxes signify approximate timing of seed availability (September–June) following large seedfall events that occurred in odd years. Horizontal black bars below seedfall data indicate the small mammal breeding season (circa May–Sept). These bars overlie coloured boxes and letters to highlight when seed availability overlapped with the breeding season (even years had early seed availability and odd years had late seed availability). Seed biomass from Hubbard Brook Experimental Forest included both viable and non-viable seeds (Cleavitt & Fahey, 2017) whereas data from Bartlett Experimental Forest included only viable seeds.

2.3 | Small mammal sampling

We sampled small mammals at Bartlett Experimental Forest as part of a (1) United States Forest Service (USFS) long-term monitoring program (data from 2011 to 2022) and (2) University of New Hampshire mark-recapture study (data from 2013 to 2022). Briefly, the USFS sampling used nine pitfall arrays that were trapped for 10 days in July, August and September centred around the new moon phase; see Stephens et al. (2018) for further sampling details. The mark-recapture study used 12 grids that were each trapped in June, July and August for 4 days using a combination of Sherman live traps and pitfall traps; see Stephens and Rowe (2020) for further sampling details. Although additional sampling was occasionally conducted outside of these windows (see Figure S2), there was no significant difference between mean sampling day for years with early and late seed availability, respectively for either the USFS (August 11 vs. August 8) or UNH mark recapture (July 14 vs. July 15) trapping.

2.4 | Ethics statement

The USFS pitfall sampling protocol (220603) and mark-recapture protocol (120708, 140304, 160507, 180401 and 210302) were approved by the University of New Hampshire Animal Care and Use Committee along with the New Hampshire Fish and Game Department. Trapping methods followed guidelines outlined by the American Society of Mammalogists for the use of wild mammals in research (Sikes & The Animal Care and Use Committee of the American Society of Mammalogists, 2016).

2.5 | Diet analyses

During tissue formation, stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes are integrated from dietary items, making isotopes a good proxy for tracking dietary niches of consumers (Newsome et al., 2007). To assess how seed availability affects diet, we used stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis of small mammal hair and diet items during 2 consecutive years with different seed availabilities (2014—early, 2015—late; Figure 1). We collected approximately 1–4 mg of hair from the dorsal posterior of sub-adult and adult individuals from our mark-recapture study. Additionally, we collected samples from dominant food sources including beech seeds ($n = 6$), hemlock seeds ($n = 5$), red maple seeds ($n = 12$), ectomycorrhizal (EM) fungal sporocarps (*Elaphomyces* and *Hydnotrya* spp., $n = 63$), arbuscular mycorrhizal (AM) fungal sporocarps

(*Glomus* spp., $n = 11$), arthropods (beetles [Coleoptera], grasshoppers [Orthoptera] and spiders [Araneae], $n = 12$) and berries (hobblebush [*Viburnum lantanoides*] and partridge berries [*Mitchella repens*], $n = 10$). All samples were collected from mark-recapture grids except AM sporocarps which were extracted from stomachs of *N. insignis* sampled at USFS pitfall sites. Hair samples were cleaned with 2:1 chloroform: methanol and food items were ground to a powder, weighed into tin capsules (1 mg for hair, 1–5 mg for food items) and analysed for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes and elemental composition (%C, %N) (see Appendix S1).

Hair integrates an isotopic signature at the time of growth and reflects the diet consumed during moult but not necessarily the time of collection (Fraser et al., 2013). In temperate forests, small mammals go through ontogenetic moults (juvenile to young-of-the-year and sub-adult to adult) and seasonal moults (late spring/early summer and late summer/early fall; Findley & Jones, 1956; Sare et al., 2005; Tabacaru et al., 2011; Whitaker & Wrigley, 1972). Based on timing, we binned hair samples into distinct summer and fall seasons. Summer hair samples were collected from young-of-the-year from June through July and from adults in July. Fall samples were collected from September 9 through October. Additionally, adults captured in June 2015 (prior to moulting) were assigned to fall 2014 (for further information and justification of seasonal bins see Stephens et al., 2019). For each seasonal bin, in each year, we analysed (stratified across sampling grids) at least 14 hair samples for each mammal species (range 14–66).

Between the 2 years and seasons, we visualized isotopic niche dynamics using biplots ($\delta^{13}C$ and $\delta^{15}N$). Additionally, we estimated the relative proportion of food sources consumed with Bayesian mixing models in the R package 'MixSIAR' (Stock & Semmens, 2013). MixSIAR uses isotopic tracers (e.g. $\delta^{15}N$ and $\delta^{13}C$) of food sources along with consumer tissues (adjusted by trophic discrimination factors) to estimate the relative proportion of food sources consumed. We accounted for differences in elemental concentration (percent carbon and nitrogen) among food sources and used field-derived trophic discrimination factors for each species (Stephens et al., 2022), with the exception of *Peromyscus* spp. in which we used 3.1 for N (Stephens et al., 2023). For all models, we used informative priors for food sources (Moore & Semmens, 2008) by scaling priors by the proportion of weeks that the food source was available during each season of hair growth (for details see Appendix S1; Figure S3). We considered summer hair to have been grown during an 11-week period between May 15 to July 31 and fall hair during a 10-week period between August 22 and October 31 (Stephens et al., 2019). Using $\delta^{15}N$ and $\delta^{13}C$ values from small mammal hair and food sources along with trophic discrimination factors, we ran each model (separate models for each species, year and season combination) with three chains for 200,000 iterations, removing the first 50,000 and thinning by a factor of 50, leaving 9000 iterations for inference (effective sample size reported in Table S1). We assessed model convergence using diagnostic tests (Gelmin-Rubin and Geweke) and visual inspection of trace plots. We visualized uncertainty around mean and median proportional dietary contributions using Bayesian credible intervals of 50%, 75% and 95%.

Arthropods and EM sporocarps occupied similar areas in isospace (Figure 2), and preliminary mixing models for *B. brevicauda* and *M. gapperi* could not distinguish their dietary contributions. Consumption of EM fungi by *B. brevicauda* is uncommon (Linzey & Linzey, 1973), as is arthropod consumption by *M. gapperi* (1%–2%; Martell, 1981; Schloyer, 1977), and we subsequently set prior probability to 0.01 for EM sporocarps and arthropods for *M. gapperi* and *B. brevicauda*, respectively.

2.6 | Reproduction analyses

Most small mammals used to assess reproduction were from the USFS long-term monitoring program ($n = 3090$; 89%) with supplementation from incidental mortalities from our mark-recapture study ($n = 380$; 11%). Collected small mammals were frozen for later processing. Following thawing, individuals were sexed, weighed, measured and prepared as museum voucher specimens. During preparation, reproductive structures were examined, with placental scars and embryos counted and the presence of mammary tissue (indicating lactation) recorded for females and testes length measured for males. From these individuals we investigated how the timing of seed availability influenced litter size and timing of reproduction of both females and males. We restricted our analyses to adults by using the minimum body mass (within lower whisker of boxplot) of reproductive females (pregnant, lactating or placental scars) as a cut-off for each species.

For each small mammal species, we compared the number of embryos that pregnant females had during early and late seed availability using a *t*-test. Further, because pregnant females were relatively uncommon in the dataset, we also compared placental scar counts between the two seed availabilities. Placental scars are a record of breeding within a season and can represent multiple litters (Adamczewska-Andrzejewska, 1969; Martin et al., 1976). In northern regions, it is extremely unlikely that small mammals have more than two litters in a season, and thus we removed five individuals (four *P. leucopus* and one *P. maniculatus*) with placental scar values that were more than twice that of the highest number of embryos for a species. Although it is difficult to determine if differences in placental scars are a result of larger litters or more litters based on counts alone, they indicate the relative output of a female for a breeding season.

We assessed the probability of reproduction in adult females between early and late seed availability across the breeding season using generalized linear mixed effects models (GLMM) in the R package 'glmmTMB' (Brooks et al., 2017). For GLMMs, we considered actively reproductive females to be either pregnant or lactating and assessed reproduction as a binomial response relative to body mass, seed availability and day of the year along with the interaction between seed availability and day of the year. For models, we included site (specific array or grid) nested within a year as a random effect

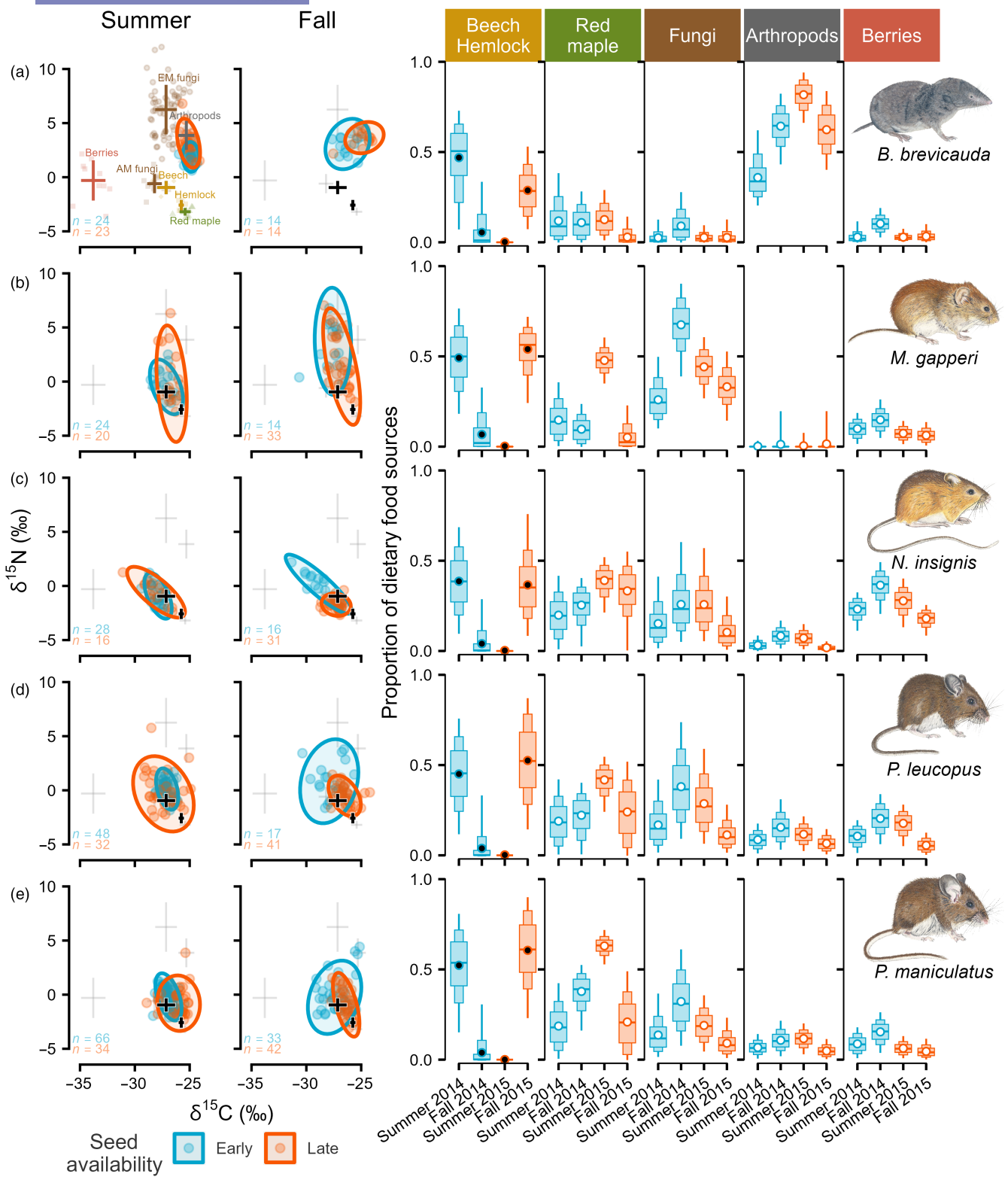

FIGURE 2 Shifts in (left) dietary niche dynamics and (right) food source consumption during the summer and fall of a breeding season with early (2014) and late (2015) seed availability for (a) *Blarina brevicauda*, (b) *Myodes gapperi*, (c) *Napaeozapus insignis*, (d) *Peromyscus leucopus* and (e) *Peromyscus maniculatus*. Mast events occurred in the fall of 2013 and 2015. (left) Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of the main food sources (individual samples are shown in top left panel with bars denoting mean and standard deviation across plots—beech and hemlock shown in black) and TDF-adjusted hair samples (individual hair samples along with 95% confidence ellipses and sample sizes for summer and fall). (right) Proportional contribution of the main food sources as indicated by Bayesian mixing models. Beech and hemlock along with AM and EM fungi were modelled separately with posteriors combined post hoc. Means and medians of dietary proportions are indicated by white circles and thick horizontal bars, respectively (beech and hemlock shown in black) and Bayesian credible intervals are denoted by box width (50% thick box; 75% intermediate box and 95% thin box). Mammal illustrations by R. Stephens.

(only year was included for *N. insignis* and *P. maniculatus* due to poor model fit with site). Model fits were assessed using the R package 'DHARMa' (Hartig, 2020). Using each year as an observation, we also compared the proportion (arcsine transformed) of adult females that were breeding between early and late seed availability using a *t*-test. We only included a year for a given species if there were at least four individuals present in the sample.

Using testes size as an indication of reproductive allocation to sperm (Kenagy & Trombulak, 1986), we assessed male reproduction between early and late seed availability across the breeding season using linear mixed-effects models in the R package 'nlme' (Pinheiro et al., 2012). For this analysis we only considered adult males, using the same body mass cutoffs as females. Because testes size is often correlated with body size ($r = 0.16–0.71$; Table S2), we standardized measurements by dividing testes length by body mass. This standardization allowed us to account for differences in body mass but did not produce qualitatively different results in models compared to unstandardized testes size. We modelled standardized testes length as a function of seed availability, day of the year and the interaction of seed availability and day of the year. For all models, we included site (specific array or grid) nested within a year as a random effect. Model fits were assessed by plotting residuals versus fitted values and by evidence of homogeneity of variances and normality of residuals and random effects (Pinheiro & Bates, 2000; Zuur et al., 2009).

We determine if the mean lactation time differed between years with early and late seed availability for each species using a *t*-test. For this analysis we used both pregnant females (adjusted by gestation time) and lactating females. Gestation times were taken from the literature with adjustments of 20 days for *B. brevicauda* (George et al., 1986), 17 days for *M. gapperi* (Merritt, 1981), 23 days for *N. insignis* (Whitaker & Wrigley, 1972), 22 days for *P. leucopus* (Lackey et al., 1985) and 24 days for *P. maniculatus* (Millar et al., 1992). Because weaning is similar, or takes longer than gestation for these species (George et al., 1986; Keane, 1990; Merritt, 1981; Millar et al., 1992; Whitaker & Wrigley, 1972), we could be confident that adjusted pregnancies fell within the time that the individual would be lactating.

All statistical analyses were performed in R version 4.0.4. (R Core Team, 2021).

3 | RESULTS

We analysed 570 small mammal hair samples collected in 2014 and 2015 for stable isotopes (Figure 2). Across all small mammal species, mixing models revealed similar patterns in dietary composition and seed consumption in response to seed availability (Figure 2). In the non-mast year when cached seeds were available early in the season (2014), species had relatively small isotopic niches and primarily consumed beech and hemlock seeds in the summer (39%–52%), whereas in the fall, isotopic niches expanded and a wider variety of food sources were consumed. Comparatively, during the masting year with late seed availability (2015), diets showed the opposite pattern with large isotopic niches in the summer (wide variety of food sources consumed) and contracted isotopic niches in the fall corresponding to increased consumption of beech and hemlock seeds (28%–61%).

We compiled a reproductive dataset of 3470 adults from our five target species collected over a 12-year period at Bartlett Experimental Forest. Of these, captures coincided with early and late seed availability, respectively, for females among *B. brevicauda* (508, 117), *M. gapperi* (170, 27), *N. insignis* (152, 257), *P. leucopus* (201, 81), *P. maniculatus* (62, 36) and for males among *B. brevicauda* (440, 191), *M. gapperi* (178, 151), *N. insignis* (129, 285), *P. leucopus* (173, 164) and *P. maniculatus* (48, 100).

Litter size was not significantly different between early and late seed availability for any species, although small samples sizes, particularly for early seed availability, precluded a robust comparison for some species. Placental scar counts differed with the timing of seed availability for two species, with *M. gapperi* having higher counts during years with early seed availability and *N. insignis* having higher counts during years with late seed availability.

Seed availability and day of the year significantly influenced probability of female reproduction (pregnant or lactating) for all species except *M. gapperi* (Figure 4a–d, Table S3). The interaction between seed availability and day of the year was also significant for *B. brevicauda*, *N. insignis* and *P. maniculatus* with a precipitous decline in reproduction in years with early seed availability (with no reproduction after August) and either constant (*B. brevicauda* and *P. maniculatus*; Figure 3a,e) or slight declines (*N. insignis*; Figure 3c) in reproduction during years with late seed availability. Reproduction in *P. leucopus* also decreased in years with early seed availability, although low levels of reproduction were evident past August. For all species, body mass had a positive effect on the probability of female reproduction (Table S3). The proportion of females breeding was also significantly higher during years with late seed availability for *B. brevicauda*, *N. insignis* and *P. maniculatus*, although all species showed the same pattern (Figure 5).

Testes size (length adjusted by body mass) was significantly smaller during years with early seed availability for all species, although the offset for *N. insignis* was slight compared to other species (Figure 4f–j, Table S4). Testes size also decreased over the breeding season for all species, except for *B. brevicauda* which stayed relatively consistent, albeit at very different sizes between seed availabilities (Figure 4f). The interaction between day of the year and seed availability was significant ($p = 0.019$) for *M. gapperi*, with a faster decrease in testes size during years with early seed availability compared to those with late seed availability (Figure 4g). Although not statistically significant at $\alpha = 0.05$, *P. leucopus* ($p = 0.072$) and *P. maniculatus* ($p = 0.147$) also showed this trend.

With the exception of *M. gapperi*, species reached peak lactation earlier in years with early seed availability compared to late seed availability, although there was a large range in this offset among species with *P. leucopus* having the smallest difference (24 days), followed by *N. insignis* (37 days), *B. brevicauda* (51 days) and *P. maniculatus* (79 days). Since we do not know when seed caches were

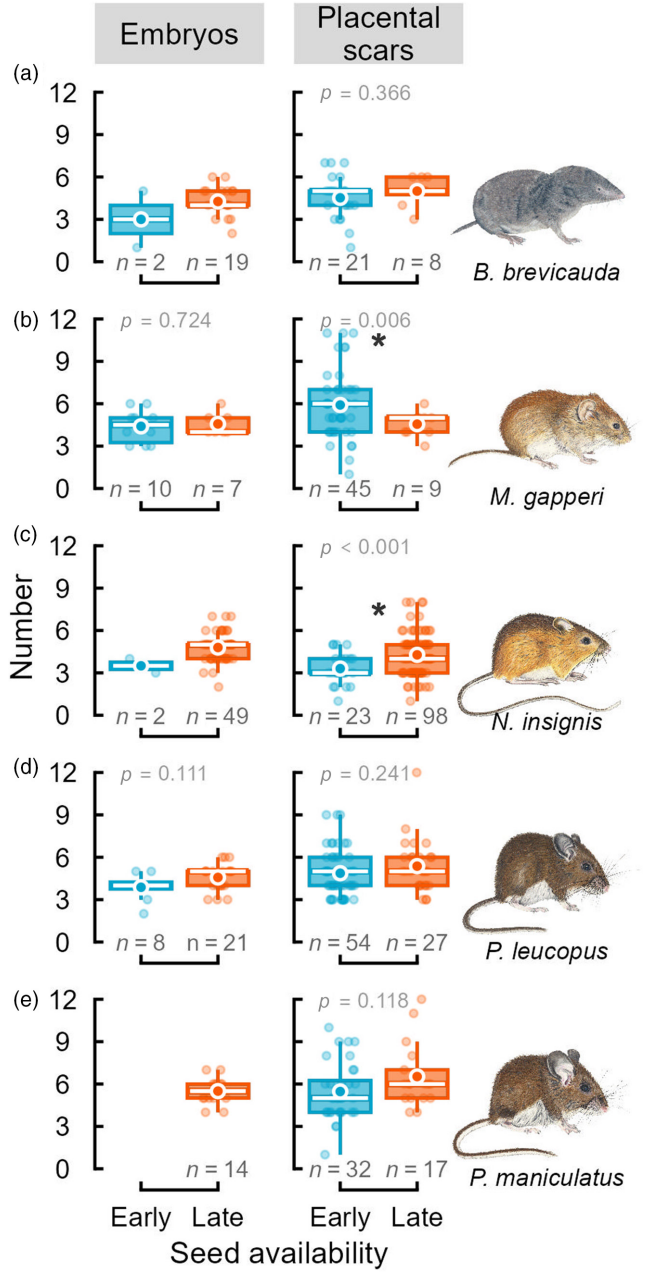

FIGURE 3 Boxplots of embryos or placental scars for periods with seed availability early or late in the breeding season for five small mammal species (a–e). Medians and means are denoted with horizontal white bars and white circles, respectively. The full data range is plotted with outlier points extending beyond boxplot whiskers. Asterisks denote significant pairs at $\alpha < 0.05$ (p-values shown in plot; only observations with >2 were tested) as indicated by t-tests: Embryos [*M. gapperi*: $t(15.0) = -0.4$ and *P. leucopus*: $t(12.0) = -1.7$] and placental scars [*B. brevicauda*: $t(19.2) = -0.9$, *M. gapperi*: $t(34.5) = 3.0$, *N. insignis*: $t(41.4) = -3.6$, *P. leucopus*: $t(46.0) = -1.2$ and *P. maniculatus*: $t(30) = -1.6$].

depleted in years with early seed availability, it is not possible to align cached seed availability with mean lactation for that timeframe; however, lactation during years with late seed availability aligned closely with peak seedfall of beech seeds (September through October; Figure 6).

4 | DISCUSSION

We investigated how timing of resource availability influences reproduction in a small mammal community experiencing pulsed masting events. We predicted that across species, seed availability would alter reproductive output and timing for females but would have little influence on males, and that the magnitude of response would be species-specific because of differences in overwintering strategies and dietary specialization. We found that resource availability had a relatively weak influence on reproductive output but a strong influence of reproductive timing and the proportion of individuals breeding. During mast years when seeds are plentiful later in the season, most species used an income breeding strategy, where the timing of female reproduction is delayed so peak lactation aligns with peak seedfall. In years with early seed availability, female reproduction for most species took place approximately 1–3 months earlier; with individuals using a capital breeding strategy by relying heavily on cached seeds during the peak reproductive period. Male testes size followed similar patterns to female reproduction. Although all small mammal species showed similar dietary responses to the timing of seed availability, the degree to which this resource pulse influenced breeding strategies, as measured by the offset in timing of reproduction, varied among species and depended on diet specificity and overwintering strategies.

Lactation is the most energy intensive part of mammalian reproduction (Stebbins, 1977). During masting years when seeds were abundant in the fall, peak lactation of most species occurred around September which coincides with the start of seedfall, particularly for beech (Leak & Graber, 1993). Thus, animals were timing the most expensive part of reproduction with peak resource availability. Nevertheless, given that the breeding season started in July (Figure 4), and beech and hemlock seeds are likely only available in low numbers in mid-summer, animals must finance the early part of reproduction (e.g. breeding and gestation) with other resources. Our isotopic analysis of diet suggests a large spike in red maple consumption during the summer preceding the mast for most species (Figure 2). In southern Québec, Canada, eastern chipmunks (*Tamias striatus*) use a similar approach by consuming large amounts of red maple seeds (approximately 77% diet) around the time of breeding in anticipation of a fall beech mast (Tissier et al., 2020). This high level of red maple consumption was irrespective of seed availability on the landscape and did not occur in non-masting years (Tissier et al., 2020). This underscores, that although fall mast is an important element for timing reproduction, other food resources are required early in the breeding season.

Although we found that most small mammals adjusted timing of reproduction to match seed availability, the strength of response varied among species and was not necessarily linked to level of granivory. Even within the granivorous mice, we found considerable differences in the reproductive delay between early and late seed availability with *P. leucopus* and *P. maniculatus* showing a 24- and 79-day delay, respectively which may reflect their relative level of specialization on seeds, with *P. leucopus* often being more of a generalist

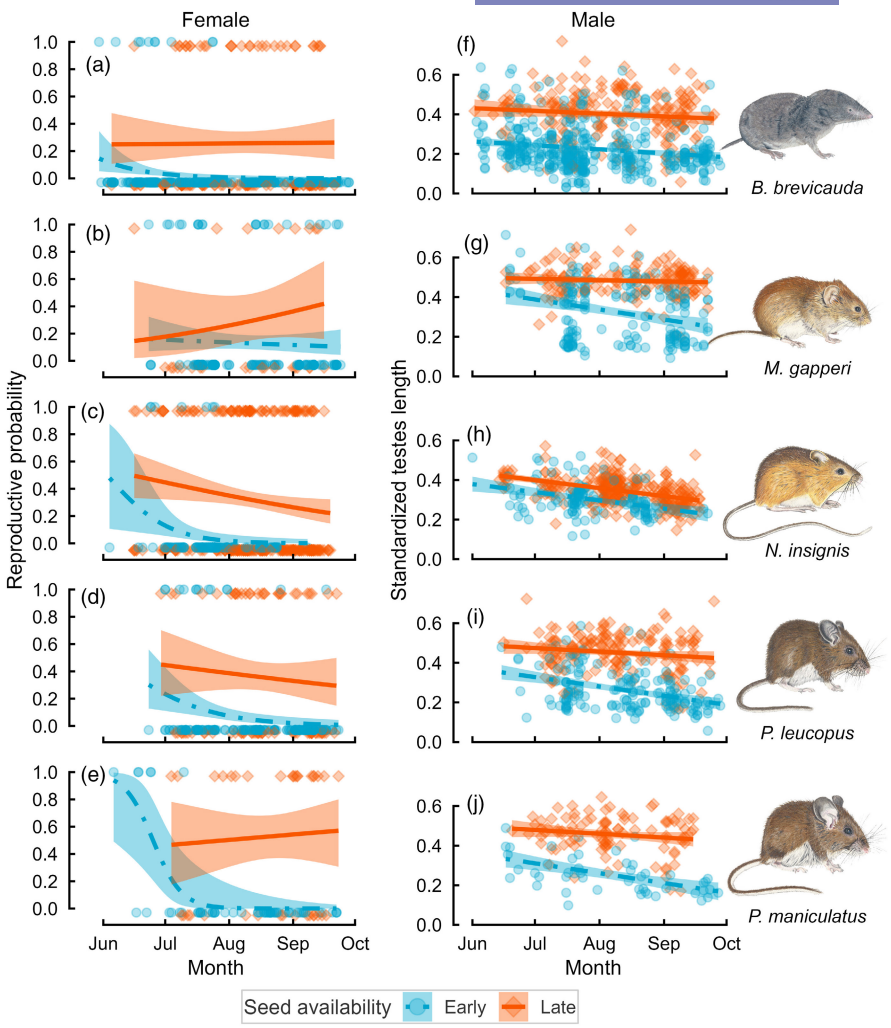

FIGURE 4 The (a–e) probability that an adult female is actively reproductive (pregnant or lactating) and (f–j) the standardized testes length (testes length/body mass) of adult males across time between early or late seed availability. Individual animals are shown as shapes (for females, 1 = reproductive and 0 = non-reproductive). Full model results for females (generalized linear mixed effects models) and males (linear mixed effects models) are in Tables S1 and S2, respectively.

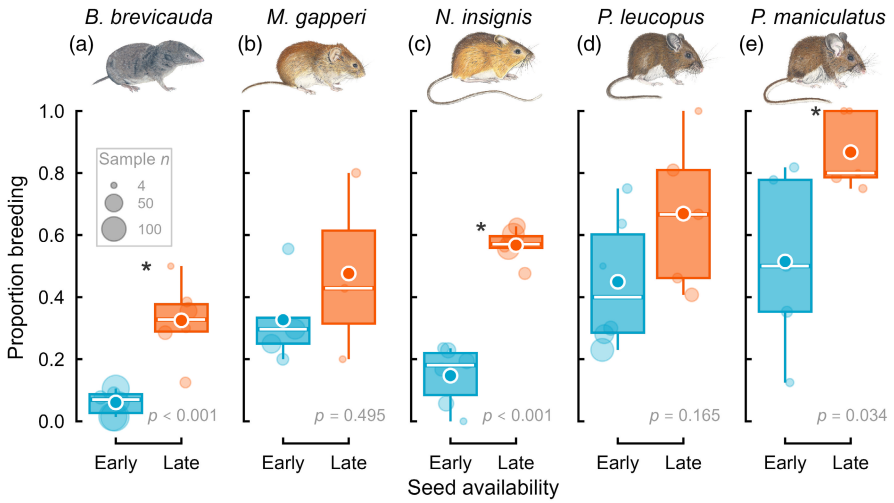

FIGURE 5 Boxplots indicating proportion of adult females of five small mammal species (a–e) that were reproductively active (pregnant, lactating or with placental scars) during years with seed availability early or late in the breeding season. Medians and means are denoted with horizontal white bars and white circles, respectively. Sample size within a year is denoted by point size with outlier points extending beyond boxplot whiskers. Asterisks denote significant pairs at $\alpha < 0.05$ (p-values shown in plot) as indicated by t-tests for *B. brevicauda*: $t(8.5) = -5.2$, *M. gapperi*: $t(2.5) = -0.8$, *N. insignis*: $t(5.7) = -5.9$, *P. leucopus*: $t(6.5) = -1.6$ and *P. maniculatus*: $t(7.8) = -2.6$.

than *P. maniculatus* (Cramer, 2014; Stephens et al., 2019). We had expected that *B. brevicauda* and *M. gapperi* would show the weakest response to seed availability since they are thought to rely less on seeds compared to the other species. However, contrary to our expectation, *B. brevicauda*, an ostensibly insectivorous shrew, showed one of the strongest responses—with a greater proportion of females

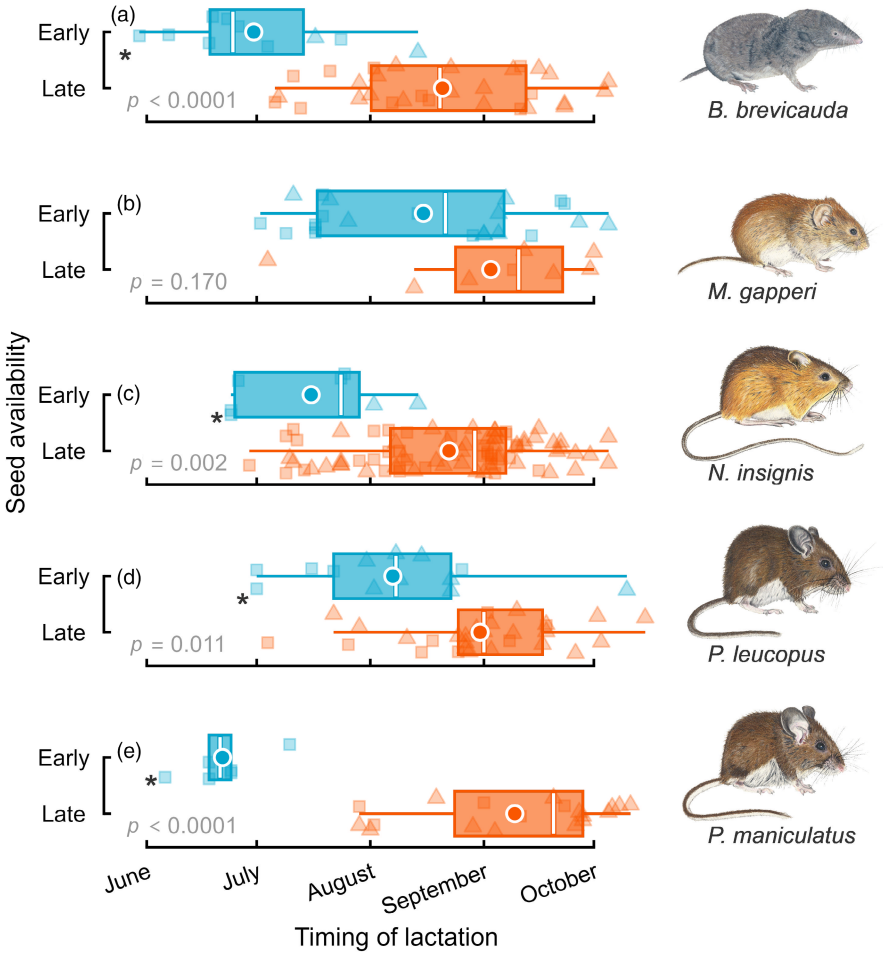

FIGURE 6 Boxplots summarizing timing of reproduction of five small mammal species (a–e), including observed lactating females (square) and embryos (triangle; adjusted by gestation duration) for years with seed availability early or late in the breeding season. Medians and means are denoted with vertical white bars and white circles, respectively. The full data range is plotted with outlier points extending beyond boxplot whiskers. Asterisks denote significant pairs at $\alpha < 0.05$ (p-values shown in plot) as indicated by t-tests for *B. brevicauda*: $t(18.2) = -5.9$, *M. gapperi*: $t(12.9) = -1.5$, *N. insignis*: $t(7.4) = -4.5$, *P. leucopus*: $t(20.3) = -2.8$ and *P. maniculatus*: $t(20.2) = -10.6$.

breeding along with reproduction occurring nearly 2 months later during years with late seed availability compared to years with early seed availability. Although *B. brevicauda* is generally considered to be insectivorous (George et al., 1986), there is evidence that seeds may be an important component of its diet. For example, *B. brevicauda* is known to cache beech seeds during the winter (Merriam, 1884; Merritt, 1986) and populations in forested systems respond numerically to beech mast (Jensen et al., 2012). We found that these cached seeds change summer diet of *B. brevicauda* from that of an insectivore (82% arthropods in 2015) to that of an omnivore (33% arthropods and 47% cached seeds in 2014), which in turn shapes the timing of reproduction. Thus, although *B. brevicauda* is generally an insectivore, masting appears to shift breeding earlier in the season. Increased abundance of insects associated with masting (e.g. Michał et al., 2018) may also contribute to diets during this time and more detailed analyses such as metabarcoding of stomach contents or scat are necessary to fully resolve the relative influence of direct and indirect trophic channels on reproduction in *B. brevicauda*.

Although *M. gapperi* also consumed more hemlock and beech seeds during masting events, its reproductive response was more nuanced than the other species. During years with early seed availability, *M. gapperi* appeared to take advantage of cached seeds to produce an early litter; however, unlike the other species, *M. gapperi* also appeared to breed again in the fall (as indicated by placental scar counts; Figure 3b). During this time, fungal consumption increased from about 25% in the summer to about 68% in the fall (Figure 2b). Thus, in years with early seed availability, *M. gapperi* uses a capital breeding strategy early in the breeding season (financed with cached seeds) and an income breeding strategy later in the season (financed with concurrently available fungal sporocarps). The larger cecum and thus ability of *M. gapperi* to process lower quality foods may allow it to take advantage of food sources that do not supply sufficient resources for the other small mammals to reproduce (Dubay et al., 2008; Moore et al., 2022).

Seasonal environments may also put limits on reproduction, particularly in our study system where winter runs from November into May (Richardson et al., 2007). These constraints are likely especially important for hibernating species such as *N. insignis*, which initiates hibernation between September and October (Wrigley, 1972). Indeed, whereas other species showed steady rates of breeding throughout the season in years with late seed availability, both female and male *N. insignis* showed declines in reproduction as the season progressed. Additionally, they tended to start lactation slightly earlier compared to other mice (Figure 6). This suggests that for hibernators, there are likely tradeoffs between waiting for seed availability and rearing young too close to winter (Zhang et al., 2006). Earlier reproduction may help time the emergence of juveniles with peak beech seed availability; allowing young to put on fat reserves before hibernation. For example, juvenile *T. striatus* wean during peak beech seedfall, which results in higher overwinter survival

(Bergeron et al., 2011; Tissier et al., 2020). *Napaeozapus insignis* also had higher placental scar counts in years with late seed availability compared to early seed availability (Figure 3c), suggesting that some individuals might have produced a second litter later in the season. Another small mammal hibernator, the common dormouse (*Muscardinus avellanarius*) also uses this strategy, with females in good condition reproducing early in the spring with the potential for another litter later in the summer, allowing them to take advantage of a relatively short breeding season (Bieber et al., 2012).

We predicted that males would show little response in terms of testes size to seed availability (Bronson, 1985). However, for most species we detected a strong response with males having smaller testes, that tended to decrease over the breeding season in years with early seed availability. In Europe, the edible dormouse (*Glis glis*) also reduces testes size in years with low seed availability, although no early reproduction occurs in the summer following a masting event (Bieber, 1998). Interestingly, in our system, testes size in males followed similar patterns to female breeding and it may be that cues from females are the proximate cause of change in testes size rather than resource availability itself (Bronson, 1985). Although resource allocation to testes in mammals is relatively small, testes are relatively large in promiscuous small mammals (Kenagy & Trombulak, 1986), and it may be that as mating opportunities with females decrease, it is not worth maintaining large testes throughout the breeding season. Unlike the other species that maintained testes size in years with fall seed availability, *N. insignis* showed a gradual decline over the breeding season with only slightly larger testes during fall compared to spring seed availability. This pattern further supports that breeding in *N. insignis* is likely constrained by hibernation.

Masting can shape mammal reproduction and interannual population cycles, although species-specific responses are often variable (Michałand et al., 2016). Our results have important implications for understanding the proximate drivers of reproductive timing of small mammals in seasonal environments which experience masting events. We found that masting drives two distinct reproductive pulses, one concurrent with seedfall during the fall season, with a high proportion of females breeding, and another occurring early the following summer, financed by cached seeds with a lower proportion of females breeding. Together, these two reproductive periods drive large interannual population fluctuations among species that are synchronized across the region (Stephens, Hocking, et al., 2017). We also found that, for most species, reproduction was uncommon outside of when seeds were available, highlighting that although photoperiod and temperature are broadly responsible for setting the bounds of the breeding season in seasonal environments (McLean & Guralnick, 2021), resource availability influences the strategies that species use, which in turn strongly influences the timing of reproduction within a year. Ostensibly this plasticity in ability to switch between breeding strategies in response to resource pulses may allow small mammals to adjust to phenological changes as a result of climate change since reproduction is not specifically linked to photoperiod cues (Bronson, 2009). However, masting is often correlated with regional weather conditions, and climate change is making masting events more variable, which may make it harder for species to track resource pulses (Janzen, 1971; Pearse et al., 2017). Moreover, asynchronous phenological changes among seasons (e.g. earlier spring and later fall) may be disruptive as our results suggest that early season resources (e.g. red maple seeds), which are important for financing gestation, may lead to lactation occurring before fall masting occurs. Such mismatches in seasonal food availability may ultimately influence survival and recruitment.

AUTHOR CONTRIBUTIONS

Ryan B. Stephens and Rebecca J. Rowe conceived the ideas and designed methodology; Christine A. Costello, Ryan B. Stephens, Joshua S. Willems and Mariko Yamasaki collected the data; Ryan B. Stephens analysed the data and led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

This work was supported by Research Joint Venture Agreement 19-JV-11242307-044 between the U.S.D.A. Forest Service and the University of New Hampshire. Support was also provided by the New Hampshire Agricultural Experiment Station (NHAES). This work was supported by the USDA National Institute of Food and McIntire-Stennis Project (1006881, 1016133, 1026211). This is NHAES Scientific Contribution Number 3019.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code used in this manuscript are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.nvx0k6f0t (Stephens et al., 2024).

ORCID

Ryan B. Stephens https://orcid.org/0000-0001-8524-9873
Rebecca J. Rowe https://orcid.org/0000-0002-0492-568X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Relationship between beech seed biomass collected at Hubbard Brook Experimental Forest and Bartlett Experimental Forest between 2017 and 2022 ($R^2 = 0.92$).

Figure S2. Summary of timing of sampling for the United States Forest Service long-term monitoring program (wide bars) and University of New Hampshire mark-recapture study (lines) during year with early and late seed availability.

Figure S3. Timing of when food items are available to small mammals during the breeding season and the period of time over which hair samples from small mammals integrate an isotopic signal of diet.

Table S1. Effective sample size of posteriors from Bayesian mixing models for each potential food source in summer and fall of 2014 and 2015.

Table S2. Correlation between body mass and testes size in males in early and late seed availability.

Table S3. Summary of best generalized linear mixed models showing the influence of body mass, seed availability (Seed—relative to late season availability), day of the year (DOY), and the interaction between day of the year and seed availability on female reproduction.

Table S4. Summary of linear mixed models showing the influence of seed availability (Seed—relative to late season availability), day of the year (DOY), and the interaction between day of the year and seed availability on standardized testes size.

How to cite this article: Stephens, R. B., Willems, J. S., Yamasaki, M., Costello, C. A., & Rowe, R. J. (2024). Resource availability alters breeding strategies in a small mammal community. *Journal of Animal Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2656.14148