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Simultaneous population fluctuations of rodents in montane forests and alpine meadows suggest indirect effects of tree masting

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Resource pulses can generate cross-habitat dispersal of consumers, and therefore affect organisms even in areas where the resource pulses do not occur. We investigated this phenomenon at the elevational treeline in the Carpathian Mountains, where beech (*Fagus sylvatica*) masting caused an increase in abundance of forest rodents and intensified their use of alpine meadows. We tested 3 hypotheses concerning the impact of forest rodent spillover on the abundance of meadow-dwelling pine voles (*Microtus subterraneus*): 1) the competition hypothesis: if the spillover affects pine voles mostly through intensified competitive interactions, then pine voles should decline when forest rodents reach their peak abundance, i.e., 1 year after masting; 2) the apparent competition hypothesis: if predators switch to alternative prey when populations of forest rodents collapse, then pine voles should decline 2 years after masting; and 3) the apparent mutualism hypothesis: if the increase of forest rodents temporarily releases pine voles from predatory pressure, pine voles should increase in synchrony with forest rodents—1 year after masting. Our results, while correlative in nature, supported the apparent mutualism hypothesis: 1 year after masting, both forest rodents and pine voles strongly increased their abundance. Two years after masting, when populations of forest rodents crashed, abundance of pine voles returned to pre-masting levels rather than collapse. These findings suggest that pulsed spillover, known mostly from negative effects on organisms in recipient habitats, can also create indirect positive interactions. Furthermore, they illustrate how density-dependent spillover of animals might increase the spatial scale of masting effects beyond the habitats where seeds are released.

Key words: *Apodemus flavicollis*, Bieszczady Mountains, *Fagus sylvatica*, indirect effects, mast seeding, *Microtus subterraneus*, *Myodes glareolus*, Poland, pulsed resources

Resource pulses, defined as brief episodes of increased resource availability, strongly affect animal communities (Yang et al. 2010). Resource fluctuations cause sequential bottom-up and top-down effects in trophic webs, changing the architecture of interaction networks and relations between consumers and resources (e.g., Carnicer et al. 2009; Cockle and Martin 2015; Levi et al. 2015; Sato et al. 2016). These types of effects are most obvious and expected in areas where the resource pulses occur. Their impact may be more spatially extensive; even when the resources themselves do not cross habitat boundaries their consumers often do (e.g., Allen and Wesner 2016). For example, resource pulses can generate dispersal of consumers into adjacent areas, causing cross-habitat “spillovers” of organisms (Tschamtko et al. 2012). This phenomenon could greatly

expand the spatial influence of resource pulses. Yet, publications on consumer spillover and on resource pulses rarely reference one another and the few studies that bridge those topics mostly focus on organism exchange in a mosaic of managed and natural habitats (e.g., Rand et al. 2006; Frost et al. 2015; Riedinger et al. 2015).

When species that are subsidized by abundant resources in one habitat spillover into adjacent habitats, exploitative competition may result if they encounter species with similar resource requirements (Polis et al. 1997; Stapp and Polis 2003; Schneider et al. 2016). This process may negatively affect the latter species. Similarly, spillover can generate strong interference competition in adjacent habitats (Oksanen et al. 1995). The interference competition results in reduced foraging

efficiency due to time lost for agonistic interactions or exclusion from the best foraging patches (e.g., Henden et al. 2010; Peck et al. 2014).

Alternatively, spillover of subsidized consumers into adjacent habitats can change predation pressure in those habitats. The best documented example of such a phenomenon is apparent competition, whereby an increase in one prey species leads to an increase in predator abundance and subsequent decline in the second prey species (Holt and Lawton 1994; Wootton 1994). However, when predators cannot respond quickly to the influx of a new prey species, predation pressure on the second prey species may decrease, providing a temporary release from predator suppression of prey abundance. Theoretical models indicate that such positive predator-mediated interactions between prey species are particularly likely when populations fluctuate (Abrams et al. 1998). Yet, this phenomenon, termed “apparent mutualism,” has received much less attention in community ecology than apparent competition (Gilg and Yoccoz 2010; Ims et al. 2011; Tack et al. 2011; van Maanen et al. 2012; Lee et al. 2016).

Synchronized fluctuations in plant seed production, or masting (Crone and Rapp 2014; Pearse et al. 2016), provide an exceptional opportunity to study consumer spillover. Masting trees create pronounced resource pulses that influence populations of numerous consumers (Clotfelter et al. 2007; Schmidt and Ostfeld 2008; Szymkowiak and Kuczyński 2015; Bogdziewicz et al. 2016). The seeds produced during masting events are generally limited to forested habitats, but many granivores that consume those seeds are highly mobile and frequently live in adjacent habitats. Thus, tree masting has the potential to create strong spillover effects.

We investigated effects of a mast event in beech (*Fagus sylvatica*) on rodent communities in beech forest and in adjacent alpine meadows. The rodent communities below treeline are numerically dominated by yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*). For both species, tree seeds are an important part of their diet (Drózd 1966; Butet and Delettre 2011; Selva et al. 2012). Their populations typically increase 1 year after beech masting and steeply decrease 2 years after masting (Jensen 1982; Pucek et al. 1993; Stenseth et al. 2002; Zwolak et al. 2016a). Rodent communities above treeline in alpine meadows are dominated by pine voles (*Microtus subterraneus*—Grodziński et al. 1966). Diet of this rodent species consists mostly of leaves, stems, tubers, and roots (Holišová 1965; Pucek 1984; Butet and Delettre 2011).

We anticipated that yellow-necked mice and bank voles, which are associated mainly with forest habitats (Grodziński et al. 1966; Schlinkert et al. 2016), would intensify their use of alpine meadows as their populations in beech forest increase 1 year after the mast event. This assumption is based on a negative relationship between population abundance and habitat selectivity (e.g., Rosenzweig 1991). Such a phenomenon has been documented in many species, including yellow-necked mice and bank voles (Zwolak et al. 2016a).

Direct effects of beech masting on pine voles would be unlikely because this species was found almost exclusively

in alpine meadows (see “Results”) and therefore did not have access to beech seeds. Yet, high abundance of yellow-necked mice and bank voles and their presumed increased use of alpine meadows might impact the abundance of pine voles in 3 ways: 1) if the increased abundance of yellow-necked mice and bank voles affects pine voles mainly through intensified interference competition, it might lead to a decline in pine voles 1 year after masting (the competition hypothesis); 2) if predator populations increase in alpine meadows when yellow-necked mice and bank voles become abundant and if predators switch to alternate prey when yellow-necked mouse and bank vole populations collapse, the abundance of pine voles might decrease 2 years after masting (the apparent competition hypothesis); and 3) if predator populations in alpine meadows are slow to respond numerically to increases in yellow-necked mice and bank voles, the numbers of pine voles might increase 1 year after masting due to the large number of prey relative to the number of predators (the apparent mutualism hypothesis). We tested these hypotheses by monitoring populations of the 3 rodent species in both habitats.

MATERIALS AND METHODS

Study sites.—The study was conducted in the Bieszczady Mountains (part of the Eastern Carpathians), located in south-eastern Poland in Podkarpackie Province, within Bieszczady National Park (22°40'E, 49° 07'N; Fig. 1). The gentle slopes of the Bieszczady Mountains (max. slope < 45°) reach an elevation of 1,300 m above sea level (a.s.l.). The area lies in the temperate continental climate zone, which is characterized by cold winters and mild summers. Mean temperature is 15°C in July and −5°C in January. Annual precipitation ranges between 1,100 and 1,200 mm, with a maximum in July (150–170 mm) and a minimum in January (70 mm) (Winnicki and Zemanek 2009). Snow cover in the study area lasts from mid-November through April. Forests, predominated by beech with some silver fir (*Abies alba*) and sycamore (*Acer pseudoplatanus*), cover about 70% of the area and extend up to an elevation of ~ 1,150 m a.s.l. This relatively low treeline consists of gnarly forms of beech (krummholz). Immediately above treeline are alpine meadows composed mainly of blueberry shrubs (*Vaccinium myrtillus*) and grasses (*Calamagrostis arundinacea*, *Deschampsia caespitosa*), with sparse forbs (Winnicki and Zemanek 2009). All economic activities (mainly cattle grazing) on the alpine meadows ceased after the Second World War (Kucharzyk and Augustyn 2008) and there is no timber harvest in high-elevation forests. This study was concentrated at the transition zone between the beech forest and alpine meadows. Four research sites, spaced approximately 7 km apart, were located at the treeline of the Park's main massifs, 2 with a southwest aspect (Połonina Caryńska, Rozsypaniec) and 2 with a northeast aspect (Połonina Wetlińska, Bukowe Berdo; Fig. 1).

Seed production.—Seedfall in beech occurs in October and November, with large inter-annual variation in crop size (Kantorowicz 2000; Packham et al. 2012; Bogdziewicz et al. 2017). As an index of seed production, we used data on the

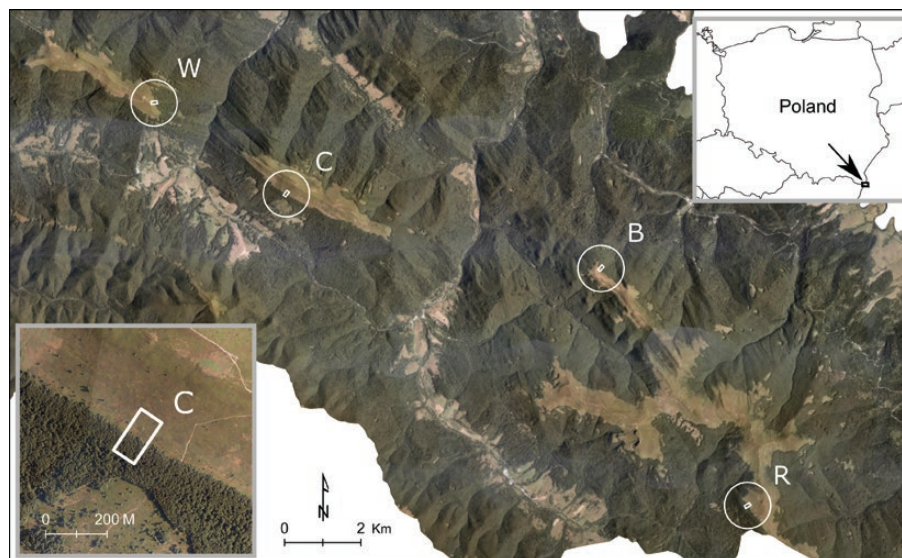


Fig. 1.—Position of small mammal trapping grids within the Bieszczady National Park, Poland. W = trapping grid situated at Połonina Wetlińska; C = Połonina Caryńska; B = Bukowe Berdo; R = Rozsypaniec. Upper box: location of study sites in Poland; lower box: position of the trapping grid at Połonina Caryńska in relation to the treeline.

annual beech seed crop in Podkarpackie Province, provided by the Regional Directorate of State Forests in Krosno. The data were collected annually from 1995 to 2015 for the Polish Forest Gene Bank. Each year, the beech seed crop was assessed on permanent forest plots, which were evenly distributed across the Regional Directorate of the State Forests. Beech seeds were collected from the forest floor and by using standard seed traps. Seed production was expressed as kilograms of seeds collected per ha of area surveyed.

Small mammal trapping.—At each site, we set up a rectangular 16×8 trapping grid (128 traps per grid), with 10 m spacing between trap stations. The grid was perpendicular to the treeline, with approximately one-half of the traps in the forest and one-half in the meadow (Fig. 1).

Trapping was conducted in 2013 (mast year), 2014 (post-mast year), and 2015 (2 years after mast), in 2 sessions per year, spring (June) and fall (September). Each session lasted 4 consecutive nights and 3 days. Total trapping effort (i.e., over 3 years of the study) was 12,288 trap-nights. Wooden traps (“dziekanówka” type, size $16.5 \times 8 \times 9.5$ cm; produced by PPUH A. Marcinkiewicz, Rajgród, Poland) were baited with a mixture of rolled oats and sunflower seeds and checked in the morning (starting at 08:00 h) and evening (starting at 18:00 h). Trapped rodents were marked with individually numbered ear tags and released immediately after recording information on their species, sex, reproductive status, and body mass (measured with Pesola spring scales). Besides yellow-necked mice, bank voles, and pine voles, we sporadically captured the following species of rodents: edible dormouse (*Glis glis*), common dormouse (*Muscardinus avellanarius*), birch mouse (*Sicista betulina*), striped field mouse (*Apodemus agrarius*), harvest mouse (*Micromys minutus*), and field vole (*Microtus agrestis*). Other captured animals (e.g., pygmy shrews [*Sorex minutus*], common shrews [*S. araneus*], alpine shrews [*S. alpinus*], least weasels [*Mustela nivalis*], and stoats [*M. erminea*]) were

released unmarked. Approval for live-trapping was granted by the Local Ethical Commission in Poznań, Poland (no. 71/2012) and the Minister of Environment (DLPpn-4102–420/47773/12/RS). The methods used conformed to the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes et al. 2016).

Data analysis.—We analyzed data in R (R Core Team 2016), using generalized linear mixed models (GLMMs). Statistical significance of fixed factors was tested with Wald type II chi-square tests. The analysis of habitat use (to verify the assumption of increased use of meadows by yellow-necked mice and bank voles when their abundances are high) was conducted with package “lme4” (Bates et al. 2015), separately for each species. We used logit link functions and binomial data distributions (captures in traps located in meadows versus forest). Explanatory variables included the index of intraspecific abundance (the number of different individuals of a given species captured per trapping session), and in the case of bank vole and pine vole models, the index of abundance of the yellow-necked mouse. The model also included the variable “season” to control for potential shifts in habitat use between June and September. Random effects included site and individual (to account for multiple captures of the same animals). While locations of traps within grids were not spatially independent, simulation studies demonstrated that this correlation structure is unlikely to bias the results of habitat use analyses, particularly when trapping effort is high (more than 10,000 trap-nights—Gorosito et al. 2016). In the analysis of abundance (necessary to distinguish among the competition, the apparent competition, and the apparent mutualism hypotheses), the response variable was the number of different individuals captured per trapping session (with separate models for yellow-necked mice, bank voles, and pine voles). Explanatory variables included year, season, and their interaction (only if significant). Trapping site was used as random effect. We used a log link function and a negative

binomial distribution. We conducted this analysis with package “glmmADMB” (Skaug et al. 2016). We did not use estimators of abundance (e.g., White and Burnham 1999) because the numbers of captures strongly fluctuated over time (see “Results”) and thus reliable estimates could not be obtained for all years of the study. In such a situation, an index might be a better measure than estimated abundance (McKelvey and Pearson 2001; Engeman 2003; Hopkins and Kennedy 2004; Johnson 2008; Schwartz et al. 2015).

RESULTS

Seed production.—Over the years 1995–2015, the average seed production was 2.12 kg/ha ($SD = 2.78$). In 2012, seed production was 0.85 kg/ha. In 2013 it reached 7.05 kg/ha, and in 2014 it fell to 0 kg/ha. Seed production in 2013 was the highest within the 20-year period surveyed (Fig. 2).

Habitat use.—In total, we recorded 1,466 captures of yellow-necked mouse (632 different individuals), 1,580 captures of bank voles (708 individuals), and 441 captures of pine voles (254 individuals). Sixty-eight percent of yellow-necked mouse captures occurred in forest and 32% in meadows (Fig. 3). Contrary to our expectations, these proportions were not influenced by changes in abundance of this species ($\chi^2 = 0.12$, $d.f. = 1$, $P = 0.73$). Similarly, the effect of season was not significant ($\chi^2 = 0.10$, $d.f. = 1$, $P = 0.75$).

As anticipated, the proportion of bank vole captures in meadows strongly increased with intraspecific abundance ($\chi^2 = 6.66$, $d.f. = 1$, $P = 0.010$). Consequently, in 2013 and 2015 (when abundance was low) only 1% of captures occurred in meadows; in 2014, this proportion increased to 55% (Fig. 3). After controlling for this effect, bank voles also were more likely to be captured in forest when the abundance of yellow-necked mice was high ($\chi^2 = 4.61$, $d.f. = 1$, $P = 0.032$) and in the fall rather than in spring ($\chi^2 = 4.86$, $d.f. = 1$, $P = 0.027$).

Pine voles were largely confined to meadows (97% of captures; Fig. 3), regardless of changes in intra- or interspecific abundance (pine vole effect: $\chi^2 = 0.57$, $d.f. = 1$, $P = 0.64$; yellow-necked mouse effect: $\chi^2 = 1.40$, $d.f. = 1$, $P = 0.24$) or season ($\chi^2 = 2.93$, $d.f. = 1$, $P = 0.09$).

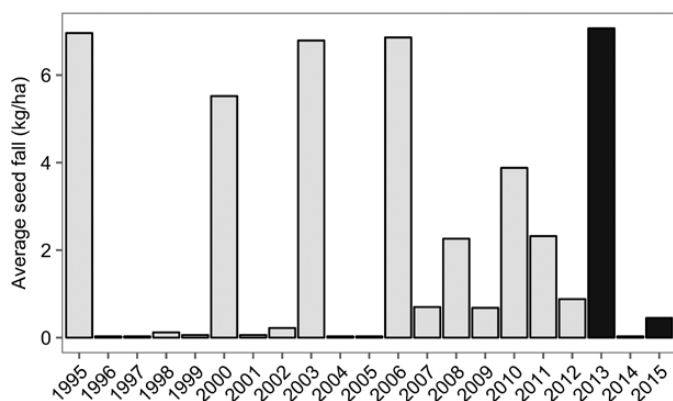


Fig. 2.—Annual beech seed crop in Podkarpackie Province, Poland. Black bars denote period of the study (2013–2015).

Competition, apparent competition, and apparent mutualism hypotheses.—The forest rodents (yellow-necked mouse and bank vole) and the pine vole increased in synchrony 1 year after masting. Two years after masting, the abundance of forest rodents was extremely low (during spring trapping, we captured only 1 yellow-necked mouse and no bank voles), but the abundance of pine voles returned to pre-masting levels (Fig. 4). This pattern is in accordance with the apparent mutualism hypothesis, but does not support the competition or the apparent competition hypotheses.

The abundance of yellow-necked mice increased about 3.6-fold from 2013 to 2014 and collapsed to very low levels in 2015, when only 11 individuals were captured over the entire trapping season (year effect, $\chi^2 = 56.17$, $d.f. = 2$, $P < 0.001$; Fig. 4). Additionally, in 2013 and 2015, abundance of yellow-necked mice was higher in the fall than in the spring, but the opposite was found in 2014 (season effect, $\chi^2 = 8.90$, $d.f. = 1$, $P = 0.003$; season \times year effect, $\chi^2 = 35.83$, $d.f. = 2$, $P < 0.001$; Fig. 4).

Only year was a significant predictor of bank and pine vole abundance (bank vole: $\chi^2 = 110.93$, $d.f. = 2$, $P < 0.001$; pine vole: $\chi^2 = 33.05$, $d.f. = 2$, $P < 0.001$); both species were relatively rare in 2013 and 2015 (with less than 10 individuals per site, on average), but extremely abundant in 2014 (with dozens of individuals per site; Fig. 4). The post-masting increase was 39-fold in bank voles and 12-fold in pine voles.

DISCUSSION

We examined 3 alternative hypotheses concerning effects of post-masting spillover of forest rodents on voles that live in alpine meadows: the competition hypothesis, the apparent competition hypothesis, and the apparent mutualism hypothesis. Our results are consistent with predictions of the apparent mutualism hypothesis, which states that the spillover can cause a synchronous increase of forest and meadow rodents through temporary release of the latter from predatory pressure. This emphasizes the notion that food webs function as dynamic, open systems, with local dynamics strongly influenced by external factors and “transient” species (Reiners and Driese 2001; Polis et al. 2004). Furthermore, our results demonstrate that pulsed spillover, known mostly from negative effects on organisms in recipient habitats (e.g., Stapp and Polis 2003; Soykan and Sabo 2009; Frost et al. 2015; Schneider et al. 2016), can also create indirect positive interactions.

The competition hypothesis.—Yellow-necked mice and bank voles strongly increased in abundance after beech masting that occurred in the fall of 2013. Additionally, bank voles, which occurred almost exclusively below the treeline when their abundance was low, in 2014 began to use the meadows as frequently as the forest. The competition hypothesis predicted that the heavy use of the meadow by these rodents would reduce the number of pine voles, which are smaller and most likely behaviorally submissive. In contrast to this prediction, pine voles drastically increased in abundance in 2014. Thus, competition was probably not a predominant effect during the spillover: the competition hypothesis can be rejected.

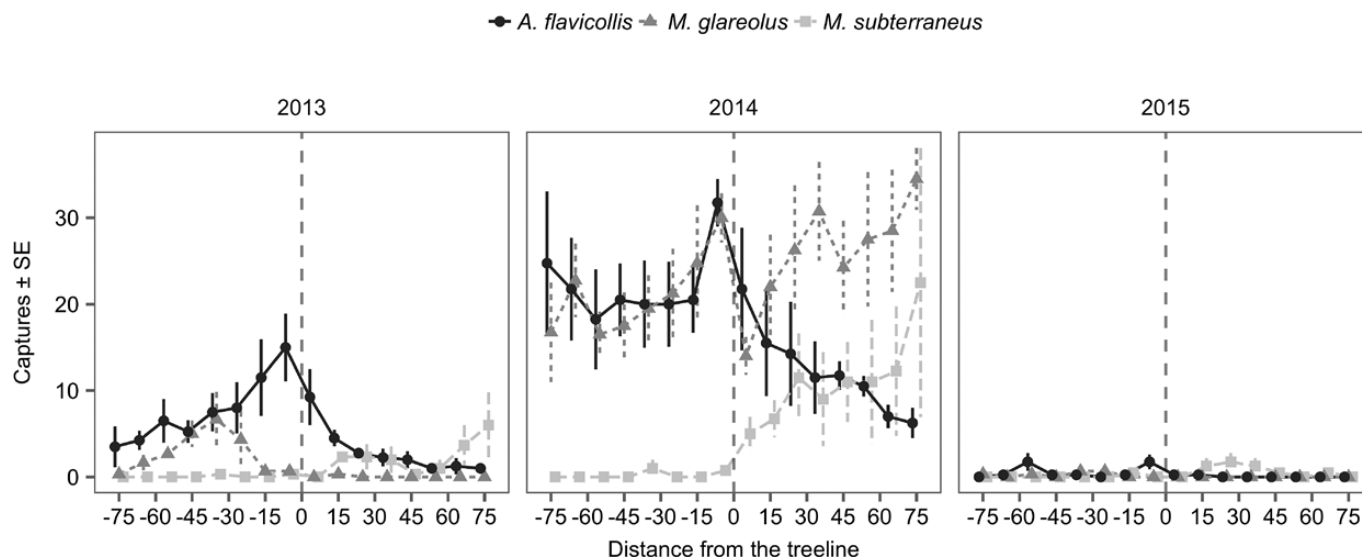


Fig. 3.—Distribution of rodent captures (means with SEs, based on using trapping sites as replicates) in relation to the beech treeline at Bieszczady National Park, Poland. Data collected during mast year (2013), 1 year after masting (2014), and 2 years after masting (2015). Positive values on the x-axis represent distance (in meters) into the meadow and negative ones distance into the forest. Captures of yellow-necked mice (*Apodemus flavicollis*, circles) occurred mostly in the forest, but also above the treeline; captures of bank voles (*Myodes glareolus*, triangles) occurred solely below treeline during periods of low abundance (2013 and 2015), but in both habitats when abundance of this species was high (2014); pine voles (*Microtus subterraneus*, squares) were captured almost exclusively in the meadows regardless of their abundance.

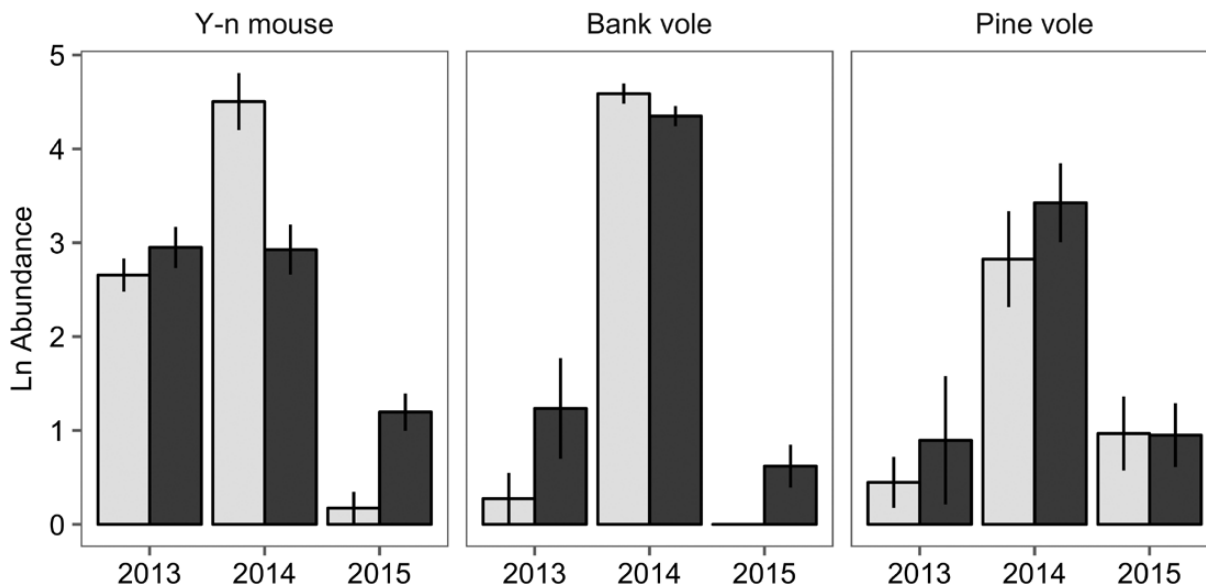


Fig. 4.—Mean abundance (\pm SE) of rodents (number of different individuals captured per trapping site; notice the logarithmic scale) during mast year (2013), 1 year after masting (2014), and 2 years after masting (2015) in Bieszczady National Park, Poland. Light bars represent spring trapping and dark bars fall trapping. Y-n = yellow-necked mouse, *Apodemus flavicollis*; bank vole = *Myodes glareolus*; pine vole = *Microtus subterraneus*.

The simultaneous post-masting population increases of yellow-necked mice, bank voles, and pine voles suggest that the positive impact of the pulsed resource on abundance was stronger than potential negative effects of competition. Studies conducted in the temperate zone often fail to find effects of competition on rodent abundance (e.g., competition between the yellow-necked mouse and the bank vole—[Amori et al. 2015](#); [Sozio and Mortelliti 2015](#); but see [Fasola and Canova 2000](#)) and some researchers question the importance of

competition in small mammal population dynamics ([Galindo and Krebs 1985](#); [Wolff and Dueser 1986](#); [Sekijima and Sone 1994](#); [Shanker 2001](#); [Huitu et al. 2004](#); [Brunner et al. 2013](#), but see e.g., [Merritt et al. 2001](#); [Lemaître et al. 2010](#)). In general, synchronized dynamics of small mammals are common because many species respond to the same bottom-up (e.g., [Singleton et al. 2010](#)) or top-down (e.g., [Korpimäki et al. 2005](#)) forces that override competition and make it difficult to detect without long-term removal experiments ([Heske et al. 1994](#)).

Similarly, we found little evidence of shifts in habitat use as populations of potential competitors increased. As competing species increase in density, they become more likely to partition habitats (Morris 2003; van Beest et al. 2014). However, yellow-necked mice and pine voles exhibited stable habitat use patterns, regardless of changes in interspecific (and intraspecific) abundance. Bank voles strongly changed their habitat use with intraspecific abundance and season. When these effects were statistically controlled, bank voles also seemed to respond to changes in the abundance of yellow-necked mice. Yet, the response was in the opposite direction than expected if driven by competition: i.e., when yellow-necked mice were abundant, bank voles tended to occur more often below the treeline, which is the main habitat of the mice. We cannot envision how such a shift would be attributed to interspecific competition (we also note that abundances of yellow-necked mice and bank voles were correlated, thus this effect has to be interpreted with caution). Perhaps these species partition habitats at finer scales (i.e., microhabitat—Amori et al. 2015; Zwolak et al. 2016a) than examined here.

The apparent competition hypothesis.—Masting-related changes in resource abundance trigger consumer reactions that often result in apparent competition (Ostfeld and Keesing 2000; Bogdziewicz et al. 2016). The best-known example of this phenomenon involves rodents, their predators (mustelids and raptors), and songbirds as the alternative prey. Populations of predators grow in response to rodent abundance and in turn generate increased predation on birds when rodents crash and become scarce (Jędrzejewska and Jędrzejewski 1998; Schmidt and Ostfeld 2008). This phenomenon causes synchronized collapses of primary and alternative prey (see also “the alternative prey hypothesis” of rodent cycles—Angelstam et al. 1984; Korpimäki et al. 2005). However, this pattern was not detected in our study system. One year after masting, when populations of forest rodents peaked, pine voles strongly increased in abundance. Two years after masting, when populations of forest rodents crashed (see e.g., Pucek et al. 1993; Elias et al. 2006; Pedersen and Greives 2008 for discussion of possible reasons for post-masting population crashes), abundance of pine voles returned to pre-masting levels rather than collapsed. These findings argue against the apparent competition hypothesis; this interaction was unlikely to be the dominant driver of rodent population dynamics.

Other possible explanations of the post-masting pine vole increase.—The pine vole is unlikely to directly benefit from masting. This species is predominantly herbivorous, feeding mostly on subterranean parts of plants and only rarely on seeds (Pucek 1984). Moreover, even though the pine vole inhabits forests (particularly with dense understory) in other parts of its range, it is not found in beech forest in the Bieszczady Mountains (Grodziński et al. 1966; this study), and beech seeds are too heavy to be transported into the meadow by wind. Some seeds may have been dispersed into the meadow by yellow-necked mice, but distances of such transport rarely exceed several meters (Zwolak et al. 2016b). Therefore, feeding on beech seeds (including pilferage of seed caches made in alpine

meadows by yellow-necked mice) can be ruled out as the reason for the pine vole’s population increase.

Alternatively, the increase in pine vole abundance could be mediated by an indirect bottom-up effect of masting. Lobo and Millar (2013) suggested that an increase in deer mice (*Peromyscus maniculatus*) after masting in Alberta, Canada, was caused not by abundant seeds, but by granivorous beetles that fed on the seeds. Lobo and Millar (2013) speculated that the beetles became abundant due to an increase in their food source (mast) and then became important in the diet of small mammals. That explanation has not been directly tested, however. In the case of the pine vole increase, this scenario seems unlikely. Apart from the fact that pine voles are mainly herbivorous, invertebrate granivores would have to travel far from forest into alpine meadows to serve as a food resource for pine voles. Moreover, if the increase of pine voles was caused by diffusion of resources (seeds or invertebrates) from the forest, we would expect the highest number of pine voles to be captured close to the forest-meadow boundary, which was not observed (Fig. 3).

Finally, abundance of pine voles could respond to changes in unmeasured food resources, which happened to coincide with beech masting. However, there was no indication of fluctuations in the biomass of grasses and forbs (eaten by pine voles) over the course of our study—and such fluctuations would have to be very substantial to account for the dramatic changes in pine vole abundance. Variation in berry production by *Vaccinium* sp. is also known to influence populations of voles (Krebs et al. 2010; Selås et al. 2013). However, if changes in berry production were responsible for the increase in pine vole that occurred in 2014, the increase would be most pronounced at sites with high cover of *V. myrtilus* and less marked at sites where such cover was low. This was not the case: site “Bukowe Berdo” differed from the other study sites by having very little *V. myrtilus* (it covered only 4% of this site while at the 3 remaining sites it covered 21–36% of the area: R. Zwolak et al., pers. obs.), yet the peak abundance of pine voles at “Bukowe Berdo” was higher than anywhere else. Thus, fluctuations in berry crops were unlikely to cause the changes in pine vole abundance.

The apparent mutualism hypothesis.—Based on our data, the most likely explanation for the post-masting increase in abundance of pine voles is a reduction in the top-down pressure of predators: the strong increases in abundance of yellow-necked mice and bank voles benefited pine voles by swamping the local predator community and diluting predation pressure (Bêty et al. 2002; Gilg and Yoccoz 2010; Ims et al. 2011). The most important predators in our study system are likely to be least weasels and stoats. We captured both of these species at all our field sites, above and below the treeline. Captures were infrequent (0–3 captures per site per season) and we did not detect an increase after masting for either species. We note, however, that mustelids may be more difficult to trap when prey is abundant (Korpimäki et al. 1991). Responses of mustelids to peaks in rodent populations are often lagged (Sundell et al. 2013; but see Jędrzejewski et al. 1995), which suggests their prey experiences temporary release from predator pressure.

Furthermore, even when lags are not detected, numerical responses of rodents to masting is overwhelmingly stronger than numerical responses of mustelids to rodents (King 1983; Jędrzejewski et al. 1995). A similar pattern holds also for other predators of rodents (Jędrzejewski et al. 1996; Jędrzejewska and Jędrzejewski 1998)—in general, post-masting increases in rodent abundance temporarily overwhelms the capability of predators to suppress populations of their prey.

Thus, according to this interpretation, peak abundance of yellow-necked mice and bank voles would be caused by bottom-up effects of masting (Stenseth et al. 2002; Shimada and Saitoh 2006; Falls et al. 2007; Boonstra and Krebs 2012; Flowerdew et al. 2017, but see Selås 2016), and peaks of pine voles would follow from spillover of forest rodents that resulted in release from top-down forces (Korpimäki et al. 2002; Huitu et al. 2003; Maron et al. 2010). We note, however, the correlative nature of our results. We did not measure predatory pressure and our explanation is based solely on the consistency between patterns of rodent abundance and predictions of the apparent mutualism hypothesis. Moreover, our study was relatively short-term and therefore included only 1 masting event (in beech, mast events usually occur in intervals of 4–8 years—Packham et al. 2012; Bogdziewicz et al. 2017).

To conclude, we demonstrated a synchronized, post-masting increase of rodents with different diets (the yellow-necked mouse, a seed specialist; the bank vole, an omnivore; the pine vole, a herbivore—Pucek 1984; Gasperini et al. 2018) and habitat affinities (forest and meadow specialists—Grodziński et al. 1966; Sozio and Mortelliti 2016). The synchrony in peak population abundance of forest and meadow rodents was predicted by the apparent mutualism hypothesis: most likely, it resulted from predatory release caused by extremely fast numerical response of forest rodents to the resource pulse. While it is widely acknowledged that cross-edge dispersal of subsidized predators can depress prey species in adjacent habitats (e.g., Kristan and Boarman 2003; Rand et al. 2006), our findings suggest that spillovers of subsidized prey can help alternative prey temporarily escape from top-down control. Furthermore, these results demonstrate how density-dependent spillover of animals increases the spatial scale of masting effects beyond the habitat where seeds are released.

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