



Beech masting modifies the response of rodents to forest management



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ABSTRACT

We investigated the impact of forest harvest and tree masting on the abundance and habitat selection of yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*). Our study was conducted in managed European beech (*Fagus sylvatica*) forest, in four closed-canopy and four shelterwood stands, during two mast and two non-mast years. We predicted that (1) forest harvest will positively affect vegetation cover, resulting in increased abundance of yellow-necked mice; (2) abundance of bank voles will not be affected by forest harvest; (3) the increased abundance of yellow-necked mice in shelterwood vs. closed-canopy stands will be more pronounced after non-mast (low rodent abundance) than after mast years (high rodent abundance), and (4) both species of rodents will select microhabitats with protective cover (provided by coarse woody debris or dense vegetation), but this preference will be stronger after non-mast than after mast years. In agreement with the first prediction, the abundance of yellow-necked mice tended to be higher in shelterwood than in closed-canopy stands, and was positively associated with average vegetation cover (generally denser in shelterwood than in closed-canopy stands). The second prediction was partially supported: while there was no clear effect of forest harvest on bank vole abundance, it was negatively affected by soil scarification conducted at two shelterwood stands. In concurrence with predictions (3) and (4), habitat associations of both rodent species were considerably weaker after mast years at both stand and microhabitat scales. Unexpectedly, after mast years, there was a negative association between bank vole abundance and vegetation cover, perhaps resulting from interference competition with yellow-necked mice. Our findings demonstrate that masting-related fluctuations in rodent abundance strongly influence their patterns of habitat selection.

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1. Introduction

Most forests in the northern temperate zone are managed for wood production or have been converted for other human use. In central Europe, for instance, only 0.2% of broad-leaf forests persist in a close-to-natural state (Hannah et al., 1995). Due to widespread forest management, silvicultural treatments change the structure of wildlife habitat and availability of food resources over vast areas. The consequences of this anthropogenic disturbance for wildlife abundance and habitat selection are of considerable conservation interest (Naughton et al., 2000; Fisher and Wilkinson, 2005; Schieck and Song, 2006; Paillet et al., 2010). However, reliable inferences on the effects of forest management on wildlife require taking into account density-dependence of habitat selection (Morris, 2003). Because the probability of choosing a particular habitat varies with population density, investigations should be conducted under conditions of both high and low population

density (Hodson et al., 2010; van Beest et al., 2014). This is particularly important when abundance fluctuates through time.

Masting, the synchronous and intermittent production of large seed crops (Kelly and Sork, 2002; Crone et al., 2011), is a primary driver of wildlife abundance cycles in many managed forests. Masting results in strong pulses of resources, with effects permeating through forest food webs (Ostfeld and Keesing, 2000; Yang et al., 2010; Bogdziewicz et al., 2015). Although it has been frequently investigated by wildlife biologists, its effects on wildlife are usually examined in unmanaged forests or without consideration of forest management. Yet, the responses of forest organisms to tree harvest might be modified or masked by masting-related changes in animal abundance.

Populations of small mammals are known for their strong reactions to masting (Jensen, 1982; Pucek et al., 1993; Choquenot and Ruscoe, 2000; Falls et al., 2007; Wang et al., 2009; Bergeron et al., 2011). Rodents in particular have generalist feeding habits and an extremely fast life history, with short generation times and large litters. Therefore, they are capable of rapid functional and numerical responses, triggered by increased food availability. In turn, changes in small mammal abundance caused by masting affect

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other organisms, such as songbirds (masting results in higher nest predation by small mammals (McShea, 2000; Clotfelter et al., 2007; Schmidt et al., 2008; Szymkowiak and Kuczyński, 2015), carnivores (masting-related increases in small mammals are associated with larger litters and higher offspring survival in many predator species: (Jędrzejewska and Jędrzejewski, 1998; Wittmer et al., 2007; Jensen et al., 2012) and even humans (high numbers of rodents caused by masting are linked to an increased risk of hantavirus infections and Lyme disease cases: Clement et al., 2009; Ostfeld, 2010). From the forestry perspective, fluctuations in small mammal abundance can affect forest functioning and regeneration because high densities of rodents help control insect pests (Hanski and Parviainen, 1985; Jones et al., 1998; Kollberg et al., 2014), but might also result in intense seed predation (Birkedal et al., 2009; Zwolak et al., 2010; Lobo, 2014).

In temperate Europe, populations of most rodent species increase after forest harvest (Bogdziewicz and Zwolak, 2014). However, even though population responses to harvest are typically positive, there is variation in the direction, shape, and magnitude of responses (e.g., Hansson, 1974; Horváth et al., 2005; Sidorovich et al., 2008; Savola et al., 2013). This variation is rarely explored and poorly understood. Moreover, almost all studies on the effects of forest harvest on European small mammals take place in the context of clearcutting (but see Ramakers et al., 2014; Sozio et al., 2014). This is a significant gap in our knowledge because alternative methods based on partial harvest are increasingly used in modern forestry (Work et al., 2003; Lindenmayer et al., 2006; Puettmann et al., 2012). One such method is called “natural regeneration with a shelterwood”, in which most trees in a stand are harvested, but some are left as seed sources. This approach is commonly used to regenerate European beech, *Fagus sylvatica*, stands in central and northern Europe (Agestam et al., 2003; Wagner et al., 2010; Övergaard, 2012).

In this study, we report effects of natural regeneration with shelterwood on rodents in beech stands after two mast and two non-mast years. We focused our investigation on the abundance and habitat selection of the two rodent species that are numerically dominant in forests of central Europe: the yellow-necked mouse, *Apodemus flavicollis*, and the bank vole, *Myodes glareolus* (Niedziałkowska et al., 2010). The pattern of habitat selection depends on scale (Morris, 1987a; Boyce, 2006; Oatway and Morris, 2007). Accordingly, we measured rodent abundance at the stand scale and microhabitat selection at the scale of individual trapping stations. We predicted that (1) forest harvest will increase vegetation cover, which in turn will have a positive effect on abundance of yellow-necked mice. This species tends to be more common in disturbed, more densely vegetated areas than in closed-canopy temperate forest (Bogdziewicz and Zwolak, 2014). We also predicted that (2) abundance of bank voles will not be affected by forest harvest. The bank vole is a generalist, reported to be similarly abundant in disturbed and undisturbed forest (Gliwicz and Głowacka, 2000; Bogdziewicz and Zwolak, 2014). Furthermore, we expected that (3) the increased abundance of yellow-necked mice in shelterwood vs. closed canopy stands will be more pronounced after non-mast (low rodent abundance) than after mast years (high rodent abundance). This prediction is based on habitat selection theory: high population densities should be associated with declines in habitat selectivity because a greater proportion of individuals settle in non-preferred, lower quality sites (Fretwell, 1972; Pulliam, 1988; Rodenhouse et al., 1997). Finally, we predicted that (4) the selection for protective cover (provided by coarse woody debris or dense vegetation) will be more pronounced after non-mast than after mast years, because foraging is less sensitive to predation risk when population density is high (Brown and Kotler, 2004).

2. Materials and methods

2.1. Study sites

We conducted research between October 2009 and September 2013 in Gorzowska Forest, situated in western Poland at an altitude of 60–80 m. The Gorzowska Forest is located in the temperate climate zone, with average annual precipitation of 523 mm and average annual temperature of 8 °C (measured for the city of Gorzów Wielkopolski, 12 km from the study sites). Common tree species include European beech, oaks, *Quercus* spp., Scots pine, *Pinus sylvestris*, and European larch, *Larix decidua*. We selected eight 0.49 ha (70 × 70 m) sites in pure beech stands: four in closed-canopy stands and four in shelterwood natural regeneration sites. Distances among sites averaged 1.6 km (SD = 0.8 km), and the two categories of sites were interspersed. In the closed-canopy stands, management actions were usually limited to light, pre-commercial thinning. In the shelterwood sites, most trees had been removed 1.5–3.5 years before the beginning of small mammal trapping, but some trees were retained as seed sources. In addition, two of the four shelterwood stands were scarified in 2009 to expose mineral soil and improve conditions for seed germination. The remaining two shelterwood sites had undisturbed soil (i.e., scarification was conducted at least 4 years prior to small mammal trapping). The area of the natural regeneration treatments ranged from 4.2 to 11.7 ha. Other details are provided in Table 1.

2.2. Small mammal trapping

We trapped small mammals from 2010 to 2013, in four-month sessions (June–September) each year. We divided sites into two sets, each consisting of two closed-canopy and two shelterwood sites (one recently scarified and one with undisturbed soil). Sites within each set were trapped simultaneously. Each monthly trapping session lasted 5 consecutive nights and 4 days, with traps checked in the morning (starting at 08:00) and in the evening (starting at 18:00). We arranged traps in 8 by 8 grids with 10 m spacing (one trap per station), and baited them with rolled oats and sunflower seeds. Total trapping effort equaled 40 960 trap-nights. We identified captured rodents to species (or, in the case of *Microtus* sp., to genus) and marked them with uniquely numbered ear-tags. Shrews (the Eurasian common shrew *Sorex araneus*, the Eurasian pygmy shrew *S. minutus*, the Eurasian water shrew *Neomys fodiens*, and the lesser white-toothed shrew *Crocidura suaveolens*) were released unmarked.

Table 1
Characteristics of the study sites.

Site category	Stand code	Stand age ^c (years)	No. of trees ^d	Basal area ^e (m ²)
Closed-canopy ^a	CC1	100	145	8.8
	CC2	85	143	17.6
	CC3	75	125	14.4
	CC4	70	143	13.7
Shelterwood ^b	ScS1	110	67	11.3
	ScS2	105	58	8.6
	S1	100	77	9.8
	S2	110	31	7.4

^a Stands before final felling, with management actions limited to precommercial thinning.

^b Even-aged seed tree stands, with soil recently scarified (sites ScS1 and ScS2) or undisturbed (S1 and S2).

^c Given for the dominating age class.

^d Within each study site (0.49 ha), quantified in 2012.

^e Total area of cross-sections of tree trunks within each study site, quantified in 2012.

2.3. Habitat sampling

We visually estimated plant ground cover (to the nearest 5%) within 1 m radius plots centered at trap stations within each site ($n = 64$ plots/site). In addition, we measured distance from the trapping station to the nearest coarse woody debris (CWD), represented at our study sites mostly by wood piles left after thinning or harvest and by tree stumps (minimal diameter = 50 cm). The sampling was conducted in July and August 2010–2013. In 2012 and 2013, we also measured the total surface (m^2) of coarse woody debris within each plot.

2.4. Beech masting

We determined beech seed availability by counting seeds on the ground (Hilton and Packham, 1997). Sampling of beech seeds consisted of collecting and counting all seeds in 0.25 m^2 squares (24 per site in 2009 and 12 per site in 2010–2012) centered on randomly selected trap stations. The sampling was conducted once per year, in late October. The sampling was limited to a subset of sites, used in companion studies (Wróbel and Zwolak, 2013; Zwolak et al. *unpublished manuscript*): four in 2009 (two shelterwood sites: S1, S2; two closed-canopy stands: CC2, CC3), and six in 2010–2012 (four shelterwood stands: CC1, CC2, ScS1, ScS2, and two closed-canopy stands: CC2 and CC3). This method reliably distinguished between mast and non-mast years (see Section 3).

2.5. Rodent abundance and population density

We used the number of different individuals captured as an index of relative rodent abundance. We did not estimate abundance with capture-mark-recapture models (e.g., White and Burnham, 1999) because small mammal abundance strongly fluctuated throughout the study and in two out of four years (see Section 3) there were too few captures to reliably use estimators, particularly for bank voles. In the case of yellow-necked mice, the index of abundance and estimates from capture-mark-recapture models were highly correlated (Pearson's $r = 0.99$: see Appendix 1 for details). Abundance indices and estimators should not be mixed within a study and the chosen method must be appropriate for the most sparse dataset (McKelvey and Pearson, 2001). Therefore, while we present estimates of abundance for the yellow-necked mouse in Appendix 1, we used an index rather than an estimate of abundance for all calculations for both studied species.

2.6. Statistical analysis

We analyzed data with generalized linear mixed models (GLMMs) implemented via the lme4 package (Bates et al., 2013) in R (R Core Team, 2013). We assessed vegetation cover using a model with percentage vegetation at a given trap station as a response variable, and site, year and their interaction as fixed factors. We also included year as a random factor because different researchers conducted vegetation sampling in different years of the study. We used this model to obtain estimates of average cover at each site while accounting for potential observer bias. We tested for differences in average vegetation cover among site categories using a likelihood ratio test and a model with site category (closed-canopy, shelterwood, recently scarified shelterwood), year, and their interaction as fixed factors. Here, we included year as a linear variable to account for successional changes in vegetation cover. Random factors included site and year.

Similarly, we used the likelihood ratio test to test for differences in the abundance of beech seeds among site categories (closed-canopy or shelterwood). Beech seed data were analyzed using a

model with year and site category as fixed factors and site as a random factor. In this case, we did not separate scarified and not scarified shelterwood sites because soil treatment was unlikely to affect seedfall. In all above-mentioned models we used Gaussian family error distributions.

Data on coarse woody debris were collected at the site level, thus there was no need to include random factors (lack of hierarchical data structure; Schielzeth and Nakagawa, 2013). We analyzed these data with a two-way ANOVA. Explanatory variables included site category and year (2012 and 2013).

The relationships among masting, forest management, and abundance of yellow-necked mice and bank voles were analyzed by comparing 10 candidate models, which represented *a priori* hypotheses on factors that influence abundances of these rodent species. The models were tested separately for yellow-necked mice and bank voles and evaluated using Akaike's Information Criterion corrected for small sample size, AICc (Burnham and Anderson, 2002). The best candidate model has a $\Delta AICc$ of zero. As a rule of thumb, models with substantial empirical support have $\Delta AICc < 2$; models with $\Delta AICc$ between 4 and 7 have considerably less support, and models with $\Delta AICc > 10$ are essentially not supported (Burnham and Anderson, 2002). Fixed effects included masting (occurrence or absence in the previous fall), stand category (closed-canopy or shelterwood), recent scarification (presence or absence of effects in 2010), and the estimated vegetation cover, in various combinations (Table 2). We did not include models with more persistent impacts of scarification because field observations suggested that the influence of this disturbance on small mammals was brief. Since the effect of month on rodent abundance was not related to any of our hypotheses, we explored models with different structures with regard to this variable (absence, additive or interactive effect of month), but present only the model that was consistently receiving the lowest AICc scores. Random effects included study site and year.

Microhabitat selection was analyzed by dividing trap stations into those with or without captures of yellow-necked mice or bank voles (two separate analyses) in August, when the microhabitat sampling took place. We used a model with binomial error terms and a logit link function. We constructed 10 candidate models, where fixed effects included different combinations of percent vegetation cover around trap stations, the presence or absence of coarse woody debris in a 2 m radius from the trapping station (we also explored other distances of response to coarse woody debris, but they did not improve the fit of the models), masting (presence or absence in the previous fall), and their two-way interactions (Table 3). Random effects included study site and year.

3. Results

3.1. Vegetation cover and coarse woody debris

Vegetation at all closed-canopy stands was sparse (Fig. 1) and consisted mostly of the wood anemone (*Anemone nemorosa*) and the common wood sorrel (*Oxalis acetosella*), with patches of small-flowered touch-me-not (*Impatiens parviflora*) and the common bracken (*Pteridium aquilinum*). Vegetation at the shelterwood stands strongly differed among sites (Fig. 1). At sites where soil was not scarified, vegetation was either relatively sparse and dominated by beech saplings (site S1) or dense and dominated by the European raspberry (*Rubus idaeus*), grasses (Poaceae) and beech saplings (site S2). Scarified sites were almost devoid of vegetation in 2010, and later either became dominated by rushes (*Juncus* sp.) and beech saplings (site ScS2) or remained open throughout the

Table 2

Model selection table, identifying the most parsimonious models of abundance of (a) yellow-necked mice and (b) bank voles.

Rank	Fixed effects	K	AICc	Δ AICc	w_i
<i>(a) The yellow-necked mouse</i>					
1	(Month \times Masting)	12	1117.8	0.0	0.72
2	+ (Masting \times Vegetation Cover)	13	1120.2	2.4	0.21
3	(Month \times Masting) + (Masting \times Vegetation Cover) + Scarification	14	1122.4	4.6	0.07
4	(Month \times Masting) + Masting + Scarification + Site Category + Vegetation Cover	11	1160.4	42.6	0.00
5	(Month \times masting) + Masting + Site Category + Scarification	12	1161.3	43.5	0.00
6	(Month \times Masting)	10	1161.6	43.8	0.00
7	(Month \times Masting) + (Masting \times Site Category) + Scarification	13	1161.6	43.8	0.00
8	(Month \times Masting) + (Site Category \times Vegetation Cover) + Scarification	14	1163.3	45.5	0.00
9	Month \times Vegetation Cover	10	1166.9	49.1	0.00
10	Month \times Site Category	10	1232.5	114.7	0.00
<i>(b) The bank vole</i>					
1	Month + (Masting \times Vegetation Cover) + Scarification	10	659.6	0.0	0.75
2	Month + (Masting \times Vegetation Cover) + Scarification + Site Category	11	661.8	2.2	0.25
3	Month + (Masting \times Site Category) + Scarification	10	676.9	17.3	0.00
4	Month + Masting + (Site Category \times Vegetation Cover) + Scarification	11	679.8	20.2	0.00
5	Month + Masting + Site Category + Scarification	9	696.3	36.7	0.00
6	Month + Masting \times Vegetation Cover	9	715.5	55.9	0.00
7	Month + Masting	7	760.2	100.6	0.00
8	Month + Masting + Vegetation Cover	8	760.5	100.9	0.00
9	Month + Vegetation Cover	7	770.2	110.6	0.00
10	Month + Site Category	7	772.3	112.7	0.00

Note: Masting is a categorical variable with two levels (mast or non-mast year); vegetation cover denotes estimated average vegetation cover at a trapping site; site category denotes stand type (closed-canopy or shelterwood); scarification represents the effect of soil scarification. The models were ranked according to Δ AICc; K denotes the number of parameters, and w_i can be interpreted as the weight of evidence in favor of model i (Burnham and Anderson, 2002).

study period, with few wood anemones and common wood sorrels (site ScS1). On average, shelterwood sites that were not scarified had $47 \pm 11\%$ (SE), scarified sites $12 \pm 11\%$ and closed canopy sites $11 \pm 8\%$ vegetation cover. The differences among site categories were significant ($\chi^2 = 7.63$, $df = 2$, $P = 0.022$). Additionally, there was a significant site category \times year interaction ($\chi^2 = 39.64$, $df = 2$, $P < 0.001$), although there was no clear directional change at most sites (Fig. 1). The amount of coarse woody debris did not differ among site categories (main effect: $F = 2.16$, $df = 2$, $P = 0.166$; interaction with year: $F = 0.34$, $df = 2$, $P = 0.720$).

3.2. Beech masting

Beech masting occurred in the fall of 2009 (average seed density = 281 seeds/m², 95% CI: 224–353 seeds/m²) and 2011 (310 seeds/m², 95% CI: 248–387 seeds/m²). In 2010 and 2012, seeds were not found on the ground or observed on tree branches. Seed availability did not differ between the two mast years ($\chi^2 = 0.14$, $df = 1$, $P = 0.710$), but was higher at the shelterwood sites than at the closed canopy stands ($\chi^2 = 5.25$, $df = 1$, $P = 0.022$; Fig. 2).

3.3. Captured rodents

In total, we captured 2 836 individual rodents. Yellow-necked mice represented 65.6% and bank voles 27.0% of all individuals. Other rodent species (7.3% of individuals captured) included striped field mouse *Apodemus agrarius*, harvest mouse *Micromys minutus*, and voles *Microtus* spp. The abundance of rodents strongly fluctuated throughout the study, with high numbers after beech mast years and low numbers after non-mast years (Table 1; Fig. 3).

3.4. Effects of habitat variables on the abundance and habitat selection of yellow-necked mice and bank voles

Mice tended to be more abundant in shelterwood than in closed-canopy stands. Average monthly abundance of mice was 22.8 individuals in natural regeneration stands and 17.5 in closed-canopy stands ($\chi^2 = 2.88$, $df = 1$, $P = 0.089$). Nevertheless, models that contained stand category were outperformed by models that contained vegetation cover (Table 2a). The best model for the yellow-necked mouse abundance contained an interaction between masting and vegetation cover and another between masting and month (Table 2a). Both masting and cover positively influenced the abundance of mice, but the effect of vegetation cover was considerably weaker after mast years (Table 4a). These findings support our first and third prediction (i.e., forest harvest affects yellow-necked mouse abundance through its effects on understory vegetation; the difference in abundance between closed canopy and shelterwood stands is greater after non-mast than mast years). Other supported models for mice (ranked second and third in Table 2a) contained additional, weak effects of scarification (estimate \pm SE: -0.017 ± 0.090) and site category

Table 3

Model selection table, identifying the most parsimonious models of the microhabitat selection of (a) yellow-necked mice and (b) bank voles.

Rank	Fixed effects	K	AICc	Δ AICc	w_i
<i>(a) The yellow-necked mouse</i>					
1	(Masting \times Vegetation Cover) + CWD	8	1815.5	0.0	0.52
2	(Masting \times Vegetation Cover) + (Vegetation Cover \times CWD)	9	1817.0	1.5	0.24
3	(Masting \times Vegetation Cover) + (Vegetation Cover \times CWD) + (Masting \times CWD)	10	1817.8	2.3	0.16
4	(Masting \times Vegetation Cover)	7	1819.3	3.8	0.00
5	Masting + Vegetation Cover + CWD	7	1835.5	20.0	0.00
6	Masting + (Vegetation Cover \times CWD)	8	1839.1	23.6	0.00
7	Masting	5	1844.8	29.3	0.00
8	(Vegetation Cover \times CWD)	7	1848.8	33.3	0.00
9	CWD	5	1851.7	36.2	0.00
10	Vegetation Cover	5	1852.5	37.0	0.00
<i>(b) The bank vole</i>					
1	(Masting \times Vegetation Cover) + (Vegetation Cover \times CWD)	9	1189.6	0.0	0.44
2	Masting + (Vegetation Cover \times CWD)	8	1190.2	0.6	0.33
3	(Masting \times Vegetation Cover) + (Vegetation Cover \times CWD) + (Masting \times CWD)	10	1191.6	2.0	0.16
4	(Masting \times Vegetation Cover) + CWD	8	1194.9	5.3	0.03
5	(Vegetation Cover \times CWD)	7	1196.5	6.9	0.00
6	Masting + Vegetation Cover + CWD	7	1196.5	6.9	0.00
7	Masting \times Vegetation Cover	7	1199.0	9.4	0.00
8	Vegetation Cover	5	1205.6	16.0	0.00
9	Masting	5	1227.1	37.5	0.00
10	CWD	5	1232.5	42.9	0.00

Note: Masting is a categorical variable with two levels (mast or non-mast year); vegetation cover denotes average vegetation cover in a 1 m radius around a trap station; CWD is the effect of presence of coarse woody debris in a 2 m radius around a trap station. The models were ranked according to Δ AICc; K denotes the number of parameters, and w_i can be interpreted as the weight of evidence in favor of model i (Burnham and Anderson, 2002).

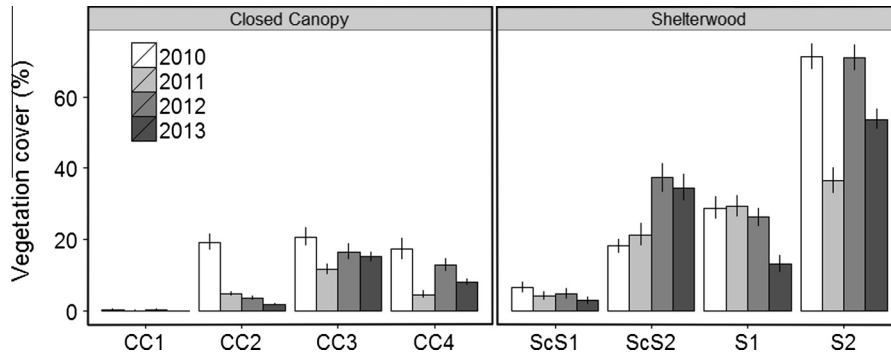


Fig. 1. Vegetation cover in successive years at closed-canopy and shelterwood sites. The shelterwood category includes sites where soil was recently scarified (ScS1 and ScS2) and sites with undisturbed soil (S1 and S2). Bars represent averages with standard errors.

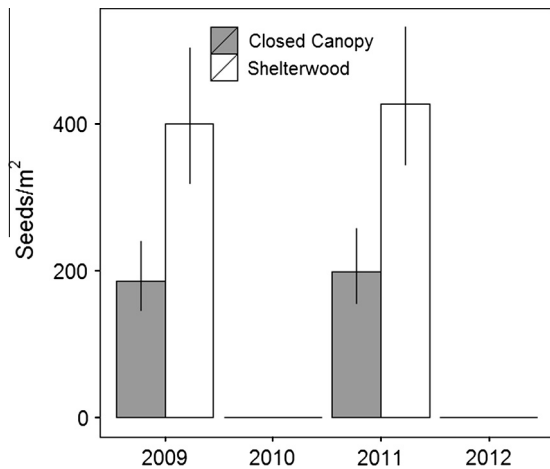


Fig. 2. Availability of beech (*Fagus sylvatica*) seeds in managed beech forest, in four closed-canopy and four shelterwood stands, measured in late October each year. No seeds were found in 2010 and 2012. Bars represent averages with standard errors.

(0.069 ± 0.116). The remaining models had virtually no support (Table 2a).

Average monthly abundance of bank voles did not differ between closed-canopy and shelterwood stands (9.1 vs. 7.5 individuals; $\chi^2 = 0.14$, $df = 1$, $P = 0.704$). For voles, the best model contained an interaction between masting and vegetation cover, a strong negative effect of scarification, and an effect of month (Table 2b). In contrast to yellow-necked mice, bank voles were less

abundant in sites with more vegetation cover, but this effect was found only after mast years (Table 4b). Bank vole abundance declined after scarification (Table 4b). The second-best model had the same structure as the first, but contained an additional, weakly positive (0.346 ± 0.832) effect of natural regeneration on vole abundance. Only these two models received substantial support. These findings are in partial agreement with our second prediction: as expected, forest harvest did not have clear effects on bank vole abundance, but scarification caused a decline.

3.5. Microhabitat selection by the yellow-necked mouse and the bank vole

All supported models for yellow-necked mice contained an interaction between masting and vegetation cover (Table 3). According to the highest ranking model, mice were more likely to choose microhabitats with dense vegetation cover (Vegetation Cover effect in Table 5a), but this effect disappeared after mast years (Vegetation Cover × Masting effect in Table 5a). This result supports prediction 4 (masting influences selection for protective cover). In addition to this effect, mouse captures were more likely to occur near coarse woody debris (CWD effect in Table 5a). Not surprisingly, captures were also more likely after mast (when mice were abundant) than non-mast years (when mice were scarce: Mast effect in Table 5a). Adding more terms (e.g. interactions masting × CWD and vegetation cover × CWD: second- and third-ranking models in Table 3) did not improve fit of the models.

In the case of the bank vole, the highest ranking model also contained the masting × vegetation cover interaction, providing fur-

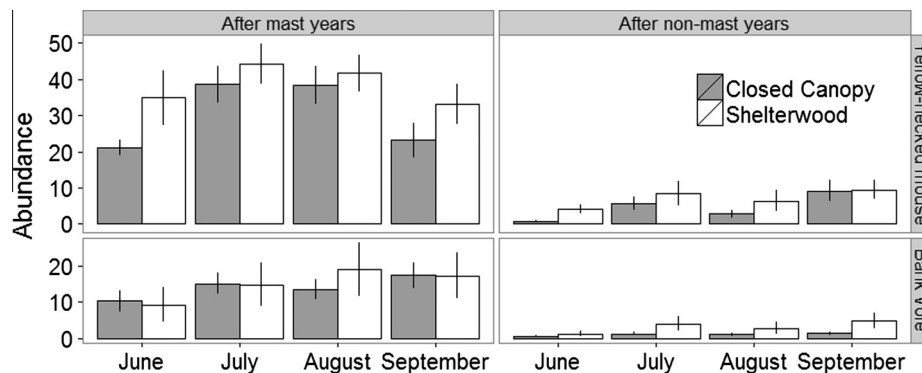


Fig. 3. Relative abundance (number of different individuals per trapping site) of yellow-necked mice and bank voles in closed-canopy and shelterwood beech stands. Bars represent averages (for four sites and two years) with standard errors.

Table 4

Influence of different variables on the abundance of (a) yellow-necked mice and (b) bank voles on the stand scale. The estimates are based on the highest-ranking candidate models ($\Delta AICc = 0$) for each studied species (see Table 2).

Variable	Regression coefficient \pm SE
<i>(a) The yellow-necked mouse</i>	
Intercept	0.359 \pm 0.186
July	1.030 \pm 0.184
August	0.601 \pm 0.197
September	1.315 \pm 0.178
Masting	2.799 \pm 0.191
Vegetation Cover	0.028 \pm 0.004
Masting \times Vegetation Cover	-0.021 \pm 0.003
Masting \times July	-0.638 \pm 0.194
Masting \times August	-0.243 \pm 0.206
Masting \times September	-1.310 \pm 0.190
<i>(b) The bank vole</i>	
Intercept	-0.579 \pm 0.464
July	0.499 \pm 0.098
August	0.527 \pm 0.097
September	0.651 \pm 0.095
Masting	2.974 \pm 0.204
Vegetation Cover	0.008 \pm 0.010
Masting \times Vegetation Cover	-0.025 \pm 0.005
Scarification	-2.282 \pm 0.307

Note: July, August and September represent change in abundance in relation to June. In the case of the yellow-necked mouse, the month effect differs between non-mast years (main effect) and mast years (interaction with masting). Masting denotes change in abundance in mast vs. non-mast years. Vegetation cover denotes change in abundance per one percent increase in vegetation cover in non-mast (main effect) and mast years (in interaction with masting). Scarification denotes change in abundance after soil scarification. The coefficients represent changes in abundance expressed on a log scale.

ther support for prediction (4). Bank voles were more likely to be captured in microhabitats with dense vegetation, although this effect was considerably weaker (yet still present) after mast years (Vegetation Cover and Vegetation Cover \times Masting effects in Table 5b). The best model also contained a negative interaction between vegetation cover and coarse woody debris: the presence of CWD increased the probability of capture, but this influence weakened when dense vegetation was present (CWD and CWD \times Vegetation Cover effects in Table 5b). The second-ranking model contained only the main effect of masting and the vegetation cover \times CWD interaction. This model was almost as well supported as the top model (Table 3).

Table 5

Factors influencing microhabitat selection of (a) yellow-necked mice and (b) bank voles. The estimates are based on the highest-ranking candidate models ($\Delta AICc = 0$) for each studied species (see Table 3).

Variable	Regression coefficient \pm SE
<i>(a) The yellow-necked mouse</i>	
Intercept	-4.873 \pm 0.651
Masting	3.762 \pm 0.380
Vegetation Cover	0.026 \pm 0.004
CWD	0.366 \pm 0.145
Masting \times Vegetation Cover	-0.025 \pm 0.005
<i>(b) The bank vole</i>	
Intercept	-4.969 \pm 0.620
Masting	2.567 \pm 0.449
Vegetation Cover	0.034 \pm 0.006
CWD	0.857 \pm 0.232
Masting \times Vegetation Cover	-0.012 \pm 0.006
Vegetation Cover \times CWD	0.014 \pm 0.005

Note: The coefficients represent changes in odds of capture probability (per trapping station) expressed on a log scale. Masting denotes change in capture probability in mast vs. non-mast years. Vegetation cover denotes change in capture probability per one percent increase in plant cover within 1 m radius from a trapping station. CWD denotes the presence of coarse woody debris in a 2 m radius from the trapping station.

4. Discussion

4.1. Effects of habitat variables on the abundance and habitat selection of yellow-necked mice and bank voles

In accordance with our predictions, the effects of stand management on yellow-necked mice were mediated by the positive influence of understory vegetation on mouse abundance. Dense vegetation helps rodents avoid predators and is often associated with abundant food resources (Schmidt et al., 2005; Kearney et al., 2007; Rosalino et al., 2011). However, while forb and grass cover tended to increase after forest harvest, this response varied among shelterwood stands. Consequently, vegetation cover was a better predictor of rodent abundance than stand category. Thus, effects of tree harvest on rodents in beech forest are likely to be idiosyncratic because development of understory is influenced by multiple factors, some of which depend on harvest type (e.g., tree retention level or severity of forest floor disturbance), but others that do not (e.g., soil water level or edaphic conditions; Roberts and Zhu, 2002; Frey et al., 2003; Macdonald and Fenniak, 2007; Craig and Macdonald, 2009).

Bank vole abundance did not differ between closed-canopy and shelterwood stands, and was not influenced by vegetation cover, at least at low population levels (see below). This lack of apparent effect is related to the diversity of harvest impacts on understory vegetation. For example, bank voles were very abundant at a natural regeneration stand that was colonized by raspberries (site S2), but relatively rare at another natural regeneration stand where vegetation was also dense, but consisted mostly of sedges (site ScS2) or beech saplings (site S1; Fig. 1; Table 1). Soil scarification, on the other hand, had a strong, negative influence on the abundance of bank voles, even after controlling for the effects of changes in vegetation cover (destroyed during the operation). Thus, this species appears to be more sensitive to litter and soil disturbance than is the yellow-necked mouse.

Patterns of microhabitat selection of both mice and voles indicated that dense vegetation and coarse woody debris are important for rodents in managed beech forests. Stronger association of bank voles with vegetation at fine than at stand level emphasizes scale-dependency of habitat relationships, a result consistent with previous studies of small mammals (Johnson, 1980; Morris, 1987a; Oatway and Morris, 2007; Wilson and Puettmann, 2007; Fauteux et al., 2012). Coarse woody debris is used by small mammals for nesting, as protective cover, foraging sites, and travel routes (Planz and Kirkland, 1992; McCay, 2000; Manning and Edge, 2004; Vanderwel et al., 2010; Fauteux et al., 2012). CWD was rare in managed beech forest and came mostly in the form of piles of slash left after harvest and stumps remaining in spots where trees were cut. We frequently observed that yellow-necked mice and bank voles fleeing from us, used them as hiding places in otherwise very open beech forests. In the case of bank voles, the positive effect of coarse woody debris was particularly pronounced when vegetation cover was low, reflecting the preference of bank voles for structurally complex microhabitats (Panzacchi et al., 2010).

4.2. Masting-related changes in habitat selection

Masting dramatically altered abundance of rodents in the managed beech forest and through changes in density affected their habitat use. After mast years, when rodent abundance was high, yellow-necked mice and bank voles used habitats more evenly both at coarse and fine scales (trapping grid and trapping station, respectively), as evidenced by their weaker associations with vegetative cover and, in the case of bank voles, coarse woody debris. This finding supports our predictions and emphasizes the need to

account for density-dependent habitat selection when evaluating the effects of forest management on animals (see also Hodson et al., 2010).

Decline in habitat selectiveness with an increase in population density is typically caused by dispersal of animals to habitats that have not yet been used (Fretwell and Calver, 1969; Rosenzweig, 1991; Rodenhouse et al., 1997; Morris, 2003). In our study, high rodent abundance was associated with increased use of stands and microhabitats with sparse vegetation cover. Such sites are probably more risky. The diminished selectiveness could be caused by increased competition for protective cover: when abundance in preferred habitats increases, aggressive interactions with other foragers are more frequent, per capita food availability declines, and individuals are more willing to forage in risky sites (Brown and Kotler, 2004). In addition, high population densities might dilute per capita predation pressure, making foraging in open habitats safer (China et al., 2008; Hodson et al., 2010).

Changes in resource availability also influence habitat selection (McLoughlin et al., 2010). Over the course of this study, beech seed abundance strongly fluctuated. In addition, seed availability was higher in shelterwood than in closed-canopy stands, probably because of higher production of seeds by trees that were older, had fewer competitors and better light conditions (Topoliantz and Ponge, 2000). However, we conducted rodent sampling either before resources were present in mast years (trapping in June–September, whereas seedfall started in October) or when resources were depleted in non-mast years. Therefore, differences in seed availability were unlikely to affect habitat selection at the time of trapping.

After mast years, when overall rodent densities were high, bank vole abundance was lower in densely vegetated stands than in stands with sparser vegetation cover. This pattern was unexpected, given habitat associations of bank voles known from previous research (Fitzgibbon, 1997; Buesching et al., 2011) and their preference for densely vegetated microsites documented in this study (Results: “Microhabitat selection”). Their apparent preference for sparsely vegetated areas may be explained by competition from the yellow-necked mouse. In this case, interference (direct) competition is more likely than exploitative (indirect) competition. Trophic niches of yellow-necked mice and bank voles overlap only during mast years, when food is unlikely to be a limiting factor (Selva et al., 2012). We found the negative response of bank voles to vegetation cover after mast years, when food resources were already depleted, but rodent abundances were still high. Thus, the shift by bank voles was likely caused by competition for dense, presumably safe, habitats. Body size is an important factor that often determines the outcome of direct competition, with larger species usually dominant over smaller species (Rychlik and Zwolak, 2006; Pasch et al., 2013). Bank voles are smaller than yellow-necked mice; in this study, body mass of the former was on average 17.6 g (SD = 4.3), and of the latter 25.3 g (SD = 8.5). Accordingly, previous studies suggested that *Apodemus* mice dominate bank voles in interspecific encounters (Gipps, 1985; Fasola and Canova, 2000; Grum and Bujalska, 2000), which could explain the observed patterns of habitat selection: when yellow-necked mice reached high abundance, they displaced bank voles from preferred, heavily vegetated sites. The putative influence of yellow-necked mice on bank vole habitat selection emphasizes the notion that species do not choose habitats in isolation, but via interactions with other species (Rosenzweig, 1991). However, while patterns of density-dependent habitat selection are a prerequisite to inferences on interspecific competition (Rosenzweig, 1991), conclusive evaluation of the interactions between *A. flavicollis* and *M. glareolus* requires experimental data or a different approach to assessing competition for habitat (e.g., isodars: Morris, 1987b, 2003).

4.3. Management implications

Our results suggest possible management actions to reduce abundance of yellow-necked mice and bank voles in beech forest, including reduction of vegetation cover (particularly raspberries: Schreiner et al., 2000) in shelterwood stands, removal of woody debris left after harvest (see also Sullivan et al., 2012), and soil scarification. However, it is debatable whether lowering abundance of small mammals would increase success of natural regeneration. While foresters tend to focus on the negative role of small mammals as seed and seedling predators, ecologists pay growing attention to their role in dispersing seeds to favorable microsites (Briggs et al., 2009; Hirsch et al., 2012). In particular, yellow-necked mice not only consume beech seeds (Nielsen, 1977; Nilsson, 1985; Nilsson and Wästljung, 1987; Nopp-Mayr et al., 2012), but also bury some of them in topsoil (so-called “scatterhoarding”), which greatly increases their germination rates (Jensen, 1985; Zwolak et al. unpublished manuscript). Thus, they serve as conditional mutualists of trees, capable both of increasing and decreasing the trees’ reproductive success (Jorge and Howe, 2009; Klinger and Rejmánek, 2010; Zwolak and Crone, 2012). One of the generalities that emerges from recent research is that the role of rodents in plant regeneration is driven by changes in the seed:scatterhoarder ratio (Theimer, 2005; Zwolak et al. unpublished manuscript). Therefore, extremely high rodent abundances could reduce plant recruitment through increased seed consumption and reduced caching. In addition, when rodents are more abundant, they use microhabitats more evenly, which probably translates into fewer safe sites for seeds. However, the masting-related increase in rodent abundance occurs with a delay, and by the time the highest densities of rodents are reached, most seeds have already produced seedlings (at our study sites, beech seedlings emerge in April and May: Zwolak, unpublished data).

The role of small mammals might also depend on the type of soil preparation undertaken before or after seedfall (Övergaard, 2012). When natural regeneration is conducted without soil preparation, seed burial by scatterhoarders will likely increase seedling recruitment. In contrast, when soil is scarified before seedfall, seeds are already in contact with soil, burial by vertebrates is unlikely to further improve regeneration (Zwolak and Crone, 2012), and many seeds will be consumed (Madsen and Löf, 2005; Birkedal et al., 2009; Jinks et al., 2012). When soil is disturbed after seedfall to bury seeds, rodents are unlikely to affect regeneration (as predators or dispersers) because the amount of seeds buried mechanically is sufficient to ensure regeneration.

5. Conclusions

Habitat selection is a crucial process to address when managing wildlife. Our study shows that mast seeding causes changes in rodent abundance that then alter the frequency of the rodents’ habitat use. This pattern is most likely widespread in ecosystems dominated by masting species (e.g., With and Morrison, 1990; Schnurr et al., 2004). Thus, confounding effects of mast-related changes in consumer abundance or seed availability should be taken into account when investigating wildlife habitat selection. More generally, snapshot patterns of species abundance in different habitats might be misleading because habitat selection is a dynamic process. For example, limiting our investigation to years with only high or only low rodent abundance would result in considerably different estimates of the strength of habitat associations. Thus, capturing the dynamics of habitat selection requires several years of data (Boyce et al., 2002; Mønbæk et al., 2009; McLoughlin et al., 2010; van Beest et al., 2014) or using spatial variation in abundance to assess density-dependence (Morris, 2003).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.10.017>.

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