



Beech masting modifies the response of rodents to forest management



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ARTICLE INFO

Article history:

Received 7 July 2015

Received in revised form 5 October 2015

Accepted 9 October 2015

Available online 22 October 2015

Keywords:

Density-dependent habitat selection

Forest harvest

Poland

Pulsed resources

Rodents

Small mammals

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.

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