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Differential demographic responses of sympatric *Parids* to vegetation management in boreal forest

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ABSTRACT

Large-scale removal of small-diameter trees (i.e. thinning from below) in boreal forest can diminish niche diversity for birds that rely on a well-developed understory for nesting and foraging. Yet, few studies have examined how reduced niche diversity in managed forests affects fitness measures in closely-related species and the ability of competing species to co-exist. We related forest thinning to population trends of the willow tit *Poecile montana* (declining) and its dominant competitor the crested tit *Lophophanes cristatus* (stable), and conducted a 3-year comparative study to determine how variation in understory spruce density differentially influences survival and reproduction in these species. In line with our prediction that crested tits would gain resource priority under conditions of reduced forest understory complexity, willow tits and their nestlings suffered a disproportionate decline in both nest and adult survival prospects relative to crested tits as understory spruce density declined. Willow tits also had increased numbers of tail feather fault bars with decreasing understory complexity, further supporting the idea that willow tits suffer from food shortage and increased predation risk in areas of reduced understory. The long-term population declines of willow tits in boreal forest appears linked to large scale harvest of small-diameter spruce trees that provide important understory vegetation. A patchy arrangement of different thinning treatments through 'Understory Retention Thinning' (URT) may provide a cost-effective way to restore long-term structural complexity and biodiversity in densely stocked conifer stands.

1. Introduction

Human-induced structural changes of boreal forests at multiple spatial scales are widely regarded as a major threat to biodiversity (Helle and Järvinen, 1986; Andrén, 1994). Empirical evidence suggests that most bird population responses to these changes can be attributed to habitat loss rather than true fragmentation effects (Schmiegelow and Mönkkönen, 2002). However, few studies have examined how vegetation management in tracts of continuous forest influence fitness correlates of forest interior species (Powell et al., 2000), and the ability of closely related species to coexist. This is important because intermediate harvest of small-diameter trees (i.e. thinning from below) is a major component of sustained yield silviculture of boreal forest in Scandinavia, Russia and North America (Thompson, 2003), with the potential to diminish niche diversity at the global scale. Thus, understanding how wildlife responds to changes in stand structure is essential to reconcile the management of multiple-use boreal forests that are expected to sustain wood production and biodiversity (Costanza et al., 1997).

The effects on wildlife of forest thinning depend strongly on species life history and habitat requirements (Kalies et al., 2010). For instance, thinning of dense, closed-canopy forests from above (i.e. harvesting the largest trees) may facilitate understory biomass and tree-crown growth, thereby providing habitat for ground and shrub foraging birds (Yuan et al., 2005), small mammals (Zwolak, 2009) and insects (Niemelä et al., 2007). Yet many tree-foraging birds respond negatively to extensive overstory removal (Kalies et al., 2010). In Scandinavia, the Baltic States and Russia, however, most thinning is done from below and removes smaller than average merchantable trees (Loman, 2005). Additionally, understory trees are often routinely cleaned away to enhance expedient handling of harvested trees. This dual practice results in a single canopy layer in the overstory and a sparse understory with little woody debris. Hence, a reduction in understory foliage may have greatest impact on habitat specialists (Norris and Harper, 2004) and less-competitive species (Wiens, 1989) that rely on the lower strata of the forest for foraging, nesting and predator avoidance (Eggers et al., 2006; Griesser et al., 2007; Chisholm and Leonard, 2008). This may be particularly problematic for behaviourally

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subordinate individuals or species that are forced into increasingly vulnerable sites by stronger competitors (Nilsson, 1984; Alatalo et al., 1986; Krams, 1996).

In this study, we use a comparative approach to test this 'habitat complexity hypothesis' for two forest dwelling species, the willow tit *Poecile montanus* and its more dominant competitor the crested tit *Lophophanes cristatus* in managed Swedish boreal forests (Ekman, 1989; Krams, 1996). Willow tits in southern Sweden and Finland have declined by more than 60% during the last 40 years, while the population size of crested tits has remained relatively stable (Väisänen, 2003; Lindström et al., 2009), despite sympatric occurrence in the region and an exceptional ecological and morphological match between the species (Glutz von Blotzhein and Bauer, 1993). However, the mechanism of large-scale willow tit declines in boreal forest is unclear. We predict that subordinate willow tits show a disproportionately steeper decline in nest and adult survival prospects relative to crested tits, as the understory structure of mixed coniferous forest simplifies. This expectation comes from these species being resident cavity-nesting birds for which understory spruce vegetation and dead wood provide safe foraging and nesting substrate (Ekman, 1987; Lathi et al., 1998) while pine trees provide more food supplies and seem to be the preferred option for foraging (Ekman, 1987). A reduction of safe sites from forest thinning should increase resource competition (i.e. food and nest site shortage) and force willow tits into more vulnerable sites (i.e. increased predation risk; Alatalo et al., 1987). Willow tits are therefore expected to develop more fault (or stress) bars in tail feathers (Møller et al., 2009), be less likely to find a mate (Bortolotti et al., 2002), and suffer from reduced survival and breeding success (Jansson et al., 1981) than crested tits under these stressful conditions. However, it is also possible that the development of fault bars precedes settlement, reduces the ability to compete for preferred habitat and thus are a cause rather than (or as well as) a consequence of habitat quality.

Because the effects of vegetation management on anticipated niche shifts are rarely translated into population responses, we also tested if relationships between understory complexity and demography at the local scale were consistent with national population trends for the two species relative to long-term changes in forest area subject to commercial thinning.

2. Methods

2.1. Study species

Willow and crested tits co-exist throughout most of their southern range in Fennoscandia (Glutz von Blotzhein and Bauer, 1993). They spend a large part of the non-breeding season together in small sedentary groups with complex dominance hierarchies (Ekman, 1989) that influence individual fitness through rank-related access to safe foraging opportunities. They inhabit mixed conifer forest within a ∼25 ha winter territory (Ekman, 1979), use food storage for winter survival and feed on seeds and arthropods (Jansson et al., 1981). Crested tits are dominant over willow tits (Ekman, 1979) and have priority access to cover from avian predators (Suhonen et al., 1993). Both species establish breeding territories of approximately 2–3 ha within their overlapping winter territories and use nest sites in dead woody debris, where they excavate nest-holes.

2.2. Study area and design

The fieldwork was carried out in managed mixed-coniferous forest at five study sites in southern Uppsala county, central Sweden (3500 km^2 centred at N59.73260°, E17.58680°) between January 2003 and June 2005 (Fig. S1). We selected sites (1–2 km^2 each with 5–25 km between sites; ∼600 ha in total) in late thinning stages of mixed stands (age 60–80 years) of Scots pine *Pinus silvestris* (47% of total volume), Norway spruce *Picea abies* (42%) and birch *Betula* sp. (9%). Approximately 20% (range 10–40%) of the total forest area within each study site is less-intensively managed or has remained unmanaged for the last 10–30 years (i.e. nature reserve). This allowed us to test our 'habitat complexity hypotheses' along a gradient from unmanaged sites with a complex vertical vegetation structure, to more simplified, even-aged stands with little or no understory (Fig. S2). Thinning management of most areas is carried out at 10–25 years intervals, 20–40% of the basal area being removed on each occasion (Skogsstyrelsen, 2010). This commercial thinning removes predominantly smaller spruce trees of merchantable size and reduces between-tree competition among the remaining large-diameter trees, which are harvested at ∼80 years old. Pine is typically restricted to the overstory while shade-tolerant spruce grows in the overstory and understory. Small understory trees, shrubs and woody debris are typically cleaned away to enhance handling of harvested trees (Fig. S2). The two study species established nesting sites within overlapping home ranges and were thus monitored at the same sites. This comparative design controlled for the effects of environmental differences between study sites and home ranges that could potentially confound the impact of stand structure on bird demography and numbers.

2.3. Capture and feather evaluation

Between January and March, birds from mixed-species flocks in 27 winter territories were mist netted and banded with metal rings and unique combinations of colour bands. Trapping efforts were constant within each winter home range (twice a month) on each visit (3 h) and between years; because birds were in mixed flocks, trapping effort for the two species remained constant across years and between sites. The 9 m mist net was within understory vegetation and near a feeder with sunflower seeds. At the time of capture, individuals were aged according to Svensson (1992). Rectrices of 114 individuals were inspected for fault bars (crested tit: 33 adults, 21 juveniles; willow tit: 43 adults, 17 juveniles); these narrow, translucent bands across the feather are produced under stressful conditions (e.g. resource shortages) during feather formation and are clearly visible (Witter and Lee, 1995; Bortolotti et al., 2002; Møller et al., 2009). We used the total number of fault bars per bird for analysis. Because tail feathers were primarily grown in the nestling phase (juveniles prior to natal dispersal) and in summer (adults), fault bars were not primarily caused by (local) winter conditions but were indicative of intrinsic individual quality coupled with conditions, especially nutritional stress, during feather growth (Møller et al., 2009). Mark-recapture allowed estimation of apparent survival relative to species, age, forest structure and fault bars. To obtain estimates on winter territory size (maximum polygon) we followed mixed-species flocks twice a month for approximately 1 h at each occasion.

2.4. Nest observations

We found nest-holes by following pairs every third day, for 1 h at each occasion throughout the breeding season or until the nest was found, and monitored the progress of 57 first-brood nests (crested tit = 33; willow tit = 24) by visiting territories every third day from April to the end of June each year. The status of nests (success/failure) was determined from a 50 m distance to minimize disturbance. If no parental nest visits were observed within 30 min, the nest was examined. Nest success was defined by the