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Population patterns in relation to food and nesting resource for two cavity-nesting bee species in young boreal forest stands

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ABSTRACT

Wild bees have separate food and nest sites, two essential resources that potentially could limit bee populations. Many solitary bee species nest in holes in deadwood. Female bees collect pollen and nectar, which is stored in the nests as a food supply for their offspring. It is not well understood how availability of either resource affects bee species with different life histories. This study aimed to demonstrate the relative importance of food and nesting resources on population size of two cavity-nesting wild bee species that differ in their requirements regarding food- and nesting resource. Standardized trap nests consisting of wooden poles with pre-drilled holes were deployed in 15 young boreal forest stands to monitor bee abundance. At each site the food resource (flowering plants) and nesting resource (holes in deadwood) for hole-nesting solitary bees were surveyed in the nearby surroundings. The food resource was differentiated into flowers occurring in young forest stands and flowers occurring along forest roadsides. Generalized and general linear models were used to predict nest abundance in the trap nests of two bee species. A total of 166 nests of a pollen-specialist species, *Megachile lapponica*, and 38 nests of a pollen-generalist species, *Hylaeus annulatus* were found in the traps. The nest abundance of *M. lapponica* across the sites was predicted only by this species' specific food resource, fireweed, *Chamerion angustifolium*, whereas the nest abundance of *H. annulatus* was predicted by both food and nesting resources. In a simple linear regression, the density of suitable nesting holes for *H. annulatus* explained 38% of the variation in the number of nests. Corresponding values for the food resource density along sun exposed gravel roadsides and in young forest stands were 63% and 41% respectively. In a multiple regression, the three variables – nesting resource density, food resource density in young forest stands and food resource density along sun exposed roadsides – explained 86% of the variation in abundance of *H. annulatus* nests. Nesting and food resource densities for *H. annulatus* were not correlated with each other. Our results imply that creation and retention of standing dead wood are conservation measures that favor *H. annulatus* since the availability of nest holes in standing dead wood limited population sizes. To locate the high stumps near sun-exposed forest roads with a dense flora should increase the efficiency of this measure since *H. annulatus* was particularly favored by flower rich roadsides.

1. Introduction

For long-term species conservation to be successful, it is necessary that critical resources are available in sufficient amounts to sustain viable populations. For many organisms, critical resources are spatially separated, and it is essential that all of them are available within their activity range (Bailey et al., 2014; Catry et al., 2013; Kovács-Hostyánszki et al., 2013). Wild bees have separate food and nest sites, two essential resources that must be present within their relatively small activity range (Zurbuchen et al., 2010). In many parts of Europe, there is strong evidence that many populations of wild bees are declining (Biesmeijer et al., 2006; Patiny et al., 2009). In Sweden about one third of the solitary wild bee species are red-listed (The Swedish Species Information Center, 2015). To ensure effectiveness of conservation measures, it is crucial to identify which resource that is most critical, and thus likely to limit the population size (Perrins et al., 1991; Westrich, 1996). Although many studies emphasize the importance of feeding resource there is still little evidence that nesting resources limit wild bee populations (Roulston & Goodell, 2011; Winfree, 2010).

The food resource for bees consist of nectar and pollen (flowers). There are many levels of specialization concerning pollen collection among bees (so called oligolectic species), ranging from bee species

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collecting pollen from several non-related plants to bee species collecting pollen from one plant family, genus and even one single plant species (Radenchenko & Pesenko, 1994; Westrich, 1990). The nest resource for bees differ among species, commonly divided into; ground-nesting bees and cavity-nesting bees, where the latter breed in cavities above ground. Nest specialization is not a well-established concept like food specialization (oligolecty). Still, bees can be very demanding when choosing nest site, i.e. they have specific requirements on the ground or cavity used for breeding (Cane, 1991; Gathmann et al., 1994; Polidori et al., 2010; Potts & Willmer, 1997; Sardiñas & Kremen, 2014; Westerfelt et al., 2015).

High abundance and high species richness of flowers have both been shown to favor abundance or species richness of bees (Holzschuh et al., 2007; Rubene et al., 2015), but this should apply only to bees limited by food resource. There are other studies which do not show any effect of flower availability on bee abundance or species richness (Fabian et al., 2013; Hopfenmüller et al., 2014; Steffan-Dewenter & Leschke, 2003). Apparently, there are other factors than flower availability that could limit wild bees. There are calls for more studies on how availability of natural nesting resources affects solitary bee populations (Bogusch & Horák, 2018; Senapathi et al., 2017; Winfree, 2010), since this resource is also essential for bee existence. As pointed out by Roulston and Goodell (2011), although nest site limitation of bee populations should be plausible, there is little evidence in the literature that supports this. One study found positive relationships between the abundance of ground-nesting bee species and bare ground (i.e. nesting resource) (Potts et al., 2005), but bare ground was also positively associated with fire disturbance, which has been shown to correlate with floral resources for pollinators as well (Campbell et al., 2007; Moretti et al., 2009).

To our knowledge, no study has quantified both food- and nesting resource for any species and tested which of these resources that mostly limits population size. The most limiting resource probably varies depending on bee species and type of landscape. Still, a reasonable pattern should be that the population size of a food specialist will largely be limited by the size of the food resource whereas the population size of a nest specialist will be largely limited by the size of the nesting resource.

In the present study, we sampled two solitary bee species and their food- and nesting resources and tested which resource that best explained population size. The bee species; *Megachile lapponica* and *Hylaeus annulatus*, are cavity-nesting and breed their offspring in holes in dead wood in young forest stands. These two species differ in their requirements concerning food- and nesting resource. *Megachile lapponica* is a food resource specialist, collecting pollen from one plant species; fireweed *Chamerion angustifolium* (Westrich, 1990). *Hylaeus annulatus* is a pollen generalist (Holmström, 2017). In a previous study (Westerfelt et al., 2015) it was found that *H. annulatus* was specific in its nest choice. All the nests were found in proper sized holes situated in standing dead wood objects being more than 1 m high, a dead wood feature which exist mainly as a result of retention, i.e. conservation within forestry. *M. lapponica* was a nest-generalist, nesting in proper sized holes situated in all types of dead wood, including stumps which occur in dense numbers in recently cut forests, often more than 500 per hectare. The food resource was differentiated into flowers occurring in young forest stands and flowers occurring along forest roadsides, because it was apparent during the field work that forest road sides had a rich flora that differed in species composition compared to young forests. Forest roads are a common feature in Swedish forests, having a total length over 200.000 km (The Swedish Forest Agency, 2007), and could therefore offer a dense resource for foraging bees in forest landscapes. However, empirical evidence that forest road sides have positive impact on bee populations is lacking.

The overall aim of the present study is to clarify how population size of each of the two bee species is affected by resource density for foraging and nesting. More precisely, we predicted that the abundance of the pollen generalist with high nesting site requirements will be affected mainly by nesting resource density whereas the abundance of the pollen specialist will be affected mainly by food resource density. We also explore the relative importance of flowers along forest roadsides and flowers in young forest stands for each species.

2. Methods

2.1. Study system

Female nest-provisioning solitary bees collect pollen and nectar to store as food for their offspring. A nest typically consists of one or several cells where each cell contains one egg and a food supply for the larva. If there are several cells in one nest, they are separated by cell walls built by the female. Many species construct their cells in holes or cavities above ground, often in dead wood. These holes or cavities are made by various wood-boring insect species, most often beetles, and should have proper characteristics to be approved as breeding chamber by the egg-laying female (Westerfelt et al., 2015). After having completed egg-laying and food collecting, the female seals the opening with a plug made from some material which varies among aculeate genera, some plug materials are genus specific and some material are shared between several genera (Lomholdt, 1975; O'Neill, 2001). Since the plugs differs among aculeate genera, it is possible to know which genus/genera that inhabit the hole without further inspection of the nest interior, but solely by examination of the plug. The two species in the present study differ both in plug type and preferred diameter of the hole. *M. lapponica* prefers relatively large holes (7–10 mm) and the plugs are made of wood fibers mixed with soil (Westerfelt et al., 2015). *H annulatus* prefers smaller holes (3–5 mm) and the plug consists of a cellophane-like membrane (Westerfelt et al., 2015). Forage- and nesting sites for bees in the boreal forest landscape are found in open and sun-exposed areas. This is because closed forests have too shady conditions (Westerfelt, 2015) and poor flower availability (Korpela et al., 2015; Romey et al., 2007).

2.2. Study area

The study took place during the summer of 2011 in a 300 km^2 area of forest landscape near the village Nyhammar, situated in southern part of the province of Dalarna in the southern boreal zone (60°N, 14°E) of Sweden. It is a typical managed forest landscape in the boreal coniferous forest belt with a low proportion of agricultural land and rural settlements. The dominant tree species in the mature forest are Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, but in young forest stands, deciduous species, mainly birch *Betula* spp., are common. Young forest stands (< 15 years old) constitute about 20% of the forest area in the landscape. The forest region was environmentally certified (FSC – Forest Stewardship Council) in 1998 and had therefore relative high levels of dead wood for a managed forest landscape. FSC-certification require that all dead trees are left and at least three high stumps per hectare are created during final felling (FSC-Sweden, 2014). The studied forest landscape had a distributed network of permanent forest roads. Forest roads are a common feature in Swedish forests, having a total length over 200.000 km (The Swedish Forest Agency, 2007). They have been constructed to transport machines, timber and seedlings in a cost-efficient way.

Using stand databases provided by a forest company, 15 young forest stands were selected as study sites. The sites fulfilled the following criteria: (1) > 4 years old and < 15 years old; (2) not pre-commercially thinned; (3) about half of the stands should have been replanted with Norway spruce, and half with Scots pine; (4) at least 500 m apart, separated largely by older forest stands; (5) of intermediate fertility (increment 4.3–6.6 m^3 ha^{-1} a^{-1}). The selection resulted in stands ranging in age from 4 to 13 years since clear-cutting, all having a forest road running through or along one edge of the stand.