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Niche partitioning based on nest site selection in the small carpenter bees *Ceratina mikmaqi* and *C. calcarata*

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Nest site selection can have important fitness consequences for bees: nest location and substrate influence conditions experienced by developing broods, and competition for nesting substrate influences the structure of bee communities. One approach to investigate how bees respond to limitations in nesting resources is to compare patterns of resource usage in the field to the outcome of choice experiments. If different species show overlapping resource preferences but nonoverlapping resource use, this suggests that interspecific competition results in resource partitioning. We investigated nest site selection and its fitness consequences in two closely related dwarf carpenter bee species (*Ceratina mikmaqi* and *C. calcarata*) in southern Ontario. *Ceratina* nests were found in the exposed pith of common teasel, *Dipsacus fullonum*, which grows in full sun, and in wild raspberry, *Rubus strigosus*, and staghorn sumac, *Rhus typhina*, which grow in shade. When experimentally given the opportunity to choose among equal numbers of nests in any combination of substrate (raspberry, teasel, sumac) and site (sunny, shady), both species preferred to nest in raspberry twigs in sunny sites. Collections from naturally occurring nests showed that *C. calcarata* nests occur primarily in the preferred substrate (raspberry), while *C. mikmaqi* nests occur in the preferred site (sun). Thus, competition for nesting substrate is partially offset by spatially partitioning nesting resources. *Ceratina calcarata* nesting in sunny microclimates produced larger and more offspring, and experienced less parasitism, whereas *C. mikmaqi* showed no effect of microclimate. Overall, this suggests that *C. mikmaqi* is the superior competitor for nesting substrate.

Gause's (1934) competitive exclusion principle states that ecologically similar, sympatric species come to occupy slightly different niches as a consequence of competition for resources. Species that occupy similar niches may reduce interspecific competition by partitioning resources in space or time. For example, two species of spittlebug occupy different areas of the same plant (McEvoy 1986) and two sympatric sweat bees forage on the same flowers, but at different times of the day (Plateaux-Quenu 1992). Interspecific competition may also be reduced by character displacement, in which morphological differences among species are associated with resource partitioning. The most famous example is beak size and shape differentiation in Darwin's finches (Grant 1986).

Among bee communities, most research on interspecific competition has focused on floral resources (Inouye 1978; Johnson 1986; Graham & Jones 1996; Steffan-Dewenter & Tscharntke 2000; Dupont et al. 2004), however, recent evidence suggests that nest sites also play an important role in structuring bee communities (Potts et al. 2003, 2005). Nest site selection can have important fitness consequences for individual bees. Bees are central place foragers, commuting from their nest sites to gather floral resources within flight distance (Cresswell et al. 2000), so location of nest sites may influence how food resources are accessed (Peterson & Roitberg 2006a, b; Zurbuchen et al. 2010). Nest location and substrate also influence conditions such as temperature and humidity experienced by individuals inside nests. Broods in nests that get overly warm or that are in arid landscapes may be prone to desiccation or heat shock (Hranitz & Barthell 2003; Hranitz et al. 2009), while broods in nests located in cold, moist areas may have slower developmental rates and may also be more prone to mould. Nest site selection can also influence the structure of bee communities, because the availability of appropriate nesting substrate can limit bee populations (Cane & Tepedino 2001; Cane et al. 2006).

Whether there is significant competition for nesting substrate or for nests is difficult to document. Aggressive interactions among nest-founding females are one possible indication of competition

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for scarce nesting resources, but might also be a strategy by which some females avoid the costs of nest construction, even when a surplus of apparently suitable substrate is available (McIntosh 1996). A pattern of differential usage of nesting resources under natural conditions suggests resource partitioning in response to competition, but could also result if currently sympatric species evolved different resource preferences in allopatry. One approach to investigate whether resources are partitioned is to compare species' resource preferences as expressed in choice experiments to their realized patterns of resource usage in the field. If potential competitors show overlapping resource preferences but nonoverlapping resource usage, this logically suggests that interspecific competition results in resource partitioning.

Ceratina mikmaqi Rehan and Sheffield, 2011 and *C. calcarata* Say, 1837 are common, morphologically and ecologically similar small carpenter bees with very similar sympatric distributions encompassing most of eastern North America (Grothaus 1962; Kislow 1976; Michener 2007; Rehan & Richards 2010; Rehan & Sheffield 2011; Vickruck et al. 2011). Their similar geographical distributions, life history patterns, and choices of nesting substrates suggest the possibility of ongoing interspecific competition for nesting substrate. Both species make their nests in woody stems of plants such as raspberry (*Rubus* sp.), sumac (*Rhus* sp.), rose (*Rosa* sp.), plume grass (*Erianthus* sp.) and teasel (*Dipsacus* sp.) (Grothaus 1962; Johnson 1988; Rehan & Richards 2010). In the Niagara region of southern Ontario, Canada, pan trap studies indicate that the population densities of *C. mikmaqi* and *C. calcarata* are similar (Richards et al. 2011; Vickruck et al. 2011). However, nest collections reveal different proportions of the two bee species in the common nesting substrates, *C. mikmaqi* nesting most often in teasel (*Dipsacus fullonum* L.) and *C. calcarata* in raspberry (*Rubus strigosus* Michx.; Vickruck et al. 2011). Moreover, since teasel plants grow in sun and raspberry plants often grow in shade, this interspecific difference in nesting substrate is associated with a further difference in microclimate that could have important consequences for raising broods, because *C. mikmaqi* nests would be significantly hotter during the daytime than would *C. calcarata* nests.

We hypothesized that differences in nesting substrate usage by *C. mikmaqi* and *C. calcarata* represent the outcome of interspecific competition, specifically the most commonly used plant species in the local area (namely raspberry, teasel and sumac (*Rhus typhina* L.)). However, a drawback of field collections is that we do not know how bees find and choose nesting substrate, and so we cannot estimate the relative availability of nest sites in each substrate. Although we can compare bee species ratios within nest substrates to assess whether the two bee species use the substrate similarly, we cannot compare the frequencies of nest substrates within bee species to assess their actual nest site selection preferences. Therefore, we devised a field choice experiment in which equal numbers of newly cut woody stems of raspberry, teasel and sumac were presented to female *Ceratina* in both sunny and shady locations, allowing them to choose nesting sites by either plant substrate type or microclimate, or both. The experiment had two possible outcomes. First, patterns of nesting substrate and site usage in the experiment could resemble the patterns observed in the field. This would suggest species-specific nest site selection (*C. mikmaqi* more often choosing sunny, teasel nests and *C. calcarata* more often choosing shady, raspberry or sumac nests), which might reflect competition. Alternatively, a contrasting nest usage pattern in experimental versus natural settings would suggest that bees use nesting substrate differently when a surplus of sites is provided experimentally. This in turn would suggest that realized nesting patterns in the field result from competitive interactions in which one species is more likely to obtain the preferred resource.

METHODS

Life History Patterns of C. mikmaqi *and* C. calcarata

Ceratina calcarata and *C. mikmaqi* are univoltine, twig-nesting, small carpenter bees that are among the most common bee species in southern Ontario (Richards et al. 2011). Both females and males overwinter as adults. In spring, females emerge from their hibernacula to mate and to search for new twigs to use as nesting substrate; hibernacula are never reused as nests (Rehan & Richards 2010; Vickruck et al. 2011). Foundresses are nest loyal, and once they have provisioned all of their brood, they remain at the nest entrance to guard their offspring until their emergence as adults (Rau 1928; Kislow 1976; Rehan & Richards 2010; Vickruck et al. 2011). Females live for approximately 1 year and produce a single clutch of eggs within a single nest, and the offspring reared from that nest represent that female's lifetime reproductive output. Newly eclosed offspring overwinter in their natal nest or disperse in the autumn to find or excavate new hibernacula.

Nesting Substrates and Field Sites

The three most common nesting substrates for *Ceratina* in our study sites are recently dead stems of raspberry (*Rubus strigosus*), teasel (*Dipsacus fullonum*) and staghorn sumac (*Rhus typhina*) (Vickruck et al. 2011). Teasel is a biennial weed that grows in sunny, open field settings. In its second summer, it produces a single stalk that grows up to 1 m in height, and each teasel plant can provide only a single potential nest site. Raspberry and sumac are typically found at shaded wood margins and are multibranched, perennial shrubs that provide multiple potential nest sites.

Nest collections were conducted on the Brock University campus (Global Positioning System, GPS, coordinates: 43°07′08″N, 79°14′56″W), at the Glenridge Quarry Naturalization Site (GQNS; 43°07′19″N, 79°14′13″W), and old abandoned fields adjacent to Glenridge Avenue in St Catharines, Ontario, Canada (43°08′49″N, 79°10′48″W). The Brock University sites comprised several old fields replete with teasel, as well as two raspberry patches and two sumac stands. The GQNS was similar in that it had several large open fields containing teasel as well as two raspberry patches and several areas where sumac was present. The abandoned fields along Glenridge Avenue were used for teasel collections only. Experimental nest sites in 2009 were all located on the Brock University Campus and had been chosen because they had been good *Ceratina* collecting sites in 2008.

Microclimate Differences among Nesting Substrates

To investigate microclimate temperature differences between shady wood margins and sunny open fields, small temperature-recording devices ('iButtons', Thermochron) were inlaid in a piece of wood and covered with masking tape for protection. Two devices were deposited in each of six sites where *Ceratina* nests were collected in 2008. Three sites were located in full sun where teasel nests were collected (two on the Brock University campus and one at the GQNS), and three sites were located at shady wood margins in raspberry patches (two sites on the Brock campus and one at the GQNS). From 1 April to 30 September 2008, the data loggers collected synchronized temperature readings every 30 min. Every 2 weeks, one data logger from each of the six sites was collected for data downloading and replaced with a new one. Readings from paired data loggers were compared to ensure that temperature recordings were equivalent and that all data loggers were functional.