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PHENOLOGY AND TRAP SELECTION OF THREE SPECIES OF *HYLAEUS* (HYMENOPTERA: COLLETIDAE) IN UPPER MICHIGAN

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ABSTRACT

Hylaeus basalis, *H. ellipticus* and *H. verticalis* nested in wooden traps during a two-year study in Upper Michigan. Bees were given a choice of traps with varying bore diameters, heights, and entrance orientations. Nests were completed between 1 July and 15 September. These three *Hylaeus* species partitioned available nest site resources (traps) based on diameter and height. *H. ellipticus* selected traps with smaller bore diameters than did the other two species which selected traps of the same bore diameters. *H. verticalis* nested in traps at higher locations than *H. basalis* which limited its nesting to only the two lowest heights available. Entrance orientation had no effect on trap selection by any of the species. Seasonal differences in choice of traps are discussed.

Nesting biologies of some groups of solitary bees have been reported in detail, while other groups remain relatively unstudied. The lack of biological information on North American *Hylaeus* may be attributed to several factors. The most obvious of these is their small size which makes field observation difficult. Unlike all other North American bee genera these relatively hairless bees carry pollen internally, and thus have not been included in pollination studies. In addition, the genus continues to have a reputation for taxonomic problems despite the excellent contributions of Snelling (1966a, 1966b, 1966c, 1968, 1970, 1975, 1983).

Information on nest site selection of North American *Hylaeus* is mostly limited to short papers or notes based on few nests (Davidson 1895, Rau 1922, 1930; Hicks 1926; Brandhorst 1962; Fye 1965a, 1965b; Medler 1966; Krombein 1967; Eickwort 1973; Barrows 1975; Tepedino 1980; Torchio 1984). From these, we know that North American *Hylaeus* nest in pithy stems including *Rhus* and *Sambucus*. Some species nest in other cavities such as abandoned galls or old mason bee (*Osmia*) cells. Rarely, they nest underground as in abandoned halictid burrows. Because of their cavity nesting habit, some species will accept trap-nests.

A trap-nesting study in Upper Michigan was undertaken to gather basic information on the nesting biology of *Hylaeus basalis* (Smith), *H. ellipticus* (Kirby), and *H. verticalis* (Cresson). Since these three species all nest in traps, the following questions were raised. Do these three species partition the provided traps in some way? If so, what role does nesting phenology, and the trap

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variables of bore diameter, height and entrance orientation play in trap selection?

The focus of this portion of the *Hylaeus* study will be to determine if each of these three species select only a certain subset of traps provided and what factors contribute to any observed differences.

MATERIALS AND METHODS

This study took place during the summers of 1984 and 1985 in Dickinson and Iron Counties in Michigan's Upper Peninsula. Five study sites, C5 (T.42N, R.31W, S.14), CH (T.43N, R.30W, S.18), CL (T.43N, R.30W, S.19), F1 (T.43N, R.29W, S.14), and F2 (T.43N, R.29W, S.14) were open fields bordered by second growth forest.

Trap-nests (traps) consisted of white pine blocks (19 × 19 × 150 mm) in which a single hole was drilled lengthwise to a depth of roughly 125 mm. Six drill bits (4.5, 5.2, 6.0, 7.2, 9.4, and 11.0 mm) were used to provide a variety of bore diameters. Twelve traps were bound with plastic strapping into a bundle so that one trap of each bore diameter faced each direction and no two trap entrances were adjoining.

In April, well before nesting began, four bundles of traps were randomly placed crosswise on each shelf of four-shelved wooden hutches located along the field edges. Shelf heights measured roughly 0.1, 0.4, 0.8, and 1.1 m above ground level. A small roof covered the uppermost shelf of each hutch to protect traps from rain and provide shade. During 1984, four hutches were placed at each site. During 1985, six hutches were placed at all sites, except CH, which continued to have four. In all cases the hutches were grouped in pairs so that one hutch had trap entrances facing east and west while the other had trap entrances facing north and south.

Data on bore diameter, height, and entrance orientation were recorded for each *Hylaeus* nest. During 1984, complete nests were removed from the hutches as soon as a nest cap was noticed and replaced with an empty trap. Incomplete nests (without nest caps) were collected at the end of the summer. During 1985, all traps were checked for *Hylaeus* nesting activity at 9-to 12-day intervals by reflecting sunlight into the tunnels with a mirror. Nest contents or presence of nest caps were noted for all nests. During 1985, complete nests were left in the bundles at the hutches until after the first hard freeze (11 September 1985). All nests from both nesting seasons were stored for the winter in an unheated garage near site CH.

Completed nests constructed during 1985 are divided into two categories, early season and late season nests. Early season nests were completed before 22 July 1985. Late season nests were completed on or after 22 July 1985. Completion dates were used since beginning dates were difficult to detect, and thus not accurate.

Statistical analyses include log-likelihood (G) contingency tables and Chi-square (χ^2) goodness of fit tests (Zar, 1984). G contingency tables were used to compare yearly differences in trap selection for each bee species. If years did not differ significantly from each other, data from the two years were combined. This analysis was also used to compare trap selection among species. Before data from the five study sites were combined, G tests were conducted to insure that data from the different study sites were not significantly different ($a > 0.05$). Chi-square goodness of fit tests were performed to determine whether trap selection by each species was significantly different from an equal distribution.

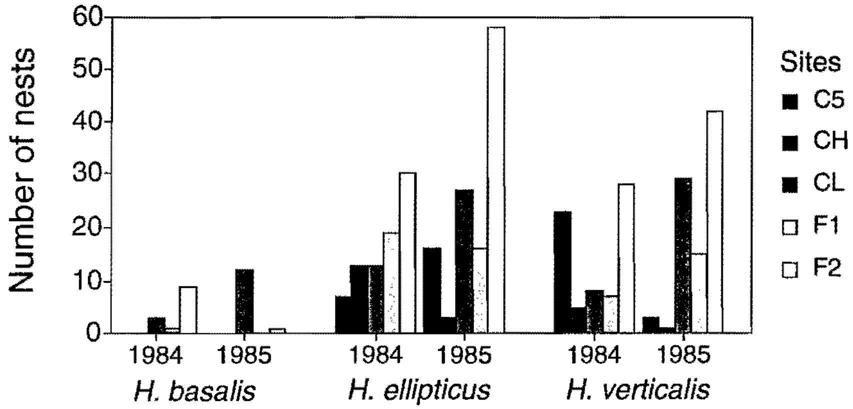

Figure 1. Number of nests completed by three *Hylaeus* species during two years at five study sites in the Upper Peninsula of Michigan.

RESULTS

During the two-year study, *H. basalis* completed 26 nests (13 during each year), *H. ellipticus* completed 203 nests (83 in 1984 and 120 in 1985), and *H. verticalis* completed 163 nests (73 in 1984 and 90 in 1985). In this study, it appears that female *Hylaeus* often constructed more than one nest during the nesting season, since new nests were periodically started throughout the summer despite the fact that all three species were univoltine.

Phenology: *Hylaeus basalis*, the largest species to nest (female thorax diameter = 2.66 mm, N = 31), nested at only some of the study sites (Fig. 1). It was present at sites CL and F2 both years and at site F1 during 1984. It was entirely lacking from sites C5 and CH. When present, this species nested in small groups at only one or two hutches. This species completed nests between 9 July and 13 August, with a peak on 22 July 1985 (Fig. 2).

Hylaeus ellipticus was the smallest species to nest (female thorax diameter = 1.89 mm, N = 41). This species nested at all sites and generally completed the most nests of any of the *Hylaeus* species at each site (Fig. 1). This species completed nests from 1 July to 15 September, with a peak on 22 July 1985 (Fig. 2).

Hylaeus verticalis was the medium size species (female thorax diameter = 2.17 mm, N = 33). It nested at all sites, but was found in low numbers at site CH during both years (Fig. 1). This species completed nests between 9 July and 15 September, with a peak on 1 August 1985 (Fig. 2).

In general, these three species nested during the same time period (Fig. 2). *Hylaeus ellipticus* completed some nests one week before either of the other species. *Hylaeus basalis* had the shortest nesting season, completing all of its nests one month before the two other species.

Bore diameter: Bore diameters selected by *Hylaeus* were limited to the three smallest diameters provided (4.5, 5.2 and 6.0 mm) with each *Hylaeus* species nesting in traps of each of these three bore diameters.

Hylaeus basalis primarily selected traps with diameters of 4.5 and 5.2 mm, with traps of 6.0 mm diameters making up only a small portion of the traps selected (Fig. 3). This selection of bore diameters was significantly dif-

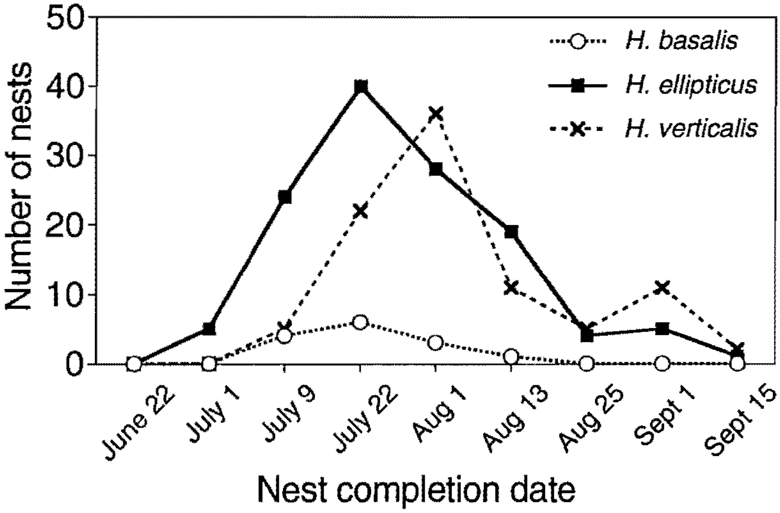

Figure 2. Phenology of nest completion by three *Hylaeus* species during 1985.

ferent from equal (χ^2=7.000, 2 df, 0.05<P<0.025). During early season (before 22 July) 1985 (N=9), *H. basalis* completed 11.1% of its nests in 4.5mm traps, 77.8% in 5.2 mm traps and 11.1% in 6.0 mm traps. During late season (on or after 22 July) 1985 (N=4) this species constructed 50.0% of its nests in each of the 4.5 and 6.0 mm traps. The trend toward greater use of 4.5 mm bores during late season was not tested statistically because of low sample sizes.

Hylaeus ellipticus preferred traps with bore diameters of 4.5 mm, although a smaller number of 5.2 mm and a few 6.0 mm traps were also used (Fig. 3). This selection of bore diameters was significantly different from equal (χ^2=192.010, 2 df, P<0.001). During early season 1985 (N=63), *H. ellipticus* completed 85.7% of its nests in traps with 4.5 mm bore diameters, 14.3% in 5.2 mm, and 0.0% in 6.0 mm traps. During late season (N=54), this species completed 66.7% of its nests in 4.5 mm traps, 20.4% in 5.2 mm, and 13.0% in 6.0 mm traps. Selection of trap diameters during early and late season were significantly different from each other (G=12.836, 2 df, 0.001<P<0.005) with a greater proportion of the early season nests being completed in traps with 4.5 mm bore diameters, and all nests in traps with 6.0 mm bore diameters being completed during late season.

Hylaeus verticalis mainly selected traps with 4.5 and 5.2 mm bore diameters, although a small number of 6.0 mm traps were selected (Fig. 3). The selection of bore diameters varied significantly between years (G=9.176, 2 df, 0.01<P<0.025), with a greater use of traps with 6.0 mm bore diameters during 1985. The selection of bore diameters was significantly different from equal for each year (1984 χ^2=28.795, 2 df, P<0.001; 1985 χ^2=8.6000, 2 df, 0.025<P<0.01). During early season 1985 (N=25), *H. verticalis* completed 40.0% of its nests in traps with 4.5 mm bore diameters, 44.0% in 5.2 mm, and 16.0% in 6.0 mm traps. During late season (N=65), this species completed 38.5% of its nests in 4.5 mm traps, 41.5% in 5.2 mm, and 20.0% in 6.0 mm

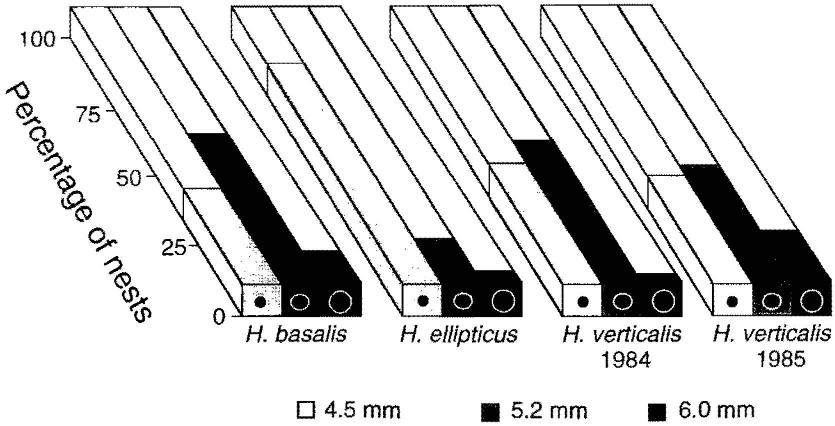

Figure 3. Percentage of nests constructed by each of three *Hylaeus* species in traps of three different bore diameters.

traps. Selection of bore diameters during early and late season 1985 did not differ significantly (G=0.195, 2 df, ns).

In a comparison among the three *Hylaeus* species (Fig. 3), *H. ellipticus* selected traps with smaller bore diameters than either *H. basalis* (G=20.507, 2 df, $P<0.001$) or *H. verticalis* (1984 G=33.185, 2 df, $P<0.001$; 1985 G=44.878, 2 df, $P<0.001$). Bore diameter selection was not significantly different between *H. basalis* and *H. verticalis* (1984 G=1.953, 2 df, ns; 1985 G=1.374, 2 df, ns).

Height: Heights selected by *Hylaeus* included all four heights available (0.1, 0.4, 0.8, and 1.1 m) however, not all *Hylaeus* species nested at all heights.

Hylaeus basalis selected traps at only the two lowest heights available, 0.1 and 0.4 m above ground level (Fig. 4). During early season 1985 (N=9), *H. basalis* completed 11.1% of its nests at 0.4 m height and 88.9% at 0.1 m. During late season (N=4), this species completed 75.0% of its nests at 0.4 m height and 25.0% at 0.1 m. The shift toward using higher traps during late season was not tested statistically due to low sample sizes.

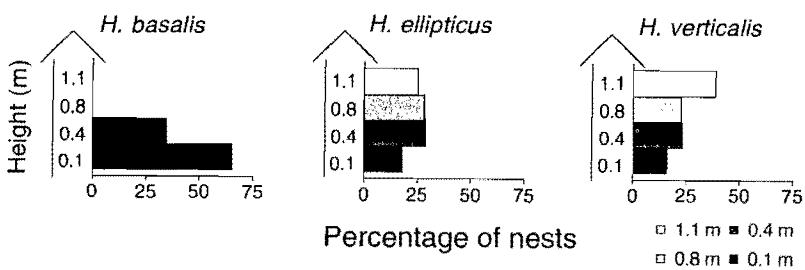

Figure 4. Percentage of nests constructed by each of three *Hylaeus* species in traps at four different heights.

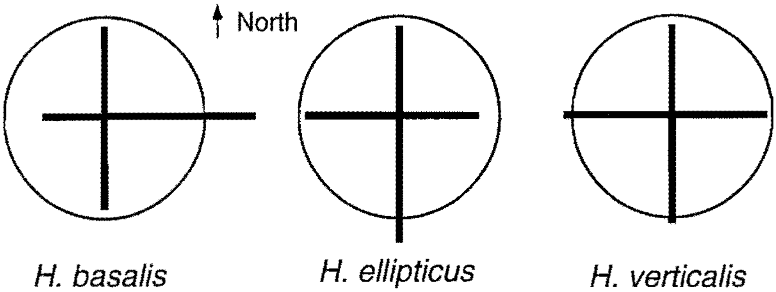

Figure 5. Percentage of nests constructed by each of three *Hylaeus* species in traps with four different entrance orientations. Circles represent an equal selection of traps with the four entrance orientations.

Hylaeus ellipticus selected traps at all four available heights (Fig. 4) with no specific height preference. Selection of heights by this species was not significantly different from equal (χ^2=5.759, 3 df, ns). During early season 1985 (N=62), *H. ellipticus* completed 22.6% of its nests at 1.1 m height, 25.8% at 0.8 m, 38.7% at 0.4 m, and 12.9% at 0.1 m. During late season (N=53), this species completed 20.8% of its nests at 1.1 m height, 32.1% at 0.8 m, 28.3% at 0.4 m, and 18.9% at 0.1 m. Selection of height during early and late seasons were not significantly different from each other (G=2.005, 3 df, ns).

Hylaeus verticalis selected traps at all four available heights, but had a preference for the higher traps (Fig. 4). Selection of heights was significantly different from equal (χ^2=16.019, 3 df, P<0.001). During early season 1985 (N=25), *H. verticalis* completed 48.0% of its nests at 1.1 m height, 12.0% at 0.8 m, 24.0% at 0.4 m, and 16.0% at 0.1 m. During late season (N=64), this species completed 43.8% of its nests at 1.1 m height, 25.0% at 0.8 m, 14.1% at 0.4 m, and 17.2% at 0.1 m. Selection of height during early and late seasons were not significantly different from each other (G=2.665, 3 df, ns).

In a comparison of heights selected by the three *Hylaeus* species (Fig. 4), *H. basalis* selected traps at lower levels than either *H. ellipticus* (G=42.090, 3 df, P<0.001) or *H. verticalis* (G=47.246, 3 df, P<0.001). Trap heights selected by *H. ellipticus* and *H. verticalis* did not differ significantly from each other (G=6.885, 3 df, ns).

Entrance orientation: Entrance orientations selected by each of the three *Hylaeus* species included all four directions available (north, south, east and west) with each *Hylaeus* species nesting in traps of all orientations.

Hylaeus basalis selected traps with each of the four entrance orientations available (Fig. 5). Selection of trap orientation was not significantly different from an equal distribution (χ^2=2.923, 3 df, ns). During early season 1985 (N=9), *H. basalis* completed 33.3% of its nests in traps with entrances facing north, 22.2% facing east, 44.4% facing south, and 0.0% facing west. During late season (N=4), this species completed 25.0% of its nests in traps facing north, east, south and west. Seasonal differences in selection of traps facing different orientations were not tested statistically because of low sample sizes.

Hylaeus ellipticus selected traps with each of the four entrance orientations available (Fig. 5). Selection of entrance orientation was not significantly different from equal (χ^2=7.196, 3 df, ns). During early season 1985 (N=62), *H. ellipticus* completed 29.0% of its nests in traps with entrances facing north, 21.0% facing east, 33.9% facing south, and 16.1% facing west. During late season (N=52), this species completed 23.1% of its nests in traps with entrances facing north, 13.5% facing east, 36.5% facing south, and 26.9% facing west. Seasonal differences in selection of traps facing different orientations were not significantly different from each other (G=2.928, 3 df, ns).

Hylaeus verticalis selected traps with each of the four entrance orientations available (Fig. 5). Selection of entrance orientation was not significantly different from equal (χ^2=1.671, 3 df, ns). During early season 1985 (N=25), *H. verticalis* completed 28.0% of its nests in traps with entrances facing north, 16.0% facing east, 40.0% facing south, and 16.0% facing west. During late season (N=64), this species completed 17.2% of its nests in traps with entrances facing north, 25.0% facing east, 29.7% facing south, and 28.1% facing west. Seasonal differences in selection of traps facing different orientations were not significantly different from each other (G=3.399, 3 df, ns).

None of the three *Hylaeus* species showed a preferred entrance orientation (Fig. 5). Selection of entrance orientation among the three species did not differ significantly (G=6.329, 6 df, ns). In addition, entrance orientations selected did not differ between any pair of species, *H. basalis* and *H. ellipticus* (G=4.484, 3 df, ns), *H. basalis* and *H. verticalis* (G=3.301, 3 df, ns), or *H. ellipticus* and *H. verticalis* (G=2.239, 3 df, ns).

DISCUSSION

During this two-year study, three species of *Hylaeus* completed nests in traps with bore diameters of 4.5, 5.2 and 6.0 mm, at heights of 0.1, 0.4, 0.8, and 1.1 m and in traps whose entrances faced north, south, east and west. Their selection of different bore diameters and different trap heights shows some resource partitioning.

Nesting began in late June. The first nests nests were completed by *H. ellipticus* at the beginning of July. The two other species completed their first nests one week later. *Hylaeus basalis* completed nesting by mid-August, while the two other species continued nesting through mid-September. Phenology probably plays little role in avoiding competition by *Hylaeus* as they partition trap resources since most selection of nesting sites occurred at a time when all three species were actively nesting. Only *H. ellipticus* nesting very early in the season would have selected traps in the absence of the two other species, and another factor (bore diameter) seems to play the most important role in the selection of traps by that species.

Of the three different trap variables, bore diameter, height and entrance orientation, the latter had no effect on trap selection by any of the *Hylaeus* species, whereas, bore diameter and height both play major roles in the partitioning of nesting sites available to these bees.

Hylaeus ellipticus was the smallest of the three species to nest in these traps. It selected traps with the smallest diameters provided (4.5 mm). It may have also selected traps with even smaller bore diameters (<4.5 mm), had they been available. During 1985, *H. ellipticus* completed nests in traps with the largest bore diameter (6.0 mm) during late season only. Because completed *Hylaeus* nests were not removed from the hutches and replaced with empty traps during 1985, the availability of smaller bores became more limited late in the nesting season. Therefore, selection of traps during early season shows the preferred bore diameter, while selection of traps during late season show a less preferred, but still acceptable range. *Hylaeus ellipticus* was clearly choosing the traps with the smallest bore diameters when available. And thus, it appears as though this species may be avoiding completion with the other *Hylaeus* species for nesting sites by selecting traps with smaller diameters.

Both *H. verticalis*, the medium size bee, and *H. basalis*, the largest species studied, showed a preference for the smallest- and medium-sized bore diameters (4.5 and 5.2 mm). Traps with larger bore diameters were available at the hutches, and thus, *H. basalis*, the largest species, was not being forced to select traps with diameters smaller than "normally" accepted. Since these two species were selecting traps with the same bore diameters, they were competing for these nesting sites.

Height seems to play a role in the selection of traps by *H. verticalis* and *H. basalis*, the two species competing for traps with the same bore diameters. *H. basalis* had the most dramatic preference for a certain trap heights, nesting at only the two lowest heights (0.1 and 0.4 m) available. *Hylaeus verticalis* showed a preference for higher traps. Since *H. basalis* and *H. verticalis* are competing for nest sites with similar tunnel diameters it is not unexpected to find that they are partitioning these resources in some way, in this case, by height. In this study, *H. basalis* was uncommon. It was found in low numbers and was entirely absent from two of the study sites. Therefore, present day competition between *Hylaeus* species for nest sites does not account for the differences in trap selection observed in this study. Perhaps the observed patterns are the result of past competition between these two species, or present competition with non-*Hylaeus* species also nesting in the traps.

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