Nesting biology and behavioral interactions of two solitary halictine bees Lasioglossum (Lasioglossum) sp. and Lasioglossum (Chilalictus) platycephalum (Hymenoptera : Halictidae)

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NESTING BIOLOGY AND BEHAVIORAL INTERACTIONS
OF TWO SOLITARY, HALICTINE BEES,
LASIOGLOSSUM (LASIOGLOSSUM) SP. AND
LASIOGLOSSUM (CHILALICTUS) PLATYCEPHALUM
(HYMENOPTERA: HALICTIDAE).

by

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Nesting Biology and Behavioral Interactions of Two Solitary, Halictine Bees, _Lasioglossum (Lasioglossum) sp._ and _Lasioglossum (Chilalictus) platycephalum_ (Hymenoptera: Halictidae).

Director: Penny F. Kukuk

The purpose of this study was to collect data on the nest structure of two solitary, halictine bees and to investigate the behavioral interactions of solitary species. Results from behavioral experiments with the solitary species were then compared with results previously reported from two related, social species.

Halictine bees (Hymenoptera: Halictidae) exhibit a wide variety of nest structures. Studies of nest architecture are useful in comparative analyses to reinforce systematic positions. Nests of two solitary, Australian species, _Lasioglossum (Lasioglossum) sp._ and _Lasioglossum (Chilalictus) platycephalum_, were excavated to obtain measurements of nest dimensions and record nest contents. _L. (Lasioglossum) sp._ constructs a primitive nest type while nests of _L. (Chilalictus) platycephalum_ may contain some derived characteristics.

The family Halictidae is also an ideal group for studies of the evolution of sociality in Hymenoptera, as it contains species which exhibit nearly the entire array of social structures. Recent studies generated an interest in communal species, whose colonies consist of two or more reproductively active females of the same generation. It was suggested (Kukuk & Schwarz 1987) that communal behavior is an evolutionarily stable alternative to eusociality.

Circle tube experiments were conducted to collect data on the behavioral interactions of _L. (Lasioglossum) sp._ and _L. (Chilalictus) platycephalum_. The results were compared with those previously reported from identical tests with the communal species _L. (Chilalictus) hemichalceum_ and the eusocial species _L. (Dialictus) zephyrum_. These experiments also tested the hypothesis that individuals of solitary species will be highly aggressive toward all conspecifics.

Both solitary species exhibited low levels of aggressive and cooperative (passing) acts, yet nearly all females were reproductively active, as determined by subsequent dissections. Neither ovarian width nor size was associated with aggression in either species.

Interspecific comparisons reveal large differences in cooperation and aggression among the four congeneric species. The communal species exhibits significantly more passing and less aggression than all other species, suggesting that communal behavior is not intermediate between solitary and eusocial behavior. Further, the behavior of the three Australian species (one communal and two solitary) is mapped onto an independently derived phylogeny, and the results suggest that communal behavior is a derived trait in the subgenus _Chilalictus._
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Chapter I


Introduction

The nest architecture and nest contents of two soil-dwelling, solitary bees in the family Halictidae were examined by excavating nests of each species. Thus far, no descriptions of nesting biology are available in the literature for both species. Therefore, this project will contribute to the continuously expanding data base on the nesting biology of halictid bees.

Studies of halictine bees often emphasize the great diversity of social structure found in this cosmopolitan family. Another aspect of halictine biology that is also highly variable and a useful comparative trait is nest architecture. In their review of of halictine nesting biology, Sakagami and Michener (1962) stated that nest architecture and social structure evolved independently. Rather, nest architecture studies are useful references to reinforce systematic positions (Packer & Knerer 1986). The majority of halictines nest in the soil. Sakagami
and Michener (1962) defined the most primitive type of soil nest as one with a main burrow extending down from the nest entrance, off of which narrower, lateral tunnels branch. Cells are located at the ends of these branches, which may vary in length. The cells are coated with a waxy secretion, provisioned with a pollen ball upon which the female oviposits, then typically sealed off from the main burrow by filling the lateral tunnels with dirt. Derived conditions include reduced length of lateral branches and construction of cells in series or in clusters (Eickwort & Sakagami 1979; Packer & Knerer 1986). Sakagami et al. (1985) suggest two different evolutionary routes from a primitive nest type with regards to cell construction. One route leads to the formation of serially arranged cells and likely passes through a step involving formation of two cells at the end of one lateral. The second route initially leads to construction of a cell cluster and excavation of burrows around the cluster. More evolved nest types involve formation of a cell cluster within an already excavated cavity (Sakagami et al. 1985). All of the above nest types are represented in the subfamily Halictinae. Within the Halictinae, a general trend exists in which primitive nest types are found in solitary and communal species but not in eusocial species; however, the construction of serial cells, clustered cells, and sessile cells is not associated with social system (Eickwort & Kukuk 1990; Kukuk & Eickwort 1987). Three additional features of nest structure common in halictines are the presence of a blind burrow below the deepest cells, a narrow entrance,
and lateral branches which are narrower than the main burrow (Eickwort & Sakagami 1979; Sakagami et al. 1985).

Australian halictine bees are interesting behaviorally due to the lack of eusociality— all known species are solitary or apparently communal. The majority of Australian halictines belong to the worldwide genus *Lasioglossum* and include seven endemic subgenera, such as *Chilalictus* and *Parasphecodes*, and two subgenera, *Lasioglossum* s.s. and *Ctenomia*, with centers of species diversity in Asia and the Holarctic region, respectively. Typical nests of some representative species from these groups are illustrated in Knerer & Schwarz (1976). They report cases in which species of the same subgenus, *Chilalictus*, have very different nest structures.

Nest structure data were collected for two solitary, Australian species, an undescribed species of *Lasioglossum* (*Lasioglossum*) and *Lasioglossum* (*Chilalictus*) *platycephalum*. No published descriptions of nest architecture were found for either species in the literature. Recent DNA sequencing research indicates that *Lasioglossum* s.s. may be ancestral to *Chilalictus* (Kukuk, Koulianos & Crozier, in prep). Results suggesting that *L*. (*Lasioglossum*) sp. constructs a more primitive nest type than does *L*. (*Chilalictus*) *platycephalum* would be consistent with these classifications.

*Lasioglossum* s.s. is most diverse in North America and Europe. Currently, six Australian species have been placed in this group (Ken Walker, Museum of Victoria, pers. comm.). Very few descriptions of
Lasioglossum s.s. nesting biology are available. All holarctic species studied are solitary with primitive nest types (Eickwort, pers. comm.; Atwood 1933; Knerer 1968).

The subgenus *Chilalictus* contains highly variable nest structures. The communal species *L. (Chilalictus) inclinans* and *L. (Chilalictus) lanarium* construct nests consisting of one vertical main burrow with laterals leading to single cells or three or more cells in series (Knerer & Schwarz 1976, 1978). In contrast, *L. (Chilalictus) hemichalceum*, also a communal species, forms nests in which the initial main burrow gives rise to a network of chambers or short branches where single cells or cell clusters are found (Kukuk, unpubl. data). *L. (Chilalictus) victoriellum* constructs unicellular nests which consist of a single burrow leading to a single cell. Unicellular nests are common in wasps and possibly the most primitive nest type of aculeate Hymenoptera, but are rarely seen in halictines. This nest type may have evolved secondarily in *L. (Chilalictus) victoriellum* as an adaptation to nesting in loose sand (Sakagami & Michener 1962). The data from excavations of *L. (Chilalictus) platycephalum* will contribute additional information to the currently limited sources available on this speciose Australian subgenus.
Materials and Methods

Nests were excavated at two sites in Cobboboonee State Forest located in southwestern Victoria, Australia. One site, a grassy, open area at a five way intersection, including Fishholes Road and Cutout Dam Road, contained a large aggregation of *L. (Lasioglossum)* sp. (Fig. 1.1). A smaller, sparse aggregation of *L. (Chilalictus) platycephalum* was known about seven kilometers away on the bare, northwest corner of the intersection of Fishholes Road and Beaugleholes Road, and served as the second site (Fig. 1.2).

Nest data for *L. (Lasioglossum)* sp. were obtained between 19 Nov. 1992 and 27 Nov. 1992. Data for *L. (Chilalictus) platycephalum* were collected between 21 Dec. 1992 and 29 Dec. 1992. Based on observation of females and contents of the nests, it appeared that most females were foraging by these dates. Subsequent excavations of *L. (Lasioglossum)* sp. nests were done on 7 Jan. 1993 to reexamine the progress of nest construction and verify the accuracy of our earlier results. Nest structures were very similar to those excavated previously, and measurements taken for three nests were included in the analysis.

Nests were excavated in the morning, late afternoon, or on cool, rainy days when all bees were in the nests. Excavations followed the procedure described in Abrams & Eickwort (1980) except colored talcum powder was substituted for plaster of paris. The talcum powder was
sprayed down into the main tunnel, allowing it to be clearly followed and easing detection of side tunnels, without injuring nest inhabitants.

Measurements of tunnel widths and lengths, the number of cells and contents of each, and the number of adult bees found were recorded for each nest. Although more nests were excavated, data included in the analysis are from 19 nests of *L. (Lasioglossum)* sp. and 22 nests of *L. (Chilalictus*) *platycephalum*. It was not always possible to make every desired measurement for each nest, thus data sets for some nests are incomplete. Still the data are sufficient to confidently describe general nest structure and determine that both species are primarily solitary. The bees collected from excavations were taken to the laboratory for behavioral experiments, and then dissected to evaluate reproductive condition of each female. The results from behavioral tests are reported in a separate paper (McConnell & Kukuk, in prep). Bees were dissected with a Wild-M5A stereoscope equipped with an ocular micrometer. Values recorded include ovarian width as the sum of the maximum width of each ovary when viewed dorsally, ovarian state assigned according to the number and size of developing oocytes, head width, intertegular span, and wing wear as the number of wing nicks on the left wing. The opacity of the spermatheca was also noted to determine whether or not females were inseminated.

Mean values for nest dimensions and measurements of females are reported with standard deviations in parentheses.
Results

Nest dimensions

*L. (Lasioglossum)* sp.-- Table 1.1 reports the mean values and standard deviations of nest dimensions, including diameter and length of the main shaft and lateral branches, number of laterals, depth of the shallowest lateral or cell, and width and length of cells.

Nest entrances were often sealed due to the inclement weather during which many nests were excavated, therefore, burrows were usually located a few centimeters below the surface. The few that were not sealed were round with no tumulus, an accumulation of loose soil around the entrance observed in many other halictine species. The main burrow was typically vertical, occasionally meandering briefly in a subhorizontal direction, and extended beyond the deepest lateral branch to terminate in a blind end. The number of lateral branches ranged from zero to three and length of laterals ranged from 3.5 mm to 20.0 mm. Lateral branches were typically horizontal and extended in any direction from the main burrow. Only four measurements of the entrance diameter of a lateral were obtained, averaging 2.23 mm (± 0.52) The majority of branches (n=15) simply ended blindly, whereas nine led to a cell. Measurements obtained from two cells in different nests excavated in January were 3.6 mm x 6.8 mm and 3.5 mm x 6.0 mm. Figure 1.3 illustrates a representative nest of this species.

The mean diameter of nests excavated earlier in the season was
3.04 mm (± 0.27, n=9), whereas mean diameter of nests excavated in January was 4.10 mm (± 0.36, n=3). These values are not significantly different due to small sample sizes (t=1.732, p=.2). The mean number of laterals in early season nests was 1.44 (± 0.89, n=16) and in January nests was 1.67 (± 0.58, n=3). Again the difference was not significant (t=0.425, p>.5). The length of laterals shows the most striking difference between early season nests (x̄=1.26 cm ± 0.59, n=10) and January nests (x̄ = 0.43 cm ± 0.11, n=2). Using the Smith-Satterthwaite procedure for comparing means with unequal variances, this difference is significant (t=4.106, p=.01).

_L. (Lasioglossum) platycephalum_-- Table 1.1 reports the mean values and standard deviations of nest dimensions. As with the first species, most entrances were sealed at the time of excavations. However, because nests were more scattered than those of _L. (Lasioglossum)_ sp., we located and marked nests on sunny, warm days when the bees were flying. This allowed us to note that entrances were round, usually with no tumulus. Four entrance diameters were recorded at 2.5, 2.8, 2.8, and 4.0 mm. The first three values are lower than the diameter of the main burrow for that nest, while the fourth was equal to the main burrow diameter. The main tunnel was vertical for most of its length, however short subhorizontal diversions were noted for several nests.

All nests of _L. (Chilalictus) platycephalum_ had at least one cell
constructed and as many as 12 cells associated with one nest were found. Most cells were sealed off from the main tunnel thus lateral branches were often difficult to recognize. However, the diameter of 9 open laterals was measured (Table 1.1). On average, the distance between a cell and the main burrow was 15.55 mm. This value was used as an estimator of lateral length (Table 1.1). Figure 1.4 depicts two representative nests that illustrate two characteristics of cell positioning in this species described below.

Nest contents

*L. (Lasioglossum)* sp.—Table 1.2 reports the contents of each nest of *L. (Lasioglossum)* sp. excavated. Few cells were found, therefore only minimal descriptive data are presented. Cells were positioned horizontally at the ends of laterals. No clusters or series of cells were found. Eight empty cells were excavated, six of which were polished. The three nests excavated later in the season collectively contained five of these empty cells, all polished. In a different, early season nest, two cells at different depths were located (nest #14, Table 1.2). The shallower cell contained a prepupa and the deeper cell contained a pollen ball with an egg. This nest was unique because two adult females were also found in it, yet it is unknown whether this was simply a coincidence of catching the nest in a temporary state with an intruding female in another female's nest or if both females were utilizing the same nest. One additional nest with
two females was excavated, however solitary females prevailed, accounting for 20 of 22 nests occupied at the time of excavation. The females from both two-female nests were used in preliminary behavioral experiments and were not dissected to determine ovarian development and wing wear. However, neither of the two nests contained any cells with pollen excrement to suggest recent emergence of offspring.

Mean ovarian width was 0.75 mm (± 0.15, n=38) and mean intertegular span was 1.21 mm (± 0.06, n=46). Coefficients of variation were 20.06 for ovarian width and 5.30 for intertegular span. Frequency distributions of both variables do not show any gross deviations from normality (Fig. 1.5). Thirteen of 38 females dissected had one oocyte ready or nearly ready to be laid. Wing wear, determined as the number of wing nicks on the left wing, ranged from 0 to 5 and averaged 1.71 (± 1.89, n=38). Ten of 38 females showed no wing wear. Head widths and condition of the spermathecae were not recorded for this species.

L. (Chilalictus) platycephalum-- A total of 87 cells were excavated. All cells were either horizontal or slightly angled. Most were single cells sealed off from the main burrow, however four cases of two or three cells in series were noted, as well as four instances in which two or three cells were situated close to one another at the end of one lateral but were not distinctly clustered or in series (illustrated in Fig. 1.4). Cells were scattered in all directions
around the main burrow.

Although several nest contained an abundance of cells, they included a mixture of old or moldy cells, freshly excavated cells, and sealed cells housing offspring (Table 1.3). It is possible that nest reuse is prevalent in this species as the soil can become very hard in dry conditions, yet substantiating this would require more extensive observations. In addition, the summer during which this study was conducted was unusually cool and rainy. Average high temperatures for November and December were $18.6^\circ\text{C}$ and $22.1^\circ\text{C}$, respectively, and total precipitation was 92.8 mm in November and 50.4 mm in December (recorded at Heywood, Victoria, Bureau of Meteorology). This may account for the numerous moldy cells found and possibly skewed the results if cell construction or provisioning was altered that year in response to greater losses from wet weather.

The total number of cells with provisions and/or offspring was 28. An additional 23 cells were fresh but empty; at least 12 of these cells were polished. Fifteen cells appeared old or contained moldy pollen while eight more cells contained wet, unshaped pollen. Thus the total number of old or non-viable cells was 23, over one-fourth of the total cell count.

Females were present in thirteen nests, eleven of which contained only one adult female and the remaining two inhabited by two adult females at the time of excavation (Table 1.3). Both females from one of the two-female nests were dissected (nest #17, Table 1.3). One
female had an ovarian width of 1.04 mm, pollen in the crop, and no wing wear, while the second female had an ovarian width of 0.74 mm, nectar in the crop, and 3 wing nicks. The opaque condition of the spermatheca in both females suggested that they were inseminated. Only one female from the other two-female nest was dissected (nest #10, Table 1.3). She had an ovarian width of 1.12 mm, pollen in the crop, and appeared to be inseminated. Neither of these nests contained cells from which offspring recently emerged.

Overall, mean ovarian width was 0.83 mm (± 0.18, n=38) and mean intertegular span was 1.23 mm (± 0.07, n=39). Coefficients of variation were 21.63 for ovarian width and 5.97 for intertegular span. For the sample of bees dissected, both measurements do not severely deviate from normality (Fig. 1.6). The frequency distribution of ovarian width appears to be slightly skewed to the left, however there is no indication of bimodality. Mean head width was 1.59 mm (± 0.05, n=39) and the coefficient of variation for head width was 2.97. Thirteen of 38 females examined for ovarian state had one oocyte ready or nearly ready to be laid and all but three females appeared to be inseminated by the opaque condition of their spermathecae. Wing wear ranged from 0 to 10 with a mean of 2.26 (± 2.36, n=39) wing nicks. Ten of 39 females showed no wing wear.

Evidence of parasitism was found in five nests and was primarily due to an Ichneumonid wasp, *Labium* sp. (Table 1.3). One adult, one teneral, one prepupa, and two pupae of *Labium* sp. were excavated, as
well as one unidentified Dipteran larva. When the site was visited on sunny days, numerous adult females of *Labium* sp. were seen flying over *L. (Chilalictus) platycephalum* nests.
Discussion

Information on nest structure and contents was collected by nest excavation for two Australian species *L. (Lasioglossum)* sp. and *L. (Chilalictus) platycephalum*. Descriptions of the nesting biology of both subgenera in the literature are very limited. Based on excavations and dissection data, both species are solitary, yet we did find two nests in each species that contained two adult females. No recently vacated cells were found in any two-female nests and dissection data from *L. (Chilalictus) platycephalum*, although incomplete, indicated that these females had developed ovaries, full crops, and were apparently inseminated. Therefore, it is unlikely that one of the adults was newly emerged, but two other possible situations remain in question. Two females may have been utilizing the same nest or one female may have intruded upon another's nest. Additional field observations examining the nesting behavior of these species are necessary before conclusions can be reached.

Both species construct nests consisting of a main burrow with cells located at the end of lateral branches. Lateral branches on average are relatively long, extending between 1.5 and 3.5 times the length of cells. Nests of *L. (Lasioglossum)* sp. contained very few laterals and cells and only one cell was formed at the end of a lateral. Three nests of this species were excavated later in the season to verify the earlier results and the only significant
structural change detected was a decrease in the length of lateral branches. No cells in the late season nests contained provisions or offspring. In comparison, two cells, one containing a prepupa and the other a pollen ball with egg, were found in an early season nest. The process of cell provisioning requires sufficient availability of resources and foraging trips to obtain those resources. The general lack of provisioned cells in *L. (Lasioglossum)* sp. may be a consequence of a reduction in either resources or foraging. The latter is a more likely explanation considering the cool, rainy conditions that persisted throughout the season of this study. If the frequency of foraging trips is significantly reduced in wetter years, the effects may be reflected in nest structure as a reduction in the number of cells per nest. This assumes that females cannot provision as many cells and decrease cell construction in wetter years as opposed to years with consistently warmer and drier weather. Although this is only speculation, it raises concern that the results presented in this paper do not accurately describe typical nests of this species. Additional excavations would be beneficial to confirm or expand upon these data.

Each *L. (Chilalictus) platycephalum* nest had more associated cells on average, yet in contrast to *L. (Lasioglossum)* sp., moldy cells were also found and accounted for 25% of the total cell count. Four instances of two or three cells occurring in series were recorded, as well as four cases of cells that seemed to be formed off of the same
lateral yet were not in an organized cluster. The general nest type of this species is more similar to nests of *L. (Chilalictus) inclinans* and *L. (Chilalictus) lanarium* than those of *L. (Chilalictus) hemichalceum*. The observation that serial cells occur in one solitary species and two communal species of the subgenus *Chilalictus* suggests that the construction of serial cells is a trait associated with *Chilalictus* and not with sociality. This conclusion is consistent with some previous reports of halictines (Eickwort & Kukuk 1990; Eickwort & Sakagami 1979), but contradicts others (Knerer 1969; Knerer & Schwarz 1976).

In comparison to *L. (Lasioglossum) sp.*, *L. (Chilalictus) platycephalum* appears to exhibit some derived nest characteristics not seen in the very primitive nest structure of the former. This would be consistent with the current tentative phylogeny developed from DNA sequencing (Kukuk, Koulianos & Crozier, in prep) which suggests that *Lasioglossum s.s.* may be ancestral to *Chilalictus*.

Parasitism may be an important factor in *L. (Chilalictus) platycephalum*. Evidence of parasitism, most notably by an Ichneumonid wasp, *Labium* sp., was found in five nests and numerous individuals of *Labium* were observed flying over bee nests on sunny days. Additional studies addressing this problem and the severity of parasitism on fitness of solitary species would provide interesting results that could possibly serve as a basis for comparison to test the notion that parasitism is a factor promoting sociality, particularly in communal species.
Literature Cited


Chapter II

Behavioral interactions in two solitary, halictine bees, *Lasioglossum* (*Lasioglossum*) sp. and *Lasioglossum* (*Chilalictus*) *platycephalum*, and behavioral comparisons among solitary, communal, and eusocial species.

Introduction

Laboratory behavioral experiments were conducted with two solitary, halictine bees to examine the nature of behavioral interactions between females of solitary species, which are often presumed to be highly aggressive (Kukuk 1992). The experimental design of this study was identical to work previously done on a communal, halictine bee (Kukuk 1992) and a eusocial, halictine bee (Breed et al. 1978). All four species belong to the genus *Lasioglossum*. Therefore, the results from this project, focused on solitary species, can be compared to those obtained from two related, social species. The purpose of these comparisons is to test the hypothesis that communal behavior is not intermediate between the behaviors of solitary species and eusocial species.

The evolution of sociality in Hymenoptera has long been the object of theoretical work. The extreme forms of altruism, exemplified by sterile worker castes in eusocial species, sparked a majority of the
interest (Hamilton 1964a,b, 1972; Lin & Michener 1972; West Eberhard 1975). The primary reason for the attention given to other forms of sociality in Hymenoptera was to assist in reconstructing the transition from solitary to eusocial life. Many of the alternative social structures were thought to be evolutionarily unstable, an idea generated by the discovery that many eusocial colonies pass through a temporary stage resembling the sociality of certain non-eusocial species, primarily semisocial wasps (Lin & Michener 1972; Michener & Lange 1958; West 1967).

More recent studies have begun investigating the possibility of alternative, evolutionarily stable social structures in Hymenoptera (Knerer & Schwarz 1976; Kukuk & Schwarz 1987). Cooperative societies seen in various communal hymenopteran species provide support for this proposal. Other work focused on explaining the occurrence of cooperative foundress associations, a temporary stage of some eusocial ant species (Pollock & Rissing 1985; Rissing & Pollock 1986, 1987; Rissing et al. 1989). Foundress associations are a separate phenomenon; this paper deals only with societies that live cooperatively throughout the colony cycle. The formation of such cooperative societies is already a valid strategy in theory (Axelrod & Dion 1988; Axelrod & Hamilton 1981; Vehrencamp 1983), and is beginning to accumulate empirical support as an alternative social system to eusociality (Danforth 1991; Kukuk 1992; McCorquodale 1989; Wcislo 1993). Halictine bees are very useful for such studies. The
family Halictidae is a very large, diverse group distributed worldwide and comprised of over 2,000 species which exhibit nearly the entire array of social structures observed in Hymenoptera as defined by Michener (1974).

Communal Behavior

Communal colonies are defined as two or more females of the same generation inhabiting a nest yet acting independently of one another. Each female is reproductively active, provisioning and ovipositing on her own cells (Michener 1974). There is no cooperation in reproductive activities, however females share a nest entrance and are likely to encounter nestmates frequently, so there must be a tolerance to conspecifics.

At present, there is minimal information available regarding the relatedness of colony members in communal species. McCorquodale (1988) reported significant intracolony relatedness values of 0.5 and 0.3 for two aggregations of the apparently communal wasp Cerceris antipodes, and estimates of about 0.3 for two additional aggregations which were not statistically distinguishable from zero. These levels of relatedness, he concluded, were consistent with kin selection theory, emphasizing the importance of relatedness in the evolution of colonial living. In contrast, Kukuk and Sage (in press) reported a low overall coefficient of relatedness of 0.13 for Lasioglossum (Chilalictus) hemichalceum. Intracolony relatedness values for a subset of 25
reproductively active colonies averaged 0.07 and were statistically indistinguishable from zero. Danforth et al. (in prep) used DNA fingerprinting to evaluate relatedness of nestmates in the communal bee *Perdita texana*. The results indicate that several nests contain small groups of related females, probably half-sib sisters, but on average, nestmates are not more closely related than non-nestmates.

Abrams and Eickwort (1981) observed a high degree of nest switching in *Agapostemon virescens*. In one aggregation, they report that 58% of the parent females moved from one nest to another during one season, suggesting that communal colonies of this species do not exist as discrete units but rather experience a lot of individual interchange which would effectively lower intra-colony relatedness values. This information leads one to believe that communal behavior in the halictine bees studied thus far is being reinforced by mutualistic benefits of group living. Additional studies of various communal Hymenopteran groups suggest several different forms of mutualistic benefits received by communal species, including reduced cost of time and labor in nest construction, reduced parasitism, and protection from predation (Abrams & Eickwort 1981; Alcock 1980; Danforth 1991; Evans & Hook 1986; McCorquodale 1989; Wcislo 1993).

The hypothesis that communal halictines, forming highly tolerant societies lacking a reproductive division of labor and the associated dominance relationships, are evolutionarily stable, is also supported by theoretical models as well as by phylogenetic and behavioral data.
Theory

Several theoretical models lend support to the notion that cooperative societies can be evolutionarily stable. Vehrencamp (1983) applied optimality theory to predict the occurrence of no dominance or varying degrees of dominance in social groups. Dominance strategies are determined by the degree of relatedness, the probability of successful dispersal, and the mean group fitness relative to fitness of solitary individuals. Conditions that would decrease the amount of reproductive bias a dominant can impose on a group are a low degree of relatedness, a low cost of dispersal, and a low benefit of group living relative to solitary living. The first two conditions may pertain to some communal species as discussed above. The third condition, fitness benefits to individuals in a colony compared with solitary individuals, has yet to be quantified. Thus far, reports on two species indicate little or no increase in reproductivity, given as the number of offspring per female, as colony size increases (Abrams & Eickwort 1980; Kukuk & Sage, in press).

A second theoretical approach used game theory to explain the evolution of cooperative behavior (Axelrod & Dion 1988; Axelrod & Hamilton 1981). A computer simulation game demonstrated that a simple individual cooperative strategy based on reciprocity, TIT FOR TAT, can become established in a group of predominantly noncooperative individuals and be maintained with a high resistance to invasion by cheaters. Relatedness may aid the initiation of cooperative behavior
in groups of closely related individuals, however it is not a prerequisite. Axelrod and Hamilton (1981) describe mechanisms by which cooperation can become established and persist without relatedness if the probability of two individuals encountering each other again is high. Further work indicated that the evolution of cooperation is restricted by high numbers of players (Axelrod & Dion 1988) and mobility of organisms (Enquist & Leimar 1993). Some of these conditions may be compatible with communal species in which individuals share a nest entrance and colonies tend to be small relative to eusocial species.

The high tolerance levels typical of communal species may also be promoted by low individual variation in fighting ability. Sequential interactions between two individuals allow assessment of relative fighting ability (Enquist & Leimar 1983), which, if interpreted to be about equal, may result in an unresolved conflict. Repeated interactions of this type may stabilize into an egalitarian relationship (Hand 1986).

The above models support the idea that cooperative behavior may be promoted by two types of selection--kin selection and/or mutualism--and can theoretically be a stable strategy.

Mapping Behavior onto Phylogeny

Communality has evolved independently in several different phylogenetic lines in the Hymenoptera, including the sphecid and
pompilid wasps, as well as the bee families Oxaeidae, Andrenidae and Halictidae (Abrams & Eickwort 1980; Danforth 1991; Kukuk & Schwarz 1987; McCorquodale 1988, 1989; Michener 1974). Within the halictines, according to Michener's classifications (1974), communality is seen in the subfamilies Nomiinae and Halictinae, with origins in the Agapostemon complex and groups of Lasioglossum s.l. such as Chilalictus, Ctenonomia, and Evylaeus (Eickwort 1969; Kukuk & Schwarz 1987; Sakagami 1968; Sakagami et al. 1966). For the most part, these lineages differ from those in which eusocial species occur (Eickwort & Sakagami 1979; Kukuk & Schwarz 1987; Michener 1974, 1985).

The Australian halictines are a very interesting and valuable source of information about communal behavior. The majority of Australian halictines are in the genus Lasioglossum which has a worldwide distribution and exhibits a wide range of social structures. The Australian components are comprised of seven endemic subgenera and include additional species belonging to two subgenera with centers of species diversity elsewhere, primarily Asia and the Holarctic region (Michener 1979; Walker, pers. comm.). All of the known Australian species are either solitary or apparently communal. This observation motivated studies of communal behavior in Australian halictines and speculation on why communality is so prevalent in these species (Knerer & Schwarz 1976; Kukuk & Schwarz 1987).

The behavioral interactions of one communal species, L. (Chilalictus) hemichalceum, were investigated by Kukuk (1992). These
results were compared to those from similar experiments with *L. (Dialictus) zephyrum*, a North American, behaviorally and cyclically eusocial species (Breed et al. 1978; the terms 'behaviorally' and 'cyclically' are used here to replace 'primitively,' see Kukuk, in press). The communal species exhibits little or no agonistic behavior toward nestmates and non-nestmates although such behaviors are part of their repertoire. In contrast, the eusocial species exhibited a substantially greater degree of aggression and proportionally fewer acts that require cooperation. Moreover, *L. zephyrum* responded differently to nestmates, as compared to non-nestmates. From these initial comparisons, Kukuk (1992) concluded that communal species are behaviorally very different. They show a universal acceptance of all conspecifics as opposed to the differential responses reported for the eusocial species (Kukuk 1992).

The intent of this project was to expand upon these comparisons by including the ancestral lifestyle, represented by two solitary, congeneric species. Identical behavioral experiments were performed with the Australian species, *Lasioglossum (Chilalictus) platycephalum* and *L. (Lasioglossum)* sp. Including information on behavioral interactions of solitary species enables identification of differences in behavioral patterns between solitary species and social species. These data may then indicate whether communal behavior in the Australian species represents a possible intermediate evolutionary stage, or if it appears more likely to be diverged from both solitary
and eusocial behaviors. The latter is expected if communality is an
alternative, stable social strategy in Australian halictines.

As in any comparative study, the results of these behavioral
experiments must be mapped onto an independently established phylogeny
in order to confirm independent evolutionary events (Carpenter 1991;
Harvey & Pagel 1991). Current research is underway to establish the
phylogeny of the Australian subgenera of Lasioglossum s.l. Four groups
have been suggested as possible ancestors to the Australian subgenera,
including L. (Lasioglossum) and L. (Ctenomia), both of which contain
some Australian species, L. (Nesohalictus), with species in Asia, New
Guinea and Madagascar; L. kinabaluense, from Borneo; and African
subgenera of Lasioglossum s.l. (Michener 1965, 1986; Pauly 1980, 1981,
sequencing analysis of three subgenera of Lasioglossum s.l. (Kukuk,
Koulianos & Crozier, in prep), suggest that the subgenus Lasioglossum
may be ancestral to Chilalictus. Mitochondrial DNA sequence data were
obtained from four Australian halictid species: Nomia (Austronomia)
australica, used as an outgroup; L. (Chilalictus) hemichalceum; L.
(Parasphecodes) sp.; and L. (Lasioglossum) sp. Two methods were used
to analyze the data, one based on maximum likelihood and the other on
the principle of parsimony, and both grouped Chilalictus and
Parasphecodes together (Fig. 2.1; Kukuk, Koulianos & Crozier, in prep).
These results clearly indicate that Chilalictus is not ancestral to
Lasioglossum, and do not eliminate Lasioglossum as a possible ancestor
to *Chilalictus*, however the phylogeny is still incomplete.

Since one solitary species and the communal species belong to the subgenus *Chilalictus*, while the other solitary species belongs to *Lasioglossum* s.s., further evaluation will reveal whether behavioral patterns reflect the phylogenetic classification of these species. If so, *L. (Chilalictus) platycephalum* and *L. (Chilalictus) hemichalceum* should be more similar behaviorally than either is to *L. (Lasioglossum)* sp. The alternative conclusion may be that behavior is more highly correlated to sociality than phylogeny, if the data suggest that the two solitary species do not differ behaviorally from one another, yet both differ from the communal species.

The data will also provide additional information on the nature of solitary halictine bees. It has been suggested that solitary species will exhibit a very high aggression level toward all conspecifics (Kukuk 1992). Batra (1968) and Stockhammer (1966) observed a higher degree of aggressiveness in solitary halictine bees than in social species and found aggression to be related to reproductive activity. Although it seems a safe assumption that solitary bees will be highly aggressive toward all conspecifics, the situation becomes more complicated by the occurrence, in some normally solitary species, of a few multifemale nests, indicating that these species may be exhibiting some social tendencies (Alcock 1975; Sakagami & Maeta 1984, 1987).

An additional point raised by Michener (1974) is the inherent
difficulty in classifying species into discrete behavioral categories. Some solitary species have a slight overlap of generations; in others, sisters are likely to live together during the emergence and dispersal stage but do not constitute a colony according to Michener. This information suggests that some degree of tolerance may be favorable, or even necessary, at least during the non-reproductive phases for most species. As a final objective, this project investigated the behavior of two solitary species placed in a laboratory environment, testing the hypothesis that individuals of solitary species exhibit a high level aggression, greater than that seen in eusocial species, toward all conspecifics in the reproductive stage of the life cycle.

In summary, the primary goal of this project was to examine the behaviors and behavioral states of two solitary, halictine bees in a circle tube environment. The results were used for two purposes: 1) To test the hypothesis that solitary species are highly aggressive toward conspecifics, and 2) To compare the behavioral patterns of two solitary species with two social congeners, including one communal species and one eusocial species, to investigate the notion that communal behavior is not intermediate between solitary life and eusociality.
Materials and Methods

Cobboboonee State Forest in Southwestern Victoria, Australia served as the study area from November 1992 through January 1993. Female bees were collected from two sites, separated by about seven kilometers, and taken to the laboratory for experiments. One site, an open, grassy area located on the northwest corner of a five way intersection, including Fishholes Road and Cutout Dam Road, contained a dense aggregation of *Lasioglossum (Lasioglossum)* sp. The other, located at the bare northeast corner of the intersection of Fishholes Road and Beauglehole Road, contained a much smaller aggregation of *Lasioglossum (Chilalictus) platycephalum*. Both species are ground nesting, therefore, most bees were obtained by nest excavation. This was done when all bees were in the nest, either in the morning, the evening, or on cool, rainy days. Excavations followed the procedure described in Abrams and Eickwort (1980), except that colored talcum powder replaced plaster of paris. Talcum powder sprayed down into the main tunnel allows it to be followed easily and side branches to be located, yet it does not injure inhabitants of the nest. Excavations provided information on nest architecture and sociality for each species, since neither species has been previously studied in detail. Sufficient data from 32 nests of *L. (Lasioglossum)* sp. and 22 nests of *L. (Chilalictus) platycephalum* were collected to confidently describe general nest structure and identify both species as primarily solitary
(McConnell & Kukuk, in prep). At this point, the remainder of the bees used in laboratory experiments were collected using more efficient methods, either sweep netting or by placing an inverted vial over the nest entrance and digging out the bees as they appeared at the entrance. Bees were transported to the lab in a cooler and kept chilled until used in behavioral experiments the same day. Bees that were not put through experiments on the day of collection were maintained overnight in petri dishes supplied with a moistened tissue and a 1:1 mixture of honey and water.

Behavioral data were collected in the lab by conducting circle tube experiments, as described by Breed et al. (1978) and Kukuk (1992) to allow for comparison of results (Fig. 2.2). Each circle tube trial was a ten minute observation period during which all behaviors and behavioral states, individual and interactive, were recorded for two bees. For each trial, two females, each from a different nest, were put into a section of clear nalgene tubing with an internal diameter of 3 mm, which is approximately equal to the average diameter of the bees' main nest tunnels (McConnell & Kukuk, in prep). One of the females was marked on the thorax with a quick drying, enamel paint pen (Magic Brand) for individual identification during the observation period. The ends of the tube were joined and held together by another short piece of tubing cut lengthwise and wrapped around the junction. Observations then began immediately and all behaviors and behavioral states of each bee were continuously recorded for ten minutes. A
magnifying lamp (Magi Lamp) aided the observations and a stopwatch placed next to the circle tube allowed for accurate records of the time and duration of each behavior and behavioral state. Two observers were present for each trial— one called out the behavior and time while the other recorded the information. A tape recorder was used as a backup to ensure that all behaviors were noted in proper sequence when the bees were especially active. We conducted 26 circle tube trials with L. (Lasioglossum) sp. from 3-8 December 1992 and 20 trials with L. (Chilalictus) platycephalum between 21 December 1992 and 12 January 1993. Each bee was used only once and immediately frozen. All bees were dissected to obtain data on head width, intertegular span, ovarian development, and wing wear of each female using a Wild-M5A Stereomicroscope equipped with an ocular micrometer. The values reported for ovarian width represent the sum of the maximum width of both ovaries when viewed dorsally and those for wing wear are the total number of wing nicks on the left wing. The opacity of the spermatheca was also noted to determine whether or not females were inseminated.

Prior to the above experiments for comparative analysis, preliminary circle tube tests were conducted with L. (Lasioglossum) sp. to determine if activity level was affected by confining the normally solitary bees in a circle tube with another bee. Thirteen trials were completed, each of which involved observing one circle tube containing two bees and two circle tubes, each containing a single bee, for ten minutes. The amount of time spent active, defined as either walking
forward or backward, or turning, was compared between the single bees and the paired bees (interactions were not included). Because nests of L. (Chilalictus) platycephalum were sparse, these preliminary tests were not conducted on this species to ensure that enough bees were available for a sufficient number of trials to include in the comparative analysis.

For each species, all data used in comparisons were obtained by observing interactions between females belonging to different nests. All mean values are reported with standard deviations. To analyze differences in behavioral patterns among the eusocial, communal, and two solitary species, chi-square tables were set up with the observed number of times a particular behavior occurred or did not occur for each species. Expected values were computed as the product of row totals and column totals divided by the grand total. The individual cells whose observed values were significantly different from expected values were identified by computing \( z = \frac{O - E}{\sqrt{E}} \) for each cell, with significance levels determined from a standard normal distribution. Subsequently, the equality of proportions of each behavior was tested between the two solitary species, and separately for each solitary species with the communal species. These tests were corrected for multiplicity with the Bonferroni method. Frequency distributions, scattergrams, and stepwise regression analysis were done with the statistical package Statview (Table 2.2, Figs. 2.3, 2.4, 2.5, 2.6).
Results

Confining two bees in one circle tube did not significantly raise or lower activity level compared to bees placed alone in tubes. Overall, the paired bees were active (excluding interactions) for an average of 73.12 seconds (+ 83.02, n=26) and the single bees were active for an average of 142.92 seconds (+ 189.75, n=26). To determine whether these differences were significant, for each trial (n=13), the average time spent active was calculated for the paired bees and the two single bees separately, then ranked. There was no difference between treatments (Kruskal-Wallace adjusted H = 1.216, p>.05). The Smith-Satterthwaite procedure for comparing means with unequal variances was also applied to these data and did not indicate a significant difference in mean activity level of single and paired bees (t=1.719, p=.10).

For comparative analysis, the primary interactive behaviors observed during circle tube trials were categorized and described. Several of the behaviors are typical of halictine bees and are named according to previously published descriptions (Breed et al. 1978, Kukuk 1992), facilitating inter-specific comparisons.

**Frontal Encounter (FE)**- an encounter between two females facing each other involving some contact.
Pass- One possible consequence of a frontal encounter. The two head-to-head females must rotate so their ventral surfaces are facing and they can move past each other in the narrow tube.

C-posture- A behavior in which the female curls her abdomen under so her body is in a c-shaped position and thus her mandibles and sting are pointed at the other female.

Lunge- A quick, sharp forward motion by one female toward the other with mandibles open.

Bite- A behavior in which one female opens and snaps shut her mandibles at the other female, physically contacting her.

Avoid- Occurring as a result of a frontal encounter or a response from a distance, it is a very quick retreat by a female.

Withdraw- Also a retreat by either backing or turning and walking forward, however a withdraw does not appear to be as strong of a response as avoid. It is often difficult to determine whether a withdraw is influenced by the frontal encounter or is an independent act. Since there is no clear boundary between avoidance and withdrawal, and also to facilitate comparisons, the two categories were combined for statistical computations.

Overall, the number of frontal encounters per trial was highly variable. At least one frontal encounter occurred in 24 out of 26
trials with *L. (Lasioglossum)* sp. and in 17 out of 20 trials with *L. (Chilalictus) platycephalum*. The trials with no frontal encounters were omitted from the analysis. Both passing and acts of aggression, which includes c-postures, lunges, and bites, were uncommon in each of the solitary species, while withdrawal and avoidance behaviors occurred much more frequently. Aggressive acts were nearly always c-postures, however two lunges and one bite were noted, therefore the three behaviors were combined into one category, termed aggressive acts, for analysis. Mean proportions of these three behaviors per frontal encounter were calculated. The methods used require some explanation due to the nature of the interactions. Passing requires both females and can occur only once per frontal encounter, thus was considered a single act. On the other hand, withdrawal, avoidance and aggression are individually performed. Under these categories, both bees need not exhibit the same behavior. In addition, a female may exhibit more than one of these behaviors at a given frontal encounter although this was rare (Breed et al. 1978; Breed, pers. comm.). Therefore aggressive and withdrawal events were scored individually, accounting for values such as that reported by Breed et al. (1978) which exceeds one.

* L. (Lasioglossum) sp.  

Frontal encounters (FE) occurred 114 times in 24 trials with *L. (Lasioglossum)* sp., with a range of duration from less than one second to 80 seconds (n=105). Passing (n=31) was seen in 13 of 24 trials.
Aggressive acts (n=29) occurred in only 8 of 24 trials. In contrast, withdrawal and avoidance (n=72) occurred in 20 of 24 trials. Table 2.1 reports the mean numbers of frontal encounters per trial, passes per trial, aggressive acts per trial, and withdrawals or avoidances per trial. Also reported are the mean durations of frontal encounters and passes. The frequency of each behavior was highly variable across trials (Fig. 2.3). For example, in one trial, no passes followed 12 FE while in another, the bees passed following all 6 FE. Displays of aggression were very similar, ranging from 0 of 12 FE to 11 aggressive acts in 10 FE.

The mean proportions of each behavior per FE were 0.326 (± 0.386) for passing, 0.216 (± 0.362) for aggression, and 0.610 (± 0.492) for withdrawal/avoidance (Table 2.5).

Mean ovarian width was 0.75 mm (± 0.15, n=38). All females were in an active reproductive state with developing oocytes in at least one ovary. Thirteen of 38 females had one oocyte nearly ready to be laid. There was one exception in which the female had very slender ovaries (width = 0.32 mm). However, it is not known if this female was inseminated because the spermathecae were not examined in this species. The mean intertegular span was 1.21 (± 0.06, n=46). Wing wear ranged from zero to five wing nicks with a mean of 1.71 nicks (± 1.89, n=38). Head widths were not recorded for this species.
We recorded 115 frontal encounters in 17 trials with *L. (Chilalictus) platycephalum*. The duration of frontal encounters ranged from less than one second to 40 seconds (n=100). Passes (n=41) occurred in 10 of 17 trials. Aggressive acts (n=17) were displayed in 6 of 17 trials. Withdrawal and avoidance behaviors (n=77) were seen in 15 of 17 trials. Table 2.1 reports the mean numbers of frontal encounters, passes, aggressive acts, and withdrawals or avoidances per trial, as well as mean durations of frontal encounters and passes. As in *L. (Lasioglossum)* sp., there was a lot of variability across trials in occurrence of each behavior (Fig. 2.4). In one trial, no passes followed 11 FE while in two others, females passed following 5 of 6 and 13 of 19 FE. The frequency of aggression was similar, ranging from no aggressive acts in 19 FE to 7 aggressive acts in 11 FE.

The mean proportion of passing per FE was 0.297 (± 0.310), of aggression per FE was 0.111 (± 0.181), and of withdrawal/avoidance per FE was 0.548 (± 0.525; Table 2.5).

Mean ovarian width was 0.83 mm (± 0.18, n=38). With two exceptions, every female was reproductively active and appeared to be inseminated. Thirteen of 38 females had one oocyte nearly ready to be laid. The two exceptions included one female with an ovarian width of 0.24 mm, no wing nicks, little or no crop contents, and a transparent spermatheca, suggesting that she was not inseminated. The other had a slightly larger ovarian width (0.36 mm), 2 wing nicks, a full crop, and
appeared to be inseminated. The mean intertegular span was 1.23 mm (± 0.07, n=39) and mean head width was 1.59 mm (± 0.05, n=39). Wing wear ranged from zero to ten wing nicks with a mean of 2.26 nicks (± 2.36, n=39).

Relationships between behavior and the variables ovarian width, body size, and time

For both species, there was no correlation between either the intertegular span or ovarian width of a female and the number of aggressive acts performed by that female (Fig. 2.5, 2.6). Stepwise regression was used to evaluate the relation between the number of passes per trial and three potentially influential independent variables: the number of frontal encounters, difference in ovarian width, and difference in intertegular span (Table 2.2). However, the large percentage of trials in which no passing occurred statistically weakens this test, thus it primarily provides descriptive information about factors that may influence the number of times females pass. For L. (Lasioglossum) sp., neither differences in ovarian width nor size were significantly correlated with the number of passes. In contrast, for L. (Chilalictus) platycephalum, all three variables were entered into the model (F = 14.81, p=.001). The number of FE showed the highest correlation, while difference in ovarian width was entered second (positively correlated with passing), and difference in size was entered third (negatively correlated with passing).
One might suspect that the nature of behavioral interactions between two individuals may change over time as they interact more. This does not seem to be the case for females of either solitary species in the ten minute time interval used. In \textit{L. (Lasioglossum)} sp., the mean number of FE before the first pass occurred was 2.77 (± 2.55, n=13). Females passed at the first FE quite frequently, in 6 of 13 trials. The upper limit of the range was set by one trial in which the two females first passed at the ninth FE. In \textit{L. (Chilalictus)} platycephalum, the mean number of FE before the first pass was 2.60 (± 2.72, n=10). Females passed on the first FE in 4 of 10 trials and on the second or third FE in 5 additional trials. The one remaining trial established the upper extent of the range at 10 FE before the first pass.

For \textit{L. (Lasioglossum)} sp. the mean number of FE before an aggressive act was 1.75 (± 0.71, n=8), ranging from 1 to 3. For \textit{L. (Chilalictus)} platycephalum, the mean number of FE before an aggressive act was 2.50 (± 2.35, n=6), ranging from 1 to 7. Six trials with \textit{L. (Lasioglossum)} sp. and four trials with \textit{L. (Chilalictus)} platycephalum contained both passing and aggression, but the two behaviors did not appear to occur in a predictable sequence (i.e. aggression always preceding passing or vice versa).

The data from each trial were divided into two halves--the first five minutes and the second five minutes of observation--and the numbers of passes, aggressive acts, and frontal encounters were totaled
for each half. Chi-square tables were set up for each behavior and for each species to test whether the behaviors observed in the first half of the trials were independent of those observed in the second half (Tables 2.3, 2.4). The chi-square value for passing in *Lasioglossum* sp. is significant ($X^2 = 4.523$, $df=1$, $p=.05$), however none of the z-values computed for individual cells were significant. The chi-square test for differences in aggression between first and last five minutes of trials was not significant ($X^2 = 2.185$, $df=1$, $p>.10$). In *L. CChilalictus* platycephalum, chi-square tests for both passing ($X^2 = 0.213$, $df=1$, $p>.50$) and aggression ($X^2 = 0.501$, $df=1$, $p>.25$) were not significant suggesting that the occurrence of these behaviors in the last half of trials was independent of events in the first half of trials.

**Comparisons**

Table 2.5 reports the mean proportions of passing, aggression, and withdrawal per frontal encounter for the two solitary species, the communal species *L. (Chilalictus) hemichalceum* (Kukuk 1992), and queens, foragers, and guards of the behaviorally and cyclically eusocial species *L. (Dialictus) zephyrum* (Breed et al. 1978).

Chi-square tests were performed to determine if the observed levels of passing and aggression were independent of the species. The results indicate significant differences among the groups in passing
(Table 2.6; $X^2 = 533.24$, df=5, p<.001) and aggression (Table 2.7; $X^2 = 734.63$, df=5, p<.001). The frequency of withdrawal is negatively correlated to passing and is the most likely candidate for inconsistent scoring by different observers, therefore this behavioral state was omitted from further analysis.

**Passing**

All individual z-values are significant (p=.01) except for those of queens (Table 2.6). Of the rest, only the communal species passes more frequently than expected; foragers, guards, and the two solitary species pass less frequently than expected.

The two solitary species did not differ from each other in the proportion of passes yet both differ significantly from the communal species (Table 2.8; p=.01 with Bonferroni correction for multiple tests).

**Aggression**

The highly significant chi-square value for aggression is due primarily to *L. zephyrum* and *L. hemichalceum* (Table 2.7). All groups of *L. zephyrum* displayed higher levels of aggression than expected while *L. hemichalceum* exhibited significantly lower levels (p=.01). The proportion of aggressive acts shown by *L. hemichalceum* is also significantly lower than both solitary species, which do not differ from one another (Table 2.9; p=.01 with Bonferroni correction).
Discussion

**Behavior of solitary species**

The low frequency of aggressive acts and high frequency of withdrawal observed for both solitary species suggest that females of solitary species are not highly aggressive toward all conspecifics as was suggested. These results contradict Batra's (1968) and Stockhammer's (1966) reports of the behavior of solitary females in observation nests. Many of the interactions they observed, however, were between mothers and newly emerged daughters, a period in the life cycle not included in this paper. Yet, the artificial situation of the circle tube experiments, while useful and necessary for interspecific comparisons, may alter the behavior of solitary species. Placing each bee in an unfamiliar environment may have affected its behavioral responses to encountering another female such that more avoidance rather than aggression was exhibited. Still notable, however, is that the results for the two solitary species are consistent and statistically indistinguishable from one another. We also showed with *L. (Lasioglossum)* sp. that activity levels of paired bees were not higher or lower than that of bees alone in a tube. Additional experiments in a more natural setting are suggested; for example, allowing females to establish themselves in artificial nests, then adding a second female to each nest would provide more detailed data regarding behavioral interactions between the nest 'owner' and
'intruder.' Such data would indicate whether the bees' behavior is flexible depending of their position as 'owner' or 'intruder.'

If the results reported are indicative of the behavior of solitary females in the nest, the question becomes what advantages do solitary females gain from not being highly aggressive toward conspecifics. In his study of solitary Cerceris wasps, Alcock (1975) reported high degrees of nest switching, changes of nest ownership, and communal provisioning. Alcock offers several mechanisms by which females may benefit from these behaviors. Further field observations of solitary halictines would be necessary to reveal whether these females tend to consistently return to the same nest or rather attempt to usurp others' nests.

Neither size nor ovarian width was associated with aggression level in either solitary species, although the results may be influenced by a lack of data points with one or more aggressive acts. In L. (Lasioglossum) sp., passing did not appear to be associated with differences between the two females in size or ovarian development. In contrast, both variables were significant predictors of passing in L. (Chilalictus) platycephalum. However, the test was weakened by a high number of cases in which no passes occurred. The data suggest that difference in ovarian width is a more important indicator of passing than size difference, and that the females are more likely to pass as the difference in ovarian width increases, but less likely to pass as size difference increases. However, whether or not a female is
actually able to assess the ovarian state of other females relative to herself and, further, is behaviorally responding to this is unknown. The nature of the signals responsible for different behavioral responses following frontal encounters cannot be determined from these data.

Previous interactions do not appear to greatly influence the outcome of a present interaction in either solitary species. Although the choice of time is arbitrary, splitting the data into two halves allowed us to test whether behaviors occurred independently of one another throughout the ten minute trials. The only significant result obtained suggests that *L. (Lasioglossum)* sp. may pass more frequently in the last half of a ten minute trial, although this was not confirmed by individual significant z-values. In addition, it was fairly common for females to pass at the first frontal encounter (6 of 13 trials), indicating that previous interactions are not required for a pass to occur. However, it is possible that the probability of a pass at a given encounter increases as the number of previous interactions or passes increases for this species. The results obtained from tests of aggression in *L. (Lasioglossum)* sp. and tests of both passing and aggression in *L. (Chilalictus) platycephalum* were insignificant and suggest that these behaviors are independently performed over the course of the ten minute trials.
Interspecific comparisons

The amount of passing and aggression was compared among two solitary, one communal, and one eusocial species, all belonging to the genus *Lasioglossum*, to investigate the hypothesis that communal behavior is not an intermediate state of sociality between solitary and eusocial behavior. Passing requires that both females position themselves with their ventral surfaces facing one another, thus it is considered a cooperative event. The communal species is more cooperative than both solitary species and the eusocial species, indicated by the significantly greater frequency of passing. Both solitary species, along with foragers and guards of *L. zephyrum* pass less often than expected. The solitary species appear to pass in frequencies most similar to eusocial foragers. Thus, regarding passing as an indicator of cooperation, *L. hemichalceum*’s behavior is not intermediate but rather, the predominance of cooperative acts represents one extreme among the four species examined.

A similar situation exists for aggression. All groups of *L. zephyrum* exhibited significant amounts of aggression. In contrast, aggression is rare in interactions between females of *L. hemichalceum*. Both solitary species displayed intermediate levels of aggressive behaviors, yet the frequencies are still significantly greater than those of *L. hemichalceum*. Again, the behavioral patterns in the communal species seem indicative of a social system that has evolved from a solitary lifestyle along a different pathway than that of
eusociality.

Considering only the three Australian species, behavioral patterns were mapped onto the currently available phylogeny (Fig 2.7), and tested statistically (Tables 2.8 and 2.9). *Lasioglossum s.s.* may be ancestral to *Chilalictus* according to recent DNA sequencing research (Fig. 2.1; Kukuk, Koulianos & Crozier, in prep), yet behavioral patterns of *L. (Lasioglossum)* sp. do not differ from those of *L. (Chilalictus) platycephalum*. Both solitary species, however, differ behaviorally (in terms of cooperation and aggression) from the communal species *L. (Chilalictus) hemichalceum*. These results suggest that interactive behaviors do not reflect phylogeny, but are instead related to social structure. They further indicate that communal behavior is a derived trait in *Chilalictus*. This information, along with the above data, support the notion that the highly cooperative, non-agonistic behaviors exhibited by *L. (Chilalictus) hemichalceum* do not represent an intermediate state of sociality between solitary life and eusociality.

Apparently communal behavior has been reported for many distantly related Hymenopteran species and appears to have evolved independently in several lineages (Eickwort 1969; Kukuk & Schwarz 1987; Michener 1974; Sakagami 1968; Sakagami et. al. 1966). Whether these species are exhibiting cooperative behavior under similar selective pressures is unknown and will require much more extensive integration between behavioral, genetic, and phylogenetic work. However, the results
reported here suggest that within the Australian halictine bees, communal behavior in *Chilalictus* is a derived trait that is not an intermediate form of social behavior.
Literature Cited


Table 1.1: Mean values and standard deviations of nest dimensions from excavations of nests of two solitary species, *L. (Lasioglossum)* sp. and *L. (Chilalictus) platycephalum*. The sample size is reported in parentheses.

<table>
<thead>
<tr>
<th>Nest dimensions</th>
<th><em>L. (Lasioglossum)</em> sp.</th>
<th><em>L. (Chilalictus) platycephalum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Main shaft diameter (mm)</td>
<td>$3.31 \pm 0.55$ (n=12)</td>
<td>$3.11 \pm 0.43$ (n=19)</td>
</tr>
<tr>
<td>Main shaft length (cm)</td>
<td>$23.60 \pm 6.68$ (n=11)</td>
<td>$19.12 \pm 2.86$ (n=17)</td>
</tr>
<tr>
<td>Number of laterals</td>
<td>$1.41 \pm 0.87$ (n=17)</td>
<td>*</td>
</tr>
<tr>
<td>Depth of first lateral or cell (cm)</td>
<td>$13.71 \pm 5.47$ (n=12)</td>
<td>$10.03 \pm 2.37$ (n=21)</td>
</tr>
<tr>
<td>Lateral length (mm)</td>
<td>$11.18 \pm 6.22$ (n=12)</td>
<td>$15.55 \pm 8.11^*$ (n=58)</td>
</tr>
<tr>
<td>Lateral diameter (mm)</td>
<td>$2.38 \pm 0.61$ (n=9)</td>
<td>$2.90 \pm 0.50$ (n=9)</td>
</tr>
<tr>
<td>Cell width (mm)</td>
<td>$3.55 \pm 0.07$ (n=2)</td>
<td>$3.20 \pm 0.38$ (n=31)</td>
</tr>
<tr>
<td>Cell length (mm)</td>
<td>$6.40 \pm 0.57$ (n=2)</td>
<td>$5.60 \pm 0.86$ (n=21)</td>
</tr>
</tbody>
</table>

* In nests of *L. (Chilalictus) platycephalum*, the majority of lateral branches were filled with soil and, therefore, it was difficult to determine the total number of laterals constructed in each nest and their lengths with complete accuracy.
Table 1.2: Nest contents of *L. (Lasioglossum)* sp. All cells excavated were fresh and viable. An additional 13 nests with only one adult female were excavated, however no nest structure or content data were collected for these nests.

<table>
<thead>
<tr>
<th>Nest</th>
<th># Adult Females</th>
<th># Cells</th>
<th># Laterals</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>13</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>15</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>16</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>17</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>18</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>19</td>
<td>0</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 1.3: The contents of each excavated nest of *L. (Chilalictus) platycephalum*, including the number of adult females (#Ad Fem), the number of viable cells, the number of non-viable cells, and the number of parasitized cells.

<table>
<thead>
<tr>
<th>Nest</th>
<th>#Ad Fem</th>
<th>#Viable Cells*</th>
<th>#Non-viable Cells*</th>
<th>#Paras. Cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>6</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>7</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>12</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>13</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>16</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>17</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>18</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>19</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>20</td>
<td>1**</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>21</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>22</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>23</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

* Viable cells include freshly excavated, empty cells or cells containing live offspring; Non-viable cells include old or moldy cells and cells containing wet, unshaped pollen.

** One adult female of *L. platycephalum* plus one adult female of *Labium* sp. were found in this nest.
Table 2.1: Mean numbers of frontal encounters per trial (FE/T), passes per trial (P/T), aggressive acts per trial (A/T), and withdrawal or avoidance per trial (W/T) for 24 trials of *L. (Lasioglossum)* sp. and 17 trials of *L. (Chilalictus) platycepalum*. Standard deviations are in parentheses. Also reported are mean durations of frontal encounters (FE) and passes.

<table>
<thead>
<tr>
<th></th>
<th><em>L. (Lasioglossum)</em> sp.</th>
<th><em>L. (Chilalictus) platycepalum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>FE/T</td>
<td>4.75 (3.83)</td>
<td>6.77 (4.87)</td>
</tr>
<tr>
<td>P/T</td>
<td>1.29 (1.73)</td>
<td>2.41 (3.51)</td>
</tr>
<tr>
<td>A/T</td>
<td>1.21 (2.77)</td>
<td>1.00 (1.87)</td>
</tr>
<tr>
<td>W/T</td>
<td>3.00 (3.27)</td>
<td>4.53 (3.72)</td>
</tr>
<tr>
<td>FE duration (sec)</td>
<td>7.51 (12.02)</td>
<td>6.43 (12.85)</td>
</tr>
<tr>
<td>Pass duration (sec)</td>
<td>4.00 (2.81)</td>
<td>1.83 (0.83)</td>
</tr>
</tbody>
</table>
Table 2.2: Results from stepwise regression of the number of passes per trial with the number of frontal encounters per trial (FE), difference in ovarian width of the two females in each trial (OvWd), and difference in intertegular span (ITS). In both species, FE was entered first. Neither OvWd nor ITS were significantly correlated with passes in *L. (Lasioglossum)* sp. and were not entered into the model. For *L. (Chilalictus) platycephalum*, OvWd was entered second and ITS third. The correlation values reported for FE, OvWd, and ITS are the successive adjusted $R^2$ for the model as additional variables were entered.

<table>
<thead>
<tr>
<th>Correlation (R²)</th>
<th>FE</th>
<th>OvWd</th>
<th>ITS</th>
<th>F ratio</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. (Lasioglossum)</em> sp.</td>
<td>0.776</td>
<td>---</td>
<td>---</td>
<td>21.76</td>
<td>.01</td>
</tr>
<tr>
<td><em>L. (Chilalictus) platycephalum</em></td>
<td>0.484</td>
<td>0.609</td>
<td>0.734</td>
<td>14.81</td>
<td>.001</td>
</tr>
</tbody>
</table>
Table 2.3: Results of chi-square tests comparing the amount of passing (a) and aggression (b) between the first and second five minutes of trials with *L. (Lasiglossum)* sp. Reported values include the number of times a pass or aggressive act occurred and the number of times a potential pass or aggressive act did not occur (0), the expected values (E), and z-values for each cell (z = \( \frac{0 - E}{\sqrt{E}} \)). The total possible number of aggressive acts is assumed to be twice the number of FE observed in the first or second five minutes of the trials.

(a) Passing

<table>
<thead>
<tr>
<th></th>
<th>1st 5 minutes</th>
<th>2nd 5 minutes</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0=</td>
<td>15</td>
<td>16</td>
<td>31</td>
</tr>
<tr>
<td>E=</td>
<td>19.85</td>
<td>11.15</td>
<td></td>
</tr>
<tr>
<td>z=</td>
<td>-1.088</td>
<td>1.452</td>
<td></td>
</tr>
<tr>
<td>No Pass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0=</td>
<td>58</td>
<td>25</td>
<td>83</td>
</tr>
<tr>
<td>E=</td>
<td>53.15</td>
<td>29.85</td>
<td></td>
</tr>
<tr>
<td>z=</td>
<td>0.665</td>
<td>-0.888</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>73</td>
<td>41</td>
<td>114</td>
</tr>
</tbody>
</table>

\( x^2 = 4.523, \ df=1, \ p=.05 \)

(b) Aggression

<table>
<thead>
<tr>
<th></th>
<th>1st 5 minutes</th>
<th>2nd 5 minutes</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggression</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0=</td>
<td>15</td>
<td>14</td>
<td>29</td>
</tr>
<tr>
<td>E=</td>
<td>18.57</td>
<td>10.43</td>
<td></td>
</tr>
<tr>
<td>z=</td>
<td>-0.828</td>
<td>1.105</td>
<td></td>
</tr>
<tr>
<td>No Aggression</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0=</td>
<td>131</td>
<td>68</td>
<td>199</td>
</tr>
<tr>
<td>E=</td>
<td>127.43</td>
<td>71.57</td>
<td></td>
</tr>
<tr>
<td>z=</td>
<td>0.316</td>
<td>-0.422</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>146</td>
<td>82</td>
<td>228</td>
</tr>
</tbody>
</table>

\( x^2 = 2.185, \ df=1, \ p>.10 \)
Table 2.4: Results of chi-square tests comparing the amount of passing (a) and aggression (b) between the first and second five minutes of trials with *L. (Chilalictus) platycephalum*. Reported values include the number of times a pass or aggressive occurred and the number of times a potential pass or aggressive act did not occur (0), expected values (E), and z-values for each cell ($z = \frac{O - E}{\sqrt{E}}$). The total possible number of aggressive acts is assumed to be twice the number of FE observed in either the first or second five minutes of the trials.

(a) Passing

<table>
<thead>
<tr>
<th></th>
<th>1st 5 minutes</th>
<th>2nd 5 minutes</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pass</td>
<td>$O$= 22</td>
<td>$E$= 23.17</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>$z$= -0.244</td>
<td>$E$= 0.278</td>
<td></td>
</tr>
<tr>
<td>No Pass</td>
<td>$O$= 43</td>
<td>$E$= 41.83</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>$z$= 0.182</td>
<td>$E$= -0.207</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>$O$= 65</td>
<td>$E$= 50</td>
<td>115</td>
</tr>
</tbody>
</table>

$X^2 = 0.213$, df=1, $p > .50$

(b) Aggression

<table>
<thead>
<tr>
<th></th>
<th>1st 5 minutes</th>
<th>2nd 5 minutes</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggression</td>
<td>$O$= 11</td>
<td>$E$= 9.61</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>$z$= 0.449</td>
<td>$E$= 0.512</td>
<td></td>
</tr>
<tr>
<td>No Aggression</td>
<td>$O$= 119</td>
<td>$E$= 120.39</td>
<td>213</td>
</tr>
<tr>
<td></td>
<td>$z$= -0.127</td>
<td>$E$= -0.144</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>$O$= 130</td>
<td>$E$= 100</td>
<td>230</td>
</tr>
</tbody>
</table>

$X^2 = 0.501$, df=1, $p > .25$
Table 2.5: Mean proportion of passing, aggression, and withdrawal or avoidance per frontal encounter (FE) for foragers, queens, and guards of the eusocial species *L. (Dialictus) zephyrum* (Breed et. al. 1978), the Australian, communal species *L. (Chilalictus) hemichalceum* (Kukuk 1992), and two solitary, Australian species, *L. (Chilalictus) platycephalum* and *L. (Lasioglossum) sp.* (n = the number of circle tube trials, #FE = the total number of frontal encounters that occurred in n trials).

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>#FE</th>
<th>Pass/FE</th>
<th>Aggression/FE</th>
<th>Withdraw/FE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. zephyrum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Queens</td>
<td>11</td>
<td>82</td>
<td>0.573</td>
<td>1.280</td>
<td>0.451</td>
</tr>
<tr>
<td>Foragers</td>
<td>22</td>
<td>182</td>
<td>0.214</td>
<td>0.599</td>
<td>0.516</td>
</tr>
<tr>
<td>Guards</td>
<td>12</td>
<td>71</td>
<td>0.000</td>
<td>0.606</td>
<td>0.915</td>
</tr>
<tr>
<td><em>L. hemichalceum</em></td>
<td>26</td>
<td>682</td>
<td>0.813</td>
<td>0.018</td>
<td>0.153</td>
</tr>
<tr>
<td><em>L. platycephalum</em></td>
<td>17</td>
<td>115</td>
<td>0.297</td>
<td>0.111</td>
<td>0.548</td>
</tr>
<tr>
<td><em>L. (Lasioglossum)</em></td>
<td>24</td>
<td>114</td>
<td>0.326</td>
<td>0.216</td>
<td>0.610</td>
</tr>
</tbody>
</table>
Table 2.6: Chi-square test comparing passing for queens, foragers, and guards of *L. (Dialictus) zephyrum* (values calculated from Table 1 of Breed et. al. 1978), *L. (Chillalictus) hemichalceum* (Kukuk 1992), *L. (Chillalictus) platycephalum*, and *L. (Lasiosoglossum)* sp. The column totals are equal to the total number of frontal encounters observed for each group. Reported values include the observed number of passes and number of frontal encounters at which no pass occurred (0), expected values (E), and individual z-values (z = 0 - E).

\[ \chi^2 = 533.235, \text{ df}=5, \ p<.001 \]

* indicates significant z-values (p = .01).

<table>
<thead>
<tr>
<th></th>
<th>Queens</th>
<th>Foragers</th>
<th>Guards</th>
<th>L. hemichalceum</th>
<th>L. platycephalum</th>
<th>L. (Lasiosoglossum) sp.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pass</td>
<td>0=</td>
<td>47</td>
<td>39</td>
<td>0</td>
<td>603</td>
<td>31</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>E=</td>
<td>50.08</td>
<td>111.16</td>
<td>43.36</td>
<td>416.53</td>
<td>70.24</td>
<td>69.63</td>
</tr>
<tr>
<td></td>
<td>z=</td>
<td>-0.435</td>
<td>-6.844*</td>
<td>-6.585*</td>
<td>9.137*</td>
<td>-4.682*</td>
<td>-3.431*</td>
</tr>
<tr>
<td>No Pass</td>
<td>0=</td>
<td>35</td>
<td>143</td>
<td>71</td>
<td>79</td>
<td>84</td>
<td>73</td>
</tr>
<tr>
<td></td>
<td>E=</td>
<td>31.92</td>
<td>70.84</td>
<td>27.64</td>
<td>265.47</td>
<td>44.76</td>
<td>44.37</td>
</tr>
<tr>
<td></td>
<td>z=</td>
<td>0.545</td>
<td>8.573*</td>
<td>8.247*</td>
<td>-11.445*</td>
<td>5.865*</td>
<td>4.298*</td>
</tr>
<tr>
<td>Total</td>
<td>82</td>
<td>182</td>
<td>71</td>
<td>682</td>
<td>115</td>
<td>114</td>
<td>1246</td>
</tr>
</tbody>
</table>
Table 2.7: Chi-square test comparing aggressive acts for *L. (Dialictus) zephyrum* (values calculated from Table 1 Breed et al. 1978), *L. (Chilalictus) hemichalceum* (Kukuk 1992), *L. (Chilalictus) platycephalum* and *L. (Lasioglossum) sp*. It was assumed that the total number of possible aggressive acts was equal to the number of frontal encounters multiplied by two. Reported values include observed number of aggressive acts and number of times a potential aggressive act did not occur (0), expected values (E), and individual z-values (z = 0 - E).  

\[ \chi^2 = 734.626, \text{ df}=5, p<.001 \]

* indicates significant individual z-values (p = .01).
Table 2.8: Z-values reported from tests comparing the proportion of passing among the three Australian species, including *L. (Chilalictus) hemichalceum*, a communal species; *L. (Chilalictus) platycephalum*, and *L. (Lasioglossum)* sp., both solitary species.

<table>
<thead>
<tr>
<th>Solitary Species</th>
<th>L. (Lasioglossum) sp.</th>
<th>L. (Chilalictus) platycephalum</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. (Chilalictus) platycephalum</em></td>
<td>-1.468</td>
<td>---</td>
</tr>
<tr>
<td>Chilalictus sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. (Chilalictus) hemichalceum</em></td>
<td>13.189 *</td>
<td>15.116 *</td>
</tr>
</tbody>
</table>

* indicates a significant difference; p = .01 with Bonferroni correction for multiple tests.
Table 2.9: Z-values reported from tests comparing the proportion of aggression for the three Australian species, including *L. (Chilalictus) hemichalceum*, a communal species; *L. (Chilalictus) platycephalum* and *L. (Lasioglossum)* sp., both solitary species.

<table>
<thead>
<tr>
<th>Solitary Species</th>
<th>L. (Lasioglossum) sp.</th>
<th>L. (Chilalictus) platycephalum</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. (Chilalictus) platycephalum</em></td>
<td>1.175</td>
<td>---</td>
</tr>
<tr>
<td><em>Chilalictus</em> sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. (Chilalictus) hemichalceum</em></td>
<td>9.899 *</td>
<td>7.684 *</td>
</tr>
</tbody>
</table>

* indicates a significant difference; p = .01 with Bonferroni correction for multiple tests.
Figure 1.1: Site containing a large aggregation of *L. (Lasioglossum)* sp.

Figure 1.2: Site containing an aggregation of *L. (Chilalictus)* *platycephalum.*
Figure 1.3: Representative nest of *L.* (*Lasioglossum*) sp.
*E* = empty cell. Cell dimensions and tunnel diameters are not drawn to scale.
Figure 1.4: Two representative nests of *L. (Chilalictus)* *platycephalum* illustrating the positions of three cells about one lateral and cells in series. E = empty; L = Larva; M = male pupa; F = female pupa; W = wet pollen; O = moldy pollen; P = Labium prepupa. Cell dimensions and tunnel diameters are not drawn to scale.
Figure 1.5: Frequency distributions of ovarian width (mm) and intertegular span (mm) for L. (Lasioglossum) sp.
Figure 1.6: Frequency distributions of ovarian width (mm) and intertegular span (mm) for *L. (Chilalictus) platycephalum*.
Figure 2.1: One possible phylogenetic tree constructed from preliminary DNA sequence data of an outgroup, *Nomia (Austronomia) australicus*, and three subgenera of *Lasioglossum* s.l. (Kukuk, Koulianos & Crozier, in prep).
Figure 2.2: The set up for circle tube experiments, including magnifying lamp (Magi Lamp), circle tube, stopwatch, and tape recorder.
Figure 2.3: Frequency distributions of the proportion of passing and aggression for *L. (Lasioglossum)* sp.
Figure 2.4: Frequency distributions of the proportion of passing and aggression for *L. (Chilalictus) platycephalum.*
Figure 2.5: Scattergrams of the number of aggressive acts plotted against ovarian width (mm) and intertegular span (mm) for *L. (Lasioglossum)* sp. The correlations (*R*²) between aggressive acts and both independent variables are reported.
Figure 2.6: Scattergrams of the number of aggressive acts plotted against ovarian width (mm) and intertegular span (mm) for *L. (Chilalictus) platycephalum*. The correlations ($R^2$) between aggressive acts and both independent variables are reported.
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X = Solitary nesters, moderately cooperative, moderately aggressive.

O = Communal colonies formed, highly cooperative, non-agonistic

Figure 2.7: Behavior of the three Australian species, including two solitary species, L. (Lasioglossum) sp. and L. (Chilalictus) platycephalum, and the communal species L. (Chilalictus) hemichalceum, mapped onto a tentative phylogeny constructed from DNA sequence data (Kukuk, Koulianos & Crozier, in prep).