The effect of *Bombylius pulchellus* (Diptera; Bombyliidae) and other mortality factors upon the biology of *Halictus ligatus* (Hymenoptera; Halictidae) in southern Ontario

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Two factors were important in causing brood mortality in a southern Ontario population of *Halictus ligatus*: parasitism by larvae of the bombyliid *Bombylius pulchellus* and various forms of microbial infection of bee immatures or their pollen ball food. Bombyliid larvae consumed host prepupae or, less commonly, young pupae, restricted their attack mostly to the reproductive brood, and were contagiously distributed within the nest population. All immature stages were susceptible to fungal infection or disease but such pathogens did not seem to spread among cells within nests, indicating that bees may be able to prevent the spread of disease from one brood cell to another. Filling affected cells with earth may accomplish this brood hygiene. The survival rate of worker and reproductive brood immatures approximated 90%. Reproductive brood mortality affected females more than males. Reproductive brood mortality was probably underestimated: filled-in cells that may represent brood mortality were not included in these estimates.

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Deux facteurs sont principalement responsables de la mortalité de la progéniture chez une population d'*Halictus ligatus* du sud de l'Ontario : le parasitisme par les larves du bombyle *Bombylius pulchellus* et diverses formes d'infections bactériennes des larves ou des boules de pollen. Les larves de bombyles consomment les prénymphes ou, ce qui est plus rare, les petites nymphes d'halictes; elles limitent leurs attaques à la progéniture de reproducteurs et ont une répartition contagieuse au sein de la colonie. Tous les stades immatures de l'abeille sont sujets aux infections ou maladies causées par les champignons, mais les pathogènes ne semblent pas se répandre dans les cellules du nid, ce qui indique que les halictes sont probablement capables d'empêcher la maladie de se propager d'une cellule à l'autre. Il se peut que le remplissage des cellules affectées avec de la terre permette d'enrayer la contagion. Le taux de survie des stades immatures d'ouvrières et de reproducteurs est d'environ 90%. La mortalité affecte plus les femelles que les mâles. La mortalité des reproducteurs est probablement sous-estimée : les cellules condamnées par remplissage, qui représentent peut-être un certain pourcentage de la mortalité, n'ont pas été comptabilisées dans les estimations.

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Introduction

One of the major advantages that sociality may confer is increased survival of immature brood (Lin 1964; Michener 1974). This may be facilitated by nest defense during foraging, an option not available to solitary species. Halictine bees are excellent subjects for studies of the selective advantages associated with sociality because they exhibit a wide range of social levels often within narrow taxonomic confines. Although natural enemies of halictine bees are often mentioned in the literature, accurate estimates of the magnitude of their depredations upon the brood, or whole nests, have not been made. Such investigations are only possible when large numbers of nests are excavated (it should be noted that following tiny bee burrows through a metre or more of soil is a rather daunting task). This paper enumerates the various brood mortality factors acting in an aggregation of the primitively social halictine bee *Halictus ligatus* in southern Ontario. Previous papers have dealt with the social organization (Packer 1986*a*), selective advantages associated with multiple-foundress associations (Packer 1986*b*), and nest architecture (Packer and Knerer 1986) of this population.

Dense aggregations of bees provide large quantities of resource for potential predators and parasites. Therefore, it is not surprising that host aggregations often support a diverse assemblage of natural enemies which may include microbial pathogens, fungi, nematodes, mites, bombyliid, conopid, and miltogrammine flies, and strepsipteran, meloid, and rhipiphorid beetles in addition to cleptoparasitic bee species. The most detailed account of the natural enemies of any halictine is that of Batra (1965) on the small, primitively social species *Lasioglossum zephyrum*: 27 species were recorded as being associated with this bee in Kansas, 9 of which were parasites.

At Victoria, southern Ontario, only two categories of brood mortality were important: parasitism by larvae of the bombyliid *Bombylius pulchellus* and microbial or fungal infection of the pollen mass and (or) developing host immatures. The effects of these factors upon the production of workers and reproductives are described here. The influence of these natural enemies upon host nest architecture has been assessed elsewhere (Packer and Knerer 1986).

Bee flies of the genus *Bombylius* are parasitoids of ground-nesting bees and wasps. Bees of the genera *Colletes*, *Andrena*, *Lasioglossum*, and *Halictus* have been recorded as hosts (Lucas 1852; Chapman 1878; Yerbury 1902; Nielsen 1903; Buzzard 1954; Batra 1965). Adult female bee flies may be seen flying over host nest aggregations or feeding at flowers. Hitherto, studies of bee fly biology have largely been restricted to observations of adult foraging behaviour at flowers or notes on host associations. The large number of *B. pulchellus* larvae found in this study permits certain conclusions on the biology of adult and immature bee flies to be made.

Contents of brood cells that were mouldy or diseased were not cultured, making accurate identification of the pathogens impossible. Indeed, even if this had been done it would often have been difficult to ascertain whether mortality had been caused by the recorded organism or had been the result of some

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TABLE 1. Occurrence of *Bombylius pulchellus* larvae and prepupae associated with nests of *Halictus ligatus* in different 10-day periods

	Time period						
	4	5	6	7	8	9	11
No. of nests	18	26	16	7	9	10	8
No. of nests with *Bombylius*	1	2	8	4	4	4	2
% of nests with *Bombylius*	5.5	7.7	50.0	57.1	44.4	40.0	25.0
Total no. of *Bombylius*	1	2	17	12	12	9	3
No. of *Bombylius* per nest	0.06	0.08	0.88	1.71	1.22	0.90	0.38

NOTE: Day 1 of time period 1 was June 13.

TABLE 2. Comparison of the incidence of *B. pulchellus* larvae and microbial infection in *H. ligatus* nests with expected Poisson frequencies

	Bombylius larvae		Infection	
No./nest	No. of nests observed	No. of nests expected	No. of nests observed	No. of nests expected
0	22	14.0	90	82.6
1	5	15.3	27	37.5
2	10	12.7	11	9.9
3	0		0	
4	4		0	
5	1		2	

NOTE: Because of temporal variation in the occurrence of bombyliids in nests, only those nests excavated in time periods 6 to 9 inclusive are included in the analysis of bee fly parasitism.

other factor followed by secondary infection. This category of mortality is likely somewhat heterogeneous.

Methods

The methods used to study the biology of *H. ligatus* have been described elsewhere (Packer 1986*a*; Packer and Knerer 1986). Only those details of direct relevance to the present study are outlined below.

The active season for the host was divided into 10-day periods with day 1 being the first date that pollen foraging was observed in the aggregation, June 3, 1984. Reproductive brood pollen balls were "sexed" on the basis of differences in shape (for more details, see Chandler 1955, p. 300; Packer 1986*a*). The possibility that mortality affects male and female reproductive brood differentially was analysed as follows. Mortality per nest was calculated for each 10-day period separately for brood up to the fully grown larval stage and from the prepupa (post-defecating larva) onwards. These figures were partitioned into male and female reproductive mortality by multiplying pre-prepupal deaths by the pollen ball sex ratio for that 10-day period and mortality for post-fully-grown larvae by the pupal sex ratio at that time. These effects were then summed across time blocks.

Most nests were excavated when bees were inactive, either late in the afternoon or during inclement weather. Diagrams were made of the nests showing the position of all brood cells. Descriptions of cell contents were appended to the drawings as excavation proceeded. Bombyliid larvae could be easily distinguished from those of the host and were usually found within brood cells. It appeared that fully grown *B. pulchellus* larvae burrow away from the host nest and overwinter in a hibernaculum nearby. Such individuals could be associated with particular nests but not with individual brood cells.

The presence or absence of adult bee flies was recorded on each visit to the nest site in spring. No detailed analyses of adult parasite behaviour were carried out, although bee flies were observed inspecting host burrow entrances and other holes in the ground.

Other parasitoids found in nests were extremely uncommon. Thus, only four brood cells contained larvae or pupae of miltogrammine flies and one contained a fully grown rhipiphorid larva. Two brood cells contained tiny colonies of ants of the genus *Brachymyrmex*, one cell contained nematodes (probably a secondary invasion of a cell whose occupant had died of other causes), and three nests showed signs of damage by earthworms. Collembola were frequently found within nests but did not appear to affect brood survival in any way. Adults of the cleptoparasitic bee species *Sphecodes dichrous* were seen at the nest site. However, despite the excavation of over 130 nests, not one adult or immature of this species was detected and it appears that *H. ligatus* is not its host at this locality.

Fungal or microbial infection of brood was commonly observed. These factors affected pollen balls and all stages of immature development. Where possible, the bee instar affected was noted; this was not possible in some cases of advanced infection.

Brood cells that have suffered mortality are often filled in with soil, which pushes the contents to the back of the cell (Chandler 1955). Such cells are often difficult to distinguish from those that have been filled in after emergence of the occupant. An attempt was made to estimate the magnitude of this "hidden" mortality as follows. Before the period of adult worker eclosion, any filled-in cells will have suffered mortality at some earlier stage. Similarly, in the deeper parts of summer nests, where only reproductive brood cells are constructed, earth-filled cells found before any males or young gynes have emerged will represent immature mortality. Thus, rough estimates of "hidden" mortality can be made and compared with those obtained from cells whose fates were more readily identifiable. It should be noted that filled-in cells are more difficult to detect during excavation than those containing brood and that their numbers are probably slightly underestimated in the following analyses. It could be argued that the most accurate estimates of mortality are those obtained at the end of a brood-raising period, when all brood cells can be censused. However, the difficulty in distinguishing between cells filled in after adult eclosion from those that have suffered some mortality precludes such an analysis.

Results

Bombylius pulchellus

Adult *B. pulchellus* were observed flying around the study site between June 3 and 12, 1984. None were observed thereafter despite intensive observations on June 13, 16, 19, and 22. The first *B. pulchellus* larva was excavated on July 21 and the first fully grown larva was observed on August 9. Parasite larvae located within nests were almost always comparatively large, apparently representing the last and penultimate instars only. Some host larvae transferred to the laboratory were later discovered to have been attacked by early instar *Bombylius*. In the laboratory, bee fly larvae attained quite a large size within a few days. Nonetheless, it is clear that the early larval stages of the parasites were often missed.

TABLE 3. Temporal variation in the incidence of microbial infection of brood cells

	Time period								
	1	2	3	4	5	6	7	8	9
No. of nests	7	8	8	18	26	16	7	9	10
No. of nests infected	2	0	2	3	7	9	5	4	5
% of nests infected	28.6	0.0	25.0	16.7	26.9	56.2	71.4	44.4	50.0
No. of infected cells	2	0	3	5	11	14	11	7	7
Infection per nest	0.26	0.0	0.37	0.28	0.42	0.87	1.57	0.78	0.70

The occurrence of bee fly larvae excavated during different time periods is shown in Table 1. The decrease in frequency towards the end of the season is probably an artifact of the parasites being more difficult to locate after they have burrowed away from the host nest to overwinter. It is likely, therefore, that host nests receive, on average, one or two bombyliid larvae.

The distribution of the number of parasite larvae found in nests is compared with expected Poisson frequencies in Table 2. The data are highly contagiously distributed (χ^2 goodness of fit test, $\chi^2 = 11.9, p < 0.001$). This indicates either that the same nests are parasitized repeatedly or that ovipositing females direct more than one egg towards the same burrow in the same egg-laying bout.

The precise locations of 53 of the 56 total bee fly larvae were recorded. Eight (15%) were found attached to host immatures. Seven parasitoids were feeding upon host prepupae and one was feeding upon a white-eyed pupa, the youngest pupal stage. Ten (19%) bee fly individuals had burrowed away from the host nest and were found in hibernacula nearby. Such individuals were found disproportionately later in the samples (Mann–Whitney U-test, $U_s = 328$, $t_s = 1.97, p < 0.05$).

More bee fly larvae were found in nests with the entrance obscured by vegetation than in those that were out in the open. Statistical analysis of these data was made difficult by small sample sizes and large temporal variation in frequency of larvae (Table 1). The best data are those from time period 6. A Fisher's exact test with variables nest entrance hidden or not hidden and presence or absence of bombyliid larvae gave nonsignificant results ($p > 0.2$). It should be noted that a similar analysis presented elsewhere (Packer and Knerer 1986) was in error (bombyliid parasitism was accidentally overestimated) although the result of the statistical analysis was the same.

The host individuals attacked by bombyliid larvae could be assigned to worker or reproductive brood in 46 cases. Only four (8.5%) had parasitized worker brood immatures.

Large bombyliid larvae were found on comparatively intact hosts on two occasions. This suggests that the parasitoids sometimes require more than one host immature to complete their development. One of these larvae was found in a cell joined to an adjacent one by a narrow burrow that had clearly not been excavated by a host bee. In one nest, two comparatively small bee fly larvae were found not associated with particular brood cells. It could not be ascertained whether they were in a host burrow or in the soil very close to a burrow; however, it seems certain that they were attempting to move from one cell to another.

Microbial infection

The incidence of such brood cell infection in different time periods is indicated in Table 3. It was shown previously that there is an association between this mortality factor and recent rainfall (Packer and Knerer 1986). This indicates that cell waterlogging, or at least high soil humidity, promotes brood infection.

TABLE 4. Stage of development of worker and reproductive brood affected by microbial infection

	No. infected	
	Worker brood	Reproductive brood
Pollen ball	3	7
Larva	8	19
Prepupa	4	6
Pupa	1	3

The frequency of infected brood cells within nests did not show any departure from expected Poisson frequencies (Table 2, χ^2 goodness of fit test, $\chi^2 = 4.43, p > 0.1$). This indicates that microbial pathogens do not spread from one brood cell to another.

Microbial infection of brood occurred at all stages from pollen ball construction to pupation (Table 4). Without detailed data on the duration of different stadia it is not possible to state whether the pathogenic organisms differentially affect particular life-history stages. However, the pupal stage lasts longer than any other but seems to suffer the least mortality, indicating that pupae may be comparatively protected against infection.

Twenty of 59 (33.9%) infected cells had been destined to become worker brood individuals.

"Hidden" mortality

The frequency of filled-in cells increased to 0.5 per nest just before worker brood emergence. This is similar to the value of approximately 0.4 per nest recorded as suffering from mortality likely to result in cells being filled in.

There were approximately 2.4 filled-in brood cells per nest just before the emergence of the first reproductives. This is substantially greater than the 0.94 cells per nest discovered to be suffering from infection just before this time. It is likely that most of this excess "hidden" mortality resulted from cell infection, as bombyliids appeared to remain in host cells for some time after completing their growth.

The effect of natural enemies upon the biology of the host

A total of 965 host brood cells with identifiable contents were excavated during the course of this study. Of these, 56 (5.8%) had been attacked by *B. pulchellus* larvae and 59 (6.1%) had become infected by microbial or fungal pathogens.

Bombyliids differentially attacked reproductive brood hosts; 52 of 770 (6.8%) male or gyne brood cells contained these parasites whereas only 4 of 195 worker brood individuals

(2.1%) were affected. This difference was significant ($\chi^2 = 6.14, p < 0.02$).

Microbial pathogens affected proportionately more worker than reproductive brood cells ($\chi^2 = 7.33, p < 0.01$), with 20 of 195 (10.2%) worker brood and 39 of 770 (5.1%) reproductive brood individuals being affected.

The combined effect of these mortalities resulted in the death of 12.3% of the worker and 9.3% of the reproductive brood. When the minor mortality factors are added these figures increase to 13.3 and 9.7%, respectively. The prevalence of hidden mortality in the reproductive brood indicates that the latter figure is certainly underestimated, probably by at least 150%. With a worker brood averaging 6.65 individuals per nest, a total mortality of 13.3% represents an average loss of 0.9 worker brood individuals per nest.

The larger size and complexity of late summer nests plus the difficulty of distinguishing some filled-in reproductive and worker brood cells made it difficult to estimate reproductive brood productivity accurately. However, the total number of cells found in late summer nests averaged 25.5 ($N = 8$, time period 8; accurate estimates of the number of filled-in cells were not made later in the season but provisioning had almost completely ceased by that time), of which approximately 18.9 would be reproductive brood. Taking a total reproductive brood mortality of 9.7% to be underestimated by 150% as described above, an estimate of 24.25% mortality is obtained, representing 4.6 individuals per nest.

Table 5 indicates that pollen ball and larval mortality affected female reproductives disproportionately, in a ratio of 3.5:1. Prepupal and pupal mortality also affected female brood more than male but only slightly so, in a ratio approximating 1.1:1. The pollen ball sex ratio found in this study was 1:1.94 males to females whereas that based upon pupae was 1:1.52 (L. Packer, unpublished data). The latter figure clearly represents the sex ratio after most mortality had occurred. A primary sex ratio of 1:1.94 is transformed into a ratio of 1:1.62 when differential mortality of the sexes is taken into consideration (assuming a reproductive brood of 18.9 individuals before mortality), considerably closer to the estimate based upon pupae.

Guarding

Halictine colonies commonly contain a bee that spends most of its time guarding the nest entrance. In spring, solitarily founded nests must remain unguarded while the female forages. Multiple-foundress nests are often guarded by the dominant female at that time (Packer 1986*b*); however, no significant differences in brood survival between haplometrotic and pleometrotic nests were discovered.

Guarding was observed during the summer phase, but was intermittent, and a rigid division of labour between guarding and foraging workers was not observed. In pleometrotic nests, the dominant foundress guarded in spring and often retained this behaviour during worker foraging ($N = 3$). No further observations were made on this aspect of the biology of *H. ligatus*.

Discussion

The most important brood parasite found in this study was the bee fly *Bombylius pulchellus*. Depredations of this parasite may have been underestimated: bombyliids may sometimes require more than one host to complete their development and some prepupal and pupal deaths attributed to microbial infection may have resulted from partial consumption by bee fly larvae. This parasite has previously been reported from other halictine bees such as *Lasioglossum zephyrum* (Batra 1965). Batra found that adult bee flies were active for a period of only 9 days and their first larvae were found in host nests 23 days after the first adult bombyliids were observed. In the laboratory, she found that bee fly larvae consumed one or two host pupae and prepupae. In the present study, adult bee flies were observed over a period of 10 days and their first larvae were detected 48 days after the first adults. Because *H. ligatus* is a much larger species than *L. zephyrum* it seems likely that more than one immature of the latter species would normally be required for bee fly larval development.

A long period elapsed between the observation of adult parasite oviposition and the excavation of the first larvae. Studies of the related bombyliid, *Heterostyla robustum* (Bohart *et al.* 1959), indicated that first-instar larvae locate a host cell and then remain inactive (usually inside the pollen ball) until the host attains the prepupal stage. Most *B. pulchellus* larvae attacked reproductive brood hosts even though oviposition occurs during the spring provisioning phase when worker brood is being produced. This indicates that the eggs or first-instar larvae remain inactive for a long period before searching for a host brood cell. The life cycle of this parasitoid appears to be synchronized to attack reproductive brood hosts. The shorter period between adult and larval activity observed by Batra (1965) resulted in host workers being parasitized rather than reproductives, as in the present study. It is difficult to provide an adequate explanation for this difference in strategy between populations of *B. pulchellus*. However, it is possible that multiple hosts are used by each population, making precise adaptations to the phenology of one individual host species difficult.

Both *H. robustum* and *B. pulchellus* larvae attack when the host is at its largest biomass, in the prepupal stage. This delayed feeding results in a larger host for parasite larvae to feed upon. Additionally, the delay ensures that large numbers of host brood are available for later parasitism if more than one prepupa is required for parasite development. Such long periods of inactivity are well known in parasitic insects in which eggs or newly emerged larvae wait for the host to reach a suitable stage before feeding begins.

Bee flies have been observed to flick their eggs down or around host burrows while hovering over them (Bohart *et al.* 1959). The clumped distribution of frequency of *B. pulchellus* larvae within nests indicates that either the same nests are used repeatedly for oviposition or that more than one egg is laid in an egg-laying bout. Nests with entrances obscured by vegetation were more likely to suffer from these parasites. This association was not significant but was in the opposite direction from that which might be expected if the adults were using purely visual cues to locate nests. First-instar *B. pulchellus* may exhibit negative phototaxis or positive olfactory responses to odours building up around nests with entrances situated under leaves. Both of these responses may result in higher rates of parasitism in nests with hidden entrances. Further research on the oviposition behaviour of bee fly adults and the behavioural responses of their first-instar larvae are required to verify the exact mechanism whereby successful parasitism is achieved.

Some diseased larvae were observed to have turned purple. Batra (1965) found *L. zephyrum* larvae that had turned red as a result of some disease and suggested that it might be the

TABLE 5. The effect of mortality upon reproductive brood sex ratio

	Time period							
	4	5	6	7	8	9*	11	Total
No. of nests	17	24	16	7	9	10	8	81
Pollen ball								
Mortalities	0	10	4	4		9		27
Sex ratio (% males)	52.2	44.1	12.4	11.8		25.0		
Mortality per nest								
Male	0.0	0.19	0.03	0.07		0.11		0.08
Female	0.0	0.23	0.22	0.50		0.45		0.28
Pupa								
Mortality	—	2	28	19	14	11	3	77
Sex ratio (% males)	—	75.0	64.4	66.7	11.8	36.0	20.0	
Mortality per nest								
Male	—	0.06	1.13	1.81	0.21	0.50	0.08	0.63
Female	—	0.02	0.62	0.90	1.54	0.88	0.30	0.71

*Pollen ball data for time periods 8 to 11 are pooled and listed here because of the very small number of provision masses produced at that time.

bacterium *Serratia marcescens*. This pathogen, or a related species, may have been the cause of some mortality in this study. Batra identified mycelia of the fungi *Fusarium* and *Penicillium* from *L. zephyrum* brood. No attempt was made to identify fungi in the current study.

It is likely that the filling-in of infected cells serves to decrease the spread of pathogens. It is interesting to note that some halictine species are known to leave their brood cells open for most of the immature developmental period (Knerer and Plateaux-Quénu 1966). This allows inspection of cell contents and, presumably, the rapid detection of diseased larvae. Species that plug their brood cells with soil have been observed to open them periodically and inspect cell contents (Batra 1964, 1968). Laboratory experiments with *H. ligatus* indicated that foundresses that had lost their entire brood through microbial infection (probably resulting from overwatering of the soil) began to forage for pollen before the brood was expected to eclose from the pupa (L. Packer, unpublished data). This indicates the adaptive significance of cell inspection; it enables a female to make up for brood mortality earlier than would otherwise be the case.

Halictus ligatus exhibited high productivity in this study. Nest survival until worker emergence was high, at approximately 90%; whole-nest mortality after worker emergence was negligible; and the survival rate of individual brood was high, around 90% for the worker brood and between 70 and 90% for reproductives. Longer-term studies are required to establish whether this pattern is usual. However, the observations of Knerer (1973) on *Lasioglossum malachurum* and those of Bohart *et al.* (1959) on *Nomia melanderi* indicate that parasites and predators can build up very large populations at host–prey aggregations and can cause catastrophic population crashes. Nonetheless, the data presented here indicate that high levels of host recruitment are possible, although the effects of mortality between reproductive brood eclosion and nest establishment the following spring remain to be made.

The levels of mortality recorded here are low in comparison to those found in trap-nesting megachilid bees for which 40 to 60% brood cell mortality appears to be common with extreme values ranging from 25 to 87% (Tepedino and Frohlich 1982; Tepedino and Parker 1983, 1984). Michener (1985) has argued that ground-nesting bees probably suffer more mortality from predators and parasites than do twig-nesting ones such as megachilids and some xylocopines. This is because enemies of ground-nesting species search for host nests in a two-dimensional environment whereas parasites and predators of twig-nesting bees have to locate more sparsely distributed hosts in three dimensions. It is interesting to note that despite the generally lower rates of mortality of *H. ligatus* brood in comparison to those of the megachilids studied by Tepedino and Parker (1983, 1984), the percentage of nests attacked by one or more parasites was comparatively high at 57% (using the values from time period 7, before the parasite larvae moved away from the host brood cell to overwinter, as being the most accurate census of bombyliid parasitism) whereas corresponding figures for megachilids ranged from 38 to 63%. It is not possible to state whether differences in social organization, choice of nesting substrate, or simple annual fluctuations in mortality are responsible for the observed variation in mortality rates. Clearly, long-term studies of brood mortality across a range of solitary and social species would be most welcome, particularly if such behavioural diversity can be found within a single mixed-species nest aggregation.

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