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The Biology of a Subtropical Population of *Halictus ligatus* Say (Hymenoptera; Halictidae).
II. Male Behaviour

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With 3 figures

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Abstract

In the subtropical climate of the Florida Keys, *Halictus ligatus* has a continuously brooded, multivoltine colony cycle. This results in young gynes and workers being active at all times of year, potentially causing problems for males with respect to mate choice. Males responded to females by ignoring them, touching them briefly or by knocking them off of flowers into the surrounding vegetation, where mating takes place. Over half of the females at this locality are mated although males prefer large, young individuals. Multiple mating of females does occur. Males search for females around flowers and, less commonly, near nest sites. Because females of this social insect offer varied returns to male mating effort, it is not surprising that males exhibit mate choice.

Introduction

Behaviours exhibited by males in their attempts to make a genetic contribution to the next generation can have far reaching effects upon the general biology of an organism. Recent reviews of insect mating behaviour in general (THORNHILL & ALCOCK 1984) and of bees in particular (ALCOCK et al. 1978; EICKWORT & GINSBERG 1980) have demonstrated the importance of differences in male mating strategy to other aspects of behaviour and ecology.

Local mate competition has been suggested as an explanation of female biased sex ratios in social Hymenoptera (ALEXANDER & SHERMAN 1977). However, it is possible that this effect could promote female biased sex ratios that would favour the evolution of sociality. Thus, local mate competition could produce conditions favourable to the evolution of worker altruism via kin selection. This adds another dimension by which male behaviour can influence social evolution.

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BARROWS was the first author to realize the importance of male behaviour in primitively eusocial halictidae. He showed that most male halictids patrol rendezvous places where females are likely to be found (BARROWS 1976), some hold territories around nest entrances (BARROWS 1975c), that females of some species may mate more than once (BARROWS 1975b), that pheromones and aphrodisiacs are produced by females (BARROWS 1975b) and that males recognise females and habituate to them by using odour cues (BARROWS 1975b, BARROWS et al. 1975). More recently, KUKUK (1985) has shown that males of *Lasioglossum* (*Dialictus*) *zephyrum* produce an antiaphrodisiac with which they mark females.

The subject of the present paper is the reproductive biology of male *Halictus ligatus* in the subtropical climate of the Florida Keys. An analysis of female reproductive success will be given elsewhere. This population exhibits several remarkable deviations from the social patterns found in other species and at other localities of the same species (PACKER & KNERER 1986a): there is a continuously brooded multivoltine colony cycle and even though discrete queen and worker castes may be identified, there is a marked reduction in the reproductive division of labour. Most social insects have phenological and/or behavioural mechanisms that serve to reduce the probability that males will mate with workers. At this locality males, newly emerged gynes and workers co-occur throughout the year and no behaviours that would isolate unmated gynes from other females were observed. Clearly, this poses interesting problems for males with respect to mate choice.

Male behaviour was investigated in four ways. 1) Male-female interactions were observed, the females captured and their various biological attributes assessed so that factors that may have influenced the observed male behaviour could be examined. 2) Diurnal variation in male and female activity patterns was investigated. 3) Diurnal variation in the suitability of available females was assessed. 4) Females caught and dissected as part of other studies into the biology of *H. ligatus* at this site were analysed to see which female categories were more likely to have mated.

Methods

Male-Female Interactions

These were observed over a period of several days in Dec. 1982. Females that were feeding or foraging on a large bush of *Bidens pilosa* were watched until a male had approached and his behaviour towards the female categorized. The female was then captured and preserved in Kahle's fixative. Males proved to be extremely fast and it was impossible to capture both participants in the interaction. Females were dissected to assess their reproductive status — ovarian condition and insemination, and their head widths and relative age recorded. The latter was done by adding the number of nicks in the wing to the score for mandibular wear to give a generalized index of wear which is a rough estimate of age.

Three categories of females were identified upon the basis of male response. A different terminology from that of BARROWS (1975b) is adopted here because of differences in the details of the interactions between the sexes observed in *H. ligatus* compared to the species that he studied.

1. *Untouched.* Many males were observed to orient towards a female and hover over her from a distance of several cm for a few s before flying away. The females that elicited this lack of

interest on behalf of the males were placed in the "untouched" category. This response is similar to that of male *L. (D.) zephyrum* when presented with female models marked with odour cues (KUKUK 1985).

2. *Touched.* Once having oriented towards the female many males descended, made very brief contact with the female and flew away immediately afterwards. These females were referred to as having been "touched". This type of interaction was the one most commonly observed.
3. *Mated.* On several occasions, males were observed to fly straight at a female and knock her off the flower and into the surrounding vegetation. Previous observations had indicated that mating takes place amongst the herbiage and does not last very long, in the order of 10—20 s. Females that were dislodged from flowers in this manner would have received a successful mating attempt.

Daily Activity Patterns

On the 12th, 14th, 15th and 16th of Feb. 1984 half-hourly transects were made through the study site. On each occasion the same path was taken and the number of males observed feeding or searching and the number of females on flowers was recorded during a period of 10 min. Every precaution was taken to ensure that the area was covered at about the same rate so as not to concentrate upon areas of spatially or temporally high bee density. Air temperature at ground level and 1 m above the soil surface was recorded, by an assistant, at the mid point of the sampling period. Soil temperature at a depth of 15 cm was also noted and brief descriptions of general weather conditions were made.

Diurnal Variation in Suitability of Females

Two sets of collections were made to investigate whether there was any diurnal variation in the time of flight of different categories of females that might be differentially suitable as mates. On the 17th of Feb. 1984, females were collected from flowers at half-hourly intervals. The head width and number of nicks in the forewing margin of each female were noted using a hand lens with an ocular micrometer — accurate to 0.1 mm. The bees were then released so that any differences observed in later samples would be due to different activity patterns of different categories of bees and not simply because the earlier flying bees had already been caught.

On the 23rd of Dec. 1982, samples of females from flowers were collected and preserved in Kahle's fixative at 9.00, 11.00, 13.00 and 15.00 h. They were dissected and measured as described above.

Other Samples

Males are expected to mate preferentially with the more productive females. At this locality these females will be the queens and ovipositing workers. A cuckoo-like caste, which must lay fertilized eggs, is also found (PACKER 1986).

During the course of investigations into the biology of *H. ligatus* at Knights Key, 858 females were caught at flowers and 420 excavated from nests. Individuals in the latter sample could be classified as queens, laying workers or non-laying workers. Size variation of queens and laying workers, compared to non-laying individuals were used to predict the probability that males should mate with females of a given size. Females were divided into size classes of .1 mm and multiple linear regression was performed on the arcsin transformation of the three variables. The dependent variable was the proportion of females in the various size classes in the flower-caught samples that had mated. Some of the youngest females may not have had sufficient time to mate. Therefore, only flower caught females with an index of wear above zero were included in the analysis. The proportions of queens and laying workers in each of the size classes were used as predictor variables. For this analysis, a worker that contained one half of an oocyte or more was considered to be a laying worker (for details of ovarian categories see PACKER & KNERER 1986a).

Because cuckoo-like individuals were collected in special samples (PACKER 1986) an unbiased estimate of their relative frequency in the population is not available. These females were intermediate in size between queens and workers with a wide overlap with each. Further, it is not expected that they make up a large proportion of the population — only 24 were found during the duration of the study even though their behaviour makes them particularly obvious. It seems unlikely that the omission of these females alters the general nature of the results in any meaningful way.

Additional observations were made of male behaviour during the course of the field work at this locality. In particular, two sleeping aggregations of males were studied. On the late afternoons of Apr. 16th to 18th 1982 the nocturnal aggregating behaviour of males was studied by means of the capture-mark-release-recapture technique. One aggregation of "sleeping" males was found on the 16th of Apr. amongst the berries of a broken branch of a Brazilian pepper tree. Several males escaped but five were marked with yellow testors PLA enamel paint. On the following afternoon another sleeping aggregation site was discovered near the first, amongst the berries of the same species. These males were marked with red paint and released. On the same day four bees from the first site were recaptured and a further 23 were marked with blue. Male bees were recaptured on the 18th but no further marking was performed because it was felt that this procedure was greatly altering the probability that the bees would return to a repeatedly disturbed spot.

Results

Mating Behaviour

Males of *H. ligatus* seem to exhibit non-sequential patrolling (terminology of BARROWS 1976): individual males fly around certain restricted portions of the study site. They pay particular attention to patches of *Bidens pilosa* which grew commonly, was the main pollen and nectar source for foraging females and serves as the main rendezvous site for the sexes. This type of searching behaviour has been reported for many halictines (BARROWS 1976). Although detailed observations of marked males were not made, it appears from studies of sleeping aggregations (described above) that males may stay in the same general area at least for several days. Males actively searched for females on flowers of *B. pilosa* and were attracted to areas where there were nests containing young emerging gynes, indicating that attractive pheromones may be given off by sexually receptive females. This was confirmed by the fact that forceps used to remove young gynes from nests during excavation were attractive to males for several min. after the female had been released.

In addition to patrolling, males would chase some suitable mates in-flight and attempt to knock them down. This was not observed in any of the halictid species studied by BARROWS (1976). Males would also pay some attention to areas around a nest in which large numbers of young gynes were emerging, but no successful matings were observed to result from either of these behaviours.

59 females were caught after their interactions with males had been recorded. 6 females were caught in copula, 40 after being touched and 13 were ignored by males. These bees, taken together, did not differ in any of the measured attributes from the sample of 90 females collected on Dec. 8th as part of the investigation into the phenology of *H. ligatus* at this site. Thus, the mean size of the bees did not differ ($t = .36$, $p > 0.5$); the proportion of bees that had already mated were the same (χ^2 .015, $p > 0.9$); the frequency of different ovarian categories did not differ ($\chi^2 = 5.2$, $p > 0.05$) and neither did the proportion of females with different degrees of wing wear ($\chi^2 = 1.04$, $p > 0.5$). Therefore, it is legitimate to consider the 90 females of the Dec. phenology sample as being a control group against which variation in the three interaction categories may be tested.

Summary statistics for the three interaction categories and the Dec. sample are shown in Fig. 1. Neither the untouched or touched categories differ in size from the general sample ($t = 0.09$, $p > 0.9$; $t = 1.30$, $p > 0.1$ respectively), but the mated bees were significantly larger ($t = 2.80$, $p < 0.02$). Differences between the interaction groups and control sample with respect to the proportion of bees that had already mated were not significant ($\chi^2 = 0.80$, $p > 0.5$; $\chi^2 = .14$, $p > 0.5$; $\chi^2 = .0036$, $p > .95$ for mated, touched and untouched bees respectively). Mated bees were more likely to have undeveloped ovaries compared to the control sample (Fisher's exact test $p = 0.017$) but neither of the other categories gave significant results ($\chi^2 = .41$, $p > 0.5$ and $\chi^2 = .69$, $p > 0.2$ for touched and untouched bees respectively). Mated bees were significantly more likely to be unworn than the controls (Fisher's exact test, $p = 0.010$) whereas the other two groups did not differ ($\chi^2 = .003$, $p > 0.95$; $\chi^2 = .014$, $p > 0.8$ for touched and untouched bees respectively).

8 (20 %) of the touched bees and 4 (31 %) of the untouched individuals were unmated. All but one of the touched, virgin bees were unworn, two of the four untouched, unmated individuals were also unworn. It would be expected that these individuals would be attractive to males. They were significantly smaller than the monthly sample (mean head width unmated, touched or ignored females = 2.86 mm, SD = 0.14, $t = 3.52$, $p < 0.001$). Thus, males actively avoid mating with particularly small females even if they are young and have not mated.

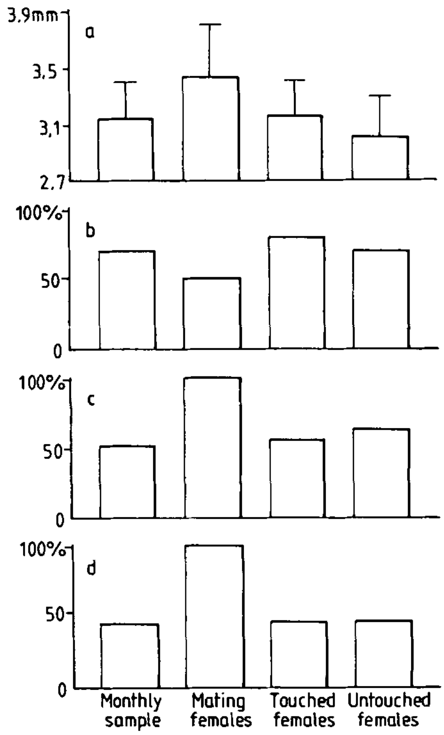

Fig. 1: Data for the monthly sample and females involved in the three categories of male-female interaction. a) Head width (Mean and SD), b) % mated, c) % with no ovarian development, d) % with an index of wear of zero

Daily Activity Patterns

Results of the half-hourly censuses of bee activity and temperature variation are shown in Fig. 2. Much of the between-day variation in activity can be attributed to the weather conditions on the four days. The 12th and 16th were the hottest days and bees began foraging at 8.00 h on the former, but were delayed until 9.15 h on the 16th as a result of an early morning shower. The 14th was a cool, misty day with intermittent showers which did not stop completely until noon.

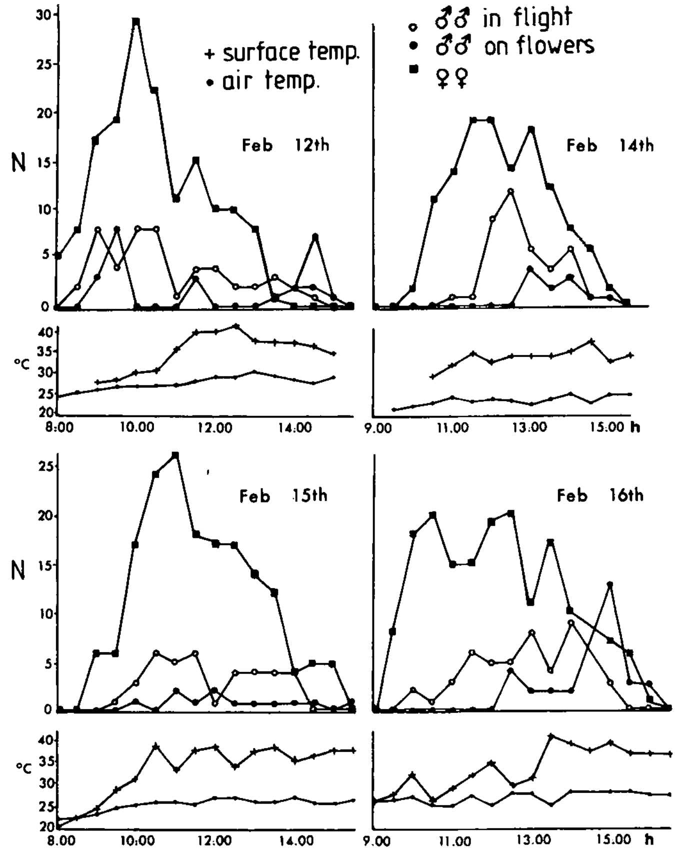

Fig. 2: Number of males and females on flowers and males flying at ½-h intervals on four days in 1984 (upper graphs) and variation in air and surface temperature for the same day (lower graphs)

The females show a peak of activity before midday with an at first rapid and then gradual decrease until about 15.00 h. When females begin foraging early (12th and 15th) the peak is well defined, but when delayed by cool weather or rain a longer period of maximum activity occurs (14th and 16th).

Male feeding behaviour seems to occur mostly well after the peak in female activity, but on hot, dry days they may feed before the females attain maximum abundance, as occurred on the 12th. The only other day when males were observed to feed before mid-day was the 15th when a high air temperature was reached at an unusually early time (38 °C at 10.30 h). Male searching behaviour peaks a little later than the activity patterns of females. Additionally, they are disproportionately more active later in the day.

Males begin to congregate around sleeping sites after 15.00 h when very few females are to be observed flying. The brief attempts at studying male sleeping aggregations indicate that some males may return to the same nocturnal resting place for at least two days running. It is quite likely that if left unmolested they would have returned in larger numbers, but unfortunately they remain sensitive to even slight disturbances until well after dusk. Thus it was not possible to get close enough to observe the spots of paint: the bees had to be captured as a result.

Diurnal Variation in the Suitability of Females

It seems that males preferentially mate with younger, larger females. Therefore, the samples of bees collected at different times of the day were analysed to see if there was any diurnal variation in the size or age of females or in their reproductive condition.

Analysis of variance revealed no difference in size or number of nicks in the wing margin amongst the ten samples collected at ½-h intervals on the 17th of Feb. This may be due to the small sample sizes. Therefore the tests were repeated with samples divided into morning and afternoon captures only. A t-test revealed no significant difference in head width between the bees caught in the morning and those caught in the afternoon. However, there were significantly more unworn bees in the afternoon sample ($\chi^2 = 4.73$, $p < 0.05$). The samples collected at 9.00, 11.00, 13.00 and 15.00 h on the 23rd of Dec. showed no significant variation in age or size when tested separately or in morning and afternoon samples. No diurnal variation in the frequency of unmated bees was found. However, when only unworn bees were considered, those collected after midday were significantly larger than those captured earlier (mean head width of morning bees = 3.18 mm, SD = 0.25, N = 40; afternoon bees = 3.31, SD = 0.20, N = 27; $t = 2.26$, $p < 0.05$).

Other Samples

Taken together, all of the 852 bees caught from flowers throughout the duration of the study of *H. ligatus* at Knight's Key indicate a positive correlation between the probability that a female will have mated and her size (Fig. 3). The results of the regression analysis indicate that both the probability that a bee will be a queen and that of it being a laying worker are taken into account. Over 88 % of the variation in the frequency of flower-caught female matings are explained by these two variables, both of which have significant effects (queens $p < 0.0005$, ovarially developed workers $p < 0.05$). The regression equation is

$$\arcsin \sqrt{x} = 1.23 \arcsin \sqrt{y} + 0.97 \arcsin \sqrt{z} + 0.04$$

where x is the mating frequency of flower-caught females, y is the frequency of queens and z the frequency of laying workers as a proportion of all active females excavated from nests. A comparison of the observed data and that predicted from the regression analysis is shown in Fig. 3.

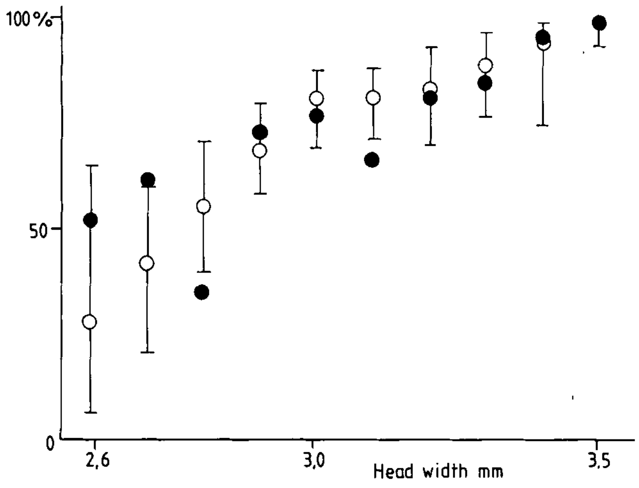

Fig. 3: Variation in percentage of females of different sizes that had mated in the flower-caught samples (open circles) and the expected frequencies from the multiple regression analysis (closed circles). 95 % confidence limits are shown for the flower-caught sample data

Discussion

It has often been stated that males should not be choosy but mate with any female. For example, DAWKINS (1976) states that "excess has no meaning for a male". However, this viewpoint probably stems more from anthropomorphic wishful thinking than scientific fact. Thus, although males often make no more contribution to the next generation's well-being than the drop of semen that leads to fertilization, recent investigations of mate choice in species in which the males contribute either prolonged parental care or a large amount of nutrients along with the sperm mass have indicated that there are many situations in which males will be choosy mates (GWYNNE & MORRIS 1983; THORNHILL & ALCOCK 1983). In addition, DEWSBURY (1982) has argued that males should always exhibit some degree of caution because of the energetic cost associated with ejaculation plus the possibility that a more productive mating may be missed.

Social insects have high variance in female reproductive output; gynes will produce many offspring whereas workers have low fecundity or lay only male-producing, unfertilized eggs. Therefore, male choice may well be expected in these organisms. Many social insects have extremely different queen and worker castes and mating behaviours that preclude worker/male matings. Less advanced social species often have annual colony cycles and there is some phenological differentiation between the time of year that workers and young gynes are flying; even if there is some overlap the workers are usually older and smaller thus giving the males some cues as to which females are worthy mates. In addition, many species have a sex attractant pheromone which is produced only early in the life of a female, thus by the time males have emerged most of the workers will not be attractive to them. Some primitively eusocial bees have a colony cycle which involves queen replacement during the summer and therefore some members of the "worker" brood must mate and become ovarially developed. These species also have a high proportion of males in the first brood to accomplish the fertilization of the replacement queens (BREED 1976). In at least one of these species, *Lasioglossum (D.) zephyrum,* the presence of a queen causes the workers to actively repel male advances (GREENBERG & BUCKLE 1981). Also, in the same species, males will habituate to the odours of females that they have already mated with (BARROWS et al. 1975), and even deposit an antiaphrodisiac compound on them (KUKUK 1985). All of these mechanisms result in a reduced probability that a male will make an unprofitable mating attempt.

The unusual colony cycle of *Halictus ligatus* at Knight's Key offers some interesting problems for males. This is because young gynes and workers of all ages are active at all times of year yet provide very different returns on mating effort.

Males of *H. ligatus* at Knight's Key were observed to fly around the preferred pollen and nectar source (*Bidens pilosa*) in search of females. They would also fly around open areas where there were nests of *H. ligatus* and chase some females at such sites. However, rendezvous sites that only young gynes and males might visit were not observed. In addition, males were constantly abundant around the study site, and were so common that it is unlikely that a female could ever complete a foraging trip (average length approx. 20 min) without being detected by at least one searching male. It is unlikely that the probability of worker mating is decreased by differences in flight behaviour between the castes. Indeed, the fact that over 50 % of the bees classified as workers were mated (PACKER & KNERER 1986 a) indicates that there cannot be much in the way of such a mechanism.

It is to be expected that males of *H. ligatus* distinguish between different types of females in order to detect which individuals are worthy mates. Observations of interactions between males and females indicate that males preferentially mate with large, young females; i.e. those that are most likely to be young gynes. The females caught in copula also tended not to have any ovarian development, this presumably resulting from them being too young to have developed their ovaries. The advantage to a male in mating with females too small to be queens may lie in the fact that such individuals do often lay at least some diploid eggs and some become replacement queens after the death of the foundress (PACKER & KNERER 1986 a). However, many of the worker-laid eggs may well produce males and thus not be fertilized. Additionally, any one worker will lay comparatively few eggs that are destined to become young reproductives in comparison to those produced by queens, thus the advantage of mating preferentially with large individuals remains. This may explain why males avoid mating with small, virgin females.

The observation that the majority of interactions between males and females result in the male touching a female but flying off again immediately is of some interest. It is possible that they are detecting some contact pheromone that gives them information concerning the females' suitability as a mate. However, the observation that all real mating attempts were initiated without intermediate touching (the males would fly at the females from some distance and knock them off of a flower or follow them as they flew) indicates that this is not the case. It could be that the males are marking the females to ensure that they do not make a rash mating attempt the next time they come across them. The searching behaviour of males seemed to fit in with the patrolling behaviour described by BARROWS (1976) for a wide range of sweat bees. It is quite likely that a male will come across the same female several times during the course of a day if not during the same foraging flight, and it may be advantageous for them to mark females that they perceive as being unworthy of a mating attempt to give them a longer distance cue for the next time. The fact that males oriented towards some females without making any further advances before flying away indicates that this might be the case. Untouched females differed from those that were touched in none of the variables tested (although in the above account interacting females were tested against a control sample, the same general results were obtained when the three groups were tested amongst themselves). The recent discovery of just such marking behaviour with an antiaphrodisiac compound by males of the confamilial *L. (D.) zephyrum* (KUKUK 1985) further strengthens this possibility. A long-distance acting pheromone can release the complete male sexual response. Observations that males would fly at some females from a comparatively great distance (10—20 cm) or follow them through fairly dense undergrowth, where visual stimulation is likely to be insufficient, indicates that this is the case.

In addition to the in-flight detection mechanism of suitable females, males seem to maximize their chances of finding a suitable mate by their periods of flight activity. Males search for females at approximately the same time that the females forage on flowers, but disproportionately so later in the day. It was found, in two separate investigations, that females caught in the afternoon are more likely to be young or larger, unworn individuals. Thus, some slight behavioural differences between young females that are more suitable mates and older or smaller individuals may be responsible for the timing of male searching behaviour. Nonetheless, such temporal separation of suitable mates is weak.

ALCOCK et al. (1978) have shown that species that nest in dense aggregations tend to mate at the nest site, whereas more dispersed nesters are more likely to mate at flowers. *H. ligatus* nests at Knight's Key are fairly well dispersed with minimum inter-nest distances varying from 15 cm to over 10 m. Thus it is not surprising that males tended to search for females at flowers. However, they were also observed flying around areas that contained a nest towards the end of the colony cycle in which young reproductive females were emerging in large numbers. In southern Ontario, where this species forms dense nesting aggregations (PACKER & KNERER 1986b), mating was never observed at the nest site but took place on flowers nearby. Interestingly, in southern Mexico where nests are much more widely dispersed, as many as 13 males were observed congregating around a single nest entrance (PACKER, unpubl. obs.). These males did not form microterritories as described for *L. (D.) rohweri* by BARROWS (1975a); the composition of individuals at the nest entrance was very unstable, with males pursuing individual females as they left the nest or flying to wait outside other nests several m away.

One of the most interesting findings of this study is that males will mate with females that have already mated. Three of the 6 females caught in copula had already mated. It is not thought likely that the sperm found in the spermathecae of these three females had come from the male that was observed in the mating attempt: the females were caught well before mating was complete. Additionally, it is known that it takes from 12—18 h for the sperm from one mating to reach the spermathecae of a honey bee queen (RUTTNER 1960), complete transfer taking up to 40 h (WOYKE 1983). Delayed sperm transfer has also been established for a different halictine species, *L. (D.) zephyrum* (BATRA 1966). Further evidence of multiple mating comes from observations that gynes "resting" in their natal nest after the end of the colony cycle at colder times of year were highly attractive to males even though 85.7 % of them had already mated (PACKER & KNERER 1986a). These nests were the ones that attracted searching males.

Multiple mating is a phenomenon that has caused some controversy amongst theorists of social evolution. COLE (1983) has argued that multiple mating is more prevalent in species with large colonies and therefore serves to ensure that the queen does not run out of sperm. Alternatively, it has been suggested (PAGE 1980; PAGE & METCALF 1982) that multiple mating reduces variance in brood viability resulting from the production of diploid males. Unfortunately, the data for primitively eusocial species with small colonies is very sparse. The only data available are for *L. (D.) rohweri* which mates from one to four times (BARROWS 1975b) and *L. (D.) zephyrum* which was thought to mate once (BATRA 1966; BARROWS 1975b). However, evidence from electrophoresis indicates that as many as 36 % of the females of the latter species may be multiply inseminated (KUKUK 1985). Thus, *L. (D.) zephyrum*, *H. ligatus* (the Florida population) and also *Lasioglossum (Evylaeus) malachurum* (PACKER & KNERER 1985) may be added to the list of multiple mating primitively eusocial species. Thus, multiple mating amongst primitively social species with small colonies may be more prevalent than the present literature suggests. The possibility that multiple mating by gynes in this population has had deleterious effects upon the degree of sociality will be explored elsewhere (PACKER, in prep.).

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Literature Cited

ALCOCK, J., E. M. BARROWS, G. GORDH, L. J. HUBBARD, L. KIRKENDALL, D. W. PYLE, T. L. PONDER & F. G. ZALOM, 1978: The ecology and evolution of male reproductive behaviour in the bees and wasps. Zool. J. Linn. Soc. Lond, **64**, 293—326.

ALEXANDER, R. M., & P. W. SHERMAN, 1977: Local mate competition and paternal investment in social insects. Science **196**, 494—500.

BARROWS, E. M. 1975a: Mating behavior in halictine bees (Hymenoptera: Halictidae): II. Microterritorial and patrolling behavior in males of *Lasioglossum rohweri*. Z. Tierpsychol. **40**, 377—389.

——, 1975b: Mating behavior in halictine bees (Hymenoptera: Halictidae): III. Copulatory behavior and olfactory communication. Insectes Soc. **22**, 307—331.

——, 1975c: Individually distinctive odors in an invertebrate. Behav. Biol. **15**, 57—64.

——, 1976: Mating behavior in halictine bees (Hymenoptera: Halictidae): I. patrolling and age-specific behavior in males. J. Kans. Entomol. Soc. **49**, 105—119.

——, W. J. BELL, & C. D. MICHENER, 1975: Individual odor differences and their social functions in insects. Proc. Nat. Acad. Sci. USA **72**, 2824—2828.

BATRA, S. W. T., 1966: Life cycle and behavior of the primitively social bee *Lasioglossum zephyrum*. Univ. Kans. Sci. Bull. **46**, 359—423.

BREED, M. D., 1976: The evolution of social behavior in primitively social bees: a multivariate analysis. Evolution **30**, 234—240.

COLE, B. J., 1983: Multiple mating and the evolution of social behavior in the Hymenoptera. Behav. Ecol. Sociobiol. **12**, 191—201.

DAWKINS, R., 1976: The Selfish Gene. Oxford Univ. Press, Oxford.

DEWSBURY, D. A., 1982: Ejaculate cost and male choice. Am. Nat. **119**, 601—610.

EICKWORT, G. C., & H. S. GINSBERG, 1980: Foraging and mating behavior in Apoidea. Ann. Rev. Ent. **25**, 421—446.

GREENBERG, L., & G. R. BUCKLE, 1981: Inhibition of worker mating by queens in a sweat bee, *Lasioglossum zephyrum*. Insectes Soc. **20**, 347—352.

GWYNNE, D. T., & G. K. MORRIS, eds., 1983: Orthopteran Mating Systems. Westview Press, Boulder.

KUKUK, P., 1985: Evidence for an antiaphrodisiac in the sweat bee *Lasioglossum* (*Dialictus*) *zephyrum*. Science, **227**, 656—657.

METCALF, R. A., 1980: Sex ratios, parent-offspring conflict and local competition for mates in the social wasps *Polistes metricus* and *Polistes variatus*. Am. Nat. **116**, 642—654.

PACKER, L., 1986: The biology of a subtropical population of *Halictus ligatus* Say (Hymenoptera; Halictidae). IV. A cuckoo-like caste. J. New York Ent. Soc. (in press).

——, & G. KNERER, 1985: Social evolution and its correlates in bees of the subgenus *Evylaeus*. Behav. Ecol. Sociobiol. **17**, 143—149.

——, & ——, 1986a: The biology of a subtropical population of *Halictus ligatus* Say. I. Phenology and social organization. Behav. Ecol. Sociobiol. (in press).

——, & ——, 1986b: An analysis of variation in the nest architecture of *Halictus ligatus* in Ontario. Insected Soc. (in press).

PAGE, R. E., 1980: The evolution of multiple mating by honey bee queens (*Apis mellifera* L.). Genetics **96**, 263—273.

——, & R. A. METCALF, 1982: Multiple mating, sperm utilization, and social evolution. Am. Nat. **119**, 263—281.

RUTTNER, F., 1960: Fortpflanzung und Vererbung. In: Biene und Bienenzucht. (BUDEL, A., E. HEROLD, eds.) Ehrenwirth, München, pp. 5—22.

THORNHILL, R., & J. ALCOCK, 1983: The Evolution of Insect Mating Systems. Belknap, Harvard, Cambridge.

WOYKE, J., 1983: Dynamics of entry of spermatozoa into the spermatheca of instrumentally inseminated queen honeybees. J. Apic. Res. **22**, 150—154.

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