INTRODUCTION

Insects are the largest and most diverse group of animals and consequently demonstrate a great array of courtship patterns. Courtship and mating behaviour includes most of the activities performed by animals in the sexual reproduction (Mertins, 1971). Mating is of interest in the natural population process. It derives an added importance from the possibility of controlling the pest species by removing the adult males as with sex pheromone baited traps (Lyons et al., 1972). Courtship behaviour has been widely studied in many insects and there is much known about mating behaviour. However, few detailed studies of parasitoid courtship and mating behaviour exist. A large number of casual and fragmentary observations made on the diverse species suggest a complex sequence of reciprocal behaviour, worthy of greater attention. The behavioural changes of the parasitoids during mating of adults in the field are of concern to many researchers. Likewise, the effect of long term rearing on the physiology is little understood (Raulston et al., 1976).

The ethology of an insect can directly influence the genetic control programme, biocontrol programme, release of the sterilized species, competitiveness of field released species, etc. The high genetic diversity has been linked with a wide spread success of some of the biological control agents (Simmonds, 1963). In initiating mating, observation to elucidate the responses of males to virgin females or vice versa and details on activities may prove worthy to gain knowledge about this important life activity. A better understanding of the relationship between the control techniques and mating behaviour may prove useful in pest management (Dowell & Horn, 1975).
The sequence of mating typically consists of number of components (Bousch & Baerwald, 1967; Cole, 1970). Mating behaviour is obviously an aspect of sexual reproduction (Chapman, 1983). In the parasitic wasps it implies separate reproductive strategies for males and females, producers of sperm and eggs, respectively. The quintessence of sexual reproduction is the recombination of genetic material in the offspring. In general, fertilization is required for the production of a viable offspring. In the parasitic wasps this applied to daughters only, since sons result from unfertilized eggs. The insemination precedes fertilization. The male products are introduced into a female's genital tract by means of sexual contact, i.e. copulation and the sperms are stored in a spermatheca until recruited for fertilization (King and Radcliffe, 1969). As a rule, potentially inseminable females do not simply allow copulation; rather, males have to induce readiness to copulate by means of some sort of effort. Usually, it occurs in some form of a display, which may be called as courtship (Bastock, 1967).

The courtship and the copulation are by no means restricted to the parasitic wasps and the nature of their performance is a characteristic of their way of life. Frequently, however, due to parasitic way of life, the mating pool is very limited in space and time. This has implications for the way in which contributors can maximize reproductive success. For males, it is of paramount importance to be present ahead of female emergence since the inseminable females usually become available only for relatively short periods.
The reproductive success of females may also increase with multiple copulations. This would be the case if they were able to assess and compare the genetic quality of the potential partners, or if a copulation involve an energetic gain of some kind (Borgia, 1979; Thornhill and Alcock, 1983), or both. For enhancing the reproductive rate in the parasitic wasps, sperms of a second male can be utilized in certain circumstances (van den Assem, 1986).

In general, male parasitic wasps are the most active sex in courtship. On an encounter, a male will manoeuvre in such a way that he comes to take up a stereotypical position relative to the female, either on top of her or on the substrate. After accomplishing this, a display behaviour will start. In principle, displays consist of a repetition of fixed patterns of movements in which several limbs may participate. These repetitions occur continuously or at intervals, separated by short or long pauses (van den Assem, 1975).

The female's role in courtship is not conspicuous (van den Assem, 1986). A female need not release the stimuli periodically, as if responding to the male, to keep him going, nor does she influence the characteristic form of this movements or the precise timing of the repetitions. Once initiated, his display proceeds in a highly stereotypical fashion, on a living partner just as well as on a dead female or on a dummy. The external stimuli, that originates from female, are continuously perceived by the male.

In past, Genleys (1925), Seiltner & Notzi (1925), Fink (1926), Jackson (1928), Matthews (1962), Leong & Oatman (1968), Broodryk (1969)

Considering the importance of mating behaviour in the pest management programme, the present studies were carried out with the four biocontrol agents viz., Cotesia diurnii Rao & Nikam, Campoletis chlorideae Uchida, Eriborus argenteopilosus (Cameron) and Apanteles prodendae Viereck. Some of the preliminary observations on mating of C. diurnii and C. chlorideae have been noted by Sathe (1985b) and Sathe & Nikam (1986).

MATERIAL AND METHODS

Laboratory cultures of the parasitoids were used for the experiments. Mating behaviour of the parasitoid species were studied by caging the newly emerged individuals of both the sexes (1 α and 1 φ) in a test tube (size: 19 x 2.5 cm) at laboratory conditions (25 ± 1°C; 60 ± 6% R.H.). Twenty pairs of each parasitoid species were observed for their premating, mating and postmating behaviours. Simultaneously, the food preference for both sexes after and before mating were also noted. For observing mating interruptions, newly emerged one female and five males were caged in the test tube. The test tubes containing C. diurnii and A. prodendae were exposed to zero volt red bulb from 6 p.m. to 10 p.m.
for recording mating behaviour. During the course of experiment, adult parasitoids were fed with 50% honey. The assumption of the terms premating period, mating period, postmating period, high phase and low phase are as follows:

Premating period:

The period between the emergence of adult and initiation of the courtship behaviour.

Mating period:

The period from the initiation of the courtship up to the termination of the coitus.

Postmating period:

The period after the termination of the coitus till the death of the parasitoid.

High-phase:

In this, the male's head held away from the female's dorsum. He vibrates his wings very conspicuously over a large amplitude at the same time he performs a kind of movements with his hind legs on the female's wings. In addition, the male's body is also involved in slight forward-backward movements.

Low-phase:

During this, the wings were not vibrated, but remain elevated and the hind legs were kept in place. The male arches his entire body in such a way that the underside of his head, including palpi and mouth parts, comes near to the female's thorax and synchronously he presses the tip of his gaster on the upper side of the female's wings.
RESULTS

Mating behaviour of C. diurnii:

Premating:

The premating period was 40'. If food was provided, both sexes were attracted toward it prior to mating. During the premating period excitement behaviour in both sexes was not observed.

Mating:

The mating was not observed during day time in this species. However, it was accomplished during night immediately after the exposure of both sexes in test tube. The males usually respond immediately (attraction) and move rapidly and excitedly when in the immediate vicinity (recognition) of newly emerged virgin females. The female moved more slowly. As the male approaches the female, he shows considerably to orient to her. At the same time, wing vibrations (fanning) of varying intensities were common and repeated. The male antennae were spread and forwardly directed (antennation). When the female stopped moving, the male appeared to touch her abdomen. At that time, his antennae were posteriorly directed, contacting or touching the female's abdomen with up and down head movements. This phenomenon was repeated 10-15 times and mounting was attempted. Mounting consisted of high-low phases, including pauses alternate rapidly. High-phase, pause and low phase averaged 2"., 1.5", 1.5" respectively. After two phase shifts, the female has shown receptivity and then copulation occurred. Virgin females were normally responsive. Mounting and mating occurred after courtship, when the male was behind the female and begun to extend his genetalia by
curling the abdomen under his body until full contact was made with the female genetalia. Male mounted female dorsally. When mounting was complete the antennae remained stationary. Copulation lasted from 25"-30" (Ave. 28"). Presence of excess number of males have always interrupted a copulating pair. Coitus was terminated by both the sexes but, mostly by males. After copulation, the male and female were separated and moved rapidly away from each other. Males were polygamous whereas, females were monogamous.

Postmating:

Males have performed grooming behaviour. But females have not shown receptivity. Both sexes attracted toward food after separation. The postmating period averaged 7 days. The females were receptive till two days after their emergence.

Mating behaviour of C. chlorideae:

Premating:

The males were not attracted to food in the presence of females. As mating occurred immediately after emergence, there was no premating period.

Mating (Fig. 35-39):

The adults of C. chlorideae mated immediately after their emergence. Change in the behaviour of male occurred when a female was at a distance of 2.50 to 5.00 cm. The antennae of male were raised, vibrated speedily in air and for a moment spread the wings. Male held his wings at a 60° angle and kept vibrating them in short bursts. During display the antennae were held at a 60° angle. The courtship behaviour
lasted 7-12 revolutions. The females demonstrated receptivity to copulation by remaining stationary and continuously holding her antennae parallel with the substrate. Upon termination of courtship behaviour the male stroked the antennae of the receptive female with his antennae and then mounted. The high phase, pause and low phase averaged 4", 1", 2.5". After a phase shift female allowed the male to copulate. Upon mounting the female, the male grasped her thorax with his legs and then curved his abdomen under her's until he inserted his aedeagus into her vagina. During insertion of the aedeagus female didn't exhibit any movements. They remained stationary during copulation. Average time for copulation was 3.45' (range: 2' to 7.30'). Presence of more than one male always interrupted a copulating pair. Newly emerged males mated easily with one day old females.

It was found that 3-4 attempts were made by the males within a period of 2' for mating. The males showed intention to mate very soon than females. After 3 hr females allowed males to mate again. Females have shown long period of sexual receptivity i.e. till 96 hr after emergence. Males and females were polygamous.

Postmating:

Both sexes were attracted toward food after copulation. Males were found to show the intention to mate by orienting antennae, up-down movements of abdomen and walking towards female, but, females were not receptive. Females responded negatively to the trials of males. Postmating period averaged 11 days.
Mating behaviour of *E. argenteopilosus*:

**Premating:**

Females of *E. argenteopilosus* were attracted towards food immediately after emergence. They took some time for cleaning their bodies and thus the premating period averaged 8'. During premating period, the presence of male and female has not brought about any exiting behaviours.

**Mating:**

After introduction, males and females moved around in the test tube. Male after locating a female, stopped moving forward, elevated the wings, and began fluttering or vibrating them in arcs of 60° for several seconds. Such beats of fluttering often ends in an intense flutter in which the wings were vibrated faster and in longer areas than in fluttering itself. Intense flutters typically lasts not more than 5". After an intense flutter, the male usually moves to the female with wings elevated, briefly taps her thorax and abdomen with his antennae and mounts her from the side while folding his wings. He orients body, so that their heads are pointed in the same direction. Occasionally a male mounts a female with his head toward the female's abdomen but, quickly changes the direction to 180°, while antennating the female. Once mounted in the proper (dorsally) the male immediately moves back, bends his abdomen down and copulates with the female. The time from termination of flutter to beginning of copulation was of 12"-14". The average periods required for high phase, pause and low phase were 3", 1", 1.5". After two phase shifts copulation occurred. Receptive females make no obvious movements throughout the process of mating. The male during coitus
made number of noddings with his body. The mating period averaged 4.8'.
The coitus was terminated by males. Males and females were polygamous. The females were receptive till 4 days after their emergence. The presence of excess males resulted in interrupting copulation.

Postmating:

After mating both sexes moved away and remained motionless for a while. Both sexes were attracted toward food after separation. No multiple matings occurred. Even though the male showed intention to mate, by fluttering the wings, etc. but, female didn't allow the male to mount. The postmating period averaged 13 days.

Mating behaviour of *A. prodeniae*:

Premating:

After emergence the adults spent a brief time in cleaning their bodies. If food was available, feeding could occur immediately after the emergence. Premating period averaged 34'.

Mating:

During the day time mating was not observed. However, at night mating was noticed. A male when excited by the presence of female, walked toward her, fanning the wings. He simultaneously started moving antennae and abdomen. Female, after locating the male started moving her antennae and abdomen followed by movement of 3rd pair of legs. Often when the pair was close to each other, the female tried to run away and the male pursued her. Change in the behaviour of male occurred, when the female was at a distance of 2.50 to 3.00 cm. Male raised his antennae, vibrated speedily in the air and for a moment spread the
wings. Later he moved closer to female and grasped. Upon grasping the 
female, the male suddenly jumped upon the female's back from behind, 
mounted dorsally and then clasped her with his legs. The high phase, 
pause and low phase periods averaged 2.5", 1" and 2" respectively. After 
five phase shifts, the female has shown the receptivity and copulation 
occurred. During insertion of aedeagus the female didn't exhibit any 
movements. The males during coitus made a number of noddings with 
his body. Copulation period averaged 40". The coitus was terminated 
by either sex but, mostly by males. It was observed that males mated 
more than once in a single day (polygamous). Females were monogamous 
but, shown longer period (till three days after emergence) of sexual 
receptivity than males.

Postmating:

Within a period of 60-80' males tried again to mate, but females 
refused. During the trials males have performed orientation of antennae, 
circular movements around females. Both sexes get attracted towards 
the food after separation. Postmating period averaged 6 days.

DISCUSSION

The behavioural studies of parasitic wasps on courtship and mating 
exist though a large number of casual and fragmentary observations 
on diverse species, suggest a complex sequence of reciprocal behaviours. 
In so far as is known, this sequence typically consists of a behaviour 
chain including most of the following components (Bousch & Baerwald, 
orientation, wing fanning or vibration, mounting, antennation, copulation 
and post-copulatory grooming.
A premating period may be characteristic of some groups of hymenopterous parasitoids but, most species are ready to mate upon emergence from the cocoon (Laing & Caltagirone, 1969). Leong and Oatman (1968) reported the mating behaviour of Campoplex haywardi (Blanchard) (Hymenoptera: Ichneumonidae), a parasitoid of the potato tuber worm, Phthorimaea operculella (Zeller) in which the adults were mated soon after emergence (Premating period absent). In Orgilus lepidus Muesebeck and Apanteles (= Pseudoapanteles) dignus Muesebeck (Hymenoptera: Braconidae) the solitary, endo-larval parasitoids of the potato tuber worm and Kelseyia lycopersicella (Walsingham) respectively, premating periods were absent (Oatman et al., 1969; Cardona & Oatman, 1971) whereas, in Bathypectes curculionis (Thompson) (Hymenoptera: Ichneumonidae), a larval parasitoid of the Alfalfa weevil, Hypera postica (Coleoptera: Curculionidae) it was 35'-40' (Dowell & Horn, 1975).

In C. chlorideae, premating period was absent whereas, in C. diurnil, E. argenteopilosus and A. prodeniae premating periods were 40', 8' and 34' respectively.

In C. haywardi there was some indication that copulation was more successful with younger than older females. The females more than 24 hr old were rather reluctant to mate and those over 3 days old often rejected the pursuing males but, mating activities of the male were less affected by the age (Leong & Oatman, 1968). Weseloh (1977) reported that, females of Apanteles (= Cotesia) melanoscelus Ratzeburg (Hymenoptera: Braconidae), a solitary larval parasitoid of the gypsy moth Lymantria dispar (L.) remained receptive to males for at least 11 days of their adult life, and were courted. C. chlorideae females have
shown long period of sexual receptivity i.e. of 96 hr after emergence. The females of *A. prodeniae* were receptive till 3 days of their emergence, the females of *C. diurnii* were receptive for only first 2 days of their adult life while, males of *E. argenteopilosus* showed longer sexual receptivity (four days after eclosion) than females.

The actual copulation time was quite brief, normally less than one minute in many parasitoids (Biliotti & Daumal, 1969; Harbo & Kraft, 1969; Lewis, 1970 and Cardona & Oatman, 1971). The average copulation period, 6.8' was noted in *C. haywardi* (Leong and Oatman, 1968); in *Priopoda nigricollis* (Thos.) a parasitoid of the Birch leaf miner, *Fenusa pusilla* (Lepidoptera : Tenthredinidae) it was lasted from 3'' to 70'' (Quednau & Guevremont, 1975), in *B. curculionis* it was 3.58' + 16'' (Dowell & Horn, 1975) while, in *Neodiprion sertifer* (Geoff.) 9.2 + 0.2' (Lyons, 1976). In the present study, the copulation periods were 28'', 3.45'', 4.8' and 40'' in *C. diurnii*, *C. chlorideae*, *E. argenteopilosus* and *A. prodeniae* respectively.

In *P. nigricollis* the coitus was terminated by females (Quednau & Guevremont, 1975). The presence of excess males interrupted a copulating pair and the absence of resistance from females resulted copulation in *C. haywardi*. Similar observations were noted in the present forms. There was severe competition between males for inseminable females the male who was able to court at all have proven his male qualities in competition. Therefore, the female's ability to choose may be absent; hence, virgins females usually copulated with the first conspecific male encountered.
Multiple mating appears common for males but, females of several species were reported to be refractory after mating once (Fink, 1926; Oatman et al. 1969 and Cardona & Oatman, 1971). This may be variable, however, Apanteles (=Cotesia) flavipes females reported by Kajita & Drake (1969) mated only once were observed by Gifford & Mann (1967) to mate as many as eight times.

The males of Chelonius curvimaculatus Cameron (Hymenoptera: Braconidae), a parasitoid of potato tuber moth, *P. operculella* were polygamous, and females mate twice in rapid succession (Broodryk, 1969). In *A. digus* males were polygamous and females monogamous (Cardona & Oatman, 1971), in *B. curculionis* both sexes were polygamous (Dowell & Horn, 1975) while, the females of *B. anurus* were monogamous (Gordh & Hendrickson, 1976). In the present study, it was found that, the males of *C. diurnii* and *A. prodeniae* were polygamous and females monogamous whereas, both sexes of *C. chlorideae* and *E. argenteopilosus* were polygamous. A male of high quality should replenish a spermatheca or replace its contents with his own sperm in multiple copulation for enhancing the reproductive rate. However, in parasitic wasps, sperm of a second male can be utilized in certain circumstances; complete replacement does not occur (van den Assem, 1986).

The orientation during courtship is probably accomplished by several means. The wing vibration by excited males which seems to be an almost universal component of braconid courtship perhaps serves to orient the male to the female's odor (Cole, 1970 and Vinson, 1972). Miller (personal communication to Matthews, 1974) suggests that wing
vibration and antennation may involve acoustical communication, since dealated males of the chalcid, *Nasonia vitripennis* have reduced mating success. The orientation was probably accomplished by visual means as well, the observations suggested that males of some species were indifferent to a female's presence until she came within a few centimeters (Genleys, 1925 and Matthews, 1969).

In *A. dignus*, before mating the male parasitoids have performed fanning movements of wings and walking movements toward females and male made several attempts to catchup the female (Cardona & Oatman, 1971). The males of *P. nigricollis*, slowly approach females with half unfolded wings, grasp the wings of the other sex with his fore legs and bends abdomen to accomplish union (Quednau & Guevremont, 1975). In *B. curculionis* male exhibited courtship behaviour by holding antennae at 45°C with the body and the mating dance lasted for 2 to 8 revolutions (Dowell & Horn, 1975). After premating period the males exhibited courtship behaviour (dance) whenever within 1 cm of a receptive female. In the present study, the males of *C. chlorideae* raised their antennae, vibrated speedily in air and held wings at 60°C angle during courtship behaviour. The courtship behaviour comprised of 7-12 revolutions. Male exhibited this behaviour whenever a female was in a distance of 2.5 to 5 cm.

In *N. sertifer* mating sometimes began as soon as the insects were put into cages; about 28% of the matings began within 15', 63% by the end of the 1st hr and 74% by the end of the 2nd hr, and when allowed to continue longer than 2 hr, mating occurred in the 3rd, 4th and 5th hr. Usually, there was a brief disorderly struggle during which
the male faced the same direction as the female and second genital contact; he then reversed the direction and the pair assumed the motionless "end-to-end" pose characteristic of strophandrious sawflies (Lyons, 1976).

Generally, the male mounts the female dorsally and copulation position has rarely been noted in braconids (Matthews, 1974). The Chelonine, Phanerotoma torteuta, assumes an end-to-end position (Herbo & Kraft, 1969). However, the two euphorines, Dinocampus coccinellae (Jackson, 1928) and Cosmophorus henschell. Seiltner assume a position with the male upside down (Seiltner & Notzl, 1925) whereas, in the present braconids the males mounted females dorsally.

The courtship pattern of A. melanoscelus contains a number of stereotyped elements including wing elevations, flutters and intense flutters which occur before mating. Copulation occurs immediately after mounting. Males respond to females under a variety of conditions, but females effectively determine mating success. Non-satiated females released in the mating chamber invariably began feeding on the honey provided. They were not so easily disturbed as satiated females and so permitted males to mate more often. When females were physically restrained, mating success was maximal. In the present form, C. chlorideae one day old female when placed with newly emerged males mating took place immediately but, the older males do not respond vigorously to females, possibly because of general enfeeblement. The results indicate that for good success of the mating, age of the sex and receptivity are important.
In *N. sertifer* copulation tended to be slightly briefer in early afternoon than at other times of the day, while, in *C. chlorideae* and *E. argenteopilosus* mating usually occurred during the day time and there was no specific period observed in the day. Similar observations were recorded by Sathe & Nikam (1983) in *Diadegma trichoptilus* (Cameron). In *A. prodeniae* and *C. diurnii* mating was observed at night. These results are in agreement with the investigation made by Sathe and Nikam (1984a) in *Cotesia orientalis* Chilkwar & Nikam.

If food was available, feeding could occur immediately in *A. dignus* and both sexes when present, mating could take place prior to feeding or while the virgin female was feeding. In the present forms, *C. diurnii*, *E. argenteopilosus* and *A. prodeniae* feeding occurred prior to mating. In *C. chlorideae*, presence of a female with male immediately brought about mating. Both males and females of all the present species attracted toward food immediately after copulation.

In the eulophid, *Aceratoneuromyia granularis* Domenichini, Bosch & Assem (1986) have reported a primitive type of mating behaviour; the role of male's antennae (an important source of a variety of movements in many species) was not significant, as they held side ways throughout the courtship behaviour. Whereas, in the present forms, advanced type of mating behaviour was noted; antennal movements (antennation) have played the significant role throughout the courtship behaviour.

In *A. granularis* high-phase, pause and low-phase periods averaged 1.5", 1.5", 0.2" while in the present forms, these periods averaged 2", 1.5", 

...
1.5" in C. diurnii, 4", 1", 2.5" in C. chlorideae, 3", 1", 1.5" in E. argenteopilosus and 2.5", 1", 2" in A. prodeniae respectively.

Very little is known about postmating behaviour in the parasitic hymenoptera. In Temeleucha sp. Oatman & Platner (1974) reported that there was no postmating period. While, in C. diurnii, C. chlorideae, E. argenteopilosus and A. prodeniae the postmating periods were 7, 11, 13 and 6 days respectively.

The present data will serve as a basis for the assessment of the present parasitoids and further, for utilization in biological control programmes.
Table - 24: Comparative account on the premating, mating and postmating of the adults of *C. diurni*, *C. chlorideae*, *E. argenteopilosus* and *A. prodeniae*.

<table>
<thead>
<tr>
<th>Observations</th>
<th><em>C. diurni</em></th>
<th><em>C. chlorideae</em></th>
<th><em>E. argenteopilosus</em></th>
<th><em>A. prodeniae</em></th>
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<tr>
<td>Premating period (ave)</td>
<td>40'</td>
<td>-</td>
<td>8'</td>
<td>34'</td>
</tr>
<tr>
<td>Mating period (ave)</td>
<td>28''</td>
<td>3.45'</td>
<td>4.8'</td>
<td>40''</td>
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<tr>
<td>Post-mating period (ave)</td>
<td>11 days</td>
<td>13 days</td>
<td>6 days</td>
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<td>attracted towards food</td>
<td>attracted towards food</td>
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<td>Mating occurred at</td>
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