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THE COMPARATIVE PREDATORY AND SEXUAL BEHAVIOR OF
HANGINGFLIES (MECOPTERA:BITTACIDAE)

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INTRODUCTION

ADULTS of the Family Bittacidae (Fig. 1), commonly called hanging-flies because between flights they hang by their front legs from the foliage, occur on every continent and are typically inhabitants of the lush herbaceous stratum of moist forests. Miyake (1913) first observed the connection between predatory and sexual behavior in bittacids. He briefly described nuptial feeding behavior in the laboratory in *Bittacus nipponicus*. Males of this species were observed to capture a prey insect and feed it to the female during copulation. Setty (1940), in laboratory observations on several bittacid species, found nuptial feeding to be a component of their sexual behavior. Brownson (1964) and Newkirk (1957, 1970) investigated the behavior of *B. apicalis* and *B. strigosus* under field conditions in Ohio, and Bornemissza (1964, 1966) investigated the behavior of four species of *Harpobittacus* in Australia under both field and laboratory conditions. *Bittacus strigosus* was found to not exhibit nuptial feeding behavior. Females of *Harpobittacus* apparently do not catch their own prey but depend entirely on nuptial prey provided by males. The observations by Newkirk suggested that the duration of copulation in *B. apicalis* is dependent on the palatability of the nuptial prey provided by the male.

A detailed study (Thornhill, 1976a) of mating behavior in *Bittacus apicalis* revealed that copulation duration and male reproductive success is dependent upon the male's choice of nuptial prey and that females discriminate against males with suboptimal nuptial prey. Male-male competition and female choice were found to be important selective forces in the evolution of nuptial feeding behavior in *B. apicalis*. These same selective agents may have been important in the

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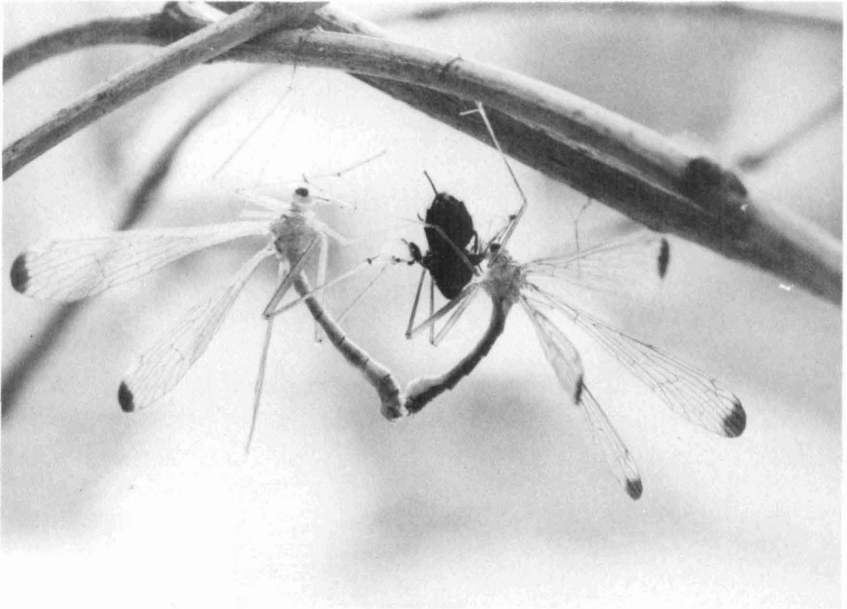


Fig. 1. Copulating pair of *Bittacus apicalis*. The female is feeding on the nuptial prey (a blow fly) provided by the male.

evolution of nuptial feeding in other arthropods and in birds (Thornhill, 1976b).

Comparative studies in behavior have been critical in elucidating general behavior patterns in numerous animal groups as well as in understanding the selective forces in operation that resulted in the evolution of behavioral diversity within groups of animals (e. g., see Alexander, 1962, 1969; Lloyd, 1966; Otte, 1970). The information presented here represents the beginning of a comparative behavioral study of the eleven described species of Bittacidae in North America and includes analyses of the reproductive behavior of four of the ten species in the genus *Bittacus* represented in our fauna: *B. apicalis*, *B. pilicornis*, *B. stigmaterus* and *B. strigosus*. I attempt to answer the following questions: (1) How do the behavioral events surrounding pair formation and copulation differ among species of *Bittacus* investigated? (2) What is the function of each of the behavioral events surrounding copulation in hangingflies? (3) Do premating reproductive isolating mechanisms other than probable species-specific male pheromones exist in bittacids?

MATERIAL AND METHODS

Behavioral studies of adults of *Bittacus apicalis*, *B. pilicornis* and *B. strigosus* were conducted in the field and laboratory during June, July and August of 1971, 1972 and 1973. Observations of *B. stigmaterus* were conducted only in the laboratory during August of 1973. Most field observations on these species were made in moist deciduous forests with a dense herbaceous stratum near Ann Arbor in Washtenaw County, Michigan (see Thornhill, 1974 for descriptions of study sites). A few field observations were made on the behavior of *Kalobittacus* in southern Mexico during late August and early September of 1972.

All laboratory studies on hangingflies were conducted with specimens collected in Washtenaw County, Michigan. For laboratory studies, individuals were collected in the field with an insect net, placed in screen cages or glass jars containing leafy branches, and transported to my home in Ann Arbor. Very little mortality results while transporting bittacids from the field to the laboratory if the containers are kept cool and crowding is avoided. Hangingflies were maintained in glass aquaria in the basement of my home and in screen enclosures in shady areas in my backyard. All containers were provided with leafy branches as resting places for the insects. Water was supplied by a stoppered glass tube fitted with a cotton wick. Blowflies (*Phaenicia sericata*) were used as food for the hangingflies.

In both the field and laboratory, many behavioral observations were recorded in notebooks and also by using a Sony cassette tape recorder, Sony 1/2-inch Rover television equipment, and motion pictures. The Sony TV equipment was ideal for recording the behavior of the hangingflies in the field because it could be used under low light levels at dawn and dusk and under heavily shaded forest conditions. Both motion pictures and TV tapes were extensively used for recording behavioral sequences under laboratory conditions for later analysis.

Prey arthropods captured by *Bittacus apicalis*, *B. pilicornis* and *B. strigosus* were obtained by netting individuals with prey for later identification. Sizes of prey utilized by bittacids were estimated by measuring in millimeters the body length and width of prey taken from both males and females. Totals of 524, 234, and 294 prey arthropods were measured after being taken from males and females of *B. apicalis*, *B. pilicornis* and *B. strigosus*, respectively.

To obtain information on mating frequency and intercopulatory behavior, a total of 42 males of *Bittacus apicalis* were collected,

individually marked with a spot of quick-drying airplane dope either on the hind femora, front femora, or wings, and released in the same area. Each marked male was then followed continuously through a sequence of four copulations, and detailed notes were kept by means of a tape recorder on the hunting behavior of the male, the duration of each copulation, the taxon and size of the nuptial prey used in each copulation, the fate of the prey item after each copulation, and interactions with other males and females between copulations. The copulatory and inter-copulatory behavior of several females was also observed. Both sexes of *B. apicalis* are easily followed in the field because they are slow flyers and make only short flights (usually less than four feet) in the low woodland vegetation. Also their normal behavior is not disturbed if one follows marked specimens slowly and with a minimum amount of disturbance. Since these marked males could not be collected between copulation without disrupting natural interactions it was necessary to estimate the size of each prey they obtained by recording the taxon of the prey and comparing it to the same species or a similar species whose size was known.

A two-tailed student's t-test was used to statistically analyze the data. The t-statistics were calculated using a console-oriented statistical computing program, "Constat," developed by The University of Michigan Statistics Research Laboratory in conjunction with the University Computing Center. The level of significance for all t-tests was chosen at $p = 0.5$. Differences at 5%, 1% and 0.1% levels are marked with one, two and three asterisks, respectively.

RESULTS AND DISCUSSION

Predatory Behavior

In moist deciduous woods in southeastern Michigan, *Bittacus apicalis* and *B. strigosus* reach population numbers in the thousands and several specimens may be collected with one sweep of an insect net. The typical woodland habitat of these species has a dense herb stratum often comprised primarily of jewelweed (*Impatiens* spp.) and nettle (*Laportea canadensis*). In such habitats in southeastern Michigan, *B. apicalis* and *B. strigosus* often occur with smaller populations of *B. pilicornis*, and occasionally with very small populations of *B. stigmatetus*.

The three common species of hangingflies in southeastern Michigan (*Bittacus apicalis*, *B. pilicornis* and *B. strigosus*) have the same diurnal habitat preference: they all occur in the low vegetation, and primarily

in the most mesic portion of the woods in which they are found. There is a seasonal succession of these three species with considerable seasonal overlap, and the males emerge and reach peak population numbers slightly before females (Thornhill, 1974; Thornhill and Johnson, 1974).

These three species differ greatly in many aspects of their adult behavior. No population of *Bittacus stigmaterus* was located until 1973, and the population was too small (only 15 individuals were collected) for field study. All known bittacids are predaceous on arthropods; however, adults of the three common species of *Bittacus* I studied are either active at different times or are active in different parts of the woods at the same time. *Bittacus apicalis* is a diurnal species, feeding and mating during the day, whereas both *B. strigosus* and *B. pilicornis* are crepuscular and nocturnal species. *Bittacus strigosus*, however, feeds primarily in the trees well above the herb stratum at night, and *B. pilicornis* apparently feeds only in the low vegetation at night. Individuals of *B. strigosus* feed in the low vegetation to some extent at dusk, prior to ascending into the trees, and at dawn after descending from the trees. *Bittacus pilicornis* was never observed feeding during full daylight hours (i.e., exclusive of the hours around dawn or dusk) in nature, and *B. strigosus* was only observed feeding during full daylight hours on 21 occasions. The 21 daytime feeding observations make up only five per cent of the total feeding observations recorded for *B. strigosus*.

Three types of feeding behavior are apparent in bittacids: 1) individuals hang from the vegetation by their front legs and when a prey item comes into range, they grab it with their prehensile hind or middle tarsi; 2) individuals fly out rapidly from a hanging position and grab a prey item off a plant part or from midair; 3) finally, individuals may sweep their hind and/or middle legs as they fly and crawl up and down the stems and leaves of the herbs in the habitat, and when a prey insect is contacted they wrap their prehensile tarsi around it. The first and second feeding methods are utilized primarily by the diurnal species, *Bittacus apicalis*; however, this species also employs the third technique to a limited extent. Probably because *B. pilicornis* and *B. strigosus* are active under conditions of low light intensity they primarily utilize the third strategy in capturing prey. At dusk and dawn these two species can be seen sweeping the vegetation with their long legs during flights among the low herbs and perhaps employ only this means of hunting at night.

Newkirk (1957, 1970) and Brownson (1964) studied the food habits of *Bittacus apicalis* and *B. strigosus* in Ohio and their results were

summarized by Newkirk (1970). Newkirk (1970) was especially interested in testing Felt's (1895) suggestion that bittacids reduce mosquito numbers, and concluded that *B. apicalis* and *B. strigosus* only occasionally eat mosquitoes because only 21 cases of mosquito predation out of a total of 689 were observed. Newkirk (1970) reported that Homoptera form the largest part of the food of *B. apicalis*. Newkirk (1957) states that in 1955, *B. apicalis* preyed on aphids more often than any other insect, and on fulgoroids in 1956; the other homopterans were cercopids, cicadellids, membracids and psyllids.

My observations on the feeding of *Bittacus apicalis*, *B. pilicornis* and *B. strigosus* are contained in Table 1. Homopterans made up the largest percentage of each species' diet, with Diptera second for *B. apicalis* and Lepidoptera second for both *B. pilicornis* and *B. strigosus*. Homopterans are very common in the low vegetation where the feeding observations were made and this alone probably explained the preponderance of this group in the diets of the three species. The difference in the second most preponderant group in the diet of *B. apicalis* compared to the diets of *B. strigosus* and *B. pilicornis* probably involves the difference in the feeding time of *B. apicalis*, compared to that of the other two species. Lepidopterans are most active under low light intensities around dusk, dawn and at night and this could explain the larger percentages of this group in the diets of the nocturnal species, *B. strigosus* and *B. pilicornis*.

My findings differ somewhat from those of Newkirk. He reported larger percentages (46%) of homopterans in the diet of *Bittacus apicalis* than I observed (28%). Also, he found that the largest percentage of the diet of *B. strigosus* was Diptera (45%) followed by Homoptera (13%) and then Lepidoptera (12%), whereas I found about equal numbers of Homoptera (20%), Lepidoptera (18%) and Diptera (17%) in the diet of this species.

The information obtained on the prey of *Bittacus apicalis*, *B. pilicornis* and *B. strigosus* suggests that the diets of these species depend on the prey insects available, and that there is no preference for a certain species of insect or taxonomic group of insects. Palatability and size are important criteria in the prey selected by males and used to feed the female during copulation in *B. apicalis*. Males selecting large palatable prey are more successful in terms of a copulation with a single female and in multiple copulations with different females (Thornhill, 1976a). Females of *B. apicalis* are indiscriminate in the prey sizes they have in their possession, whereas males prefer prey in the

TABLE 1

Summary of prey taken from *Bittacus apicalis*, *B. pilicornis* and *B. strigosus* in Washtenaw County, Michigan, during 1971, 1972 and 1973. Number in parentheses is percentage of each group eaten by the predator.

| Prey (By Group) | Predators | | |
|--------------------|--------------------|----------------------|---------------------|
| | <i>B. apicalis</i> | <i>B. pilicornis</i> | <i>B. strigosus</i> |
| Diptera | 198 (20.60) | 53 (14.88) | 74 (17.49) |
| Homoptera | 273 (28.40) | 69 (19.38) | 85 (20.09) |
| Hymenoptera | 105 (10.92) | 42 (11.79) | 34 (8.03) |
| Hemiptera | 78 (8.11) | 27 (7.58) | 22 (5.20) |
| Lepidoptera | 84 (8.74) | 63 (17.69) | 78 (18.43) |
| Psocoptera | 26 (2.70) | 9 (2.52) | 10 (2.36) |
| Orthoptera | 41 (4.26) | 25 (7.02) | 32 (7.56) |
| Ephemeroptera | 9 (0.93) | 8 (2.24) | 5 (1.18) |
| Neuroptera | 17 (1.76) | 13 (3.65) | 9 (2.12) |
| Trichoptera | 20 (2.08) | 17 (4.77) | 15 (3.54) |
| Coleoptera | 11 (1.14) | 3 (0.84) | 7 (1.65) |
| Plecoptera | 0 (0.00) | 2 (0.56) | 6 (1.41) |
| Mecoptera | 31 (3.22) | 0 (0.00) | 7 (1.65) |
| Araneae | 25 (2.60) | 11 (3.08) | 18 (4.25) |
| Phalangida | 43 (4.47) | 14 (3.93) | 21 (4.96) |
| TOTAL | 961 | 356 | 423 |

size range of about 19 mm² to 50 mm². This range corresponds to prey sizes that maximize male reproductive success. Prey smaller than 19 mm² do not result in maximally effective copulations, i.e., few sperm are transferred, and males usually discard prey smaller than 19 mm² soon after their capture (Thornhill, 1976a). The prey sizes taken from males and females of *B. pilicornis* suggest that this species exhibits predatory and pre-copulatory behavior similar to *B. apicalis* (Fig. 2). Males of *B. strigosus* do not present a nuptial meal to the female during courtship or copulation, and show less selectivity with respect to prey size than the males of *B. apicalis* and *B. pilicornis* (Fig. 3).

Sexual Behavior

Bittacus apicalis

Newkirk (1957) provided the first general description of the sexual behavior of *Bittacus apicalis*. My study of *B. apicalis* was considerably more detailed than Newkirk's and included observations on marked males during and between copulations. Females were also followed in a few cases.

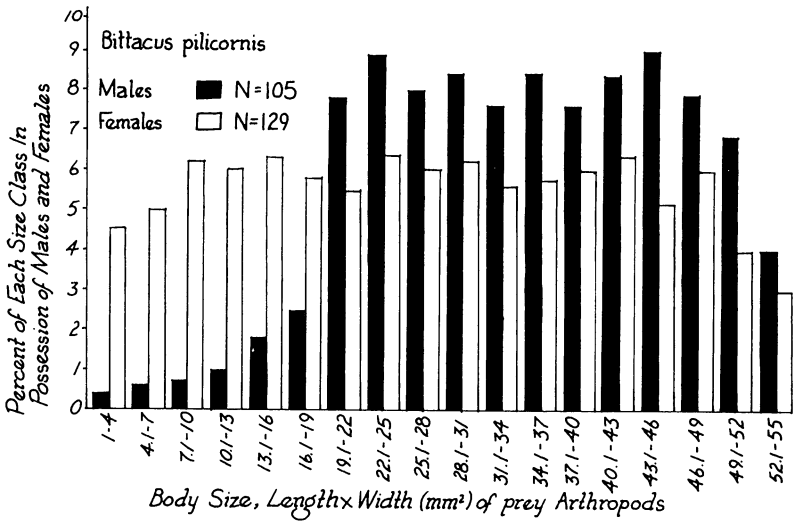


Fig. 2. The sizes of prey taken from males and females of *Bittacus pilicornis* in Washtenaw County, Michigan, during 1971 through 1973.

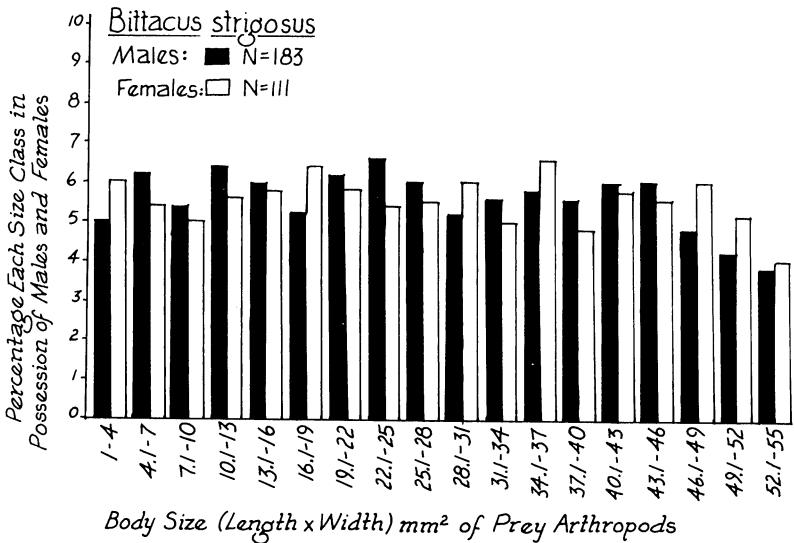


Fig. 3. The sizes of prey taken from males and females of *Bittacus strigosus* in Washtenaw County, Michigan, during 1971 through 1973.

The sequence of sexual behavior in *Bittacus apicalis* begins when a male catches for himself or steals from another male a prey arthropod—usually an insect—and begins to feed on it. After briefly feeding he either discards the prey and obtains another if the prey is unpalatable or less than 19 mm² or, while still holding the prey in his hind tarsi, initiates a behavior pattern which I refer to as searching behavior.

During the searching phase a male makes short flights (usually less than four feet) through the dense herbaceous stratum. After each flight the male, while hanging by his forelegs from a leaf or twig, vibrates his wings (usually only his hind wings) and exposes his abdominal pheromone-dispersing vesicles intermittently, suggesting that air driven by wing movements may aid in the dispersal of the sex attractant; this I refer to as calling behavior. Males are subject to prey-piracy, usually by other males, while feeding, searching or calling.

Females initially respond to males by olfaction, and the visual stimuli emitted by the searching male, i.e., the wing vibrations and the prey, are not necessary to attract females to his vicinity (Thornhill, 1974). Visual cues could only be important at very close range because the dense herb stratum where *Bittacus apicalis* lives surely ordinarily precludes long distance viewing. The prey of copulating or searching males is often stolen by other males. Under these conditions, a pirated male may briefly continue his search for females but without holding any prey. Females are sometimes attracted to these males, but never copulate with them. This suggests that the possession of prey is not important in pair formation, but only becomes important after the pair is formed and courtship is initiated. I have shown that females only evaluate the prey offered by a male after feeding upon it during courtship and that some prey items are more likely to enhance copulation than others (Thornhill, 1976a).

One or more females can be seen approaching a calling male, and on occasion a female may actually collide with such a male. The attracted female(s), commonly come to rest by hanging by their front legs in the vegetation near the calling male. When a male sees a female he terminates his calling behavior; then, either the male approaches the female, or the female approaches the male by a short flight. At this time the two individuals are facing each other and are hanging by their front legs from the vegetation. The male then presents his prey to the female by extending his hind legs in her direction. During approach, the male usually covers the prey with his abdominal tip. The male withdraws his abdominal tip as the female thrusts her mouth parts into the prey and grasps it with her hind tarsi. The female, now holding the

prey with one or both hind tarsi, feeds as the male couples with her. Figure 1 shows a copulating pair of *Bittacus apicalis*. The male still holds on to the prey with one or both hind tarsi and may also grasp the female's legs by means of his middle tarsi. If the male succeeds in coupling with the female, the duration of the ensuing copulation is dependent on the size and palatability of the male's nuptial prey. If the prey is of suitable size and palatability, the copulation will be male-terminated after a mean of about 23 minutes; otherwise, the copulation will be terminated earlier by the female (Thornhill, 1976a). Only the female feeds during copulation. Copulations are often interrupted by intruding hangingflies (usually males).

If a male is unsuccessful in coupling with a female on the first attempt, he takes the prey from the female and presents it to her again. If she continues to avoid his coupling attempts, he will terminate the encounter, flying away with the prey. In copulations terminated by the male, he pulls his abdominal tip from that of the female. At this time there is a struggle lasting a few seconds during which both male and female disentangle their legs but retain a hold on the prey. The male usually retrieves the prey after copulation; occasionally it may be dropped, or if the prey is large, the female usually retains it. After separation of the pair, the male again feeds briefly on the retrieved prey, and if it is still palatable again begins searching for females. Depending on the size of the prey, it may be used in up to three successive copulations. If the prey is found to be unpalatable by a male it is usually discarded and he begins hunting for another prey item before resuming calling.

It has been determined (Thornhill, 1976a) that male-terminated copulations (i.e., copulations of 20 or more minutes and a mean of 23 minutes), but not copulations of shorter duration stimulate oviposition and induce sexual non-receptivity in females. These females remain unreceptive for about three hours, during which they lay an average of 3.5 eggs. Females drop their eggs among the ground litter while hanging from the vegetation. Females which copulate at the end of each mating refractory period, i.e., about every three hours, maximize their fecundity throughout the day. Under average conditions, in a 12-hour day a female mates four times and in the four mating periods lays a total of 14 eggs. During these four matings a female feeds for about 90 minutes since the mean copulation duration is 23 minutes. Females feeding on the nuptial meals of their mates alone are as fecund as females which have continuous access to prey. Also, females seldom hunt on their own when males emerge and become abundant, but depend primarily on nuptial prey provided by males during copula-

tion. Therefore, the prey fed upon by the female during copulation may supply enough protein for egg development and maintenance of the female during the three hour mating refractory period.

Tables 2 and 3 contain data obtained by observing a total of 42 males of *Bittacus apicalis* from mark and release through four successive copulations each. Table 2 contains information on the copulatory and inter-copulatory behavior of 22 males in which at least one of the copulations in each sequence of four was interrupted by an intruding hangingfly, whereas Table 3 contains similar information on 20 males in which none of the copulations were interrupted by intruders. Tables 4 and 5 summarize data for the males from Tables 2 and 3, respectively, on prey-piracy between copulations, as well as on other aspects of their intercopulatory behavior not included in Tables 2 and 3.

As discussed later, the interruption of copulations by intruding individuals (usually males) is one major factor contributing to variance in male reproductive success. In 1971, the copulations that were uninterrupted and those interrupted by intruding hangingflies were recorded for three days when the population of *Bittacus apicalis* at the study site was at high density, for three days when the population was at a moderate density, and for four days when the population was at low density. Data on relative seasonal abundance of *B. apicalis* were obtained by walking for 1/2 hour at the study site at intervals throughout the seasons and recording by tape recorder the number of individuals of each sex that were seen (see Thornhill, 1974). High population densities were recorded on the dates July 2, 8, and 14, 1971, because at least 200 and up to 225 individuals were counted in 1/2 hour periods on these dates. Moderate population sizes were recorded on July 23, 25, and 26, 1971 because by this time females had begun to predominate numerically and only about 30 males and 40 females could be counted in a 1/2 hour period. Low population densities were recorded on July 30, 1971 and August 2-6, 1971 because only about 20 males and 30 females could be observed in a 1/2 hour period.

Eighty-eight percent of the copulations (71 of 81) observed at times of high densities were interrupted, and 30% (25 of 65) and 21% (12 of 57) were interrupted during times of moderate and low population numbers, respectively. When all three population densities are considered, 53% of the observed copulations (108 of 203) were interrupted, and males were responsible for most of the disruptions (94%). The data on disrupted copulations observed by the following 22 marked males under conditions of moderate to high population densities during 1971, 1972, and 1973 are similar to those discussed above:

TABLE 2

The copulatory and inter-copulatory behavior of 22 marked *Bittacus apicalis* males in nature. Each male was observed through four consecutive copulations, each with a different female. Each row contains the sequence of copulations of one male. Time is in minutes. Prey size is estimated and expressed in mm² (length times width of the prey item).

| Male No. | Time From Marking to 1st Cop. | Copulations | | | | | | | | | | | | | | | |
|----------|-------------------------------|-----------------|-----------|-------------------|-----------------------|-----------------|-----------|-------------------|-----------------------|-----------------|-----------|--------------------------------|-----------------------|-----------------|-----------|---------------------|--|
| | | 1 | | | | 2 | | | | 3 | | | | 4 | | | |
| | | Prey Size | Cop. Time | Term. By | Time Between Cops. | Prey Size | Cop. Time | Term. By | Time Between Cops. | Prey Size | Cop. Time | Term. By | Time Between Cops. | Prey Size | Cop. Time | Term. By | |
| 1 | 45(1MR ^c) | 42 | 24 | male | 10 | 42 ^a | 21 | male ^f | 21 | 37 | 22 | IM ^b 1 | 25 | 19 | 20 | male ^f | |
| 2 | 25 | 22 | 23 | male ^f | 31(2MR ^c) | 35 ^d | 3 | IM ^b 5 | 20 | 16 | 15 | female ^g | 42(2MR ^c) | 20 | 22 | male ^g | |
| 3 | 45(2MR ^c) | 39 ^d | 5 | IM ^b 1 | 22 | 30 ^d | 24 | male ^f | 55(4MR ^c) | 45 ^d | 23 | male | 10 | 45 ^a | 20 | male ^g | |
| 4 | 33(1MR ^c) | 20 | 20 | male ^g | 10 | 52 ^d | 10 | IM ^b 5 | 29 | 27 ^d | 21 | male ^f | 25(1MR ^c) | 22 | 26 | male ^f | |
| 5 | 20 | 43 | 25 | male | 50(4MR ^c) | 20 | 22 | male ^g | 45(2MR ^c) | 30 ^d | 2 | IM ^b 1 | 19 | 34 ^d | 24 | male | |
| 6 | 55(3MR ^c) | 26 ^d | 2 | IM ^b 1 | 25(1MR ^c) | 28 | 21 | male ^g | 40(1MR ^c) | 22 | 20 | male ^g | 45(3MR ^c) | 29 | 11 | IM ^b 1 | |
| 7 | 17 | 48 ^d | 20 | IM ^b 4 | 22(1MR ^c) | 45 | 25 | male | 2 | 45 ^a | 1 | IM ^b 1 | 30 | 26 | 23 | male ^g | |
| 8 | 27 | 36 | 24 | male | 2 | 36 ^a | 5 | IM ^b 1 | 38(1MR ^c) | 33 ^d | 20 | male | 22(1MR ^c) | 43 ^d | 4 | IM ^b 1 | |
| 9 | 30(1MR ^c) | 21 ^d | 10 | IM ^b 3 | 62(4MR ^c) | 24 ^d | 16 | IF ^b 4 | 6(1MR ^c) | 28 | 26 | male ^f | 49(2MR ^c) | 21 ^d | 22 | male ^g | |
| 10 | 38 | 29 | 21 | male ^f | 15 | 41 ^d | 23 | male | 27(1MR ^c) | 54 ^d | 4 | IM ^b 1 | 33(2MR ^c) | 30 | 8 | IF ^b 2 | |
| 11 | 46(2MR ^c) | 43 ^d | 14 | IM ^b 5 | 65(3MR ^c) | 21 | 24 | male ^g | 30(2MR ^c) | 22 | 22 | male ^g | 13 | 40 ^d | 23 | IM ^b 4 | |
| 12 | 21 | 32 | 11 | IM ^b 3 | 20(1MR ^c) | 42 ^d | 21 | male | 35(3MR ^c) | 40 ^d | 8 | IM ^b 1 | 40(3MR ^c) | 29 | 6 | IM ^b 1 | |
| 13 | 39(1MR ^c) | 48 ^d | 26 | IM ^b 1 | 17 | 27 | 17 | IM ^b 1 | 26(1MR ^c) | 33 | 12 | IM ^b 1 | 35(1MR ^c) | 35 ^d | 22 | male | |
| 14 | 44(1MR ^c) | 30 | 21 | male ^f | 32(1MR ^c) | 50 | 9 | IM ^b 5 | 31 | 34 | 4 | IM ^b 4 | 48(4MR ^c) | 19 | 12 | IM ^b 1 | |
| 15 | 19 | 35 ^d | 3 | IM ^b 3 | 22(1MR ^c) | 22 | 5 | IM ^b 5 | 10 | 19 | 23 | male ^g | 31(2MR ^c) | 27 | 20 | IF ^b 3 | |
| 16 | 52(4MR ^c) | 27 | 22 | male ^f | 56(3MR ^c) | 24 ^d | 16 | IM ^b 1 | 25(1MR ^c) | 43 ^d | 4 | IM ^b 1 | 38(3MR ^c) | 40 ^d | 9 | IM ^b 1 | |
| 17 | 20 | 51 ^d | 1 | IM ^b 1 | 24 | 29 | 2 | IM ^b 3 | 28(2MR ^c) | 51 ^d | 22 | male ^c | 67(4MR ^c) | 18 | 13 | IM ^b 1 | |
| 18 | 29 | 22 | 17 | IM ^b 5 | 38(2MR ^c) | 39 | 5 | IM ^b 1 | 47(3MR ^c) | 36 ^d | 10 | IM ^b 5 | 35(1MR ^c) | 9 | 10 | female ^f | |
| 19 | 33(2MR ^c) | 36 ^d | 5 | IM ^b 1 | 15 | 33 ^d | 3 | IM ^b 1 | 52(2MR ^c) | 40 ^d | 6 | IM ^b 1 | 22 | 25 ^d | 1 | IM ^b 1 | |
| 20 | 39(1MR ^c) | 20 | 8 | IM ^b 5 | 12 | 42 ^d | 1 | IM ^b 5 | 20 | 21 | 9 | IM ^b 3 ^g | 19 | 42 ^d | 6 | IM ^b 4 | |
| 21 | 49(1MR ^c) | 23 | 10 | IM ^b 1 | 48(1MR ^c) | 38 | 11 | IM ^b 3 | 36(1MR ^c) | 19 ^d | 3 | IM ^b 1 | 37(2MR ^c) | 24 | 8 | IM ^b 1 | |
| 22 | 57(4MR ^c) | 29 | 3 | IM ^b 4 | 29(1MR ^c) | 20 ^d | 14 | IM ^b 1 | 29(1MR ^c) | 24 | 4 | IM ^b 1 | 55(3MR ^c) | 33 ^d | 13 | IM ^b 5 | |

^a Same nuptial prey as used in preceding copulation.

^b IM = intruding male, IF = intruding female; ¹intruding male gets prey, ²intruding female gets prey, ³original male gets prey, ⁴original female gets prey, ⁵prey is dropped in struggle.

^c MR = male robbed of a nuptial prey between copulations or between marking and first copulation; the number preceding this abbreviation is the number of robberies between two copulations.

^d Male stole another male's or a copulating pair's nuptial prey.

^e Female obtains prey after a struggle with the male during the termination of a copulation.

^f Prey was dropped during struggle at the termination of a copulation.

^g Prey was discarded by the male after feeding on it between copulations.

TABLE 3

The copulatory and inter-copulatory behavior of 20 marked males of *Bittacus apicalis* in nature. Each male was observed through four consecutive copulations, each with a different female. Each row contains the sequence of copulations of one male. Time is in minutes. Prey size is estimated and expressed in mm² (length times width of the prey item).

| Male No. | Time From Marking to 1st Cop. | Copulations | | | | | | | | | | | | | | | |
|----------|-------------------------------|-----------------|-----------|---------------------|-----------------------|-----------------|-----------|---------------------|-----------------------|-----------------|-----------|-------------------|-----------------------|-----------------|-----------|---------------------|--|
| | | 1 | | | | 2 | | | | 3 | | | | 4 | | | |
| | | Prey Size | Cop. Time | Term. By | Time Between Cops. | Prey Size | Cop. Time | Term. By | Time Between Cops. | Prey Size | Cop. Time | Term. By | Time Between Cops. | Prey Size | Cop. Time | Term. By | |
| 1 | 25 | 5 | 8 | female ^f | 55(2MR ^c) | 24 | 21 | male ^g | 29 | 29 | 21 | male ^f | 23 | 21 | 22 | male ^g | |
| 2 | 29 | 12 | 14 | female ^g | 28 | 21 | 21 | male ^g | 33 | 28 | 21 | male | 11 | 28 ^a | 22 | male ^g | |
| 3 | 38 | 16 | 17 | female ^g | 31 | 22 | 20 | male ^g | 37(1MR ^c) | 31 | 24 | male | 18 | 31 ^a | 20 | male | |
| 4 | 31(1MR ^c) | 19 | 23 | male ^f | 40(1MR ^c) | 20 | 20 | male ^g | 26 | 29 | 22 | male | 3 | 29 ^a | 21 | male ^g | |
| 5 | 36 | 19 | 23 | male ^g | 31 | 24 | 25 | male ^g | 12 | 47 ^d | 20 | male ^c | 49(1MR ^c) | 29 ^d | 25 | male ^f | |
| 6 | 26 | 22 | 23 | male ^f | 29(1MR ^c) | 35 ^d | 22 | male | 7 | 35 ^a | 21 | male ^f | 36 | 19 | 22 | male ^g | |
| 7 | 33(1MR ^c) | 23 | 24 | male ^g | 20 | 19 | 21 | male ^f | 17 | 51 ^d | 22 | male ^c | 34 | 39 | 25 | male ^f | |
| 8 | 18 | 25 ^d | 23 | male ^g | 32 | 14 | 15 | female ^g | 29(1MR ^c) | 40 | 21 | male | 5 | 40 ^a | 26 | male ^g | |
| 9 | 35(1MR ^c) | 25 ^d | 20 | male ^f | 25 | 16 | 15 | female ^g | 13 | 29 | 20 | male ^f | 17 | 21 | 23 | male ^g | |
| 10 | 23 | 27 ^d | 25 | male ^f | 19 | 38 ^d | 20 | male | 6 | 38 ^a | 25 | male ^g | 69(3MR ^c) | 48 ^d | 21 | male ^c | |
| 11 | 38 | 30 | 26 | male ^f | 19 | 22 ^d | 23 | male ^f | 27(1MR ^c) | 43 | 21 | male | 8 | 43 ^a | 22 | male ^g | |
| 12 | 34(1MR ^c) | 30 | 25 | male | 6 | 30 ^a | 20 | male | 21 | 54 ^d | 25 | male ^c | 52(2MR ^c) | 23 | 23 | male ^f | |
| 13 | 52(2MR ^c) | 37 | 23 | male | 61(2MR ^c) | 27 ^d | 25 | male ^g | 26 | 39 | 21 | male | 4 | 39 ^a | 24 | male ^g | |
| 14 | 33 | 38 | 23 | male | 6 | 38 ^a | 20 | male ^f | 12 | 19 | 23 | male ^g | 10 | 24 ^d | 23 | male ^f | |
| 15 | 20 | 45 | 21 | male | 14 | 45 ^a | 23 | male | 5 | 45 ^a | 21 | male ^c | 15 | 21 | 21 | male ^g | |
| 16 | 39 | 44 | 21 | male ^f | 15 | 42 | 25 | male | 44(1MR ^c) | 21 | 22 | male ^f | 31 | 23 | 21 | male ^g | |
| 17 | 22 | 45 | 26 | male | 10 | 45 ^a | 21 | male ^g | 20 | 22 ^d | 27 | male ^g | 32(1MR ^c) | 47 ^d | 25 | male | |
| 18 | 17 | 50 ^d | 24 | male ^c | 57(2MR ^c) | 22 | 23 | male ^f | 24 | 26 | 24 | male ^f | 19 | 33 ^d | 20 | male ^f | |
| 19 | 21 | 52 ^d | 27 | male ^c | 25 | 25 | 24 | male ^g | 30 | 32 | 24 | male | 35(1MR ^c) | 26 | 25 | male ^g | |
| 20 | 34(1MR ^c) | 55 | 22 | male ^c | 9 | 36 ^d | 24 | male | 4 | 36 ^a | 22 | male | 9 | 11 | 12 | female ^g | |

^{a-g}See footnotes Table 2

TABLE 4

Activities of marked males of *Bittacus apicalis* between copulations and between marking and the first copulation. Data is for males observed under conditions of moderate to high population densities (see Table 2).

| Male No. | No. Prey | | | Min. (%) Spent Feeding on Prey | Min. (%) Spent Locating Prey Used in the 4 Copulations | Min. (%) Spent Finding Sexually Cooperative Females | No. Females Interacted With | Total Time (Min.) Between Cops. and Between Marking and First Cop. |
|------------------------|----------------|------------------|------------------------------------|--------------------------------|--|---|-----------------------------|--|
| | Stolen by Male | Stolen from Male | Discarded by Male After Evaluation | | | | | |
| 1 | 0 | 1 | 2 | 32 (31.7) | 56 (55.4) | 13 (12.9) | 5 | 101 |
| 2 | 1 | 4 | 3 | 40 (33.9) | 58 (49.2) | 20 (16.9) | 6 | 118 |
| 3 | 3 | 6 | 1 | 46 (34.8) | 62 (47.0) | 24 (18.2) | 4 | 132 |
| 4 | 2 | 2 | 3 | 27 (27.8) | 60 (61.9) | 10 (10.3) | 5 | 97 |
| 5 | 2 | 6 | 3 | 50 (37.3) | 64 (47.8) | 20 (14.9) | 6 | 134 |
| 6 | 1 | 8 | 2 | 69 (41.8) | 52 (31.5) | 44 (26.7) | 5 | 165 |
| 7 | 1 | 1 | 2 | 18 (25.4) | 44 (62.0) | 9 (12.7) | 6 | 71 |
| 8 | 2 | 2 | 4 | 28 (31.5) | 50 (56.2) | 11 (12.4) | 4 | 89 |
| 9 | 3 | 8 | 5 | 56 (38.1) | 69 (46.9) | 22 (15.0) | 7 | 147 |
| 10 | 2 | 3 | 2 | 35 (31.0) | 68 (60.2) | 10 (8.85) | 6 | 113 |
| 11 | 2 | 7 | 3 | 52 (33.8) | 81 (52.6) | 21 (13.6) | 5 | 154 |
| 12 | 2 | 7 | 3 | 42 (36.0) | 53 (45.7) | 21 (18.1) | 6 | 116 |
| 13 | 2 | 3 | 1 | 36 (30.8) | 66 (56.4) | 15 (12.8) | 8 | 117 |
| 14 | 0 | 6 | 4 | 58 (37.4) | 60 (38.7) | 37 (23.9) | 4 | 155 |
| 15 | 1 | 3 | 3 | 26 (31.7) | 44 (53.7) | 12 (14.6) | 6 | 82 |
| 16 | 3 | 11 | 5 | 82 (47.9) | 37 (21.6) | 52 (30.4) | 5 | 171 |
| 17 | 2 | 6 | 2 | 49 (35.3) | 67 (48.2) | 23 (16.5) | 6 | 139 |
| 18 | 0 | 6 | 4 | 66 (44.3) | 52 (34.9) | 31 (20.8) | 4 | 149 |
| 19 | 4 | 4 | 2 | 27 (22.1) | 83 (68.0) | 12 (9.84) | 6 | 122 |
| 20 | 2 | 1 | 1 | 19 (21.1) | 62 (68.9) | 9 (10.0) | 4 | 90 |
| 21 | 1 | 5 | 3 | 57 (33.5) | 81 (47.6) | 32 (18.8) | 7 | 170 |
| 22 | 2 | 9 | 2 | 74 (43.5) | 48 (28.2) | 48 (28.2) | 5 | 170 |
| X/Male in 4 cops: | 1.73 | 4.95 | 2.73 | 45.0(35.3) | 59.9(47.9) | 22.5(17.7) | 5.45 | 127.4 |
| X Between each cop: | 0.432 | 1.24 | 0.682 | 11.2(35.2) | 15.0(47.2) | 5.63(17.7) | 1.36 | 31.8 |

TABLE 5

Activities of marked males of *Bittacus apicalis* between copulations and between marking and the first copulation. Data is for males observed under conditions of low population density (see Table 3).

| Male No. | No. Prey | | | Min. (%) Spent Feeding on Prey | Min. (%) Spent Locating Prey Used in the 4 Copulations | Min. (%) Spent Finding Sexually Cooperative Females | No. Females Interacted With | Total Time (Min.) Between Cops. and Between Marking and First Cop. |
|------------------------|----------------|------------------|------------------------------------|--------------------------------|--|---|-----------------------------|--|
| | Stolen by Male | Stolen from Male | Discarded by Male After Evaluation | | | | | |
| 1 | 0 | 2 | 3 | 45 (36.3) | 52 (41.9) | 27 (21.8) | 8 | 124 |
| 2 | 0 | 0 | 2 | 32 (31.7) | 40 (39.6) | 29 (28.7) | 9 | 101 |
| 3 | 0 | 1 | 3 | 28 (24.6) | 50 (43.9) | 36 (31.6) | 8 | 114 |
| 4 | 0 | 2 | 2 | 32 (32.0) | 55 (55.0) | 13 (13.0) | 4 | 100 |
| 5 | 2 | 1 | 2 | 40 (31.3) | 46 (35.9) | 42 (32.8) | 9 | 128 |
| 6 | 1 | 1 | 2 | 20 (20.4) | 35 (35.7) | 43 (43.9) | 8 | 98 |
| 7 | 1 | 1 | 3 | 25 (24.0) | 39 (38.0) | 40 (38.5) | 7 | 104 |
| 8 | 1 | 1 | 3 | 22 (26.2) | 36 (42.9) | 26 (31.0) | 9 | 84 |
| 9 | 1 | 1 | 3 | 26 (28.9) | 30 (33.3) | 34 (37.8) | 7 | 90 |
| 10 | 3 | 3 | 2 | 35 (29.9) | 43 (36.8) | 39 (33.3) | 9 | 117 |
| 11 | 1 | 1 | 2 | 22 (23.9) | 30 (32.6) | 40 (43.5) | 8 | 92 |
| 12 | 1 | 3 | 2 | 39 (34.5) | 51 (45.1) | 23 (20.4) | 9 | 113 |
| 13 | 1 | 4 | 3 | 32 (22.4) | 70 (49.0) | 41 (28.7) | 8 | 143 |
| 14 | 1 | 0 | 2 | 23 (37.7) | 31 (50.8) | 7 (11.5) | 6 | 61 |
| 15 | 0 | 0 | 2 | 15 (27.8) | 15 (27.8) | 24 (44.4) | 11 | 54 |
| 16 | 0 | 1 | 4 | 47 (36.4) | 44 (34.1) | 38 (29.5) | 8 | 129 |
| 17 | 2 | 1 | 3 | 30 (35.7) | 34 (40.5) | 20 (23.8) | 6 | 84 |
| 18 | 2 | 2 | 2 | 26 (22.2) | 41 (35.0) | 50 (42.7) | 9 | 117 |
| 19 | 1 | 1 | 4 | 29 (26.1) | 38 (34.2) | 44 (39.6) | 8 | 111 |
| 20 | 1 | 1 | 0 | 22 (37.3) | 15 (25.4) | 22 (37.3) | 8 | 59 |
| X/Male in 4 cops: | 0.95 | 1.34 | 2.45 | 29.7(29.2) | 39.9(39.3) | 31.6(31.5) | 7.95 | 101.2 |
| X Between each cop: | 0.238 | 0.337 | 0.612 | 7.38(29.2) | 9.93(39.2) | 7.98(31.5) | 1.99 | 25.3 |

61% of the copulations were disrupted (54 of 88) and most disruptions were caused by intruding males (94%) (see Table 2). The data in Table 3 were largely collected under conditions of low to very low population sizes during 1971, 1972, and 1973, and this accounts for the absence of observed disrupted copulations.

The behaviors of marked males followed through four successive copulations under conditions of low to high population densities are diagrammed in Figures 4 and 5. Figure 4 is based on the behavior of 22 marked males under moderate to high population densities (see Table 2). Figure 5 is based on the behavior of 20 marked males when the population density was low (see Table 3).

The data in Figures 5 and 6 allow an analysis of both the copulatory and inter-copulatory behavior of *Bittacus apicalis*. The 106 male-terminated copulations in Tables 2 and 3, in the absence of intruding hangingflies, averaged 22.6 minutes (standard deviation = 1.87, $R = 20-27$), and the eight female-terminated copulations, in the absence of intruders, averaged 13.3 minutes (standard deviation = 3.01, $R = 8-17$). The 54 copulations which were interrupted by intruders were of short duration lasting a mean of 8.78 minutes (standard deviation = 6.18, $R = 1-25$). A two-tailed student's *t*-test comparing the mean durations of male-terminated and female-terminated copulations reveals a highly significant difference ($t = 13.0$, $p < 0.001$), as does the difference between male-terminated copulations which are not disrupted versus intruder interrupted copulations ($t = 21.2$; $p < 0.001$). Copulations in which the female of the pair terminates the interaction always involve prey smaller than 19 mm^2 , or distasteful prey such as ladybird beetles, and copulation-duration depends on the size and palatability of the prey presented by the male to the female (Thornhill, 1976a).

At the termination of a copulation, both the male and the female struggle to gain a hold on the nuptial prey. In 34 uninterrupted copulations (see Table 2), and in the 80 uninterrupted copulations (see Table 3), the male retains the prey 64% of the time, the female gets it 8% of the time, and it is dropped in the struggle 28% of the time. Newkirk (1957) also found that males usually retain the prey at the termination of the copulations. He reported that out of 46 copulations observed in one day, the male gets the prey 28 times (61%), the female got it two times (3%) and it was dropped 16 times (35%). These percentages generally conform with my observations on the fates of the nuptial prey after a larger number of copulations.

Figure 6 relates the size of the nuptial prey to its use in more than one copulation by a male. The data plotted are from Tables 2 and 3, but include only the instances in which it was clear that the prey had

B. APICALIS: MODERATE TO HIGH POPULATION DENSITY

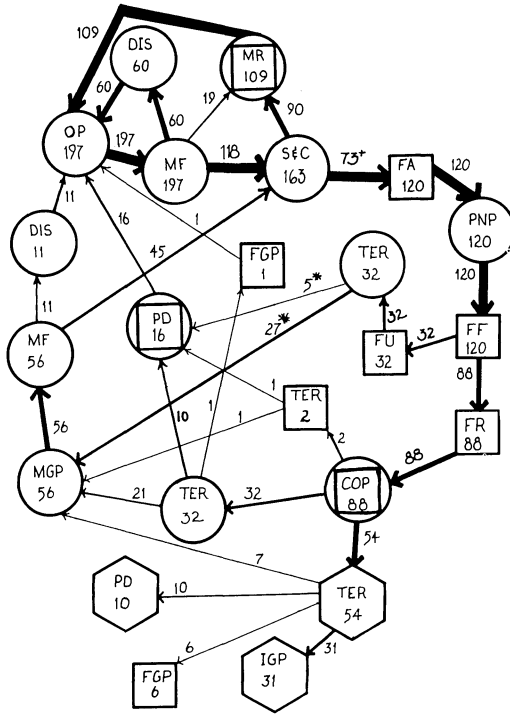


Fig. 4. Alternative sequences of pair formation, copulatory and inter-copulatory behavior in *Bittacus apicalis* under conditions of moderate to high population densities. This figure is based on data obtained in nature following 22 marked males through four successive copulations (see Table 2). Circles indicate male actions and squares female actions. Hexagons denote the intruding behavior of either males or females which interrupt copulations. The numbers above or to the right of the lines, and the relative thicknesses of the lines, indicate the number of behavioral events following a particular pathway. Numbers within the symbols indicate the number of times that event occurred. The circle (OP) at the left top of the diagram is a logical starting point. The events indicated by numbers followed by asterisks are not contained in Table 3. The events on the line between S & C and FA indicated by a plus may not match numerically the events within the symbols because several females may be attracted to each searching and calling (S & C) male. Key to Abbreviations: COP, Copulation; DIS, Male discards prey after feeding on it; FA, Females are attracted to the pheromone of the male; FF, Female feeds on nuptial prey; FGP, Copulating female gets prey upon termination of encounter; FR, Female is sexually unresponsive; FU, Female is sexually unresponsive; IGP, Intruding hangingfly gets prey upon termination of encounter; MF, Male feeds on prey; MGP, Copulating male gets prey upon termination of encounter; MR, Male robbed of his prey by another hangingfly; OP, Male catches prey or steals prey from another hangingfly; PD, Prey is dropped upon termination of encounter; PNP, Male presents nuptial prey to attracted female; S&C, Male makes short flights through the herbs searching for females and exposing his pheromone vesicles (calling) while still holding the prey; TER, Encounter (copulation or courtship) terminated.

B. APICALIS: LOW POPULATION DENSITY

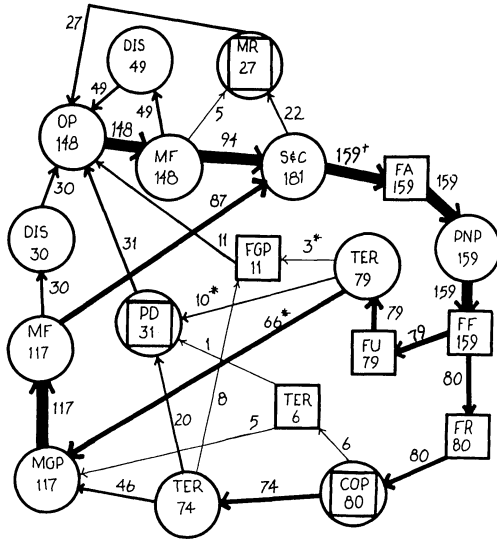


Fig. 5. Alternative sequences of pair formation, courtship, copulatory, and inter-copulatory behavior in *Bittacus apicalis* under conditions of low population density. This figure is based on data obtained in nature by following 20 marked males through four successive copulations (see Table 3). Circles indicate male actions and squares female actions. Hexagons denote the intruding behavior of either males or females which interrupt copulations. The numbers above or to the right of the lines, and the relative thicknesses of lines, indicate the number of behavioral events following a particular pathway. Numbers within the symbols indicate the number of times that event occurred. The circle (OP) at the left top of the diagram is a logical starting point. The events indicated by numbers followed by asterisks are not contained in Table 3. The vents on the line between S & C and FA indicated by a plus may not match numerically the events within the symbols because several females may be attracted to each searching and calling (S&C) male. Abbreviations as in Fig. 4.

either been a) rejected for further use in copulations by the male after one or more male-terminated copulations, or b) obtained by the female at the termination of a copulation, or c) pirated by another male after the initial male's behavior indicated that the prey item was still suitable for use in a subsequent copulation. These data suggest that prey items smaller than 28 mm² are normally used only for one male-terminated copulation. The male's inter-copulatory behavior of feeding for a couple of minutes on these prey and then discarding them is the criterion establishing that they are not suitable for use in a subsequent copulation. Prey items between about 28 mm² to about

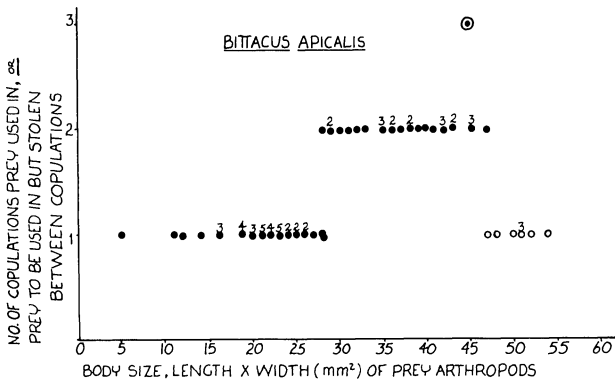


Fig. 6. The relationship between the multiple use of prey in successive copulations by males of *Bittacus apicalis* and the body size of the prey. The numbers above the data points indicate the number of observations when more than one observation for a prey size was recorded. ● = Male retained prey after copulation; ○ = Female obtained prey after copulation; ⊙ = Female obtained prey after its use in three successive copulations.

47 mm² are commonly used in two male-terminated copulations. Prey in this size range are not discarded after the brief feeding following the first copulation. In one case, a large crane fly with an estimated body size of 45 mm² was used by one male in three successive male-terminated copulations. At the termination of copulations involving prey items larger than 47 mm² the copulating female always got the prey after a brief struggle with the male, probably because it is more difficult for a male to maintain a grasp on prey larger than 47 mm² (see Thornhill, 1974).

A two-tailed t-test was used to compare the mean inter-copulatory times when males use a prey arthropod in one copulation only and catch or steal another prey for the next copulation (N = 50) versus when males use the same prey item in two successive copulations (N = 18). Only those inter-copulatory times were included in which males experienced no prey-piracy by hangingflies between copulations. There is a statistically significant reduction (t = 7.65; p < 0.001) in a male's inter-copulatory time when he uses prey in two successive copulations, rather than in only one copulation—from means of 21.7 to 7.28 minutes. Since prey in the size range of 28 mm² and 47 mm² are used in multiple copulations most frequently (see Figure 6), the time gain alone might be expected to select for males which initially catch prey of these sizes. However, males do not show discrimination quite this limited in the sizes of prey they utilize in copulations. The

predominant sizes of prey involve categories from 19 mm² to about 50 mm², with prey smaller than 19 mm² being discarded. I have shown that the prey preference of males has probably been dictated in part by intersexual selection, i.e., female choice (Thornhill, 1976a).

The durations between copulations in which males catch prey (N = 46) versus those in which males steal prey from another male or copulating pair (N = 26) were also compared by a t-test. The analysis only includes inter-copulatory times in which males experienced no prey-piracy themselves. The time interval from marking and release until the first copulation was considered as an inter-copulatory period since handling did not significantly delay the initiation of reproductive activities by males. A male significantly reduces his mean inter-copulatory time from 25.2 to 17.2 minutes by stealing rather than catching prey between copulations ($t = 4.72$; $p < 0.001$). My observations of males between copulations suggest that males display a mixed hunting response. If a hunting male first encounters a searching or feeding male, or a copulating pair, he usually attempts to steal the prey (and also to copulate with the female in the case of a copulating pair). However, if a hunting male first encounters a prey arthropod, before seeing a copulating pair or another male with prey, it becomes his victim. The incidence of prey-piracy both between copulations and during copulations is dependent on the size of the population of *Bittacus apicalis*. Under low population density (Table 3; Fig. 5) none of the copulations were interrupted and thus no piracy of prey in possession of copulating pairs was observed. However, under moderate to high population numbers (Table 2; Fig. 4) 54 of the 88 copulations were disrupted, and the nuptial prey was stolen in 57% of the disruptions. Under low density conditions prey was stolen from males 27 times and stolen by males 19 times between copulations (Table 5). Under moderate to high population densities prey-piracy between copulations increased to 109 prey stolen from males and 38 stolen by males (Table 4).

It is interesting that an intruding individual (almost always a male) is successful in stealing prey from a copulating pair about 57% of the time (31 out of 54 observations; see Fig. 4). I do not have comparable data on the success of hangingflies in attempts to steal the prey from searching or feeding males, but I feel that it is about 50%. Males that steal a male's or a copulating pair's prey have been observed to behave in one of two ways; first, some males fly directly against the individual or pair with some force (this behavior probably increases the efficiency of prey-piracy by males); second, some males merely fly up and strugle with the original male or pair for the prey.

In 85% (46 of 54) of the interrupted copulations observed, no copulation resulted after interruption, but in 15% the intruding male copulated with the female. The resumption of copulation by the original pair, or copulation by an intruding female with the original male, was never observed.

T-tests were used to determine if an increase in the number of times a male experienced prey-piracy between any two copulations listed in Tables 2 and 3 (including interval from marking to first copulation) resulted in an increase in inter-copulatory time. Mean inter-copulatory duration increases as the number of prey stolen from males between copulations increases (Table 6). These results were expected since it is necessary for a male to obtain prey before his next copulation each time his prey is stolen.

I also recorded the number of prey stolen by males, number of prey stolen from males, number of prey discarded after capture and evaluation by males, and number of males interacted with by males between copulations and between marking and release and first copulation (see Tables 4 and 5). A comparison of these behavioral data by means of a t-test under conditions of moderate to high and low population densities is shown in Table 7. Significantly more prey are stolen by males, and from males, under conditions of moderate to high population densities than when populations are at low levels. No significant difference was found between the mean number of prey discarded by males under conditions of varying population densities. This indicates that a male is likely to capture small prey which he subsequently judges unsuitable and discards, without regard to population density as expected. The mean number of females that a male interacts with between copulations is significantly greater under low population density than when populations are at moderate to high levels. This may seem anomalous, but is easily explicable in terms of the greater number of receptive females when population densities are high. In the early and mid flight season of *Bittacus apicalis* individuals are everywhere abundant and at least in the early season individuals are still emerging (Thornhill, 1974). A greater portion of the females are sexually receptive at this time and little time elapses between the initiation of calling behavior by a male and the attraction of a receptive female. However, some nonreceptive females are attracted to the searching males and steal or feed upon their prey, but do not copulate with them. Late in the season when population numbers have decreased many females are unreceptive, possibly due to disease or senility, and although they are attracted to males a large number of them refuse to copulate and only steal or feed upon the male's prey.

TABLE 6

The relationship between the incidence of prey piracy between copulations and the inter-copulatory time (minutes).

| No. Times Prey Stolen From Males Between Copulations | N | Inter-cop. Time | Std.Dev. | Range |
|--|----|-----------------|----------|-------|
| 0* | 73 | 22.9 | 7.59 | 5-39 |
| 1 | 40 | 32.8 | 8.79 | 6-49 |
| 2 | 19 | 43.0 | 10.30 | 28-61 |
| 3 | 10 | 50.5 | 11.40 | 35-69 |
| 4 | 7 | 55.9 | 6.77 | 48-67 |

Student's T-Test Analysis:

| | |
|--------------------|----------------------|
| 0 VS. 1: T = -6.19 | p(2 Tail) = 0.000*** |
| 1 VS. 2: T = -3.96 | p(2 Tail) = 0.000*** |
| 2 VS. 3: T = -1.80 | p(2 Tail) = 0.083 |
| 3 VS. 4: T = -1.12 | p(2 Tail) = 0.286 |

*Exclusive of situations where male used the same prey in two successive copulations.

Tables 4 and 5 summarize for the four copulations of each male, the time spent between copulations, time between release and the first copulation, time spent in finding sexually receptive females, the time locating prey used in copulations, and the time spent feeding on prey. Table 8 shows highly significant differences in the mean durations of each of these inter-copulatory activities as well as the mean total durations between copulation for males under conditions of high to moderate and low population densities. The total time between copulations is greater at moderate to high population levels because of increased time involved in feeding on prey and in locating prey to be used in copulations; and these increases, in turn, are the result of more prey-piracy during moderate to high population levels. The high level of prey theft, both during copulations and between copulations results in the necessity to spend more time hunting for and making gustatory evaluations of prey. A total of 197 prey were captured or stolen and fed upon by the 22 males followed under conditions of moderate to high population levels. The high level of prey theft, both during copulations and between copulations results in the necessity to spend more time hunting for and making gustatory evaluations of prey. A total of 197 prey were captured or stolen and fed upon by the 22 males followed under conditions of moderate to high population density, whereas under conditions of low populations levels, 20 males handled only 148 prey (see Figs. 4 and 5). The time required for the

location of sexually receptive females by males was significantly greater at low population levels than at moderate to high densities.

Sperm Competition and Variance in Reproductive Success of Males and Females of Bittacus apicalis

The intrasexual component of sexual selection (competition between males) in insects does not necessarily end when a male inseminates a female because of the phenomenon of sperm competition, i.e., competition between the sperm from two or more males for the fertilization of the eggs of a single female (see review by Parker, 1970a). Relative to other animal groups insects have high levels of sperm competition resulting from the frequency of multiple insemination of females by different males and from the extent of temporal overlap of the stored ejaculates from two or more males. Any male which possesses an attribute that would decrease competition between his sperm and the sperm of another male during the fertilization of the

TABLE 7

Mean number of prey stolen by males, stolen from males, discarded by males after evaluation, and mean number of females males interacted with between copulations and between the release of marked individuals and the first copulation under conditions of low and moderate to high population densities of *Bittacus apicalis*.

| Population Density | N | Behavior | Mean No. | Std.Dev. | Range |
|--------------------|----|-------------------------|----------|----------|-------|
| Mod. to High | 88 | Prey Stolen By Males | 0.432 | 0.583 | 0-3 |
| Low | 80 | Prey Stolen By Males | 0.238 | 0.484 | 0-2 |
| Mod. to High | 88 | Prey Stolen From Males | 1.240 | 1.050 | 0-3 |
| Low | 80 | Prey Stolen From Males | 0.337 | 0.526 | 0-2 |
| Mod. to High | 88 | Prey Discarded By Males | 0.682 | 0.558 | 0-2 |
| Low | 80 | Prey Discarded By Males | 0.612 | 0.684 | 0-3 |
| Mod. to High | 88 | Females Interacted With | 1.360 | 0.529 | 1-3 |
| Low | 80 | Females Interacted With | 1.990 | 0.562 | 1-4 |

Students T-Test Analysis:

Moderate to high vs. low population density:

| | | |
|--------------------------|-----------|----------------------|
| Prey stolen by males: | T = 2.340 | p(2 Tail) = 0.021 * |
| Prey stolen from males: | T = 6.920 | p(2 Tail) = 0.000*** |
| Prey discarded by males: | T = 0.722 | p(2 Tail) = 0.471 |
| Females Interacted With: | T = 7.410 | p(2 Tail) = 0.000*** |

eggs of a female would gain a selective advantage. Parker discusses probable sexually selected adaptations of male insects which would reduce or prevent sperm competition. Here I mention two adaptations—sperm displacement and non-receptivity induced in the female—that may be important in maximizing a male's reproductive success in *Bittacus apicalis*.

Sperm displacement is defined by Parker (1970a) as "the displacement of previously stored sperm and its replacement with sperm from the last male to mate." He cites evidence from the literature and from his own work suggesting that sperm displacement may occur in multiple matings in *Drosophila* and dung flies (Scatophagidae). Recently, Economopoulos and Gordon (1972) have shown that in *Oncopeltus fasciatus* (Hemiptera: Lygaeidae), a species in which the male places semen directly into the spermatheca of the female through a long penile tube (Bonhag and Wick, 1953), the sperm of the first male is replaced by a "washing out" of the spermathecal contents by the flow of the semen of the second male to mate. In *Bittacus apicalis*, as in other bittacids, the aedeagus of the male is extended into a penile filament which is coiled when not in use. The lengths of the filaments in *B. apicalis*, *B. pilicornis* and *B. strigosus* correspond to the lengths

TABLE 8

Mean total time (minutes) between copulations for males and mean time for males in each of three activities between copulations under conditions of moderate to high and low population densities of *Bittacus apicalis*.

| Population Density | N | Activity | Mean Time For Activity | Std.Dev. | Range |
|--------------------|----|---------------------------|------------------------|----------|-------|
| Med. to High | 88 | Feeding on Prey | 11.20 | 5.90 | 3-30 |
| Low | 80 | Feeding on Prey | 7.38 | 3.97 | 2-20 |
| Med. to High | 88 | Locating Prey | 15.00 | 6.63 | 2-35 |
| Low | 80 | Locating Prey | 9.93 | 5.26 | 2-30 |
| Med. to High | 88 | Locating Receptive Female | 5.63 | 4.56 | 1-30 |
| Low | 80 | Locating Receptive Female | 7.98 | 4.02 | 1-20 |
| Med. to High | 88 | Total time between Cops. | 31.80 | 11.10 | 17-65 |
| Low | 80 | Total time between Cops. | 25.30 | 8.05 | 10-50 |

Students T-Test Analysis:

Moderate to high vs. low population density:

| | | |
|---------------------------------|----------|----------------------|
| Feeding on prey: | T = 4.92 | p(2 Tail) = 0.000*** |
| Locating prey: | T = 5.42 | p(2 Tail) = 0.000*** |
| Locating receptive female: | T = 3.51 | p(2 Tail) = 0.000*** |
| Total time between copulations: | T = 4.34 | p(2 Tail) = 0.000*** |

of the spermathecal duct in each species. This suggests that the aedeagus is extended into the spermatheca for sperm transfer during copulation, and it is tempting to infer that a replacement of stored sperm by the copulating male may take place. Any male capable of displacing all or part of the sperm would have a tremendous selective advantage over males without this ability.

The mating refractory period in females of *Bittacus apicalis* after copulations of 20 minutes or more probably maximizes the copulating male's egg gain (number of eggs fertilized) by reducing sperm competition that would result if additional matings took place during that time. During the refractory period following a male-terminated copulation, a male gains all the eggs laid if a female is a virgin, and probably most of the eggs if she is not a virgin. That the male fertilizes most of the eggs laid during the refractory period subsequent to a mating with a nonvirgin is of course an assumption but is based on data from studies on other insect groups (see review by Parker, 1970a). In most insects that have been studied, the last male to inseminate a female in a multiple mating sequence fertilized most (50% to 95%) of the subsequent eggs prior to another mating, at which time the sperm of the last male takes precedence in fertilization. In multiple insemination of females, sperm competition is an important factor in determining a male's reproductive success, and usually sperm from matings prior to the last compete for the percentage of eggs not fertilized by the last male to mate. For example, Parker (1970b) has shown that in dung flies the last male to mate fertilizes about 80% of the succeeding batch of eggs irrespective of the number of previous matings. Also, sperm from previous matings compete for the remaining 20% of the batch in the same proportion as they did for the previous batch. I presume that a somewhat similar situation exists in bittacids; however, if sperm replacement is complete, the last male to mate would fertilize all the eggs of a female during her refractory period.

The concept of sexual selection is based on the idea that variance in the reproductive success of one sex (usually the male) is greater than the variance in the reproductive success of the other sex. Thus, in any study of sexual selection it is important to obtain data on differential reproductive success of each sex. Estimation of the egg gains of the 42 marked males of *Bittacus apicalis* that were followed through four successive copulations allows a means of assessing the variance in male reproductive success. First, I must make the following two assumptions: 1) the last male to mate for 20 minutes with a female in a multiple mating sequence fertilizes most of the eggs laid until she copulates with another male. In quantifying egg gains I use 85% as the

percentage of eggs fertilized by a male until another mating takes place. The remaining 15% of the eggs are fertilized by the sperm of the male(s) which copulated with the female prior to the last copulation. 2) Copulations of durations less than 20 minutes resulting from interruptions by intruding males or from premature termination by the female lead to no egg gain for a male. It was shown that copulations of less than 20 minutes do not initiate nonreceptivity and oviposition in females and that those females immediately seek another male with which to mate.

The first assumption is very reasonable because of the information available from studies on sperm competition in insects. However, in *Bittacus apicalis* 85% may be much too conservative an estimate of the last male's egg gain, especially if complete sperm replacement by the last male to mate takes place. Of course, 85% egg gain by a male in the refractory period following mating is too low when a male mates with a virgin, in which case the male would presumably fertilize all the eggs during the refractory period of three hours. A female lays an average of 3.5 eggs during a refractory period. Eighty-five percent of this is 2.98 or three eggs gained by a male copulating with a female 20 or more minutes.

The second assumption will probably not be substantiated unless complete sperm replacement takes place during copulations of 20 or more minutes. Despite the problems with these assumptions, I believe that male reproductive success can be more meaningfully measured this way than merely by the number of copulations. Male reproductive success undoubtedly varies as a function of the number of copulations that a male obtains, but in *Bittacus apicalis* copulations lasting less than five minutes result in the transfer of very few or no sperm and therefore cannot be considered to increase a male's reproductive success (Thornhill, 1976a).

Variance in male reproductive success in *Bittacus apicalis* is primarily influenced by four factors: 1) interrupted copulations by intruding males, 2) the time necessary for prey location and capture, 3) prey-piracy by males between copulations, and 4) mistakes in prey selection and evaluation by males (this paper and Thornhill, 1976a). The frequencies of interrupted copulations and prey-piracy are directly related to population density. Interrupted copulations reduce a male's time *in copulo* and therefore the number of sperm transferred. The number of times a male is robbed of his prey between copulations is positively correlated with intercopulatory duration; therefore, more time is required by robbed males for prey acquisition resulting in less copulatory time. Mistakes in prey selection and evaluation result in time

wasted by males because the females either refuse to copulate or copulate for a short duration.

The egg gain (9 or 12) and egg gain per minute (0.046-0.080) by the 20 males followed through four copulations under conditions of low population density (see Table 3) show relatively little variation. A better estimate of the variation in egg gain by males is based on observations of 22 marked males in four successive copulations under moderate to high population densities (see Table 2). Sixty-one percent of the 88 copulations recorded for these 22 males were interrupted by intruding hangingflies. The egg gains of the 22 males in four copulations ranged from 1 to 12, and the eggs gained per minute ranged from 0 to 0.064. Five males (22.7%) had egg gains of zero since they were unable during any of their four copulations to remain coupled for 20 minutes because of intruding males. One male had an egg gain of 12 thus being more than twelve times as successful as those five males with zero egg gains. If the egg gain per minute is extrapolated to egg gain per day, assuming a 12 hour day (e.g., 6:00 a.m. to 6:00 p.m.) and that the male's reproductive success would not change during the day, egg gains per day vary from zero to 46 eggs. Copulations and time between copulations require on the average about 23 and 25 minutes, respectively. A male under these average conditions might be expected to effect 15 successful copulations per 12 hour day. If a male fertilized 85% of the eggs that the 15 females laid during their refractory periods (i.e., three eggs per mating), he would fertilize 45 eggs per 12 hour day. One male had an egg gain of 0.080 per minute during four copulations and would gain 57.6 eggs per 12 hour day if he maintained this rate all day.

Thus there appears to be considerable variation in the reproductive success of males if measured in terms of egg gain in four copulations or in egg gain per minute. Females, on the other hand, do not exhibit this degree of variation in the number of eggs they produce. Females lay about 3.5 eggs per four-hour non-receptive period and experience four matings and four refractory periods per day under average conditions. The only factor observed to influence importantly the variance in number of eggs a female laid in nature was interrupted copulations by intruding males, which delays the insemination of a female and delays oviposition. However, these delays are short because a female may occasionally resume copulation with the original male, or she copulates with the intruding male, or she locates another male rapidly ($x = 2.5$ minutes in nature) (Thornhill, 1974. 1976a).

Bittacus pilicornis

My analyses of the behavior of *Bittacus pilicornis*, *B. stigmaterus* and *B. strigosus* were not as detailed as that for *B. apicalis*. *Bittacus pilicornis*, *B. stigmaterus* and *B. strigosus*, unlike *B. apicalis*, are active after dark and under conditions of low light intensities at dawn and dusk which makes field observations difficult. This problem was offset somewhat by laboratory studies since bittacids are easily kept and observed under laboratory conditions.

Figure 7 shows the alternative sequences of the sexual behavior of *Bittacus pilicornis*, based on observations of individuals and pairs, and unmarked males between copulations. Although the males of *B. pilicornis* that were followed were not marked, I am reasonably sure of individual identity in all observations reported in Figure 7. These observations were obtained in the period of low light intensities around daybreak and dawn. The broken lines connecting actions in Figure 7 were not observed in the field, but are based on laboratory observations. For example, I never observed a male catch or steal a prey item and then use it in a copulation in the field; however, this was often observed in the laboratory. Instead my time in the field was spent following males which had already captured or stolen prey and were feeding, or males which had already initiated their searching and calling behavior.

Bittacus pilicornis was never seen feeding or mating during full daylight. During the day both sexes hang by their front legs from leaves and stems of herbs with their wings lowered along the sides of their abdomen and fly only when disturbed. As light intensities fall in late afternoon, individuals become active and begin to fly among the herbs in search of food. At this time, both sexes can be seen capturing and feeding upon prey. No matings, mating attempts, or pheromone dispersing behavior by males were observed in the late afternoon in *B. pilicornis*. This species is apparently active at night in nature, because both sexes commonly feed at night in the darkness of the laboratory. *Bittacus pilicornis* was not observed to mate or attempt to mate in the laboratory at night. *Bittacus pilicornis* apparently does not ascend into the trees at dusk and remain in the tree-top until the following dawn as does *B. strigosus* (as discussed later). No behavior associated with mating was observed in *B. pilicornis* at times other than at daybreak and dawn; at which times, the capture of prey and feeding by both sexes are also commonly observed.

Males of *Bittacus pilicornis* initiate the sequence of sexual behavior by catching a prey arthropod, usually an insect, which will serve as the

B. *PILICORNIS*: IN NATURE

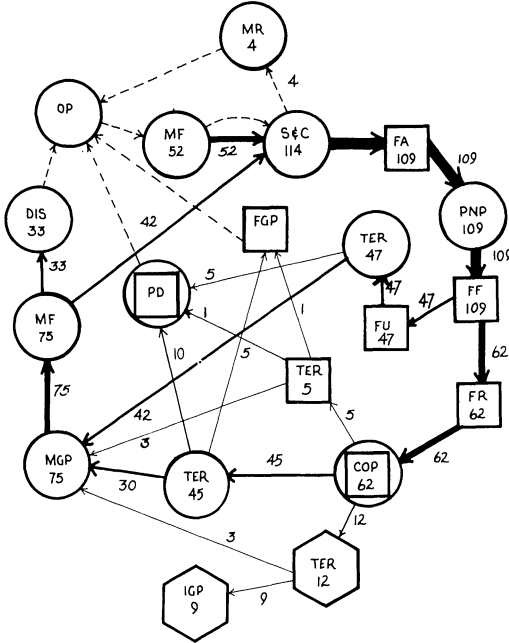


Fig. 7. Alternature sequences of pair formation, copulatory and inter-copulatory behavior in *Bittacus pilicornis*. Circles indicate male actions and squares female actions. Hexagons denote the intruding behavior of males which interrupt copulations. The numbers on the lines, and the relative thicknesses of the lines, indicate the number of behavioral events following a particular pathway. Numbers within the symbols indicate the number of times that event occurred. The circle (OP) at the left top of the diagram is a logical starting point. The broken lines connecting behavioral actions were not actually observed, but are based on laboratory observations. Abbreviations as in Fig. 4.

nuptial meal (Fig. 7). The mean duration of feeding by a male after he obtains prey and before he begins his searching and calling behavior is about six minutes ($\bar{x} = 5.95$ minutes, $N = 24$); however, all these feedings had been initiated prior to my first observation of the males. None of the feeding males observed were robbed of prey by other males or female hangingflies. After feedings of approximately six minutes, males begin making short flights (5-20 feet) through the low vegetation while still holding the prey, i.e., they initiate searching behavior. After each flight a male raises his wings and may or may not vibrate them. At the same time, he everts and inverts his pair of pheromone dispersing structures by flexing the abdomen forward. The

pheromone dispersing vesicles in *B. pilicornis* are bifurcate, unlike the vesicles in *B. apicalis* which are rounded. Four males were robbed by intruding males during their searching and calling behavior out of a total of 14 robbery attempts. In all observed thefts in nature, it appeared that the intruding male flew against a searching or calling male and then the two wrestled for the prey.

Fifteen searching and calling males required an average of 11.3 minutes to attract a sexually cooperative female. This is somewhat longer than the average time required for males of *Bittacus apicalis* to attract a receptive female (see Tables 4 and 5), probably because the populations of *B. pilicornis* were smaller and also because females of *B. pilicornis* remain sexually unreceptive for up to two days after mating (*B. apicalis* females are unreceptive for about three hours after mating; Thornhill, 1974, 1976a). These two factors probably contributed to fewer sexually receptive females of *B. pilicornis* being available. Unreceptive females of *B. pilicornis* were attracted by searching and calling males; in fact, 43.1% (47 out of 109) of the females attracted to males would not mate with them, but attempted to get their nuptial meals. These unreceptive females were not successful in stealing the male's prey, but did manage to feed briefly (\bar{x} = 4 minutes in lab., N = 17) on the prey before the male terminated the interaction. At the termination of interactions with unreceptive females, as in *B. apicalis*, the male of *B. pilicornis* pulls the prey from the grasp of the female, who is also attempting to pull it from the grasp of the male. The male retained the prey at the termination of most (90%) encounters with unreceptive females, but the prey was dropped in 10% of these terminations. Unreceptive females may also gain possession of the prey at the termination of copulation, but this was not observed in nature (Fig. 7).

After a female is attracted to within a few inches of a calling male, either sex may approach the other. Sometimes females actually collide with calling males. At the end of pair formation, the sexes are a few inches apart and facing each other while suspended from the vegetation by their front legs. At this time the male presents the prey to the female. Unlike *Bittacus apicalis*, the male of *B. pilicornis* does not cover the prey with his abdominal tip while it is being passed to the female. The female grabs the prey with her hindlegs and sometimes also her middle legs and begins to feed on it while it is still being held securely by the hind legs of the male. The tarsi of the middle legs of the male are usually wrapped around the femora or tibiae of the female. The male begins to search out the tip of the female's abdomen by sliding his opened genital claspers down the length of the abdomen

of the female. The male may couple with the female on the first attempt, but occasionally three or four attempts are required even if the female is sexually receptive. An unreceptive female pulls her abdomen back each time the male attempts to couple with her and after two or five minutes of unsuccessful mating attempts the male terminates the encounter and flies away, feeds briefly on the prey, and then resumes his searching and calling behavior if the prey is still suitable.

Duration of copulation is apparently dependent on the size and palatability of the prey, as is the case in *Bittacus apicalis*. Males are selective in their choice of prey (Fig. 2) and their prey preferences may have been determined in part by intersexual selection (Thornhill, 1974, 1976a). Timed male-terminated copulation in both the field (N = 45) and laboratory (N = 22), in the absence of intruding males, averaged 22.7 and 21.4 minutes, respectively. Blow flies (*Phaenicia sericata*) served as nuptial prey in the 22 male-terminated copulations observed in the laboratory. Five copulations observed in nature were female-terminated after a mean of 13 minutes; no female-terminated copulations were observed in the laboratory.

Copulating males of *Bittacus pilicornis* are often seen with their beaks inside the prey at the same time the female is feeding; simultaneous feeding by the pair during copulation was rarely seen in *B. apicalis*, where only the female feeds during copulation. Perhaps the male of *B. pilicornis* is not feeding during copulation, but is only secreting digestive enzymes into the prey which could facilitate his feeding of the female.

Of the 62 copulations observed in nature from beginning to end (Fig. 7), 45 were terminated by the copulating male, five by the copulating female and 12 by intruding males. None of the intruding males were able to effect a copulation with the original female. As in *Bittacus apicalis*, the male of *B. pilicornis*, reclaims the prey most of the time (66%; Fig. 7) when the copulations are terminated by either mating partner. In the 12 copulations terminated by intruding males, the intruder stole the prey nine times, with the copulating male retaining it three times. The prey was dropped at the termination of 11 of these 62 copulations. If the female gets the prey or it is dropped, I assume (as indicated by the broken lines in Fig. 7) that the male would then seek another prey item for his next copulations, as was observed in the laboratory. When the copulating male retains the prey after the termination of an encounter, he feeds on it briefly and then if it is still palatable he begins his search for another female. If the male judges the prey to be of low food value after a copulation he

discards it and probably seeks another arthropod to use in his next copulation. That males of *B. pilicornis* discard unpalatable prey after a copulation is based on my observations of males of *B. apicalis* discarding prey after a copulation of normal duration and the assumption that *B. pilicornis* behaves in a similar way in this context. Males of *B. pilicornis* were seen to use prey in two successive copulations on three occasions in nature.

Bittacus stigmaterus

Bittacus stigmaterus was not studied in nature, because only one small population of this species was found in Washtenaw County, Michigan. This species occurs in relatively small numbers in Michigan (Thornhill and Johnson, 1974). My laboratory observations on *B. stigmaterus* reveal that its reproductive behavior is most similar to that of *B. pilicornis*. *Bittacus stigmaterus* is undoubtedly nocturnal and crepuscular since no individuals were seen feeding or mating in nature during the day, and mating did not occur during the day in the laboratory. However, this species was observed to feed during the day in the laboratory; but this is probably not normal behavior because *B. strigosus*, also a nocturnal and crepuscular species, rarely feeds during the day in nature, but readily feeds in the laboratory during daylight hours. Although a considerable amount of time was spent observing *B. stigmaterus* in the laboratory at night and at dusk, all mating pairs (nine) were observed around dawn; hence, this species may mate only at this time, as is probably the case for *B. pilicornis*.

After a short feeding period ($\bar{x} = 13.5$ minutes, $N = 18$) following the capture of a blow fly in the laboratory, a male of *Bittacus stigmaterus* assumes a calling posture similar to that of *B. pilicornis*. While calling, the wings are raised and the pheromone-dispersing vesicles are everted and inverted intermittently. Since the precopulatory behavior of *B. stigmaterus* was not observed in nature, and because the calling males were somewhat confined in the terraria, it is not known if this species exhibits searching behavior similar to that in *B. apicalis* and *B. pilicornis*. Males of *B. stigmaterus* were seen, however, making short flights from one area to another in the terraria and then assuming the calling posture after each flight, which suggests that searching is part of the behavioral repertoire of this species. Prey-piracy of searching or calling males by other males was observed several times.

Females are attracted to calling males, and the male passes the prey to the first female that arrives. The male's abdomen is not placed over the prey while it is being presented to the female. As in *Bittacus apicalis* and *B. pilicornis*, some females of *B. stigmaterus* pull their

abdomens back when the male attempts to copulate with them, but receptive females do not behave in a coy manner and readily unite with the male. Both the male and the female grasp the prey while the female feeds during copulation. The male may also occasionally be seen with his beak in the prey while the pair copulates. During the presentation of the prey to the female and during copulation, the male holds his wings in a raised position, while the female keeps her wings lowered along the sides of her abdomen.

Nine copulations in *Bittacus stigmaterus* with blow flies as nuptial prey were observed from beginning to end and timed; all were male-terminated and lasted a mean of 20.6 minutes (Range = 17-23 minutes). This is similar to the means of about 23 minutes and 21 minutes for *B. apicalis* and *B. pilicornis*, respectively. The male retained the prey after a brief struggle with the female at the termination of all nine copulations in *B. stigmaterus*. The disruption of copulating pairs of *B. stigmaterus* by intruding males was observed on several occasions in the laboratory. An intruding male would fly against the copulating pair and attempt to copulate with the female and gain possession of the nuptial meal, or merely fly against the pair and attempt to steal the prey. Intruding males commonly stole the prey and then the female terminated the copulation with the original male. Intruding males were never seen to effect a copulation with the female.

Bittacus strigosus

The behavior of *Bittacus strigosus* is more complex than that of the other species studied. Like *B. pilicornis* and *B. stigmaterus*, *B. strigosus* is a crepuscular and nocturnal species. During my three-year study of populations of *B. strigosus* in Michigan, I have only seen 21 individuals out of a total of 423 carrying prey during full daylight, and no matings were observed during the day. During daylight hours both males and females hang by their front legs in the lower woodland vegetation and only fly when disturbed. The inactivity of *B. strigosus* during the day was also observed by Brownson (1964) in Ohio. Both sexes of *B. strigosus* become active at dusk and can be seen flying through the low herbage while sweeping it with their hind and middle legs. When the tarsi contact a prey arthropod, the hangingfly grabs it and begins to feed. *Bittacus strigosus* also catches flying prey by rapid flights out from a hanging position in the herbage. At dusk individuals of both sexes, which may or may not be carrying prey, can be seen flying slowly into the trees. Some of the ascending hangingflies appear to

sweep branches and leaves of the trees as they ascend. At dawn hangingflies can be seen fluttering down from the trees, and it is during this time that *B. strigosus* again becomes abundant in the low vegetation of the woods. Individuals of either sex may be seen feeding during a one to two hour interval after their descent from the trees—i.e., they feed until light intensities rise to approximate daylight levels. Brownson (1964) first noticed the ascent of *B. strigosus* into the trees at dusk and their descent at dawn. To determine what the hangingflies were doing in the trees at night, he made observations from a 36-foot extension ladder and a 40-foot tower. Although his vision from the tower and ladder was severely limited, he observed 20 individuals of *B. strigosus* at heights ranging from 10 to 46 feet (\bar{x} = 34.6 feet). Only three of the 20 individuals he observed possessed prey. No mating pairs or calling males were observed in the forest canopy.

The behavior of the males of *Bittacus strigosus* at dusk is the most perplexing aspect of the behavior of hangingflies I have observed. As light levels fall in the late afternoon most males raise their wings, after hanging quietly in the herbs during the daylight hours with their wings lowered along the sides of the abdomen. Brownson (1964) felt that the initiation of wing-raising in males correlated with about 10 foot-candles of light. All four wings vibrate intermittently and may remain in the raised position continuously until dark; the males periodically evert the pair of bifurcate pheromone-dispersing vesicles when the wings are vibrated. The wing and body postures of male *B. strigosus* are identical to those of a calling male of *B. pilicornis*, but the males of *B. strigosus* rarely are holding prey. Other males of *B. strigosus* approach calling males by short flights through the herbage, and upon contact an attracted male raises his wings and the two hangingflies appear to attempt to engage their genitalia. These interactions between two males may last as long as two minutes, but actual genital contact usually lasts only a few seconds. During these interactions both males have their wings raised, but the pheromone dispersing structure is never exposed by either male. The homosexual encounters sometime lead to a grouping of the males. The results of pheromone attraction tests with *B. strigosus* indicate that males show an olfactory response to calling males at dusk (Thornhill, 1974). Males calling at dusk rarely have prey in their possession; Brownson (1964) observed them with prey only two times, and I observed this only four times during my three-year study, which included observations on several hundred males. In three of the four instances I observed, males were attracted on the calling males holding or feeding on prey, but there appeared to be no struggle between two males for the prey itself.

Brownson's (1964) study indicates that both males and females of *Bittacus strigosus* spend the night feeding in the tree-tops, returning at dawn to the herb stratum where mating takes place. The males assume the same calling posture as they did the previous dusk; however, at dawn males never interact. I observed 69 complete matings and numerous partial matings during my investigation of *B. strigosus*; all these matings occurred at dawn. Brownson (1964) observed nine matings by *B. strigosus*, eight were at dawn and one occurred after dark. At dusk, females are not attracted to calling males; females respond olfactorily to calling males only at dawn (Thornhill, 1974).

Brownson (1964) speculated on the adaptive significance of the homosexual encounters of males at dusk. He suggested that the behavior "may serve to attract the attention of any predators to the male rather than the more valuable female." This is not a very likely explanation because of the movement of males and females at dusk, dawn and during the day. When pairs separate after copulation, both individuals separately move away from the mating site. Also, males move around at dusk to feed and locate other males, and females move at dusk to feed; and both sexes move to a limited extent during the day. Therefore although a male may have mated with one or more females the preceding dawn chances seem slight that his mate(s) would remain near enough to him to benefit from his "display to predators" at dusk. A male attracting the attention of predators would then be protecting females in the vicinity, but probably not females he had inseminated, i.e., his behavior would be genetically selfless or altruistic and only explicable in terms of the differential survival of groups. It is now generally agreed that selection at the individual level is a much more potent evolutionary force than is group selection (Williams, 1966; Emlen, 1973; Ricklefs, 1973; Pianka, 1974).

Another interpretation of the male encounters at dusk based on group benefit was provided by Newkirk (1970). He states that while the males are engaged at dusk, the females ascend into the trees, and that the period of male homosexual behavior gives the females a period of feeding free of male interference. He goes on to say that this is a population adaptation resulting from the need to eliminate the competition between feeding and mating. Brownson (1964) did not observe a distinct separation of the sexes at dusk, and my observations indicate that the males and females move into the trees during the same period.

Brownson (1964) also suggested the male homosexual behavior at dusk may provide the needed stimulus to ejaculate the sperm and couple with the female the following dawn, i.e., the behavior serves as

a necessary component in the events leading to copulation. I tested this hypothesis by allowing males which had and males which had not experienced homosexual encounters at dusk to mate the following dawn. Eighteen males which were observed to have had genital contact with other males at dusk in the laboratory were isolated individually overnight in pint jars containing blow flies as food and each was mated to a virgin female (collected as teneral individuals) the following morning. Fifteen males which were isolated individually for 48 hours were also mated with virgin females. In all matings by both types of males, sperm was transferred as seen by examination of the spermathecae of the previously virgin females. Thus, it seems that a homosexual encounter by a male at dusk is not necessary for successful sperm transfer the following dawn.

I suggest the following hypothesis to explain the homosexual encounters of males at dusk. Perhaps the male encounters at dusk involve an evaluation and prediction of the nature and extent of competition for females the next dawn in an area. Males may, by attracting and responding to other males, be able to judge whether a particular area is suitable for their return the next dawn in terms of its potentiality for successful copulations. Males that could determine if a habitat was likely to contain females at dawn and was also likely to contain the fewest males would gain a selective advantage. When this idea was first formulated I thought that it would be easily tested by marking males and seeing if they returned to the same area at dawn where they had been calling and interacting with other males the previous dusk. This was attempted under laboratory conditions by placing marked males and females in a shaded screened enclosure (16 ft. x 8 ft. x 8 ft.). I found no pattern in the return of the males at dawn in this small experimental area. However, this does not negate my hypothesis because the arena of a male at dawn would be considerably larger than the floor space of this enclosure; it would be circular theoretically, and with a radius of 40 feet since this is the maximum effective distance of the male's sex attractant (Thornhill, 1974). I now realize that this hypothesis must be tested in the field. If it is found that males space themselves at dawn according to the nature and extent of male encounters the previous dusk, this would suggest that the encounters may enhance spacing, thus reducing male-male competition and result in greater reproductive success for individual males.

Heterosexual interactions in *Bittacus strigosus* apparently take place only during the time of low light intensities around dawn. Males at dawn assume the same calling posture as they do at dusk; however, at dawn only females respond to calling males. Calling males do not

possess prey, and nuptial feeding is not a part of the copulatory behavior of this species. The male grasps the female's abdominal tip with his genital claspers; at the same time he releases his hold on the vegetation and wraps his fore tarsi around the neck or wing bases of the female. Thus the female supports both the male and herself by her forelegs during copulation. During copulation the wings of the female are held down along the sides of the abdomen or ventral of the abdomen, whereas those of the male are held in an elevated position.

Sixty-nine copulations in nature and 78 copulations in the laboratory were observed from beginning to end. In both situations the mean duration was about nine minutes (8.60 and 9.24 minutes, respectively). Some of the copulations, both in nature and in the laboratory, were female-terminated and some were male-terminated, but careful notes were not kept on the terminating sex of each copulation. Brownson (1964) observed that copulation duration varied from one to nine minutes in the nine copulations he observed in nature. Thus, *B. strigosus* has a much shorter copulation duration than the other species of hangingflies investigated.

Parker (1970b) has explained the adaptive significance of copulation duration in the dung fly, *Scatophaga stercoraria* in terms of male strategies to reduce intrasexual competition. I have explained copulation duration in *Bittacus apicalis* in terms of a male's strategy to reduce the effect of male-male competition and in terms of female choice (Thornhill, 1976a, and above). In addition I have speculated as to how opposing selective forces should influence the evolution of copulation duration in insects (Thornhill, 1976b,c).

It is of interest to speculate why *Bittacus strigosus* copulates for a shorter duration than the other three species of *Bittacus* studied, and why nuptial feeding behavior has apparently been lost in *B. strigosus*. *Bittacus strigosus* is the only known bittacid which moves from the herb stratum to the forest canopy as light levels drop at dusk and returns to the herb stratum the following dawn. *Bittacus strigosus* does not feed or mate during the daylight hours which are spent in the low vegetation. This species does not mate in the low vegetation at dusk and apparently does not mate at night, but only mates upon return from the tree-tops to the herb stratum at dawn. Some feeding occurs at dawn and dusk in the low vegetation, but most of the feeding apparently takes place at night up in the trees. Possibly in the past selection pressures from interspecific competition or predators favored individuals that moved into the tree-tops at night to feed. The pheromones of at least some bittacids are species-specific and function at short distances of 40 feet or less (i.e., relative to the long distance

pheromones in some other insects—e.g., as in many Lepidoptera; Thornhill, 1974). That the pheromones are species-specific and work only over short distances indicates that they are heavy molecules since the effective distance and the species-specificity of a pheromone are inversely related to the size of the molecule (see Chapman, 1971). Very heavy molecules would be much less effective, because of their weight, in the tree-tops than at ground level and might result in all pair forming attempts being unsuccessful. Under these conditions individuals that refrained from reproduction and concentrated on feeding while in the tree-tops and placed all their reproductive effort in matings at dawn might be favored by selection. However, mating only at dawn has a disadvantage in that it allows only a short period of one to two hours when matings can take place. A short period for copulations would place a high premium on males capable of rapid and numerous matings. Therefore, males which did not feed the female during copulation and which maximally inseminated a female in a short time would be favored. Females that preferred such males would gain a selective advantage because their male offspring would behave similarly.

Copulation disruption by intruding individuals was never observed in *Bittacus strigosus* in nature; however, occasional interruptions by intruding males were observed in the laboratory. In a few cases the intruder managed to copulate with the female, but usually the pair was merely separated by the intruding male.

Other Bittacidae

Although only four species of Bittacidae were investigated in the present study, some information is available from the literature on other species of bittacids which allows a comparison with my findings. Table 9 summarizes certain aspects of the copulatory behavior of all species of bittacids for which this information is available. The family Bittacidae is the second largest family of Mecoptera, with about 75-100 described species. The behavior of only six of the 14 species of Bittacidae listed in Table 9 has been studied in any detail. *Bittacus apicalis*, *B. pilicornis*, *B. stigmaterus* and *B. strigosus* were investigated in the present study, and Bornemissza (1966) reported the behavior of *Harpobittacus australis* and *H. nigriceps* in Australia. Bornemissza states that he extended his studies to two additional Australian species, *H. similis* and *H. tillyardi*, and found their mating habits to be "comparable in every respect with those of *H. australis*"; therefore, I used his observations on *H. australis* to fill in information on *H. similis* and

TABLE 9

Some aspects of the copulatory behavior of the species of bittacids which have been investigated.

| Species | Range | Investigator | Copulation Duration | Prey Involved | Nature of Study |
|--------------------------|-----------|--------------------|----------------------|---------------|-----------------|
| <i>Bittacus</i> | | | | | |
| <i>italicus</i> L. | Europe | Brauer (1853,1855) | "short time" | yes | Lab |
| <i>tipularius</i> Latr. | Europe | Brauer (1853,1855) | "short time" | yes | Lab |
| <i>nipponicus</i> Nav. | Japan | Miyake (1913) | ? | yes | Lab |
| <i>apicalis</i> Hagen | U.S. | Newkirk (1957) | 1-24 min.* | yes | Lab & Field |
| <i>apicalis</i> Hagen | U.S. | Thornhill | $\bar{X} = 23$ min.* | yes | Lab & Field |
| <i>occidentis</i> Walk. | U.S. | Setty (1940) | ? | yes | Lab |
| <i>pilicornis</i> Westw. | U.S. | Thornhill | $\bar{X} = 22$ min.* | yes | Lab & Field |
| <i>punctiger</i> Westw. | U.S. | Setty (1940) | 25 min. | yes | Lab |
| <i>stigmaterus</i> Say | U.S. | Thornhill | $\bar{X} = 21$ min.* | yes | Lab |
| <i>strigosus</i> Hagen | U.S. | Brownson (1964) | $\bar{X} = 9$ min. | no | Field |
| <i>strigosus</i> Hagen | U.S. | Thornhill | $X = 9$ min. | no | Lab & Field |
| <i>Harpobittacus</i> | | | | | |
| <i>australis</i> (Klug) | Australia | Bornemissza (1966) | 3-12 ⁺ | yes | Lab & Field |
| <i>nigriceps</i> (Selys) | Australia | Bornemissza (1966) | 3-12 ⁺ | yes | Lab & Field |
| <i>similis</i> E.-P. | Australia | Bornemissza (1966) | 3-12 ⁺ | yes | Lab |
| <i>tillyardi</i> E.-P. | Australia | Bornemissza (1966) | 3-12 ⁺ | yes | Lab |
| <i>Kalobittacus</i> | | | | | |
| A Mexican species | Mexico | Thornhill | ? | yes? | Field |

*Copulation duration depends on size and palatability of nuptial prey.

+Copulation duration probably dependent on size and palatability of nuptial prey.

H. tillyardi in Table 9. The information on the species of *Bittacus* contained in Table 9 and not listed above, is based on only one or a few observations for each of these species.

I made a couple of behavioral observations on a species of *Kalobittacus*, undescribed according to Dr. George W. Byers (pers. comm.), in a small patch of cloud forest at an elevation of 4,000 feet, about five miles northeast of Coscomatepec, Vera Cruz, Mexico. *Kalobittacus* is apparently diurnal, as is *B. apicalis*. Both sexes of *Kalobittacus* keep their wings raised after short flights through the vegetation; this behavior is also typical of males and females of *B. apicalis* while resting between flights, but the other North American *Bittacus* species do not elevate their wings while resting and males of these species only raise their wings during calling and copulation. A male of *Kalobittacus* was collected at 4:30 p.m. while carrying a fulgoroïd homopteran as prey. Another male was seen at about 1:00 p.m. carrying prey and making short flights through the dense herb stratum of the tropical forest. After each flight the male everted his abdominal vesicles, but I did not notice any wing vibrations associated with this behavior. These observations suggest that the male feeds the female during copulation. Dr. George Byers (pers. comm.) feels that, based on morphological criteria, *B. apicalis* is only distantly related to the other North American Mecoptera placed in the genus *Bittacus* and is apparently more closely related to the genus *Kalobittacus*. The similarities of diurnal activity and the positioning of the wings in *B. apicalis* and *Kalobittacus* add credence to Byers' interpretation.

Prey-piracy by males between copulations and the disruption of copulating pairs by intruding males are apparently widespread components of the behavior of bittacids. Prey-piracy was noted in the three species in the present study that utilize prey in copulation and the disruption of copulating pairs was noted in all four of the species. Also, Bornemissza (1966) observed both prey-piracy and disruptions of copulating pairs by males of *Harpobittacus* in Australia.

The male feeds the female during copulation in all species whose copulatory behavior is known, except *Bittacus strigosus*, as shown in Table 9. Table 9 also reveals that the duration of copulation is dependent upon the palatability and size of the prey provided by the male in *Harpobittacus* species, in *B. apicalis*, and probably in *B. pilicornis*.

Of the 11 bittacid species in North America (10 *Bittacus* and one *Apterobittacus*), only one, *B. apicalis*, is known to be diurnal. Nothing is known about adults of *Apterobittacus apterus* MacLachlan, which is apparently restricted to the vicinity of San Francisco Bay in central

California (Byers, 1954). Data presented separately indicate that at least in *B. pilicornis* and *B. strigosus*, which are sympatric over most of their ranges, species-specific pheromones are produced (Thornhill, 1974). Bornemissza (1966) has shown that species-specific pheromones are also produced by *Harpobittacus* species. Perhaps olfactory discrimination is the chief means by which sympatric species of bittacids prevent or reduce interspecific mating mistakes. Sympatric species of bittacids in North America are partially separated on a seasonal basis (Thornhill, 1974), and temporal isolation could be important in preventing gene exchange between species. It is still uncertain how courtship differences between species, such as presence or absence of nuptial prey, relate to reproductive isolation. If species-specific pheromones are found to be the case in all the species in multi-species populations of nocturnal hangingflies (e.g., mixed populations of *B. pilicornis*, *B. stigmaterus*, *B. punctiger* and *B. strigosus* in the southeastern United States), this would suggest that courtship differences, which in the bittacids are perceived only after pair formation and therefore at very close range, are unimportant and that the longer ranging pheromones are the primary mechanisms preventing or reducing interspecific matings.

SUMMARY

Palatability and size are important criteria in the selection of prey arthropods by males and their use to feed the female during copulation in *Bittacus apicalis* and probably in *B. pilicornis*. Males selecting large palatable prey experience greater reproductive success than males that do not. I have shown separately that the prey preferences of males have probably been dictated in part by intersexual selection, i.e., female choice. Males of *B. strigosus* do not present a nuptial meal to the female in the prelude to copulation and show less selectivity with respect to prey size than the males of *B. apicalis* and *B. pilicornis*. In non-reproductive contexts females of the three species of hangingflies are indiscriminate in terms of the prey captured. There is apparently no preference for prey in any taxonomic group, and the diets of the three species of hangingflies depend on the prey arthropods available.

Bittacus apicalis is a diurnal species, feeding and mating during the day, whereas *B. strigosus*, *B. pilicornis*, and *B. stigmaterus* are crepuscular and nocturnal species. *Bittacus strigosus* feeds in the trees well above the herb stratum at night and *B. pilicornis* apparently feeds only in the low vegetation at night. *Bittacus stigmaterus* was not studied in the field.

Male-male competition in *Bittacus apicalis* is intense and is proportional to the size of the population. The reproductive success of males in nature is much more variable than that of females and is influenced by four factors: 1) interrupted copulations by intruding males, 2) the time necessary for prey location and capture, 3) prey-piracy by males between copulations, and 4) mistakes in prey selection and evaluation.

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