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### Recommended Citation

Cross, Earle A., and George E. Bohart. 1969. Phoretic Behavior of Four Species of Alkali Bee Mites as Influenced by Season and Host Sex. *J. Kansas Entomol. Soc.* 42: 195-219. April, 1969.

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*Reprinted from the*  
JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY  
Vol. 42, April, 1969, No. 2  
pp. 195-219  
*Made in United States of America*

**PHORETIC BEHAVIOR OF FOUR SPECIES  
OF ALKALI BEE MITES  
AS INFLUENCED BY SEASON AND HOST SEX**

EARLE A. CROSS AND GEORGE E. BOHART

# PHORETIC BEHAVIOR OF FOUR SPECIES OF ALKALI BEE MITES AS INFLUENCED BY SEASON AND HOST SEX<sup>1</sup>

EARLE A. CROSS<sup>2</sup> AND GEORGE E. BOHART<sup>3</sup>

## ABSTRACT

The phoretic relationships of four species of mites [*Caloglyphus boharti* Cross, *Glyphanoetus nomiensis* Cross, *Imparipies americanus* (Banks), and *Trochometridium tribulatum* Cross] to both immature and adult stages of the alkali bee, *Nomia melanderi* Cockerell, were investigated during the summers of 1955-1956 and 1965-1966. Degree and incidence of infestation of these mites were analyzed in time, space, and by host sex. Each species occurred in specific location(s) on adult *Nomia*. Two species, *C. boharti* and *G. nomiensis*, located differentially according to bee sex. The same mite species attached in different locations on different bee species. At least two, and probably all, of the species studied were distributed on adult hosts in approximately bilaterally symmetrical fashion. All four of the species used the adult host only for transportation. There was no evidence that phoresy, per se, was responsible for bee mortality. The phoretic population of each species followed a unique pattern in time which was at least partly dependent upon bee sex. In *I. americana*, both bee sexes appeared to be infested equally at emergence, but new males apparently lost mites much more rapidly than new females. Hypopi of *C. boharti* infested a higher percentage of, and occurred in greater numbers on, male bees.

## INTRODUCTION

### THE MITES

The presence of various mites as associates of many kinds of insects is well known to acarologists and entomologists alike, but until recently, formal studies of their interrelationships have been rare.

Phoresy is defined herein as "a form of behavior characteristic of certain animals which attach themselves to other animals to be carried about" (Webster's New Internat. Dict., 2nd Ed., 1957). We purposely omit from our definition the complex interactions initiating and resulting from this relationship (see Vitzthum, 1943).

A significant consequence of phoresy, implicit in the definition, is dispersal of the phoretic species. Its importance in the evolution of the Acarina is indicated by the fact that it has evolved a number of times in different ways in the three major mite groups, Mesostigmata, Prostigmata, and Astigmata. It is also functionally implicit in most members of the parasitic suborder Ixodides.

<sup>1</sup> This work supported in part by Research Grant No. AI-05657 from the National Institutes of Health. Accepted for publication September 5, 1968.

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Specializations for phoresy vary widely within each group. The phoretic specializations of parasitic forms (e.g., the transfer of sanguivorous forms directly from one individual to another or to a new host species following a molt) are often inseparable from their parasitic specializations per se. At the other extreme are species whose phoretic immature stages (nymphs of Uropodina and Acaridia) or adults (certain Antennophorina and Heterostigmata) regularly or intermittently exhibit unusual, often bizarre, structural and behavioral modifications.

We have found that many species of native North American bees carry mites belonging to one or more of the three major suborders mentioned above. Broadly speaking, mites are common on bees of the families Halictidae and Megachilidae and on the apid subfamilies Apinae and Xylocopinae (*sensu* Michener, 1944), and uncommon on most genera of the remaining groups. North American genera having the highest percentage of infested species appear to be *Xylocopa* (*sensu* Hurd and Moure, 1963), *Bombus*, *Nomia*, *Megachile*, *Anthidium*, *Lithurge*, *Agapostemon*, *Halictus*, and *Lasioglossum* (*sensu* Michener).

Broad correlations exist between bee taxa and those of associated mites; e. g., mites of the Family Chaetodactylidae are by far the most common associates of bees of the Family Megachilidae, and mites of the Superfamily Tarsonemoidea are the most common forms found on various genera of the Family Halictidae. A genus of bees is commonly associated with more than a single genus of mites, and vice versa. To what extent these relationships are phylogenetically parallel and to what extent they are merely a reflection of a common behavior or habitus (such as wood-nesting) is not known.

Many phoretic relationships are transitory, and sometimes they are purely accidental. Homann (1933), investigating bee-mite relationships in the honey bee (*Apis mellifera* L.) in Germany, found that relatively few of the 18 phoretic species studied by him had any permanent relationship to the individual or the colony.

Permanence of relationship, whether the latter be parasitism, paraphagism, symphorism, or some other type of association, is usually indicated by a high frequency of infestation and a dense mite burden. Examples of such relationships in North America include species of *Pneumonyssus* (Mesostigmata) and *Scutacarus acarorum* (Goeze) (Prostigmata) associated with most species of *Bombus*, *Chaetodactylus* sp. (Astigmata) found with certain *Osmia*, and *Sennertia* sp. (Astigmata) with *Xylocopa* sp., as well as the cases to be discussed herein.

Infestation by any mite species may be geographically continuous within the range of the host, or may occur only in isolated populations. *Caloglyphus boharti*, discussed below, has been found in association with the alkali bee at only one nesting site. The Holarctic *Scutacarus acarorum*, found with many, perhaps most, boreal species of North American *Bombus*, becomes progressively less frequent on all species at lower latitudes. These cases suggest that climatic factors may play an

important part in regulating mite distribution in the presence of a suitable host.

**DISTRIBUTION OF MITES WITHIN THE HOST POPULATION.** Most authors have noted that phoretic acarines form clusters upon certain members of a host population while leaving a relatively large portion of the population uninfested, i. e., form contagious distributions, but few have analyzed their data in this respect. Efford (1963) found that the distribution of *Feltria romijni* Besseling upon its host *Tanytarsus flavidulus* Edwards departs significantly from a Poisson distribution but fits closely to that of a negative binomial. Hunter and Mollin (1964), and Hunter and Davis (1965) found that the distribution of certain Mesostigmata phoretic upon the passalid beetle *Popilius disjunctus* (Illiger) does not follow that of a binomial. They likewise found a significant positive correlation between the percent of infested beetles and the mean number of mites per beetle.

In the case of the species of *Imparipes* and *Glyphanoetus* treated herein, it seems clear that the bees obtain their mite burdens largely or entirely from the natal cell. Since this microhabitat furnishes the environment for the mite to pass through its complete life cycle, thereby building its populations, one would expect to find these species contagiously distributed. The host emerges from the same cell in which the mites have developed and there is no need for the latter to migrate through the burrows or soil. On the other hand, although both *Caloglyphus* and *Trochometridium* build large populations in individual cells, these always contain dead or unhealthy brood, and both species must disperse in order to find a host bee. In this case, the time, rate, and type of dispersion must be considered in addition to any factors deemed important in the case of *Imparipes* and *Glyphanoetus*, and a contagious distribution would perhaps be less likely.

To test the degree to which distributions of the mites on alkali bees were contagious, we fitted counts of all four species (categorized according to age and sex of the adult host) into a Poisson series containing 11 classes, bees carrying 10 or more mites being lumped into the 11th class. In all cases, the observed distribution showed marked overdispersion, resulting in very large Chi-squares.

We also tried to ascertain whether infested cells were distributed randomly throughout the nesting site or existed in "pockets." Certain data for *Imparipes* were, therefore, analyzed by a non-parametric "runs" test (Siegel, 1956). Results are discussed under the section treating that species.

**DISTRIBUTION AND ATTACHMENT OF MITES ON INDIVIDUAL BEES.** Mites attach themselves to their host bees in two general fashions, reflecting the morphology and behavior of the species concerned: (1) clinging to the pile, nearly always of the thorax, and (2) attached to the integument, usually of the propodeum, metasoma, and vertex. Mites using the first method (Prostigmata and Monogynaspida) possess rel-

atively few specializations for attachment, excluding, perhaps, enlarged claws on one or more pairs of legs. Those using the second (most Acaridia, certain Uropodina) are usually furnished with various corporeal and appendicular suckers, mucilaginous hairs, or anal secretory glands, all special modifications for clinging. Members of the first group often ride as adults, whereas those of the second group almost always ride as nymphs.

Two of the four species dealt with here (*Glyphanoetus nomiensis* and *Caloglyphus boharti*) are phoretic only in a strikingly modified second nymphal instar commonly called a "hypopus." In the other two species—*Imparipes americanus* and *Trochometridium tribulatum*—adult females alone practice phoresy. These females differ markedly from immatures and adult males, exhibiting, for example, harder and seemingly less permeable integument, more compact body form, and stouter claws, particularly on legs I. The phoretic stages of all species discussed herein can survive at least two months without food, and use the adult host only as a transporting agent. In contrast, the phoretic stages of most water mites feed on their host while they use them as vehicles (Mitchell, 1967).

Areas of the integument inhabited by clustering mites are often called "acarinaria" (Cooper, 1955; Krombein, 1967). Some bees possess structures thought to be modified expressly for phoresy, but it is not clear whether or to what extent mite and carrier have interacted in the evolution of such structures. *Nomia* (*Dicunomia*) *heteropoda* Say possesses an enlarged propodeal-metascutellar sulcus often filled with *I. americanus*, but the most obvious acarinaria occur in certain African subgenera of *Xylocopa* (*Kophthortosoma*, *Mesotrichia*, and others). These consist of a chitinous pouch invaginated into the anterior face of the first metasomal tergum.

*Location of Attachment According to Host Species.* A single species of mite may attach to the same or different locations upon different host species. *I. americanus*, for example, is most commonly found on the anterior mesonotal angles of both *Nomia* (*Acunomia*) *melanderi* and *N. (A.) nortoni* Cresson, whereas *Glyphanoetus nomiensis*, most often found on the wings and modified male metasterna of *N. melanderi*, is commonly found in large, paired clusters on the vertex of *N. nortoni*.

*Symmetry.* The location of phoretic acarines on their hosts has been a matter of interest since the early work of Sylvestri, Berlese, and others. The four species of concern here all form clusters on the host, and to this extent are non-randomly distributed. However, the sizes and disposition of these clusters are perhaps of greater interest.

Bilateral equality of mite numbers on the host has been claimed for many, perhaps most, phoretics, this equality sometimes cited as helping to maintain a balanced load, thereby minimizing aerodynamic interference. Such a symmetrical distribution could be attributed either to random progress of the mites upon the host, given certain assumptions,

or to various non-random processes. Although several authors have described non-random, symmetrical clustering, we know of no instance where bilaterally symmetrical loads have been shown to be acquired solely through random mite movement.

Treat (1957 and earlier), in his work with the moth ear mite *Dicrocheles* (= *Myrmonyssus phalaenodectes* Treat, found that the first female mite to infest a moth chooses an ear, apparently at random. Nearly all succeeding females choose the same ear, so that only rarely do both ears of the same host become infested. The resulting distribution is, of course, unilateral. Here, site selection apparently depends only on the location of other mites of the same species. Mitchell (1967) analyzed the distribution of two species of *Arrenurus* on their adult dragonfly hosts, finding them to be contagious and asymmetrical. Mites on adult hosts were restricted in both time and space, and their asymmetry reflected that on the naiad prior to the final molt. Naiad asymmetry was ascribed to the formation of clusters to the right or left of (but rarely across) the center line. This situation is similar to that found by Treat.

A different type of site selection is seemingly characteristic of *Kennethiella* (= *Ensliniella trisetosa* (Cooreman), according to Cooper (1955) in his interesting study of the relationships between this mite and the eumenine wasp *Ancistrocerus antilope* (Panzer). Young males of this wasp often carry large hypopial burdens of the mite distributed in three clusters, two on the lateral faces and one on the posterior face of the propodeum. The lateral loads are approximately equal. If one lateral load is experimentally removed from a wasp isolated in a glass vial in the laboratory, the remaining hypopae usually redistribute themselves within a day or so in a symmetrical fashion. Here, the attachment of a hypopus seems to depend not only on the presence of others, but on their numbers as well.

Aspects of the symmetrical distribution of *Imparipes* and *Glyphanoetus* are discussed in more detail below.

Our observations, like those of many previous authors (Cooper, 1955; Krombein, 1962, 1967), indicate that the mites are attached, generally speaking, in equal numbers on each side of *N. melanderi*, although we noted that occasional bees showed striking asymmetry.

FREQUENCY AND DEGREE OF INFESTATION ACCORDING TO HOST SEX AND AGE. Any analysis of the distribution of mites upon individual bees must consider (1) the initial distribution of mites on the two bee sexes prior to the latter's emergence, and (2) the nature of mite or host loss in time. The first implies the possibility that the mites are capable of host sex discrimination at some time between the construction of the cell and the emergence of the adult, or that mite fecundity during that period is dependent upon bee sex. It is also possible that, after emergence, one host sex may be more "successful" in actively dislodging or passively losing the mites than the other, or again, that there is a dif-

ferential mite mortality on male and female hosts. Finally, there could be a differential mortality of the host according to sex for a given mite burden. Combinations of these may, of course, exist.

That some Hydracarina are able to distinguish and differentially parasitize hosts according to their sex seems well established. Davies (1959) and Mitchell (1967) report the differential parasitization, at time of host emergence, of simuliid flies and dragonflies, respectively, in Canada and the United States. On the other hand, Efford (1963), analyzing trap records of 1,577 newly-emerged flies, found that *Feltria romijni* attached equally to the sexes of the chironomid *Tanytarsus flavidulus* in England.

To our knowledge, stimuli directly responsible for discrimination by host sex have not been studied. Davies (1959) suggested that the presence of sexual differences in fat body size and/or the presence of developing ova in female flies might be valuable in determining the rate of attachment of *Sperchon* sp. Aspects of the changes in incidence and degree of infestation of mites on alkali bees according to sex and age are discussed in more detail below.

#### THE BEE

The alkali bee, *Nomia melanderi*, the host bee, is one of the most important and best known of all native North American bees. It ranges from central Washington and Idaho eastward to eastern Wyoming (*vide* Ribble, 1965), thence southward through west-central Colorado to northwestern Sonora and most of Baja California. Ribble (1965) separated the southernmost populations into a distinct subspecies (*melanderi howardi* Crawford). The alkali bee is the most important indigenous pollinator of alfalfa, with economically important populations in Wyoming, Idaho, Utah, Washington, Oregon, and California. It nests in dense aggregations of varying sizes, ranging from less than a square yard to several acres. Adults appear, depending upon temperature, from mid-June to mid-August and have a flight season of four to six weeks per generation. Most nesting sites in the Northwest have only one generation but in some, presumably where conditions are warmer, at least a partial second generation appears. In California and Arizona, normally at least two, and sometimes three, generations occur. Nesting "typically" occurs in bare or lightly vegetated soils that may vary in composition but are nearly always alkaline and moistened from the cell level to the surface by subsurface water. Females lay their eggs on flattened pollen spheres placed in the bottoms of vertically-oriented jug-shaped cells located between 7 and 12 inches deep. Cell interiors are smoothed and lined with a waxy coating. They are sealed, after provisioning and oviposition, with a spirally coiled layer of mud which often partially deteriorates during the winter, allowing increased communication between cells and burrow-inhabiting organisms. Under ideal conditions, single females make and provision about one cell per day, and



completed nests usually contain between 12 and 20 cells (Bohart and Cross, 1955).

Males emerge from the soil first, preceding females by several days. They spend the sunlight hours alternately feeding and patrolling the nesting area. At night or during cool, cloudy weather, they rest in emergence holes or cluster together in soil pockets or on the tips of tall, slender plants.

Females emerge throughout the day, but often spend a day, or even longer, at the burrow entrance before taking flight. As soon as they leave their burrows, they are pounced on by the patrolling males. Nest construction usually begins the same day. If the soil surface temperature is high, "digging in" is usually delayed until late afternoon. The second day after emergence, females often have completed their first pollen ball but do not oviposit on it until the third day. A period of about 11 days is necessary for the egg to develop to the overwintering stage, a modification of the final larval instar commonly called the prepupa.

Females divide the daylight hours between the nest and the flowers and spend the night within their own burrows. Contacts with males at the nesting site and on nearby forage are brief but frequent, the latter constantly seeking mates.

The metasomal sterna of the male are longer and more loosely arranged than those of the female and are provided with depressions and apophyses characteristic of the species. These differences appear to influence the distribution of hypopial *Glyphanoctus* and *Caloglyphus* upon the bee, and may be important in determining their numbers and duration of attachment as well.

Ten species of mites are known to be associated with the alkali bee. The four discussed here [*Imparipes americanus* (Scutacaridae), *Trochometridium tribulatum* (Pyemotidae), *Glyphanoctus nomiensis* (Anoetidae), and *Caloglyphus boharti* (Tyroglyphidae)] are associated in the greatest numbers with the bee in the Intermountain portion of its range.

#### PROCEDURES

The studies reported upon here were carried out in the summers of 1955-1956 and 1965-1966 at eight alkali bee nesting sites situated as follows: Hunter, Flowell, and Travertine, all near Fillmore, Millard Co., Utah, 1965-1966 only; Work's, near Delta, Millard Co., Utah, 1955 only; Airport, Cache Co., Utah, 1966 only; near Preston, Franklin Co., Idaho, 1965-1966; Hidden Valley, and Pavillion, both near Riverton, Fremont Co., Wyoming, 1955-1956, 1965.

Data were collected by noting presence and degree of infestation of mites (1) *in situ* upon adult bees collected over the nesting sites and on nearby flowers and (2) in bee cells containing immatures in various stages of development. Bees in the cells or burrows were categorized into eight classes, only six of which are pertinent here: (1) "old" prepupae,

(2) "new" prepupae, (3) white pupae, (4) pigmented pupae, (5) teneral in closed cells, and (6) teneral in opened cells or in the burrows. "New" prepupae belonged to the current year's brood; "old" prepupae belonged to the brood of the preceding year. White pupae were unpigmented or had darkened eyes only; pigmented pupae showed some darkening in addition to that of the eye. We sexed prepupae of the 1965-1966 brood, using the technique of Nielsen and Bohart (1967). The amount of wear exhibited by the wings, mandibles, and body pubescence was used to place adult bees into one of the following categories: (1) teneral, (2) very young, (3) young, (4) moderately old, (5) old, and (6) very old. Except in the case of teneral, which were nearly always found (unemerged) within the nest or whose wings were still soft, no absolute division separated any of these categories, and assignment in borderline cases was arbitrary. However, classification was always done by one or the other (usually both) of the authors, who consulted frequently.

Original procedure called for counting all the mites on each bee and in each cell, but this was found to be impractical. Subsequently, although accurate counts were always made of light and moderate infestations, mite numbers on heavily infested bees were usually estimated. These estimates were deliberately biased to be conservative and were periodically checked against actual counts. In all such cases, actual numbers exceeded the estimates. Consequently, although low and moderate counts were absolute, high counts (over 30) probably underestimated the actual number. Calculations of the mean mite burden based wholly or partly on estimates are marked with a superscripted "a" in figures and tables.

Our data were gathered from approximately 1,100 *Nomia* cells and 940 adult bees. Tables 2 and 5 show data arranged by sex according to sample. It should be remembered that adult male bees emerged about a week before the females and were, therefore, on the average, a week older in any given sample. Tables 3 and 4 and Figures 1 to 6 show the data arranged by sex according to age of emerged adult or stage of development. In these instances, it was necessary to lump the data from the different samples. We assumed variation within time and space as regards mite incidence and population size but made the further assumption that both types of variation were independent of bee sex. Spatial variation was important in *Imparipes*, where large samples of female bees at the Preston site showed both a low incidence of infestation and light mean burdens, whereas male bees did not differ greatly from those at other sites. Lumping, in this case, had the consequence of decreasing the differences between sexes, and was therefore conservative.

Bilateral symmetry of mite loads of two species was evaluated by means of total and pooled Chi-squares, utilizing a 1:1 bilateral distribution as a hypothesis.

Presence-absence data were analyzed in  $2 \times 2$  contingency tables

using Yates' correction for continuity, and by the non-parametric "runs" test (Siegel, 1956) to estimate randomness of distribution. Means of certain samples containing only absolute counts were compared by the non-parametric Rank-Sum Test of Wilcoxon and Wilcox (1964) or by a difference of means test using Student's "t."

## RESULTS AND CONCLUSIONS

### *Imparipes americanus*

This ubiquitous species was present wherever we found the alkali bee. It was found on every visit to each site, and was accordingly studied more intensively than the other species.

The adult females comprise the phoretic stage. They usually attach themselves to the thoracic pile of the bee, clinging to the hair bases and appressing themselves closely to the integument. When only a few are present, they are usually found in the subalar pits, where they tend to cluster three to nine to a side. Small clusters, usually of fewer than four, are also frequently found on the hind femora and on the posterior face of the propodeum. When present in larger numbers, the mites layer along the anterior margin of the mesonotum, especially at the sides, giving the bee the appearance of having rusty-red "shoulder pads." Particularly female bees may carry as many as 95 mites, but a more usual burden is 15 to 20. Generally speaking, *Imparipes* is distributed in a similar fashion upon either bee sex, but tends to be slightly more concentrated on the anterior mesonotal angles of males. The proportion of bees infested, as judged by examination of both cells and young adults, varies from site to site.

#### DISTRIBUTION OF *IMPARIPE*S WITHIN THE HOST POPULATION.

Because of the widespread availability of this mite, two analyses of random distribution within the host population were performed in addition to the one for adults mentioned previously. In the first, mites from two samples of cells containing prepupae were counted, arrayed into a Poisson distribution, and tested by Chi-square in the manner described for the adults. Sample 1, containing 32 cells, was collected in the Fillmore area on April 6, 1966. Sample 2, of 65 cells, was collected at the same site shortly prior to pupal transformation on June 30 to July 1, 1966. Both showed a high degree of overdispersion.

To check the possibility that infested cells might exist in "pockets" in the site, the above data of June 30 to July 1 (for the post-prepupal stage only) were analyzed by a "runs" test, cells being arrayed in the order in which they were dug. Although the first test, consisting of the first 41 cells taken without regard to contents, was barely significant at 0.05, a similar test of the entire array of 169 cells showed no such significance. The entire sample was then arrayed according to sex and the following stages of development: teneral, pigmented pupae, white pupae. Each category was tested separately; in no case was "r" significant.

We conclude that, although *Imparipes* exhibits a markedly contagious distribution on individual adult bees, the distribution of infested cells within the nesting area appears to be random and independent of bee sex or stage of development.

**DISTRIBUTION OF *IMPARIPIPES* UPON INDIVIDUAL BEES.** Although the largest numbers of *Imparipes* are found on the anterolateral mesonotal angles of both sexes of *Nomia*, these areas may not be occupied first, at least on female bees. Of a sample of 37 teneral and newly-emerged females carrying *Imparipes* on August 10-11, 1965, and June 30, 1966, in the Fillmore area, 34 carried one or more in either or both subalar pits, 8 had one or more on the mesonotal angles, 16 carried at least one on the posterior face of the propodeum, and 19 had one or more on the bases of legs III. The most heavily loaded bees carried mites in all of these areas.

A rather different pattern is indicated by our limited data for male *Nomia*. Here, of a sample of 19 infested teneral and newly-emerged bees, 15 possessed at least one *Imparipes* on the mesonotal angles, whereas only 7 had mites in the subalar pits, 5 carried one or more on the scutellum, and only 1 had them on legs III.

In both bee sexes, mites apparently migrate initially to the anterior thoracic region, perhaps later to seek other areas. Those on females find the subalar pits quickly. These seemingly serve as refugia, since they are usually occupied to the exclusion of other sites in female *Nomia* carrying but few mites, and they are usually the last areas from which mites are lost. Space in these pits is limited, the maximum number of mites observed in any one pit being 9; however, they are often unfilled, carrying 3 or fewer, even in females bearing heavy mite burdens.

The pattern of distribution in teneral and newly-emerged females applies in older females as well. In a sample of 34 infested females in the "young" and "moderately old" classes, 30 had mites in the subalar

TABLE 1. Symmetrical distribution of *Imparipes americanus* on female *Nomia melanderi*.

Site, date	Area of attachment	Bee age class	d.f.	Total mites/side		Total Chi-square
				Right	Left	
Fillmore, 8/10-11/65	Subalar pits	teneral & very young	28	65	61	19.20 N.S.
Fillmore, 8/10-11/65	Anterior mesonotal angles	teneral & very young	22	170	138	37.44*
Riggs' home, 7/27/56	Subalar pits	young & moderately old	15	37	38	6.22 N.S.
Riggs' home, 8/3/55	Subalar pits	young & moderately old	11	18	27	5.75 N.S.
Riggs' home, 8/3/55	Anterior mesonotal angles	young & moderately old	5	20	22	2.48 N.S.

pits, 25 carried them on the anterior mesonotal angles, 8 retained them on the posterior face of the propodeum, and none had them on the hind legs. We have insufficient data to make statements concerning still older females.

*Imparipes* were scarce on older male bees. Of 9 available males "moderately old" or older, the distribution of *Imparipes* was variable. Four of the 9 carried mites on the "shoulders," 3 on the scutellum, 2 on the legs, and only 1 carried any mites in the subalar pits.

*Symmetry.* We evaluated the symmetry of *Imparipes* in the subalar pits and on the anterior mesonotal angles of female *Nomia* of various ages by the use of Chi-square, utilizing a 1:1 bilateral distribution as mentioned previously. Mite loads on males were too small for analysis but appeared to be symmetrical. In most instances, the thesis of equal distribution was upheld (Table 1), but the sample of bees in the youngest age classes from the Fillmore area shows a departure from the expected ratio (significant at the 5-percent level). The associated heterogeneity Chi-square was also significant at 0.05, indicating no trend as to numbers found on a single side.

Significance was caused by only a few specimens carrying asymmetrical loads, e.g., the two most deviant specimens (carrying 14-3 and 16-5 mites) contributed about 37 percent of the total Chi-square. The same degree of symmetry appears to be maintained in time, and it is

TABLE 2. *Imparipes americanus* phoretic on *Nomia melanderi* taken in flight, 1955-1956, 1965-1966, by locality and date.

Site, date	No. of bees (all ages)		Percent bees infested		Mean mite burden/ infested bee	
	♂	♀	♂	♀	♂	♀
WYOMING						
1. Hidden Valley, 7/12/55	20	15	20	93	2.5	19.5
2. Hidden Valley, 8/3/55	2	25	0	56	0.0	7.4
3. Riggs' home, 8/3/55	2	23	0	35	0.0	6.4
4. Hidden Valley, 7/26/56	20	20	0	65	0.0	16.8
5. Riggs', near, 7/26/56	20	20	5	80	1.0	6.4
6. Hidden Valley, 7/21/65	55	0	5	...	3.3	...
UTAH						
7. Work's, Delta, 8/15/55	24	0	8	...	— <sup>b</sup>	....
8. Flowell, 7/19/65	100	4	2	100	1.0	10.0
9. Travertine, 7/19/65	80	2	5	50	1.3	26.0 <sup>a</sup>
10. Travertine, 8/10/65	26	34	4	44	1.0	7.9
11. Hunter-Flowell, 8/11/65	57	37	12	87	2.0	26.2 <sup>a</sup>
IDAHO						
12. Preston, 7/1/65	21	63	5	10	1.0	4.3
13. Preston, 7/9/65	20	97	0	24	0.0	10.9
14. Preston, 6/28/66	16	69	6	20	3.0	8.3 <sup>a</sup>

<sup>a</sup> Figures include some estimates of mite numbers.

<sup>b</sup> Reliable counts not made.

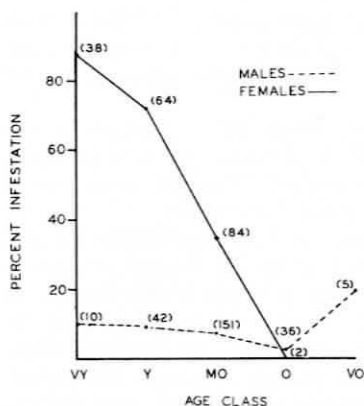


FIG. 1. Percentage of *Nomia melanderi*, captured in flight, infested by at least one specimen of *Imparipes americanus*. Bees are divided into five age classes, Class I being "very young," Class V, "very old." The figures in parentheses refer to sample size.

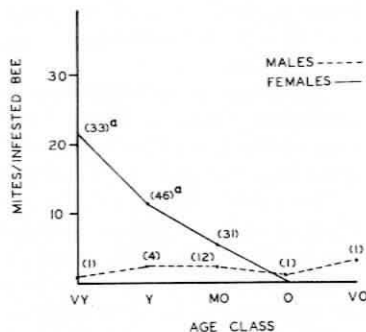


FIG. 2. Mean mite burden of *Imparipes americanus* on the infested specimens of *Nomia melanderi* plotted in Figure 1. Superscript "a" indicates that some estimates are included in calculation of the mean.

possible that a phenomenon of redistribution similar to that mentioned by Cooper is occurring. The analyses strengthen Cooper's suggestion that marked imbalances may be temporary and result from the loss of a block of mites. Further studies are needed on this point.

Perhaps the strength of clustering response is of prime importance in determining the degree of bilateral symmetry in certain phoretic acarines. In forms such as *Dicrocheles phalaenodectes* this response may be so strong that mites will not seek other, equally preferred sites except under conditions of the most severe crowding. In other forms in which the response might be less highly canalized, emigration to such sites might begin at a much reduced cluster density.

*Frequency and Degree of Infestation according to Host Sex and Age.* Table 2 shows the proportion of infestation and mean *Imparipes* burden on male and female bees (without regard to age) captured in flight over the various nesting sites. The mean age of males in any sample exceeded that of females by about one week, the former therefore having had more opportunity to lose mites. However, the consistent, large differences between sexes is largely independent of this age difference. Samples 6-9, all consisting mostly of "very young" and "young" males examined prior to female emergence, clearly indicate the early low incidence and degree of infestation of *Imparipes* on male *Nomia*.

Figures 1 and 2 refer to bees captured in flight over the various nesting sites and sorted into age classes by sex. Of particular interest is the wide discrepancy in the proportion of infested males and females, especially in the "very young" class (Fig. 1). In this class, 87 percent

of the females and only 20 percent of the males were infested. Moreover, a time factor was involved in the difference between sexes, the proportion of infested females declining sharply with advancing age while that of infested males remained essentially constant. Figure 2 shows the mean mite burden of infested bees from the same sample. Its similarity to Figure 1 indicates that numbers of mites, as well as proportions of infested bees, also decrease with age at a differential rate according to sex.

Table 3 summarizes the numbers and incidence of *Imparipes* on the two sexes in the late developmental stages. Data were first analyzed by sample, then lumped and re-analyzed. Incidence of infestation according to host sex was tested for each group in a  $2 \times 2$  contingency table. The resulting Chi-squares are given in the fifth column. The mean mite burden per infested bee was tabulated in the same manner and, in those samples containing no estimates, differences in mean burden per infested bee were tested by either the Wilcoxon Rank Sum Test or Student's "t," depending upon sample size.

The data indicate two interesting points: First, the incidence of infestation on overwintered prepupae is not independent of host sex ( $\chi^2 = 9.77^{**}$ ). Furthermore, the surplus is found on males rather than females. The higher incidence of mites in the cells of male prepupae was unexpected since it did not occur in any of the later developmental stages observed and directly countered the data obtained from adults captured in flight. Breakdown of the data into developmental components reveals that the Chi-square value resulted almost entirely from the

TABLE 3. Proportion and degree of infestation of late developmental stages of *Nomia melanderi* by *Imparipes americanus*.

Stage, site, date	No. of cells		Percent infested		Chi- square	Mean mite burden/in- fested bee		Signifi- cance value
	♂	♀	♂	♀		♂	♀	
Overwintered prepupae								
Travertine								
4/6/66	13	31	85	68	0.602	....	....	.....
6/30-31/66	9	42	100	43	3.658	15.8 <sup>a</sup>	10.4 <sup>a</sup>	.....
Hunter								
4/6/66	33	18	100	100	.....	9.7 <sup>a</sup>	9.9 <sup>a</sup>	.....
6/30-31/66	7	21	100	95	0.045	10.2	18.1	T <sup>a</sup> = 80
Total or Average	62	112	97	73	9.771 <sup>**e,d</sup>	11.1 <sup>a</sup>	12.8 <sup>a</sup>	.....
White pupae	56	58	78	68	2.349 <sup>c</sup>	15.2	19.9	t <sup>b</sup> = 0.998
Pigmented pupae	41	30	59	73	1.077 <sup>c</sup>	14.1 <sup>a</sup>	15.6 <sup>a</sup>	.....
Tenerals	52	35	58	74	2.696 <sup>c</sup>	16.1 <sup>a</sup>	19.3 <sup>a</sup>	.....

<sup>a</sup> Figures include some estimates of mite numbers. <sup>b</sup> Student's "t." <sup>c</sup> Data from all samples lumped. <sup>d</sup> Significant at  $P < .01$ . <sup>e</sup> Significance figure for the Wilcoxon Rank Sum Test.

single sample taken at the Travertine site on June 30-31, 1966. We cannot explain it except as sampling error.

Second, and of greater consequence, the data for subsequent un-emerged stages of *Nomia* do not foretell the markedly greater numbers and incidence of mites on females of the "very young" class (Figs. 1-2). Data for white and pigmented pupae are similar to each other and to that of the teneral as regards both frequency and degree of infestation. Chi-squares for all three groups are similar and non-significant, as is the "t" for white pupae (Table 3). Fifty-eight percent of 52 teneral males and 74 percent of 35 teneral females were infested (Chi-square = 2.70) as compared to only 10 percent of 10 emerged males and 87 percent of 38 emerged females (Chi-square = 19.97\*\*) in the "very young" class. Likewise, the mean mite burden on tenerals of the two sexes differed but little (16.1 and 19.3, respectively), whereas in the "very young" class, 33 infested females carried an average of approximately 22 mites, and the single measurable male carried only two. The dependence of infestation upon host sex was even more pronounced in "young" and "moderately old" bees, Chi-squares for these being 37.1\*\*\* and 27.8\*\*\*, respectively. Figure 2 shows that a pronounced discrepancy in mean mite burden still existed between the sexes in the "young" age class, where the average mite burden of 46 females was 11.2 and that of 4 males, 2.2. All data here were absolute, and a difference of means was therefore calculated by the Rank-Sum method. "T," equal to 46, was significant at 0.05 for the sample sizes quoted. Since the two sexes of bees emerged about equally infested, there must have been a rapid loss of mites from male bees almost immediately after they left their cells. Later, as a consequence of a steady loss of mites from the females, infestation on the two sexes equalized by the time the bees were "old." In the "very old" category, there even appeared to be a higher infestation on the males, although the numbers by this time were too small to yield significant data (Fig. 2).

The mechanism by which the rapid initial loss of mites on male bees was accomplished is not clear. Perhaps males, because of morphological or behavioral peculiarities, are more effective than females in removing mites from the anterolateral portions of the mesonotum. Furthermore, mites on male bees would presumably be more subject to the temperature and moisture extremes characteristic of the arid flatlands inhabited by the bee, since males, in contrast to females, spend most of their time above ground.

Veneral transfer was considered, but it seems unlikely. The numbers of mites lost by males are not accounted for by the very small increase in mite burden and incidence of infestation noted upon females. This increase could more easily be accounted for by sampling error. Moreover, the positions of the mites upon the host bees are such that quick transfer would be hampered, and *Imparipes* appears to be inactive on field-caught bees of either sex.



Davies (1959) found that larval numbers of the water mite *Sperchon* sp. decreased rapidly upon simuliids after the latter's emergence, and he attributed this to an increased mortality of heavily infested flies. Mitchell (1967), noting a similar phenomenon, compared the Coefficients of Variability of loads of the water mite *Arrenurus* upon teneral and "mature" male dragonflies and found no decrease. He therefore believes that a significant loss of heavily parasitized hosts does not occur during the maturation period. *Imparipes* is not a parasite, and there is no evidence that it harms emerged *Nomia*, although we have not adequately explored such a possibility. However, it seems unlikely that mortality would be restricted to one sex.

The relatively constant rate of mite loss from active females is more easily explained than the early loss of mites from the males. It would appear that cell-provisioning activity by the female bee stimulates the mites to leave the bee and infest the cell. Female mites have been found in fewer than a dozen completed but unprovisioned cells, whereas they are found commonly, sometimes in large numbers, in newly provisioned cells with unhatched eggs. Apparently, phoresy by the mites on males is a "dead end" phenomenon, resulting in a loss of nearly half of the adult population each generation.

In summary, (1) immature and unemerged adult *Nomia* appear to be equally infested with *Imparipes*, without regard to sex. (2) Shortly after emergence, male bees presumably lose most of their mite burden, after which the proportion of infestation and mean mite burden per infested bee remains approximately constant in time. Female bees show a steady decline in both proportion of infestation and mean mite burden with age. (3) *Imparipes* females attach themselves principally to the anterior mesonotal angles and within the subalar pits of *Nomia*. Sites of attachment are the same for either bee sex, but distribution per site differs slightly. The subalar pits of female bees are among the first sites to be occupied and are usually the last to be emptied. Mites concentrate more heavily upon the anterior mesonotal angles of male bees and are less frequently found in the subalar pits when in small numbers. (4) *Imparipes* females attach themselves in a bilaterally symmetrical fashion upon their host, whether female or male. Symmetry appears to be maintained in time. (5) *Imparipes* is contagiously distributed among members of the bee population regardless of bee sex. (6) The pattern of infestation of cells within a site appears to be random.

#### *Trochometridium tribulatum*

This pyemotid mite is known to infest several species of soil-dwelling bees and wasps (Cross, 1965; Shinn, 1967). It is distributed from coast to coast in the United States, but records of its appearances are sporadic and uncommon. It was found only at the Preston site in 1965-1966 and at the Airport site in 1966. Only one previous record of association with the alkali bee (near Adrian, Oregon, 1958) is known to us.

Phoresy is practiced solely by adult females. Unlike those of *Imparipes*, which always burrow to the hair bases, and which always form distinct clusters, females of *T. tribulatum* may attach anywhere along the hairs and tend to be more loosely scattered over the mesosoma, favoring, however, its posterior half. They likewise commonly attach to the pile of the lateral or dorsal surfaces of coxae and femora III. Sites of attachment appear to be similar on either host sex, but the mites seem to be more loosely scattered on males. Distribution appears to be symmetrical on the individual host, but we lack sufficient data to be positive on this point.

In contrast to *Imparipes*, which reaches maximum development in association with healthy bee brood, and whose reproducing females may be found in most or all cells they infest, gravid females of *T. tribulatum* are scarce and invariably associated with dead bee larvae. Such females were found in only four of 197 *Nomia* cells examined at the Preston site. Dead, or living but non-gravid females were found in three additional cells. This scarcity is partly offset by a high intrinsic rate of natural increase. One infested cell—of a cricket-storing wasp, *Motes argentata* (Palisot-Beauvais)—found at the Preston site contained 2,256 young female mites.

Although no bee is present to provide attachment for the young females and to open the cell, the latter are evidently able to disperse by actively moving through the soil of the site. This assumption is reinforced by the following evidence: (1) The rather small number of mites per infested bee, when one considers the enormous number produced per cell, indicates a rather low degree of contagion. (2) The indiscriminate attack on various cell-making Hymenoptera and their cleptoparasites (*Oreopasites*, *Sphecodes*, *Dasymutilla*, etc.), indicates that the only common feature in invaded cells is their presence in the soil of the site. The season of mite dispersal is unknown, but the earliest bees of the 1965 season to emerge (June 26) were infested.

Preliminary counts of *Trochometridium* on adult bees, made early in the 1965 season without regard to bee age, showed infestations on 33

TABLE 4. *Trochometridium tribulatum* phoretic on *Nomia melanderi* taken in flight, 1965-1966, at Preston, Idaho.

Age class	No. of bees		Percent bees infested		Chi-square	Mean Mite burden/infested bee		Significance value
	♂	♀	♂	♀		♂	♀	
Very young	10	109	20	16	0.01	9.5	3.4	....
Young	20	32	40	25	0.57	6.8	3.8	T = 74
Moderately old	11	11	9	0	....	0.1	0.0	....
Old	2	0	0	...	....	...	...	....
Total or Average	43	152	25	16	1.30	...	...	....

percent of 25 males and 17 percent of 81 females. A similar count, made a week later, indicated that only 13 percent of 23 males and 4 percent of 99 females were infested. In neither case could the incidence of infestation be shown to differ significantly between the sexes (Chi-squares = 1.70 and 1.38, respectively). Similar analyses, performed by age classes (Table 4), gave like results, as did the same type of analysis performed on the pooled data. In no case was the incidence of infestation found to be dependent upon bee sex, although a somewhat higher percentage of males in each age class carried mites.

Likewise, the mean mite burden of infested individuals did not differ greatly between the sexes. Differences were greatest in young bees and least in older ones but, unlike *Imparipes*, males carried more mites than females. Sample sizes were generally too small to test the data, but a Rank-Sums Test performed on the bees of the "young" class indicated that the means did not differ significantly between the sexes. Of interest is the fact that bees of both sexes in this class showed a higher apparent rate of infestation than those in the "very young" class.

In summary, (1) when compared to the other three species discussed herein, females of *T. tribulatum* infested a relatively low percentage of newly-emerged bees, and infested hosts carried, on the average, a small number of mites. (2) Although differences according to sex in the rate of infestation or in the mean number of mites per infested individual were non-significant, the data suggest that males tend to be higher in both respects. (3) The data also suggest that, although mite burdens of both bee sexes may decrease with bee age, proportionately more bees in the "young" class carry mites than do those of the preceding class. (4) *Trochometridium* females cling in loose clusters along individual hairs of the thoracic pile and basal leg segments of *Nomia*.

#### *Glyphanoectus nomiensis*

Known previously only from the Riverton sites, this anoetid was recently found to be common on specimens of *Nomia (Acunomia) nortoni* Cresson collected in southern Louisiana (Cross, 1968). In 1955-1956, specimens were more numerous in healthy *N. melanderi* cells than those of the other mite species discussed herein, but in 1965-1966, in the face of greatly reduced bee populations, the mite could not be found. Consequently, it was studied less intensively than the others.

The phoretic stage is a clumsy, slow-moving hypopus which attaches to the integument and, unlike the two preceding forms, may cluster on different areas of the host according to the latter's sex. In general, the mites attach themselves to the upper surfaces of all four wings of both sexes, but they are often found in even larger numbers in the lateral depressions of the modified fifth metasomal sternum of males. Average mite populations in these depressions are much higher than wing populations in each age class. Hypopae are not known to occur in

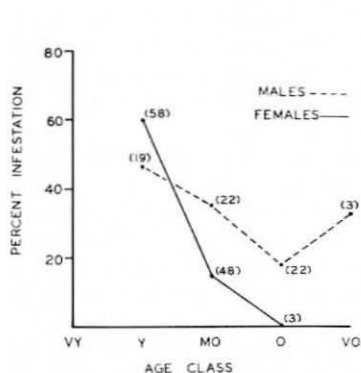


FIG. 3. Percentage of *Nomia melanderi*, captured in flight, infested by at least one specimen of *Glyphanoetus nomiensis*. Bees are divided into five age classes; figures in parentheses refer to sample size.

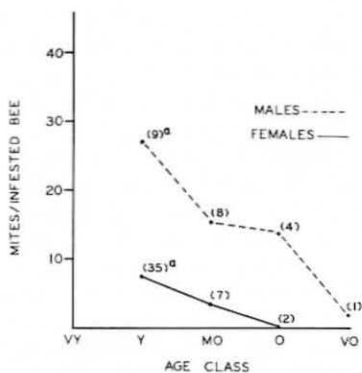


FIG. 4. Mean mite burden of *Glyphanoetus nomiensis* on the infested specimens of *Nomia melanderi* plotted in Figure 3. Superscript "a" indicates that some estimates are included in calculation of the mean.

significant numbers under the metasomal sterna of females. The largest burden noted upon an emerged male bee was 62 hypopae, 32 of which were located under sternum 5. A maximum of 50 mites was counted on the wings of one "young" female.

**Symmetry.** No samples of teneral or freshly emerged bees were available for analysis, and therefore original patterns of attachment are perhaps obscured. Female bees of the two youngest age classes available ("young" and "moderately old") were tested for symmetry of mites on the wings by total Chi-square, using the hypothesis that the mites were in equal abundance on each side of the body. Neither group showed a significant departure from the hypothesis (Chi-square = 24.02, .05 < P < .10, d.f. = 16, and Chi-square = 12.68, d.f. = 9, respectively), although the first approaches significance at the 5-percent level.

Concerning the clusters inhabiting the modified fifth sternum of the male, it can only be stated that in seven of nine instances there was no marked discrepancy in mite numbers between sides. In the remaining two instances counts of 14-3 and 22-0 were found on the two sides.

**Distribution according to Host Sex and Age.** Because of the absence of data in the pupal and youngest adult classes, it is not possible to state with certainty whether *Glyphanoetus* infests *N. melanderi* differentially at emergence according to host sex. Analysis of the "young" sample fails to show that the incidence of infestation was sex-dependent (Chi-square = 0.75). Although the average mite load of "young" infested males was considerably higher than that of infested females (27.2 to 7.3), the difference was not statistically significant (T = 277 for M = 9, N = 33).

The proportion of "moderately old" males infested was 0.36, that of females 0.15 (Chi-square = 3.06,  $.1 > P > .05$ ). Infested males of the same age class carried a mean burden of 15.1 hypopae compared to 2.71 for females ( $T = 40$ ,  $.1 > P > .05$ ). Possible differences in older age classes were not analyzable.

Examination of wing loads alone revealed that 6 "young" infested males and 34 "young" infested females carried nearly the same average load, 7.0 and 7.5 mites, respectively. Wing infestations were no more common on one sex than the other in members of this class, although the Chi-square value (3.19) approached the 5-percent level. In the "moderately old" class, the mean wing burden of females decreased to 2.7 ( $N = 7$ ) while the male burden remained approximately constant (7.5,  $N = 6$ ). The difference between these means remained statistically non-significant ( $T = 46$ ). Approximately the same proportion of males and females carried wing infestations (Chi-square = 0.88). No females were available in the "old" class, but three of the four infested males carried wing burdens.

It is thus clear that, regardless of the presence or absence of mites in the modified sternal pockets of male bees, neither incidence nor density of wing infestations of the age classes examined could be shown to differ between sexes.

In summary, (1) there is no demonstrable difference between sexes in incidence of infestation or in the mean mite burden of infested bees of the "young" class, although the mean mite load of infested males was much higher than for infested females. No samples of teneral or of "very young" bees were available; therefore, mite density and incidence at time of bee emergence is unknown. (2) Subject to the same shortage of data as the preceding, bees of the "young" class indicated that *G. nomiensis* hypopae were attached in symmetrical fashion to the wings, and probably to male metasomal sternum V. (3) Overall, infested males of all ages seemingly carried a heavier mite burden than females and appeared to retain at least one mite for a longer period of time. (4) Wing burdens were similar in any age class regardless of bee sex, a great portion of the observed difference between sexes therefore being due to the mites clustered on sternum V of the males. Large clusters of mites on older bees were most often found on the latter structure.

#### *Caloglyphus boharti*

This species is presently known only from *N. melanderi* at the Riverton sites, where it was found in small numbers (usually < 10) in about 20 percent of all cells containing healthy developing brood. It was significantly more common (56 percent, Chi-square = 18.9\*\*\*) in cells containing dead bees in any stage and in cells containing yeasty pollen. In these, it commonly achieved populations of several hundred individuals.

The phoretic hypopae are nearly always found on the metasomal

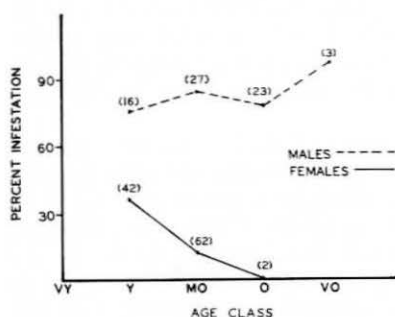


FIG. 5. Percentage of *Nomia melanderi*, captured in flight, infested by at least one specimen of *Caloglyphus boharti*. Bees are divided into five age classes; figures in parentheses refer to sample size.

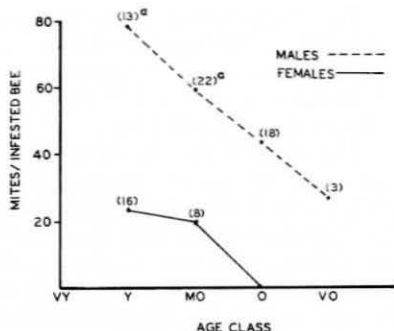


FIG. 6. Mean mite burden of *Caloglyphus boharti* on the infested specimens of *Nomia melanderi* plotted in Figure 5. Superscript "a" indicates that some estimates are included in calculation of the mean.

integument, crowded into the intersegmental spaces, where they pattern themselves into partially overlapping layers, their orientation opposite to that of the bee. They are found clinging to the underside of the overlapping segment or, more usually, to the upper surface of the segment following, and are thereby often hidden from casual observation. The presence of hypopae in appreciable numbers on the thorax was always accompanied by a heavy metasomal infestation, and it seems likely that the thorax is a marginal area, utilized for attachment only when the metasoma is crowded.

As in *G. nomiensis*, the hypopae exploit secondary sexual differences for use as sites of attachment, and are distributed in different fashion within the intersegmental spaces of the two bee sexes.

To estimate the distribution of hypopae beneath the different metasomal segments, infested bees were lumped by sex without regard to age, and counts of mites beneath each segment were made. Segments were then tallied and ranked inversely according to the proportion of each bearing at least one hypopus.

Although the lumping procedure assumes several patterns of mite loss not necessarily found in our data, we believe that our presence-absence data are not seriously in error since we found no evidence that loss rates were uneven in either sex (Figs. 5, 6) and/or that segments were abandoned on a sequential basis. Moreover, a high percentage of even "very old" males retained relatively large mite loads, and all females fell into one of two consecutive age classes. The number of mites under the various segments are subject to the same assumptions and are, moreover, weighted according to frequency of the bees in any age class. They are presented as an estimate of relative density only.

On 56 male bees, the most frequent sites of attachment, followed

by percent of total males infested at that site, were as follows: metasomal sternum IV (93), sternum III (79), and sternum II (71), followed by sternum I (52), metasomal tergum II (50), and metasomal tergum III (26). Hypopae were found least commonly beneath metasomal segment V (tergum and sternum) and beneath metasomal terga I and IV.

Of 24 infested females, all in the "young" and "moderately old" age classes, the variance of distribution was greater, the most frequent sites of attachment being: metasomal tergum V (53), sternum I and V (each 41), tergum II (35), and terga III and IV (each 24). Mites were least commonly found beneath sternum II to IV.

In the sample of males, the modal location, sternum IV, also held the highest mean number of mites (23.2), followed by tergum II (22.6), and sternum III (20.0). On the females, the modal location, tergum V, held comparatively few mites, the mean number being 6.8. Terga II to IV were the most heavily populated (16.5, 15.8, and 13.8, respectively).

*Symmetry.* Because individuals of this species tend to form band or ringlike clusters around each segment, we did not attempt to arbitrarily divide and analyze segmental loads. It may be said, subjectively, that loads appeared to be approximately symmetrical in most instances.

*Distribution according to Host Sex.* Male bees were much more commonly infested than females and carried, on the average, markedly greater mite burdens (note above, Table 5 and Fig. 6). The overall proportion of infested bees for 124 males and 106 females was 0.63 and 0.25 respectively (Chi-square = 30.8\*\*\*). Although lumping was again done without regard to age, analysis of members of the youngest available class alone ("young") gave similar results (0.81 males and 0.38 females infested, Chi-square = 6.99\*\*), and the data in Table 5 and Figures 5 and 6 agree in uniformly indicating higher mite numbers and greater incidence on males.

It is not possible to confirm that this discrepancy exists at the time of emergence because our sampling did not include newly emerged bees. The limited number of pigmented pupae and unemerged healthy

TABLE 5. *Caloglyphus boharti* phoretic on emerged *Nomia melanderi* 1955-1956, 1965 data.

Site, date	No. of bees		Percent bees infested		Mean mite burden/in-fested	
	♂	♀	♂	♀	♂	♀
Hidden Valley, 7/12/55	18	17	88	35	49.4	1.7
Hidden Valley, 8/3/55	8	25	100	8	30.0	8.5
Riggs', near, 8/3/55	1	25	0	8	....	2.5
Hidden Valley, 7/26/56	19	21	52	33	72.4	33.3
Riggs', near, 7/26/56	20	20	100	35	73.2	28.6
Hidden Valley, 7/21/65	55	0	40	...	28.6	....

tenerals examined indicated a surprisingly low percentage of infested bees of either sex. In one sample of 26 tenerals (13 of each sex), none carried mites, nor were mites present in their cells, while 40 percent of emerged males from the same population, captured in flight at the same time over the nesting site, were infested (flying females were not available for comparison). Since *Caloglyphus* breeds in large numbers only in cells containing dead or unhealthy bees, it, like *Trochometridium*, must leave its natal cells in order to attach to a host. The hypopae, unlike those of *Glyphanoctus*, are quite active, and they are capable of traversing several inches of soil as indicated by the difference in infestation rates between healthy and unhealthy brood. These facts indicate that *C. boharti* hypopae probably find their hosts in bee emergence tunnels rather than in the cells. This could explain any host sex preference at the time of emergence, since male bees are the first to emerge and would therefore be the earliest targets of the waiting hypopae. Males also presumably offer more easily accessible areas for attachment and may, therefore, attract more hypopae per unit time.

If, as seems less likely, hypopae do attach themselves indiscriminately to either sex at the time of emergence, perhaps females can more effectively dislodge or otherwise lose them than males, e.g., by dropoff in cells or elsewhere in the nest. Some support for this hypothesis came from one "moderately old" female bee that carried 16 hypopae, all clustered tightly beneath one side of tergum II. This side of the tergum was deformed in such a manner that the segment was nearly immovable against the one following. The deformity possibly hindered or prevented active or passive departure of the mites. However, two normal females of approximately the same age carried even larger mite burdens.

The assumption that the majority of hypopae occur initially upon male bees might imply a waste of hypopae, since females presumably offer more efficient transportation into nests. However, this may not be the case. Our laboratory studies show that, because of the dispersal abilities of the hypopae and, perhaps, their sensitivity to various odors, their efficiency in locating and invading localities suitable for colonization is high. Consequently, the species becomes a contaminant in most or all nearby suitable places unless it is specifically prohibited from doing so. The comparatively light loads associated with female bees therefore may be adequate to insure the distribution and population size optimal to its long-range survival.

Again, of the species reported upon here, *C. boharti*, because of its active hypopus and because it is usually found on the metasoma, dorsally in females and ventrally in males (sometimes on structures modified for copulation), is the species most likely to effect venereal transfer. Although we have no evidence that this is so, a system unbalanced in favor of males would have the advantage of keeping a large, mobile population in reserve, while virtually insuring young



females of repeated contacts with a source of infestation. Since sexual contacts are less frequent with advancing age, the decline in numbers of hypopae on older females could be explained by the gradual loss of those acquired earlier.

In summary, (1) in all bee age classes studied, *C. boharti* was found to infest a higher percentage of and to be present in higher density on male *Nomia*; however, newly-emerged bees were not available for study. (2) Although *C. boharti* built up large populations in cells containing dead bees (prepupal or later stages), it was uncommon in cells containing healthy hosts. (3) Hypopae probably infest bees in the burrow as they emerge rather than in the natal cell. Since male bees emerge before females, they thereby receive the majority of the waiting hypopae. (4) *C. boharti* is found nearly exclusively beneath the metasomal segments of *Nomia*. It attaches differentially according to bee sex. Generally speaking, it is most likely to be found ventrally on males but either dorsally or ventrally on females. Hypopae are most densely concentrated ventrally on males and dorsally on females. (5) Hypopae appear to be attached in symmetrical fashion, but we did not analyze this feature.

#### SUMMARY

(1) Phoresy is an important mechanism enabling small arthropods to find specialized microniches with a relatively high probability.

(2) Mites may be associated with a bee throughout the latter's range or be restricted to small portions of that range.

(3) Broad taxonomic correlation in bee-mite relationships occurs, particularly in higher categories, e. g., mites of the astigmatid family Chaetodactylidae are most commonly associated with bees of the family Megachilidae.

(4) Mites of all species in our study except *Trochometridium*, at least if attached to female *Nomia*, showed marked overdispersion when compared to a Poisson series. *Imparipes* was similarly shown to be distributed contagiously on pupae and teneral bees in cells.

(5) Although numbers of *Imparipes* were contagiously distributed on hosts, spatial infestation of bee cells was apparently random, as shown by "runs" tests.

(6) Mites phoretic on bees exhibit two broad morphological divisions, depending upon whether they cling to the pile or attach to the integument. Those phoretic as adults belong nearly exclusively to the first group.

(7) The four species treated here utilized the adult host only as a means of transportation.

(8) Each species had a major area of attachment to *Nomia*. These often differed according to species or sex of host.

(9) Certain locations, e.g., the subalar pits in the case of *Imparipes* and the lateral "pockets" of the male fifth sternum in the case of

*Glyphanoctus*, more commonly contained mites and were less likely to lose mites than the other locations utilized.

(10) All four species of mites appeared to be distributed in an approximately bilaterally symmetrical fashion.

(11) The strength of the clustering stimulus appears to be of importance in determining the symmetry of phoretic mites on their host.

(12) Only for *Imparipes* was meaningful information found on infestation of immature, emerging, and newly-emerged bees. Bee sexes appeared to be equally infested at time of emergence but most of those attaching to males were apparently lost within three days after emergence. *Caloglyphus*, in particular, appeared to prefer male bees, but a study of mite populations on teneral and newly-emerged bees is necessary to confirm this.

(13) The phoretic population of each species followed a unique pattern in time which is at least partly dependent upon bee sex.

(14) There was no evidence that any of the four species treated here have an important effect upon *Nomia* populations by causing mortality as phoretics. There was some suggestion of mortality of males infested with *Imparipes*, but this should have little effect upon long-term population size.

#### ACKNOWLEDGMENT

The authors wish to thank Dr. P. E. Hunter, Department of Entomology, University of Georgia, for critical reading of the manuscript.

#### LITERATURE CITED

- Bohart, G. E., and E. A. Cross. 1955. Time relationships in the nest construction and life cycle of the alkali bee. *Ann. Entomol. Soc. Amer.* 48: 403-406.
- Cooper, Kenneth W. 1955. Venereal transmission of mites by wasps and some evolutionary problems arising from the remarkable association of *Ensigniella trisetosa* with the wasp *Ancistrocerus antilope*. *Biology of eumenine wasps II. Amer. Entomol. Soc., Trans.* 80: 119-174.
- Cross, E. A. 1965. The generic relationships of the family Pyemotidae (Acarina: Trombidiformes). *Univ. Kansas Sci. Bull.* 45: 29-275.
- Cross, E. A. 1968. Descriptions of three new species of mites phoretic upon native bees. *Southwestern Natur.* 13: 325-334.
- Davies, D. M. 1959. The parasitism of black flies (Diptera, Simuliidae) by larval water mites mainly of the genus *Sperchon*. *Can. J. Zool.* 37: 353-369.
- Efford, I. E. 1963. The parasitic ecology of some water mites. *J. Anim. Ecol.* 32: 141-156.
- Homann, H. 1933. Die Milben in Gesunden Bienenstöcken. *Z. Parasitenkunde Berlin* 7: 350-415.
- Hunter, P. E., and K. Mollin. 1964. Mites associated with the passalus beetle I. Life stages and seasonal abundance of *Cosmolaelaps passali* n. sp. (Acarina: Laelaptidae). *Acarologia* 6: 247-256.
- Hunter, P. E., and R. Davis. 1965. Mites associated with the passalus beetle III. Life stages and observations on the biology of *Eusercon latus* (Banks) (Acarina: Euserconidae). *Acarologia* 7: 30-42.
- Hurd, P. D. and J. S. Moure. 1963. A classification of the large carpenter bees (Xylocopini) (Hymenoptera: Apoidea). *Univ. California Pub. Entomol.* 29: 1-365.

- Krombein, Karl. 1962. Biological notes on acarid mites associated with solitary wood-nesting wasps and bees (Acarina: Acaridae). Proc. Entomol. Soc. Washington 64: 11-19.
- Krombein, Karl. 1967. Trap-nesting wasps and bees. Life histories, nests, and associates. Pub. No. 4670, Smithsonian Institution Press, vi + 570 p.
- Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Natur. Hist. 82(6): 158-326.
- Mitchell, R. 1967. Host exploitation of two closely related water mites. Evolution 21: 59-75.
- Nielsen, R. A., and G. E. Bohart. 1967. Sex characters of larval bees (Hymenoptera: Apoidea). Ann. Entomol. Soc. Amer. 60: 414-419.
- Ribble, D. W. 1965. A revision of the banded subgenera of *Nomia* in America (Hymenoptera: Halictidae). Univ. Kansas Sci. Bull. 45: 277-359.
- Shinn, Alvin. 1967. A revision of the bee genus *Calliopsis* and the biology and ecology of *C. andreniformis* (Hymenoptera, Andrenidae). Univ. Kansas Sci. Bull. 46: 753-936.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 p.
- Treat, Asher E. 1957. Unilaterality in infestations of the moth ear mite. J. New York Entomol. Soc. 65: 41-50.
- Vitzthum, H. G. 1943. Die Acarina. In Bronns' Klassen und Ordnungen des Tierreichs, Bd. 5 (Arthropoda), Abt. IV (Arachnoidea), Buch 5. xi + 480 p. Akademische Verlagsgesellschaft, Leipzig.
- Wilcoxon, Frank, and R. A. Wilcox. 1964. Some rapid approximate statistical procedures (revised). Lederle Laboratories, Pearl River, N. Y. 60 p.