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**PARASITISM OF *NEPHILA CLAVIPES*  
(ARANEAE, TETRAGNATHIDAE) BY AN ICHNEUMONID  
(HYMENOPTERA, POLYSPHINCTINI) IN PANAMA**

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**ABSTRACT**

An apparent outbreak of *Hymenoepimecis* sp., a heretofore unknown ectoparasite of the giant orb weaver, *Nephila clavipes* is documented in Panama during 1984-1985. Parasitism was highest (25-30%) among intermediate-sized, juvenile female spiders. During the second year the wasps became less discriminating in selecting host spiders. Female wasps were significantly larger than males, and the size of the wasp ectoparasite was positively correlated with the size of the host spider. Although intermediate-sized females that had males in their webs were less likely to be parasitized than such females without males, results from an insectary experiment showed that male spiders did not prevent an established wasp larva from killing its host.

**INTRODUCTION**

The Pimplinae is a diverse subfamily of Ichneumonid wasps, within which the tribe Polysphinctini are ectoparasites of spiders. Currently there are no published accounts of the biology of any neotropical Polysphinctine (Wahl pers. comm.; Fitton et al. 1988), nor of their effect on the host population. In Panama we witnessed high levels of parasitism by an undescribed polysphinctine wasp, *Hymenoepimecis* sp., whose host was the golden orb weaver spider, *Nephila clavipes* (L.). Herein we describe the life cycle of the parasitoid wasp, and document the frequency of the parasitoid in the host population over a two-year period.

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## MATERIALS AND METHODS

The study was conducted on Barro Colorado Island (hereafter designated BCI) in the Republic of Panama. There, the lowland moist forest experiences a dry season from January to May (see Leigh et al. 1982 for habitat description). The host spider, *Nephila clavipes*, normally has two generations per year, with mature adults peaking in early wet season and in late wet to early dry season (Lubin 1978; Vollrath 1980).

The frequency of *Hymenoepimecis* sp. on *N. clavipes* was measured during two study periods that encompassed both dry and wet seasons in 2 consecutive years: from March to August 1984, and from February to December 1985. In 1984 *N. clavipes* was sampled by noting individuals encountered along roughly 1.5 km of trails transecting mature forests, and in the clearings adjacent to these trails. We marked the location of the web and measured the total length of the spider's cephalothorax-abdomen with calipers, recorded the number of males present in the web, and noted the presence of any parasitoid eggs or larvae on the female spider. Webs were checked on average of once every 3 days, until the spider could no longer be found in its original spot, or until the end of the study period.

In 1985, spiders were checked weekly or bi-weekly along 2 km of trails on BCI and the size of the spider was measured by the tibia-patella length. The cephalothorax-abdomen length of female spiders was highly correlated with tibia-patella length ( $r = 0.96$ ,  $N = 21$  females,  $P < 0.05$ ). For comparisons between years, we converted body length data to estimates of tibia-patella length using the regression equation. To determine whether the outbreak was a localized phenomenon, monthly surveys of *N. clavipes* over roughly the same length of trail were conducted on the mainland peninsula of Gigante from February 1985 to February 1986.

The life cycle of the *Hymenoepimecis* sp. parasitoid was studied by maintaining field collected, parasitized spiders in an outdoor insectary ( $2 \times 2 \times 2.5$  m). The spiders readily built webs and fed on small insects thrown into their webs. We measured the length of the parasitoids daily, noting when the host spider died, and when the larva pupated. The wasp pupae were removed from the webs and kept individually in small screen vials. The size and sex of the emerging adult wasps was recorded. Oviposition behavior and the reaction of female *N. clavipes* to wasps was noted opportunistically in the field.

Juvenile females with male spiders in the web were parasitized less frequently than were those in the presence of male spiders. To determine if this effect was a consequence of the male's behavior, one or two males were placed in the webs of 12 recently parasitized female spiders that were maintained in the insectary. Interactions between the parasitoids and the male spiders were noted during hour-long daily observation periods until the host spider was killed or the parasitoid disappeared.

## RESULTS

**Frequency and distribution of the parasitoid.**—Parasitism by *Hymenoepimecis* sp. on *N. clavipes* in 1984 and 1985 is shown in Table 1. In both years, female spiders of intermediate size (corresponding to instars 5-8) were disproportionately

Table 1.—Occurrence of parasitism by *Hymenoepimecis* sp. and of males in the webs of female *N. clavipes* of different sizes. For comparison of percentage of parasitism, 1984 samples were combined. \* = The smallest instars were not sampled in 1984.

Tibia-patella length (mm)	Year	N	Parasitized		Females with males
			n	%	
≤0.4	1984 (BCI) *	18	0	0	0
	1985 (BCI)	117	7	5.9	0
	1985 (mainland)	14	0	0	0
>0.4 ≤0.7	1984 (BCI)	24	2	8.3	2
	1985 (BCI)	81	8	9.9	1
	1985 (mainland)	36	5	14.0	3
>0.7 ≤1.2	1984 (BCI)	113	29	25.0	54
	1985 (BCI)	77	23	30.0	9
	1985 (mainland)	55	8	14.6	19
>1.2	1984 (BCI)	112	1	1.0	92
	1985 (BCI)	85	1	1.2	41
	1985 (mainland)	78	0	0	50

parasitized. Most (68%) sexually mature adult *N. clavipes* females were found in association with one or more males whereas only 32% of the intermediate-sized females had males in their webs. However, only 4 of the 154 (3%) *N. clavipes* females that had males in the web were parasitized ( $\chi^2 = 8.4$ ,  $df = 1$ ,  $P < 0.05$ ). Of the 5-8th instar females (i.e., those most heavily parasitized), 69 of 341 (20%) had males in the webs. Only three of these females (4%) were parasitized as opposed to a 27% parasitism rate in the 272 females (27%) that lacked males ( $\chi^2 = 12.8$ ,  $df = 1$ ,  $P < 0.05$ ).

In 1985, the incidence of parasitism in the BCI sample was about twice that found in the mainland sample of *N. clavipes* (Table 1). In this year on BCI, the normal peak in abundance of mature females in December never materialized (Higgins, unpubl.). Concomitantly, ovipositing wasps were less discriminating in their selection of host spiders. Eleven juveniles too small to sex (<4 mm tibia-patella length) and 3 of the 61 juvenile males censused were parasitized. Four cases of double parasitism were also observed.

**Lifecycle of *Hymenoepimecis* sp.**—We do not know how *Hymenoepimecis* sp. detects *N. clavipes* hosts. However, once the wasp located a potential host, it was not always successful in parasitizing the spider. On three occasions female *N. clavipes* were found off of the web (either in the leaf litter or on a lateral branch) while the wasp rested at the web center. The spiders approached the web, plucked it, and then dropped into the leaf litter. The wasps reacted by flying off of the web, circling it, and then flying away. Two of these spiders were later found parasitized. The third already had an early instar larva attached to it. We did not witness interactions that led to a wasp successfully landing on a spider host.

*Hymenoepimecis* sp. appeared to temporarily paralyze its host. On one occasion a female wasp was seen to sting a spider between the sternum and the coxae (see also Nielson, 1935; Eason et al., 1967). Typically, a wasp sat on the dorsal or dorsal-lateral side of the spider's abdomen, grasping the posterior end of the abdomen with her first pair of legs (Fig. 1). The wasp then moved her ovipositor back and forth for up to 5 min before attaching a single egg to the cuticle

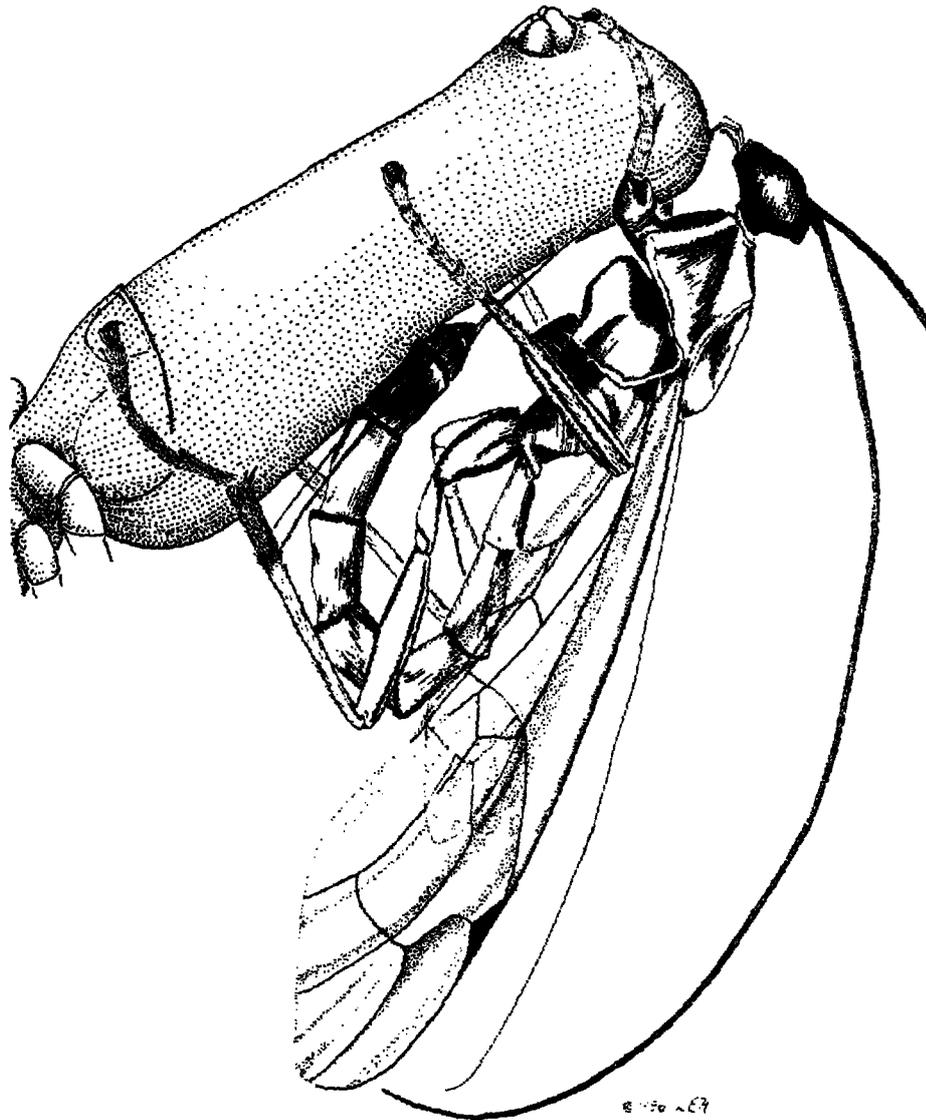


Figure 1.—A female *Hymenoepimecis* sp. ovipositing on a female *N. clavipes*.

of the spider. Fifteen min after the wasp oviposited, the host spider had fully recovered.

Within 24 h the eggs ( $N = 4$ ) hatched into larvae roughly 1 mm in length. One newly hatched larva was unable to attach itself to the spider and died within 24 h. Although this female spider grew to maturity (at below average size), she retained a scar on the abdomen where the egg had been attached. Wasp larvae grew slowly for the first week, after which they increased rapidly in size (Figs. 2, 3). Parasitized female *N. clavipes* built increasingly irregular, reduced webs but continued to feed up to 1-2 days before they died. By the end of 2 weeks the larvae had completely sucked out their host, leaving only the exoskeleton which dropped to the ground. Three of the 25 larvae maintained in the insectary



Figure 2.—*Hymenoepimecis* sp. larva at 7 days post-hatch, attached to a female *N. clavipes*.

disappeared after killing the host. Remaining larvae took 3-5 h to build golden, spindle-shaped cocoons that hung conspicuously within the frame lines of the host web (Fig. 4).

*Hymenoepimecis* sp. larvae failed to complete development if the host spider was too small or if it had already been parasitized. All of the larvae on juvenile males and on the small females (<4 mm tibia-patella length) that were brought into the insectary failed to pupate before the spider died. In all four cases of double parasitism, the larger, first-laid larvae was the only one of each pair to survive (one of these larvae ate the other). Two of the 22 pupae formed in the insectary failed to emerge for unknown reasons. In the field, one pupa was eaten by a kleptoparasitic spider (*Argyrodes*), and three were found crushed by heavy rains.

Even though male *Hymenoepimecis* sp. were smaller ( $\bar{X}$  body length  $\pm$  SE =  $14.8 \pm 0.1$  mm,  $N = 6$ ) than the females ( $\bar{X} \pm$  SE =  $17.6 \pm 0.1$  mm,  $N = 11$ ), the time required to emerge after pupation did not differ significantly between the sexes ( $\bar{X} = 10.4 \pm 0.7$  days,  $N = 5$  males;  $\bar{X} = 11.0 \pm 0.4$ ,  $N = 11$  females). The

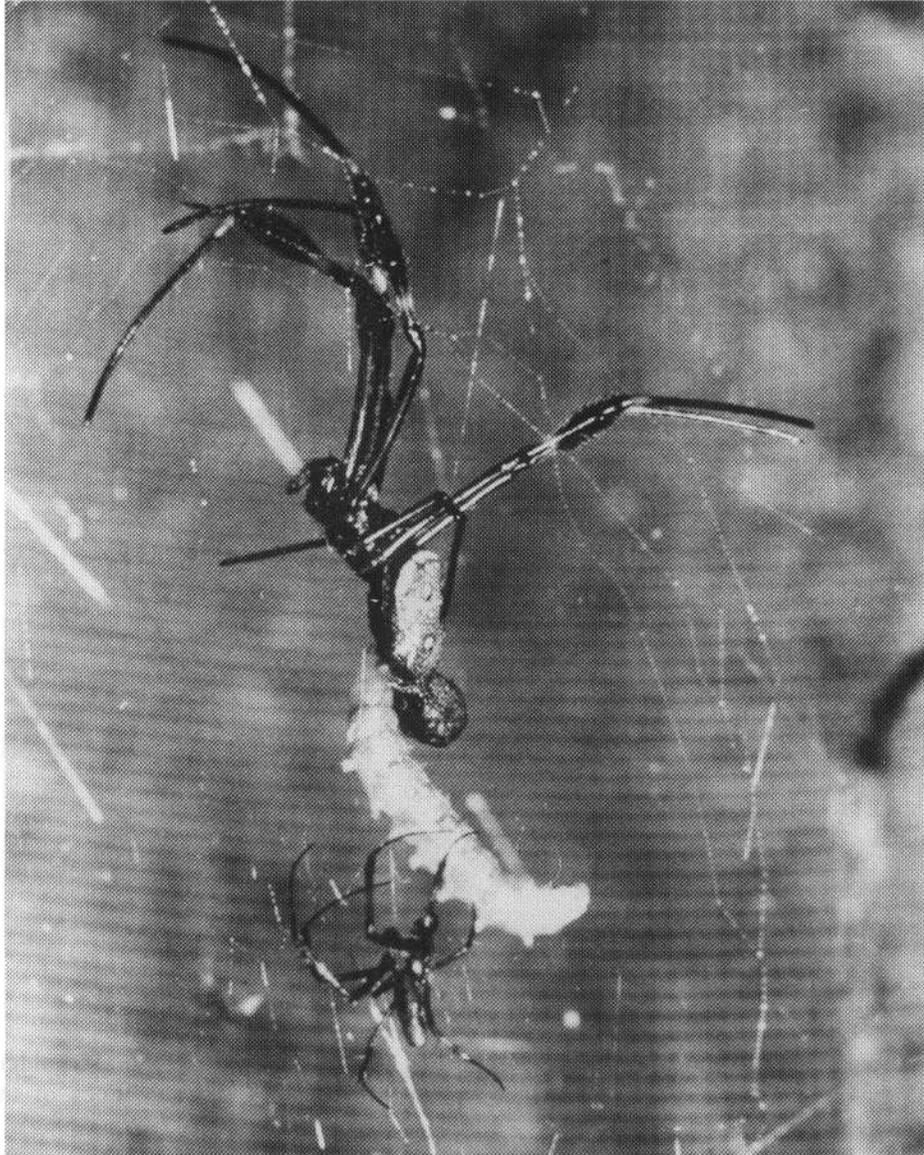


Figure 3.—Male *N. clavipes* touching a wasp larva as the larva feeds on a female *N. clavipes*. Pupation occurred 2 days later.

total time from egg to adult was 27 and 28 days for the two female wasps for which the date of oviposition was known (we lack similar data for males). Newly emerged adult *Hymenoepimecis* sp. released in the insectary with large *N. clavipes* females did not mate nor orient to any of the spiders.

In both years the sex ratio of emerging wasps was significantly biased towards females (1984, 7 males: 13 females; 1985, 6 males: 12 females,  $P < 0.05$ ,  $\chi^2$  tests). There was a significant correlation between size of the host spider (tibia-patella length) and body length of the emerging wasp ( $r = 0.91$ ,  $N = 7$ ,  $P < 0.05$ ).

**Effects of male *N. clavipes* on success of the parasitoid.**—In the insectary experiment, all of the 12 parasitized female spiders with male *N. clavipes* in their

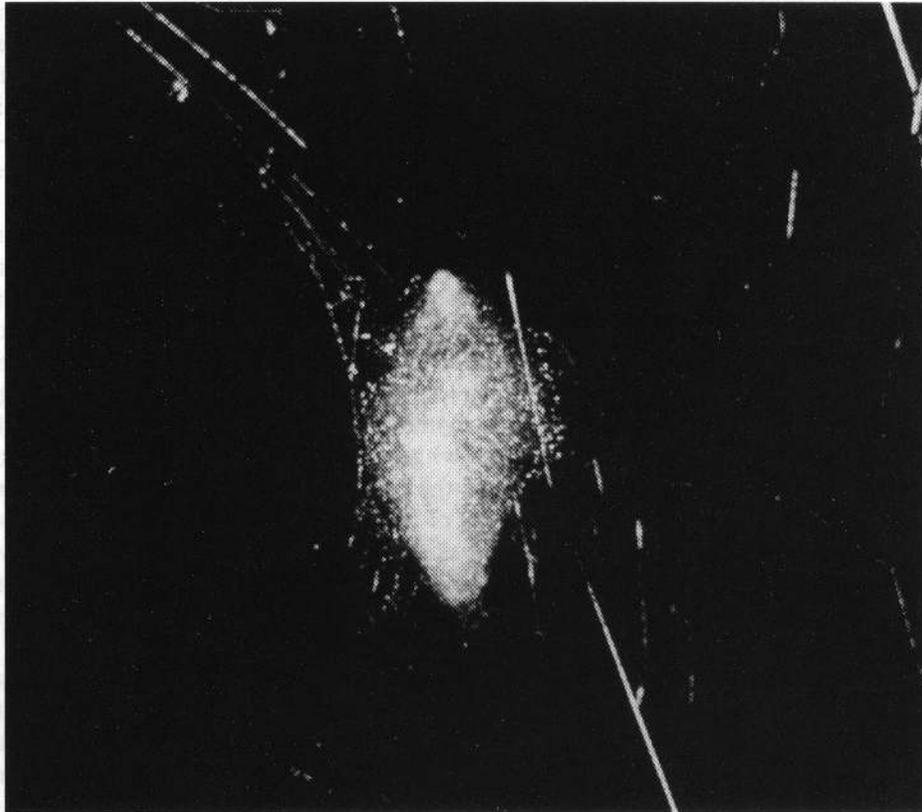


Figure 4.—Pupa of *Hymenoepimecis* sp. in the web of the dead host female *N. clavipes*.

webs were eventually killed by the parasitoids, of which all but one pupated successfully. The one exception was a larva that, after killing its host, failed to pupate before it was eaten by a second *N. clavipes* female that wandered onto the web. Periodically a larva raised its anterior end to reposition its mouth on another area of the spider's abdomen. During such times, male *N. clavipes* occasionally touched the larva (Fig. 3), but they never removed nor ate larvae. We cannot rule out the possibility that males interfere with successful oviposition by the adult wasps.

#### DISCUSSION

The fact that *N. clavipes* host spiders continued to build webs and feed for nearly two weeks after being parasitized indicates that *Hymenoepimecis* sp. conforms with other known polysphinctines in being koinobiotic (i.e., paralyzing their hosts only temporarily) (Askew and Shaw 1986). Many temperate polysphinctines overwinter as small instars on the spider host and develop over several months during which the host spider molts. *Hymenoepimecis* sp., however, developed rapidly and killed the host before the spider molted. The larva of some parasitoids may actively inhibit molting, but the only parasitized *N. clavipes* that we observed molting did so after losing its parasitoid. Because newly emerged female *Hymenoepimecis* sp. did not react to male wasps nor to potential

host spiders, their ovaries are probably undeveloped. The two periods during which we sampled *N. clavipes* in 1984 corresponded closely to the peaks of subadults and early adults of the biannual generations (Lubin 1978; Vollrath 1983). Unless it uses more than one host (unlikely for a koinobiotic polysphinctine, see Fitton et al. 1988), the wasp parasitoid must live at least 1-2 months in order to persist during periods of low juvenile female densities, between January and March, and August and October.

Because *Hymenoepimecis* larva were rarely seen to disappear from the host spider, we conclude that the observed size-specific parasitism did not result from differential larval success after oviposition. At present we do not know if the disproportional use of intermediate-sized spiders results from a choice preference by ovipositing wasps (e.g., Eason et al. 1967; Fitton et al. 1988) or from the superior ability of larger *N. clavipes* females to avoid ovipositing wasps. Although mature females that had male spiders in their webs suffered disproportionately less parasitism than did mature females without males, male *N. clavipes* did not interfere with successful development of the parasitoid. Limitation of parasitism of *N. clavipes* to intermediate size classes of the host spider provides one adaptive advantage to small size in male *N. clavipes*. By being too small to nourish a larva to pupation, males effectively escaped attack by the wasp. In this study, mature males were never observed to be parasitized, and juvenile males were parasitized only in late 1985, when large juvenile females were scarce.

Male *Hymenoepimecis* sp. were significantly smaller than females, and wasp size was correlated with the size of the host spider (see also Jowyk and Smilowitz 1978; Samson 1984), suggesting that an ovipositing female can assess the relative size of a potential host, and control the sex of her eggs (e.g., Cole 1981; Sandlan 1979b; Askew and Shaw 1986). *Hymenoepimecis* sp. females may assess host size and/or the presence of ectoparasitic larva by moving the ovipositor over the host's body prior to egg-laying.

Although *Hymenoepimecis* sp. becomes a large and conspicuous ectoparasite on *N. clavipes*, parasitism by these wasps has not previously been reported by other researchers working with *N. clavipes* on BCI (Robinson and Robinson 1977; Vollrath pers. comm). Nor were the ectoparasitoids noticed during three months in 1982, when *N. clavipes* webs were monitored as part of a study of spider predation by damselflies on BCI (Fincke unpub.). On mainland Panama where the density of *N. clavipes* was greater than on BCI, Vollrath (pers. comm.) found parasitoids only rarely. The high level of parasitism we found during 1984-1985 suggests that this was an uncommon outbreak of *Hymenoepimecis*. The environmental and biological factors that normally control the density of *Hymenoepimecis* sp. are unclear. In 1985 both the dry and the wet seasons were dryer than average (D. Windsor 1990). Because pupae were sometimes found to be killed by the heavy rains, the parasitoids may benefit from dry weather. Parasitism in 1984 probably contributed to the decline of the BCI *N. clavipes* population found in 1985 which was coupled with double parasitism and the use of host spiders of sub-standard size.

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