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EXTERNAL MORPHOLOGY AND DEVELOPMENT OF IMMATURE STAGES OF *ELACHERTUS SCUTELLATUS* (HYMENOPTERA: EULOPHIDAE) IN FLORIDA: THE FIRST NORTH AMERICAN RECORD

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ABSTRACT

The first North American record for *Elachertus scutellatus*, a parasitoid of *Calpodes ethlius* Stoll, occurred August 1999, in Florida. A simple rearing protocol was established to allow the morphology and development of this wasp to be examined. The egg and larval morphology and development of *E. scutellatus* resemble other *Elachertus* species. The freshly-ecdysed pupa, on the other hand, is rare among parasitoids in that it secretes a fluid from its anus which, when dry, fastens the pupa to its substrate. The death of the colony after eight months has many possible explanations including a laboratory-induced castration, inappropriate food source(s), and pathogenic infection.

Key Words: *Elachertus scutellatus*, *Calpodes ethlius*, koinobiont, ectoparasitoid, development, morphology.

RESUMEN

Le premier rapport nord-américain pour le *scutellatus* d'*Elachertus* s'est produit en août 1999, en Floride. Un protocole d'élevage a été établi pour permettre la morphologie et le développement de cette guêpe à examiner. L'oeuf morphologie et développement larvaires de *E. scutellatus* ressemblent à l'autre espèce d'*Elachertus*. Des chrysalides fraîchement "ecdysed", d'autre part, est rare parmi des parasitoids parce qu'il sécrète un fluide de son anus qui si sec attache les chrysalides à son substrat. La mort de la colonie après huit mois a beaucoup d'explications possibles comprenant une castration induite dans le laboratoire, source(s) inadéquate de nourriture et infection pathogène.

Translation provided by the authors.

The names *Elachertus scutellatus* and *Ardalus scutellatus*, were used by Howard (1897) and Ashmead (1900) to describe what is now considered to be a single species of eulophid wasp (Boucek 1988). *Elachertus scutellatus* Howard, within the tribus Elachertini, is the name now used by convention (Boucek 1988). Boucek (1988) has provided a complete key to the genus *Elachertus*.

Although the genus *Elachertus* is cosmopolitan, it is especially well represented and diverse in Central America (Hanson & Gauld 1995). *E. scutellatus* has been recorded in the Caribbean (Howard 1897; Ashmead 1900). It was collected in southern Florida, the first North American record for this species, by the first author in August 1999 (identification confirmed by Dr. Michael Schauff, USDA, ARS, at the National Museum of Natural History, Washington, D.C.). With the exception of a few studies on the taxonomy of *E. scutellatus* and its distribution (Howard 1897; Ashmead 1900; Ulrich 1932; Bennett & Hughes 1959; Boucek 1977; Cock 1985; Boucek 1988), very little is known of the biology of this wasp.

Elachertus scutellatus is an ectoparasitoid of the caterpillar of the Brazilian skipper, *Calpodes ethlius* Stoll (Lepidoptera: Hesperidae) (Ulrich

1932; Clausen 1978; Boucek 1977; Cock 1985). There are no recorded alternate hosts for *Elachertus scutellatus*. The Brazilian skipper is a serious pest of *Canna* species (Cannaceae) (Scudder 1889; Moore 1928; Young 1982; Reinert et al. 1983; Smith et al. 1994) and arrowroot, *Maranta arundinacea* (Marantaceae) (Cock 1985) in tropical and subtropical regions. Arrowroot is grown for the starch obtained from its rhizomes and is native to northern South America and the Lesser Antilles (Cock 1985). St. Vincent is the principal world producer, although it also has been grown in Barbados, Bermuda, Dominica, Jamaica, and St. Lucia (Cock 1985). The Brazilian skipper has been recorded in Bermuda since 1910 (Bennett & Hughes 1959; Cock 1985). Because of the severe damage caused to *Canna* by this caterpillar, ornamental *Canna* species are not planted extensively (Bennett & Hughes 1959; Cock 1985). In Florida, for instance, which is the northern-most permanent range of this skipper, the Miami Parks Authority discontinued the use of ornamental *Canna* plants because of the voracious feeding of skipper larvae (Smith et al. 1994).

Attempts have been made to introduce *E. scutellatus* into several Caribbean islands as a

biocontrol agent of *C. ethlius* caterpillars feeding on arrowroot. In 1951, *E. scutellatus* wasps were introduced from Trinidad to St. Vincent to control *C. ethlius* on commercial arrowroot crops (in Cock 1985). The Caribbean Agricultural Research and Development Institute (1982) made additional releases of *E. scutellatus* into St. Vincent and initiated introductions into Barbados. Biocontrol attempts in Bermuda began in 1953, when twenty adult *E. scutellatus* wasps were imported from Trinidad (Bennett & Hughes 1959). In 1960, more wasps were imported into Bermuda from Jamaica (Cock 1985).

In 1960 and 1962 the United States Department of Agriculture introduced *E. scutellatus* wasps (under the name *E. meridionalis*) into Bermuda in an attempt to control *C. ethlius* feeding on canna (Clausen 1978; Cock 1985). A successful rearing protocol was developed, but not published (F. D. Bennett, pers. comm.). Although an initial establishment of the parasitoid was confirmed, surveys in 1963 indicated that *E. scutellatus* was not maintained in Bermuda, likely due to the lower winter temperature and seasonal depletion of hosts, conditions not present at the collection sites (F. D. Bennett, pers. comm.). The Brazilian skipper is still a severe pest of canna and arrowroot plants in tropical areas (Cock 1985).

This paper provides a detailed description of the external morphology and development of *Elachertus scutellatus* with accompanying photographs.

MATERIALS AND METHODS

A colony of *E. scutellatus* was established from parasitized *C. ethlius* caterpillars collected in residential gardens in southern Florida, where *Canna* is common as a perennial ornamental plant. Three main sites in the Fort Lauderdale and Pompano Beach area with persistent *E. scutellatus* wasp populations were identified between May 8 and June 30, 2000.

Elachertus scutellatus was reared in an incubator at 25°C (77°F), the average annual temperature for Fort Lauderdale, Florida as recorded by the National Oceanic and Atmospheric Administration (1998), and high RH under a L:D 14:10 regime.

Host *C. ethlius* caterpillars were reared in a greenhouse at 22°C, high RH and under long-day conditions. This caterpillar is a near-monophagous leaf-rolling species and was fed *ad libitum* on leaves of the *Canna* lily. Caterpillars were exposed to adult wasps early in the third larval stadium (MacDonald & Caveney 2004).

Pre-adult *E. scutellatus* Rearing

After exposure to wasps, the caterpillars were placed under a dissecting microscope to examine whether eggs had been laid on their integument. Parasitized caterpillars were placed individually

in 100-mm diameter Petri dishes together with a damp piece of filter paper and a fresh piece of *Canna* leaf as food. Fresh leaf material was given daily as long as the hosts continued to feed. As a check for parasitism, apparently non-parasitized caterpillars were placed in 100-mm diameter Petri dishes with a damp filter paper and leaf material. These caterpillars were fed and observed until they completed the molt to the next instar. As molting confirmed the caterpillars were not parasitized, they were discarded.

Each Petri dish was sterilized daily with 70% ethanol, rinsed with distilled water and a new piece of damp filter paper was placed in the bottom. The host leafroll was kept folded to conserve moisture for parasitoid larvae and only opened briefly for observation each day. Upon pupation of the parasitoid, the leafroll was opened and stapled to filter paper to prevent curling of the leaf as it dried, and to allow easy observation. Observations of the immature wasp stages were made each day and the development of the parasitoid on the host was described.

Adult *E. scutellatus* Rearing

Adult wasp broods were held in Nalgene® transparent styrene-acrylonitrile utility boxes (7 × 6 × 12 cm). The wasps were provided with pure Billybee® clover honey brushed onto small yellow "Post-it"® notes (3.7 × 5 cm) stuck to the inside of the box (Hagley & Barber 1992; Pitcairn & Gutierrez 1992; Zaviezo & Mills 1999). Humidity was kept high in the container by placing moist filter paper in the bottom of the dishes. Moisture was not allowed to collect into droplets on the container walls, as the adults drowned easily within them. The wasps were removed daily with a mouth aspirator and the container was sterilized with 70% ethanol and rinsed with distilled water. The adults were sexed, mortality recorded and the healthy wasps then returned to the container with fresh honey.

One early third instar host caterpillar was provided per one or two adult female wasps. Host caterpillars were removed from the colony and exposed to adult wasps in the breeding population several times a week for an average of 24 h, although oviposition occasionally was completed within a few h.

RESULTS

External Morphology and Development of *E. scutellatus*

Egg: The egg of *E. scutellatus* is a large, yolk-rich anhydropic structure with a thick, tough chorion (Fig. 1a). A simple anchor on the egg, possibly an extension of the chorion (Clausen 1940; Kasparyan 1981), penetrates the host cuticle and secures the egg to the host integument. The egg

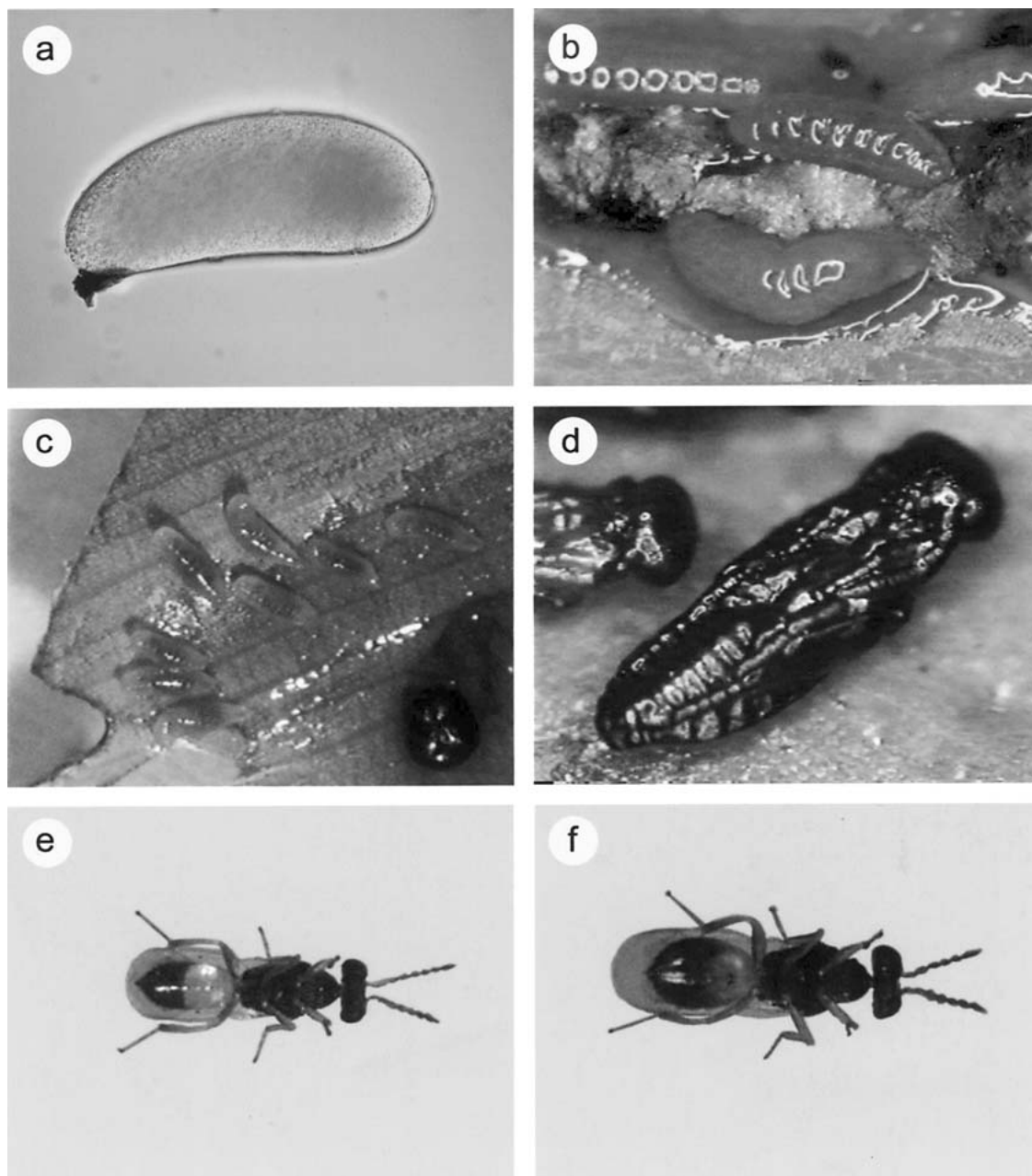


Fig. 1. Developmental stages of *Elachertus scutellatus*: a) large, proteinaceous, anhydropic egg with a portion of the egg stalk intact (magnification $\times 200$); b) 4-day-old larvae feeding on dead, necrotic host (magnification $\times 20$); c) 5-day-old larvae have completed feeding and wandered from host prior to pupation. They will expel their gut contents and pupate within 24 h (magnification $\times 10$); d) 4-day-old pupae after hardening and tanning their cuticle (magnification $\times 30$); e) adult male wasp (magnification $\times 20$) f) adult female wasp (magnification $\times 20$).

has the shortest developmental duration of the immature stages. Embryogenesis is completed in about two days (2.1 ± 0.2 , $n = 39$).

Larva: *E. scutellatus* larvae are hymenopteriform, 13-segmented (Gauld & Bolton 1988) and lack any tubercles or spines (Fig. 1b). The number

of instars was not determined. Following parasitoid hatching, the host caterpillar ceases to feed but continues to expel fecal pellets. The parasitoid larvae feed externally on the caterpillar for six days (6.0 ± 0.6 , $n = 13$). During this time, the host turns from green to a dull yellow color, presumably

due to the absence of gut contents and hemolymph normally visible through its translucent cuticle. Initially, the gut contents of the wasp larvae appear white, but as feeding ensues the gut turns yellow or brown. The host caterpillar dies several days after the parasitoids begin feeding and is often entirely consumed before the wasps pupate. Frequently the hosts died prematurely, usually within two days of wasp feeding, from what appeared to be a pathogenic infection. This caused the death of the associated parasitoid larvae.

Pupa: When feeding is complete, approximately one day prior to pupation, *E. scutellatus* larvae leave the host carcass but remain within the leafroll (Fig. 1c). They then expel their gut contents and pupate. *E. scutellatus* does not spin a cocoon for pupation (Fig. 1d) but instead, as seen in most chalcidoid wasps, the pupa is obtect (appendages are held against the body by a secretion produced at the last larval molt and the exposed surfaces of the appendages are heavily cuticularized) (Richards & Davies 1964) and adecticous (has reduced mandibles not used in adult eclosion) (Richards & Davies 1964). The pupae actively pump a clear fluid from their anus (Fig. 2) prior to tanning and hardening of their exterior. When dry, this fluid becomes fibrous and attaches the pupae to the inner surface of their host's leafroll.

One to two days prior to eclosion in the female wasp, a dark ovipositor becomes visible through the pupal casing as it stands out against her yellow abdomen. Adult wasps emerge within one week of pupal ecdysis (6.5 ± 0.5 , $n = 10$).

Adult: The adult wasp is black, approximately 1.5 mm long, with reddish eyes and ocelli (Howard 1897). The anterior portion of the ventral side of the adult male abdomen is translucent (Fig. 1e). The anterior portion of the ventral side of the female abdomen is honey-yellow (Howard

1897). The clearly visible ovipositor is positioned on the ventral midline of the female abdomen, but does not extend past its tip (Fig. 1f). Females were typically larger than males within a brood, although between broods the size range of the sexes overlaps considerably.

DISCUSSION

As seen in many ectoparasitoids, *E. scutellatus* wasps lay anhydropic eggs that have a large enough quantity of yolk that the embryo can complete its development to the larval stage without the need to sequester protein and nutrients from the host (Quicke 1997). The yolk of anhydropic eggs is rich in protein, of which vitellin is the major component, and has numerous lipid droplets (Quicke 1997). A large amount of egg protein is associated with the consumption of host fluids by female wasps (Flanders 1950; Le Ralec 1995). The eggs of most parasitoids are roughly oval and many ectoparasitoid eggs have stalks or pedicels to anchor the egg to the host (Quicke 1997). The morphology of *E. scutellatus* eggs is much like the eggs of the ichneumonid subfamily Tryphoninae, another group of ectoparasitic koinobiont wasps (Mason 1967; Kasparyan 1981).

The egg of *E. scutellatus* is unusual in that it is very large with a tough chorion. This presumably protects against both desiccation (Mason 1967) and physical damage that may occur when the host is allowed to remain active and mobile after attack by a parasitoid wasp (Mason 1967). To protect against the dehydration of eggs, female wasps often will attack only hosts living in humid or partially concealed situations (Mason 1967). To protect the eggs from the active host, female *E. scutellatus* wasps most often place the eggs between the host prolegs where they are difficult

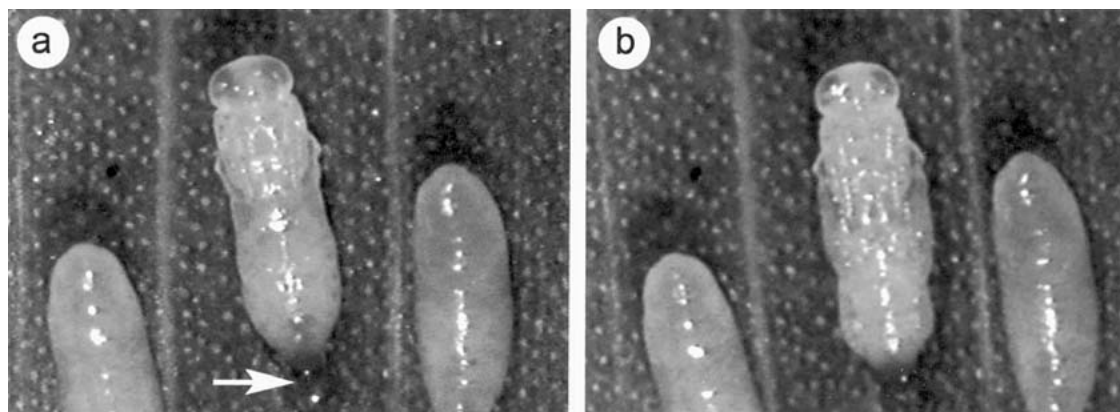


Fig. 2. Video images of a freshly-ecdyed *E. scutellatus* pupa secreting fluid from the anus. When dry, this fluid will form a fibrous attachment, fastening the pupa to the inside of the host leafroll: a) abdomen of pupa is relaxed, some fluid has been expelled from the anus (indicated by arrow); b) abdomen of pupa is contracted, actively expelling fluid from anus (magnification $\times 20$).

for the host to detect and destroy. These constraints are claimed to account for the rarity of ectoparasitic koinobionts (Gauld 1988; Godfray 1994; Mayhew & Blackburn 1999).

The larval morphology of *E. scutellatus* resembles that of other eulophids (Gauld & Bolton 1988). The white appearance of first instars of the wasp probably is due to the prenatal yolk resorbed during embryogenesis (Anderson 1973) and as feeding ensues, the larvae take on the color of the consumed host fluids, which can be seen through the translucent cuticle. Although the number of instars for *E. scutellatus* was not determined, Hanson & Gauld (1995) determined that in other eulophids there are three to five instars.

Parasitoid larvae are capable of altering the physiology of their active hosts, increasing or arresting developmental rates (Harvey et al. 1998; Doury et al. 1995; Hemerik & Harvey 1999) and changing host feeding habits (Shaw 1981; Powell 1989). Oral secretions from larval *E. scutellatus* may be the cause of the observed cessation in caterpillar feeding (Godfray 1994; Morales-Ramos et al. 1995; Richards & Edwards 1999) as well as the lack of a host phenoloxidase reaction at larval feeding sites (Richards & Edwards 1999). Interestingly, the larvae of pimpline ichneumonids that parasitize lepidopteran pupae are capable of producing toxic anal secretions from modified Malpighian tubules that inhibit host phenoloxidase activity (Godfray 1994). Although the presence and targets of larval secretions have not been closely studied, it seems parasitoid larvae possess specific adaptations that may alter host physiology and result in an increase in their own chance of survival.

The Eulophidae are exceptional within the Chalcidoidea in that silk cocoon formation is rare (Quicke 1997). *Elachertus scutellatus* do not produce a cocoon but instead harden and tan their cuticle (Richards & Davies 1964) and fasten the pupa to the substrate with a clear fluid that becomes fibrous when dry. Fidgen and Eveleigh (1998) state that *Elachertus cacaoeciae* pupae attach themselves by their meconium ["waste material excreted by an insect upon eclosion as an adult (a few parasitic wasps) or, in the case of the majority of parasitic wasps, just prior to pupation" (Quicke 1997)]. It seems unlikely that the fluid is simply a waste product in *E. scutellatus*, as the prepupae expel their gut contents far in advance of the active production of the clear fluid they use for attachment. It has been reported that many chalcidoids produce a cocoon-like structure from a liquid secreted by the anal end (and occasionally also the oral end) of the final instar (Flanders 1938; Quicke 1997). In several endoparasitoids, the fluid flows over the larvae under the pressure of the host hemolymph, then dries and hardens into an amorphous sheath often associated with host tracheae (Flanders 1938; Co-

lazza & Bin 1992; Ceresa-Gastaldo & Chiappini 1994). In the Chalcididae, the origin of the liquid is the iliac glands, structures homologous to the specially modified Malpighian tubules found in many ichneumonoid larvae (Quicke 1997). Freshly-ecdysed *E. scutellatus* pupae may not need to produce a protective cocoon with this liquid (as they are ectoparasitic) and instead make use of the host shelter. In *E. scutellatus* the excreted fluid is restricted to the anal area and is used to fasten the pupa to its substrate. This behavior seems to be intermediate between the formation of endoparasitic or silk cocoon produced anally and a lack of anal silk excretion in most parasitoids. The hindgut of chalcid larvae is very muscular and adapted to active expulsion of cocoon-forming secretions (Flanders 1938).

Generally, adult male wasps emerge before females (Harvey et al. 1998; Hanson & Gauld 1995; Jyothi et al. 1999; Zaviezo & Mills 1999). This was also seen in *E. scutellatus*, and is likely an advantage to the male in securing a female for mating immediately upon her emergence. The observed size differences between broods is likely due to differences in available resources and competition for food as the size of parasitoids is often related positively to host size (Wen et al. 1995; Fidgen et al. 2000;) and negatively to brood size (Hardy et al. 1992; Harvey et al. 1998).

Population Mortality

The rearing of *E. scutellatus* in the laboratory ended eight months after the colony was first established. Despite close care, the size of the population declined slowly without an obvious cause until the entire population died out. The highest mortality of *E. scutellatus* occurred in the larval stage. In a closely related species, *Euplectrus plathypenae* (Eulophidae), a similar pattern of mortality was observed (Parkman et al. 1981).

The demise of the colony may have been a result of adult female behavior or physiology. According to Schneider (1941), ovarian regression (ovarialkrise) "is a tendency toward ecological castration and may so decrease the readiness to oviposit that under laboratory conditions egg deposition does not continue" (in Flanders 1950). Ovarialkrise is considered characteristic of tropical wasps (in Flanders 1950). Similarly, phasic castration (atrophy of ovaries resulting in sterility) was frequently observed in laboratory mating studies of *Chrysocharis larinellae* (Eulophidae) (Quednau 1967).

Most laboratory-reared wasp populations are sustainable when the females are provided with a source of honey and hosts for host-feeding, and the males are provided with honey water (Hagley & Barber 1992; Pitcairn & Gutierrez 1992; Zaviezo & Mills 1999). The brand of honey routinely used to rear *E. scutellatus* was replaced for a

short duration of time with another brand, whereupon oviposition decreased. When the original brand of honey was restored, oviposition increased but failed to recover fully. It is possible the colony did not recuperate from the decline in female egg laying, but it seems unlikely that this was the cause of the death of the population. Synovigenic wasps such as *E. scutellatus* are capable of resorbing mature eggs (oösortion) should a food source become limited (Jervis & Kidd 1986).

Prior to the complete extirpation of the wasp colony, host caterpillars often turned black or bright red with yellow patches and sometimes developed a sweet odor, like that of citronella. Death of the host consequently resulted in the early death of the parasitoids. Several studies have concluded that the act of parasitoid oviposition can increase the host's susceptibility to viral infections resulting in the death of the host and associated parasitoids (Irabagon & Brooks 1974; Levin et al. 1981; Eller et al. 1988). Ectoparasitic larvae also have been shown to compromise host immune systems (Richards & Edwards 1999). The larvae of an ectoparasitic koinobiont eulophid wasp, *Eulophus pennicornis*, are known to produce factors that decrease the number of host hemocytes in order to reduce the host immune response (Richards & Edwards 1999). A reduction in host defences could result in pathogenic infection and death of both the host and the larval parasitoids. Although no direct evidence of infection was obtained, this is a possible explanation for the death of the parasitoid colony.

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REFERENCES CITED

- ANDERSON, D. T. 1973. Embryology and Phylogeny in Annelids and Arthropods. Pergamon Press, New York. 495 pp.
- ASHMEAD, W. H. 1900. Report upon the aculeate Hymenoptera of St. Vincent and Grenada, with additions to the parasitic Hymenoptera and a list of the described Hymenoptera of the West Indies. Trans. R. Entomol. Soc. London, Part II—July, 207-367.
- BENNETT, F. D., AND I. W. HUGHES. 1959. Biological control of insect pests in Bermuda. Bull. Entomol. Res. 50: 423-436.
- BOUCEK, Z. 1977. Descriptions of two new species of Neotropical Eulophidae (Hymenoptera) of economic interest, with taxonomic notes on related species and genera. Bull. Entomol. Res. 67: 1-15.
- BOUCEK, Z. 1988. Australasian Chalcidoidea (Hymenoptera): A Biosystematic Revision of Genera of Fourteen Families, with a Reclassification of Species, C.A.B. International, Oxon, UK. 832 pp.
- CARIBBEAN AGRICULTURAL RESEARCH AND DEVELOPMENT INSTITUTE. 1982. Integrated pest control programme in Barbados and the Eastern Caribbean, Progress Report October 1981-September 1982. Barbados; Caribbean Agricultural Research and Development Institute. 13 pp.
- CERESA-GASTALDO, L., AND E. CHIAPPINI. 1994. Observations on the cocoon of *Oligosita krygeri* Girault (Hymenoptera: Trichogrammatidae) oophagous parasitoid of *Cicadella viridis* (L.) (Homoptera: Cicadellidae). Norwegian J. Agr. Sci. 16: 131-140.
- CLAUSEN, C. P. 1940. Entomophagous Insects. McGraw-Hill Book Co. 688 pp.
- CLAUSEN, C. P. 1978. Hesperidiidae, p. 192. In C. P. Clausen [ed.], Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review. Agricultural Research Service, U.S. Dept. of Agriculture, Agricultural Handbook #480, Washington, D.C.
- COCK, M. J. W. 1985. A Review of Biological Control of Pests in the Commonwealth Caribbean and Bermuda up to 1982. Commonwealth Institute of Biological Control 218 pp.
- COLAZZA, S., AND F. BIN. 1992. Introduction of the oophage *Edovum puttleri* Griss. (Hymenoptera: Eulophidae) in Italy for the biological control of Colorado Potato Beetle. Redia 75: 203-225.
- DOURY, G., D. ROJAS-ROUSSE, AND G. PERIQUET. 1995. Ability of *Eupelmus orientalis* ectoparasitoid larvae to develop on an unparalysed host in the absence of female stinging behaviour. J. Insect Physiol. 41: 287-296.
- ELLER, F. J., D. G. BOUCIAS, AND J. H. TUMLINSON. 1988. Interactions between *Microplitis croceipes* (Hymenoptera: Braconidae) and a nuclear polyhedrosis virus of *Heliothis zea* (Lepidoptera: Noctuidae). Environ. Entomol. 17: 977-982.
- FIDGEN, J. G., AND E. S. EVELEIGH. 1998. Life history characteristics of *Elachertus cacoeciae* (Hymenoptera: Eulophidae), an ectoparasitoid of spruce budworm larvae, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 130: 215-229.
- FIDGEN, J. G., E. S. EVELEIGH, AND D. T. QUIRING. 2000. Influence of host size on oviposition behaviour and fitness of *Elachertus cacoeciae* attacking a low-density population of spruce budworm *Choristoneura fumiferana* larvae. Ecol. Entomol. 25: 156-164.
- FLANDERS, S. E. 1938. Cocoon formation in endoparasitic chalcidoids. Ann. Entomol. Soc. Amer. 31: 167-180.
- FLANDERS, S. E. 1950. Regulation of ovulation and egg disposal in the parasitic Hymenoptera. Can. Entomol. 82: 134-140.
- GAULD, I. D. 1988. Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae) Biol. J. Linnean Soc. 35: 351-377.
- GAULD, I. D., AND B. BOLTON. 1988. The Hymenoptera, British Museum (Natural History). Oxford University Press, London. 332 pp.
- GODFRAY, H. C. J. 1994. Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, NJ. 473 pp.
- HAGLEY, E. A., AND D. R. BARBER. 1992. Effect of food sources on the longevity and fecundity of *Pholetesor ornigis* (Weed) (Hymenoptera: Braconidae). Can. Entomol. 124: 341-345.
- HANSON, P. E., AND I. GAULD. 1995. The Hymenoptera of Costa Rica. Oxford University Press, London. 893 pp.

- HARDY, I. C. W., N. T. GRIFFITHS, AND H. C. J. GODFRAY. 1992. Clutch size in a parasitoid wasp: a manipulation experiment. *J. Animal Ecol.* 61: 121-129.
- HARVEY, J. A., L. E. M. VET, N. JIANG, AND R. GOLS. 1998. Nutritional ecology of the interaction between larvae of the gregarious ectoparasitoid, *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae), and their pupal host, *Musca domestica* (Diptera: Muscidae). *Physiol. Entomol.* 23: 113-120.
- HEMERIK, L., AND J. A. HARVEY. 1999. Flexible larval development and the timing of destructive feeding by a solitary endoparasitoid: an optimal foraging problem in evolutionary perspective. *Ecol. Entomol.* 24: 308-315.
- HOWARD, L. O. 1897. On the Chalcididae of the island of Grenada, B.W.I. *J. Linnean Soc.* 26: 129-178.
- IRABAGON, T. A., AND W. M. BROOKS. 1974. Interaction of *Campoletis sonorensis* and a nuclear polyhedrosis virus in larvae of *Heliothis virescens*. *J. Econ. Entomol.* 67: 229-231.
- JERVIS, M. A., AND N. A. C. KIDD. 1986. Host-feeding strategies in Hymenopteran parasitoids. *Biol. Rev.* 61: 395-434.
- JYOTHI, H. K., G. VEERANNA, AND G. BALI. 1999. Biology and life table studies of *Dirhinus anthraciae* Walker (Hymenoptera: Chalcididae) a parasitoid of *Exorista bombycis* Louis (Diptera: Tachinidae) at various constant temperatures. *J. Biol. Control* 12: 93-100.
- KASPARYAN, D. R. 1981. Ichneumonidae (Subfamily Tryphoninae) tribe Tryphonini. Fauna of the USSR, 106: 1-414. [English translation of Russian original published 1973, in Leningrad].
- LEVIN, D. B., J. E. LAING, AND R. P. JACQUES. 1981. Interactions Between *Apanteles glomeratus* (L.) (Hymenoptera: Braconidae) and granulosis virus in *Pieris rapae* (L.) (Lepidoptera: Pieridae). *Environ. Entomol.* 10: 65-68.
- LE RALEC, A. 1995. Egg contents in relation to host-feeding in some parasitic Hymenoptera. *Entomophaga* 40(1): 87-93.
- MACDONALD, K. E., AND S. CAVENEY. 2004. Unusual life history characteristics of *Elachertus scutellatus* Howard (Hymenoptera: Eulophidae), a koinobionic ectoparasitoid. *Environ. Entomol.* 33(2): 227-233.
- MASON, W. R. M. 1967. Specialization in the egg structure of *Exenterus* (Hymenoptera: Ichneumonidae) in relation to distribution and abundance. *Can. Entomol.* 99: 375-384.
- MAYHEW, P. J., AND T. M. BLACKBURN. 1999. Does development mode organize life-history traits in the parasitoid Hymenoptera? *J. Animal Ecol.* 68: 906-916.
- MOORE, M. B. 1928. A study of the life history and habits under Florida conditions of the canna butterfly (Brazilian Skipper) *Calpodus ethlius* (Cramer): An insect pest of the canna. M.S. Thesis, University of Florida.
- MORALES-RAMOS, J. A., M. G. ROJAS, AND E. G. KING. 1995. Venom of *Catolaccus grandis* (Hymenoptera: Pteromalidae) and its role in parasitoid development and host regulation. *Ann. Entomol. Soc. Amer.* 88: 800-808.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1998. Climatological Data Annual Summary: Florida. 102(13).
- PARKMAN, P., M. SHEPARD, AND J. POWELL. 1981. Oviposition biology and population dynamics of *Euplectrus plathypenae* Howard (Hymenoptera: Eulophidae). *J. Georgia Entomol. Soc.* 16: 336-341.
- PITCAIRN, M. J., AND A. P. GUTIERREZ. 1992. Influence of adult size and age on the fecundity and longevity of *Tetrastichus incertus* (Hymenoptera: Eulophidae). *Ann. Entomol. Soc. Amer.* 85(1): 53-57.
- POWELL, J. E. 1989. Food consumption by tobacco budworm (Lepidoptera: Noctuidae) larvae reduced after parasitization by *Microplitis demolitor* or *M. croceipes* (Hymenoptera: Braconidae). *J. Econ. Entomol.* 82: 408-411.
- QUEDNAU, F. W. 1967. Notes on mating behavior and oviposition of *Chrysocharis larinellae* (Hymenoptera: Eulophidae), a parasite of the larch casebearer (*Coleophora laricella*). *Can. Entomol.* 99: 326-331.
- QUICKE, D. L. J. 1997. Parasitic Wasps. Chapman & Hall, London. 470 pp.
- REINERT, J. A., T. K. BROCHAT, AND H. M. DONSELMAN. 1983. Resistance of *Canna* spp. to the Skipper Butterfly, *Calpodus ethlius* (Lepidoptera: Hesperidae). *Environ. Entomol.* 12: 1829-1832.
- RICHARDS, E. H., AND J. P. EDWARDS. 1999. Parasitization of *Lacanobia oleracea* (Lepidoptera: Noctuidae) by the ectoparasitic wasp, *Eulophus pennicornis*. Effects of parasitization, venom and starvation on host haemocytes. *J. Insect Physiol.* 45: 1073-1083.
- RICHARDS, O. W., AND R. G. DAVIES. 1964. A General Textbook of Entomology Including the Anatomy, Physiology, Development and Classification of Insects. Butler & Tanner Ltd., London. 886 pp.
- SCHNEIDER, F. 1941. Eientwicklung und Eiresorption in den ovarien des puppenparasiten *Brachymeria euploae* West. (Chalcididae). *Z. Angewandte Entomol.* 28: 211-228.
- SCUDDER, S. H. 1889. The Butterflies of the Eastern United States and Canada with Special Reference to New England. S. H. Scudder, Cambridge, MA. 1757 pp.
- SHAW, M. R. 1981. Delayed inhibition of host development by the nonparalysing venoms of parasitic wasps. *J. Invert. Path.* 37: 215-221.
- SMITH, D. S., L. D. MILLER, AND J. Y. MILLER. 1994. Butterflies of the West Indies and South Florida. Oxford University Press. 264 pp.
- URLICH, F. W. 1932. The arrowroot leaf roller (*Calpodus ethlius*). *Trop. Agric.* 9(10): 299-300.
- WEN, B., D. K. WEAVER, AND J. H. BROWER. 1995. Size preference and sex ratio for *Pteromalus cerealellae* (Hymenoptera: Pteromalidae) parasitizing *Sitotroga cerealella* (Lepidoptera: Gelechiidae) in stored corn. *Environ. Entomol.* 24: 1160-1166.
- YOUNG, A. M. 1982. Notes on the interaction of the skipper butterfly *Calpodus ethlius* (Lepidoptera: Hesperidae) with its larval host plant *Canna edulis* (Cannaceae) in Mazatlan, State of Sinaloa, Mexico. *New York Entomol. Soc.* 40: 99-114.
- ZAVIEZO, T., AND N. MILLS. 1999. Biological control aspects of the biology of *Hyssopus pallidus* (Hymenoptera: Eulophidae), a parasitoid of the codling moth (Lepidoptera: Olethreutidae). *Environ. Entomol.* 28: 748-754.