

Reproductive Strategies of Primary Parasitoids of the Green Cloverworm (Lepidoptera: Noctuidae)

S. K. BRAMAN¹ AND K. V. YEARGAN

Department of Entomology, University of Kentucky,
Lexington, Kentucky 40546

Environ. Entomol. 20(1): 349-353 (1991)

ABSTRACT *Cotesia marginiventris* (Cresson), *Diolcogaster facetosa* (Weed), and *Rogas nolophanae* Ashmead, which respectively parasitize progressively older green cloverworm, *Plathypena scabra* (F.) larvae, produced ($\bar{x} \pm \text{SE}$) 362.7 \pm 24.1, 83.2 \pm 11.4, 66.3 \pm 6.1 offspring, respectively, during their lifetimes. Adult female longevity at 24°C averaged 18.1 \pm 0.8, 13.0 \pm 0.9, and 29.9 \pm 2.7 d for these species, respectively. Numbers of mature eggs from dissections of 2-d-old females were 105 \pm 7.1, 57 \pm 5.9, and 5.2 \pm 0.9. Primary braconid and tachinid parasitoids of the green cloverworm exhibited decreasing observed or estimated fecundities with respect to increasing age of host larvae attacked. Decreasing fecundities of these parasitoid species may reflect increasing potential for survival until time of parasitoid emergence of the progressively older host larvae which these species attack. Other factors suggested as influencing fecundity are breadth of host range and complexity of host location, capture, and oviposition behaviors.

KEY WORDS Insecta, *Cotesia marginiventris*, *Diolcogaster facetosa*, *Rogas nolophanae*

THE GREEN CLOVERWORM, *Plathypena scabra* (F.), is a noctuid defoliator and an occasionally serious pest of soybean, especially in the midwestern states (Pedigo et al. 1973). Species composition and relative abundance of members of the large guild of parasitoids that attack the green cloverworm vary according to geographic location, type of host plant, and time of year (Daigle et al. 1988 and references therein). In general, early instar (1-4) green cloverworms are parasitized by hymenopterans, whereas later instar larvae are attacked primarily by tachinids. In Kentucky, *Cotesia* (= *Apanteles*) *marginiventris* (Cresson), *Diolcogaster* (= *Protomicroplitis*) *facetosa* (Weed), and *Rogas nolophanae* Ashmead are the most common primary parasitoids that attack early instar green cloverworms in soybean (Sloderbeck & Yeargan 1983).

Basic biological studies allow us to interpret and to more reliably predict seasonal phenology and abundance of parasitoids effecting reductions in pest populations. Developmental biology of *C. marginiventris*, *D. facetosa*, and *R. nolophanae* has been reported (e.g., Lentz & Pedigo 1974, Kunalaca & Mueller 1979, Yeargan & Braman 1986). Knowledge of the reproductive biologies of these species is less complete. Price (1975) reported the empirical relationship between ovariole number and fecundity for tachinids and ichneumonids. Fecundity for a particular species of tachinid or ichneumonid may be estimated when the number of ovarioles is known by applying the following formula: $(20.66) \times (\text{number of ovarioles per ovary}) - 96.69$. Yeargan (1979) found good agreement

between estimated and actual fecundities for two of three *Bathyleptes* species (Hymenoptera: Ichneumonidae) when using this formula. Departure from agreement appeared to occur when the parasitoid species was particularly long lived.

Price (1975) further reported a relationship between number of ovarioles and placement of eggs or planidia by tachinid parasitoids. When type of oviposition (x) was placed on a continuum from deposition of eggs on food (1) to oviposition within an adult host (13), the corresponding relationship with number of ovarioles per ovary (y) was best described by the equation $y = 138.29 - 22.77x + 1.00x^2$. The tachinid species *Blondelia hyphantriae* (Tohill), *Chaetophlepsis plathypenae* Sabrosky, and *Winthemia sinuata* Reinhard are commonly reported parasitoids of *P. scabra* and other Lepidoptera (e.g., Barry 1970, Lentz and Pedigo 1975, Sabrosky 1975, Deitz et al. 1976). The corresponding relationship between ovariole number (y) and stage of host attacked (x) by ichneumonids was described by the equation $y = 48.99 - 8.61x - 0.42x^2$. We report the comparative reproductive potential of the most abundant parasitoid species which attack young green cloverworm larvae in Kentucky. We further examine the various life history attributes of these parasitoids which may influence reproductive potential of a particular species.

Materials and Methods

Parasitoid Dissections. Colonies of *C. marginiventris*, *D. facetosa*, and *R. nolophanae* were initiated with adults reared from field collected green cloverworms. Ten females of each of the braconid

¹ Current address: Department of Entomology, University of Georgia, Georgia Station, Griffin, Ga. 30223-1797.

parasitoid species were fed 10% honey solution, held at an air temperature of 24°C, and a photoperiod of (L:D) 15:9 (the regime maintained for all experiments herein), and dissected when they were 2 d old. Data recorded included number of ovarioles per ovary, number of mature eggs, and number of developing ova. Four to six adult females of the tachinid species *B. hyphantriae*, *C. plathypenae*, and *W. sinuata*, which had been reared from field collected green cloverworm larvae, were dissected when they were 1-2 d old, at which time the number of ovarioles per ovary was determined.

Cotesia marginiventris, *D. facetosa*, and *R. nolophanae* are braconids, a family to which Price's (1975) formulae may not apply. Therefore, fecundities for these parasitoids were measured by following daily parasitoid production throughout the life of adult females.

Fecundities. Newly emerged females were paired with males and each pair was transferred to individual acrylic cylinders (30.5 cm high, 10 cm diam) that fit snugly over potted, V4-5 stage (Fehr et al. 1971) 'Essex' variety soybean plants. Preliminary observations of parasitoid behavior suggested an appropriate number of green cloverworm larvae to present to parasitoid females on a daily basis to ensure that parasitoids would not be host limited. *C. marginiventris* females were provided with 50 first instars per day, *D. facetosa* females were provided with 20 second instars, and *R. nolophanae* females were presented with 15 third instars per day as indicated by host instar acceptability data reported by Kunnalaca & Mueller (1979), Lentz & Pedigo (1974), and Yeargan & Braman (1986). Male-female pairs were transferred to new cylinders with a new set of hosts every day. Ten percent honey solution was streaked on the interior of the container and water was beaded on the interior of the containers using a wash bottle. A petri dish modified with a 52-mesh saran screen served as a lid for the cylinder. Larvae that had been exposed to parasitoid females were individually reared in 32-ml plastic cups with paper lids and were fed with excised soybean leaflets until parasitoid emergence from the host (*C. marginiventris* and *D. facetosa*) or pupal formation within the host integument (*R. nolophanae*). When males died, they were replaced. Daily parasitoid production was measured for the entire length of the parasitoid's lifetime. Sample sizes were 10 *C. marginiventris*, 10 *D. facetosa*, and 7 *R. nolophanae* females.

Survivorship of host larvae also was recorded for all green cloverworms that had been exposed to parasitoids. *R. nolophanae* is known to kill hosts not only via parasitism, but also through host-feeding (Lentz & Pedigo 1974). Therefore, cylinders of host larvae, which were treated similarly to cylinders of larvae exposed to *R. nolophanae*, were maintained but not parasitized. Those larvae were individually reared and used to provide back-

Table 1. Observed and predicted ovariole number and fecundities for three tachinid parasitoids of the green cloverworm

Species (n)	Age of larval host ^a	Observed no. of ovarioles per ovary	Predicted no. of ovarioles per ovary (fecundity)
<i>C. plathypenae</i> (6)	Mid-old	16	11-14 (110-193)
<i>W. sinuata</i> (5)	Old	10	11 (110)
<i>B. hyphantriae</i> (4)	Old	96	11 (110)

Predictions are based on Price's (1975) demonstrated relationship between fecundity and ovariole number, and stage of host attacked and ovariole number (as indicative of fecundity). See text for further explanation.

^a Age of host attacked determined from literature cited in text.

ground mortality to assess degree of mortality inflicted by host-feeding alone.

Differences in parasitoid fecundity, longevity, and host survivorship per day for the duration of a parasitoid's lifetime were detected using the Tukey-Kramer method (Sokal & Rohlf 1981) following a significant analysis of variance. Survivorship of green cloverworm host larvae and control larvae was compared as percent survival per original number of larvae exposed to parasitoids or control conditions with number of days of exposure to these experimental conditions serving as replication as follows: controls, 108 d; *R. nolophanae*, 200 d; *D. facetosa*, 130 d; *C. marginiventris*, 180 d. A replicate therefore consisted of all larvae exposed to one given parasitoid on a given day of exposure. Regression analysis tested predictions of parasitoid fecundity, based on age of host attacked. Voucher specimens of all parasitoid species have been deposited in the Entomology Department Museum, University of Kentucky, Lexington, Ky.

Results and Discussion

Parasitoid Dissections. All three braconid species have two ovarioles per ovary. They differ, however, in number of mature eggs as 2-d-old females. *C. marginiventris* ovaries were found to contain the greatest number of mature eggs upon dissection (105 ± 7.1), whereas *R. nolophanae* ovaries contained the fewest (5.2 ± 0.9). Neither variation in diet (provision with host hemolymph in addition to honey solution) nor age (5-d-old versus 2-d-old) of *R. nolophanae* females resulted in any increase in number of mature eggs upon dissection (S.K.B., unpublished data). *D. facetosa* ovaries contained an average of 57 ± 5.9 mature eggs. Mean \pm SE immature eggs were 43.4 ± 2.9 (*C. marginiventris*), 44.5 ± 2.6 (*D. facetosa*), and 53.7 ± 2.2 (*R. nolophanae*). Observed number of ovarioles compared closely with predicted ovariole number for two of three tachinid species examined (Table 1). *B. hyphantriae*, however, presents an anomaly. Little published information concerning the biology of this species exists that would provide an explanation for the high fecundity suggested by the large

Table 2. Mean \pm SE fecundity, female longevity, and host survivorship of braconid parasitoids of the green cloverworm

Species (n)	Fecundity ^a	Longevity (d)	Host survivorship ^b
<i>C. marginiventris</i> (10)	362.7 \pm 24.1a	18.1 \pm 0.8b	89.5 \pm 0.5a
<i>D. facetosa</i> (10)	83.2 \pm 11.4b	13.0 \pm 0.9c	89.5 \pm 0.2a
<i>R. nolophanae</i> (7)	66.3 \pm 6.1b	29.9 \pm 2.7a	84.5 \pm 0.1b

Means within a column followed by a different letter are significantly different ($P < 0.05$).

^a Number of offspring which emerged from host larvae.

^b Percent survival to parasitoid emergence or host pupation.

number of ovarioles. Tothill (1922) described this parasitoid as *Lydella hyphantriae* parasitizing the fall webworm. Adult tachinids deposited larvae in the third to last stage larvae of that host.

Fecundities. *C. marginiventris* females produced the greatest number of offspring during their lifetimes (Table 2). *R. nolophanae* and *D. facetosa* produced comparable numbers of offspring and far fewer than *C. marginiventris*. *R. nolophanae*, however, was much longer lived than *D. facetosa* (Fig. 1). While there was no preoviposition period subsequent to emergence from the cocoon, daily ovipositional rates for the three species were greater after day two. Kunnalaca & Mueller (1979) found that when 50 first-instar green cloverworm larvae were provided for *C. marginiventris* females ($n = 4$), total number of larvae parasitized ranged from 73 to 110, and none of the females survived >5 d. *C. marginiventris*, tested as an exotic parasitoid against a *Spodoptera* sp. in India, survived for 5.3 d at 27°C and parasitized 111.8 \pm 16.8 larvae (Jalali et al. 1987). The fecundity we recorded for this species was considerably higher (362.7 \pm 24.1) and possibly reflected greater adult parasitoid survival, or greater survival of host larvae, or both (Table 2). Nevertheless, parasitoid progeny production reported here may be a conservative figure. Under the experimental conditions described, superparasitism could have occurred although only one parasitoid per host was produced. Also, host larvae that died prior to parasitoid emergence were not dissected, and some of those may have been parasitized.

Survival to host pupation or parasitoid emergence of the 3,000 green cloverworm larvae that were exposed to *R. nolophanae* was slightly, but significantly ($P < 0.05$) less than that of 1,620 control larvae (84.5 \pm 0.1% versus 88.6 \pm 0.1%). Survival to parasitoid emergence of 11,550 host larvae exposed to parasitism by the other two braconid species was higher than for larvae exposed to *R. nolophanae* (Table 2), but did not differ from the survivorship of the previously mentioned unexposed (control) larvae. These data indicate that paralysis and host feeding by *R. nolophanae*, in addition to actual parasitism, contributes to parasitoid-induced mortality of green cloverworms, as suggested by Lentz & Pedigo (1974). The magnitude of such mortality was rather low in our study, perhaps because parasitoids were not offered larger or smaller larvae than that preferred for parasitism.

Host feeding may be more extensive on larvae which are otherwise unsuitable for parasitism.

Price (1975), using tachinids and ichneumonids as models and ovariole numbers as predictors of fecundity, advanced an hypothesis that suggested that parasitoid fecundities should be related to the life stage of host attacked. This relationship, he noted, should reflect differences in the expected probability of survival of successive life stages of a host. Endoparasitic larvae will be subjected to the same mortality factors that affect their hosts. Therefore, parasitoids that attack the egg stage of a host, for example, should be more highly fecund than those that attack later stages because their hosts may be expected to suffer higher mortality from all causes than a later host stage. Higher offspring numbers would presumably tend to offset this higher mortality.

Pedigo et al. (1983) presented partial life tables for the green cloverworm (data summarized in Fig. 2A). Observed and estimated (based on ovariole number) parasitoid fecundities decreased with increasing age of host larva attacked (Fig. 2A). The three braconid species discussed here (*C. marginiventris*, *D. facetosa*, and *R. nolophanae*, respectively) attack progressively older larvae although there is some overlap in parasitism of various instars. Fecundities of these species tend to fit the predictions of Price (1975) (Fig. 2B). Fecundity predicted on the basis of age of host attacked (equations presented earlier) was tested using observed fecundity of the braconid and estimated fecundity of tachinid parasitoids. When the outlier (*B. hyphantriae*) was omitted from analysis, a significant

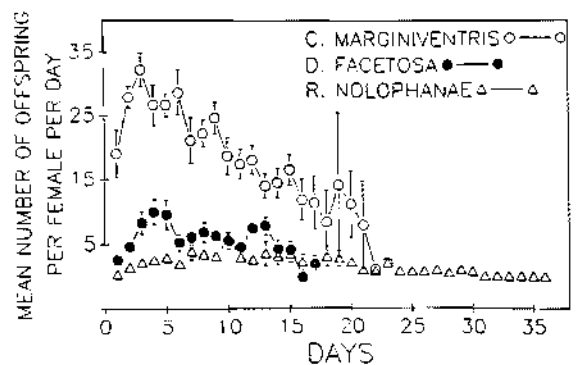


Fig. 1. Daily ovipositional rate of three braconid parasitoids of the green cloverworm.

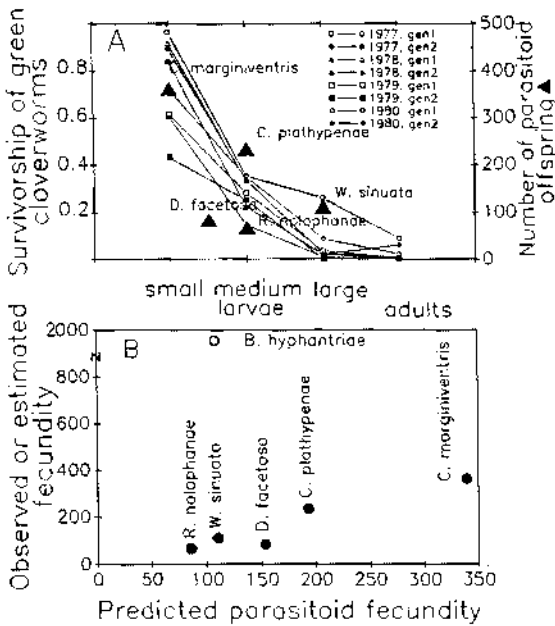


Fig. 2. (A) Survivorship of host (data from Pedigo et al. 1983) and fecundity of parasitoid species attacking small (instar one through two), medium (instar three through four), or large (instar five through six) larvae. (B) Relationship between parasitoid fecundity predicted on the basis of age of host attacked (see text for further discussion), and fecundity measured in the laboratory or estimated using number of ovarioles as determined by dissection.

regression ($y = 1.2x - 39.5$; $P = 0.01$; adj. $R^2 = 0.88$) was obtained.

Factors other than a presumed balanced mortality could influence the type of reproductive strategies that parasitoids possess. Host lists vary according to the parasitoid species mentioned here from extremely polyphagous (*C. marginiventris*) to having two recorded host species (*R. nolophanae*, Marsh 1979). Host capture and oviposition behavior, as well as associated time (and presumed energy expenditures), vary widely among these species (Yeargan & Braman 1986, 1989). These aspects of a parasitoid's life history may influence resource allocation to egg production. *R. nolophanae*, for example, is dependent upon few host species for survival. It would perhaps benefit this species to devote more energy to adult longevity and efforts involved in host location than for *C. marginiventris* whose wide host range might make timing of parasitoid emergence and location of suitable hosts less critical.

Diolcogaster facetosa also has a somewhat restricted host range. Three other noctuids in addition to the green cloverworm, as well as a tortricid, have been reported as hosts for this parasitoid (Marsh 1979; P. M. Marsh, personal communication). This species and *R. nolophanae* possess elaborate and time-consuming host-capture behaviors. This involves head-first descent on the suspending

thread of the green cloverworm host for *D. facetosa* (Yeargan & Braman 1986) or diving capture after as long as a 10-min surveillance of the host followed by host paralysis and extended handling time, in the case of *R. nolophanae* (Yeargan & Braman 1989, Lentz & Pedigo 1974). Our observations indicate that host capture by *C. marginiventris* is much less complex and time consuming than the behaviors described above. This species captures its host on the foliage or immediately dives after an escaping larva; oviposition is accomplished quickly.

Knowledge of the reproductive biologies and the selective factors that may be acting on egg production allows a better understanding of parasitoid population dynamics. The information here details the reproductive capabilities of parasitoids attacking successively older larvae of the same host and some of the factors that may influence the number of offspring a female is able to produce in a lifetime.

Acknowledgment

D. A. Potter and L. H. Townsend (University of Kentucky, Lexington), G. D. Buntin and W. A. Gardner (University of Georgia, Griffin), and two anonymous reviewers improved the manuscript by their helpful comments on an earlier draft. Identifications of parasitoids were kindly provided by P. M. Marsh (USDA Systematic Entomology Laboratory). Valuable technical assistance was provided by W. E. Barney. The investigation reported in this paper (#90-7-35) is in connection with a project of the Kentucky Agricultural Experiment Station and is published with the approval of the director.

References Cited

- Barry, R. M. 1970. Insect parasites of the green cloverworm in Missouri. *J. Econ. Entomol.* 63: 1963-1965.
- Daigle, C. J., D. J. Boethel & J. R. Fuxa. 1988. Parasitoids and pathogens of green cloverworm (Lepidoptera: Noctuidae) on an uncultivated spring host (Vetch, *Vicia* spp.) and a cultivated summer host (soybean, *Glycine max*). *Environ. Entomol.* 17: 90-96.
- Deitz, L. L., J. W. Van Duyn, J. R. Bradley, Jr., R. L. Rabb, W. M. Brooks & R. E. Stinner. 1976. A guide to the identification and biology of soybean arthropods in North Carolina. North Carolina Agricultural Experiment Station Technical Bulletin 283.
- Fehr, W. R., C. E. Caviness, D. T. Burmood & J. S. Pennington. 1971. Stages of development descriptions for soybeans, *Glycine max* (L.) Merrill. *Crop Sci.* 11: 929-931.
- Jalali, S. K., S. P. Singh & C. R. Ballal. 1987. Studies on host age preference and biology of exotic parasite *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae). *Entomon* 12: 59-62.
- Kunnalaca, S. & A. J. Mueller. 1979. A laboratory study of *Apanteles marginiventris*, a parasite of green cloverworm. *Environ. Entomol.* 8: 365-368.
- Lentz, G. L. & L. P. Pedigo. 1974. Life history phenomena of *Rogas nolophanae* and *Winthemia sinuata*, parasites of the green cloverworm. *Ann. Entomol. Soc. Am.* 67: 678-680.

1975. Population ecology of parasites of the green cloverworm in Iowa. *J. Econ. Entomol.* 68: 301-304.
- Marsh, P. M. 1979. Family Braconidae, pp. 144-295. In K. V. Krombein, P. D. Hurd, Jr., D. R. Smith & B. D. Burks [eds.], *Catalogue of Hymenoptera in America north of Mexico*. Smithsonian Institution, Washington, D.C.
- Pedigo, L. P., J. D. Stone & G. L. Lentz. 1973. Biological synopsis of the green cloverworm in central Iowa. *J. Econ. Entomol.* 66: 665-673.
- Pedigo, L. P., E. J. Bechinski & R. A. Higgins. 1983. Partial life tables of the green cloverworm (Lepidoptera: Noctuidae) in soybean and a hypothesis of population dynamics in Iowa. *Environ. Entomol.* 12: 186-195.
- Price, P. W. 1975. Reproductive strategies of parasitoids. In P. W. Price [ed.], *Evolutionary strategies of parasitic insects and mites*. Plenum, New York.
- Sabrosky, C. W. 1975. *Chaetophlepsis plathypenae*, a new parasite of the green cloverworm, with a key to *Chaetophlepsis* and *Parahypochaeta* (Diptera: Tachinidae). *Ann. Entomol. Soc. Am.* 68: 43-50.
- Sloderbeck, P. E. & K. V. Yeargan. 1983. Green cloverworm populations in conventional and double-crop no-till soybeans. *J. Econ. Entomol.* 76: 785-791.
- Sokal, R. R. & F. J. Rohlf. 1981. *Biometry*, 2nd ed. Freeman, San Francisco.
- Tothill, J. D. 1922. The natural control of the fall webworm (*Hyphantria cunea*, Drury) in Canada, together with an account of its several parasites. Canada Department of Agriculture, Ottawa, Bulletin New Series 3 (*Entomol. Bull.* 19), 107 pp.
- Yeargan, K. V. 1979. Ovipositional rate, fecundity, and longevity of *Bathyplectes stenostigmata*. *Environ. Entomol.* 8: 150-153.
- Yeargan, K. V. & S. K. Braman. 1986. Life history of the parasite *Diolcogaster facetosa* (Weed) (Hymenoptera: Braconidae) and its behavioral adaptation to the defensive response of a lepidopteran host. *Ann. Entomol. Soc. Am.* 79: 1029-1033.
1989. Comparative behavioral studies of hemipteran predators and hymenopteran parasites of the green cloverworm (Lepidoptera: Noctuidae). *J. Kansas Entomol. Soc.* 62: 156-163.

Received for publication 5 March 1990; accepted 18 September 1990.