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Review Article

Biology, ecology and use in pest management of *Telenomus remus*

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Abstract

Telenomus remus parasitizes the eggs of several lepidopterous insects. It is currently reared and released in many countries for control of *Spodoptera* spp. that are crop pests, particularly *Spodoptera litura* and *Spodoptera frugiperda*. The biology, ecology, historical use in pest management and taxonomic quandries of *T. remus* are reviewed. Suggestions for greater use of this parasitoid and research needed for improving its pest control capabilities in the field are discussed.

Introduction

Telenomus remus Nixon (Hym., Scelionidae) is an egg parasitoid of lepidopterous insects, many of which are pests of crops in Asia and the Americas. Its high reproductive rate and ease of mass rearing makes this wasp a good agent for the biological control of lepidopterous pests, particularly those of the genus *Spodoptera* (Noctuidae). Currently, it is being reared and released in seven Latin American countries.

This report reviews the published literature on *T. remus*, including its biology, ecology and use in pest management programmes. Problems with the taxonomy and recognition of *Telenomus* spp. similar to *T. remus* are discussed. Also, recommendations for amplifying the use of this parasitoid and research needed for improving its effectiveness in pest control are presented.

Biology and Ecology

The adult of *T. remus* measures 0.5-0.6 mm in length. The body is shiny black. The femora and tibiae are dark in the female, but pale brown in the male. The female's antenna has a four-segmented club, whereas no detectable club is present in the male's antenna. The forewing is slightly more than three times longer than wide and its margins are subparallel.

The developmental biology of *T. remus* was studied by Gerling (1972), Gómez de Picho (1987) and Hernández & Díaz (1995, 1996). An overview of the information described in these works is presented here. The female deposits a single egg in the interior of the developing host embryo. Superparasitism has been observed in the laboratory, but mortality by competing larvae and/or nutrient limitation in the host egg permits only one *T. remus* larva to complete its development. Only eggs less than 72 hours old are parasitized (Dass & Parshad, 1983); an egg in which the embryo has completed development is rarely susceptible to parasitization by *T. remus*. The duration of the egg stage varies from 10 hours at 30°C (Hernández & Díaz, 1996) to 18-24 hours at 15.5°C (Gómez de Picho, 1987).

The larva of *T. remus* has two instars. The first instar is unsegmented. It has a pair of mandibles which move vertically and two caudal spines, one short and one long and curved. The mandibles and caudal spines may be used to macerate and move host tissues; they may also be used to kill other parasitoid larvae within the host. A series of circumabdominal setae possibly assist in mobilizing the larva. The second instar is clearly segmented and has no caudal spines; the mandibles are short and straight. This instar assimilates nutrients from the host until they are entirely consumed. Upon completion of host feeding and larval development, the *T. remus* larva exudes a meconium when it enters the prepupal stage. Duration of the larval stage varies from 4 days at 30°C (Hernández & Díaz, 1996) to 7 days at 15.5°C (Gómez de Picho, 1987).

Pupation occurs within the host egg. Initially the pupa is opaque white with slightly reddish eyes. Gradually the body turns grey and later black. The duration of the pupal stage varies from 112 hours at 30°C (Hernández & Díaz, 1996) to 15 days at 15.5°C (Gómez de Picho, 1987). Gautum (1986a) reported that total development time from egg deposition to emergence of the adult varied from 13.7 days at 23ºC to 7 days at 34ºC and that ambient relative humidity had no influence on development rate.

When the development of the immature *T. remus* is complete, the adult chews a small hole in the host egg chorion through which it emerges. In general, males emerge 24 hours before females. After emerging the males will remain on the egg mass from which they emerged or search out other egg masses with parasitized hosts to

await the emergence of females. Male sexual behaviour is apparently triggered by pheromones from the females (Schwartz & Gerling, 1974). Copulation occurs immediately or soon after the female emerges from her host egg.

Telenomus remus females respond to (Z)-9-tetradecene-1-ol acetate and (Z)-9-dodecene-1-ol acetate (Lewis & Nordlund, 1984), which are components of the sex pheromone of *Spodoptera frugiperda* (J. E. Smith) (Nordlund *et al.*, 1983). The presence of these chemicals increases parasitism rates. Also, kairomones present in the secretion of the *S. frugiperda* female accessory gland stimulate oviposition by *T. remus* (Lewis & Nordlund, 1984). However, Nordlund *et al.* (1983) suggested that many factors may act synergistically to determine if *T. remus* accepts and oviposits in a host.

Plant synomones also play an important role in parasitism by *T. remus*. Lewis & Nordlund (1984) applied extracts from maize and tomato leaves to cowpea plants in the greenhouse and found that parasitism on treated plants was two times greater than on plants without extracts.

Telenomus remus females tolerate the presence of other conspecific females ovipositing in the same egg mass (Schwartz & Gerling, 1974; author, pers. obs.). After ovipositing, the females rub or scratch the host's chorion with the ovipositor (Gerling & Schwartz, 1974; van Welzen & Waage, 1987). However, Gerling & Schwartz (1974) gave evidence that this action, common among species of the family Scelionidae (Rabb & Bradley, 1970; Johnson, 1984; Cave *et al*., 1987), does not prevent superparasitism within the first hour after oviposition.

Females contain the maximum number of eggs in their ovaries at 2-3 days of age (van Welzen & Waage, 1987) and produce more than 76% of their progeny during their first 5 days of adult life (Schwartz & Gerling, 1974). The sex ratio of the progeny is normally 60-70% females, but declines to 22% as the female ages (Schwartz & Gerling, 1974). The first male egg is generally placed within the second host attacked; subsequent male eggs are deposited afterwards at variable intervals between depositions of female eggs (van Welzen & Waage, 1987). Greater proportions of male eggs are produced when the number of female *T. remus* is much greater than the number of hosts (van Welzen & Waage, 1987), although this may possibly be due to superparasitism and differential mortality (Schwartz & Gerling, 1974). Van Welzen & Waage (1987) explain that the change in progeny sex ratio in relation to parasitoid density is due to other factors. During simultaneous oviposition by two or more females on one egg mass, there is a reduction in the number of eggs deposited by each female, which increases the proportion of male eggs because of the sequential effect described above. Since female *T. remus* have a strong tendency to avoid superparasitism, there are fewer eggs laid per female when multiple females occur simultaneously on the same egg mass (in comparison to a lone female on an egg mass). Because females deposit a greater proportion of male eggs early in an ovipositional series, females that deposit fewer eggs produce a greater proportion of male progeny. Also, there is an increase in the probability of depositing a male egg that is independent of sequence, which indicates a direct response by the female to the presence of other females (van Welzen & Waage, 1987). Therefore, inadequate ratios of egg masses to female *T. remus* in mass-rearing facilities could lead to suboptimal sex ratios of progeny.

The sex allocation sequence of the second female to alight on an egg mass has a different pattern to that of the first female (van Welzen & Waage, 1987). There is a greater probability that the second female will assign a male egg to the first host egg encountered, a behaviour not usually displayed by the first female. Therefore, females oviposit a greater proportion of male eggs in egg masses already visited, but only when the ratio of non-parasitized eggs to parasitized eggs is small.

Except for two known exceptions, the host range of *T. remus* is restricted to the family Noctuidae (Table 1). In the Old World, ten species of Noctuidae, one species of Pyralidae and one species of Arctiidae are known hosts of *T. remus*. In the New World, Wojcik *et al*. (1976) tested 43 species of Lepidoptera belonging to six families. Eggs of 15 noctuid species and a pyralid species were attacked and parasitized; eggs of species of Arctiidae, Geometridae, Mimallonidae and Notodontidae were not parasitized. Nordlund *et al.* (1987) remarked that eggs of *Helicoverpa zea* (Boddie) (Noctuidae) are probably not common hosts in the field since the *T. remus* female usually stands on and braces herself against one egg while parasitizing an adjacent egg in the egg mass; *H. zea* eggs are laid singly in the field.

Ballal *et al.* (1989) demonstrated that host plant species may influence the level of parasitism by *T. remus*. In choice tests, parasitism of *Spodoptera litura* (F.) eggs was higher on cauliflower, beets and okra than on castor bean (*Ricinus communis*), cabbage, cowpea and tobacco.

The interspecific competition between *T. remus* and the braconid *Chelonus insularis* Cresson in *Spodoptera exigua* (Hübner) eggs was studied by Earl & Graham (1984). Only *T. remus* emerged from eggs exposed simultaneously to females of both species. This was probably due to physical attack by the first-instar larva of *T. remus*, which emerges from its egg earlier than the first-instar larva of *C. insularis*, which does not eclose until the larval stage of the host. From hosts 6-16 hours old and exposed to the two parasitoids with a temporal separation of 24 hours, the emergence rate of *T. remus* was significantly greater than the emergence rate of *C. insularis*, whether *T. remus* was the first parasitoid exposed or the second. *Telenomus remus* apparently does not discriminate between non-parasitized eggs and eggs already parasitized by *C. insularis*. However, *C. insularis* females can discriminate eggs that have been parasitized by *T. remus* for more than 24 hours.

Spodoptera spp. egg masses are sometimes parasitized by *Trichogramma* spp. (Hym., Trichogrammatidae) (Cave & Acosta, in press). When the female *Spodoptera* lays an egg mass she covers it with scales from her body; these scales and the multiple layers of eggs make a formidable barrier to *Trichogramma* females (which are smaller and more delicate than *Telenomus remus*), thus they can parasitize only some (usually only those in the top layer) of the eggs in the egg mass. *Telenomus remus* is a more aggressive parasitoid on a *Spodoptera* spp. egg mass due to its larger, more robust size, which allows it to penetrate all layers of the egg mass and parasitize each egg.

Mass Rearing

The multiplication and mass rearing of *T. remus* in the laboratory/ insectary have been studied by a number of researchers for almost 20 years. In India, eggs of *S. litura* (Joshi *et al.*, 1976; Gupta & Pawar, 1985), *Agrotis biconica* Kollar (Noctuidae) (Gautum & Gupta, 1994) and *Corcyra cephalonica* Stainton (Pyralidae) (Kumar *et al*., 1986) have been used as hosts. Gautum (1986b) observed that females of *T. remus* attacked infertile eggs of *S. litura*, but progeny development occurred only in fertile eggs. He also noted that eggs from the first 6 days of oviposition by female *S. litura* are parasitized without ill effects on the parasitoid's biological attributes; parasitoid emergence was reduced in eggs from later ovipositions. Gautum (1986c) suggested the use of *Agrotis* spp. eggs as an alternate host for one generation to improve the biological efficacy of *T. remus*, because adults reared in these eggs are bigger, live longer and are more fecund than adults reared in *Spodoptera* spp. eggs. Kumar *et al.* (1986) noted that parasitism in eggs of *C. cephalonica* was low initially, but after seven generations reached 100%. No differences in development time and sex ratio were detected in comparison with *T. remus* reared in eggs of *S. litura*.

Table 1. Species of Lepidoptera whose eggs are known hosts for *Telenomus remus*.

Family	Species	Reference
Noctuidae	*Achaea janata* (L.)	Sankaran 1974
	Agrotis biconica Kollar	Gautum 1986b
	Agrotis ipsilon (Hufnagel)	Gautum 1986b
	Anicla infecta (Ochsenheimer)	Wojcik *et al*. 1976
	Anticarsia gemmatalis Hübner	Wojcik *et al*. 1976
	Argyrogramma signata (F.)	Joshi *et al*. 1989
	Autographa nigrisigna (Walker)	Dass and Parshad 1984
	Condica videns (Guenée)	Wojcik *et al*. 1976
	Elaphria chalcedonia (Hübner)	Wojcik *et al*. 1976
	Elaphria festivoides (Guenée)	Wojcik *et al*. 1976
	Feltia subterranea (F.)	Wojcik *et al*. 1976
	Grammodes stolida (F.)	Gautum 1987a
	Helicoverpa armigera (Hübner)	Bughio *et al*. 1994
	Helicoverpa zea (Boddie)	Wojcik *et al*. 1976
	Neoerastria apicosa (Haworth)	Wojcik *et al*. 1976
	Mythimna loreyi (Duponchel)	Dass and Parshad 1984
	Mythimna unipuncta (Haworth)	Wojcik *et al*. 1976
	Spodoptera albula Walker	Cave and Acosta (in press)
	Spodoptera dolichos (F.)	Wojcik *et al*. 1976
	Spodoptera eridania (Stoll)	Wojcik *et al*. 1976
	Spodoptera exigua (Hübner)	Wojcik *et al*. 1976
	Spodoptera frugiperda (J. E. Smith)	Wojcik *et al*. 1976
	Spodoptera latifascia (Walker)	Wojcik *et al*. 1976
	Spodoptera littoralis (Boisduval)	Gerling 1972
	Spodoptera litura (F.)	Joshi and Rao 1980
	Spodoptera mauritia (Boisduval)	Gautum 1987a
	Trichoplusia ni (Hübner)	Wojcik *et al*. 1976
Pyralidae	*Nomophila noctuella* (Denis & Schiffermüller)	Wojcik *et al*. 1976
	*Corcyra cephalonic*a Stainton	Kumar *et al*. 1986
Arctiidae	*Creatonotos gangis* (L.)	Bughio *et al*. 1994

In Honduras, Cave & Acosta (in press) described a method of mass rearing *T. remus* using *S. frugiperda* eggs. Strips of waxed paper or recycled typing paper, with several egg masses deposited on them in *S. frugiperda* oviposition cages, are hung from the glass tops of sleeve cages. A quantity of adult *T. remus*, determined by the number of egg masses exposed but usually 30,000-40,000 in a full cage, are released in the cages. The paper strips are removed after 3 days and the individual egg masses are cut from the paper strips. Fifty eggs masses are placed in a plastic bag with a paper towel and the bag is closed with a knot with a second paper towel passing through the knot. Bags are then stored in a rearing room for 10 days. One day before adult emergence, the paper towel passing through the knot in the plastic bag is moistened with honey + water using a syringe, thus emerging adults have an immediate food source. With an average 200 eggs per egg mass and 50 egg masses per bag, each bag produces approximately 10,000 wasps.

Linares (1998) reported that farmers in El Palmar, Venezuela maintain their own colonies of *T. remus*, using eggs of *S. frugiperda* whose larvae are reared on the leaves of castor bean; supposedly the leaves of castor bean eliminate the cannibalistic tendencies of *S. frugiperda* larvae, so that five or more larvae can be reared together in a 5 litre container.

Nagarkatti & Jayanth (1980) noted that eggs of *S. litura* stored at 10ºC for 8 days were accepted for parasitization. Gautum (1987b) reported low parasitism when host eggs were stored at -6º, 5º, 15º or 20ºC for 48-96 hours before parasitization.

Temperature and relative humidity are the most important abiotic factors during rearing of *T. remus*. Gupta & Pawar (1985) obtained parasitism levels greater than 90% only when relative humidity (RH) was greater than 50% at temperatures of 25-41ºC. Gautum (1986a) stated that parasitism was greatest at 27ºC and 75% RH.

Storage of parasitized hosts in order to synchronize production in the insectary is a very important aspect of mass rearing. Nagarkatti & Jayanth (1980) observed that parasitized eggs of *S. litura* could be stored without detriment at 10ºC for two weeks beginning 2-8

days after the initiation of parasitization. Kumar *et al*. (1984) noted that eggs of *C. cephalonica*, parasitized for up to 8 days at room temperature, could be stored at 5ºC for just two weeks. Gautum (1986d) reported that parasitized eggs stored for 7 days at 10ºC did not suffer negative effects; temperatures of 5ºC and 15ºC were not favourable. The optimum age for initiating storage was 7 days after initiation of parasitization.

Storing adult parasitoids for later release in the field is another option. Gautum (1986d) found that adult females of *T. remus* stored at 5ºC or 10ºC survived up to 7 days, without negative effects on their biological attributes; males did not survive for more than 3 days. Storage of adult females for more than 7 days significantly reduced fecundity. Linares (1998) related that farmer-produced *T. remus* adults may be stored at 8-14°C for up to 7 days.

Use in Pest Management

The first use of *T. remus* in classical biological control apparently occurred in 1963 when the parasitoid was introduced from Papua New Guinea to India (Sankaran, 1974). It was later introduced to other Asian countries (Joshi *et al.*, 1976; Patel *et al.*, 1979). Braune (1985) reported that the increase in population density of *T. remus* was responsible for the reduction of *S. litura* eggs in taro during an integrated pest management programme in Samoa. Releases of *T. remus* with two other parasitoids (*Trichogramma chilonis* Ishii and *Tetrastichus howardi* (Olliff) (Hym., Eulophidae)) and a predator reduced the incidence of *S. litura* in potatoes by 60% in India (Ansari *et al.*, 1992).

In the New World, the first introduction of *Telenomus remus* took place during 1971-1972 in Barbados, where levels of parasitism greater than 60% were reported in a number of crops; this parasitoid is considered to contribute substantially to reductions in populations of *Spodoptera* spp. (Alam, 1974, 1979). Later the parasitoid was released and established in Antigua, Dominica, Monserrat, St Kitts, St Vincent and Trinidad & Tobago (Yaseen, 1979; Cock, 1985).

On more than two occasions since 1978, establishment of *T. remus* has been attempted in El Salvador (Cortés & Andrews, 1979) and Nicaragua (Lacayo, 1987). Establishment was never detected (at least never reported), probably due to unfavourable environmental conditions at the release sites and/or low quantities released. (In Nicaragua *T. remus* was reared on just a few field-collected egg masses, then released (T. Anton, pers. comm.).)

Waddill & Whitcomb (1982) attempted to establish *T. remus* in southeastern Florida (USA), releasing more than 660,000 adults in maize and sorghum during 1975-77. The parasitoid was recovered from only March to May during the last two years of releases, however, parasitism levels during this period did not surpass 43%. No parasitoid recovery was made in the field after releases were terminated in May 1977. The authors commented that the biology of *S. frugiperda*, not climate, had most to do with lack of establishment.

Although *T. remus* did not become established in Florida, Lewis & Nordlund (1984) proposed that the parasitoid would be a good candidate in inundative release programmes for controlling *S. frugiperda* because it is easily mass reared. Moreover, it would complement control programmes that utilize the pest's sex pheromone for mating disruption; the same semiochemical stimulates searching and parasitization by *T. remus*.

In Venezuela, Hernández *et al*. (1989) released 5000 *T. remus* in maize in each of three releases during three consecutive weeks. Parasitism reached 78-100% at distances of 30-1400 m from the release point up to two months after the releases; 60-83% parasitism was obtained between 2000 and 2200 m from the point of release after two months. The authors concluded that well-timed spot releases can help maintain a low population of *S. frugiperda* and that more research is needed to determine optimum release densities per unit area. Also in Venezuela, farmers produced 350,000 *T. remus* adults over ten weeks to control the pest on 87.5 ha, releasing 4000-6000 wasps per hectare of maize (Linares, 1998). These farmers place 1000-1500 parasitized eggs in 750-ml plastic containers with honey and distribute the containers in the crop.

In Honduras, *T. remus* was experimentally released in maize and sorghum fields during 1991-1994 (Cave & Acosta, in press). Parasitism rates fluctuated widely (20-92%) between months. High release rates (75,000-105,000 wasps/ha/week) and low release rates (35,000-50,000 wasps/ha/week) were tested. Although no differences in parasitism were detected between release rates, parasitism was notably higher in plots with good crop growth and flowering weeds (65-92%) than in plots with poor crop growth and no weeds (20-60%). Releasing parasitized egg masses in the field a day before parasitoid emergence, by stapling pieces of waxed paper with an egg mass to the underneath side of a maize leaf, was futile since predators (ants, earwigs, ladybirds) devoured many of the eggs before the wasps had a chance to emerge. Therefore, in all experimental releases adult wasps were released in the field. Santos Erazo (1998) showed that parasitism by *T. remus* in the field is not negatively affected by applications of *S. frugiperda* baculovirus.

Telenomus remus is currently mass reared for commercial or experimental purposes in seven Latin American countries. Private insectaries in Venezuela and Colombia produce the parasitoid for sale. Public institution laboratories in Honduras, the Dominican Republic, Peru, Bolivia and Cuba produce small numbers for experimental releases.

Taxonomy

Nixon (1937) described *T. remus* from individuals which emerged from *Spodoptera* spp. eggs collected in Malaysia. He commented that "this species is probably *Telenomus spodopterae* Dodd", which is a species described from females reared from *Spodoptera* spp. eggs in Java, Indonesia. However, according to Nixon (1937) the forewings of *T. spodopterae* are very narrow. Owing to the brief description of *T. spodopterae*, Nixon was not confident enough to apply this name to his Malaysian specimens.

Distinguishing *T. remus* from native species of the genus that also parasitize noctuid eggs in the region is often difficult. In Guatemala and Honduras *Telenomus solitus* Johnson attacks the eggs of *Trichoplusia ni* (Hübner) (Noctuidae) and an unidentified noctuid (Johnson, 1983), *Mocis latipes* (Guenée) (Noctuidae) (Cave, 1992) and *S. frugiperda* (author, pers. obs.). *Telenomus minutissimus* Ashmead is a native species in the Caribbean where it parasitizes *Spodoptera* spp. eggs (Cock, 1985). The external morphologies of *T. solitus* and *T. minutissimus* are extremely similar to those of *T. remus*, so that the only reliable diagnostic method for separating these species is comparison of male genitalia, although they are quite similar in this respect also. Cock (1985) states that a species of *Telenomus* which commonly parasitizes eggs of *Spodoptera* spp. in the Dominican Republic crosses with *T. remus* and produces fertile offspring. His interpretation is that the '*T. remus'* introduced and established in Barbados and later distributed in the Caribbean is possibly a race of *T. minutissimus.* The material subsequently released in Florida and Central America originates from Barbados.

Confusion also occurs with *Telenomus nawai* Ashmead, an Old World species introduced into the region and which parasitizes the

same hosts of *T. remus*. *Telenomus remus* does not cross with *T. nawai* (Cock, 1985). *Telenomus nawai* was released in St Kitts and Trinidad in 1980 for control of *Spodoptera* spp. (Cock, 1985). Although there is no record of its importation and release in Central America, there is the possibility (although small) that it exists in the region due to natural dispersion.

Conclusions, Recommendations and Future Research

Due to the existence of native and exotic *Telenomus* spp. that parasitize *Spodoptera* spp. eggs in the region, the need for a clear taxonomy and reliable recognition methods is obvious. Crossing studies and molecular biology would certainly do much to clarify the distinction of species and the origins of exotic species.

The technology for mass production of *T. remus* in the laboratory is well developed and relatively easy and cheap. Cost estimates for producing 1000 *T. remus* range from US$0.50 (Santos Erazo, 1998) to US$2.20 (Linares, 1998). Sophisticated equipment and precise climate control are not needed. Although certain imported materials (e.g. agar, vitamins, sorbic acid and ascorbic acid) may be needed for an artificial diet for rearing *Spodoptera* spp., the limiting factor in commercial production is labour costs (Román Suárez, 1998). In a cottage industry situation where farmers rear their own wasps, labour costs may be significantly reduced.

More research is needed to develop more effective and efficient methods for releasing *T. remus* in the field. Timing of releases according to crop and pest phenology needs to be fine-tuned. The quantity of wasps released and release frequency must be studied in different agricultural areas with different climatic conditions in order to optimize the ratio of *T. remus* to host egg masses.

The future successful use of *T. remus* to control populations of *Spodoptera* spp. in Latin America probably lies in the ability to develop a cottage industry of commercial and semi-commercial insectaries dedicated to mass multiplication of the parasitoid. There already exists in Venezuela one private company (Servicio Biológico, C.A., Barquisimeto), which has commercially produced *T. remus* since 1991. There are commercial insectaries in Colombia, also. Linares (1998) described how farmers in Venezuela rear their own *T. remus*. This type of applied technology could be easily and effectively transferred throughout the region. Therefore, rural development programmes in Central America ought seriously to consider the potential of *T. remus* for improving the economies of agricultural communities with limited resources.

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