

**Egg retention in *Trichogramma*
(Hymenoptera: Chalcidoidea: Trichogrammatidae):
learning or diapause?***

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Abstract. It is well known that insects are capable of modifying their oviposition behaviour and oogenesis in response to environmental conditions. These responses come in a continuum of steps: from learning to reproductive diapause. Some *Trichogramma principium* Sugonayev et Sorokina, 1978 females oviposited in *Sitotroga cerealella* Olivier eggs whereas other females of the same strain delayed oviposition or totally refuse to parasitize this host. The 'refusing' females had a high number of mature eggs, suggesting that refusal to oviposit may be considered as egg retention. About one third of the females delayed oviposition for up to 8 days. Of the *Trichogramma* females that oviposited in *Sitotroga cerealella* eggs, most oviposited again when offered another batch of host eggs. This tendency to parasitize remained stable both in the presence of hosts and when deprived of hosts and even when preferred and less preferred hosts were sequentially offered. This phenomenon shows certain properties peculiar to learning: it is a behavioural response not associated with oogenesis; it is determined by the immediate environment and is not an anticipatory response triggered by token stimuli, and it is not associated with reduced activity or marked increase in longevity. On the other hand, separation of females into those that oviposited and those that did not revealed that the 'parasitization state' is almost irreversible, whereas learning usually induces reversible gradual changes. We suggest that the stability of the parasitization state is endocrine based and refusal to oviposit may be considered a specific state not controlled by oogenesis, and oviposition behaviour is subject to neurohormonal regulation.

Physiology, behavior, oviposition, learning, diapause, parasitoids, Hymenoptera, Apocrita, *Trichogramma*

INTRODUCTION

Entomologists have intensively studied the physiological and behavioural mechanisms that regulate oviposition (host parasitization) in insect parasitoids. It is well known that most insect parasitoids do not lay eggs at random, but select an appropriate host for the development of their progeny. They achieve this by going through a sequence of behavioural steps, which usually include habitat location, host location, host acceptance, and oviposition proper. In the absence of appropriate stimuli, females do not oviposit. However, conditions vary in time and space and sometimes unpredictably. To cope with this diversity, insects are capable of modifying their oviposition behaviour and oogenesis.

Changes in behaviour are often based on learning, i.e. they are short-term (from seconds to days), usually reversible and modified by experience and based on neural mechanisms (Hansell 1985, Vinson 1985, Vet 1988, Vet & Groenewold 1990, Reznik 1993, Vinson 1998). Learning may

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accelerate and facilitate the search for a given host species, but can also result in a temporary specialization on the most abundant or suitable of the available hosts. In addition to learning, the responsiveness of a female to specific stimuli depends on its motivation to oviposit and hence can be modulated by numerous endogenous factors: age, satiation, and egg load, what is the number of mature eggs in their ovary (Collins & Dixon 1986). These changes in motivation may be pronounced, but always gradual and often reversible (Pak et al. 1985, Donaldson & Walter 1988, Mangel 1989, Minkenberg et al. 1992, Barton Brown 1993, Heimpel et al. 1996, Reznik et al. 1997b, Bjorksten & Hoffmann 1998a). If no acceptable host is found, females can store mature eggs; referred to as egg retention. Mature eggs can even be resorbed, which provides an opportunity to switch energy allocation from oviposition to survival, search or dispersal. In insects parasitoids, resorption and oogenesis may occur simultaneously (Flanders 1942, Fleury & Boulétreau 1993) and females can oviposit immediately when a suitable host is found.

The more profound step is variation in oogenesis in response to host stimuli and/or other environmental cues (Papaj 2000). As indicated above, egg load can exert a variety of effects on behaviour. Finally, females can enter reproductive (imaginal) diapause (when oogenesis is terminated) and so survive a long period of host deprivation and other unfavorable conditions (Tauber et al. 1986, Danks 1987). Reproductive diapause is typical for many insects, although it is relatively rare in parasitoids (e.g., Numata 1993). Diapause and reproduction are two alternative states, thus essential and often irreversible physiological changes are necessary before starting oviposition.

Both learning and diapause are well-defined, clearly distinct, and have been much studied, while changes in motivation and ovarian dynamics have only quite recently attracted the attention of scientists.

For some years we have been studying a particular type of behaviour (supposedly based on changes in motivation), which manifests properties peculiar to diapause as well as typical features of learning. For this we have used *Trichogramma*, a small hymenopteran egg parasitoid employed worldwide for the biological control of insect pests and as a model insect in research (see reviews: Schmidt, 1994; Smith, 1996). Under natural conditions, *Trichogramma* females encounter different egg hosts and each is either accepted or rejected. In the laboratory, some host species are parasitized by certain *Trichogramma* females, while other females of the same strain delay oviposition or totally refuse to parasitize the same host (Liu et al. 1995, Losey & Calvin 1995, Song et al. 1997, Basso et al. 1998, Bjorksten & Hoffmann 1998a, 1998b, Silva 1999 see Reznik et al. 200a for more references). It is noteworthy that the study of the reaction to a poor quality host is more likely to reveal small variations in behaviour because near the threshold all reactions are usually more variable. The present paper is the first to summarize the results of these studies and includes both original and previously published data.

MATERIALS AND METHODS

In our experiments, we used a laboratory line of *Trichogramma principium* Sugonayev et Sorokina, 1978, collected in Chimkent district (Kazakhstan) from the eggs of Noctuidae and cultured for more than 50 generations on eggs of the grain moth, *Sitotroga cerealella* (less than 1 day old) *T. principium* females were placed individually into small (40×5 mm) tubes. The wasps were fed honey (50% aqueous solution) streaked on the glass walls of the tube. Host eggs were presented on a paper strip to which they were pasted with a non-toxic water soluble glue. *Trichogramma* usually lay a single egg in each grain moth egg. Parasitized eggs become markedly darker in colour than unparasitized eggs. The number of dark eggs indicated the approximate number of *Trichogramma* eggs laid. In certain experiments, some of the *Trichogramma* females were dissected to determine the number of mature eggs present in the posterior part of their ovaries. When estimating stability of host acceptance, females which were dissected or died during the experiment were excluded from the statistical analysis. Details of particular experimental designs are given below along with the results or are described in the relevant publications.

RESULTS AND DISCUSSION

First, the females that did not parasitize a host were not merely 'left end of the distribution curve'. Although in a sample 'females with zero fecundity' were in the majority, wasps that started to parasitize, usually parasitized many hosts so the fecundity distribution curve is distinctly bimodal (Fig. 1). Thus, separation of females into those that oviposited and those that did not is of the 'all-or-none' type, similar to active or in diapause, in contrast to learning, which usually results in a gradual change in host searching preference, or oviposition behaviour (Hansell 1985, Vinson 1985, Papaj & Prokopy 1989, Vet & Groenewold 1990, Papaj & Lewis 1992, Reznik 1993, Vinson 1998).

However, this difference in the tendency to oviposit could be determined by differences between females and/or variations in the age of host eggs. The easiest way to settle this is to present the parasitoid with two or several ages of host eggs in sequence.

Our experiments showed that *Trichogramma* females tend to continue to oviposit when sequentially offered host eggs of similar age (Tab. 1, exp. 1–3) or even when fresh (more preferred) and 6-day old (less preferred) grain moth eggs were offered in sequence (Tab. 1, exp. 4). In a more long-term experiment, batches of grain moth eggs of similar age were sequentially offered on four occasions and the wasps were allowed to parasitize each batch over a period of two days. Data for 1710 females, obtained in 15 replicates of this experiment are summarized and presented in Fig. 2. Many females did not oviposit initially but started to oviposit 2–6 days later, which means that their 'refusal' was more a 'delay' in oviposition. Once a parasitoid began to oviposit it usually continued to do so: only 1.3% showed egg retention after a certain period of oviposition (for simplicity these individuals are not indicated in the figure). In certain experiments, a period elapsed between the presentation of the two batches of host eggs to the parasitoids. Following two- and

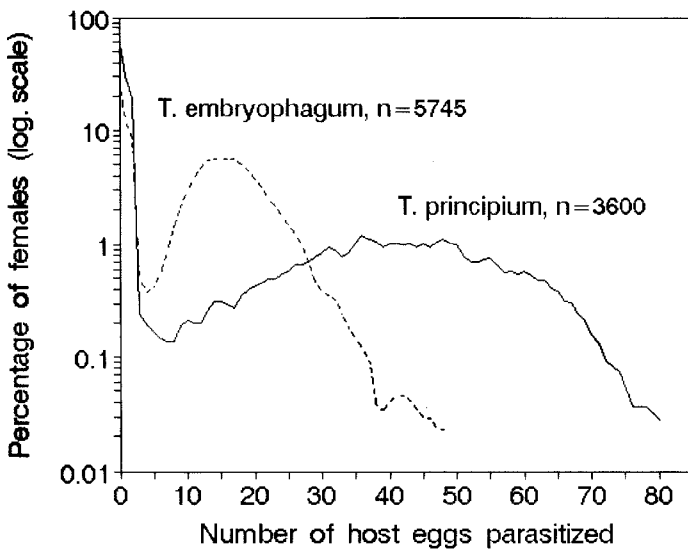


Fig. 1. Frequency distribution of the percentage *Trichogramma principium* and *T. embryophagum* that oviposited in different numbers of host eggs over a period of 48 h.

Tab. 1. The effect on the oviposition behaviour of *T. principium* of sequentially offering two batches of host eggs (in certain cases separated by a period of host deprivation)

exp.	host species and age		host deprivation (days)	oviposition behaviour		reference
	1st batch	2nd batch		host acceptance ¹	stability of parasitization ²	
1	<i>S. cerealella</i> , 1-day old ³	<i>S. cerealella</i> , 1-day old	0	37.8% (n=437) ⁴	89.2% (n=165)	Reznik et al. 1997a
2	<i>S. cerealella</i> , 1-day old	<i>S. cerealella</i> , 1-day old	0	42.9% (n=387)	95.1% (n=166)	Reznik et al. 1998
3	<i>S. cerealella</i> , 6-day old	<i>S. cerealella</i> , 6-days old	0	13.1% (n=459)	78.0% (n=60)	Reznik et al. 1997a
4	<i>S. cerealella</i> , 1-day old	<i>S. cerealella</i> , 6-days old	0	45.2% (n=454)	79.4% (n=205)	Reznik et al. 1997a
5	<i>S. cerealella</i> , 1-day old	<i>S. cerealella</i> , 6-days old	2	36.3% (n=102)	84.8% (n=37)	original data
6	<i>S. cerealella</i> , 1-day old	<i>S. cerealella</i> , 6-days old	4	34.2% (n=79)	81.5% (n=27)	original data
7	<i>E. kuehniella</i> 1-day old	<i>S. cerealella</i> , 1-day old	0	63.4% (n=354)	96.8% (n=224)	original data
8	<i>E. kuehniella</i> 1-day old	<i>S. cerealella</i> , 5-day old	0	61.4% (n=260)	96.7% (n=160)	original data

¹ host acceptance – the percentage of females ovipositing in the first batch of eggs offered

² stability of parasitization – the percentage of females that oviposited in the first batch of eggs, which also oviposited in the second batch of eggs

³ host age was measured in days at 20°C

⁴ sample size

four-day periods of host deprivation most parasitoid that oviposited at the first presentation did so at the second (“stability of parasitization”) when fresh and 6-days old eggs were offered in sequence (Tab. 1, exp. 5–6). When fresh eggs were presented on both occasions, even after 8 days of host deprivation the “stability of parasitization” was ca 90% (Reznik et al. 2001a).

Moreover, this stability remained high when relatively preferred and usually rejected host species were offered sequentially (Tab. 1, exp. 7), and even when 5-days old eggs were offered on the second occasion (Tab. 1, exp. 8). In another experiment, 70±7% of the *T. principium* females oviposited in 5-day old eggs of *S. cerealella* when previously offered *Ephestia kuehniella* eggs, while only 33±5% of the females that were sequentially offered two batches of 5-day old grain moth eggs oviposited in the second batch of eggs (in both cases n= 260, difference is significant p<0.01 [Kruskal-Wallis distribution-free test]). Thus, previous experience of oviposition in preferred host species lowered the threshold of acceptance of a less preferred host species. In contrast, in most cases of learning, experience of *Trichogramma* females of a given host species either did not influence the level of affinity for other hosts (e.g., Kaiser et al. 1989a) or the acceptance of a low-quality host decreased after a high-quality (preferred) host was encountered, as occurs in the discrimination between parasitized and unparasitized hosts (Klomp et al. 1980, Alphen & Dijken 1988). Similar reactions occur in other insects (Papaj & Prokopy 1989, Papaj & Lewis 1992, Reznik 1993).

Dividing parasitoids into those that oviposited and those that did not revealed a clear difference between females. This may be due to: (1) inherited or acquired morphological deformities, which prevent oviposition; (2) sterility or no mature eggs (Nagarkatti & Nagaraja 1978); and (3) differences in host recognition, acceptance, or oviposition behaviour.

The hypothesis of morphological deformities was rejected because many females that at first did not oviposit, did so several days later (Fig. 2). To test the sterility hypothesis, the number of mature eggs stored in the posterior part of the ovaries of certain of the females used in the long term experiment (Fig. 2) was determined by dissection. At emergence these females had 19.2 ± 1.0 mature eggs (hereafter, mean \pm SEM is given), significantly fewer eggs (7.6 ± 1.4) were found in females that oviposited for 2–4 days, and in females that did not oviposit for more than two days it was insignificantly (Tukey HSD test) higher (22.5 ± 1.6), than at emergence. These results conform with our earlier studies (Reznik et al., 1997a) and data on other *Trichogramma* species (Pak et al. 1985, Pavlik 1993, Volkoff & Daumal 1994, Bai et al. 1995). Our earlier experiments demonstrated that females that terminate oviposition and survive for more than two days, have 24.5 ± 3.3 mature eggs and, consequently, have ceased oviposition, not oogenesis. It is notable that the mean number of eggs laid during the first 48 h of oviposition is not dependent on whether parasitization is delayed or not. Moreover, lifetime fecundity is practically independent of when oviposition starts (Reznik et al. 1998, 2001a).

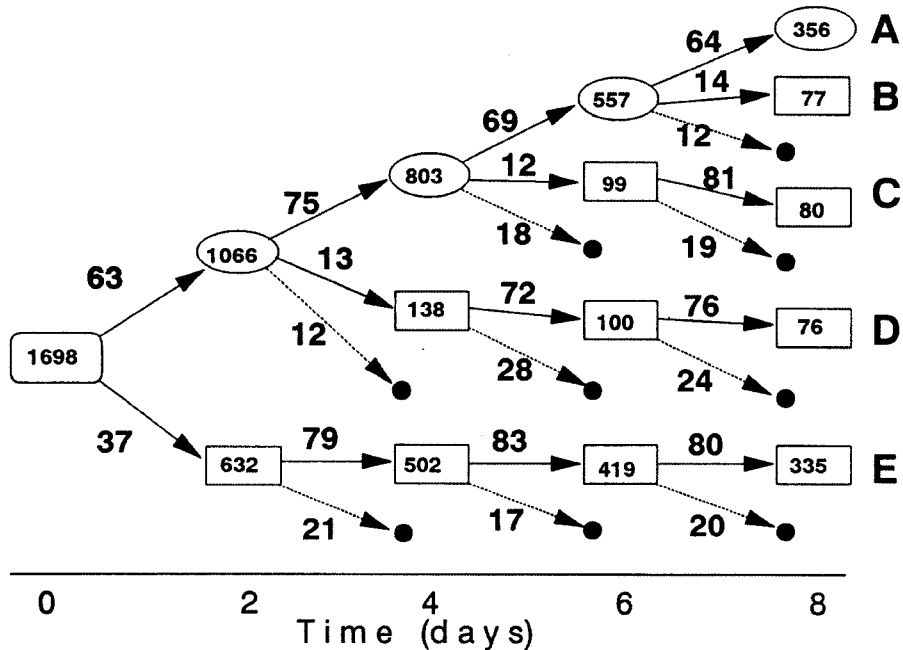


Fig. 2. Survival, egg retention and oviposition of *Trichogramma principium* females over a period of 8 days. Data are presented as a Markov chain. Symbols: rounded rectangle, ellipses, rectangles, and black circles indicate, respectively, emerging females, egg retention, oviposition, and death of female. Number close to on arrow indicates transition probability percentage (sample size, i.e. number of females in a given state, is indicated in each symbol at the point of an arrow). Letters A, B, C, D, E indicate cohorts of females in which egg retention period lasted, respectively, for >8, 6–8, 4–6, 2–4, and <2 days. Horizontal axis indicates time in days.

Thus 'refusing' females are not sterile and have a considerable number of mature eggs. Changes in host acceptance behaviour are not associated with 'low egg load', as previously recorded in many other parasitoid species (Donaldson & Walter 1988, Mangel 1989, Minkenberg et al. 1992, Heimpel et al. 1996). We conclude that the egg retention is connected with oviposition behaviour rather than the intensity of oogenesis. In this respect, the phenomenon under study is similar to learning, but markedly different from reproductive diapause.

Naturally, the next step in our studies was a comparative analysis of the oviposition behaviour of *Trichogramma* females. Direct observations of *Trichogramma* behaviour suggested that females, which did not oviposit, were active, moved around, and sometimes encountered the host (these encounters may have been accidental in such small tubes). However, these females did not show the characteristic parasitization behaviour, the usual sequence of behaviour resulting in parasitization was interrupted at the stage of arrestment and host recognition (Reznik & Umarova 1991). Long-term observations suggested that females suddenly, rather than gradually, showed the arrestment reaction to the host and switched from egg retention to parasitization behaviour (Reznik et al. 2001b).

Reproductive diapause is usually accompanied by a marked increase in longevity. This was not observed in learning. As for egg retention, our experiments revealed only a slight (although significant) increase in longevity of females that did not oviposit compared with those that oviposited for wasps kept under the same conditions. In particular (Fig. 2) 21% of the females that oviposited and 12% of those that did not oviposit died during the first two days of the experiment. In this experiment, the mean lifetime of the females that oviposited in the first batch of eggs was 5.98 ± 0.10 days, while that of the females that did not oviposit in the first batch of eggs was 6.29 ± 0.07 days (sample size is indicated in Fig. 2, Student's t-test $p < 0.001$). The females, that started to oviposit when the second batch of eggs was presented, survived for 6.55 ± 0.15 days, while those wasps that did not oviposit in either batch of eggs lived for 6.91 ± 0.06 days ($p = 0.02$).

Another difference between diapause and 'refusal to oviposit' is that the latter is of short duration (Fig. 2). However, in some insects, e.g. in leaf beetles *Leptinotarsa decemlineata* Say (De Wilde et al. 1969) and *Zygogramma suturalis* F. (Reznik 1991, Vinogradova & Pantyukhov 1995) diapause may also result in a short-term delay or interruption in oviposition. Earlier, Flanders (1942) noted that in insect parasitoids temporary cessation of oogenesis may occur either spontaneously or as a result of an environmental influence.

In comparison with diapause learning usually results in a short-term effect (Eisenstein & Reep 1985, Hansell 1985, Vinson 1985, Papaj & Prokopy 1989, Papaj & Lewis 1992, Reznik 1993). Certainly, there are exceptions to this rule. For example, Bjorksten & Hoffmann (1998b) have demonstrated that learning induces an increase in the acceptance of *S. cerealella* eggs by *Trichogramma*, which persisted for 5 days, although it resulted in nothing but an increase in the number of hosts parasitized (bearing in mind that oviposition is qualitatively different not ovipositing). Thus this phenomenon is intermediate between a neural reaction (learning) and a neurohormonal response (diapause). However the underlying mechanism is unknown.

Oviposition behaviour is subject not only to nervous, but also to endocrine control (Raabe 1986, Barton Brown 1993). We suppose that the "stability of parasitization" in *Trichogramma* females is under endocrine control. Possibly, a hormone is released at the first oviposition, which influences female behaviour, similar to the sharp increase in the titer of juvenile hormone observed when a burying beetle finds a carcass (Trumbo 1997) and the hormonal control of sexual and maternal behaviour in various insects (e.g., Webster & Carde 1984, Gadenne 1993, Rankin et al. 1997). In this case, long-term egg retention might be a result of a special physiological state in which oviposition behaviour is under hormonal control.

It is also possible that this stability is a consequence of learning. In various *Trichogramma* species, and other parasitoid wasps, host searching, recognition and acceptance behaviour may be influenced by experience (Klomp et al. 1980, Gross et al. 1981, Alphen & Dijken 1988, Vet 1988, Godfray & Waage 1988, Kaiser et al. 1989a, 1989b, Bjorksten & Hoffmann 1995, 1998a, 1998b). As was demonstrated above, the phenomenon studied here shows a number of characteristics that differentiate it from most of the reported cases of learning. However, it is difficult to differentiate between learning and changes in motivation determined by an insect parasitoid's internal state (e.g., Henneman et al. 1995).

The adaptive role of egg retention and refusal to oviposit in an immediately available host, may be its association with dispersal and search for new patches of host eggs, i. e. risk-spreading in time, in space, and in different host species (Cronin & Strong 1993, Hopper 1999, Reznik 2001a). Some other species of insect parasitoids also have a 'preoviposition' or 'dispersal' period and, for oviposition, have to switch on the 'oviposition state' or 'host find and attack cycle' (Vinson 1985, 1998).

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REFERENCES

- ALPHEN J. J. M. van & DIJKEN M. J. 1988: Host discrimination: the learning hypothesis revisited. *Coll. l'INRA* **48**: 35–36.
- BAI B., ĆOBANOGLU S. & SMITH S. M. 1995: Assessment of *Trichogramma* species for biological control of forest lepidopteran defoliators. *Entomol. Experiment. Appl.* **75**: 135–143.
- BARTON BROWNE L. 1993: Physiologically induced changes in resource-oriented behavior. *Ann. Rev. Entomol.* **38**: 1–25.
- BASSO C., GRILLE G., POMPANON F., ALLEMAND R. & PINTUREAU B. 1998: Comparacion de los caracteres biológicos y etológicos de *Trichogramma pretiosum* y de *T. exiguum* (Hymenoptera: Trichogrammatidae). *Revista Chilena Entomol.* **25**: 45–53.
- BJORKSTEN T. A. & HOFFMANN A. A. 1995: Effect of pre-adult and adult experience on host acceptance in choice and non-choice tests in two strains of *Trichogramma*. *Entomol. Experiment. Appl.* **76**: 49–58.
- BJORKSTEN T. A. & HOFFMANN A. A. 1998a: Separating the effects of experience, size, egg load and genotype on host response in *Trichogramma* (Hymenoptera, Trichogrammatidae). *J. Insect Behav.* **11**: 129–148.
- BJORKSTEN T. A. & HOFFMANN A. A. 1998b: Persistence of experience effects in the parasitoid *Trichogramma nr. brassicae*. *Ecol. Entomol.* **23**: 110–117.
- COLLINS M. D. & DIXON A. F. G. 1986: The effect of egg depletion on the foraging behaviour of an aphid parasitoid. *Zitschr. Angew. Entomol.* **102**: 342–352.
- CRONIN T. & STRONG D. R. 1993: Substantially submaximal oviposition rates by a mymarid egg parasitoid in the laboratory and field. *Ecology* **74**: 1813–1825.
- DANKS H. V. 1987: Insect dormancy: an ecological perspective. *Biol. Surv. Can. Monogr.* **1**: 1–439.
- DONALDSON J. S. & WALTER G. H. 1988: Effects of egg availability and egg maturity on the ovipositional activity of the parasitic wasp *Coccophagus atratus*. *Physiol. Entomol.* **13**: 407–417.
- EISENSTEIN E. M. & REEP R. L. 1985: Behavioral and cellular studies of learning and memory in insects. In: KERKUT G. A. & GILBERT L. I. (eds.): *Comprehensive Insect Physiology, Biochemistry and Pharmacology* **9**: 513–547.
- FLANDERS S. E. 1942: Oosorption and ovulation in relation to oviposition in the parasitic Hymenoptera. *Ann. Entomol. Soc. Amer.* **35**: 251–266.
- FLEURY F. & BOULÉTREAU M. 1993: Effect of temporary host deprivation on the reproductive potential of *Trichogramma brassicae*. *Entomol. Experiment. Appl.* **68**: 203–210.
- GADENNE C. 1993: Effects of fenoxycarb, juvenile hormone mimetic, on female sexual behavior of the black cutworm, *Agrotis ipsilon* (Lepidoptera, Noctuidae) *J. Insect Physiol.* **39**: 25–29.
- GODFRAY H. C. J. & WAAGE J. K. 1988: Learning in parasitic wasps. *Nature* **331**: 211.

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REFERENCES

- ALPHEN J. J. M. van & DIJKEN M. J. 1988: Host discrimination: the learning hypothesis revisited. *Coll. l'INRA* **48**: 35–36.
- BAI B., ĆOBANOGLU S. & SMITH S. M. 1995: Assessment of *Trichogramma* species for biological control of forest lepidopteran defoliators. *Entomol. Experiment. Appl.* **75**: 135–143.
- BARTON BROWNE L. 1993: Physiologically induced changes in resource-oriented behavior. *Ann. Rev. Entomol.* **38**: 1–25.
- BASSO C., GRILLE G., POMPANON F., ALLEMAND R. & PINTUREAU B. 1998: Comparacion de los caracteres biológicos y etológicos de *Trichogramma pretiosum* y de *T. exiguum* (Hymenoptera: Trichogrammatidae). *Revista Chilena Entomol.* **25**: 45–53.
- BJORKSTEN T. A. & HOFFMANN A. A. 1995: Effect of pre-adult and adult experience on host acceptance in choice and non-choice tests in two strains of *Trichogramma*. *Entomol. Experiment. Appl.* **76**: 49–58.
- BJORKSTEN T. A. & HOFFMANN A. A. 1998a: Separating the effects of experience, size, egg load and genotype on host response in *Trichogramma* (Hymenoptera, Trichogrammatidae). *J. Insect Behav.* **11**: 129–148.
- BJORKSTEN T. A. & HOFFMANN A. A. 1998b: Persistence of experience effects in the parasitoid *Trichogramma nr. brassicae*. *Ecol. Entomol.* **23**: 110–117.
- COLLINS M. D. & DIXON A. F. G. 1986: The effect of egg depletion on the foraging behaviour of an aphid parasitoid. *Zischr. Angew. Entomol.* **102**: 342–352.
- CRONIN T. & STRONG D. R. 1993: Substantially submaximal oviposition rates by a mymarid egg parasitoid in the laboratory and field. *Ecology* **74**: 1813–1825.
- DANKS H. V. 1987: Insect dormancy: an ecological perspective. *Biol. Surv. Can. Monogr.* **1**: 1–439.
- DONALDSON J. S. & WALTER G. H. 1988: Effects of egg availability and egg maturity on the ovipositional activity of the parasitic wasp *Coccophagus atratus*. *Physiol. Entomol.* **13**: 407–417.
- EISENSTEIN E. M. & REEP R. L. 1985: Behavioral and cellular studies of learning and memory in insects. In: KERKUT G. A. & GILBERT L. I. (eds.): *Comprehensive Insect Physiology, Biochemistry and Pharmacology* **9**: 513–547.
- FLANDERS S. E. 1942: Oosorption and ovulation in relation to oviposition in the parasitic Hymenoptera. *Ann. Entomol. Soc. Amer.* **35**: 251–266.
- FLEURY F. & BOULÉTREAU M. 1993: Effect of temporary host deprivation on the reproductive potential of *Trichogramma brassicae*. *Entomol. Experiment. Appl.* **68**: 203–210.
- GADENNE C. 1993: Effects of fenoxycarb, juvenile hormone mimetic, on female sexual behavior of the black cutworm, *Agrotis ipsilon* (Lepidoptera, Noctuidae) *J. Insect Physiol.* **39**: 25–29.
- GODFRAY H. C. J. & WAAGE J. K. 1988: Learning in parasitic wasps. *Nature* **331**: 211.

- GROSS H. R., LEWIS W. J. & NORDLUND D. A. 1981: *Trichogramma pretiosum*: effect of prerelease parasitization experience on retention in release areas and efficiency. *Environ. Entomol.* **10**: 554–556.
- HANSELL M. 1985: Ethology. In: KERKUT G. A. & GILBERT L. I. (eds.): *Comprehensive Insect Physiology, Biochemistry and Pharmacology* **9**: 3–93.
- HEIMPEL G. E., ROSENHEIM J. A. & MANGEL M. 1996: Egg limitation, host quality, and dynamic behavior by a parasitoid in the field. *Ecology* **77**: 2410–2420.
- HENNEMAN M. L., PAPAJ D. R., FIGUEREDO A. J. & VET L. E. M. 1995: Egg-laying experience and acceptance of parasitized hosts by the parasitoid *Leptopilina heterotoma* (Hymenoptera; Eucoilidae). *J. Insect Behav.* **8**: 331–342.
- HOPPER K. R. 1999: Risk-spreading and bet-hedging in insect population biology. *Ann. Rev. Entomol.* **44**: 535–560.
- KAISER L., PHAM-DELEGUE M. H. & MASSON C. 1989a: Behavioural study of plasticity in host preferences of *Trichogramma maidis* (Hymenoptera: Trichogrammatidae). *Physiol. Entomol.* **14**: 53–60.
- KAISER L., PHAM-DELEGUE M. H., BAKCHINE E. & MASSON C. 1989b: Olfactory responses of *Trichogramma maidis* Pint. et Voeg.: effects of chemical cues and behavioral plasticity. *J. Insect Behav.* **2**: 701–712.
- KLOMP H., TEERINK B. J. & WEI CHUN MA 1980: Discrimination between parasitized and unparasitized hosts in the egg parasite *Trichogramma embryophagum*: a matter of learning and forgetting. *Netherl. J. Zool.* **30**: 254–277.
- LIU S. S., ZHANG G. M., SHI Z. H. & ZHANG F. 1995: The effect of rearing host species and host age on the parasitization of the Asian corn borer, *Ostrinia furnacalis*, by *Trichogramma dendrolimi*. *Colloques de l'INRA* **73**: 87–90.
- LOSEY J. E. & CALVIN D. D. 1995: Quality assessment of four commercially available species of *Trichogramma* (Hymenoptera, Trichogrammatidae). *J. Econom. Entomol.* **88**: 1243–1250.
- MANGEL M. 1989: Evolution of host selection in parasitoids: does the state of the parasitoid matter? *Amer. Natur.* **133**: 688–705.
- MINKENBERG O. P. J. M., TATAR M. & ROSENHEIM J. A. 1992: Egg load as a major source of variability in insect foraging and oviposition behavior. *Oikos* **65**: 134–142.
- NAGARKATTI S. & NAGARAJA H. 1978: Experimental comparison of laboratory reared vs. wild-type *Trichogramma confusum* (Hym.: Trichogrammatidae) I. Fertility, fecundity and longevity. *Entomophaga* **23**: 129–136.
- NUMATA H. 1993: Induction of adult diapause and of low and high reproductive states in a parasitoid wasp, *Ooencyrtus nezarae*, by photoperiod and temperature. *Entomol. Exp. Appl.* **66**: 127–134.
- PAK G. A., VAN HALDER I., LINDEBOOM R. & STROET J. J. G. 1985: Ovarian egg supply, female age and plant spacing as factors influencing searching activity in the egg parasite *Trichogramma* sp. *Meded. Fac. Landbouwwet. Rijksuniv. Gent* **50**: 369–378.
- PAPAJ D. R. 2000: Ovarian dynamics and host use. *Ann. Rev. Entomol.* **45**: 423–448.
- PAPAJ D. R. & LEWIS A. C. 1992: *Insect learning: ecological and evolutionary perspectives*. Chapman and Hall, London, 398 pp.
- PAPAJ D. R. & PROKOPY R. J. 1989: Ecological and evolutionary aspects of learning in phytophagous insects. *Ann. Rev. Entomol.* **34**: 315–350.
- PAVLIK J. 1993: Variability in the host acceptance of European corn borer, *Ostrinia nubilalis* Hbn. (Lepidoptera, Pyralidae) in strains of the egg parasitoid *Trichogramma* spp. (Hymenoptera, Trichogrammatidae). *J. Appl. Entomol.* **115**: 77–84.
- RAABE M. 1986: Insect reproduction: regulation of successive steps. *Adv. Insect Physiol.* **19**: 29–154.
- RANKIN S. M., CHAMBERS J. & EDWARDS J. P. 1997: Juvenile hormone in earwigs: Roles in oogenesis, mating, and maternal behaviors. *Arch. Insect Biochem. Physiol.* **35**: 427–442.
- REZNIK S. Ya. 1991: The effects of feeding damage in ragweed *Ambrosia artemisiifolia* (Asteraceae) on populations of *Zygogramma suturalis* (Coleoptera, Chrysomelidae). *Oecologia* **88**: 204–210.
- REZNIK S. Ya. 1993: Learning in food selectivity of insects. *Proc. Zool. Inst. RAN* **193**: 5–72 (in Russian).
- REZNIK S. Ya. & UMAROVA T. Ya. 1991: Host population density influence on host acceptance in *Trichogramma*. *Entomol. Exp. Appl.* **58**: 49–54.
- REZNIK S. Ya., UMAROVA T. Ya. & VOINOVICH N. D. 1997a: The influence of previous host age on current host acceptance in *Trichogramma*. *Entomol. Experiment. Appl.* **82**: 153–157.
- REZNIK S. Ya., VOINOVICH N. D. & UMAROVA T. Ya. 1997b: Carbohydrate suppresses parasitization and induces egg retention in *Trichogramma*. *Biocontrol Sci. Technol.* **7**: 271–274.
- REZNIK S. Ya., UMAROVA T. Ya. & VOINOVICH N. D. 1998: Egg retention in the presence of a host in *Trichogramma* females. *J. Appl. Entomol.* **122**: 555–559.
- REZNIK S. Ya., UMAROVA T. Ya. & VOINOVICH N. D. 2001a: Long-term egg retention and parasitization in *Trichogramma principium*. *J. Appl. Entomol.* **125**: 169–175.
- REZNIK S. Ya., UMAROVA T. Ya. & VOINOVICH N. D. 2001b: Comparative behavioural analysis of females manifesting oviposition and egg retention in *Trichogramma principium*. *Entomol. Obozr.* **80**: 545–555 (in Russian).

- SCHMIDT J. M. 1994: Host recognition and acceptance by *Trichogramma*. In: WAJNBERG E. & HASSAN S. A. (eds.): *Biological control with egg parasitoids*. CAB International, Wallingford, UK. pp. 165–200.
- SILVA I. M. M. S. 1999: *Identification and evaluation of Trichogramma parasitoids for biological pest control*. Doctoral thesis. Wageningen Agricultural University, NL, 151 pp.
- SMITH S. M. 1996: Biological control with *Trichogramma*: advances, successes, and potential of their use. *Ann. Rev. Entomol.* **41**: 375–406.
- SONG S. J., BOURCHIER R. S. & SMITH S. M. 1997: Effect of host diet on acceptance of eastern spruce budworm eggs by *Trichogramma minutum*. *Entomol. Experiment. Appl.* **84**: 41–47.
- TAUBER M. J., TAUBER C. A. & MASAKI S. 1986: *Seasonal adaptations of insects*. Oxford University Press, N.Y., 411 pp.
- TRUMBO S. T. 1997: Juvenile hormone – mediated reproduction in burying beetles: from behavior to physiology. *Arch. Insect Biochem. Physiol.* **35**: 479–490.
- VET L. E. M. 1988: The influence of learning on habitat location and acceptance by parasitoids. *Colloques de l'INRA* **48**: 29–34.
- VET L. E. M. & GROENEWOLD A. W. 1990: Semiochemicals and learning in parasitoids. *J. Chem. Ecol.* **16**: 3119–3155.
- VINOGRADOVA E. B. & PANTYUKHOV G. A. 1995: Adult diapause and its physiological characteristic in the ragweed leaf beetle *Zygogramma suturalis* F. (Coleoptera, Chrysomelidae), introduced in Russia from North America. *Fol. Biol.* **44**: 137–141.
- VINSON S. B. 1985: The behavior of parasitoids. In: Kerkut G. A. & Gilbert L. I. (eds.): *Comprehensive Insect Physiology, Biochemistry and Pharmacology* **9**: 417–469.
- VINSON S. B. 1998: The general host selection behavior of parasitoid Hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. *Biol. Control* **11**: 79–96.
- VOLKOFF A. N. & DAUMAL J. 1994: Ovarian cycle in immature and adult stages of *Trichogramma cacoeciae* and *T. brassicae* (Hym.: Trichogrammatidae). *Entomophaga* **39**, 303–312.
- WEBSTER R. P. & CARDE R. T. 1984: The effects of mating, exogenous juvenile hormone and a juvenile hormone analog on pheromone titer, calling and oviposition in the omnivorous leafroller moth, *Platynota stultana*. *J. Insect Physiol.* **30**: 113–118.
- WILDE J. de, BONGERS W. & SCHOONEVELD H. 1969. Effects of host plant age on phytophagous insects. *Entomol. Experiment. Appl.* **12**: 714–720.