

Analysis of multiparasitism by *Eupelmus vuilleti* (Craw) (Eupelmidae) and *Dinarmus basalis* (Rond) (Pteromalidae) in the presence of one of their common hosts, *Bruchidius atrolineatus* (Pic) (Coleoptera Bruchidae)

Laurent Leveque¹, Jean-Paul Monge¹, Danielle Rojas-Rousse¹, Franz Van Alebeek², Jacques Huignard¹

¹ Institut de Biocénologie Expérimentale des Agrosystèmes, URA CNRS 1298, Avenue Monge, Parc Grandmont, 37200 Tours France

² Department of Entomology, Agricultural University, PO Box 8031, 6700 EH Wageningen, The Netherlands

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Abstract. *Bruchidius atrolineatus* (Pic) is a tropical beetle (Coleoptera Bruchidae) that develops during the larval and pupal stages in the seeds of a legume *Vigna unguiculata* (Walp). Two species of Hymenoptera, *Dinarmus basalis* (Rond) and *Eupelmus vuilleti* (Craw), solitary ectoparasitoids of the larvae and pupae of *B. atrolineatus*, were introduced successively in the presence of their hosts, varying the interval between the two introductions. When *D. basalis* females were introduced 24 h, 3 days or 7 days after *E. vuilleti*, multiparasitism was low. The females had low fecundity, and their eggs were not distributed randomly over the different available hosts. When *E. vuilleti* females were introduced second, they oviposited on the different hosts available and did not avoid multiparasitism. The presence of hosts already parasitised by *D. basalis* increased the reproduction of *E. vuilleti*, and the fecundity of the females was higher than in control batches with *E. vuilleti* alone. *E. vuilleti* seems capable of detecting the ovipositor shafts drilled by the *D. basalis* females, and by introducing its own ovipositors killing the *D. basalis* eggs or larvae. When interspecific competition was occurring the number of *E. vuilleti* adults emerging from the seeds was no different from that observed in control batches with *E. vuilleti* alone, and there were always fewer *D. basalis* adults than in control batches (*D. basalis* alone). This interspecific competition reduces the influence of the two parasitoids in the biological control of bruchid populations.

Key words: Hymenoptera – Ectoparasitoids – Oviposition – Interspecific competition – Host recognition

Studies carried out in the fields, in the Niamey region of Niger (13° N) show that two sympatric bruchid beetle species, *Bruchidius atrolineatus* (Pic) and *Callosobruchus maculatus* (F.), develop during their postembryonic growth in the seeds of the legume *Vigna unguiculata* (Walp)

causing serious losses to the harvest during storage (Alzouma 1987; Monge et al. 1989; Monge and Huignard 1991). A survey of the bruchid population and their parasitoids was made from November to September (i.e. during a major part of the dry season and during the rainy season) inside traditional stores containing cowpea (*V. unguiculata*) pods. Three species of hymenoptera were present throughout the period of the study: a egg parasitoid, *Uscana lariophaga* Steph. and two solitary ectoparasitoids of the larvae and pupae, *Eupelmus vuilleti* and (Craw) *Dinarmus basalis* (Rond).

The number of ectoparasitoids present in the store was estimated by using traps communicating with the interior of the store. More *E. vuilleti* than *D. basalis* adults were always captured whatever the period of the study (Monge and Huignard 1991). *E. vuilleti* was dominant inside the store and this dominance could be the consequence of interspecific competition between the adult females and larvae of the two ectoparasitoids. Van Alebeek (1991) and Van Alebeek et al. (1992) have analysed the reproduction and offspring of *E. vuilleti* and *D. basalis* females after an interval of 24 hours, and observed that the *E. vuilleti* females were capable of detecting the *D. basalis* eggs or larvae and of killing them by puncture. This ovicidal and larvicidal behaviour during oviposition has also been demonstrated in another ectoparasitoid *Bracon hebetor*, by Strand and Godfray (1989) in a superparasitism situation.

We analysed the competition between *E. vuilleti* and *D. basalis* in the presence of the larval and pupal stages of one of their hosts *Bruchidius atrolineatus*. Van Alebeek (1991) and Van Alebeek et al. (1992) have studied this type of competition, but the two species of parasitoids were either introduced together in the presence of their host, or successively with a 24 h time interval. In our experiments, the interval separating the introduction of the two species in the presence of the same host varied, so that the second species introduced could find a healthy host and/or parasitised hosts bearing either eggs, larvae or pupae of the first species.

In the case of multiparasitism, there will be competition between the larvae of the two parasitoid species,

which can be based on certain morphological or behavioural characteristics of the larvae of one of the species during interspecific competition in the presence of the host (Salt 1961; Mc Brien and Mackauer 1990). Early first-instar larvae can physically attack and kill the older larvae.

The study of the female fecundities of the two species when interspecific competition was (or was not) taking place and analysis of the adult emergence allowed an estimation of the impact of this competition under our experimental conditions.

Materials and methods

Rearing of the host

The *B. atrolineatus* population originated from the Niamey (Niger) region was collected in the cowpea cultures during October 1990. The females oviposited on the *V. unguiculata* seeds (variety Black Eyes California) and all post-embryonic development took place in these seeds. Post-embryonic development was carried out in photo- and thermoperiodic conditions 12 h 33°C: 12 h 23°C, 12:12 h LD, 60–70% RH (with synchronous photo- and thermoperiods). In these conditions, a high percentage of sexually active adults emerged from the seeds (Lenga et al. 1991; Lenga and Huignard 1992). The developmental time of the adults varied between 28 and 35 days.

Rearing of the parasitoids

The two parasitoid species were raised in the same climatic conditions as their hosts. The females were placed for 24 h in the presence of *V. unguiculata* seeds containing *B. atrolineatus* larvae (L3 or L4) or pupae. These stages are preferentially chosen by the laying females of both species. *E. vuilleti* researches the chorion of the *B. atrolineatus* egg, marking the entry of the larval gallery, and inserts its ovipositor. The females lay an egg 0.75 mm long prolonged by a pedicel on the host tegument (Terrasse 1986). *D. basalis*, which has a shorter and more rigid ovipositor, is unable to use this method. The female bores the seed coat and the cotyledon with its ovipositor and lays a more oblong egg without a pedicel on the host (Gomez-Alvarez 1980).

In our experiments the mean developmental time of *E. vuilleti* was 24 days and for *D. basalis* 16–17 days. The adults were sexed and isolated for the 12 h following their emergence, when they were used either for breeding or for experiments. In order to avoid the phenomenon of multiparasitism during rearing, the two parasitoid species were raised in different climate chambers.

Experimental conditions

All experiments were carried out under the same climatic conditions as those used for the rearing of the bruchids and their parasitoids. The *D. basalis* and *E. vuilleti* adults (♂ and ♀) were removed as soon as they emerged and placed for the first 3 days in the presence of the host. The females were inseminated and an oögenesis phase was induced (Terrasse and Rojas-Rousse 1986; Gomez-Alvarez 1980). After these 3 days the parasitoids were removed from the presence of hosts for 24 h and then placed in the presence of seeds containing the hosts. The introduction of the hosts always took place 5 h after the beginning of the photophase and the thermophase, when the reproductive activity of both species is maximal (L. Levêque, pers. comm.). One portion of the seeds was dampened as soon as the experiment was over and the larvae or pupae extracted to determine the number of hosts parasitised and eggs laid.

The other portion was placed in rearing conditions until the emergence of *B. atrolineatus*, *D. basalis* and *E. vuilleti* adults.

Different experimental situations were analysed: those with successive introductions of the two parasitoid species, and controls where only one of the two species was introduced.

Experiments with successive introductions of the two parasitoid species

Two types of batch were made up.

Batches Ev→Db. *E. vuilleti* was the first species introduced. Four batches were made up, and in each, ten *E. vuilleti* females were placed for only 3 h in the presence of seeds containing 20 potential hosts. Ten *D. basalis* females were then introduced after 3 h (Ev→Db 3 h), 24 h (Ev→Db 24 h), 3 days (Ev→Db 3 d), or 7 days (Ev→Db 7 d). In these four situations, the *D. basalis* females remained for 3 h in the presence of the hosts.

Batches Db→Ev. The same experimental method was used, but with *D. basalis* the first species introduced and *E. vuilleti* the second.

For each batch, there were five replications for the oviposition analysis and five for adult emergence. This number was lower in batches Ev→Db 7 d and Db→Ev 7 d.

Control treatment. In Db batches ten females were placed for 3 h in the presence of 20 potential hosts. In Ev batches, ten females were introduced in the same conditions in the presence of the hosts. There were two replications per batch for analysis of parasitoid fecundity and five for the study of adult emergence.

To ensure reliable statistical analysis of egg-laying during successive introductions, eggs laid by the second parasitoid species introduced (e.g. *D. basalis*) were compared with those laid in the control treatment. The eggs of the first introduced species in the batches Db→Ev or Ev→Db laid on the host were also added in the control batches. There were thus 21 replications for the Db batches and 19 for the Ev batches.

Parameters studied. The following parameters were determined: the rate of parasitism, i.e. the percentage of hosts receiving eggs, the rate of multiparasitism, i.e. the percentage of hosts parasitised by one species and receiving the eggs of the second species, and the average number of eggs per batch for each species.

For each replicate of the batches Db→Ev or Ev→Db the fraction of hosts parasitised by *D. basalis* (p) and by *E. vuilleti* (q) was calculated. If the second species introduced distributes its eggs randomly, then the theoretical number of multiparasitised hosts will be $p \times q \times n$, where n is the total number of available hosts (Van Alebeek 1991). A χ^2 test was used for comparison of the theoretical and observed values.

The rate of emergence of adults compared with that of total insects (hosts and parasitoids) was estimated for each batch.

Results

Egg-laying by the two species with or without multiparasitism

Control treatment. *D. basalis* females parasitised 76% of the hosts and the mean number of eggs per batch was 32.3. *E. vuilleti* females only parasitised 43.2% of the available hosts and the average number of eggs per batch was 15.2.

Batches Ev→Db. When the *D. basalis* females were introduced 3 h after those of *E. vuilleti*, the rate of parasitism and the mean number of eggs per batch were no different from those found for the control treatment Db. When the females were introduced 24 h, 3 days and 7 days later, these values were significantly lower (Tables 1 and 2).

Table 1. Analysis of the number of hosts parasitised by *Dinarmus basalis* in the control treatment or in the batches Ev→Db

Treatment	Db control	Ev→Db			
		3 h	24 h	3 days	7 days
No. of replicates	21	5	5	5	3
No. of hosts	347	88	82	79	51
No. of parasitised hosts	265	64	45	37	18
χ^2 (Ev→Db/Db)	–	0.5 NS	15.2*	27.2*	36.5*
No. of hosts multiparasitised by <i>D. basalis</i>	–	23	10	6	0
Theoretical number of multi-parasitised hosts	–	29.4	13.5	16.2	7.8
χ^2 values (comparison between theoretical and experimental values)	–	1.3 NS	0.7 NS	9.8*	7.1*

* $P \leq 0.05$, χ^2 , 1 df; NS, not significant

Table 2. Mean number of eggs oviposited on the hosts by *D. basalis* (in the control treatment or in the batches Ev→Db)

Treatment	Db control	Ev→Db			
		3 h	24 h	3 days	7 days
No. of replicates	12	5	5	5	3
Mean number of eggs per replicate	32.3	35.2	20.8	19	14.7
<i>U</i>	–	22 NS	9*	7*	–

* $P \leq 0.05$, Mann-Whitney *U*-test; NS, not significant

When Db females were introduced after 3 h or 24 h the number of multiparasitised hosts did not differ from the theoretical number, suggesting a random distribution of the *D. basalis* eggs. The difference was significant in batches Ev→Db 3 d and Ev→Db 7 d, suggesting a non-random distribution of the *D. basalis* egg. When the interval separating the two introductions was greater than 24 h the rate of multiparasitism diminished. In the batch Ev→Db 7 d, the *D. basalis* females no longer multiparasitised the hosts.

Batches Db→Ev. When *E. vuilleti* was introduced 3 h, 24 h, 3 days or 7 days after *D. basalis*, the parasitism rates were significantly higher than those obtained for the control treatment Ev. In the four batches the mean

number of eggs laid on the hosts were not significantly different (Mann-Whitney *U*-test). Many hosts already parasitised by *D. basalis* were multiparasitised by *E. vuilleti* and their number was not significantly different from the theoretical number. The *E. vuilleti* females did not avoid the hosts parasitised by *D. basalis* and distributed their eggs on the different available hosts (Tables 3 and 4).

The presence of *D. basalis* oviposition shafts could facilitate the detection of the host by *E. vuilleti* females and their subsequent oviposition. (Van Alebeek 1991). One of the behavioural characteristics of *E. vuilleti*, the spinning of a silk web after egg-laying, above the ovipositor penetration orifice, allowed the verification of this hypothesis. In the Ev batch, 82% of the silk cocoons were in the same place as the *B. atrolineatus* egg chorions, the females in this case having used the larval galleries during oviposition. In contrast, when there was multiparasitism, over 80% of the webbing was on the windows presumably over the drilling hole made by *D. basalis*.

When the *E. vuilleti* female was in the presence of a host carrying the eggs or larvae of *D. basalis* two types of behaviour were observed:

1. **Ovicide.** Of the *D. basalis* eggs found on the hosts in the Db→Ev 3 h batch 31% and 41.3% in the Db→Ev 24 h batch, were dead and most showed punctures. It was possible for several eggs to be punctured on the same host and for the same egg to show signs of several punctures. This suggests that the punctures were not accidental and

Table 3. Analysis of the number of hosts parasitised by *Eupelmus vuilleti* in the control treatment and in the batches Db→Ev

Treatment	Ev control	Db→Ev			
		3 h	24 h	3 days	7 days
No. of replicates	19	5	5	5	5
No. of hosts	326	78	84	82	80
No. of parasitised hosts	141	35	61	45	52
χ^2 Db→Ev/Ev	–	18.7*	23.1*	3.5*	12.2*
No. of hosts multiparasitised by <i>E. vuilleti</i>	–	44	50	40	40
Theoretical number of multi-parasitised hosts	–	42.6	45.7	35.4	39.4
χ^2 values (comparison between theoretical and experimental values)	–	0.1 NS	0.3 NS	1.7 NS	0.02 NS

* $P \leq 0.05$, χ^2 , 1 df; NS, not significant

Table 4. Mean number of eggs laid by *E. vuilleti* on the hosts in the control treatment or in the batches Db→Ev

Treatment	Ev control	Db→Ev			
		3 h	24 h	3 days	7 days
No. of replicates	12	5	5	5	4
Mean number of eggs per replicate	15.2±5.3	22±3.9	23.2±8.8	15.8±3	22±4.5
U-test	-	19 NS	14 NS	26 NS	66 NS

NS, all values not significant at $P \leq 0.05$, Mann-Whitney *U*-test

were probably due to perforation of the chorion by the *E. vuilleti* ovipositor. The punctured eggs were dead, probably through injury (only 13.5% of eggs did not develop in the control treatment Db).

2. *Larvicide*. When the host was carrying *D. basalis* larvae the *E. vuilleti* females punctured the larvae with their ovipositor. In the final stages of development, the *D. basalis* larvae had consumed all of their hosts. The *E. vuilleti* females thus laid on the larvae or nymphs of *D. basalis*, developing as hyperparasitoids and giving rise to smaller progeny.

Consequences of multiparasitism for the survival of the two parasitoid species

Batches Ev→Db. The rate of *D. basalis* adult emergences in all the batches was significantly lower than that found in control treatment Db. This decrease in the number of emerging adults was due to a reduction of the parasitism rate in the presence of hosts parasitised by *E. vuilleti* (as

shown by the previous study of egg-laying) and to the low chances of survival of its larvae on the multiparasitised hosts. Observations carried out on hosts extracted from the seeds showed that the highly mobile *E. vuilleti* larvae can, with their powerful mandibles, bite the eggs or larvae of *D. basalis* and kill them. The introduction of *D. basalis* did not seem to alter the survival of *E. vuilleti* because the rate of emergences was not significantly different from that found in the control treatment Ev (Tables 5 and 6).

Batches Db→Ev. Although *D. basalis* was the first species introduced, the rate of adult emergences was significantly lower than in the control treatment Db, regardless of batch, owing to several factors. The *E. vuilleti* females did not avoid hosts already parasitised by *D. basalis* and the multiparasitism rate was higher. During oviposition, ovicide and larvicide by *E. vuilleti* females caused considerable mortality of the eggs or larvae of *D. basalis*. The *E. vuilleti* larvae attacked and killed *D. basalis* larvae, completing the killer action of the *E. vuilleti* females. The reverse situation was not observed under our conditions of study.

Table 5. Analysis of the number of adults emerging from the seeds (*Bruchidius atrolineatus*, *E. vuilleti*, *D. basalis*) and the rates of *E. vuilleti* emergences in the different treatments

	Ev control	Ev→Db			Db→Ev			
		3 h	24 h	3 days	3 h	24 h	3 days	7 days
No. of emerging adults (Ba + Ev + Db)	81	73	75	62	65	73	73	37
No. of <i>E. vuilleti</i>	31	24	29	24	37	33	33	23
<i>E. vuilleti</i> emergence rates	0.38	0.32	0.38	0.38	0.56	0.45	0.45	0.62
χ^2 values		0.409 NS	0.002 NS	0.002 NS	5.04*	0.76 NS	0.76 NS	5.8*

* $P \leq 0.05$, χ^2 , 1 *df*; NS, not significant

Table 6. Analysis of the number of adults emerging from the seeds (*B. atrolineatus*, *E. vuilleti*, *D. basalis*) and the rates of *D. basalis* emergences in the different treatments

	Db control	Ev→Db			Db→Ev			
		3 h	24 h	3 days	3 h	24 h	3 days	7 days
No. of emerging adults (Ba + Db + Ev)	74	73	75	62	65	73	73	37
No. of <i>D. basalis</i>	60	35	37	34	18	30	29	8
<i>D. basalis</i> emergence rates	0.81	0.47	0.49	0.54	0.27	0.49	0.39	0.21
χ^2 values		17.65*	16.5*	10.9*	40*	24.75*	26.3*	36.75*

* $P \leq 0.05$, χ^2 , 1 *df*

The rate of *E. vuilleti* adult emergences was higher in batches Db→Ev 7 d than in the control treatment Ev. There was no significant difference in Db→Ev 24 h, and Db→Ev 3 d. The consequences of the increase in the parasitism rate during oviposition on adult emergences were found in only two batches. An increase in mortality during *E. vuilleti* larval development could be due to superparasitism and/or to interspecific competition with *D. basalis*.

Discussion

The experiments carried out in this study, in which the two parasitoid species were successively placed in the presence of the same host, confirm and complement the results of Van Alebeek (1991) and Van Alebeek et al. (1992). In interspecific competition *D. basalis* and *E. vuilleti* have different strategies for host exploitation. The females of the second species introduced are in the presence of parasitised hosts carrying the eggs or larvae of the other species. Analysis of egg-laying shows that *D. basalis* females avoid hosts parasitised by *E. vuilleti*. This behaviour is more marked in the presence of the later developmental stages of *E. vuilleti*. The cues allowing the recognition of hosts already parasitised by *E. vuilleti* and influencing the behaviour of *D. basalis* are not yet known. The ability of a wasp to recognise a host parasitised by different species has been reported by Wylie (1970, 1971), Chow and Mackauer (1986), Vet et al. (1984). Oviposition restraints have been observed in multiparasitism situation and the influence of physical or chemical markers was suggested (Arthur et al. 1964; Spradbery 1968; Read et al. 1970; Richerson and Borden 1972; Mc Brien and Mackauer 1991). So, the rejection of heterospecific parasitised pea aphids by *Aphidius smithi* could involve two mechanisms, external cues as well internal cues that required ovipositor probing (Chow and Mackauer 1986; Mc Brien and Mackauer 1991). Physiological or behavioural changes of the host associated with parasitism may be also implicated in multiparasitism (Mc Brien and Mackauer 1991).

Our experimental studies suggested that females of *D. basalis* were sensitive to all or part of the range of stimuli for detecting the larvae already parasitised by the other species. *E. vuilleti* females do not avoid multiparasitism and the presence of hosts parasitised by *D. basalis* increases the parasitism. This could be the result of opportunistic behaviour by *E. vuilleti* in using the drilling holes of *D. basalis* to gain access to the host. Ovicide and larvicide show recognition of the presence of the competitor. Such behaviour is quite rare in interspecific competition situations (Van Alebeek 1991), although it has been observed in an ichneumonid, *Pleolophus indistinctus* (Price 1970, 1971).

The strategies of the two species seem to be consistent with their respective competitive aptitudes. *D. basalis* eggs or larvae in a multiparasitism situation have a low probability of survival and the females react appropriately by avoiding hosts already parasitised by *E. vuilleti*. In contrast the aggressive behaviour of *E. vuilleti* females and

larvae, and their ability to develop as hyperparasitoids, give them a strong probability of survival in interspecific competition. There seems to be no necessity for the avoidance of multiparasitism by *E. vuilleti*.

According to Van Alphen and Visser (1990), multiparasitism is common in nature, but heterospecific discrimination is frequently observed when the two species are very close. Experiments of Rosen and De Bach (1979) on *Aphytis* sp., Vet et al. (1984) on *Asobara* sp. and Mc Brien and Mackauer (1990, 1991) on *Aphidius* sp. confirm this. The heterospecific discrimination between species *E. vuilleti* and *D. basalis* could be the result of a long coevolution between these two sympatric species exploiting the same host under natural conditions. Interspecific competition acts as powerful natural selection for modelling the parasitoid strategies.

Bakker et al. (1985) suggest that for sympatric parasitoid species exploiting the same resources, multiparasitism is the best strategy when the hosts are scarce and parasitoid females are not egg-limited. In cowpea storage systems, the availability of hosts is always important and the multiparasitism was observed regardless of the density of the available hosts.

The behavioural characteristics of *E. vuilleti* enable it to dominate over *D. basalis*, whose abilities to control bruchid populations are better (Dupont et al., in prep.). During storage multiparasitism by *E. vuilleti* reduces the density of *D. basalis*. However, *E. vuilleti* alone cannot control the bruchid population and the simultaneous presence of the two parasitoid species limits the efficiency of the biological control.

Rabb et al. (1976) noted that few studies have dealt with interactions between parasitoids in the presence of the same host, yet these are often significant and must be taken into account in the development of biological control methods.

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