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AN ANALYSIS OF THE FATE OF EGGS OF *GRATIANA SPADICEA* (KLUG, 1829) (COLEOPTERA: CHRYSOMELIDAE: CASSIDINAE) IN RELATION TO THE POSITION IN THE OOTHECA[1]

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ABSTRACT

Randomly sampled oothecae of a natural population of Gratiana spadicea *from the outskirts of Porto Alegre, RS, were dissected. The overlapping of the egg membranes makes possible to enumerate the eggs in a batch and therefore to relate mortality to position in the ootheca. The ootheca of this cassid provides a spatial refuge for some of its eggs. Successful eggs of* G. spadicea *amounted to less than one fifth of the total in each batch. Parasitoids and predators were responsible for a high mortality of eggs whatever the size of the ootheca. The main cause of mortality was the eulophid wasp* Emersonella ooecia *De Santis, 1983. A large proportion of eggs were sucked dry by the mirid* Tupiocoris cincticornis *(Stal, 1860). The sucked eggs could have contained either the embryo of* G. spadicea *or the parasitoid in the pre-emergence stages.*

INTRODUCTION

The addition of membranes and of faecal material to eggs deposited externally on plants readily suggests an extra protection for the offspring. The egg cases of the cassids are regarded as elaborate devices for the protection of the eggs against predators, parasitoids and desiccation. As early as the begining of the century Muir & Sharp (1904) and Kershaw & Muir (1907) questioned the effectiveness of the oothecae of the cassids against natural enemies. Parasitization of eggs protected either in simple or in complex oothecae have been reported by various authors (Muir &

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Sharp, 1904; Kershaw & Muir, 1907; Chittenden, 1924; Rolston et alii, 1965; Kosior, 1975; Frieiro-Costa, 1984).

Gratiana spadicea (Klug, 1829) secretes a rather complex ootheca. The ootheca consists of a compact package of piled up eggs, each egg enclosed by a double membrane (Frers, 1925); Mata & Aravena, 1926; Freire, 1982; Frieiro — Costa, 1984). The average number of eggs per ootheca in a natural population is around 10, the numbers ranging from a single egg to as many as 21 (Freire, 1982; Frieiro-Costa, 1984). The architecture of the ootheca of *G. spadicea* suggests that some of the eggs are particularly protected from the attack of natural enemies. The aim of this paper was to relate the fate of the egg to its position in the ootheca.

MATERIALS AND METHODS

Oothecae were obtained from a ramdomly sampled natural population of *Gratiana spadicea* (Klug, 1829). Field work was carried out from February to April 1980 in the outskirts of Porto Alegre, RS, 30° 01' S and 51° 13' W, 15 km from the city center, in the area known as "Morro Santana" (Santana Hill). Every third day 450 leaves of *Solanum sisymbriifolium* L. were sampled. Oothecae present were brought to the laboratory for examination. Those oothecae with live contents were studied under a binocular microscope. The content of each egg was assessed by dissection. The ootheca was positioned with the upper side facing the dissection tin so that the first egg oviposited was also the first egg to be dissected.

At each occasion 10 fresh oothecae were incubated under controlled laboratory conditions (25± 1°C, 75± 5% RH, 14 hours/day of illumination). Parasitoids emerged were preserved for identification.

Oothecae from laboratory cultures were confined with the suspected predator obtained from field samples. Following exposition to the predator the oothecae were examined under the binocular microscope.

RESULTS

Gratiana spadicea (Klug, 1829) attaches one end of the ootheca to the food plant by means of a foamy base. To this foamy base are attached the proximal parts of the egg membranes. Each egg is enveloped by two large membranes. The upper membrane is nearly twice as long as the enclosed egg and has a slight thickening longitudinally; the lower one is a long as the egg. The distal border of the lower membrane adheres to the sagital plan of the egg while the lateral margins adhere to the under surface of the upper membrane. The first egg oviposited occupies a central position. The second and third eggs are laid either side of the first; the fourth egg occupies again a central position and so forth. This arrangement determines that the membranes of successive eggs overlap. The overlapping of adjacent membranes makes possible to enumerate the eggs. Thus the sequence of oviposition can be known and eggs can be given numbers from the first to the last oviposited in a batch.

Figure 1 illustrates the relative position of the membranes of two consecutive eggs. Figure 2 illustrates the ootheca of *G. spadicea* in ventral aspect.

The arrangement of eggs and respective membranes is such that a complete ootheca is a slightly convex structure, its sides covered by the outer borders of the membranes of the last eggs deposited. A small amount for faecal material is deposited on top of the ootheca. The larva leaves the egg via the ecclosion line along the sagital plan of the egg at its distal third.

A total of 426 oothecae consisting of a little as 3 eggs to as many as 17 eggs per ootheca was studied; 3,970 eggs were dissected. The contents of the eggs were identified as follows: uninjured eggs, containing the embryo of *G. spadicea* or evidence that the larva had hatched; parasitized eggs, containing the parasitoid either in the larval or pupal stage or as an adult just prior to emergence; eggs predated, whose contents had been fully sucked up; dead eggs, nondescript contents.

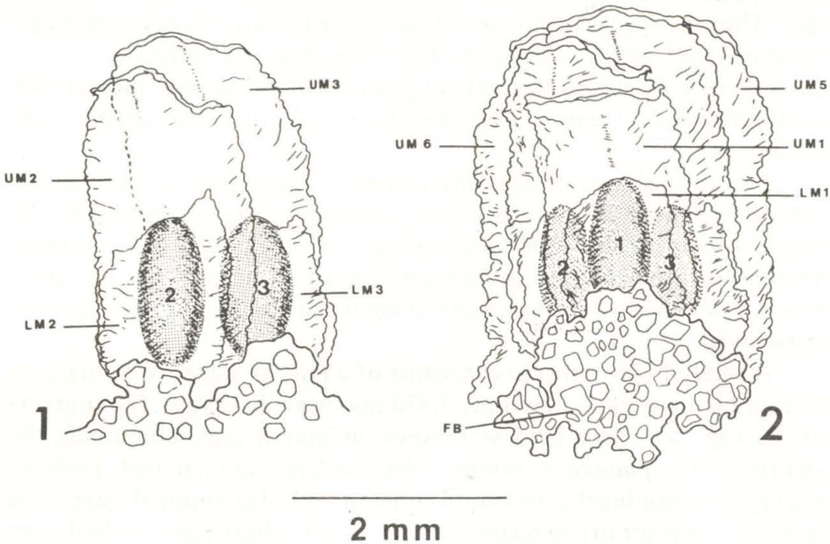
Figure 3 illustrates the relative frequencies of the four categories of egg contents according to the egg's position in 15 sizes of oothecae. Figure 4 illustrates the relative frequencies of the four categories of egg contents of the total eggs of 15 sizes of oothecae.

The four categories into which eggs were identified were found from the first to the last egg oviposited in a batch. The relative frequency of a given category varied according to the position of the egg and to the total number of eggs in a batch.

Irrespective of the number of eggs per ootheca uninjured eggs represented a small fraction of the total, never attaining 20% (fig. 4). Uninjured eggs were less frequently found among those occupying a top most position (fig. 3).

Eggs containing a parasitoid were more frquent among the first half of the eggs oviposited in a batch. The last eggs oviposited in a batch were generally devoid of yolk or any other content (fig. 3). Eggs containing the parasitoid accounted for higher proportions of the total in large oothecae (11 eggs or more) (fig. 4).

Fully sucked up eggs were particularly frequent among the three last eggs oviposited, the frequency decreasing progressively towards the first egg oviposited (fig. 3). They accounted for a high proportion of the total in very small oothecae (3 to 5 eggs) where the three rather exposed, uppermost eggs represent either the total or the majority of eggs present in the batch (figs. 3 and 4). Fully sucked up eggs represented at least 40% of the total in small to medium sized oothecae (up to 10 eggs/ootheca). Their frequency decreased in larger oothecae though they always accounted for more than 30% of the total (fig. 4).



Ootheca of *Gratiana spadicea:* Fig. 1 — Second and third eggs showing the arrangement of the egg membranes. Fig. 2 — Ventral aspect of an ootheca containing 7 eggs. (FB = foamy base; LM = lower membrane; UM = upper membrane; 1, 2, 3, 4, 5, 6 = relative to first, second, third, fourth, fifth and sixth egg in the batch, respectively).

The proportion of dead eggs with nondescript contents ranged from 6.4% (oothecae with 14 eggs) up to 23.2% (oothecae with 4 eggs) (fig. 4). The causes of mortality of such eggs remain unknown.

DISCUSSION

A single species of parasitoid was obtained from *G. spadicea* eggs, the eulophid *Emersonella ooecia* De Santis, 1983. Only one parasitoid occurs per host egg. References on either egg parasitoids of species of the genus *Gratiana* Spaeth, 1913 or of hosts of the genus *Emersonella* Girault, 1916 are scanty. *E. ooecia* was described by De Santis (1983) based on specimens bred out in this experiment. Frieiro-Costa (1984) provides the first record of egg parasitism for a neotropical species of the genus *Gratiana*. Rolston et alii (1965) refer to an undescribed eulophid, *Tetrastichus* sp., parasitizing eggs of *Gratiana pallidula* (Boheman, 1854) in Arkansas, USA. According to Boucek (1977) and De Santis (1983) the species of the genus *Emersonella* are confined to the Americas and develop as parasites in eggs of chrysomelid beetles. There are no references in Costa Lima (1962), Silva et alii (1968) and De Santis (1979, 1980) for species of this genus in Brazil. The only references for a species of *Emersonella* in Brazil besids that of Frieiro — Costa (1984) are in Carroll (1977, 1978) where *E. niveipes* Girault, 1917 is referred to as an egg parasite of

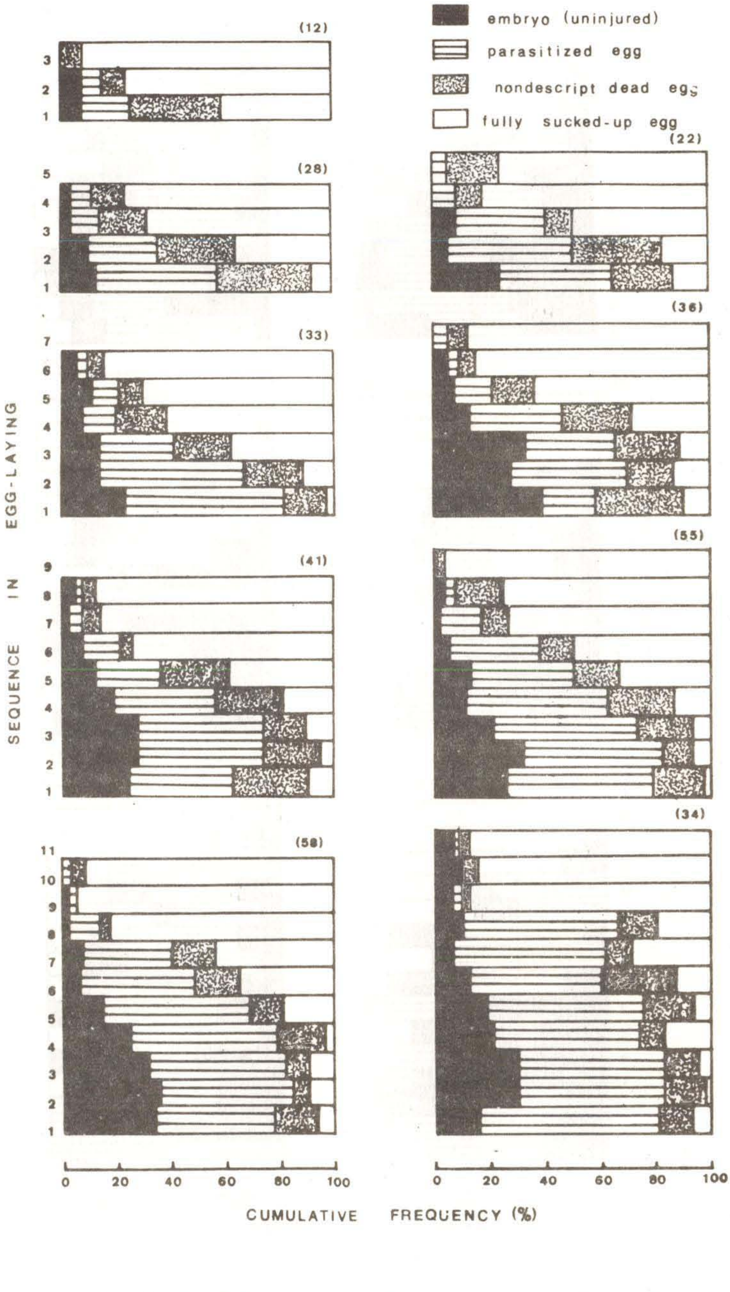


Fig. 3: Relative frequencies of four categories of egg contents according to the egg's positions in 15 sizes of oothecae of *Gratiana spadicea* (number of oothecae dissected in brackets) (Morro Santana, Porto Alegre, February-April, 1980).

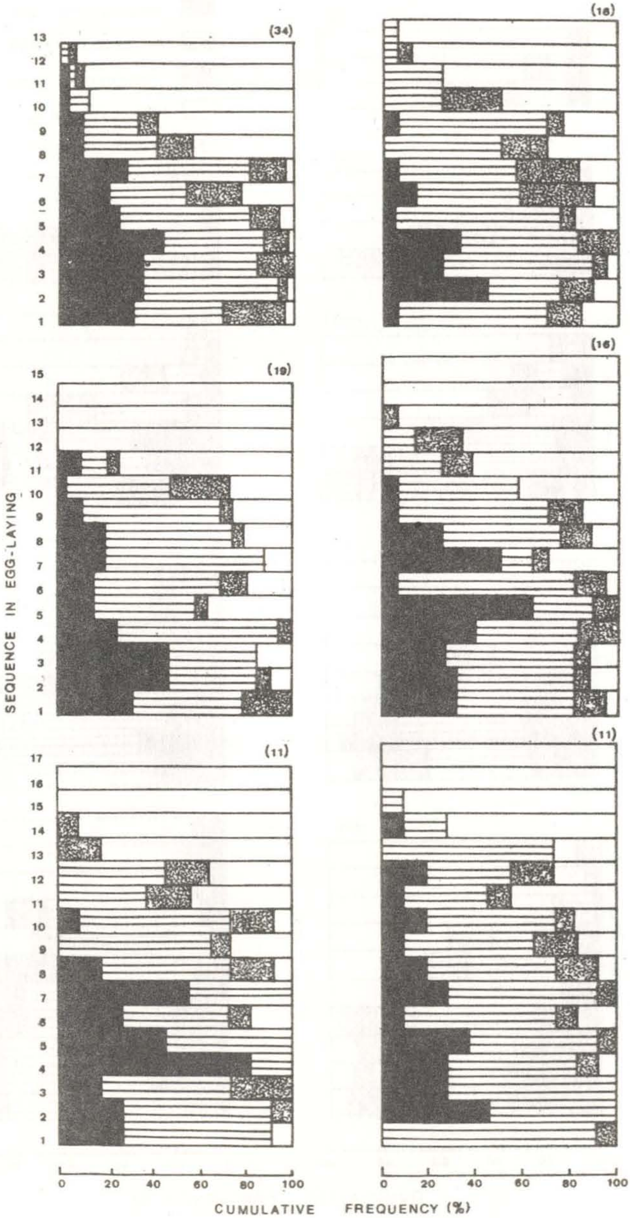


Fig. 3: Continued.

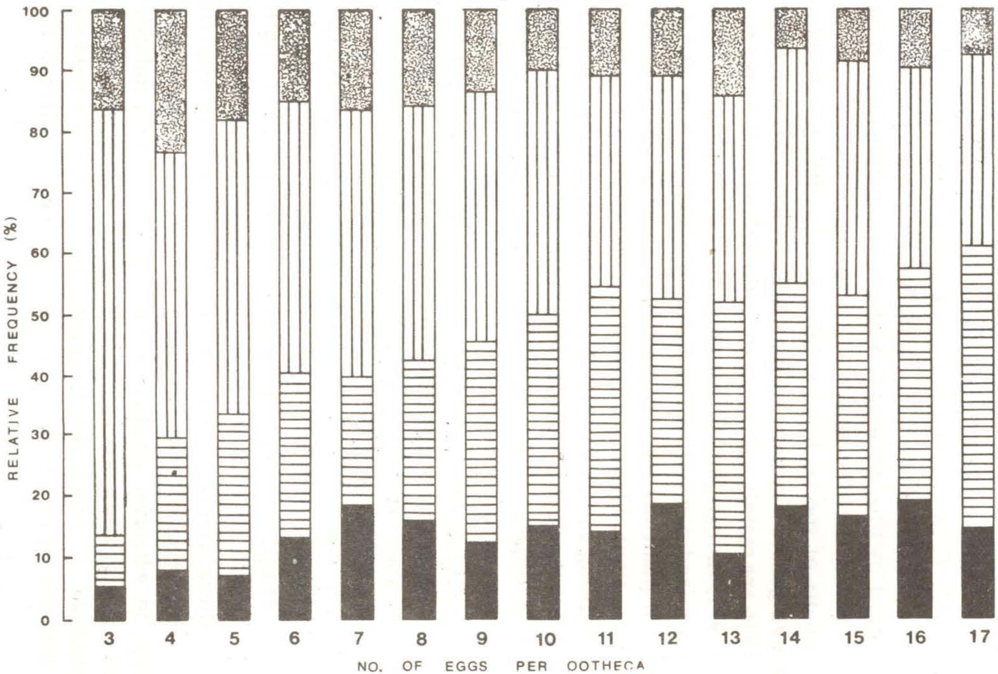


Fig. 4: Relative frequencies of four categories of egg contents of the total eggs of 15 sizes of oothecae of *Gratiana spadicea* (Morro Santana, Porto Alegre, February-April, 1980). (solid black = embryo of *G. spadicea* (uninjured); horizontal bars = parasitized eggs; vertical bars = fully sucked-up eggs; vermiculate = nondescript dead eggs).

the cassid *Stolas* sp. and they are included in De Santis (1981) supplement.

Laboratory tests confirmed the mirid *Tupiocoris cincticornis* (Stal, 1860) as the predator of *G. spadicea* eggs. This species was abundant on *S. sisymbriifolium* in the study area though the act of predation was never seen in the field. *T. cincticornis* is a rather small, delicate mirid species, only twice as long as an egg of *G. spadicea*. No trace of yolk is left in eggs fully sucked by this species and vestiges of the punctures of the stylets were not detected at the binocular microscope.

The host plants of species listed in Silva et alii (1968) for Brazil of the closely related genera *Tupiocoris* China & Carvalho, 1952 and *Engytatus* Reuter, 1876 are mainly cultivated and wild Solanaceae. As pointed out by Miller (1971) though the Miridae are mainly phytophagous, some species favour a mixed diet of plant and animal matter such as alternating the sucking of plant sap with the piercing of small insects associated with the same host plant. This is the case of *T. cincticornis*. Costa (1959) reports that its feeding causes damage to tobacco leaves in Bahia. Also, the same *Engytatus modestus* (Distant, 1893) referred to in Costa Lima (1940) as a pest of tobacco in Brazil is described by Rosewall & Smith (1930) as an efficient predator of eggs of *Heliothis* spp.

The ootheca of *G. spadicea* provides a spatial refuge in the sense of Hassell (1978) for some of its eggs. The effectiveness of a given position within the ootheca a a shelter from natural enemies differs if one considers the attack by a predator or by a parasitoid.

The eulophid *E. ooecia* is able to oviposit in all of *G. spadicea* eggs only whilst the ootheca is being laid. After oviposition is completed those eggs below the three upper ones are sheltered from the parasitoids, particularly the first, fourth, seventh and so forth, as derived from the architecture of the ootheca. Hence, *E. ooecia* needs to be on the spot when the eggs are laid to reach eggs otherwise in spatial refuges. The occurrence of parasitized eggs in whatever position within a given ootheca indicates that the act of parazitization takes place at the same occasion as oviposition by *G. spadicea*. *E. ooecia* was frequently observed in the field resting on the abdomen of *G. spadicea* females. These results suggest that *E. ooecia* overcomes the problem of spatial refuges by locating the female and waiting for the proper time to attack. A phoretic behaviour of a female wasp of the same genus is described by Carroll (1977, 1978) for *E. niveipes*, parasitoid of eggs of *Stolas* spp. Similar findings are reported by Muir & Sharp (1904) for the exensively parasitized eggs arranged in the very complex ootheca of *Aspidomorpha puncticosta*. According to Clausen (1976) phoresy among hymenopterous parasitoids of insect eggs is a much more common phenomenon than is indicated by the comparatively few instances that have been recorded. In Clausen's review of phoresy among entomophagous insects (1976) a single case of phoresy is registered for the Eulophidae. The case is that recorded by De Santis (1948) involving the entendontine *Grassator viator* De Santis, 1948, which is presumed to be parasitic in the eggs of the curculionid beetle *Naupactus xanthographus* (Germ.) in Argentina.

As discussed by Price (1975) the coevolutionary interactions between parasite and host are vital to the maintenance of both. Though *E. ooecia* is so efficient in locating females to cling to and in reaching eggs otherwise in spatial refuges, a none or all result of parasitization was seldon observed. In most of the parasitized oothecae a fraction of the total remained parasite-free, though, as determined by Frieiro-Costa (1984), 90% of the oothecae obtained in samples throughout the sampling period contained one or more parasitized eggs. Field and laboratory observations on the behaviour and biology of both host and parasitoid might provide an explanation for the mechanism preventing uninhibited exploitation once the host is located.

The frequency of fully sucked up eggs was found to be related to the degree of exposure of eggs in a batch. Those eggs at the top of the ootheca were more susceptible to predation by *T. cincticornis* than those towards the base of the ootheca. Accordingly, the last eggs oviposited in a batch were consistently devoid of yolk or any other content (fig. 3). The arrangement of the eggs and membranes provides a proportionate effect that tends to increase with the size of the ootheca. Thus, large oothecae (11 eggs or more) contain a smaller proportion of fully sucked up eggs because a higher proportion of eggs are sheltered from the predator (fig. 4).

Eggs could have been parasitized prior to the attack by the sucking predator. Accordingly, the data provided by dissections represent an underestimation of the actual level of parasitism. For an egg to result fully sucked up by *T. cincticornis* predation must have taken place at the earlier stages either of the embryo of *G. spadicea* or of the parasitoid otherwise discernible remains of cuticle would be left inside the egg shell. *T. cincticornis* was not only abundant throughout the sampling period but was also frequently in motion, moving swiftly over the host plant so that oothecae could have been located soon after deposition.

There are no evidences suggesting that there is any preferred prey age for predation. In case the egg contained either the parasitoid in later pre-emergence stages or *G. spadicea* in later embryonic development the probing itself or the partial sucking of the egg may have caused the death of the prey. At least part of the "dead eggs with nondescript contents" may be attributed to this cause of mortality.

These results, associated with those of Frieiro-Costa (1984) demonstrate that *E. ooecia* is a major mortality factor for *G. spadicea* in the egg stage. The present analysis suggest that the mirid *T. cincticornis* is not only an effective mortality factor for *G. spadicea* in the egg stage but also for *E. ooecia* in the pre-emergence stages.

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