How counter-attacking prey influence foraging and oviposition decisions of a predatory mite

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4 THE BENEFITS OF CLUSTERING EGGS: THE ROLE OF EGG PREDATION AND LARVAL CANNIBALISM IN A PREDATORY MITE

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Many arthropods produce clusters of eggs, but an unambiguous explanation for the evolution of egg clustering is still lacking. We test several hypotheses for the production of egg clusters by the predatory mite *Iphiseius degenerans*. This predator feeds on pollen, thrips larvae and nectar in flowers, but oviposits in clusters in tufts of leaf hairs (acarodomatia), where eggs run a lower risk of being killed by thrips, the prey of this predatory mite. The observed clustering is not caused by shortage of oviposition sites; females preferably oviposit in a domatium containing eggs rather than in an empty domatium. To explain this preference, we first examined the effect of egg clusters on the risk of cannibalism. We found that eggs are invulnerable to cannibalism, whereas larvae emerging from single eggs or from clusters were equally vulnerable. Subsequently, we considered the killing of eggs resulting from counter-attacks by prey, i.e. the western flower thrips. We found no indication that a cluster of eggs protects eggs from predation by thrips. However, when eggs were clustered in a domatium rather than scattered over domatia, the proportion of eggs killed by thrips was lower. Hence, oviposition in clusters has no effect on its own and oviposition in domatia reduces predation risk by thrips, but oviposition in clusters in domatia leads to a synergistic effect on survival of predator eggs. This synergism probably arises because eggs in clusters within tufts of leaf hairs are more difficult to reach by thrips. These experiments highlight a novel explanation of egg clustering, i.e. adaptation to counter-attacking prey. Moreover, they show that plant domatia protect predator eggs from predation.

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Oviposition in clusters is a common phenomenon in various insect taxa (Parker, 1965; Weseloh, 1972; Stamp, 1980; Ito et al., 1982; Chew & Robbins, 1984; Damman & Cappuccino, 1991; Stewart et al., 1991; McCauley, 1992; Agarwala & Dixon, 1993; le Masurier, 1994; Codyella & Raffa, 1995; Hunter, 1995; Clark & Faeth, 1997, 1998). Several terms have been used to describe this form of oviposition, such as egg clumping, egg pooling, aggregation of eggs or batches of eggs, but definitions regarding these terms are absent or ambiguous. In this paper, an egg cluster is defined as a group of eggs produced by one or more females, in which each egg touches the rest of the group through contact with at least one other egg.
There are three major groups of explanations for the evolution of egg-clustering. Some of these explanations are poorly supported by published data, while others are likely to be the consequence rather than the cause of such oviposition behaviour (Courtney, 1984). The first group centres around the direct effects on the ovipositing female: by reducing search for oviposition sites and laying many eggs together, the female saves energy, incurs a lower mortality risk during searching (by predation or adverse weather conditions), and/or reduces the risk of failing to find another oviposition site (Stamp, 1980). These explanations implicitly assume that moving from one oviposition site to another has associated costs and that selection therefore acts to minimise such movement.

The second group of explanations focuses on the benefits of clustering through effects on fitness of the larvae that hatch from the eggs. Larval survivorship and performance are thought to be enhanced by aggregation because of predator saturation (Lawrence, 1990), communal defence against predators and parasitoids (Labine, 1968; Tostowaryk, 1972; Stamp, 1980; Chew & Robins, 1984), an enhanced effect of warning coloration (Labine, 1968; Stamp, 1980), increased efficiency of thermo-regulation (Seymour, 1974; Porter, 1982), or increased efficiency of resource use (Young & Moffett, 1979; Tsubaki & Shiotsu, 1982; le Masurier, 1994; Clark & Feath, 1997). However, larval co-operation is likely to have evolved secondarily to egg clustering (Courtney, 1984).

The last group of hypotheses explains evolution of egg clustering through effects on the eggs. Clark & Faeth (1998) provide empirical evidence for the origin and maintenance of egg-clustering. They show that hatching success of eggs is positively related to relative humidity and hatching success is greater for larger clusters with eggs in multiple layers. Another effect of clustering on survival of the eggs is protection against predators. The association of distastefulness and aposematism of eggs with egg clustering has been proposed to account for the evolution and occurrence of egg clustering in some insects (Stamp, 1980; Agarwala & Dixon, 1993). Fisher (1999) considered kinship among gregarious individuals with distastefulness and warning coloration. He suggested that, after having fed on a distasteful egg, the nauseous predator would avoid feeding on nearby siblings of the prey and thus favour the evolution of aggregation with distastefulness and aposematism via kin selection. Thus, egg clustering is expected to have preceded the evolution of aposematic coloration rather than the reverse (Courtney, 1984). A last effect of clustering on egg survival is that egg clusters may protect eggs in the centre of the cluster from predation. Weseloh (1972) found that a smaller proportion of large egg masses of Gypsy moth was parasitised by Ooencyrtus kuwanai as compared to small egg masses.

In this paper, we study the predatory mite *Iphiseius degenerans* (Acari: Phytoseiidae). The female predatory mites alternate feeding in flowers and deposition of a single egg inside tufts of leaf hair (so-called domatia; Walter, 1996) on the underside of leaves of sweet pepper plants, where the eggs run a lower risk of being killed by counter-attacking prey, the western flower thrips *Frankliniella occidentalis* (Faraji et al. in prep.). After laying the egg, the female returns to a flower, where she feeds on pollen, thrips larvae and nectar (van Houten & van Stratum, 1995). By the time a new egg has developed, she returns to the leaf and oviposits in the same domatium. In this way, clusters of eggs are formed in leaf domatia. (F. Faraji, pers. obs.). In this system, the first group of hypotheses, i.e. direct advantage to the ovipositing female, cannot explain the evolution of egg clustering, because the female spends time and energy anyway when commuting between flowers and domatia before and after each oviposition event. In this paper, we show that clustering of eggs cannot be a by-product of scarcity of oviposition sites because females prefer occupied oviposition sites over empty
ones. Hence, we suspect that there are advantages of clustering with respect to the survival of eggs or the newly-emerged larvae (the second and third class of hypotheses).

Important mortality factors of larvae and eggs of the predatory mite are cannibalism and counter-attack by its prey. Western flower thrips are a prey of *L. degenerans*, but both adults and larvae of thrips are able to kill predator eggs, especially if eggs are laid outside domatia on leaves or in flowers (Faraji *et al.* in prep.). The mobile stages of *L. degenerans* cannibalise larvae but not eggs. If anything, cannibalism would select against clustering of eggs, as scattering the eggs reduces the risk of cannibalism among the emerging larvae. Killing of predator eggs by thrips may either favour egg clustering or not, depending on the conspicuousness of egg clusters relative to single eggs. Hence, two mortality factors, egg predation by thrips and cannibalism on larvae, are possibly involved in the occurrence of oviposition in clusters, and these are the factors under study in this article. Here we test (1) whether the eggs inside clusters are better protected against counter-attack by thrips and (2) whether cannibalism is reduced or increased when eggs are clustered and how this is affected by relatedness.

**MATERIALS AND METHODS**

**REARING**

Sweet pepper plants were grown from seeds in a greenhouse inside cages (100 x 60 x 100 cm) to prevent infestations.

Two strains of *L. degenerans*, one originating from Rabat, Morocco (M-strain) (van Houten *et al.*, 1995) and another from Givat Shmuel, Israel (I-strain) were reared separately on rectangular arenas (van Rijn & Tanigoshi, 1999) on a diet of birch pollen. Arenas consisted of a grey PVC sheet (30 x 21 cm) on a wet sponge in a water-containing tray. Paper tissues were wrapped over the edges of the arena, serving as a water source as well as a barrier. To provide more water, each arena was divided into four by three narrow filter paper strips (1 x 30 cm). Threads of sewing cotton (2 cm) were provided as an oviposition substrate.

The laboratory population of thrips was established on chrysanthemum in 1993 in our lab with individuals obtained from chrysanthemum from the Centre for Plant Breeding and Reproduction Research in Wageningen. Experiments were done either with adult thrips taken directly from this culture, or with second-instar larvae, obtained from eggs laid by adult thrips on sweet pepper leaf discs (30 mm diameter, put upside down on water-saturated cotton wool). Newly emerged larvae were transferred from this leaf disc to fresh leaf discs, where they were allowed to develop into the second instar.

**EFFECT OF CLUSTER SIZE ON OVIPOSITION DECISIONS**

Leaf discs of sweet pepper (30 mm diameter) were prepared such that the midribs were in the middle of the discs and that each disc had two domatia of approximately equal size. Leaf discs were put upside down on water-saturated cotton wool. Clusters of 1, 2, 4, 8 or 16 eggs were placed in one randomly chosen domatium while the other domatium was left empty. The number of replicates per cluster size was 15–20. A diet of birch pollen was supplied in the centre of the discs and one predatory mite was released per disc. After 24h,
the number of eggs laid on the leaf disc was counted, and their position was recorded. Based on these data, females were categorised into 3 groups: (1) females that oviposited only in domatia with eggs; (2) females that laid eggs only in empty domatia; (3) females that laid eggs in both domatia. Under the null hypothesis, eggs were expected to be distributed randomly over the two domatia, resulting in equal probabilities of ovipositing in either of the two domatia. Using a binomial test, we compared the numbers of females that oviposited exclusively in either of the two domatia.

**EFFECT OF EGG-CLUSTERING AND DOMATIA ON CANNIBALISM**

This experiment was conducted to find out whether larvae are more vulnerable to cannibalism when emerging from scattered eggs than when emerging from clusters. Branches of sweet pepper with two full-size leaves were washed with tap water in order to remove possible pollen. The stems of the branches were placed individually in small jars with water. A ring of glue was put on the stem under the lower leaf to keep mite larvae on the branches. Twenty eggs (24-48h old, within 24 hours of hatching) were placed in a cluster in the fourth domatia of the upper or lower leaf of 6 branches. As a control, the same number of eggs was distributed over 10 domatia of both leaves of another 6 branches (10 eggs on each leaf and 2 eggs in each domatium). Each branch was placed in a tray with water-saturated cotton wool on the bottom. In this way, larvae that had emerged from the eggs and subsequently dropped from the leaves were trapped in the wet cotton wool and could be detected at the end of the experiment. After 24h, the branches and cotton wool were checked for larvae, and all missing larvae were assumed to be cannibalised.

In this experiment, cannibalism among larvae was low. This could be due to the interrelatedness of females coming from the same culture. We have found previously that *I. degenerans* does discriminate between eggs from its own strain and another strain (Faraji et al., 2000). Therefore, we performed another experiment, similar to the previous one, but with 5 deutonymphs from the same strain (M-strain) as that of the eggs added to each of 6 branches with clustered eggs and 6 branches with scattered eggs. As a control for the effect of kinship on cannibalism, we added 5 deutonymphs from the other strain (l-strain) to another set of 11 branches with clustered eggs and 11 branches with scattered eggs. The experiment was carried out similar to the previous one. In all three experiments, arcsine transformed fractions of cannibalised larvae from clustered eggs were compared with those from scattered eggs with a two-tailed t-test.

**EFFECT OF EGG-CLUSTERING ON PREDATION**

We tested whether clustering provides protection for the eggs inside the cluster. The experiment was conducted on sweet pepper leaf discs (30 mm diameter) without domatia, which were put upside down on water-saturated cotton wool. Twenty predator eggs (0-18h old, which would not hatch during the experiment) were put on the disc, either scattered over the leaf disc, or in one cluster. One adult thrips or second-instar thrips larva was released per leaf disc (the number of replicates is given in Fig. 3).

Females of *I. degenerans* also add eggs to a cluster of eggshells and most oviposition sites contain a mixture of eggs and eggshells (F. Faraji, pers. obs.). Therefore, we tested whether eggshells can provide any protection to the eggs. In the centre of a leaf disc (16 replicates), 5 eggs were placed inside a cluster of around 40 eggshells. As a control 5 clustered eggs were placed in the centre of another 16 leaf discs. On second-instar thrips larva was released per disc. In both experiments, the number of surviving eggs were counted
after 24h and arcsine transformed fractions of killed eggs in treatment and control were compared with a two-tailed t-test.

**Effect of egg-clustering and domatia on predation**

This experiment was conducted to study the effect of clusters of eggs in domatia on egg predation by thrips. The branches and the position of eggs in domatia were similar to those in the experiment on cannibalism (see above). Two thrips larvae were released on the stem between the two leaves. A total of 27 replicates were carried out, each consisting of one branch with eggs and thrips larvae. In another set of experiments (24 replicates), branches were kept in a Plexiglas container and two adult thrips were released per branch. The adult thrips were first collected in a small vial in a Petri dish. The vial was opened in the Plexiglas container and the adult thrips were free to search leaves and stems. The numbers of surviving eggs were counted after 24h. Arcsine transformed fractions of killed eggs from a cluster were compared to those of scattered eggs with a two-tailed t-test.

All the experiments were conducted in a climate room at 25°C, 60±5% RH, and LD 16:8h.

**RESULTS**

**Effect of cluster size on oviposition decisions**

When clusters of different size were offered to *L. degenerans* females, they showed an increasing tendency to oviposit in clusters with increasing cluster size (Fig. 1). Although the number of females that oviposited only in domatia with one egg was higher than those that oviposited in empty domatia, this preference was not significant. For all other cluster sizes, females had a significant preference to oviposit in domatia with eggs over empty domatia (Fig. 1). Part of the females did not show preference, but oviposited in both the empty and the egg-containing domatium. The fraction of females without preference did not seem to vary with cluster size for clusters up to 8 eggs, only with the largest cluster size (16 eggs) this fraction was 0 (Fig. 1).

**Effect of egg-clustering and domatia on cannibalism**

Cannibalism among larvae from scattered eggs did not differ significantly from cannibalism among larvae from clustered eggs (Fig. 2A), with cannibalism among larvae from clustered eggs being somewhat higher. The proportion of larvae cannibalised was higher when 5 deutonymphs from the same strain (M-strain) as the eggs were added, but the difference between scattered and clustered was again not significant (Fig. 2B). To reduce the effect of kinship from the previous experiment, instead of deutonymph from the M-strain, deutonymphs from another strain (I-strain) were released on branches. The difference in proportion cannibalism between clustered and scattered eggs was again not significant (Fig. 2C). Newly emerged larvae were often found in other domatia of the same leaf or even of other leaves, where they were not clustered. This further confirms that clustering of eggs can have no effect on survival of larvae. The observed dispersal suggests that cannibalism might be further reduced in branches and plants with larger numbers of leaves, where larvae can disperse even further away from the egg cluster.
EFFECT OF EGG-CLUSTERING ON PREDATION RISK

Eggs inside a cluster of eggs were not better protected against predation than scattered eggs when the eggs were placed outside a domatium. The mean proportion of eggs killed in a cluster was not significantly different from that of scattered eggs (Fig. 3).

Eggs inside clusters of eggshells did not gain much protection against predation by thrips larvae (Fig. 4). The mean proportion of eggs killed in a cluster that was placed in eggshells was lower, but not significantly different from that of a cluster of exposed eggs.

Figure 1. Oviposition behaviour of *Iphiseius degenerans* females on leaf discs with two domatia. Egg clusters of either 1, 2, 4, 8 or 16 eggs were placed in one of the leaf domatia. The right-hand bar graph shows the preference of females that oviposited only in one of the domatia. Bars extending to the right show the percentage of females that oviposited in the domatia with eggs. Bars extending to the left show the percentage of females that laid eggs in the empty domatia. Asterisks indicate the significance level of the binomial test against an expected proportion of 0.5 for either of the two domatia: *** P<0.001, ** P<0.01, * P<0.05; two-sided binomial test. The numbers outside and inside the parentheses refer to the number of females tested and the number of eggs produced, respectively. The left-hand bar graph shows percentage of females that oviposited in both domatia (no preference).
Figure 2. Mean proportion (with standard errors) of larvae cannibalised when 20 eggs of *Lphiseius degenerans* (M-strain) were either clumped in one domatium or scattered in 10 domatia. The treatments were: (A) cannibalism of newly-emerged larvae on each other; (B) cannibalism by 5 deutonymphs on newly-emerged larvae from the same strain (M-strain); (C) cannibalism by 5 deutonymphs from another strain (I) on newly-emerged larvae.

Figure 3. Mean proportion (with standard errors) of eggs killed by adult thrips and thrips larvae. Twenty eggs of *Lphiseius degenerans* were either clustered or scattered on leaf discs. Numbers inside bars refer to the number of replicates.
Figure 4. Mean proportion (with standard errors) of eggs killed by thrips larvae. Five clustered eggs of *Iphiseius degenerans* were either exposed or were placed inside 40 eggshells on leaf discs. Numbers inside bars refer to the number of replicates.

Figure 5. Mean proportion (with standard errors) of eggs killed by adult thrips and thrips larvae. Twenty eggs of *Iphiseius degenerans* were either clumped in one domatium or scattered in 10 domatia. Numbers inside bars refer to the number of replicates.
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EFFECT OF EGG-CLUSTERING AND DOMATIA ON PREDATION RISK

When adult thrips were offered a cluster or scattered eggs in domatia, the mean proportion of clustered eggs killed was almost half of that of scattered eggs (Fig. 5, two-sided t-test on arcsine transformed fractions of eggs, \( P=0.017 \)). Although thrips larvae also killed higher proportions of scattered eggs (8.89 vs. 7.23), the difference was not significant (Fig. 5, Arcsine transformed fractions of eggs, two-sided t-test, \( P=0.27 \)). The fraction of eggs killed inside domatia was much lower than outside domatia (cf. Figs. 3, 4 and 5).

The probability of a cluster to be found by adult thrips (i.e. when at least one egg was killed) was 0.37 for clusters (a cluster of 20 eggs in a domatium) and 0.26 for scattered eggs (2 eggs per domatium). This difference was not significant (\( \chi^2 \)-test, df = 1, \( P=0.08 \)). For thrips larvae however, the probability of clusters being found was significantly higher than that of scattered eggs (0.3 vs 0.13, \( \chi^2 \)-test, df = 1, \( P=0.02 \)).

DISCUSSION

In a previous paper, we showed that \( I. \ degenerans \) females refrain from ovipositing in flowers, where they feed, but produce clusters of eggs in domatia on leaves instead. We found that egg mortality inflicted by thrips was higher in flowers than in leaf domatia. In this paper, we investigate the selective advantage for ovipositing eggs in clusters inside domatia. We found that females prefer to add eggs to clusters inside domatia even when empty domatia are available, suggesting that egg-clustering is not caused by a shortage of oviposition sites. Contrary to most cases of egg-clustering in insects, where females produce one large cluster or a few batches of eggs at a time, this predatory mite contributes one egg at a time to a cluster, after which it returns to a flower for feeding. This implies that the predator has to invest extra time and/or energy to commute in between egg depositions, suggesting that there must be an advantage to ovipositing in clusters.

One such an advantage could be the avoidance of cannibalism among kin. By preferring to oviposit close to her own eggs, a female may benefit from a lower incidence of cannibalism among her offspring. Whereas cannibalism on eggs is rare in this predatory mite (F. Faraji pers. obs.), cannibalism on larvae by adults and nymphs occurs. However, our experiments show that the rates of cannibalism of larvae from clusters or scattered eggs by nymphs did not differ. This is because the larvae leave the cluster upon hatching and move to an unoccupied domatium on the same or a nearby leaf. Possibly, this behaviour of larvae is an adaptation to avoid cannibalism.

Another possible advantage for clustering eggs inside domatia would be a further reduction of predation by thrips, the prey of this predatory mite. Indeed, when clusters of eggs were positioned inside a domatium, the predation by adult thrips was substantially reduced, whereas predation by thrips larvae was also lower (but not significantly). However, clusters of eggs and clusters of eggshells outside domatia did not protect eggs within the clusters for predation by thrips, indicating that there is a synergistic effect of clustering and the use of domatia. This suggests that clustering of eggs inside domatia is an adaptation to egg predation.

One of the hypotheses to explain the evolution of egg-clustering is that the risk for an egg cluster to be discovered by a predator is lower than for scattered eggs. In our experiment, the probability of egg clusters being found by adult thrips was not significantly different from that of scattered eggs, but the proportion of scattered eggs killed was...
significantly higher. The probability of clusters of eggs being found by thrips larvae was significantly higher than for scattered eggs, while there was no significant difference between the proportions of eggs killed. This suggests that the risk of predation for an egg in a cluster in a domatium is lower than for eggs that are scattered over domatia.

Possibly, eggs inside clusters are protected from predation because the other eggs act as a shield against thrips. We observed that eggs were not consumed entirely, and the remaining contents of the eggs dried out, thereby forming a screen that could protect eggs positioned underneath. We observed that outside domatia, thrips could lift this shield and kill the eggs underneath. Tufts of hair in domatia, however, may make it impossible for the thrips to remove such shields.

It was observed that thrips larvae without prior experience with predator eggs withdrew immediately after piercing the first egg. They only returned to the egg after a while, and started feeding on the remains of the egg. In subsequent attacks, the thrips did not leave, but were sometimes seen to kill several eggs in a row, suggesting that experience with the predator eggs resulted in enhanced effectiveness. It is still unknown whether the thrips kill the predator eggs for feeding or just to eliminate predator offspring, thus protecting vulnerable thrips larvae.

The eggs that cover a cluster may run a higher risk of predation than eggs inside or under. This raises the question of what a female should do if she adds an egg to a cluster. Females that encounter a cluster spend some time to check all sides to find a suitable place for oviposition, such as space under or inside the cluster (F. Faraji, pers. obs.). If the only option is to put the egg on the surface of the cluster, the egg may run a higher risk of predation but protect eggs underneath. If these protected eggs are related to the ovipositing female, adding an egg to a cluster may increase the inclusive fitness of the female by protecting the eggs that she oviposited previously. Indeed, we have found that *I. degenerans* prefers to add eggs to own or closely related clusters rather than to unrelated clusters (Faraji *et al.*, 2000).

Another factor that may play an important role to reinforce egg clustering in this predatory mite is desiccation. *Iphiseius degenerans* originates from the Mediterranean area, with a dry climate. Although it is claimed that the domatia can protect eggs from low relative humidity (Grostal & O'Dowd, 1994), eggs in clusters may provide further protection against desiccation (Faraji *et al.*, 2000). This hypothesis demands further investigation.

Predation and desiccation are not mutually exclusive mortality factors, and the benefits for ovipositing in clusters in domatia may depend on both these factors. It is clear that the risk of egg predation by adult thrips is reduced in clusters of eggs inside domatia. Other things being equal, this explains the preference of females to produce such clusters. If oviposition in clusters would also reduce the risk of desiccation, this would only further increase the advantage of ovipositing in clusters. Clearly, both factors fall within the group of hypotheses that explain egg clustering through effects on egg survival.

In conclusion, adult female *I. degenerans* show complex oviposition behaviour, they commute between flowers, where they feed, and leaves where they oviposit in clusters in domatia. This complex behaviour is likely to be an adaptation to egg predation by various other arthropods, including its thrips prey. This suggests that the presence of domatia on a plant affects predator-prey dynamics by offering protection to the predator. It has often been suggested that domatia offer refuge to predatory and fungivorous mites (Grostal & O'Dowd, 1994; Turner & Pemberton, 1989; Walter & O'Dowd, 1992; O'Dowd & Pemberton, 1994, 1998; Walter, 1996; O'Dowd & Wilson, 1997; Agrawal, 1997), while some studies show that the presence of domatia indeed affects predator-herbivore and predator-fungivore
interactions on plants (Agrawal & Karban, 1997; Norton et al., 2000). Together with a previous paper (Faraji et al. in prep.), our study is the first to show the benefit for predatory mites of using domatia.

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