# Ecological Interpretation of Insect Aggregation

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## I Introduction

It is recognized that aggregation of individuals is commonly observed in many species of insect, i. e. from Apterygota to highly specialized order including social insect. The stage of aggregation varies among species, such as egg and larva, and sometimes a large size of aggregation is observed even in adult stage. Egg and larval aggregations, however, are more frequent than the other stages. The adaptation of aggregation to the biology and physiology and the process of aggregation formation should differ in each systematic group and also in the stage of metamorphosis.

As Allee (1931) had pointed out, larval aggregation is due in the first place to an egg mass of individual egg being laid together, however, the other factors are probably involved as well.

The factor on the formation of aggregation may be divided into two, environmental heterogeneity and the interaction of individuals. On the latter, it can be further divided into two categories, one is due to the mutual attraction between individuals and another is due to the eggs being laid together.

Both two kinds of aggregation, however, have quite different in their ecological characters.

Recently, Ishii and Kuwabara (1967) attempted to make clear the mechanism of aggregation of the cockroach from the physiological point of view and they found that the aggregation of the german cockroach, *Blattella germanica* is due to the substance excreted from a dermal gland. They called it "aggregation pheromone". As this case, the mechanism of aggregation is needed to be clear by the physiological analysis.

The present author has studied the egg and larval aggregations of several species from the ecological point of view and he found that the effect of aggregation of eggs is important in terms of the formation of larval aggregation which is followed by the hatching synchronism of eggs within an egg mass. When the hatching of eggs within an egg mass was well-synchronized, the degree of aggregation formation was high. On the other hand, if the synchronization of hatching was disturbed by such a factor as parasitization, establishment of aggregation was also disturbed. In the present paper, the ecological significance of insect aggregation in terms of its life being specific to the species and the operation of natural control of population will be discussed.

## II Definition of Aggregation and Aggregation Effect

Generally, we use the word "density" as a measure for the number of individuals in a given unit area. But, in the same number of individuals in a given unit area, the degree of aggregation of the individuals can be different. This component of aggregation should be recognized and measured, because the degree of aggregation affects the survival and other aspects of population dynamics. Therefore, the effect of population density may be different by the degree of aggregation, i.e. whether individuals distributes in clumped or sparse in that given unit area.

Most of the species living in aggregation should disperse more or less gradually as development advances and the ecological significance of aggregation must be analyzed during each different period of aggregation being different in each species. First of all, it is necessary to define the term "aggregation".

The author may be able to say that the aggregation is an unit of group of individuals combined functionally with each other, e, g. the larvae of the tea tussock moth, *Euproctis pseudoconspersa* and those of the rice stem borer, *Chilo suppressalis*, the newly hatched larvae from their egg mass are highly aggregated and they establish the feeding-sites. In the former species the larvae persist their aggregation strongly up to the final instar, while in the latter they disperse gradually as development advances, especially after the 3rd instar. In these two species, when aggregations are disturbed by certain factors, they die out soon or if they can survive, their developments are greatly protracted. These are the cases that the disturbance for aggregation brings about a disadvantage to their survivals. When individuals are close together living in aggregation and feeding in rythm, the survival rate and the velocity of development are favoured by the aggregation as compared with the isolated larva. The author will call it a typical aggregation, which brings about a positive effect on the component individuals and no negative effect by the overcrowding at all. Needless to say, size of the aggregation varies with hazards and if it becomes small sized one, the ill effect will occur up on the individuals. Therefore, its size is important to consider the ecological significance of aggregation in each species.

## III Aggregation Effect in relation to the Degree of Aggregation

Larval aggregation may be divided into following groups according to its persistence with advancing development and in addition to the effects on the survival rate and the development.

1) Strong tendency to form aggregation up to the final instar. When a larva is isolated, serious ill effect will occur in each component individual (For instance, the tea tussock moth, *Euproctis pseudoconspersa*).

2) Strong tendency to form aggregation up to the middle instar. When a larva is isolated, the survival rate becomes low and the development is greatly protracted (For instance, the rice stem borer, *Chilo suppressalis*).

3) Aggregation may disappear after the first instar. When a larva is isolated, ill effect is not so much on the survival rate as in the case of 1) or 2) and the development is slightly protracted (For instance, the large twenty eight spotted lady beetle, *Epilachna vigintioctomaculata*).

4) The eggs are laid sparsely. This is not an egg mass in strict sense as compared with the above three cases, however, the ecological and physiological characters are favoured by rearing in several individuals together. On the contrary, when they are isolated singly or extremely crowded together, the survival rate becomes low and the development is remarkably protracted (For instance, the white cabbage butterfly, *Pieris rapae crucivora*).

It had been observed that the white cabbage butterfly has a habit to lay her eggs separately in field but frequently she lays several eggs together. This kind of diversity in the habit of oviposition may be due to the environmental heterogeneity, namely her eggs is laid continuously on a well matured leaf and *vice varsa*.

Recently, Kobayashi (1960) examined the spatial distribution of the eggs in a cabbage farm and he suggested that frequency distribution of the eggs on a cabbage was clumped because the butterfly has a habit to lay several eggs together. But it is doubtful whether this clumping comes from one adult or not. The present author examined the effect of larval aggregation on the various ecological and physiological characters of this species and he found that the survival rate and development were favoured by aggregation of several larvae as compared with isolated or extremely aggregated condition. The optimal effect of aggregation occured at intermediate degree of aggregation and it is covered completely with a deleterious effect of crowding at large aggregation.

The case of 1) or 4) is not so frequently observed as compared with that of 2) or 3) and we have to deal with the case of 2) and 3). Arrangement of eggs in a mass between 2) and 3) is different in each species. In the former, the eggs in a mass are close contact with each other and result to form strong larval aggregation. On the contrary, in the latter, eggs are associated loosely with each other and larval aggregation is not so strong as the former. Therefore, it may be postulated that the degree of larval aggregation somewhat relates to the arrangement of eggs in a mass.

Moreover, synchronization of hatching of eggs should be an important factor to form the larval aggregation. When the hatching of eggs was well-synchronized, the larval aggregation was also well-established. On the other hand, when the synchronization was disturbed, formation of larval aggregation was not raised and it brought about low survival rate followed by small size of aggregation.

This synchronization of hatching was observed in several species and the effect of larval aggregation is discussed as well, for example, the tea tussock moth, *Euproctis pseudoconspersa* (Mizuta, unpublished), the rice stem borer, *Chilo suppressalis* (Morimoto and Sato, 1962), the southern green stink bug, *Nezara viridula* (Kiritani, 1964) and the cabbage stink bug, *Eurydema rugosum* (Morimoto, 1965).

The number of eggs within an egg mass varies in a species extremely with generation and locality and the large size of egg mass is disturbed by certain accident such as climate or attack of natural enemies. The large size of larval aggregation is due to large egg mass followed by well-synchronized hatching. Therefore, it should be said that a possible mechanism of the formation of larval aggregation may be established by means of silk trail spinned by themselves in the case of the Japanese giant silk moth, *Dictyoploca japonica* (Morimoto, 1967).

It is observed that many individuals of eggs or larvae are either close contact with or loosely associated with each other in a given area. In these cases, we should check the effect of aggregation, i. e. how strong the aggregation is or whether it can be called aggregation or not. This is the reason why it is important to check aggregation by means of its effect.

## IV Mechanism of the Effect of Aggregation

It is not so clear what mechanism is taking part in the effect of aggregation. The effect of aggregation can be classified into two, namely, environmental conditioning and mutual interaction of behaviour. In the former case, aggregation affects each individual with the modification of the environment, which is conditioned by the metabolic activity of the insect, while in the latter case effect of aggregation is induced by the mutual stimulation of each individual through sensory mechanism. These two modes have been also found in the effect of population density. According to Chauvin (1957), these two modes were termed as "l'effet de masse" and "l'effet de groupe", respectively.

Utida (1967) examined the effect of larval aggregation followed by collective oviposition of the Brazilian bean weevil, *Zabrotes subfasciatus* and he postulated the mechanism of its effect being due to environmental conditioning. But this is not so frequently observed and this kind of effect will disappear when the environment is suitable for the larval life. Thus, it may be understood that aggregation is an adaptive phenomenon, in a sense, to the unsuitable environmental condition.

On the other hand, it is common case of the aggregation which is established through the mutual interaction of behaviour of each individual. Behavioural interaction plays important part to form or to maintain larval aggregation and is indispensable for taking advantage of the existing incision even when the environmental conditions are suitable for them.

## V Significance of Aggregation on the Population Dynamics

### 1) Correspondence between the spatial and chronological distributions in the population dynamics of the species deposited their eggs in a mass.

Aggregation of insect as compared with random and uniform distributions is a major characteristic of natural population. In general, the individuals of the species which deposits the eggs in a mass aggregate strongly even in an uniform area. Kono (1953) made a census of larvae of the rice stem borer, *Chilo suppressalis* in a natural field and he obtained an interesting result that distribution of individuals is strongly clumped being responsible for an egg mass and it is not only in the younger instars but in the larvae dispersed after middle instar. He called this clump "basic unit of population derived from an egg mass". The clumped distribution in the field is due to the integration of this basic unit of population.

We may consider the correspondence between the spatial and chronological distributions in the population dynamics as shown in Fig. 1.

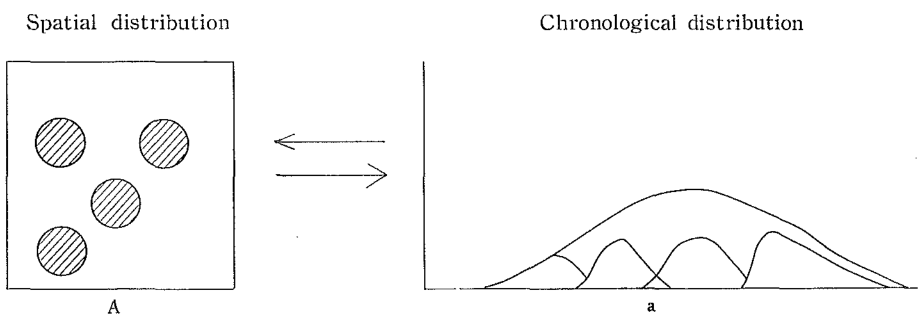


Fig. 1. Schematic representation as correspondence between the spatial and chronological distributions in the population dynamics of the species deposited their eggs in a mass.
Curve *a* shows emergence curve etc. (Morimoto, 1967)

It is considered that strongly clumped distribution as in $A$ may correspond to the curve $a$, which shows a chronological state of spatial distribution. In the spatial distibution of $A$, individuals in an aggregation is closely contact with each other and it makes them to increase mating chance. On the other hand, curve $a$ shows a possibility of adaptation to such environmental instability as various period of paddy planting and bud sprout. The aggregation has an adaptive value to prevent the elimination of population when the density becomes extremely low. The curve $a$ must be, of course, varies with adult longevity, voltinism, kinds of host plant, size of aggregation, ability of dispersion and other factors. Consequently, the aggregation plays an important role in population fluctuation.

It is possible to understand the significance of aggregation as the correspondence between $A$ and $a$, and it is suggested that the chronological state of spatial distribution as curve $a$ is more important rather than the spatial distribution itself in order to find out the mechanism of population fluctuation.

2) **The size of aggregation of eggs.**

The author examined the effect of aggregation on survival and development in several species and found that the larger the size of egg mass, the larger the larval aggregation was established by following well-synchronized hatching of eggs within an egg mass and consequently the larval survival became high. Waters (1959) also emphasized the influence of the aggregation on survival and other aspects of population dynamics and the various degree of aggregation brings about a bias in population process. Thus, the size of aggregation of eggs may be an important factor in population dynamics.

3) **Mortality pattern in the aggregation.**

The mortality factors do not act at random on the individuals within an aggregation, but on an aggregation itself as a whole. For instance, in the jack pine sawfly, *Neodiprion swainei*, its egg parasite was difficult to find out the small sized egg mass, which escaped from the parasite attack (Lyons, 1962).

The mortality factors that bring about a partial destruction of the member of aggregation such as egg parasites, predators and climatic factors may affect the mortality of the ensuing survivors. The author and other several workers made clear the effect of aggregation on survival in the several species, that is. the larger the aggregation, the higher the survival rate was brought about (e. g. Morimoto, 1960; Morimoto and Sato, 1962; Kiritani, 1964).

When the aggregation became small owing to a mortality factor, the higher mortality of ensuing survivors than expected merely from the mechanical death is brought about on the aggregation.

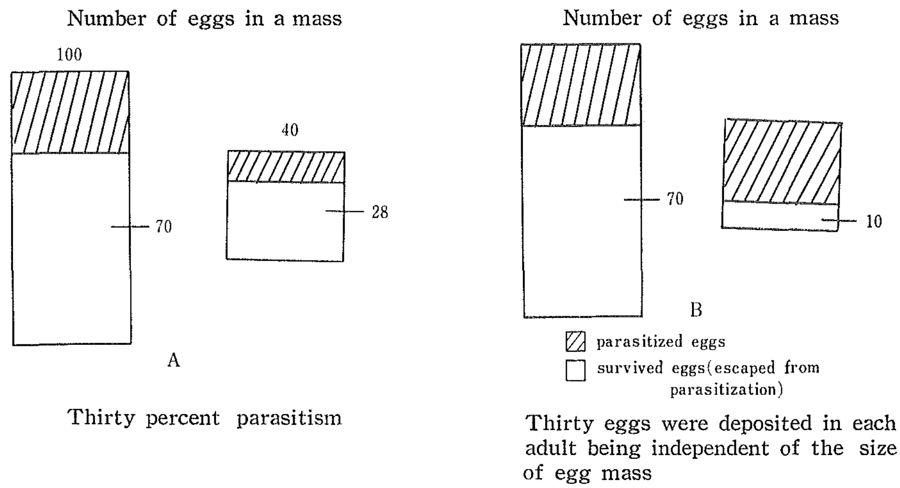


Fig. 2. Action of egg parasite on the egg mass.
A: The case of *Phanurus beneficiens*
B: The case of *Trichogramma japonicum*
(Morimoto, 1967)

This is shown in Fig. 2, which represents action of the parasites on the egg mass. Where, two kinds of egg parasites are used, that is *Phanurus beneficiens* and *Trichogramma japonicum* which inhabit in paddy field and commonly parasitize on the egg of the rice stem borer. In both parasites, the percentage of parasitized egg mass varied with the size of egg mass (Otake, 1955), and in the latter, the percentage of parasitized eggs in a mass varied with the size of egg mass accounting for her oviposition of 30 eggs in each parasite adult (Otake, 1960). Supposing 30% of individuals were attacked by *Phanurus beneficiens* on two sizes of egg mass, 100 and 40, the eggs survived are 70 and 28, respectively. On the other hand, 30 eggs were deposited by *Trichogramma japonicum* on the host being independent of the size of egg mass, 100 and 40, the eggs survived are 70 and 10, respectively. The small size of aggregation of 28 or 10 is disadvantagious for the survival of larvae hatched from it as compared with that in the size of 70, and individuals from it all die out. Mechanical death primarily caused by parasite, for instance, occurs on an aggregation and the secondary biotic factor acts on them. The higher mortality is brought about by the secondary biotic death in addition to the primary death.

Furthermore, the pattern of attack by parasite becomes important to hatching synchronism, that is whether parasite attacks the eggs singly or patchy in a mass. This secondary biotic death is due in the first place to not-synchronized hatching of the eggs in a mass. This is supported by the author's experiment that the larger the size of egg mass, the more synchronized hatching of eggs occured and the larval aggregation was smoothly established (Morimoto and Sato, 1962) and also supported by the experiment in a laboratory conditions that when the egg parasite, *Trichogramma japonicum* attacked on the eggs of the rice stem borer, the certain size of egg mass will be needed for the larvae to survive by following the well-synchronization of hatching (Morimoto, 1966).

Hokyo and Kiritani (1963) also suggested that the mortality factors act upon an aggregation as a whole rather than upon each individual in an aggregation in the population of the southern green stink bug, *Nezara viridula.*

It may become a common pattern of the mortality on aggregation. The fact that the aggregations liable to be destroyed by the mortality factors as a whole should be taken into consideration in analysing the mechanism of population dynamics.

Finally, let us turn the discussion to another consideration. Many works on the spatial distribution had been done assuming that mortality factors act randomly on the individuals in an aggregation, and clumped distribution of newly hatched larvae from an egg mass may gradually diminish and tends finally to random distribution as larval development advances. However, it may be general that the mortality factors act on the aggregation in the mode of all or none. We have to consider the new model of the spatial distribution based on it.

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# 昆虫の集合の生態学的意義

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集合は分類学的にもきわめて広い範囲にわたつて種々の昆虫にみられる一般的な現象である。集合の形成要因としては，環境のかたよりおよび昆虫自身の働きの2つが考えられ，特に後者の場合はさらに，個体相互間に何らかの誘引性がある場合と卵がかためて産みつけられる場合の2つに分けられる。

筆者は特に，卵および幼虫の集合について，集合現象を生態学的に解明し，集合の効果が昆虫の生活の中でどんな意義をもつているか，また個体数変動問題の一環として集合がどのような役割を演じているかを吟味考察した。特に後者について，自然における集合性の意義を評価する場合，集合性のために死亡要因が集合単位に all or none 的に働くことが多い事実を考えに入れる必要があることを強調した。またこのような集合を単位とした死亡のおこり方については従来ほとんど考えられていなかつたが，これが一般的であるとすれば，今までの昆虫の分布型の仮定，すなわち1卵塊から産まれた多くの幼虫個体が分散の過程でランダムに死んで行き，最初に集中的であつた個体の分布型が次第にランダムになつて行くという考えを捨てて， all or none の死亡過程に立脚した新しい分布型を考えるべきであることを強調した。