DEATH DUE TO INTERACTIONS BETWEEN RHIZOPHAGUS GRANDIS LARVAE

A THEORETICAL AND EXPERIMENTAL EVALUATION

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Summary

During rearing experiments we have often observed a decrease in the population of *Rhizophagus grandis* larvae, without ever finding the corresponding corpses. This certainly suggests necrophagy and perhaps cannibalistic-type behaviour. During the experiment described here, the mortality of the larvae was measured for different densities and food supplies. A mathematical model was constructed to evaluate the relative contributions of death which did not result from interaction (followed by necrophagy) and death due to interaction (or "cannibalism") to the total mortality. The results indicate that necrophagy and cannibalism are significant features in larval populations and that the latter is particularly important when food is scarce and the larval density is high.

1. INTRODUCTION

During rearing experiments, a decrease in the larval population was often observed, and from time to time larvae were seen eating their conspecifics.

These two observations could be explained in two ways :

1. Larvae exhibit necrophagic behaviour and their death is not influenced by their conspecifics. In this case the rate of death is proportional to the size of the population. This process will be named "individual death".
2. Death is induced by interactions between larvae; dead larvae are consumed. In this case the rate of death varies non-linearly with the size of the population. This process will be named "death by interaction".

The total mortality could result from both processes. An approach combining a mathematical model and experiments allows us to determine the relative contribution of both "individual death" and "death by interaction".

2. THE MODEL

We suppose that a larval population's death-rate (number of deaths / day) is the sum of "individual death" and "death by interaction".

"INDIVIDUAL DEATH"

The rate of "individual death" is given by :

$$- K N \qquad (1)$$

where N is the number of larvae and K the frequency of this event.

"DEATH BY INTERACTION"

The rate of "death by interaction" is proportional to the number of encounters which is a function of N^2 and a constant B. B contains the characteristics of the larvae, such as size, speed, efficiency in injuring a conspecific, and those of the environment (volume,...).
The rate of "death by interaction" is thus given by :

$$- B N^2 \qquad (2)$$

The total death rate is :

$$dN / dt = -K N - B N^2 \qquad (3)$$

If "individual death" (or "death by interaction") does not exist, K (or B) is equal to 0.
From (3) we obtain by integration :

$$1/N = e^{Kt} / N_0 + (e^{Kt} - 1) B/K \qquad (4)$$

N_0 is the size of the population at the beginning of the experiment. (4) shows a linear relationship between 1/N and $1/N_0$. This linearity will be used to determine B and K.

3. MATERIALS AND METHODS

The experimental set-up consisted of a Petri dish (diameter 9 cm; height 1.5 cm; volume 96 cm^3) with a moistened plaster base, filled with rehydrated spruce bark powder (volume 48 cm^3). Two series of experiments were realized.

GROUP OF FEEDING LARVAE

In this series of experiments, 10, 25, 50, 75 or 100 *Rhizophagus grandis* larvae with respectively 4, 10, 20, 30 or 40 *Dendroctonus micans* larvae were introduced into the dishes (2 or 3 replications were made). After 7 days, the same number of *D. micans* were reintroduced.

GROUP OF UNFED LARVAE

In this series, only 10, 25, 50, 75 or 100 *R. grandis* larvae were introduced.

After 7 and 14 days, the number of surviving <u>Rhizophagus</u> larvae was recorded. The mortality during the first week could be also due to the abrupt change in the environment of the larvae; therefore, only the results of the second experimental week were used.

4. RESULTS

Figures 1 and 2 give the experimental values of $1/N$ and $1/N_0$ (•) for the feeding and unfed larvae. The linear fitting (———) of the experimental points and its comparison with equation (4) of the model allow us to calculate K and B for the two groups of larvae (Table 1).

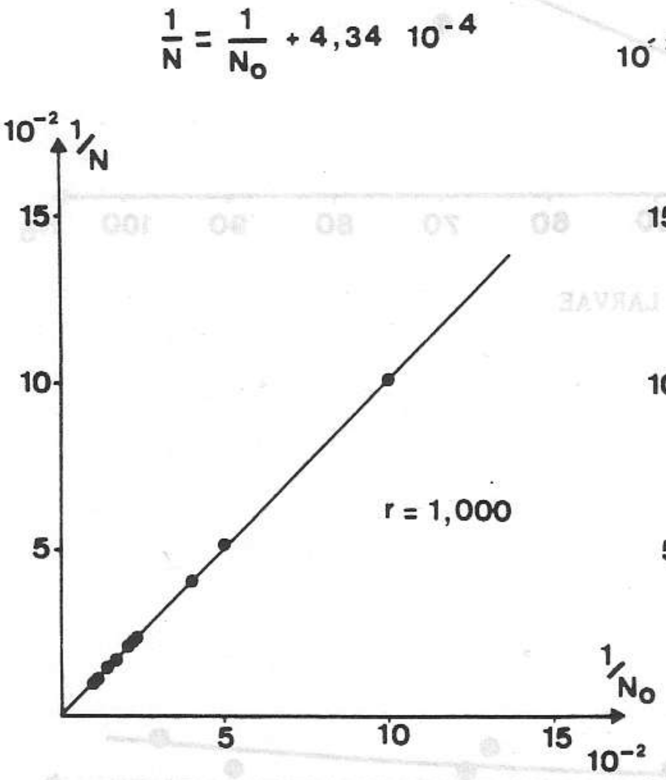

Fig. 1 : FEEDING LARVAE

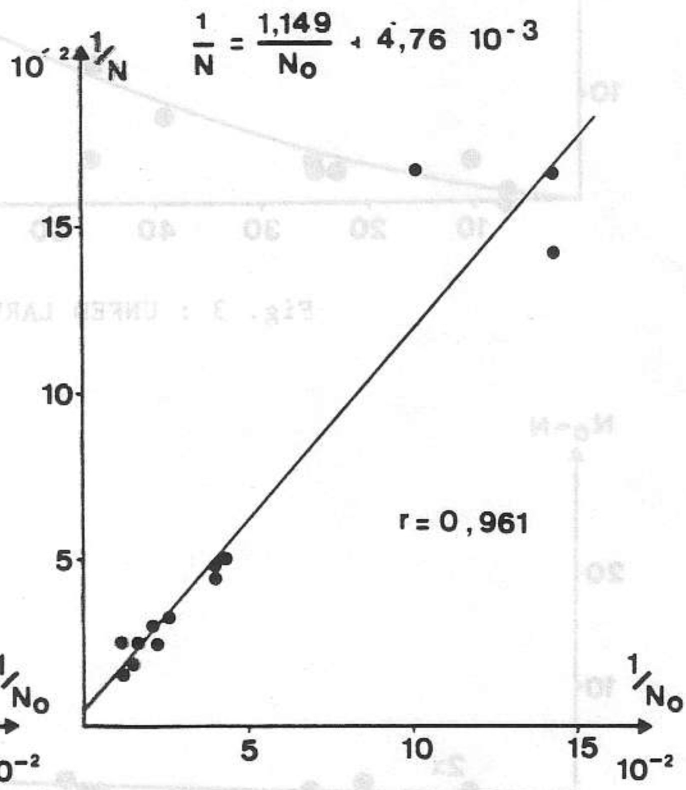

Fig. 2 : UNFED LARVAE

	K (DAY^{-1})	B (DAY^{-1} $LARVAE^{-1}$)
FEEDING LARVAE	0.00	$62\ 10^{-6}$
UNFED LARVAE	$19.8\ 10^{-2}$	$630\ 10^{-6}$

TABLE 1

Figures 3 and 4 give the number of dead (N_0-N) for the two groups of larvae and the theoretical fittings calculated with the K and B values given in table 1.

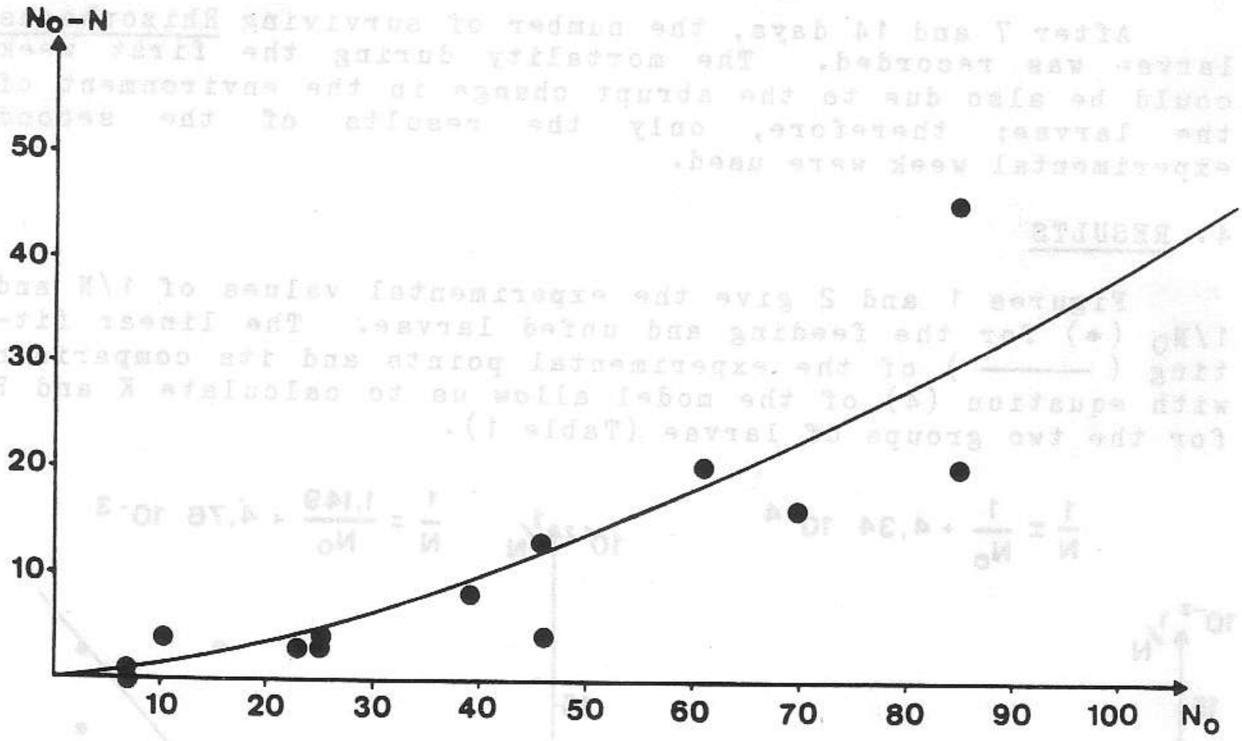

Fig. 3 : UNFED LARVAE

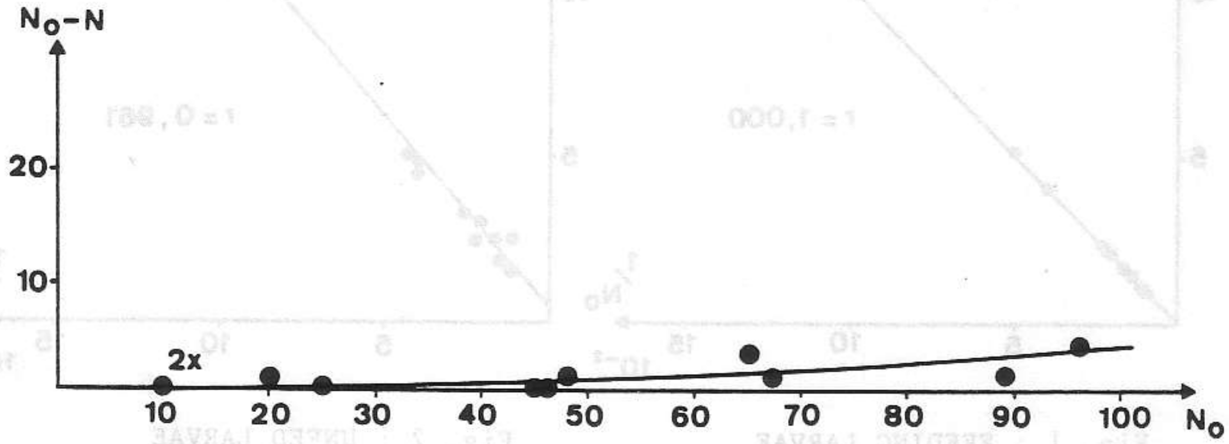

Fig. 4 : FEEDING LARVAE

From the model and the values of K and B, it is possible to estimate the number of deaths due to "individual death " and "death by interaction". Figure 5 shows each of the two contributions for the unfed larvae. There is a critical population (around 35 larvae in our experimental conditions) at which "death by interaction" becomes the dominant cause of death. At high population levels, (90 Larvae or more in our experimental conditions), "death by interaction" contributes 70 % or more of the total death. For the feeding larvae, "death by interaction" is the sole contributor (K=0).

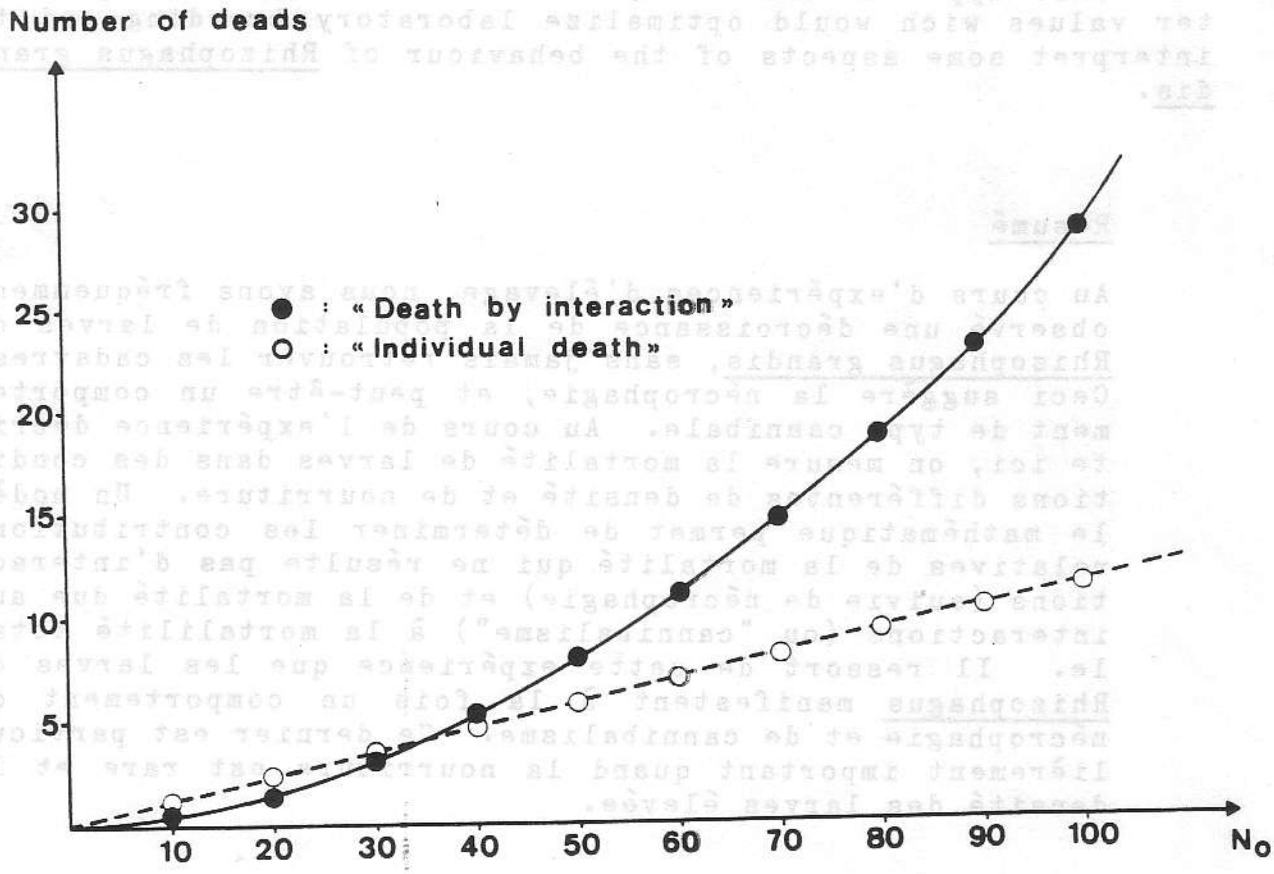

Fig. 5 : UNFED LARVAE

5. CONCLUSIONS

In the group of feeding larvae, the "individual death" is negligible or inexistent (K=0), and the "death by interaction" is low but responsable for all the deaths.

In the group of unfed larvae, the "individual death" exists and contributes in small populations (< 20 larvae in our experimental conditions) to the majority of deaths. B, which characterizes the "death by interaction", is ten times greater in this group than in feeding larvae. For a large population, "death by interaction" strongly affects the number of survivals.

The comparison between the two groups clearly shows that "individual death" is due essentially to unfavorable food-conditions (in the feeding group, "individual death" is negligible). "Death by interaction" exists in all conditions but is ten times greater for unfed larvae. High densities also favour "death by interaction".

Different factors can be involved in "death by interaction". The most probable is that contacts induce aggressive interactions, especially in conditions of deficient food supply. These aggressive interactions are either aiming at, or incidentally followed by, consumption of the killed individuals.

This approach should allow one to determine the parameter values wich would optimalize laboratory breeding and to interpret some aspects of the behaviour of Rhizophagus grandis.

Résumé

Au cours d'expériences d'élevage, nous avons fréquemment observé une décroissance de la population de larves de Rhizophagus grandis, sans jamais retrouver les cadavres. Ceci suggère la nécrophagie, et peut-être un comportement de type cannibale. Au cours de l'expérience décrite ici, on mesure la mortalité de larves dans des conditions différentes de densité et de nourriture. Un modèle mathématique permet de déterminer les contributions relatives de la mortalité qui ne résulte pas d'interactions (suivie de nécrophagie) et de la mortalité due aux interactions (ou "cannibalisme") à la mortalilité totale. Il ressort de cette expérience que les larves de Rhizophagus manifestent à la fois un comportement de nécrophagie et de cannibalisme. Ce dernier est particulièrement important quand la nourriture est rare et la densité des larves élevée.