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ANALYSIS OF VARIATIONS OF HANDLING-TIME IN *TRICHOGRAMMA MAIDIS*

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Variation in handling-time is studied in the association between *Trichogramma maidis* Pintureau & Vœgelé [*Hym.* : *Trichogrammatidae*] and one of its factitious hosts : the eggs of the Mediterranean flour moth *Ephestia kuehniella* Zeller [*Lep.* : *Pyralidae*]. It is shown that the duration of egg laying behaviour decreases exponentially from the first host egg encountered onwards. This decreasing kinetic, which corresponds to a learning ability, shows a high variability between females, but a mother-daughter regression analysis fails to demonstrate any genetic transmissibility of this learning ability over 2 successive generations. Once the learning is over, there remains a residual variability which is, in part, under genetic control. The possible consequences of these results on the stability of host-parasite associations are discussed.

KEY-WORDS : Handling-time, learning modelisation, *Trichogramma maidis*, genetic variation analysis, egg laying behaviour, behavioral analysis methods.

The response of a parasitoid in the frequency of its attack to an increase in the density of its host is usually defined under the well-known term "functional response". Among such responses, which were first described by **Solomon** (1949) but more thoroughly discussed by **Holling** (1959), the "type-II" response describes the situation where parasitism rises at a decreasing rate as host density increases, and thus approaches a plateau. This particular type of response is very common among entomophagous insects (**Holling**, 1961), at least under laboratory conditions (see **Hassell** *et al.*, 1976 for a review), and **Holling** (1959) attributes its form to the existence of a minimal handling time (Th) which must be spent in parasiting each encountered host.

Several mathematical models have been developed to study the consequenes of this response on the stability of host-parasite interactions (see **Hassell & May**, 1973 for example). In all of these models, it has been assumed that Th is a constant characteristic of a given host-parasite association.

Nevertheless, in the particular case of a true predator, **Thompson** (1975) has shown that the handling time of the damselfly *Ischnura elegans* feeding on *Daphnia magna* could vary markedly with both the age (= instar) of the predator and with the size of the prey eaten. This fact leads to a variety of functional responses for the same association, and their relative proportions depend on the age structure of both predator and prey populations. In the case of *Aphelinus thomsoni* Graham, a predator and a parasite of the aphid *Drepanosiphum platanoidis* Schrank, **Collins** *et al.* (1981) have found that mean handling time decreases with host density. For this species, it was shown that handling time for feeding is greater than handling time for oviposition. It is therefore argued that a change of mean Th with host density does not require any change in the values of these 2 types of handling time, but only in their relative frequency.

Because of the fact that handling time is directly implicated in the reproductive success of a parasitoid, this trait can be a prime target for evolutionary pressures (**Hassell,** 1976 ; **Livdhal,** 1979). It is thus possible that the determinism of this trait is partly under genetic control, and the measurement of this source of variation could contribute to a better understanding of host-parasite interactions (**Boulétreau,** 1986).

In the case of the chalcid *Trichogramma embryophagum* (*Hym. : Trichogrammatidae*), a parasitoid of the eggs of several moth species, **Klomp** *et al.* (1980) have shown that the ability of the female to discriminate between parasitized and unparasitized hosts was a matter of learning and was acquired during oviposition in the first unparasitized host egg encountered, though some authors do not agree with these conclusions (**Van Alphen** *et al.*, 1987). **Gross** *et al.* (1981), using inexperienced females of *Trichogramma pretiosum* Riley (i.e. females which have not yet oviposited) have shown that the length of time spent on the first host egg discovered (*Heliothis zea* Boddie) was significantly higher than that spent on subsequently discovered ones. This fact has also been observed by other authors on different host-parasite associations (e.g. **Samson-Boshuizen** *et al.*, 1974, on the *Drosophila-Cynipidae* relationship). It seems therefore that learning in the egg laying behaviour of *Trichogramma* spp. can be another source of variation of the handling time. Owing to the fact that *Trichogramma* also exibits a "type-II" functional response (**Kfir,** 1983), this learning ability can be implicated in the stability of all natural or artificial (i.e. Biological Control releases, **Stinner,** 1977) associations between moth eggs and these hymenopterous endoparasitoids.

In this paper, these different causes of variation of *Trichogramma maidis* Pintureau & Vœgelé egg handling behaviour duration (Th) are studied on the eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller (*Lep. : Pyralidae*). Some of them relate to learning of inexperienced females, others, that are partly under genetic control, appear when this learning ability is over. The possible consequences on the functioning of the populations are discussed.

MATERIALS AND METHODS

The *T. maidis* strain used in the experiments was reared from parasitized *Ostrinia nubilalis* Hübner eggs collected during summer 1986 in Alsace (France). This strain probably originated from the Moldavian population (**Pintureau & Vœgelé,** 1980) released in this area for biological control against the European corn borer. Its electrophoretic pattern for esterases was the same as the one described by **Pintureau & Babault** (1981) for this species. From the time of capture onwards, the strain was maintained under laboratory conditions for 16 generations on *E. kuehniella* eggs, at 25 °C.

EXPERIMENTS

Before the experiments, individual parasitized (black) host eggs were isolated in small glass tubes with a droplet of diluted honey as food for the emerging adults. After emergence, a single male was placed in the vial of each female and soon after mating, the females were introduced individually into glass vials 1 cm in diameter, 7 cm in length, with a rectangular cardboard sheet (1 × 6 cm) bearing the host eggs. The "egg cards" consisted of about 45-50 UV-killed *E. kuehniella* eggs glued with distilled water and placed at random, except that the distance between 2 consecutive eggs was never less than 2 mm. **Laing** (1937) and **Glas** *et al.* (1981) demonstrated that 2 mm was the maximal distance which allowed, by means of sight, the perception by a *Trichogramma* female of surrounding eggs, and thus promoted the movement from one host to the other. Each female was immediately observed under a stereomicroscope until 10 host eggs were parasitized.

For each parasitized host, the duration of the 3 major phases of egg laying behaviour was measured with a stopwatch. These 3 phases were : antennal drumming, ovipositor drilling and oviposition (see **Klomp** *et al.*, 1980 for a detailed description). The 3 durations obtained for each female and for each parasitized egg have been considered as a multivariate estimation of handling time (see statistical analysis below).

All experiments were done during daytime, at 24 ± 1 °C and 40-60 % RH. Females were never more than 18 h old.

Under these experimental conditions, females practically never attempt to oviposit in hosts already parasitized by themselves (self-discrimination ability). Therefore, it did not seem necessary to withdraw eggs as soon as they were attacked.

To investigate if the variations observed in the *Trichogramma* females are under genetic control, the behavioural tests were performed over 2 successive generations. The behaviour of 24 females (mothers) and, for each of them, 2 daughters was measured. The regression between mothers and the mean of the 2 daughters gives an estimation of the genetic transmissibility of the trait.

STATISTICAL ANALYSIS

The learning ability was analysed with a one-way multivariate analysis of variance procedure (**Smith** *et al.*, 1962). The 3 variates were the duration of each behavioural phase for each *Trichogramma* female and for each parasitized egg, and the factor tested was the "rank of infestation" effect (1 to 10). The corresponding overall statistical significance was studied using the **Wilks'** likelihood ratio test (**Wilks,** 1932 ; **Pearson & Wilks,** 1933), which is, in such a case, a rather robust test (**Olson,** 1974).

This statistical analysis was coupled with a factorial discriminant analysis, which is a related procedure allowing the projection of the data corresponding to the different "ranks of infestation" on successive canonical axes with decreasing importance (i.e. variance). These axes have the property of maximizing the inter/intra variance ratio, and their statistical significance can be tested with a procedure similar to the **Bartlett'**s test usually used to compare different variances with one another (**Dagnelie,** 1975).

When necessary, a **Newmann-Keuls'** test was used to separate different means.

RESULTS

The data were first analysed by pooling the results obtained on both mothers and daughters. This is justified by the fact that no statistical differences were found between the 2 successive generations.

Fig. 1 gives the changes in the mean duration of drumming, drilling, and oviposition with the rank of the host egg attacked, for the 72 females measured (i.e. 24 mothers and 48 daughters). The relative proportions of these 3 behavioural phases are about 23, 29 and 48 % respectively, which roughly correspond to the data obtained by **Pak & Van Heiningen** (1985). As shown by **Gross** *et al.* (1981), the duration of the egg laying behaviour, for the first encountered egg, is greater than for the following ones ($p < 0.01$ for the 3 egg laying phases).

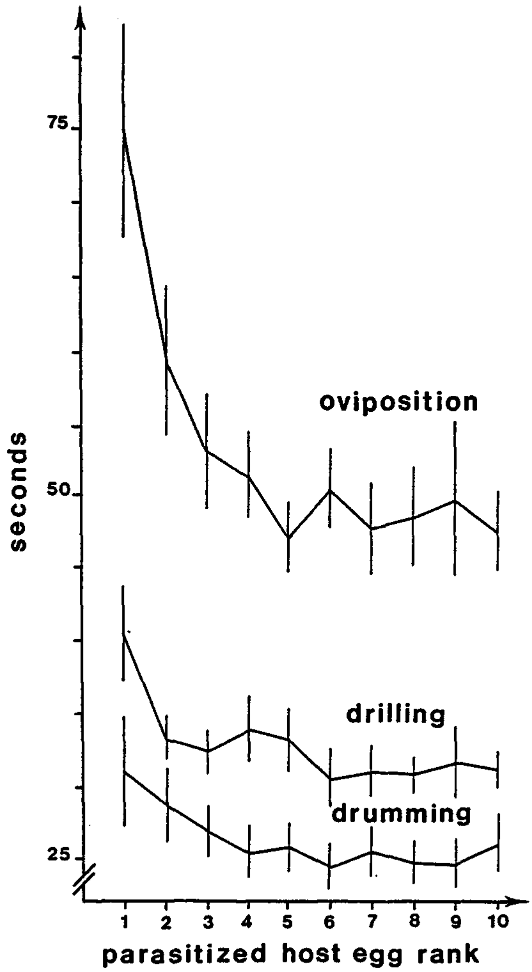

Fig. 1. Changes in the duration (in seconds) of drumming, drilling and oviposition with the rank of the host egg attacked (n = 72 ; means with 95 % confidence intervals).

Considering the three-variates feature of the data, we can project them on 3 successive canonical axes with decreasing importance. Table 1 gives a summary of the results obtained.

The first axis, which is the only significant one, explains by itself almost 90 % of the overall variance. Fig. 2 gives the changes in the mean projections of the successive "ranks of infestation" on this axis. It can be shown that mean projections corresponding to the 1st and the 2nd parasitized host egg are statistically different from those corresponding to the following ones (Newman-Keuls' test, 5 % level) ; stability is statistically obtained from the 3nd parasitized egg onwards.

Thus, there are successive decreases in the duration of egg laying behaviour for the first several eggs attacked, which is due to the experience gained by the females. Thus, according

TABLE 1

Canonical Axes number	Eigen value	Percentage of variance	Cumulative percentage	Chi^2 (d.f.)
1	.2702	89.71	89.71	169.1 ** (11)
2	.0190	6.31	96.02	13.3 NS (9)
3	.0120	3.98	100.00	8.4 NS (5)

Eigen values (i.e. variances), percentages of variance and statistical tests of each of the three canonical axes of a factorial discriminant analysis. The overall inter-"parasitized egg rank" variation is higly significant (WILKS' test : Chi^2 = 190, 8 ; 54 d.f. ; $p < .01$).
NS = Non significant ; ** : $p < .01$.

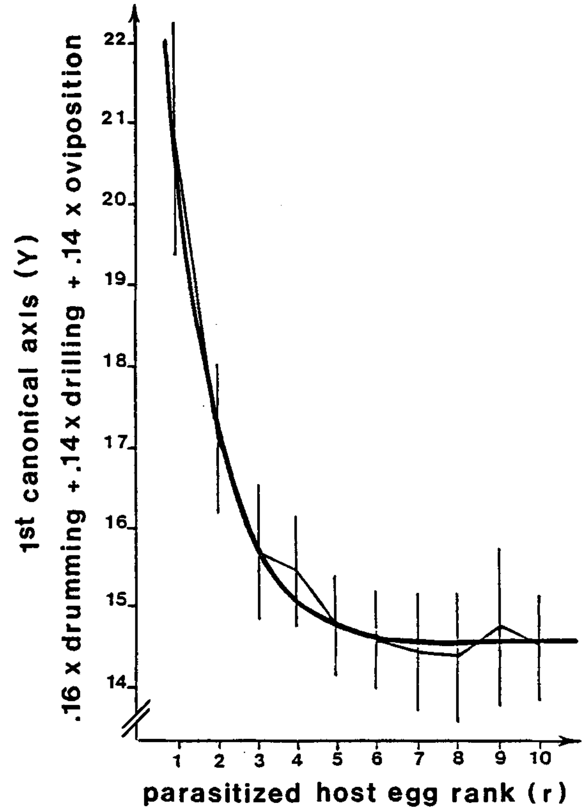

Fig. 2. Changes in the projections of the successive "parasitized egg ranks" on the first canonical axis of a factorial discriminant analysis (n = 72 ; means with 95 % confidence intervals). The model :

$$Y = YINF + C.e^{-k(r-1)}$$

has been fitted to the data using a non-linear least squares procedure, with parameter values estimates as follow (± s.e.) :

$$YINF = 14.55 \pm .09 ; \quad C = 6.19 \pm .21 \text{ and } k = .837 \pm .069 \text{ (see text).}$$

to the definition given by **Van Alphen & Vet** (1986), this phenomenon seems to be a matter of learning.

Assuming that the learning rate is proportional to the difference between the time spent for handling hosts once the learning is over (YINF) and the actual duration of the egg handling behaviour (Y), we can write :

$$dY/dr = k(YINF - Y),$$

where k is a positive constant (i.e. learning speed) and r is the rank of the parasitized host egg. This integrates to :

$$Y = YINF + C.e^{-k(r-1)},$$

where C (constant of integration) is the difference between the initial duration of the egg laying behaviour and YINF (i.e. learning effort).

As shown in fig. 2, this model fits the mean data quite well. This model can totally describe the learning behaviour of *Trichogramma* females with only 3 parameters : YINF, k and C. YINF is related to the duration of the egg laying behaviour once the learning is over ; the corresponding variation will be analysed in detail below. Concerning the 2 other parameters, the model has also been fitted to the data recorded for each female separately (i.e. for each mother and daughter), thus allowing the analysis of variations of the learning speed (k) and learning effort (C) within the population studied.

Mother-daughter regression analyses (fig. 3) show that there is substantial variations within both mothers and daughters for these 2 parameters, but no significant correlations were found in either case between the 2 successive generations. Thus, these variations do not seem to be based on some genetic mechanisms in the *Trichogramma* population studied.

As explained above, no statistical differences could be detected from the 3rd parasitized egg onwards. But, as can be seen in fig. 2, the learning behaviour seems to continue until the 6th attacked egg. So, in order to study variations that appear once the learning ability is actually over, mother-daughter regression analyses were done on the 3 behavioural phase mean durations corresponding to the last 5 eggs attacked (numbers 6 to 10). As shown in fig. 4, no correlations were found for drumming and drilling, but for oviposition there was a high correlation (i.e. heritability) between the 2 successive generations.

DISCUSSION

If we define learning in a broad sense as any change in behaviour due to female experience, as proposed by **Van Alphen & Vet** (1986), the duration of the egg laying behaviour (handling-time) of *T. maidis* females, for the 1st several host eggs encountered, is a matter of learning and follows a kinetic that can be almost perfectly fitted to a decreasing exponential function. This result complements those obtained by **Gross** *et al.* (1981) on *T. pretiosum.* Using host-seeking stimuli (Hexane extract of *Heliotis zea* Boddie moth scales), these authors found that the time spent parasitising the 1st host egg encountered was significantly longer than that spent on subsequently discovered eggs. In our results, stability is statistically obtained from the 3rd parasitized egg onwards.

Schmidt & Smith (1987) have shown that the number of eggs layed by an inexperienced *Trichogramma minutum* Riley female in a single *Manduca sexta* L. egg (*Lepidoptera ; Sphingidae*) is greater in the 1st host encountered than in the second one. It is thus possible that such effects could result in variation in host handling duration, such as observed here. In fact, as explained by these authors, egg of *M. sexta* are very large compared to *E. kuehniella* eggs, and can therefore support the development of more than 30 *Tricho-*

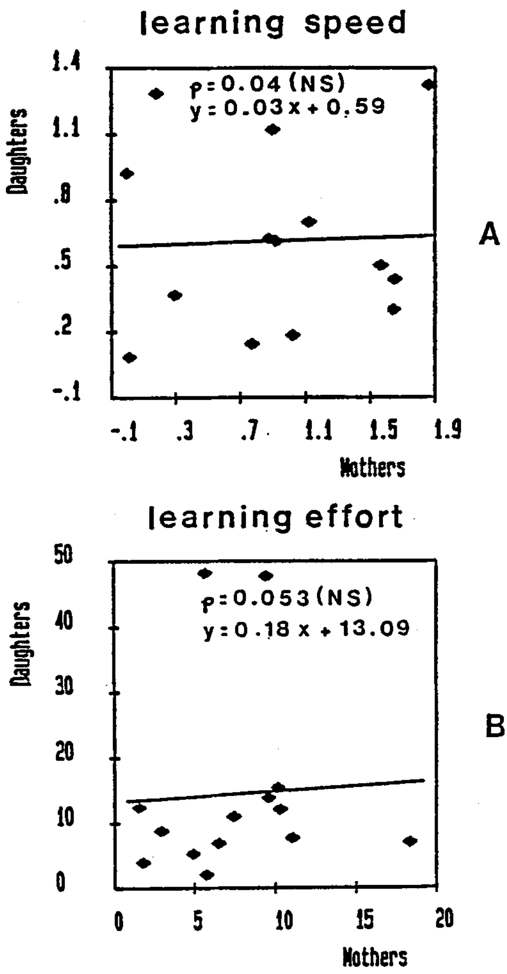

Fig. 3. Mother-daughter regression for (A) learning speed and (B) learning effort (n = 14). Values corresponding to each female have been estimated by fitting the corresponding data to the model used in fig. 2, and only points for which the non-linear least squares iterative procedure has succeeded for both the mother and her two daughters have been taken into account.

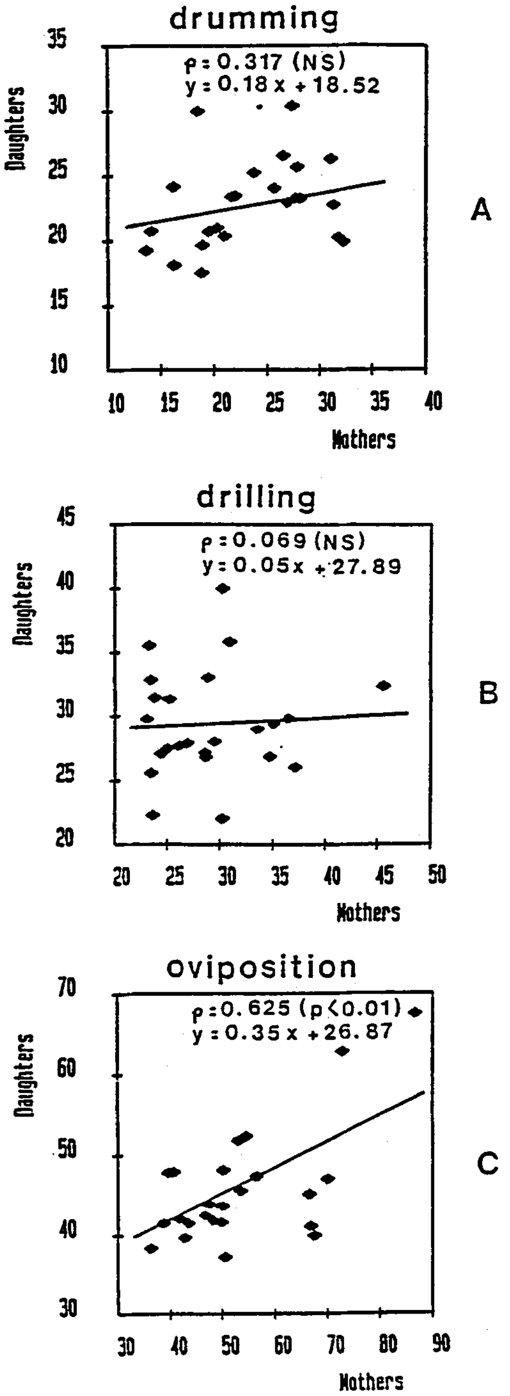

Fig. 4. Mother-daughter regression for the duration (in seconds) of (A) drumming, (B) drilling and (C) oviposition for the five last eggs attacked (numbers 6 to 10). (cf. text)

gramma without significant mortality. With *E. kuehniella,* an average of only 1 to 2 *Trichogramma* can develop in a single egg. Variation observed here could therefore be explained only in part by a change in superparasitization rates between the 1st host attacked and following ones, and other learning mechanisms must be involved.

Klomp *et al.* (1980) have shown that *Trichogramma* females learn to discriminate between parasitized and unparasitized hosts during the parasitization of the 1st host egg encountered. This ability is shown to be acquired at the end of the 3rd egg laying phase (i.e. oviposition). As shown in fig. 1, the existence of a decrease in the duration of the drumming and drilling phases seems to show that, during these 2 behavioural events, some learning mechanisms may also appear. It is possible that these learning mechanisms are related to the ability of *Trichogramma* females to measure the host volume (**Schmidt & Smith,** 1985) and to perforate the chorion, respectively. Thus, handling time does not seem to be a constant feature, even for a given female, and these variations can therefore lead also to variations in the intensity of the functional response of parasitoid females to the density of their hosts. This learning ability can thus be implicated in the stability of the associations between *Trichogramma* parasitoids and their hosts.

Up to now, learning ability of parasitoid females has not been considered in terms of variation in handling time in theoretical works, because inexperienced females have never been taken into account. Thus, concerning *Trichogramma* parasitoids, Th, for a whole population, has likely always been underestimated. Nevertheless, as can be seen in fig. 2, this phenomenon seems to concern only the first five host eggs parasitized in the whole life of a female parasitoid. The total number of parasitized hosts by a *T. maidis* female is commonly greater than 90, at least under laboratory conditions (**Pintureau** *et al.,* 1981). The incorporation of the learning behaviour should thus lead to a total increase of Th which remains small and, consequently, the possible implications in the stability of host-parasite systems seems to be negligible.

Fig. 3 shows that there is substantial variation in this learning phenomenon, but this variation does not seem to depend on genetic determinisms. This result may be a consequence of variation in the characteristics of the *E. kuehniella* eggs offered to *Trichogramma* females (i.e. : size, shape, etc., **Brindley,** 1930) : in particular, drumming and drilling duration are thought to be affected by the size of the host egg and the thickness of the chorion, respectively (**Salt,** 1938, 1940), though, as yet, this fact has not been clearly demonstrated (**Pak** *et al.,* 1986).

Although no genetic variation of the learning ability was detected here, this characteristic could, however, be an adaptive advantage for polyphagous parasites such as *Trichogramma* spp. (**Van Alphen & Vet,** 1986), where succesive generations may be exposed to different host egg species with different characteristics (volume, shape, thickness of the chorion, etc.).

The wasp population used for this experiment was reared for more than 15 generations on the same host species. It is thus possible that genetic variation in the learning ability has disappeared because of the absence of corresponding selective pressure. This hypothesis is related to the more general problem of mass-rearing of insects (**Boller,** 1972), and leads to the proposition of rearing the wasp population on the target host before field-releases to lower possible failures.

Once the learning is finished, there remains a variation in Th which is, in part, under genetic control (Fig. 4C). This genetic variation can only be detected for the oviposition duration, which represents almost half of the overall handling time.

This result suggests that handling time can be a target for selective pressures and can change according to between- and within-population variations of the characteristics of hosts. Such variations are known to occur: **Livdhal** (1979) has compared the functional response of a predatory mosquito (*Toxorhynchites rutilus septentrionalis*) on 2 populations of its prey (*Aedes triseriatis*). One prey population was sympatric with the predator, the other was allopatric. He found differences in the predator's functional response parameters for these 2 populations. As explained by **Juliano & Williams** (1984), this result does not prove that the difference is a result of adaptation by the prey to predation, but it shows that the characteristics of the functional response can change with different host populations.

It is likely that the genetic variability in handling time here observed should lead to genetic variations in the intensity of the functional response, and could thus be implicated in the stability of host-parasite interactions (**Pimentel**, 1984).

A comparison of the variations in handling time in different *Trichogramma* species that are known to attack different hosts in nature must finally be undertaken in order to better understand the different possible host exploitation strategies.

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RÉSUMÉ

Analyse des causes de variation de la durée du comportement de ponte de *Trichogramma maidis*.

Une analyse de différentes sources de variation de la durée du comportement de ponte de *Trichogramma maidis* [*Hym.: Trichogrammatidae*] sur un de ses hôtes de substitution : les œufs de la pyrale de la farine *Ephestia kuehniella* [*Lep.: Pyralidae*] est abordée ici.

L'approche expérimentale, fondée sur le chronométrage de différentes phases du comportement étudié, a pu mettre en évidence, grâce à l'utilisation de procédures statistiques multivariées, l'existence d'une capacité d'apprentissage des femelles de Trichogrammes inexpérimentées (femelles n'ayant jamais rencontré d'œufs hôtes avant l'expérimentation). Cet apprentissage se traduit par une diminution exponentielle du temps moyen de ponte entre les premiers hôtes infestés et les suivants. La cinétique d'apprentissage obtenue présente elle-même une variabilité individuelle qui ne semble pas s'expliquer par un déterminisme génétique.

Une fois cet apprentissage terminé, il reste une variabilité résiduelle de la durée moyenne de la ponte. Une analyse par régression mères/filles a pu montrer que celle-ci reposait, pour partie, sur un déterminisme génétique.

Les conséquences possibles de ces résultats sur le fonctionnement des associations parasitaires sont discutées.

MOTS CLÉS : Durée du comportement de ponte, modélisation de l'apprentissage, *Trichogramma maidis*, variations génétiques, méthodes d'analyse comportementale.

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