

Genetic variation in sex allocation in a parasitic wasp: variation in sex pattern within sequences of oviposition

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Abstract

In order to maximize their fitness under Local Mate Competition (LMC), arrhenotokous female wasps have to produce a precise sex ratio when encountering hosts. Recent progress in the theory of hymenopterous parasitoid reproduction suggest that they manage to do it by laying male and female eggs in a particular order and that such reproductive strategies are adaptive. Therefore, the determinism of such sequential patterns would be regulated by genetic control on which natural selection could act. To test this hypothesis, sequences of oviposition were recorded in a set of *Trichogramma brassicae* Bezdenko (Hymenoptera; Trichogrammatidae) females and in their daughters by providing them *Ephestia kuehniella* Zeller (Lepidoptera; Pyralidae) eggs.

In order to describe accurately sex pattern within these oviposition sequences, I present a joined non-parametric and multivariate statistical method. It is shown that *T. brassicae* females do not produce male and female eggs in random sequences. Moreover, the way they organize the sequence of the sexes in their progeny seems to be under a strong genetic control. The evolutionary consequences of such results are discussed.

Introduction

Sex allocation has been the focus of much theoretical and experimental work in recent years (Maynard Smith, 1978; Charnov, 1982; Waage, 1986). The starting point was Fisher's (1930) work in which it was pointed out that, in a random mating population with a biased sex ratio, an individual of the rarer sex would produce on average more progeny than an individual of the other sex, so that an optimal equal investment in sons and daughters would be favoured by frequency-dependent selection.

Most Hymenopterous parasitoids are haplo-diploid: males develop from unfertilized eggs and females from fertilized ones. Mated females store sperm in the spermatheca, so, at the time of oviposition, they are thus able to determine their offspring's sex ratio by controlling the proportion of fertilized eggs they lay. Due to this sex determination system, highly biased sex ratios (i.e. different from the 50:50 Fisherian sex ratio) are often found among species in response to environmental factors (Flanders, 1946). Using this mechanism, wasp females are able to adjust the sex ratio of their offspring to (1) host 'quality' (e.g. size)

(Charnov, 1979; Charnov *et al.*, 1981; Werren, 1984), (2) the size of the host patch (Waage, 1982a), (3) the encounter rate with hosts (Strand, 1988), (4) internal factors such as egg load (Putters, 1988), etc.

Moreover, in a non-random mating population where females mate as soon as they emerge and then disperse to colonize new host patches, it has been shown that the optimal sex ratio (proportion males) will shift toward a female-biased sex ratio if mating takes place between the offspring of one or a few mothers in isolated subpopulations. This is Hamilton's local mate competition model (LMC) which predicts an adjustment of the sex ratio depending on the number of females colonizing a single patch (Hamilton, 1967; Taylor & Bulmer, 1980). The result of several experimental studies are in accordance with this model which can be expected when the host population shows a significant aggregated spatial distribution (Taylor & Bulmer, 1980; Waage, 1982b; Werren, 1983; Waage & Lane, 1984; Strand, 1988).

Under such conditions, when a single female colonizes a host patch (complete LMC), her fitness will rapidly decrease if the number of sons she produces is either too large (because they will compete among themselves for mates), or too small (because some or all of her daughters will remain unmated). Therefore, under LMC, female wasps have to adjust their sex ratio accurately, and Green *et al.* (1982) have demonstrated that some wasp species do indeed produce precise sex ratios (with much lower variance than what it would be if sex determination was binomial; see Hardy, 1992 for a recent review). This strongly suggests that some mechanisms exist allowing wasp females to produce accurate sex ratios.

One mechanism could be that ovipositing mothers lay male and female eggs in a particular order (Green *et al.*, 1982; Waage, 1986). Such sequence patterns have indeed been found for several parasitoid species (Mertins, 1980; Waage, 1982a, 1982b; Putters & van den Assem, 1985; van Welzen & Waage, 1987; Strand, 1988; Hooker & Barrows, 1989; Velayudhan & Senrayan, 1989). For example, females belonging to *Trichogramma* (Hymenoptera: Trichogramma-

tidae) species, that are known to show changes in sex ratio in accordance with Hamilton's model, tend to produce proportionately more male offspring early in an oviposition bout (Suzuki *et al.*, 1984; Waage & Lane, 1984; Waage & Ng, 1984; van Dijken & Waage, 1987). However, for some species, or under some particular conditions (e.g. when there is no LMC), such sex-sequence behaviours are not observed (Strand, 1988; van Dijken *et al.*, 1989).

For species that show a change in sex ratio in accordance with the LMC model, such sequence patterns lead to an increase in the accuracy of sex allocation, and thus to an increase in females fitness, especially if just one female colonizes each host patch. Such behaviour is thus likely to be adaptive and a progressive settlement of a sex-sequence strategy during the course of generations is conceivable only if the wasp's biological traits involved are determined by a genetic variation on which natural selection could act.

Most studies of genetic aspects of sex allocation in parasitic wasps have considered sex ratio control (i.e. average values) (Wilkes, 1964; Werren *et al.*, 1981; Skinner, 1982; Parker & Orzack, 1985; Orzack & Parker, 1986, 1990) but not the mechanisms used to produce sex ratios accurately (i.e. variances).

I thus decided to look for a genetic (i.e. polygenic) variability in the sex sequence pattern in a *Trichogramma brassicae* Bezdenko (= *T. maidis* Pintureau & Voegelé) population. This wasp, which is an egg parasitoid of several moth species, was chosen because it is the insect most intensively produced over the world for inundative biological control programs (Stinner, 1977). A better understanding of its sex allocation strategy and how it may be manipulated could thus be very useful to improve its mass-production (Waage & Ng, 1984; Velayudhan & Senrayan, 1989). Furthermore, for this species, LMC is likely to exist (and thus a sex-sequence pattern is to be expected), because its natural host (the eggs of the European Corn Borer, *Ostrinia nubilalis* Hübner) shows a strong aggregated spatial distribution in natural conditions, and such results have been demonstrated for *T. evanescens* (Waage

& Lane, 1984) which is a closely related species.

This paper presents a joined non-parametric and multivariate statistical procedure developed for an accurate quantitative description of sequences of oviposition produced by *T. brassicae* females. Strong genetic variation in the way females organize the sequence of the sexes in their progeny is shown when using this method and a mother/daughter regression analysis. The adaptive significance of this result is discussed.

Materials and methods

The *T. brassicae* strain used in the experiment was founded from about thirty parasitized *Ostrinia nubilalis* Hübner (Lepidoptera; Pyralidae) egg masses collected during the summer in 1986 in Alsace (France). This strain which is also the one used in Wajnberg (1989) and Wajnberg *et al.* (1989), probably originated from the Moldavian population (Pintureau & Voegelé, 1980) released in this area for biological control against the European Corn Borer. Its electrophoretic pattern for esterases is the same as the one described by Pintureau & Babault (1981). The strain has been maintained under laboratory conditions on the eggs of one of its factitious hosts: *Ephestia kuehniella* Zeller (Lepidoptera; Pyralidae), at 25 °C, LD 12:12.

Experiments. Experiments were done with a very low female/hosts ratio. Under such conditions, females almost never superparasitize hosts (Wajnberg, 1989; Wajnberg *et al.*, 1989), and this seems to be the best condition for such experimental study. Forty-five UV-killed *E. kuehniella* eggs, 'glued' with distilled water in a regular pattern on a rectangular cardboard sheet (with about 3 mm between each of them), were offered to every isolated *T. brassicae* female (already mated and less than 16 h old) in small glass tubes (1 × 7 cm). The wasp is able to move freely between hosts and makes successive ovipositions, the interval between attacks being always less than 2 min. The sex of each laid egg can be determined by observing the abdominal movements during the

oviposition behaviour of the female (Suzuki *et al.*, 1984; Waage, 1986; van Dijken & Waage, 1987). However, in the present work, the order of parasitization of 15 eggs was recorded and then the female was removed. The parasitized hosts were then separated into individual tubes to determine, after development at 25 °C, the sex of the emerging wasp. This allows the simultaneous observation of several ovipositing females which facilitates replications per unit of experimental time. All experiments were performed during daytime, at 23 ± 1 °C. Other conditions that are known to induce changes in the sex ratio produced by females (i.e. host density, host size and quality, host's spatial distribution) were not allowed to vary in the experiment; conditions were as standardized as possible.

In order to know if the variation observed in sex sequence patterns produced by *Trichogramma* females is under genetic control, the analysis was performed over two successive generations. Sixteen mothers and 2 of their daughters were measured; the correlation between mothers and the average of the daughters gives an estimation of the genetic part of the variability observed.

Statistical analysis. Five non-parametric statistics, computed from the rank positions of sons and daughters within sequences produced by wasp females, were used to describe sequential features of the sequences. These five statistics are described in Table 1 with their corresponding null and alternative hypotheses. They are derived from standard rank test procedures (Hájek & Sidák, 1967). For example, the first one (SMR) is constructed like the well-known Wilcoxon rank sum test.

To compare the description of sequences differing in length or with different sex ratios, these five statistics were not used directly as described. For each of them and for each oviposition sequence, the exact probability to get a value lower or equal to the one obtained has been calculated by computing it over all the combinations of *M* males over *N* positions. Thus, for each of these parameters, and for each oviposition sequence, the result obtained corresponds to the exact sig-

Table 1. Formulae, null and alternative hypotheses of the five statistics used to describe sequential features in the oviposition sequences produced by *T. brassicae* females. These statistics are all computed assuming that the sequence to be described, produced by a given female, is constituted of N individuals among them M are males. $rm_{(i)}$ is the rank of the i^{th} male ($i = 1, 2, \dots, M$) and $rf_{(j)}$ is the rank of the j^{th} female ($j = 1, 2, \dots, N - M$). SMR: Sum of the males' rank position; VMR: Variance of the males' rank position; CGM: Centre-group of males; CGF: Centre-group of females; NR: Number of runs of males or females

Name	Formula	Null hypothesis	Alternative hypothesis
SMR	$\sum_1^M rm_{(i)}$	Males are not laid at the beginning of the sequence	Males are laid at the beginning of the sequence
VMR	$\sum_1^M \left(rm_{(i)} - \frac{N+1}{2} \right)^2$	Males are not laid in the middle of the sequence	Males are laid in the middle of the sequence
CGM	$\sum_1^M rm_{(i)} - Q $ (a)	There is no pooling of males within the sequence	There is pooling of males within the sequence
CGF	$\sum_1^{N-M} rf_{(j)} - R $ (b)	There is no pooling of females within the sequence	There is pooling of females within the sequence
NR	$2 + \sum_1^{M-1} d_{(i)} + \sum_1^{N-M-1} z_{(j)}$ (c)	There is no autocorrelation of males and females within the sequence	There is autocorrelation of males and females within the sequence

(a): $Q = rm_{((M+1)/2)}$ if M is odd; $Q = rm_{(M/2+1)}$ if M is even

(b): $R = rf_{((N-M+1)/2)}$ if $N - M$ is odd; $R = rf_{((N-M)/2+1)}$ if $N - M$ is even

(c): $d_{(i)} = 1$ if $(rm_{(i+1)} - rm_{(i)}) > 1$ and $d_{(i)} = 0$ otherwise; $z_{(j)} = 1$ if $(rf_{(j+1)} - rf_{(j)}) > 1$ and $z_{(j)} = 0$ otherwise

nificance level of the one-sided test of the null hypothesis given Table 1. As it can be seen from examples given in Table 2, these five parameters describe features that are not in relation with sex ratio; they just enable the description of the sequential organization of the sequences analysed. 17.35% of the parasitized eggs did not lead to the emergence of an adult wasp (i.e. developmental mortality) and 6.96% give rise to both a male and

a female wasp (i.e. superparasitism). In such cases, all the possible sequences corresponding to these missing or ambiguous data were described with the method, and average vectors were used to quantify the corresponding sequences.

For each of the five statistics, the descriptions obtained can be combined over all the analysed sequences in order to test statistically the associated null hypothesis. Indeed, if n sequences are

Table 2. Examples of the description of seven hypothetical sequences of oviposition with five non-parametric statistics. Here, males are represented by a '1' and females by a '0'. The given values are the exact probability to get a result lower or equal to those given in brackets which are computed with formulae given in Table 1. Note that all the sequences described here show the same sex ratio (i.e.: 1/3)

Sequence	SMR	VMR	CGM	CGF	NR
111100000000	0.00202 (10)	0.89697 (69)	0.01818 (4)	0.01010 (16)	0.00404 (2)
101110000000	0.01414 (13)	0.59798 (51)	0.05051 (5)	0.11717 (19)	0.10909 (4)
010001101000	0.40404 (24)	0.14545 (27)	0.28687 (8)	0.96364 (28)	0.78788 (7)
000011110000	0.53333 (26)	0.00202 (5)	0.01818 (4)	1.00000 (32)	0.02424 (3)
010001010010	0.59596 (27)	0.42626 (43)	0.64646 (11)	0.78182 (25)	1.00000 (9)
100000000111	0.92323 (34)	0.99798 (93)	0.75758 (12)	0.01010 (16)	0.02424 (3)
000000001111	1.00000 (42)	0.89697 (69)	0.01818 (4)	0.01010 (16)	0.00404 (2)

described and if P_i is the probability obtained for one of the five statistics for the i^{th} sequence, then the quantity:

$$-2 \sum_1^n \text{Log } P_i$$

is exactly distributed as a χ^2 with $2n$ d.f. (Fisher, 1954; Koziol & Perlman, 1978) and the corresponding null hypothesis can be tested.

For each recorded sequence, results were weighted by the number of combinations of placing M males over N positions in order to give more credit to sequences that are more accurately described (see Fig. 2). For example, a sequence of 15 eggs, constituted of 3 males and 12 females, is weighted by $C(15,3) = 455$. Finally, the relationship between mothers and the average of daughters was analysed with a canonical correlation analysis which allows to calculate and to test the correlation between sets of five variables simultaneously measured in two successive generations.

Results

The data were initially analysed by pooling the result obtained for both mothers and daughters. This is justified by the fact that no statistical differences were found between the two successive generations.

Figure 1 gives both sex ratio and cumulative sex ratio produced by *T. brassicae* females as a function of the sequence of oviposition. These graphs, which are similar to those obtained for *T. chilonis* by Suzuki *et al.* (1984) and for *T. evanescens* by van Dijken & Waage (1987), indicates that *T. brassicae* females also lay male eggs early in their ovipositional bout (here, on average, at the second position) and then mostly lay female eggs. This behaviour is statistically confirmed in Table 3 which shows that the hypothesis associated to the SMR descriptive parameter can be rejected. Thus, *T. brassicae* females do not lay their male and female eggs in a random sequence and tend to lay statistically male eggs early in an oviposition bout.

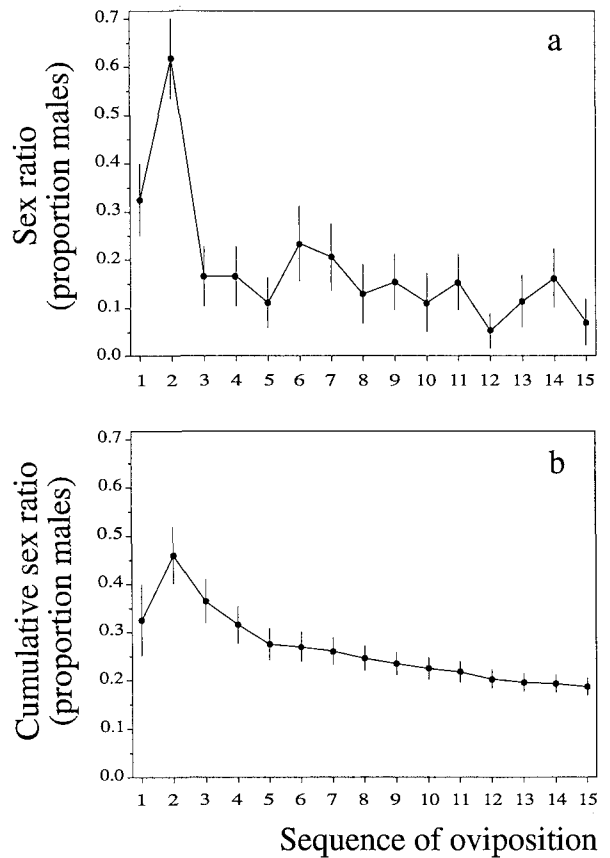


Fig. 1. Average sex ratio (a) and cumulative sex ratio (b) (\pm sd) produced by *T. brassicae* females as a function of the sequence of oviposition ($n = 48$).

Figure 2 shows a highly significant correlation between the way mothers and daughters organize the sequence of the sexes among their progeny. Contrastingly, there is no significant correlation between the mean sex ratios produced by mothers and daughters (Fig. 3). Therefore, although the variability in the sex ratios produced by fe-

Table 3. χ^2 computed on each of the five statistics used to describe the sequences of oviposition produced by 48 *T. brassicae* females (i.e. 16 mothers and 32 daughters) in order to test the associated null hypothesis (see Table 1). All χ^2 are at 96 d.f. (see text): *; $P < 0.05$; NS: Non-significant.

	SMR	VMR	CGF	CGM	NR
χ^2	125.02*	56.08 NS	38.59 NS	75.10 NS	23.66 NS

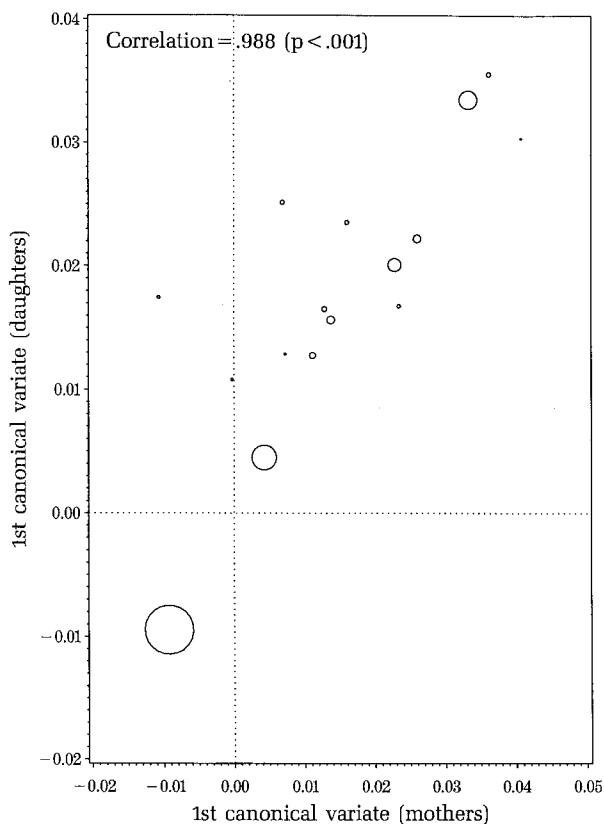


Fig. 2. Canonical correlation analysis between the sequential organization of sex allocation of 16 mothers and their daughters, as described by 5 non-parametric statistics. The canonical correlation coefficient has been tested with a standard likelihood ratio test. The weight of each point (circle surface) is proportional to the average number of combinations of M males over N positions for the corresponding mother and their two daughters. (see text). Mother-daughter correlations for each descriptive parameter taken separately are: SMR: 0.693 ($p < 0.01$); VMR: 0.252 (NS), CGF: 0.742 ($p < 0.01$); CGM: -0.073 (NS) and NR: -0.219 (NS).

males does not seem to be genetically determined in the population studied (at least for the 15 first hosts attacked), the organization of the sequence of oviposition is under a strong genetic control. In other words, within the population analysed, the way the females organize their sequences of oviposition is under genetic control, but the mean sex ratio does not seem to be heritable. This result can be explained by the fact that the statistical parameters used to describe the sequential organization of the sequences produced are built

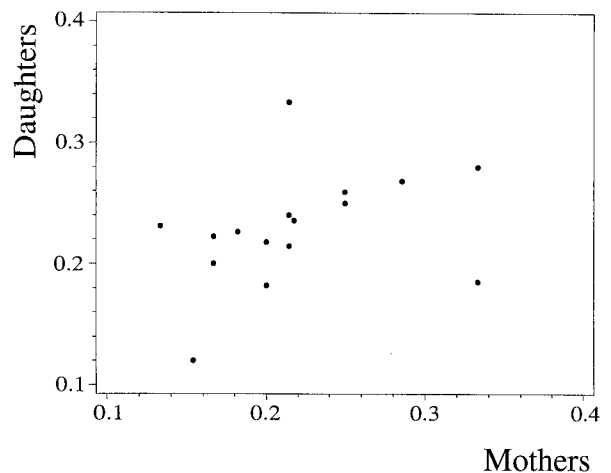


Fig. 3. Relationship between the average sex ratio (proportion males) produced by the 16 *T. brassicae* mothers and their daughters. ($r = 0.37$ (NS), on arcsin square root transformed data).

to be uncorrelated with the corresponding sex ratio.

Discussion

Sex allocation strategies in parasitic wasps have been generally considered from the point of view of mean sex ratios (Maynard Smith, 1978; King, 1987). In the present study, however, sequences in which sons and daughters are produced are studied without taking into account the corresponding sex ratio. Sex ratio determinism and sex-sequence pattern can be functionally independent. Therefore, sex ratio analysis without taking into account an accurate description of sequence behaviours could be incomplete. This especially holds for haplo-diploid species for which a LMC is likely to occur, because, in such a case, a significant part of the selective values involved is neglected.

The results presented here show that *T. brassicae* females tended to lay their male eggs at the beginning of an oviposition bout. Such a 'male-first' strategy has already been observed for *T. chilonis* (Suzuki *et al.*, 1984) and for *T. evanescens* (Waage & Lane, 1984; Waage & Ng, 1984; van

Dijken & Waage, 1987). The present work provides a statistical verification of such a sex-sequence organization.

As suggested by Waage & Lane (1984), as long as females tend to lay fewer eggs to avoid super-parasitism, this behaviour would simply explain how mothers can increase the sex ratio in their progeny under decreasing LMC. According to these authors, this would be the main mechanism by which wasp females change their sex ratio in response to their own density on a host patch. Three other mechanisms are a shift of sex allocation in response (1) to the frequency of physical contacts with other females while ovipositing (Wylie, 1976), (2) to the perception of chemical traces left by previous females on the patch (Viktorov & Kochetova, 1973) or (3) to the frequency of encounters with already parasitized hosts (Wylie, 1973).

Despite the fact that the present experiment has been done under standardized conditions, Fig. 2 shows that, in the studied population, there is a substantial variation in the sex-sequence pattern over two successive generations. The corresponding correlation strongly indicates that the way *T. brassicae* females organize the sequence of the sexes in their progeny is genetically determined. Thus, it indicates that there is a genetic variability in the strategy used by wasp females to produce a given sex ratio. In spite of this, Fig. 3 suggests that the sex ratio produced by the females does not seem to be under a genetic control. This last result, which is in contradiction with those obtained by Chassain & Boulétreau (1991) on another population of the same species, could be explained by the fact that sex ratios are estimated here from the 15 first hosts attacked by each female only. The total number of parasitized hosts by a *T. brassicae* female is commonly greater than 90, at least under laboratory conditions (Pin-tureau *et al.*, 1981). Therefore, the sex ratios analyzed here are likely poor estimations of the proportion of males really laid by wasp females in the field.

The genetic variation in sex-sequence pattern may indicate that natural selection is not acting on that trait among individuals. However, in the

species studied here, LMC is strongly suspected under natural conditions because (1) its natural host shows a strong aggregated spatial distribution, (2) usually, each egg-mass is attacked by only few females, (3) males always emerge before females and wait for them for mating, and (4) LMC has been found for *T. evanescens* (Waage & Lane, 1984) which is a closely related species. Therefore, under such conditions, females are strongly selected to produce accurate sex ratios, and the existence of the genetic variability observed suggests that *T. brassicae* females are still able to evolve in response to environmental constraints, and thus progressively increasing their fitness. In particular, the existence of such genetic variation has probably been involved in the evolution of a female-biased sex ratio under LMC.

The statistical procedure developed in the present study leads to an accurate quantification of the sex-sequence produced by each female without taking into account the corresponding average sex ratio. This procedure, which could be used to detect subtle sex-sequence patterns under different conditions, is thus likely to be a powerful tool for a better understanding of sex allocation strategies in parasitic wasps. Especially, such a procedure could be fruitfully used to look for a change in sex-sequence pattern under different levels of LMC, although no effect has been found by Van Welzen & Waage (1987) on *Telenomus remus*. This statistical tool is being used presently to compare different related wasp species or to find possible correlations between sex-patterns produced by females and different biological and/or ecological host features (i.e. size, age, spatial distribution, etc.).

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