

## Insect Parasitoids

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E. WAJNBERG

### A NEW STATISTICAL METHOD FOR QUANTIFYING SEX PATTERNS WITHIN SEQUENCES OF OVIPOSITION PRODUCED BY PARASITIC WASPS

*Abstract* - A new statistical method, using both non-parametric and multivariate analyses, is described for quantifying sex patterns within sequences of oviposition produced by hymenopterous wasp females.

KEY-WORDS: Sex Allocation, Sequences of Oviposition, Non-parametric Statistics, Parasitoids.

Hymenopterous egg parasitoids are haplodiploids, with males developing from unfertilized eggs and females from fertilized ones. Using this sex determination mechanism, females are thus able to determine their offspring sex ratio by controlling the proportion of fertilized eggs they lay. An evolutionary consequence of this is that it allows wasp females to produce a more accurate sex ratio than one stemming from a binomial (i.e. stochastic) process (GREEN *et al.*, 1982). Based on experimental results, several recent studies on parasitoid sex allocation strategy suggest that wasp females could do this by laying their son and daughter eggs in a particular order (see WAAGE, 1986; VAN WELZEN and WAAGE, 1987; STRAND, 1988 and others).

Although such sex sequence patterns have been analysed under different conditions, no efficient statistical procedure has ever been provided to quantify them accurately. The present paper proposes a procedure using both non-parametric and multivariate analyses. This procedure has been used to study the genetic (i.e. polygenic) variation in the way *Trichogramma maidis* PINTUREAU and VOEGELÉ (Hym.: Chalcidoidea) females organize the sequence of the sexes in their progeny. Other examples of the use of this method are proposed.

#### STATISTICAL PROCEDURE

Assume that the sequence to be described, produced by a given female, is

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\* I.N.R.A. Laboratoire de Biologie des Invertébrés, Unité de Biologie des Populations 37 Bd. du Cap., 06600 Antibes, France.

constituted of  $N$  individuals among which  $M$  are males, and let  $rm_{(i)}$  the rank of the  $i^{\text{th}}$  males ( $i=1, 2, \dots, M$ ) and  $rf_{(j)}$  the rank of the  $j^{\text{th}}$  female ( $j=1, 2, \dots, N-M$ ). Five non parametric statistics are computed from these rank data. These five statistics are:

1) «Sum of Males Rank Position» (SMR) =  $\sum_{(i)} rm_{(i)}$ , which is all the smaller as the males are laid early at the beginning of the sequence.

2) «Variance of Males Rank Position» (VMR) =  $\sum_{(i)} (rm_{(i)} - (N+1)/2)^2$ , which describes whether the males (resp. the females) are laid in the middle (resp. at the extremities) of the sequence or not.

3) «Center-Group of Males» (CGM) =  $\sum_{(i)} |rm_{(i)} - Q|$ , where  $Q = rm_{((M+1)/2)}$  if  $M$  is odd, and  $Q = rm_{((M/2)+1)}$  if  $M$  is even.

4) «Center-Group of Females» (CGF) =  $\sum_{(j)} |rf_{(j)} - R|$ , where  $R = rf_{((N-M+1)/2)}$  if  $N-M$  is odd, and  $R = rf_{((N-M)/2+1)}$  if  $N-M$  is even. These two last statistics describe whether there is some pooling of males (for CGM) or females (for CGF) within the sequence or not.

5) «Number of Runs of Males or Females» (NR) =  $2 + \sum_{(i)} d_{(i)} + \sum_{(j)} z_{(j)}$ , where  $d_{(i)} = 1$  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. This last parameter shows if there is an autocorrelation of males or females within the sequence or not.

Then, in order to compare the description of sequences differing in length or composed with different sex ratios, for each of these five statistics, and for each of the oviposition sequences, 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 placing  $M$  males over  $N$  positions. Each sequence of oviposition is thus described with a set of five parameters, according to their sequential organization but without taking into account the corresponding sex ratio.

#### TEST OF THE METHOD

This method has been tested with the description of all the 56 possible combinations of placing three males in a sequence of eight eggs. The raw data are given in Table 1. Figure I gives the graphical results of a corresponding principal component analysis done on this table. This multivariate descriptive method allows us to project every described sequence on different axis with an optimized representation of the distances between each of them according to the initial data. All sequences on the left side of the 1<sup>st</sup> axis (Fig. Ia) are built with the males (which are represented by a «1») in the middle, those on the right side have the males at the extremities. Concerning the 2<sup>nd</sup> axis, negative values refer to sequences where the males are overdispersed, and positive values refer to sequences where males are lumped together. Finally, on the 3<sup>rd</sup> axis (Fig. Ib), on the top, sequences where males are laid at the end are found, on the bottom, sequences where males are laid at the beginning. Therefore,

Table 1: Quantitative description, with five non-parametric statistics, of all the 56 possible sequences of placing three males in a sequence of eight eggs. (S.M.R.): Sum of males rank position; V.M.R.: Variance of males rank position; C.G.M.: Center-group of males; C.G.F.: Center-group of females; N.R.: Number of runs of males or females).

Sequences	S.M.R.	V.M.R.	C.G.M.	C.G.F.	N.R.
00000111	1.0000000	0.8571429	0.1071429	0.0714286	0.0357143
00001011	0.9821429	0.7142858	0.2857143	0.1785714	0.4285715
00001101	0.9642858	0.5357143	0.2857143	0.3928571	0.1285715
00001110	0.9285714	0.2500000	0.1071429	0.6071429	0.1428571
00010011	0.9642858	0.7142858	0.5000000	0.3928571	0.4285715
00010101	0.9285714	0.5357143	0.5000000	0.6071429	0.9285714
00010110	0.8750000	0.2500000	0.2857143	0.8214286	0.7142858
00011001	0.8750000	0.3571429	0.5000000	0.8214286	0.4285715
00011010	0.8035714	0.1071429	0.2857143	0.9285714	0.7142858
00011100	0.7142858	0.0357143	0.1071429	1.0000000	0.1428571
00100011	0.9285714	0.8571429	0.7142858	0.3928571	0.4285715
00100101	0.8750000	0.5714286	0.7142858	0.6071429	0.9285714
00100110	0.8035714	0.2857143	0.5000000	0.8214286	0.7142858
00101001	0.8035714	0.5357143	0.7142858	0.8214286	0.9285714
00101010	0.7142858	0.2500000	0.5000000	0.9285714	1.0000000
00101100	0.6071429	0.0714286	0.2857143	1.0000000	0.7142858
00110001	0.7142858	0.5357143	0.7142858	0.8214286	0.4285715
00110010	0.6071429	0.2500000	0.5000000	0.9285714	0.7142858
00110100	0.5000000	0.0714286	0.2857143	1.0000000	0.7142858
00111000	0.3928571	0.0357143	0.1071429	1.0000000	0.1428571
01000011	0.8750000	0.9285714	0.8928571	0.1785714	0.4285715
01000101	0.8035714	0.8571429	0.8928571	0.3928571	0.9285714
01000110	0.7142858	0.5357143	0.7142858	0.6071429	0.7142858
01001001	0.7142858	0.7142858	0.8928571	0.6071429	0.9285714
01001010	0.6071429	0.3571429	0.7142858	0.8214286	1.0000000
01001100	0.5000000	0.2500000	0.5000000	0.9285714	0.7142858
01010001	0.6071429	0.7142858	0.8928571	0.6071429	0.9285714
01010010	0.5000000	0.3571429	0.7142858	0.8214286	1.0000000
01010100	0.3928571	0.2500000	0.5000000	0.9285714	1.0000000
01011000	0.2857143	0.1071429	0.2857143	0.9285714	0.7142858
01100001	0.5000000	0.8571429	0.8928571	0.3928571	0.4285715
01100010	0.3928571	0.5357143	0.7142858	0.6071429	0.7142858
01100100	0.2857143	0.2857143	0.5000000	0.8214286	0.7142858
01101000	0.1964286	0.2500000	0.2857143	0.8214286	0.7142858
01110000	0.1250000	0.2500000	0.1071429	0.6071429	0.1428571
10000011	0.8035714	1.0000000	1.0000000	0.0714286	0.1428571
10000101	0.7142858	0.9642858	1.0000000	0.1785714	0.7142858
10000110	0.6071429	0.8571429	0.8928571	0.3928571	0.4285715
10001001	0.3071429	0.9285714	1.0000000	0.3928571	0.7142858
10001010	0.5000000	0.7142858	0.8928571	0.6071429	0.9285714
10001100	0.3928571	0.5357143	0.7142858	0.8214286	0.4285715
10010001	0.5000000	0.9085714	1.0000000	0.3928571	0.7142858
10010010	0.3928571	0.7142858	0.8928571	0.6071429	0.9285714
10010100	0.2857143	0.5357143	0.7142858	0.8214286	0.9285714
10011000	0.1964286	0.3571429	0.5000000	0.8214286	0.4285715
10100001	0.3928571	0.9642858	1.0000000	0.1785714	0.7142858
10100010	0.2857143	0.8571429	0.8928571	0.3928571	0.9285714
10100100	0.1964286	0.5714286	0.7142858	0.6071429	0.9285714
10101000	0.1250000	0.5357143	0.5000000	0.6071429	0.9285714
10110000	0.0714286	0.5357143	0.2857143	0.3928571	0.4285715
11000001	0.2857143	1.0000000	1.0000000	0.0714286	0.1428574
11000010	0.1964286	0.9285714	0.8928571	0.1785704	0.4285715
11000100	0.1250000	0.8571429	0.7142858	0.3928571	0.4285715
11001000	0.0714286	0.7142858	0.5000000	0.3928571	0.4285715
11010000	0.0357143	0.7142858	0.2857143	0.1785714	0.4285715
11100000	0.0178571	0.8571429	0.1071429	0.0714286	0.0357143

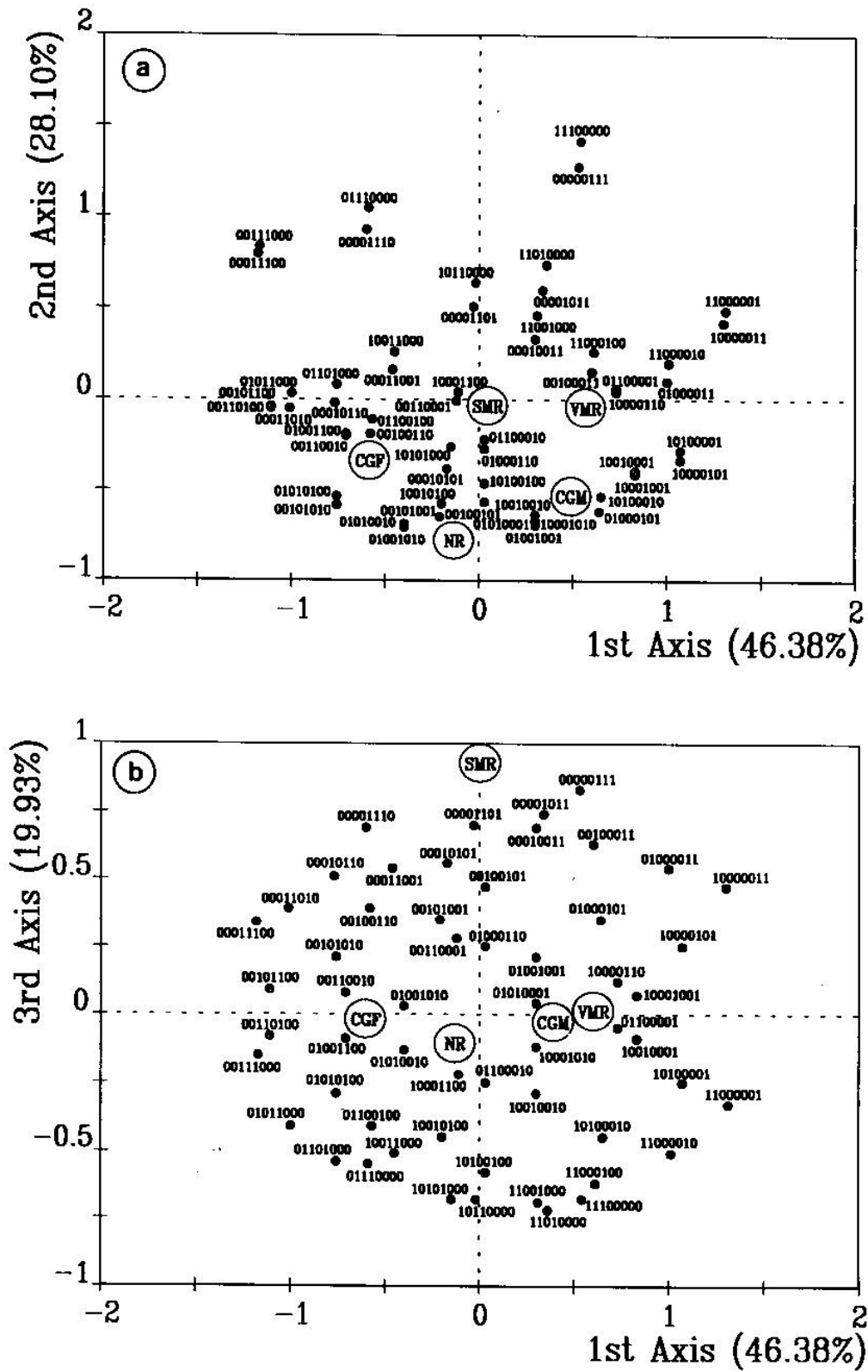


Fig. I

Graphical results of a principal component analysis done on the data presented in Table 1  
a) 1<sup>st</sup> and 2<sup>nd</sup> axis. b) 1<sup>st</sup> and 3<sup>rd</sup> axis.

although all these sequences are composed with the same sex ratio, this descriptive method enables us to quantify accurately them according only to their sequential organization.

GENETIC VARIATION IN SEX-SEQUENCE PATTERN PRODUCED  
BY *T. MAIDIS* FEMALES

This method has been used to describe oviposition sequences produced by a set of *T. maidis* females and by their daughters. Indeed, a significant relationship between the two successive generations would strongly indicate that the way females organize their sequences of oviposition would be under a genetic control.

As a matter of fact, using a multivariate regression method (i.e. canonical regression analysis) it has been shown, for a given population, that there is a strong correlation ( $p < 0.001$ ) between the way mothers and daughters organize the sequences of the sexes in their progeny (WAJNBERG, 1991). This result thus suggests that there is a genetic variability in the strategies used by the females to produce an accurate sex ratio.

FURTHER STUDIES

At the moment, further statistical methods are being developed in order to analyse sequences with missing or ambiguous data (i.e. when the sex of an egg cannot be known because of mortality before emergence, or when two or more eggs are laid in the same host without knowing their order). These developments will then be used to compare different related arrhenotokous wasp species that are known to live in different habitats and to attack different hosts. They will also be used to describe any kind of relationships between sex-sequence patterns and wasp (or host) density or host age.

REFERENCES

- GREEN R.F., GORDH G., HAWKINS B.A., 1982 — *Precise sex ratio in highly inbred parasitic wasp.* - Amer. Nat., 120: 635-655.
- STRAND M.R., 1988 — *Variable sex ratio strategy of Telenomus heliothidis (Hymenoptera: Scelionidae): Adaptation to host and conspecific density.* - Oecologia, 77: 219-224.
- VAN WELZEN C.R.L., WAAGE J.K., 1987 — *Adaptative responses to local mate competition by the parasitoid, Telenomus remus.* - Behav. Ecol. Sociobiol., 21: 359-365.
- WAAGE J.K., 1986 — *Family planning in parasitoids: adaptative patterns of progeny and sex allocation.* In: Insect parasitoids. Waage J.K., Greathead D. (eds.). Academic Press. pp 63-96.
- WAJNBERG E., 1991 — *Genetic variation in sex allocation in Trichogramma maidis: variation in the sex pattern within sequence of oviposition.* In: Trichogramma and other egg parasitoids. Wajnberg E., Vinson S.B. (eds.). Les colloques de l'IN.R.A., 56: 127-129.