Effects of Host Egg Mass Size on Sex Ratio and Oviposition Sequence of *Trissolcus basalis* (Hymenoptera: Scelionidae)

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ABSTRACT This study examines the influence of the size of the host patch (egg mass size) on the sex ratio produced by the scelionid egg parasitoid *Trissolcus basalis* (Wollaston) under laboratory conditions. The influence of this factor on the sequence in which male and female eggs are laid also is analyzed. Our detailed study shows that the size of the host patch offered to females strongly influenced both the overall sex ratio they produced, and the organization of the sequence in which male and female eggs are laid. Females adjusted their sex ratio with host number per host egg mass in qualitative agreement with the predictions of the local mate competition model and independently of oviposition sequence. Variations in the sex allocation sequences produced by *T. basalis* do not seem to depend on the ability of female wasps to assess the number of hosts per patch before oviposition. Females start egg-laying sequences by laying male eggs early in an oviposition bout in accordance with the males 1st strategy. As long as the sequences are completed, the pattern of sex allocation changes as an indirect modification in response to variation in the size of the egg mass. Such a modification in sex-sequence patterns can be considered to be an adaptive mechanism leading the females to adjust their sex ratio to different environmental conditions.

KEY WORDS *Trissolcus basalis, Nezara viridula*, sex allocation, parasitoid, egg mass size, local mate competition

MOST HYMENOPTEROUS PARASITOIDS are haplodiploid; haploid males develop from unfertilized eggs and diploid females from fertilized ones. Inseminated females store sperm in the spermatheca, and at the time of oviposition they can manipulate their offspring sex ratios according to different environmental conditions (see Hardy 1992, King 1993, Godfray 1994 for recent reviews).

Using this sex determination system, the sex ratio produced by most parasitoid species can vary from a slightly male-biased to extremely female-biased one (Flanders 1946). Extremely female-biased sex ratios have usually been observed in nonrandom mating populations (i.e., where mating takes place among the offspring of 1 or few mothers before the dispersion of the daughters to colonize new host patches). This has been described theoretically as the well-known local mate competition model (Hamilton 1967, Taylor and Bulmer 1980): When n haplodiploid females colonize a patch of hosts, the percentage of males they have to produce should be $(n - 1)(2n - 1)/n(4n - 1)$ (Taylor and Bulmer 1980). If only 1 female colonizes a patch ($n = 1$), a sex ratio of 0 is predicted. In such a case, the female should lay only enough males to fertilize all her daughters. When the number of fe-

males colonizing the patch increases, mating takes place among offspring that are not necessarily related, and the model predicts a sex ratio that progressively increases toward 50:50. Such a theoretical prediction has been verified experimentally for several quasigregarious parasitoid species, defined as those in which 1 offspring develops from each host, and the host populations show a significant aggregated spatial distribution promoting a higher level of sibling mating (Viktorov and Kochetova 1973; Waage 1982 a, b; Werren 1983; Waage and Lane 1984; Strand 1988; Wajnberg 1991a; Colazza 1994).

Under such conditions, a single female colonizing a host patch (complete local mate competition) must nonrandomly allocate male and female offspring (i.e., with less than binomial variance) (Green et al. 1982, Hardy 1992, Wajnberg 1993, Nagelkerke and Hardy 1994). Among the different mechanisms used by the female to do this, the one most often documented is that ovipositing mothers lay their son and daughter eggs in a particular order. More specifically, they usually manage to do so by laying proportionally more male eggs early in the oviposition sequence. This is the so-called "males-first strategy" (Waage and Ng 1984). Then, as the number of hosts increases, additional male eggs are laid at regular intervals (Waage 1982 a, b; Suzuki et al. 1984; Waage and Lane 1984; Waage and Ng 1984; Putters and Van den Assem 1985; van Dijken and Waage 1987; van Welzen and Waage 1987; Strand 1988; Hooker and Barrows 1989; Noda and Hirose

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1989; Velayudhan and Senrayan 1989; Wajnberg 1991a, 1993). Such a pattern of sex sequence allows female wasps to produce sex ratios approximating their optima without having to assess the size of the attacked egg mass prior to oviposition. When the foundress number increases, hosts usually are shared among females, and each female is thus likely to lay a reduced number of eggs. This results in a less female-biased sex ratio, which is in agreement with the prediction of the local mate competition model (Waage 1982a). Using a simulation model, Wajnberg (1994) quantified this phenomenon.

The scelionid wasp *Trissolcus basalis* (Wollaston) is a cosmopolitan egg parasitoid widely used in biological control (Jones 1988). Laboratory observations of life time fecundity of females reared on a honey–water solution show that they are able to produce 155.8 ± 91.2 (mean ± SD) individuals per female (Mattiacci et al. 1991). Moreover, toward the end of the oviposition period, female wasps start to lay an increasing proportion of male eggs (Mattiacci et al. 1991), suggesting that they did not receive a sufficient amount of sperm to fertilize all of their progeny (i.e., sperm depletion).

This wasp species is known to attack a wide range of pentatomid hosts (Jones 1988). In central Italy, the species was recovered mainly from egg masses of *Nezara viridula* (L.), and infrequently from egg masses of *Carpocoris mediterraneus* Tamanini and *Piezodorus lituratus* (F.) (Colazza and Bin 1995). These hosts show differences in egg mass size both within a species (e.g., *N. viridula* egg masses range from 44 to 134 eggs (91.0 ± 16.6 eggs, $n = 260$), and between species (e.g., from ≈14 eggs per egg mass on *C. mediterraneus* to ≈90 eggs per egg mass on *N. viridula*) (Colazza and Bin 1995). Such a variability in host egg mass size may induce a corresponding variation in the sex ratio laid by female wasps. As a matter of fact, laboratory observations have shown that *T. basalis* females produce different progeny sex ratios attacking *N. viridula* egg masses of different size, which is in qualitative agreement with the predictions of the local mate competition model (Colazza et al. 1991). The relationship between the sex ratio produced by ovipositing female wasps and the number of hosts attacked has already been investigated with other egg parasitoids (e.g., *Telenomus heliothidis* Ashmead; Strand 1988), showing that sex ratios become more female-biased as the number of hosts per egg mass increases. This was shown to be in agreement with the prediction of the local mate competition model, and was explained mainly by the fact that females were showing a significant males-first oviposition strategy (Strand 1988). However, it was not clear whether laying females were able to estimate the size of the host egg masses they were offered and to change the sex ratio they produced accordingly, or if the change observed in the sex ratio was only an indirect consequence of a fixed males-first oviposition strategy.

Sex ratio and sex sequence patterns can be functionally independent, so an accurate quantification and description of the sex sequence produced by female wasps could be useful for a better understanding of their sex allocation strategy (Wajnberg 1993). Hence, in this article we analyze changes in both sex ratio and oviposition sequence in response to host egg mass size on the association between *T. basalis* and *N. viridula*. For this, we use the specific statistical procedure developed by Wajnberg (1991b, 1993) for quantifying and analyzing sex sequence patterns. This method is used to verify whether mechanisms other than the males-first strategy (e.g., egg count) are used by females in response to a change in host egg mass size.

The results indicate that the number of host eggs per patch greatly affects both sex ratio and oviposition sequence of *T. basalis*. The adaptive significance of these results is discussed.

Materials and Methods

Insects. Our *T. basalis* stock originated from a colony established from wasps that emerged from *N. viridula* egg masses collected in central Italy, and they were between the F_1 and F_6 laboratory progeny of field-collected adults. Wasps were provided with honey–water solution (honey mixture 10%), containing vanilla-flavored powdered sugar 10%, yeast 10%, and benzoic acid 1% (Safavi 1968), and were caged in 16-ml glass tubes at 24 ± 2°C; 70 ± 5% RH, under a photoperiod of 16:8 (L:D) h. At emergence, *T. basalis* females were kept with males for 24 h to allow mating. Females were then isolated, provided with a drop of honey solution, and used in experiments when they were 2–3 d old (the age at which a female can produce the maximum number of progeny without previous oviposition experience) (unpublished data). Pairs of adult *N. viridula* were caged in ≈0.02-liter plastic containers ventilated with mesh-covered holes (5 cm diameter). Paper towel strips were hung from the inside edge of each cage as an oviposition substrate. Egg masses were collected daily to prevent possible cannibalism. Host eggs used in all experiments were <1 d old.

Experimental Protocol. The experimental unit consisted of a circular arena (1.5 cm diameter, 0.5 cm high) covered with a glass lid. All observations were video-recorded with a VCR system mounted on a stereomicroscope illuminated with a low-intensity light. Wasps were individually placed on patches of 4 (10), 8 (10), 16 (10), 32 (10), 64 (10), and 128 (5) host eggs (number of replicates in parentheses). Females were removed from the host as soon as all eggs were parasitized, or (for 128 eggs per egg mass) when the female failed to oviposit for 3 h. Wasps rarely tried to superparasitize; however, when they attempted to do so, the females were delicately pushed off with forceps. Parasitized host egg masses were held in a bioclimatic chamber (24 ± 1°C, 70 ± 5% RH) until parasitoids pupated in 6–7 d, then isolated in vials. The sex of all progenies was recorded at adult emergence, and the sequence in which male and female eggs were deposited was obtained using the

video record. The developmental mortality of parasitoid progeny was rare (<1%) and was recorded as missing values. All experiments were conducted in the laboratory (at 20–22°C, 30–40% RH).

Statistical Analysis. Sex ratios (expressed as male percentage) were analyzed by means of a logistic regression model, a generalized linear model specially designed for modeling binomial data using a logit link function (McCullagh and Nelder 1989). Pairwise tests were performed by choosing appropriate contrasts, and an overall significance level of 5% was maintained using a modified Bonferroni procedure (Hochberg 1988). All the corresponding computations were done with S-Plus (Venables and Ripley 1994). *T. basalis* oviposition sequences were described by the nonparametric multivariate method provided by Wajnberg (1991b, 1993). Each oviposition sequence was analyzed by a set of 5 nonparametric statistics describing different sequential features of the oviposition sequences. These statistics were as follows: (1) the sum of the males' rank position showing if males are laid at the beginning of the sequence, (2) the variance of the males' rank position showing if males are laid in the middle of the sequence, (3) the center group of males describing if there is some pooling of males within the sequence, (4) the center group of females showing if there is some pooling of females within the sequence, (5) the number of run of males or females that enables any autocorrelation of males or females within the sequence to be identified.

To describe sequences differing in length or composed of different sex ratios, these 5 parameters were first transformed into the exact probability corresponding to the 1st-level risk of the associated null hypothesis (see Wajnberg [1993] for a more detailed description). Then, using 1-way analyses of variance (ANOVA) on each parameter separately, this 5-parameter description was used to compare sequences of oviposition produced by the *T. basalis* females on *N. viridula* egg masses of different sizes. A standard factorial discriminant analysis (also called a canonical discriminant analysis) also was performed to take into account the multivariate feature of the data. This method allows describing each sequence of oviposition on successive canonical axes with decreasing importance (i.e., variance). These axes have the property of maximizing the inter–intra variance ratio. To understand the meaning of the axes obtained, their correlation with the original parameters were computed and graphically represented in the standard form of a correlation circle. All the corresponding computation were done with SAS (PROC CANDISC) (SAS Institute 1988).

Results

The sex ratios produced by *T. basalis* females differed significantly in response to the size of the host patch offered ($\chi^2 = 34.00$, df = 5, $P < 0.001$) (Fig. 1). Mean sex ratios progressively fell as the number of
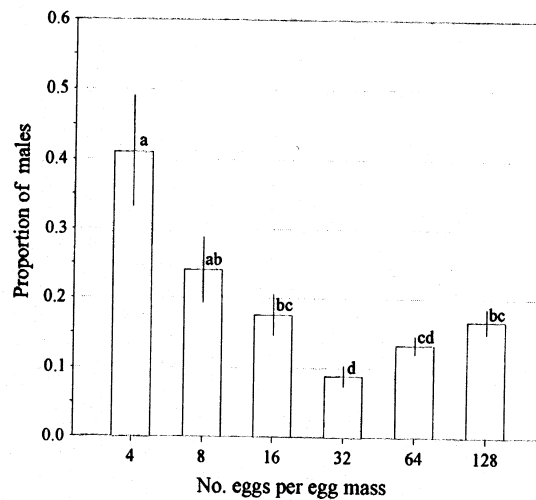

Fig. 1. Sex ratio (mean ± SD) produced by *T. basalis* as a function of *N. viridula* egg mass size. Values marked with the same letters do not differ significantly at $P < 0.05$.

host eggs per egg mass increased (from 0.405 ± 0.014 % males for 4 eggs per egg mass to 0.087 ± 0.002 for 32 eggs per egg mass). Then, sex ratios from egg masses with 64 and 128 eggs slightly increased (0.129 ± 0.005 and 0.168 ± 0.004, respectively). Fig. 2 presents both the sex ratio and cumulative sex ratio produced by *T. basalis* females as a function of the oviposition sequence on patches of different sizes. The statistical description of such sequences (Table 1) shows that, in addition to the change in their overall sex ratio (see Fig. 1), female wasps also changed the organization of the sequences in which they lay male and female eggs. Using a factorial discriminant analysis (Fig. 3), such changes were found to follow a particular trend (see also Table 1). More specifically, oviposition sequences produced on patches of 4 eggs showed relatively high values for the center group of females and number of run of males or females. This indicates that daughters are rather dispersed along the sequence; therefore, such a short sequence does not appear to be really well structured. In this case, because the 1 egg laid is always a male (Fig. 2), the absence of a particular structure concerns only the sequence in which the 3 additional eggs are laid after the 1st one. On patches of 8 eggs, the sequences showed a decrease in both center group of males and sum of the male's rank position. This is because daughters are added mostly at the end of the sequence, increasing the intensity of the males-first strategy. This effect became more evident when wasps attacked patches of 16 and 32 eggs. In these cases, very low values of the sum of the male's rank position were obtained. Finally, on patches of 64 and 128 hosts, males were progressively added at the end of the sequence (increasing value for the sum of the male's rank position), decreasing the intensity of the males-first strategy, and increasing the global dispersion of sons within the sequence (high value for the variance of the male's rank position).
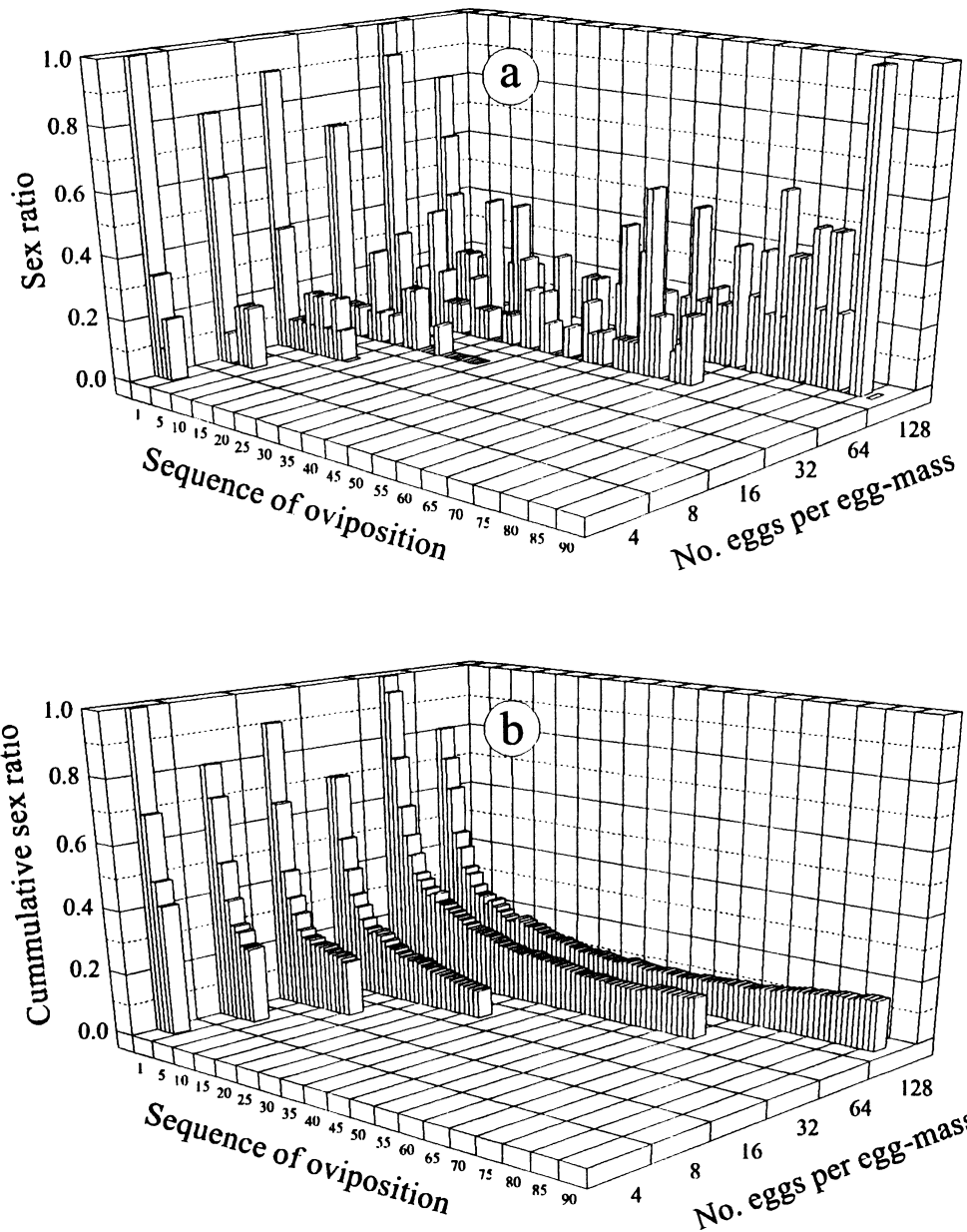
Fig. 2. (a) Sex ratio (expressed as proportion of males) and (b) cumulative sex ratio produced by *T. basalis* females as a function of the sequence of oviposition on *N. viridula* egg masses of different sizes.

Discussion

According to the prediction of the local mate competition model, a decrease in the number of hosts offered to the females should result in an increased proportion of male eggs laid (Strand 1988). Results presented in Fig. 1 show that this is indeed the case for the scelionid *T. basalis* studied here. This suggests that local mate competition operates for this species under natural conditions. In fact, local mate competition was already suspected for the following 3 reasons: (1) its natural hosts usually show a strong aggregated spatial distribution, and parasitoid females are likely to copulate at the emergence site before dispersion; (2) host egg masses are attacked by 1 female or a few females; and (3) males always emerge before females and wait for them for mating (Wilson 1961, Volkoff and Colazza 1992, Colazza and Bin 1995). Working on another scelionid egg parasitoid, *Telenomus remus* Nixon, van Welzen and Waage (1987) found that male and female

Table 1. *T. basalis* oviposition sequences (mean ± SD) laid on *N. viridula* egg masses of different sizes

No. eggs	SMR	VMR	CGM	CGF	NR
4	0.3125 ± 0.1937	0.9250 ± 0.0829	0.8083 ± 0.2292	0.5333 ± 0.1054	0.5250 ± 0.2081
8	0.2071 ± 0.1654	0.8804 ± 0.1017	0.7589 ± 0.3158	0.2821 ± 0.1769	0.4714 ± 0.3366
16	0.2178 ± 0.0849	0.7837 ± 0.1539	0.8304 ± 0.1594	0.3436 ± 0.2084	0.4034 ± 0.2704
32	0.0878 ± 0.1053	0.8430 ± 0.1169	0.5129 ± 0.2593	0.2411 ± 0.2002	0.3588 ± 0.3943
64	0.2760 ± 0.2867	0.9686 ± 0.0562	0.8928 ± 0.1164	0.0434 ± 0.0544	0.1366 ± 0.1661
128	0.7353 ± 0.2805	0.9797 ± 0.0180	0.7902 ± 0.4101	0.0415 ± 0.0381	0.1087 ± 0.1261
F	8.147	4.706	2.823	12.873	13.186
P	<0.01	<0.01	<0.05	<0.01	<0.01

SMR, sum of the males' rank poisiton; VMR, variance of the males' rank position; CGM, center-group of males; CGF, center-group of females; NR, number of runs of males or females. df = 5, 49 for all *F* tests.

eggs were not laid according to random sequence patterns. Such nonrandom sex sequences also have been observed for several other parasitoid species (Mertins 1980; Waage 1982 a, b; Putters and Van den Assem 1985; Strand 1988; Hooker and Barrows 1989; Velayudhan and Senrayan 1989; Wajnberg 1993; Colazza 1994). Moreover, a change in such sequence pattern in response to the number of contacts between females foraging on a host patch has been already found (van Welzen and Waage 1987, Colazza 1994). Here, however, we found a change in sex sequence patterns in response to the size of the host patch offered to *T. basalis* females. Because this is the case here, nonrandom sex sequences usually show proportionally more males at the beginning. Such a males-first strategy has repeatedly been considered as an efficient way for quasigregarious parasitoid females to adjust the sex ratio in response to their own density on a host patch (Waage 1986, Wajnberg 1994). As suggested by Waage and Lane (1984), as long as females tend to lay fewer eggs to avoid superparasitism, this strategy simply would explain how mothers can increase the sex ratio of their progeny when they are offered a decreasing number of hosts, which is in agreement with the results presented in Fig. 1.

Using a males-first strategy, ovipositing females do not necessarily have to evaluate the number of hosts available within a patch to decide what sex ratio they should produce before any oviposition (Green et al. 1982, Waage 1986, Waage and Ng 1984, Noda and Hirose 1989, Hardy 1992). Instead, broods are simply and progressively produced by attacking hosts 1 by 1 (Hardy 1992). Despite this, results presented here show that, in response to host density, females change the sex ratio they produce, and more specifically, the sex sequence in which they lay their male and female eggs. This suggests that females also would be able to evaluate the number of hosts they are offered and to change their sex allocation strategies accordingly.

Two mechanisms could be involved to explain the results obtained. Either *T. basalis* females can perceive the entire size of the host patch when they start ovipositing and adjust their sex ratios and sequences accordingly, or the observed changes are only an indirect result of a progressive modification in sequence structure as long as sequences are completed by laying

females. The 1st hypothesis certainly could be true because, at an oviposition site, several physical cues are probably available for females to estimate the size of the host patch they are offered. Physical factors are often cited as influencing sex ratio, host acceptance and clutch size adjustment in parasitoid wasps (Schmidt 1991). Once on a host patch, a female usually drums the entire outer edge of the egg mass with the tips of her antennae before concentrating on 1 or 2 eggs (Wilson 1961, Colazza et al. 1991, Bin et al. 1993). In all likelihood, during such host examination behavior, wasps can acquire information about the number of eggs constituting the patch on which they are foraging.

However, are female wasps really able to detect the size of the egg mass they are offered and to change their sex ratio and sequence oviposition accordingly? To answer this question, the short oviposition sequences obtained on small egg masses were compared with the beginning of the sequences obtained on larger egg masses truncated to the same length. For all 5 conditions (e.g., sequences from patches of 4–128 eggs reduced to a length of 4, sequences from patches of 8–128 eggs reduced to a length of 8) the sequences obtained were described and compared with the 5 nonparametric statistics used above (Wajnberg 1991b, 1993). In no case were the results significant. This strongly suggests that, on starting their ovipositions, females do not assess the number of hosts available within the patch they are offered. At least, if ever they are able to do so, they do not change their oviposition sequences accordingly.

Hence, changes observed in the sex sequence pattern in response to a variation in the size of the patch offered to females seem to be caused only by an indirect modification in a sequence's structure as long as sequences are progressively completed. Thus, on average, females start their egg-laying sequences with males. Then, they lay a certain number of females, and, at a particular moment in the sequence, they progressively start to lay an increasing proportion of male eggs. As stated by Waage (1982b, 1986) and other authors, such a switch in the sequence, leading the females to start laying progressively more males eggs, could be caused by some constraining factors such as
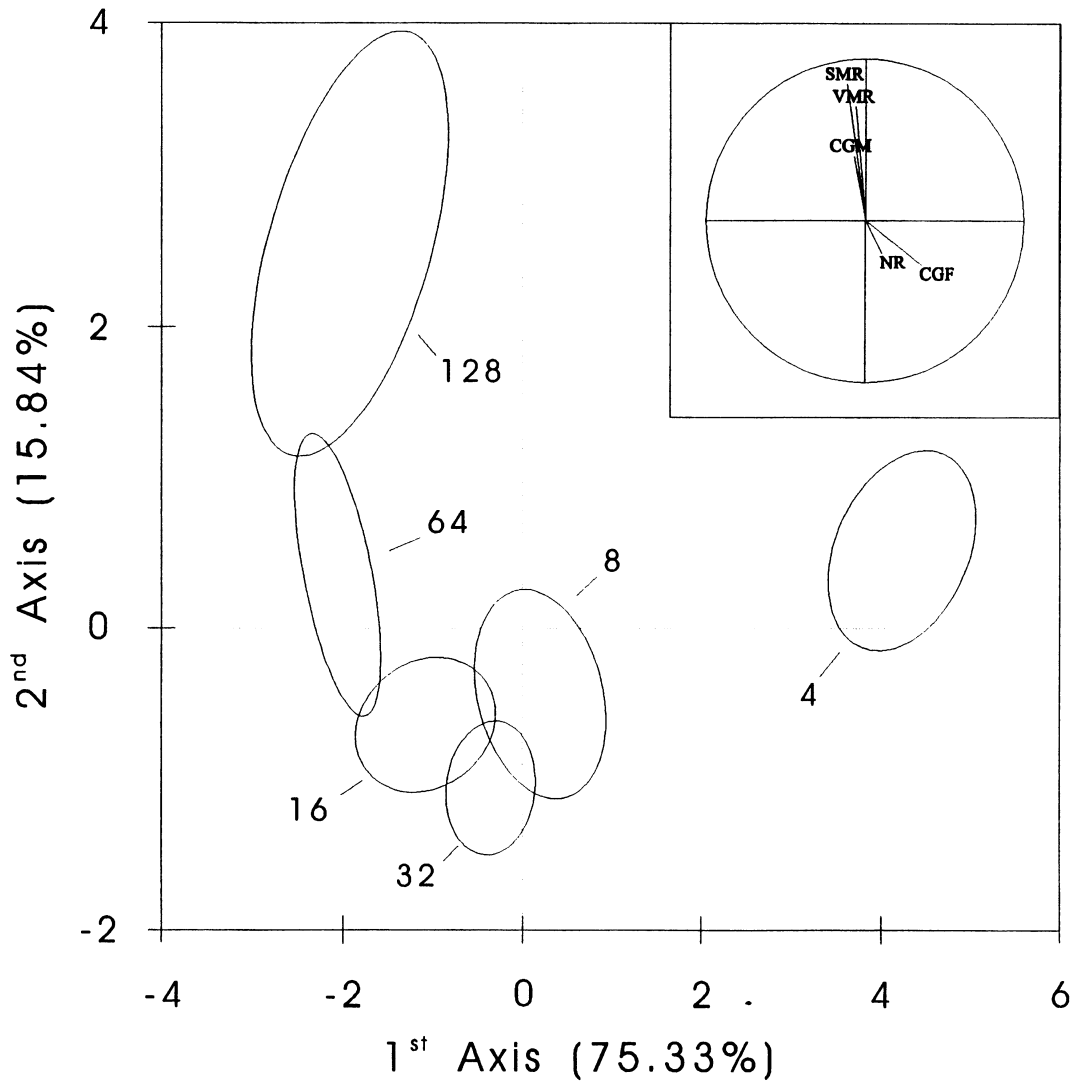
Fig. 3. First and 2nd axis (with percentage variation explained) of a factorial discriminant analysis done on the statistical description of sequences of oviposition of *T. basalis* laid on *N. viridula* egg masses of different sizes (4, 8, 16, 32, 64, or 128 eggs per egg mass). Ellipses represent 95% confidence intervals around the means. The correlation circle of the corresponding plan is provided, see text for further explanations and Table 1 for definition of oviposition sequences.

sperm depletion (Hardy 1992, King 1993). *T. basalis* females are known to mate usually only once (Wilson 1961, unpublished data). So, on large host patches, such sperm depletion is likely to occur. In return, such a mechanism will ensure the addition of extra sons, which will increase the probabilities that females are inseminated. Because both sex ratio strategy and sex sequence patterns produced by *T. basalis* females have been shown to change according to the size of the host patch they are foraging on, experiments are being considered now to compare sex ratio strategies adopted by *T. basalis* females attacking eggs of different host species that are known to be distributed in different-sized patches.

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