Sex allocation in *Telenomus busseolae*, a solitary parasitoid of concealed eggs: the influence of host patch size

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Abstract

Telenomus busseolae Gahan (Hymenoptera: Scelionidae) is an important egg parasitoid of noctuid stem borers of gramineous crops, attacking egg masses of *Sesamia* spp. Under natural conditions, and whatever the host species attacked, these egg masses are generally concealed under the leaf sheaths or other narrow spaces, and vary greatly in size. In the work presented here, the influence of host patch size (4, 8, 16, 32, 64, or 128 eggs per mass) on the sex ratio and sex sequence pattern of ovipositing *T. busseolae* was investigated in the laboratory using *Sesamia nonagrioides* (Lefebvre) (Lepidoptera: Noctuidae) as host. The results are similar to those described for other parasitoids of aggregated hosts, and are in accordance with the Local Mate Competition model. With increasing egg mass size, the overall sex ratio (proportion of males) decreased, although additional males were laid at the end of the sequence in the larger masses (64 and 128 eggs). Sex sequence pattern always followed a males-first strategy, i.e., with a higher proportion of males at the beginning, but the whole sex ratio sequence was influenced by the size of the egg mass. Such results in a parasitoid of concealed eggs are compared to those observed in parasitoids of exposed eggs and discussed in terms of parasitoid reproductive strategies and evolutionary adaptations.

Introduction

Sex allocation in arrhenotokous (haplodiploid) Hymenoptera and its evolutionary bases have been studied intensively over the last 20 years (Charnov, 1982; Cook, 1993; Godfray, 1994; Hardy, 1997). For these insects, unfertilized haploid eggs develop into males and fertilized (diploid) eggs develop into females. Under such a sex determination system, a virgin female only produces males, whereas a mated female is able to manipulate the sex ratio of her offspring in response to local conditions.

This ability is particularly effective when the assumptions of Fisher's principle of equal investment in the sexes, implying a 1 : 1 sex ratio (Fisher, 1930), do not apply – when populations are spatially structured and therefore mating is restricted to a local area or natal patch instead of being population-wide. In such non-random mating populations, there is a high probability that mating occurs between siblings before the females disperse to colonize other patches, and that brothers compete together for mates. A direct consequence of this is that sex ratios are most often female biased, as was first demonstrated by W.D. Hamilton, who called this mechanism 'local mate competition' (LMC) (Hamilton, 1967; Godfray, 1994). A sex ratio biased towards females in such populations is favoured by natural selection, as it reduces the competition among male siblings for mates, and increases the number of potential mates for each female's son (Taylor, 1981).

The LMC often applies to highly inbred gregarious parasitoid populations, where mating occurs within the offspring of one or few parental females (Werren, 1980; Waage & Lane,

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1984), and in pollinating and non-pollinating fig wasps (West et al., 1997; Flanagan et al., 1998). However, solitary parasitoid species are also under LMC when they attack patchily distributed hosts, leading to higher sib mating (Waage, 1986; Strand, 1988; Wajnberg, 1991; van Baaren et al., 1999).

The LMC model predicts that, in non-random mating populations, as the number of females ovipositing in a patch increases, the proportion of sons in the total offspring also increases (Hamilton, 1967). Such a model also predicts an increase in the proportion of sons as the number of hosts per parasitoid female in a patch decreases (Hamilton, 1967; Hardy, 1992; Godfray, 1994; Wajnberg, 1994).

Under LMC, the optimal sex ratio (proportion of males) for an haplodiploid species should be $(n-1)(2n-1)/n(4n-1)$, where n is the number of foundress females foraging on the host patch (Taylor & Bulmer, 1980). The sex ratio therefore declines from 0.5 (for large n) to 0 (when $n = 1$). The latter implies that, when patches are exploited by a single foundress female, such a parasitoid wasp should produce the minimum number of males required to inseminate all her daughters.

Variation in the brood sex ratio of a single foundress female exploiting a host patch is therefore induced by changes in host patch sizes. This has been shown for *Telenomus remus* Nixon, *Telenomus heliothidis* Ashmead (van Welzen & Waage, 1987; Strand, 1988), and *Trissolcus basalis* (Wollaston) (Colazza et al., 1991; Colazza & Wajnberg, 1998). The results from these studies fit the predictions of the LMC model, i.e., the sex ratio becomes more female biased as the number of hosts per egg mass increases.

From a mechanistic point of view, the question here is how do the ovipositing females achieve production of the optimal number of sons required to fertilize the daughters? Theoretically, parasitoids attacking exposed hosts may be able to estimate host/patch sizes by examining or walking on them (Schmidt, 1991). However, in many cases this may not be necessary. For example, although *T. basalis* females often drum the entire outer edge of the host egg mass before they start probing, they do not appear to assess the number of hosts available within the patch, as the changes observed in the sex allocation sequence appear to be caused by an indirect modification in the sequence's structure, as long as the sequence is progressively completed (Colazza & Wajnberg, 1998). This mechanism was described by Waage & Ng (1984), who reported that ovipositing females lay more males early in the oviposition sequence and, as the number of hosts increased, they laid additional males at regular intervals. Such a 'males first strategy' facilitates the production of optimal sex ratios by female parasitoids, regardless of any assessment of the egg mass size before oviposition (Waage, 1982b; Waage & Ng, 1984; van Welzen & Waage, 1987; Strand, 1988).

In the current study, we aimed to explore how females of *Telenomus busseolae* Gahan (Hymenoptera: Scelionidae), a solitary parasitoid specialized in attacking the concealed egg masses of *Sesamia* spp. and *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) (Conti & Bin, 2000), manipulates the mean sex ratio and the sex sequence of her progeny under different densities of host eggs per patch.

Telenomus busseolae is found across several parts of the Mediterranean Basin, and throughout Africa (Alexandri & Tsitsipis, 1990; Sétamou & Schulthess, 1995; Polaszek, 1998; Sertkaya, 1999), and is the most important natural mortality factor for the species attacked in these areas. Because it parasitizes egg masses concealed under leaf sheaths or ear bracts, its host location and oviposition strategies differ from other scelionid wasps. Among other special features, this parasitoid has a dorso-ventrally flattened body which allows it to reach its hosts' oviposition sites by crawling into such narrow spaces (Conti & Bin, 2000). The egg mass sizes of *Sesamia* spp. vary greatly, ranging between 5 and 160 eggs in *S. nonagrioides* (Alexandri & Tsitsipis, 1990; Sertkaya, 1999). We will show that this variability in the host's egg mass size induces a corresponding variation in the sex ratio sequences produced by *T. busseolae* females.

Materials and methods

Insects and rearing procedures

Sesamia nonagrioides was cultured from larvae and pupae collected from maize in Rome, Italy. The culture was reared on diets specifically developed by Giacometti (1995) for larvae and adults, under constant environmental conditions of 26 ± 1 °C, 70 ± 5% r.h., and L16:D8. Cardboard cylinders with parafilm strips rolled onto them were used as the oviposition substrate. Females oviposited under the parafilm strips, which allowed the eggs to be collected by unrolling the strips.

Telenomus busseolae was cultured from the parasitized egg masses of *S. nonagrioides* collected in maize fields in Adana, Turkey (37°01′N, 35°21′E). The parasitoid was reared continuously on the eggs of *S. nonagrioides* in glass tubes (3 cm diameter, 16 cm long), at 26 ± 1 °C, 70 ± 5% r.h., and L16:D8, and fed the diet devised by Safavi (1968).

Experimental protocol

The experimental arena consisted of a transparent plexiglass plate (1 mm thick, 7.5 cm long, and 2.5 cm wide) in which a special rectangular chamber (4.2 cm long and 0.6 cm wide) had been constructed by cutting out part of the plexiglass. This arena was then sandwiched between two microscope slides to complete the setup. In order to introduce the female into the arena, an entry hole (1.5 mm wide) was used. The arena was placed on a platform in order to facilitate its movement during the experiment for improved observation of parasitoid's behaviours.

Only egg masses <1 day old were used in the experiments. The egg patch sizes were of 4 (n = 16), 8 (n = 11), 16 (n = 10), 32 (n = 17), 64 (n = 10), and 128 (n = 5) host eggs. Such egg patches consisted of two egg rows of a similar size glued onto a piece of cardboard. Female wasps were transferred individually into the arena through the entry hole, which was then closed with a bamboo stopper. The parasitoids used in the experiments were 36–48 h old. To reduce variability and improve the chances of mating, just after emergence one female and one male were kept in 1 × 2 cm glass tubes with a drop of the Safavi (1968) diet.

All observations were video-recorded using a VCR system (Panasonic WV-CP230) connected to a stereoscopic binocular microscope (Wild Heerbrugg M420). All parasitized eggs were also directly recorded on a map (i.e., a diagram of an egg mass) and video records were reviewed to prevent any oversight when analysing data on egg parasitism.

Experiments were conducted at 26 ± 1 °C and 60 ± 5% r.h. under medium intensity light conditions. The observations were continued until all the eggs in a patch were parasitized, or until the wasp had failed to parasitize any eggs after a period of 3 h. Some wasps attempted to parasitize previously parasitized eggs, although self-superparasitism is rarely found in *T. busseolae* (Agboka et al., 2002). However, in such a case, because such self-superparasitism would have affected the results on the sex sequence, the arena was opened and a single-hair brush was used to gently push the wasp, thus preventing oviposition.

The parasitized egg masses obtained from the experiments were labelled and incubated at 26 ± 1 °C, 70 ± 5% r.h., and L16:D8 conditions until 1 day before emergence (15th day after parasitism). Before any offspring emerged, the parasitized eggs were placed in a deep-freezer for 4 h and dissected under a stereo binocular microscope. The males and females of *T. busseolae* were easily distinguished, based on differences in antennae, which are filiform in males and clubbed in females. This procedure led to an accurate quantification of the sex sequence of ovipositing females on each host patch size.

Statistical analysis

Sex ratios (expressed as a male percentage) were analyzed by means of a logistic regression model: a generalized linear model specifically designed for modelling binomial data using a logit link function (McCullagh & Nelder, 1989). Pair-wise tests were performed by choosing appropriate contrasts, and an overall significance level of 5% was maintained using a modified Bonferroni procedure with S-Plus (Hochberg, 1988; Venables & Ripley, 1994). The *T. busseolae* oviposition sequences were described using the non-parametric multivariate method described by Wajnberg (1991, 1993). Each oviposition sequence was analyzed using a set of five non-parametric statistics describing different sequential features of the oviposition sequences. These statistics were as follows: (1) the sum of males' rank position (SMR), showing whether males are laid in the beginning of the sequence; (2) the variance of males' rank position (VMR), showing whether males are laid in the middle of the sequence; (3) the centre group of males (CGM), describing whether there is any pooling of males within the sequence; (4) the centre group of females (CGF), showing whether there is any pooling of females within the sequence; and (5) the number of run of males or females (NR), which enables any autocorrelation of males or females within the sequence to be identified. The formulae used to compute these five parameters were as shown in Wajnberg (1993).

As explained in Wajnberg (1993), these five descriptive parameters were computed using the total length N and the number of males M and females N-M of each sex-sequence described. Therefore, these parameters could differ between sequences of different size and/or constituted with different proportions of males and females, even if they were built with exactly the same sex-sequence pattern. In order to overcome this problem, and as explained in Wajnberg (1993), these five parameters were thus first transformed into the exact probability corresponding to the 1st-level risk of the associated null hypotheses. The resulting parameters then become uncorrelated with sequence length or sex ratio, and are thus only describing the sequential organisation of males and females within each sequence described. Then, using a 1-way analysis of variance (ANOVA) on each parameter separately, this five-parameter description was used to compare parasitoid females' oviposition sequences on host egg masses of different sizes. A standard factorial discriminant analysis (also called canonical discriminant analysis) was also performed to take into account the multivariate feature of the data. This method allows a description of each oviposition sequence 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 format of a correlation circle. Such a correlation circle provides a graphical method for understanding how the computed axes are oriented in the space defined by the five original descriptive parameters used. All computations were done using SAS (PROC CANDISC) (SAS Institute, 1988).

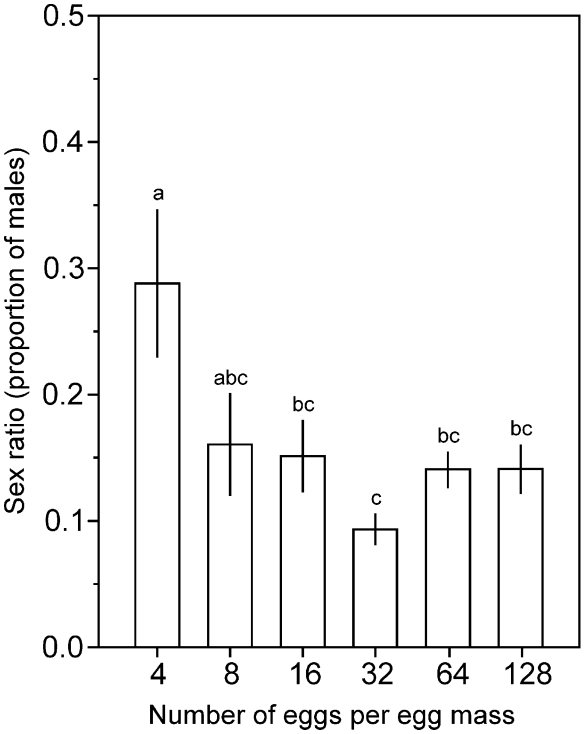

Figure 1 Sex ratio (mean ± SD) produced by *T. busseolae* as a function of *S. nonagrioides* egg mass size. Columns capped with the same letter are not significantly different at P<0.05.

Results

Male proportions of *T. busseolae* were found to be significantly different ($\chi^2 = 18.82$, d.f. = 5, P = 0.002) in response to different sizes of *S. nonagrioides* egg patches (4, 8, 16, 32, 64, or 128 eggs per mass). From 4 to 16 host eggs per mass, the mean sex ratio significantly decreased, whereas there were no significant differences from 8 to 128 eggs (Figure 1). However, when host patch size increased to 64 and 128 eggs, the sex ratio seemed to invert its trend, although not significantly (Figure 1). In addition to overall sex ratio, the sex allocation sequence of *T. busseolae* also changed significantly in response to different sizes of egg mass (Figures 2 and 3, and Table 1).

On patches containing 4–32 eggs, males are laid mostly at the beginning of the sequence (as shown by a low SMR) and both males and females are increasingly pooled (as indicated by decreasing CGM and CGF) (Table 1 and Figure 4). However, on host egg masses containing four eggs, *T. busseolae* showed higher values of SMR, CGM, and CGF than those obtained on host masses of 8–32 eggs. This mainly depends on the small size of such host patches, and indicates that both sexes of the offspring are more dispersed along the sequence, although the parasitoid still starts its oviposition sequence with male eggs, and then followed by female eggs.

In larger patches of 64 and 128 eggs, an increasing number of males are added at the end of the sex sequence (higher SMR compared to smaller patches) and sexes are relatively more dispersed (CGM highest on 64-egg patches, and higher on 128-egg compared to 32-egg patches; CGF higher on 128-egg patches compared to 32- and 64-egg patches). In all patch sizes, males are laid at the extremities of the sequence with respect to females (quite high VMR), and only a partial autocorrelation of males/females is suggested, i.e., sons and daughters are partly laid according to particular intervals (intermediate NR).

Discussion

Many factors have been shown to influence the sex allocation pattern in parasitoid wasps. In this paper we have focused on the sex ratio and sex allocation sequence as a function of the number of host eggs constituting the egg mass in the *S. nonagrioides–T. busseolae* system.

Table 1 Statistical description and comparison of *Telenomus busseolae* oviposition sequences in *Sesamia nonagrioides* egg masses of different sizes using the five descriptive parameters proposed by Wajnberg (1991, 1994) (mean ± SD). SMR, sum of males' rank position; VMR, variance of males' rank position; CGM, centre-group of males; CGF, centre-group of females; NR, number of runs of males or females. d.f. = 5,63 for all F-tests

Egg mass size	SMR	VMR	CGM	CGF	NR
4	0.3802 ± 0.2845	0.9010 ± 0.1225	0.8593 ± 0.2034	0.6562 ± 0.2212	0.4635 ± 0.2508
8	0.1659 ± 0.1125	0.8721 ± 0.1669	0.8077 ± 0.2588	0.3238 ± 0.1358	0.4258 ± 0.2715
16	0.2293 ± 0.2183	0.8140 ± 0.2030	0.7054 ± 0.3087	0.2591 ± 0.2298	0.3869 ± 0.3150
32	0.1173 ± 0.1077	0.8527 ± 0.1225	0.5517 ± 0.3102	0.1640 ± 0.1233	0.3087 ± 0.3401
64	0.4880 ± 0.2142	0.8814 ± 0.2249	0.8916 ± 0.2141	0.1433 ± 0.2548	0.4056 ± 0.2664
128	0.5439 ± 0.4271	0.7969 ± 0.1565	0.6969 ± 0. 1730	0.2166 ± 0. 1755	0.5090 ± 0.2870
F	6.33	0.57	3.37	14.10	0.64
P	<0.001	ns	<0.0092	<0.001	ns

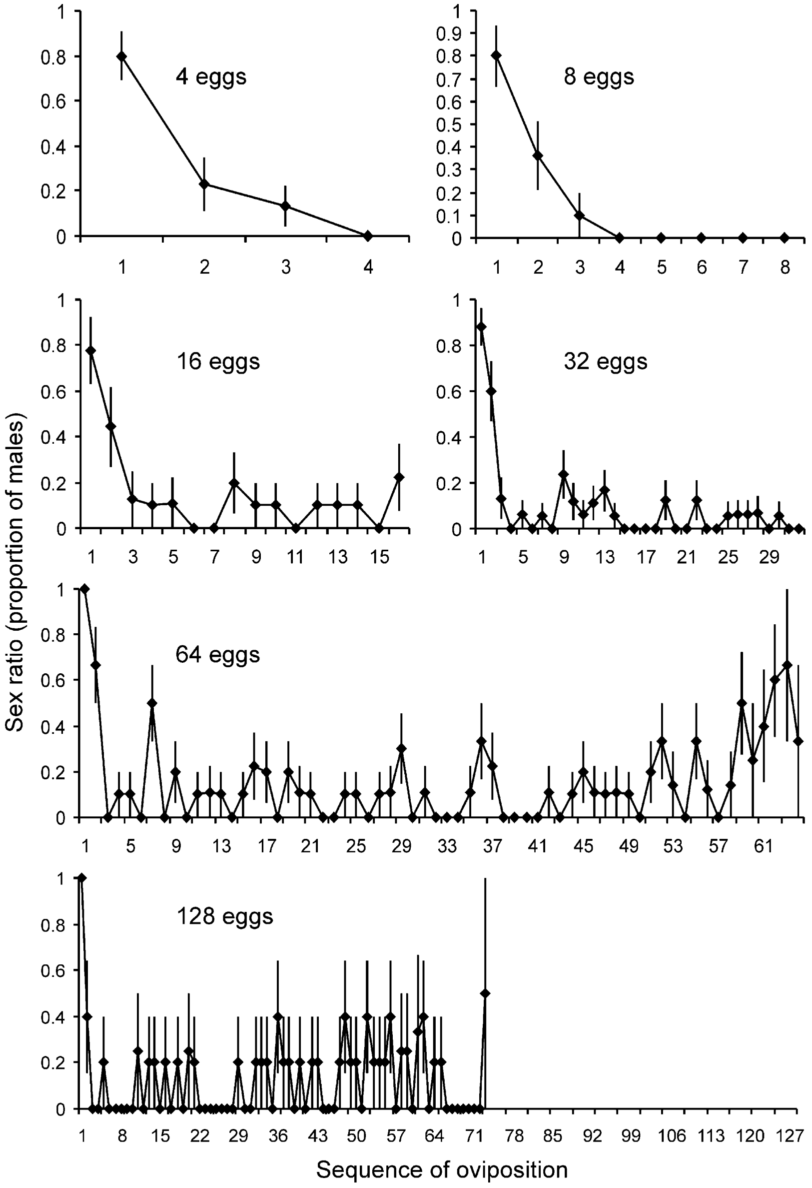

Figure 2 Sex ratios (mean ± SD) produced by *T. busseolae* as a function of the oviposition sequence on *S. nonagrioides* egg masses of different sizes.

When increasing sizes of egg masses were attacked by a single mated *T. busseolae* female, a higher female-biased sex ratio was produced, as predicted by the LMC model. Such correlation between sex ratio and host patch size is advantageous for the species as it allows the sex ratio to remain at an optimal level, i.e., by producing just enough sons to mate all daughters. Similarly, Strand (1988) showed that, with an increasing number of host eggs per mass, female *T. heliothidis* produces more female-biased sex ratios. Similar trends were also found on another scelionid egg parasitoid, *T. basalis* on *Nezara viridula* (L.) (Colazza et al., 1991; Colazza, 1994; Colazza & Wajnberg, 1998).

Such a parasitoid response to increasing host patch sizes, however, is not consistent when large egg masses (64–128) are exposed to the females, as parasitoid response shows a different pattern, i.e., the proportion of sons increases at the end of the oviposition sequence. This was also observed on other parasitoids (Waage & Ng, 1984; Strand, 1988; Colazza & Wajnberg, 1998) and, although such patterns are consistent with appropriate facultative sex ratio adjustment (West et al., 1997), suggests that in large patches the sex sequence is affected by sperm depletion (Waage, 1982b). This may also be supported by the fact that the parasitoids lay more males towards the end of their life (Chabi-Olaye et al., 1997; Sertkaya, 1999). In any case, males laid at the

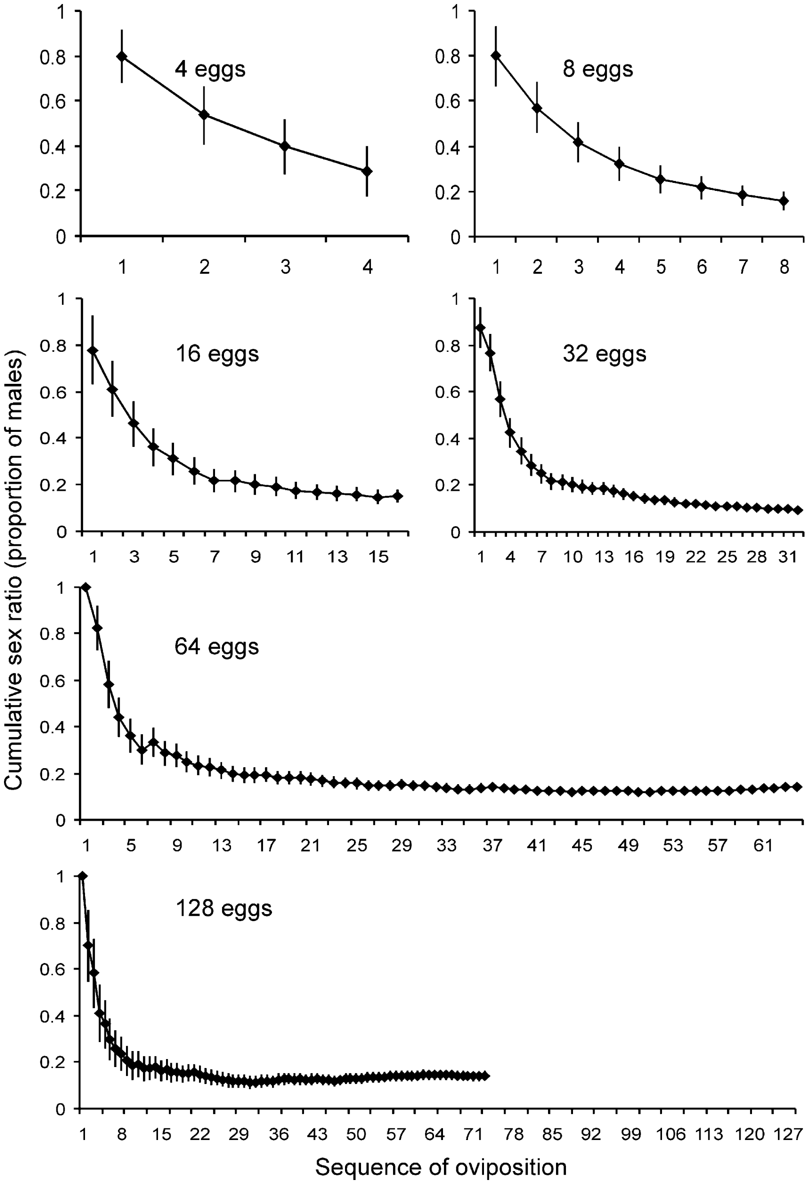

Figure 3 Cumulative sex ratios (mean ± SD) produced by *T. busseolae* as a function of the oviposition sequence on *S. nonagrioides* egg masses of different sizes.

end of the bout compensate for the possible mortality of males laid at the beginning, thus enhancing the chance for insemination of emerging siblings.

Our results, showing that *T. busseolae* females alter their offspring sex ratio in response to host density, lead to questions of whether *T. busseolae* can assess the size of an egg mass prior to the start of oviposition and, in such a case, which mechanisms are involved. Parasitoids that attack exposed egg masses may be able to collect information by walking and antennating on the host before oviposition (Colazza et al., 1991; Field, 1998). On the other hand, chemical cues produced by the host eggs could be used by the foraging parasitoids to obtain information on the amount of eggs contained in the patch before oviposition.

In the case of *T. busseolae* females, however, because the host eggs are concealed under the leaf sheath or the ear bracts and normally adhere tightly to the egg mass, assessing the number of available eggs would be difficult and may not be convenient, as the parasitoid female would have to invest a large percentage of handling time before starting the oviposition sequence.

Therefore, a 'male-first' strategy under LMC in *T. busseolae*, which was confirmed by our experiments, was already expected. Another factor that indicated LMC in *T. busseolae* was that all host eggs, belonging to *Busseola* and *Sesamia*

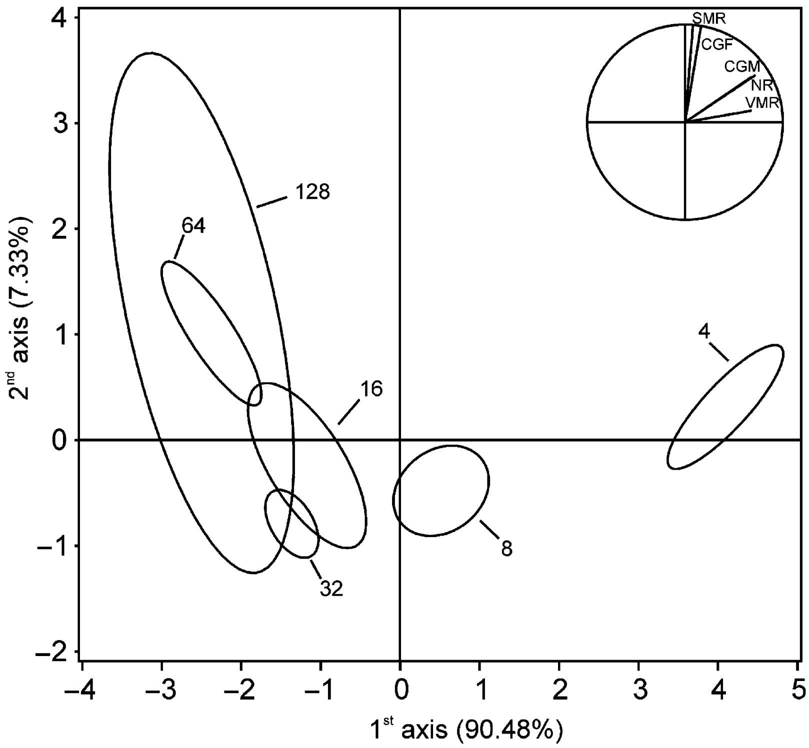

Figure 4 First and second axis (with percentage variation explained) of a factorial discriminant analysis done on the statistical description of *T. busseolae* oviposition sequences on *S. nonagrioides* egg masses of different sizes (4, 8, 16, 32, 64, and 128 eggs per mass). Ellipses represent 95% confidence intervals around the means. The correlation circle of the corresponding plan is provided.

species, are laid in clusters, i.e., they are quasi-gregarious, and can be attacked by one or few females of *T. busseolae* (Alexandri & Tsitsipis, 1990; Sertkaya, 1999; Ndemah et al., 2001; Schulthess et al., 2001). In addition, *T. busseolae* is a proterandrous species, i.e., the males always emerge several hours before females (Chabi-Olaye et al., 1997; Fatinou et al., 1998), and appear to wait for them on the egg masses; they therefore probably mate before dispersion.

Such a 'male-first' strategy was observed in other scelionid and in trichogrammatid egg parasitoids (Waage & Lane, 1984; Waage & Ng, 1984; van Dijken & Waage, 1987; van Welzen & Waage, 1987; Braman & Yeargan, 1989; Wajnberg, 1994). This resulted in a non-random sex sequences that led to the deposition of more males at the beginning of the egg-laying bouts. Using such a strategy, a foraging parasitoid does not need to assess the size of the egg mass before oviposition, and would invariably have deposited at least one male to inseminate her female offspring. This is an advantageous strategy for egg parasitoids that attack patchily distributed hosts. If an unattacked egg mass is exploited by one female parasitoid, she would produce enough males to inseminate her daughters by depositing each sex in a particular order (Waage, 1982a,b; Waage, 1986; Hardy, 1992; Godfray, 1994).

In spite of the strong morphofunctional adaptations to concealed egg masses gained by *T. busseolae* during the long host-parasitoid co-evolution, this has not resulted in differences, compared to parasitoids of exposed eggs, in sex allocation mechanisms, which are under strong genetic control. Such aspects strengthen the fact that LMC and the 'male-first' strategy provide important evolutionary advantages, both in terms of obtaining optimal sex ratios and reduced handling time.

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References

Agboka K, Schulthess F, Chabi-Olaye A, Labo I, Gounou S & Smith H (2002) Self-, intra-, and interspecific host discrimination in *Telenomus busseolae* Gahan and *T. isis* Polaszek (Hymenoptera: Scelionidae), sympatric egg parasitoids of the

African Cereal Stem Borer *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae). Journal of Insect Behavior 15: 1–12.

Alexandri MP & Tsitsipis JA (1990) Influence of the egg parasitoid *Platytelenomus busseolae* (Hym. Scelionidae) on the population of *Sesamia nonagrioides* (Lep. Noctuidae) in Central Greece. Entomophaga 35: 61–70.

van Baaren J, Landry BL & Boivin G (1999) Sex allocation and larval competition in a superparasitizing solitary egg parasitoid: competing strategies for an optimal sex ratio. Functional Ecology 13: 66–71.

Braman SK & Yeargan KV (1989) Reproductive strategy of *Trissolcus euschisti* (Hymenoptera: Scelionidae) under conditions of partially used host resources. Annals of the Entomological Society of America 82: 172–176.

Chabi-Olaye A, Schulthess F, Shanower TG & Bosque-Perez NA (1997) Factors influencing the developmental rates and reproductive potentials of *Telenomus busseolae* (Gahan) (Hym. Scelionidae), an egg parasitoid of *Sesamia calamistis* Hampson (Lep. Noctuidae). Biological Control 8: 15–21.

Charnov EL (1982) The Theory of Sex Allocation. Princeton University Press, NJ.

Colazza S (1994) Factors influencing brood sex ratio in the egg parasitoids *Trissolcus basalis* (Woll.) (Hymenoptera: Scelionidae). Entomologica 27: 211–219.

Colazza S, Vinson SB, Li YT & Bin F (1991) Sex ratio strategies of the egg parasitoid *Trissolcus basalis* (Woll.) (Hymenoptera, Scelionidae): influence of the host egg patch size. Redia 74: 279–286.

Colazza S & Wajnberg E (1998) Effects of host egg mass size on sex ratio and oviposition sequence of *Trissolcus basalis* (Hymenoptera: Scelionidae). Environmental Entomology 27: 329–336.

Conti E & Bin F (2000) Parasitoids of concealed noctuid eggs and their potential in biological control of gramine stemborers. Redia 83: 87–104.

Cook JM (1993) Sex Determination in the Hymenoptera: a review of models and evidence. Heredity 71: 421–435.

van Dijken MJ & Waage JK (1987) Self and conspecific superparasitism by the egg parasitoid *Trichogramma evanescens*. Entomologia Experimentalis et Applicata 43: 183–192.

Fatinou AA, Alexandri MP & Tsitsipis JA (1998) Adult emergence rhythm of the egg parasitoid, *Telenomus busseolae*. Biocontrol 43: 141–151.

Field SA (1998) Patch exploitation, patch leaving and preemptive patch defence in the parasitoid wasp *Trissolcus basalis* (Insecta: Scelionidae). Ethology 104: 323–338.

Fisher RA (1930) The Genetical Theory of Natural Selection. Oxford University Press, Oxford.

Flanagan KE, West SA & Godfray HCJ (1988) Local mate competition, variable fecundity and information use in a parasitoid. Animal Behaviour 56: 191–198.

Giacometti R (1995) Rearing of *Sesamia nonagrioides* Lefevbre on meridic diet (Lepidoptera, Noctuidae). Redia 78: 19–27.

Godfray HCJ (1994) Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, NJ.

Hamilton WD (1967) Extraordinary sex ratios. Science 156: 477–488.

Hardy ICW (1992) Non binomial sex allocation and brood sex ratio variances in the parasitoid Hymenoptera. Oikos 62: 143–158.

Hardy ICW (1997) Possible factors influencing vertebrate sex ratios: an introductory overview. Applied Animal Behaviour Science 51: 217–241.

Hochberg Y (1988) A sharper Bonferroni procedure for multivariate tests of significance. Biometrika 75: 800–802.

McCullagh P & Nelder JA (1989) Generalized Linear Model, 2nd edn. Chapman & Hall, New York.

Ndemah R, Schulthess F, Poehling M & Borgemeister C (2001) Natural enemies of lepidopterous borers on maize and elephant grass in the forest zone of Cameroon with special reference to *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). Bulletin of Entomological Research 91: 205–212.

Polaszek A (1998) African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control. CAB International / ACP-EU Technical Centre for Agricultural and Rural Co-operation (CTA), UK.

Safavi M (1968) Etude biologique et ecologique de hyméptéres parasites des oeufs punaises des céréales. Entomophaga 13: 281–495.

SAS Institute (1988) SAS / STAT User's Guide. SAS Institute, Cary, NC.

Schmidt JM (1991) The role of physical factors in tritrofic interactions. Redia 74: 43–93.

Schulthess F, Chabi-Olaye A & Goergen G (2001) Seasonal fluctuations of noctuid stemborer egg parasitism in Southern Benin with special reference to *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Telenomus* spp. (Hymenoptera: Scelionidae) on maize. Biocontrol Science and Technology 11: 745–757.

Sertkaya E (1999) Determination of natural enemies of corn stalk borer *Sesamia nonagrioides* Lefevbre (Lepidoptera, Noctuidae) in Cukurova, and investigations on relations with its egg parasitoids *Platytelenomus busseolae* (Gahan) (Hymenoptera, Scelionidae) and *Trichogramma evanescens* Westwood (Hymenoptera, Trichogrammatidae). PhD Thesis. Natural Applied Science Institute, Cukurova University (in Turkish).

Sétamou M & Schulthess F (1995) The influence of egg parasitoids belonging to *Telenomus busseolae* (Hym. Scelionidae) species complex on *Sesamia calamistis* (Lepidoptera: Noctuidae) population in maize fields in Southern Benin. Biocontrol Science and Technology 5: 69–81.

Strand MR (1988) Variable sex ratio strategy of *Telenomus heliothidis*: adaptation to host and conspecific density. Oecologia 77: 219–224.

Taylor PD (1981) Intra-sex and inter-sex sibling interaction as sex ratio determination. Nature 291: 64–66.

Taylor PD & Bulmer MG (1980) Local mate competition and the sex ratio. Journal of Theorical Biology 86: 409–419.

Venables WN & Ripley BD (1994) Modern Applied Statistics with S-Plus. Springer, New York.

Waage JK (1982a) Sex ratio and population dynamics of natural enemies. Annals of Applied Biology 101: 159–164.

Waage JK (1982b) Sib-mating and sex ratio strategies in scelionid wasps. Ecological Entomology 7: 103–113.

Waage JK (1986) Family Planning in Parasitoids: Adaptive Patterns of Progeny and Sex Allocation Insect Parasitoids (ed. by J K Waage & D Greathead), pp. 63–96. Academic Press, London, UK.

Waage JK & Lane JA (1984) The reproductive strategy of a parasitic wasp. II. Sex allocation and local mate competition in *Trichogramma evanescens*. Journal of Animal Ecology 53: 417–426.

Waage JK & Ng SM (1984) The reproductive strategy of a parasitic wasp I. Optimal progeny allocation in *Trichogramma evanescens*. Journal of Animal Ecology 53: 401–415.

Wajnberg E (1991) A new statistical method for quantifying sex patterns within sequences of oviposition produced by parasitic wasps. Redia 71: 401–405.

Wajnberg E (1993) Genetic variation in sex allocation in a parasitic wasp: variation in sex pattern within sequences of oviposition. Entomologia Experimentalis et Applicata 69: 221–229.

Wajnberg E (1994) Intra-population genetic variation in *Trichogramma*. Biological Control with Egg Parasitoids (ed. by E Wajnberg & S A Hassan), pp. 245–271. CAB International, Wallingford, UK.

van Welzen CRL & Waage JK (1987) Adaptive responses to Local Mate Competition by the parasitoid *Telenomus remus*. Behavioral Ecology and Sociobiology 21: 359–365.

Werren JH (1980) Sex ratio adaptation to Local Mate Competition in a parasitic wasp. Science 208: 1157–1159.

West SA, Herre EA, Compton SG, Godfray HCJ & Cook JM (1997) A comparative study of virginity in fig wasps. Animal Behaviour 54: 437–450.