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Oviposition behaviour and egg distribution of the European corn borer, *Ostrinia nubilalis*, on maize, and its effect on host finding by *Trichogramma* egg parasitoids

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Abstract

Oviposition behaviour and egg distribution of *Ostrinia nubilalis* is reviewed based on published information and new research. The position of egg masses of *O. nubilalis* on maize plants and leaves were sampled in the field. Most egg masses were found on the lower leaf side, on the middle part of the leaf or close to the stem, and close to the mid-rib. Direct observations of oviposition behaviour were made in laboratory and field cages. *O. nubilalis* moved very little on the plants and only 10 % of the females that landed on the plants oviposited. The number of actual ovipositions was quite low compared to the number of landings, with females walking only a few centimetres if at all. Shed scales of adult moths were not abundant near egg masses with only 37% of egg masses associated with scales and 45% with only a few scales. Many scales were found on other places of the plants. At the leaf and plant level, scales might serve as a useful host-cue to *Trichogramma brassicae*, an egg parasitoid of *O. nubilalis*. However, scales are not an indicator for the presence of egg masses in their immediate vicinity.

Key words: *Ostrinia nubilalis*, host-plant finding, egg laying, egg distribution, maize, moth scales, biological control, *Trichogramma brassicae*.

Introduction

Ostrinia nubilalis Hübner (Lepidoptera Crambidae), the European corn borer, is an important pest of maize in most temperate regions of the northern hemisphere. In order to understand the mating behaviour, egg distribution and density of *O. nubilalis* on maize, and its influence on *Trichogramma* egg parasitoids, we first summarized earlier published information, and, next, performed a series of experiments to collect important information that was still lacking.

Mating and oviposition behaviour of *O. nubilalis*

When maize is grown in crop rotation schemes, the fields in which *O. nubilalis* emerge will usually not be a maize field (Bigler and Brunetti, 1986). Following emergence, the moths spend the first night in the fields of emergence where they mate (Buechi *et al*., 1981; Cordillot, 1989). Although a single mating suffices to fertilize all the eggs of the female, multiple matings are possible (Poos, 1927; Cordillot, 1989). The second night, females will migrate to the maize fields (Cordillot, 1989). The males stay behind but will follow the next few days, attracted by the sex pheromones of still unmated females. From then on, the moths migrate daily in and out of the field. Daytime is spent in the grassy borders of the fields (Derridj *et al*., 1986; Cordillot, 1989). During the night *O. nubilalis* enters the maize field to oviposit, and to drink the dew from maize plants, which contains sugars (Derridj *et al*., 1986). Flight takes place in the first three hours of darkness (Broersma *et al*., 1976). The moths fly low, usually less than one meter above the vegetation (DeRozari *et al*., 1977). Mating and flight are inhibited by low temperatures (Hudon *et al*., 1989), heavy rains (Oloumi-Sadeghi *et al*., 1975) and strong winds (Loughner and Brindley, 1971; Sappington and Showers, 1983). Light rains stimulate *O. nubilalis* activity (Everett *et al*., 1958; Barlow and Mutchmore, 1963; Kira *et al*., 1969).

The oviposition period ranges from 1-28 d with a mean of 12.8 d (Poos, 1927). Oviposition, which has an endogenous circadian rhythm (Skopik and Takeda, 1980), and is influenced by the weather, mainly takes place in the first two hours after dark (Caffrey, 1928; Cordillot, 1989). Various factors stimulate or deter oviposition. Certain growth stages of the maize plant are preferred for oviposition (Ficht, 1932; Derridj *et al*., 1989; Turner and Beard, 1950), and the largest and most developed plants are preferred (Patch, 1942; Horber, 1961). Plant extracts were shown to have some attraction for *O. nubilalis* (Cutright and Huber, 1928; Moore, 1928; Cantelo and Jacobson, 1979). Burgio and Maini (1995) suggest baits of phenlylacetaldehyde to trap *O. nubilalis* adults. Compounds on the leaf surface, such as glucose, will stimulate oviposition (Derridj and Fiala, 1983; Fiala *et al*., 1985; Derridj *et al*., 1992). Pentane extracts of the whorl and tassel stages of maize stimulate oviposition, but extracts of an earlier and later developmental stage do not (Udayagiri and Mason, 1995). Eggs (Thiery and le Quere, 1991), larval frass (Dittrick *et al*., 1983) and damaged maize plants (Schurr and Holdaway, 1966) emit volatiles which repel gravid females. Thus, females avoid oviposition on plants where egg masses or larvae are already present. When egg-laying is about to begin, the moths hover about one meter above ground (Hudon and LeRoux, 1986a).

Oviposition itself was described by Poos (1927), Caffrey and Worthley (1927) and Garnier-Geoffroy *et* *al.* (1996). To oviposit, the female sits on the leaf with its head upward. The end of the abdomen is bent down and the ovipositor extruded. When the ovipositor touches the leaf, the abdomen is pulsed rapidly until an egg emerges. The round egg is pushed against the leaf, and is flattened with the tip of the ovipositor. Eggs are laid in an overlapping pattern. Females do not move substantial distances during the oviposition of an egg mass, unless they produce a long, narrow egg mass with many eggs. The production of a normal egg mass will take about 5 minutes. Leaf folds seem to be preferred as oviposition sites (Abel *et al*., 1995).

The size of egg masses varies from 1 to 64 eggs, with a mean of 15 eggs (Poos, 1927; Caffrey and Worthley, 1927). The size is not influenced by temperature (Gohari and Hawlitzky, 1986) or position on the plant (Vaillant and Hawlitzky, 1990). During its lifetime, the female can produce about 350 eggs (Caffrey and Worthley, 1927; Reh and Ohnesorge, 1988). Egg masses are held together and adhered to the leaf with a compound produced by the abdominal glands (Beck and Stauffer, 1950).

Distribution of egg masses

Within-field egg mass distributions

Most of the work on egg mass distribution in the field has been done in order to establish accurate and inexpensive sampling procedures for predicting *O. nubilalis* population densities. All three types of theoretical distribution have been observed for *O. nubilalis*. If *O. nubilalis* would choose maize plants at random, the number of egg masses per plant should be Poisson distributed, which is actually the most common distribution found in the field (McGuire *et al*., 1957; Chiang and Hodson, 1959; Calvin *et al*., 1986; Coll and Bottrell, 1991; Sorenson *et al*., 1993). If *O. nubilalis* would have a clear preference for certain plants within the field, a clumped distribution of egg masses should be found. Hudon and LeRoux (1986b) found a negative binomial distribution of egg masses over the plants, indicating some clustering. If *O. nubilalis* would avoid plants on which egg masses were laid, a uniform distribution should be the result. At higher egg mass densities indications for such uniform distributions can be found, as more plants have only one egg mass then would be expected from a Poisson distribution (Vaillant and Hawlitzky, 1990; Hawlitzky *et al*., 1994). If the egg mass density is low, it is hard to detect differences between these three types of distribution. The location of a plant in the field can also have some influence. The number of egg masses can be higher at the field edge (Lee, 1988). In general, the distribution of *O. nubilalis* egg masses in the field is not always completely random, but can be adequately described as a Poisson distribution, especially if densities are low (Shelton *et al*., 1986).

Within-plant egg mass distributions

Egg masses are mainly laid on the leaves. Depending on the source, between 0 and 6% of the egg masses are found on the stem (Everly, 1959; Burgstaller, 1974; Windels and Chiang, 1975; Shelton *et al*., 1986; Milani *et al*., 1988; Coll and Bottrell, 1991). One reason for this might be that the higher glucose levels on the leaf surface result in increased oviposition by *O. nubilalis* (Fiala *et al*., 1985).

The height distribution of egg masses over the plant has been studied by many authors, and an overview of the data from the literature is presented in table 1. Most egg masses are found in the middle strata of plants and can vary greatly from year to year and from area to area (Huber *et al*., 1928; Everly, 1959; Windels and Chiang, 1975; Vierling, 1985; Calvin *et al*., 1986; Hudon and LeRoux, 1986a; Klinger, 1979; Ohnesorge and Reh, 1987; Lee, 1988; Ismail, 1989; Lupoli *et al*., 1990; Coll and Bottrell, 1991; Sorenson *et al*., 1993; Hawlitzky *et al*., 1994). Exceptions to this were found by Burgstaller (1974) and Despins and Roberts (1986), who found most egg masses in the lower third of the plant.

Humidity and temperature influence the leaf level of oviposition (Chiang and Hodson, 1972; Despins and Roberts, 1986; Ohnesorge and Reh, 1987). The distribution over the leaf levels is symmetrical with most egg masses on the middle leaves. *O. nubilalis* apparently moves between the plants at a horizontal level to oviposit. The number of egg masses per unit surface area is higher in the upper leaves, due to the smaller leaf size.

Within-leaf egg mass distribution

The literature is very clear about the distribution of egg masses over the leaf sides: most egg masses (73-100%) are found on the lower leaf side (table 2; Poos, 1927; Everly, 1959; Windels and Chiang, 1975; Hudon and LeRoux, 1986a; Shelton *et al*., 1986; Jarvis and Guthrie, 1987; Lee, 1988; Ismail, 1989; Coll and Bottrell, 1991; Sorenson *et al*., 1993). This is not only true for maize, but also for other crops (Legg *et al*., 1986; Savinelli *et al*., 1986). Only in one case there was an equal amount of egg masses on upper (adaxial) and lower (abaxial) side of the leaves. The next season in the same area, 62% of the egg masses were on the lower leaf side (Milani *et al*., 1988). In an insectary experiment, the moth oviposited equally on both leaf sides (Hudon and LeRoux, 1986a), but in insectaries the leaves may touch the netting, which increases the chance of landing on the upper side by *O. nubilalis* flying along the cage.

Less is known on the distribution of egg masses over the leaf (table 3). Burgstaller (1974) found 49% of the egg masses on the third of the leaf closest to the stem, 35% on the middle part and 16% on the point. Vierling (1985) and Klinger (1979) found 22%, 49% and 16% and 42%, 40% and 18% respectively on the base, middle and point of the leaf. Poos (1927) and Shelton *et al*. (1986) also mention that fewer egg masses are found close to the leaf point, and that parts closer to the stem have more egg masses. Poos (1927) and Beck (1987) mention that *O. nubilalis* prefers to oviposit close to the mid-rib. Legg *et al*. (1986) observed that on sunflower the large veins are also preferred for oviposition.

Table 1. Distribution of *O. nubilalis* egg masses on maize plants.

Position	Plant size	Source
most egg masses close to silking ear	not specified	Beck, 1987
mainly at lower part of plants	not specified	Burgstaller, 1974
symmetrical distribution over leaf 2-12 most were found on leaves 6-7	13-14 leaves	Calvin *et al*., 1986
76.7% on middle leaves near silking ear	not specified	Coll and Bottrell, 1991
82% on leaf 1-4, 98% on leaf 1-6	8-10 leaves	Despins and Roberts, 1986
lower part of plant	15 leaves	Despins and Roberts, 1986
6-15% on ear leaf	not specified	Everly, 1959
95% on leaf 4-10 most were found on leaf 7	13 leaves	Hawlitzky *et al*., 1994
87% on leaf positions 1-8 17.9% on leaf 6, 16.9% on leaf 7	not specified	Huber *et al*., 1928
11% on the husks of the ear	not specified	Hudon and LeRoux, 1986a
leaf 5 to 15 most were found on leaf 8	17 leaves	Ismail, 1989
95% on leaf 5-9, 28% on leaf 7	12-14 leaves	Lee, 1988
leaf 8-13	14-16 leaves	Lupoli *et al*., 1990
83% on leaf 3-7	not specified	Ohnesorge and Reh, 1987
85% in 5 leaves around primary ear	not specified	Sorenson *et al*., 1993
leaf 2-8, 70.7% on leaf 4-6 most were found on leaf 5	10 leaves	Vierling, 1985
43.3% in ear leaf and two adjacent leaves (fodder maize)	not specified	Windels and Chiang, 1975
34.1% in ear leaf and two adjacent leaves (sweet maize)	not specified	Windels and Chiang, 1975

Table 2. Position of leaf side with *O. nubilalis* egg masses in maize and other crops.

Lower side	Crop	Source
52.2%	maize	Milani *et al*., 1988
62.4%	maize	Milani *et al*., 1988
73.4%	maize	Sorenson *et al*., 1993
79.1%	maize	Ismail, 1989
87.2%	maize	Coll and Bottrell, 1991
87.2%	fodder maize	Windels and Chiang, 1975
92.6%	maize	Everly, 1959
95.1%	sweet maize	Windels and Chiang, 1975
95.6%	maize	Lee, 1988
96.3%	maize	Everly, 1959
97.6%	maize	Poos, 1927
99%	maize	Hudon and LeRoux, 1986a
100%	maize	Jarvis and Guthrie, 1987
100%	maize	Shelton *et al*., 1986
Almost all	cotton	Savinelli *et al*., 1986
>90%	sunflower	Legg *et al*., 1986
50%	maize, insectary	Hudon and LeRoux, 1986a

Effect of *Ostrinia* egg laying pattern and scale deposition on *Trichogramma* egg parasitoids

Egg laying patters of *O. nubilalis* will affect the host-finding behaviour of its egg parasitoid *Trichogramma brassicae* Bezdenko (Hymenoptera Trichogrammatidae). *T. brassicae* is not specialized on *O. nubilalis* or maize. It parasitizes other lepidopteran eggs on other host plants (Smith, 1996; Thomson *et al*., 2003). The egg stage of lepidopterans is hard to detect, because it does not feed and thus produces no frass and excrements. Parasitoids can improve their chances to detect hosts by using host cues produced by a stage of the host that is more detectable than the stage that the parasitoid is searching for (Vet and Dicke, 1992). This semiochemical detour is used by *T. brassicae*, which reacts to scales and sex pheromones of the adult *O. nubilalis* (Smits, 1982; Kaiser *et al*., 1989; Renou *et al*., 1989, 1992; Bieri *et al*., 1990; Frenoy *et al*., 1991, 1992). Whether these adult cues are reliable depends on the behaviour of the adult, which determines where these cues will be found in time and space. Learning is used by parasitoids to connect stimuli that are easy to detect but unreliable with stimuli that are hard to detect but

Table 3. Position of *O. nubilalis* egg masses on the maize leaf.

Position	Source
49% on base, 35% middle, 16% on point	Burgstaller, 1974
22% on base, 49% middle, 16% on point	Vierling, 1985
42% on base, 40% middle, 18% on point	Klinger, 1979
fewer egg masses on point than on middle and base	Shelton *et al*., 1986
most near middle or base, few at point	Poos, 1927

reliable cues to host presence (Vet *et al*., 2003). *T. brassicae* can associate the odour of maize with the presence of *O. nubilalis* egg masses after an oviposition experience (Kaiser *et al*., 1989), but the reaction to host scales of *Mamestra brassicae* L. was not influenced by oviposition experience (Gardner and van Lenteren, 1986). A generalist might have a strong fixed response to cues that are common to all its hosts (Vet and Dicke, 1992), but in that case it is unable to optimize its responses by learning (Lewis *et al*., 2003). The more fixed the responses to scales, the stronger differences in scale distribution between host species will affect the parasitoid.

It appears that sufficient data on egg mass distribution of *O. nubilalis* over the field and on the plant are available in already published material, but that information at the leaf level is lacking. In this paper, the within-plant and within-leaf distribution of egg masses of *O. nubilalis* is presented. Observations on oviposition behaviour of *O. nubilalis* were made to collect information about the relationship between landing sites and oviposition sites, and about the distribution of moth scales over plants. The obtained information about egg distribution and scale deposition of *O. nubilalis* will be discussed in the light of understanding host finding by *T. brassicae*.

Materials and methods

Moths

O. nubilalis, which has one generation per year in Switzerland, was reared at the Swiss Federal Research Station for Agroecology and Agriculture and used for the climate room observation experiments. The colony was started in 1990 with 500 diapausing larvae collected at Cadenazzo (Ticino, Switzerland). Larvae were reared on an artificial medium for approximately 20 generations. Pupae were moved to cages (45 x 45 x 45 cm) where the adults could emerge and mate. On top of the cage, a sheet of wet filtration paper was placed for the females to oviposit. This sheet was then removed to collect the egg masses and start a new rearing cycle. Material for the observations was obtained by collecting pupae and letting them emerge. The newly emerged *O. nubilalis* males and females were kept together for 96 h to allow mating in Plexiglas containers provided with honey-water in a 25 °C climate room. For the field cage observations, *O. nubilalis* emerged from pupae collected from stubble at the Swiss Federal Research Station for Agroecology and Agriculture and *O. nubilalis* from second generation pupae collected near Cadenazzo (Ticino, Switzerland) were used.

Plants

For the climate room observation experiments, greenhouse grown maize plants with 9 leaves and 1.50 m high (cv LG11) were used. For the insectary observations, field-grown plants with 9 leaves and 1.70 m high (cv. Atlet) were potted for use. Field grown plants have thicker stems and a much larger leaf area compared to greenhouse grown plants of the same height.

Distribution of egg masses over plants in the field

Egg masses were counted during the summer of 1993 in Schinznach (Canton Aargau) and Wasterkingen (Canton Zürich) in Switzerland. A total of 18 maize fields (9 from each region) were used for the study. A total of 144 and 110 plots, each plot containing 10 plants, were sampled in Schinznach and Wasterkingen respectively: a total of 2540 plants were carefully examined for *O. nubilalis* egg masses. Positions of egg masses within plants and within leaves were recorded. For within-plant distribution, leaves of the maize plants were numbered with the lowest leaf on the plant as leaf one. To record within-leaf distribution of egg masses the position of each egg mass was marked on a sketch of the leaf. Relative positions of the egg mass to the maize stem and to the mid-rib were later measured with a ruler on the leaf sketch. Plants at Schinznach were checked on 22 June and 7, 21 July and at Wasterkingen on 23, 30 June and 13, 27 July. This time covered most of the oviposition period of *O. nubilalis*. All data were combined to determine *O. nubilalis* oviposition distribution on the leaf.

Oviposition behaviour and distribution of egg masses over plants in a cage in the laboratory

Observations in the laboratory were done to make an initial description of *Ostrinia* oviposition behaviour and to be able to design a field cage set-up. A maize plant was placed in a Plexiglas cage (58 x 58 x 126 cm). Observations were made during 8 nights in a 25 °C climate room (16L/8D) during 8 nights. Light was turned off at 17.00, observations started at 20.00 and finished at 22.30. Illumination for the observer was provided by low-intensity red light. A container with 6 to 28 *O. nubilalis*, of which about half were female, was placed on the bottom of the cage and the lid removed. Some of the individuals left the container and the movement of these *O. nubilalis* individuals over the plant was recorded for 2.5 hours. To be able to do this a drawing of the plant and the leaves was made prior to the experiment. During the observation period, the place and time where certain activities took place were noted on the drawing of the plant. Usually, only a few *O. nubilalis* individuals were active as the same time, so continuous observations of each individual could easily be made despite the fact that several individuals where in the cage. The following activities were scored: (1) time of landing on and departure from the leaf, including leaf side, and (2) time, position and type of activity (walking, standing still, probing the leaf with abdomen) on the leaf, including leaf side. Movement and activities on the Plexiglas walls were not recorded, though oviposition on the walls was regularly observed. The maize plants were left in the cage overnight and checked the next day for egg masses. *O. nubilalis* was observed for eight nights in the climate room.

Oviposition behaviour and distribution of egg masses over plants in a field cage

Four maize plants were placed in a 2.5 x 2.5 x 2 m field insectary with a metal frame covered with fine plastic netting. Fresh *O. nubilalis* were released in the cage as they became available, resulting in a population

Table 4. Number of *O. nubilalis* egg masses found in 18 maize fields in Schinznach and Wasterkingen (Switzerland).

Date	Place	Side of leaf		
		Lower	Upper	Total
22.06.1993	Schinznach	25	0	25
23.06.1993	Wasterkingen	36	2	38
30.06.1993	Wasterkingen	51	3	54
07.07.1993	Schinznach	130	2	132
13.07.1993	Wasterkingen	49	2	51
21.07.1993	Schinznach	69	2	71
27.07.1993	Wasterkingen	26	0	26
Total number of egg masses		386 (97%)	11 (3%)	397 (100%)

of mixed age classes. Approximately 20 *Ostrinia* individuals were in each cage during observations, of which about 2/3 were females. After sunset, behaviour was observed for 2 h during 10 nights.

Distribution of moth scales over plants in laboratory and field cages

To see whether *O. nubilalis* left any moth scales behind that could be used as host cues close to oviposition sites and on other places of the plant, plants were checked under the microscope for the presence of moth scales. Four of the plants used for observations in the climate room, and four plants from the field cage were carefully checked for moth scales.

Scales of *Ostrinia* that were found on the maize leaves were divided in two categories: large (length 0.234-0.167 mm, width 0.033-0.007 mm) and small (length 0.067, width 0.033-0.007 mm). When a single scale or scale cluster was closer than 3 cm to an egg mass, the two were assumed to be associated.

Results

Distribution of egg masses over plants in the field

A total of 397 *O. nubilalis* egg masses were recorded in the field, with an average of one egg mass for every 6.4 plants checked. The date, place, number of egg masses found on the lower and upper part of the leaf and total number of egg masses found are reported in table 4.

Except for one egg mass found on the stem, all other egg masses (99.7%) were found on the leaves. Only 3% of the egg masses were found on the upper leaf side. The egg masses were mainly found on leaves three, four, five, six and seven (18, 25, 23, 16 and 8% respectively), as illustrated in figure 1.

Figure 2 illustrates the position of egg masses relative to the leaf mid-rib. Forty-two percent of the egg masses were found on or very close to the leaf mid-rib (10% of total leaf width), and 64 percent in 20% of total leaf width. Very few egg masses are found close to the edge of the leaf.

Position of egg masses relative to the plant stem are represented in figure 3. A large proportion of egg masses were found on the middle section of the leaf. Approximately 80% of the egg masses were found between the relative distance of 20 and 60% from the stem.

Oviposition behaviour and distribution of egg masses over plants in cages in the laboratory and the field

Results of climate room and field insectary observations are shown in table 5. In both experiments, not all moths were active or moths just flew against the walls of the cage without landing on a plant. In the climate room, the cage was small so accidental contact with the plant was quite likely, which might explain the higher number of contacts observed than in the field insectary. Females landed proportionally more then males. A few of the females were very active, and made many short visits to the plant. In the climate room, 27 landings had a duration of only five seconds or less, while in the insectary, 38 landings lasted only five seconds or less. This explains why the median duration of a visit was so much lower than the mean duration. In the climate room, one female landed ten times and walked much further over the leaf than all other females observed. In the insectary, the largest number of landings by a single female was eight times.

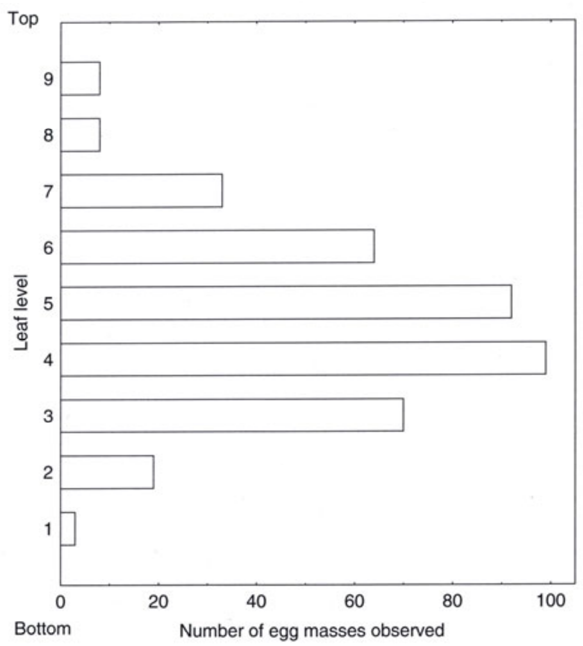

Figure 1. Distribution of 396 *O. nubilalis* egg masses over the leaf levels of maize in the field. Level one is the lowest leaf.

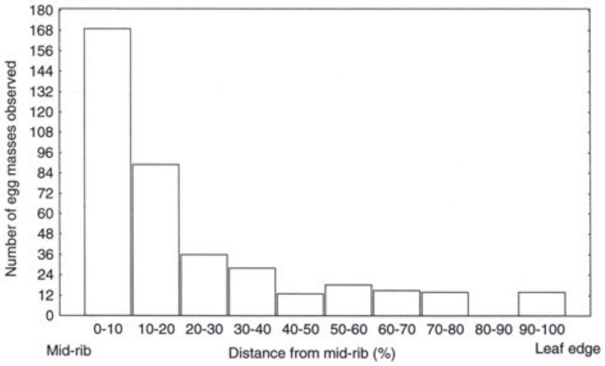

Figure 2. Distribution of 396 *O. nubilalis* egg masses over the leaf width of maize leaves in the field. Distance relative to the mid-rib.

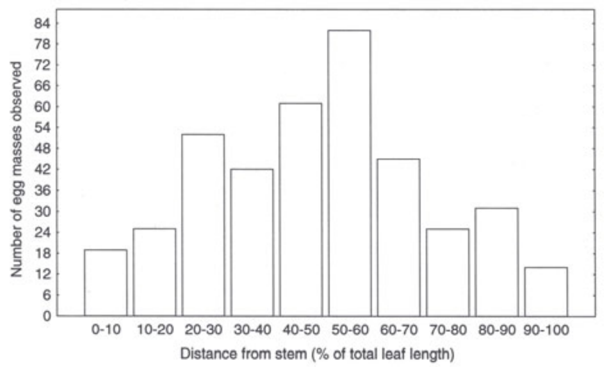

Figure 3. Distribution of 396 *O. nubilalis* egg masses over the leaf length of maize leaves in the field. Distance relative to the stem.

Table 5. Observation of *O. nubilalis* landing on maize plants in a cage in a climate room and in an insectary in the field.

	Climate room cage	Field insectary
Number of observation nights	8	10
Number of landings	93	76
Female	69	71
Male	24	5
Number of moths landing	57	33
Mean number of landings per moth	1.63	2.30
Percentage of landings on lower side	66	84
Mean leaf level of female landings	4.9 ± 0.2*	5.5 ± 0.3*
Mean time on plant (min)	20.5 ± 4.2*	11.6 ± 2.8*
Median time on plant (min)	2	1
Number walking	15	9
Number of females walking	12	8
Mean distance walked (cm)	4.9 ± 1.7*	2.5 ± 0.3*
Median distance walked (cm)	2	3
Number of probes with abdomen seen	44	12
Ovipositions	7	8
Mean oviposition leaf level	4.4 ± 0.8*	5.8 ± 0.6*

*Mean ± s.e.

Walking after landing was observed in only a few of the cases, both for males and females. However, some of the *O. nubilalis* were discovered on the leaves without the landing being observed. In these cases, it was not possible to say whether they had walked or not. The distance walked was usually short. The mean distance in the climate room was higher only because of the behaviour of one single female. Walking only occurred on the leaves. *O. nubilalis* stayed on the same leaf side during the entire search with the exception of two cases in the climate room. In the climate room, probing with the abdomen was observed in many cases. In the field insectary, light conditions were less good making such detailed observations harder. The number of actual ovipositions was quite low compared to the number of landings. In both the climate room and the insectary, the mean leaf level of oviposition was close to the mean leaf landing level (4.4 in the climate room and 5.8 in the field insectary). The distribution of landings of females over the leaf levels is shown in figure 4.

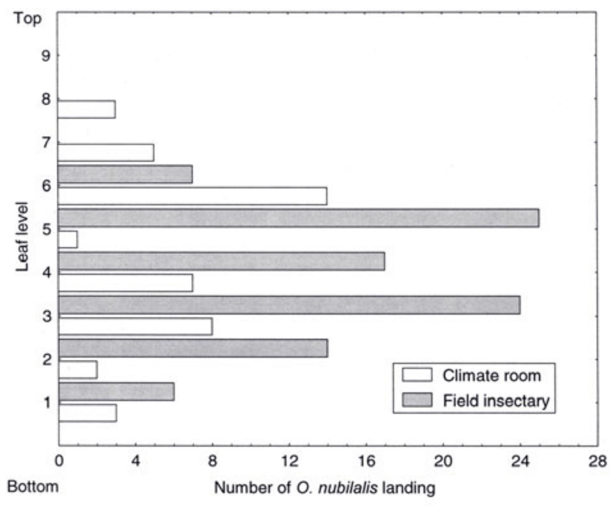

Figure 4. Distribution of female *O. nubilalis* landings over the leaf levels of maize in a cage in a climate room cage and in an insectary in the field. Level one is the lowest leaf.

Table 6. Distribution of *O. nubilalis* egg masses and scales observed on maize plants in a cage in a climate room.

	Number	Percentage
Number of plants checked	8	
Number of egg masses	62	
Egg masses on lower side	39	65
Total scales/scale patches associated with egg masses	39	45
Total scales/scale patches not associated with egg masses	48	55
Egg masses		
No scales	23	37
Few scales on or near egg mass	28	45
Dense scale area around egg mass	11	18
Scales not associated with egg masses		
Single scales or few scales	29	61
Large area with single scales	4	8
Track of scales	5	10
Dense scale area	10	21

Distribution of moth scales over plants in laboratory and field cages

Clusters of scales can be detected with the naked eye because of their "shiny" appearance. Single large scales were easily discernable on the leaf under a microscope, but single small scales were hard to detect. Most of the scales found were not directly associated with egg masses (table 6). Of the 62 egg masses, 82% had no or only a few scales (1-10) on or around them, while only 18% had an area with many large and small scales around (table 6). The number of dense scale patches without egg masses was almost the same as those associated with egg masses. Such patches had sizes from 2 to 20 mm in diameter, and were irregularly formed. Five very long and narrow scales patches were found (20-100 mm long), none of which was associated with an egg mass. Large scales were sometimes found single or in groups (1-10 scales) on the leaves. In four cases, single scales (both large and small) were spread over a large part of one leaf side.

The combination of the behavioural observations and the scales found showed that some of the dense patches of scales resulted from oviposition and abdominal probing. For each oviposition in the direct observations, 9.33 landings were made. Combined with the scale data, it is found that a landing resulting in oviposition has a 63 % chance of leaving scales behind, while landings not resulting in oviposition have only a 9% chance of leaving scales on the leaf. The distribution of egg masses and scales over the leaf levels was similar to the *O. nubilalis* landing distribution shown in figure 4.

Discussion

Distribution of egg masses over plants in the field

Distribution of *O. nubilalis* egg masses on maize plants in the field shows that egg masses are mainly found on the middle strata of the plant. As previously noted by other researchers, very few egg masses were laid on the upper leaf side. The within-leaf distribution of eggs shows that most egg masses were laid close to the mid-rib. A large proportion of egg masses were found on the middle section of the leaf relative to the plant stem, and oviposition on the tip of the leaf was rare.

Oviposition behaviour and distribution of egg masses over plants in cages in the laboratory and the field

During the experiments in the laboratory and field cages it was observed that oviposition almost always took place close to the place of landing. Few *O. nubilalis* move over the plant by walking, and those that do walk do so only for short distances. This means that the distribution of egg masses found on the plant also indicates the landing distribution over the plant. In our observations, 34% of landings in the climate room cage and 16% of the landings in the field insectary were on the upper leaf side. We consider the relatively frequent oviposition on the upper leaf side in the laboratory and field cages as an artefact of these cages. We do not think that this artefact is caused by the relatively high number of *O. nubilalis* which we released in the cages, as very few individuals were simultaneously active and contacts between individuals were rarely observed. We suppose that egg laying on the upper site is an effect of very restricted possibilies for movement which the cages offer to *O. nubilalis*.

Although landing and oviposition sites are similar, the number of landings is much higher than the number of ovipositions. In the experiments, the walls and ceiling of the cage or the insectary were often used as a resting place. In more than half of the landings in the cage, ovipositor probing was observed. This suggests that after most landings the plant is not used as a resting place only. The abdomen contains most of the receptors for perceiving plant substances indicating plant quality, such as fructose, saccharose, malate and aconitate (Baur *et al.*, 1994).

Distribution of moth scales over plants in laboratory and field cages

At distances of one to three centimetres (i.e. the maximum walking distance of *O. nubilalis* on the leaf), we found no strong relationship between egg masses and the presence of scales. Many egg masses had little or no scales in the vicinity, while on the other hand many scales and patches of scales were found on leaves with no egg masses. Scales or scale patches on leaves without egg masses could be the result of landings by males and females. We already indicated that in the laboratory and field cages, more ovipositions took place on the upper side of the leaves, and, similarly, altogether a higher than normal number of landings might have occurred on the leaf upper side than in the field. These artefacts should be kept in mind when discussing the current data in relation to the host searching behaviour of *Trichogramma*.

From the number of egg masses with little or no scales, it is clear that probing or ovipositing will not necessarily leave scales on the leaf. In natural field conditions, the number of egg masses and scale patches will be lower, with a maximum of two or three egg masses per plant. The position of the scales will be different too. Since moth landings in the field will be mostly on the lower leaf side, the host cues will also be more concentrated on the lower leaf side than in the observation experiments in cages. Scales in the field will indicate that there probably is an egg mass on the plant or on the leaf, but this egg mass might not be close to the point where the scales are encountered.

Effect of *Ostrinia* egg laying pattern and scale deposition on *Trichogramma* egg parasitoids

The egg parasitoid *T. brassicae* shows a distinctive landing and searching pattern on clean maize plants. *T. brassicae* land on both sides of the leaf, and although their landing positions are not often near the mid-rib of the leaf, landing distributions over the length of the leaf are quite similar with those of *O. nubilalis* egg masses (Suverkropp, 1994). Both sides of the leaf are searched, but *T. brassicae* spends up to 10% of time close to the mid-rib and also spends more time searching the middle and base part of the leaf (Suverkropp, 1997). Apparently, the searching and landing pattern of *T. brassicae* is quite similar with the *O. nubilalis* egg laying pattern, apart from the time that *T. brassicae* spends on the upper leaf side. Since both the amount of egg masses and scales on upper leaf sides is low in the field, it would be more efficient for *T. brassicae* to spend most time on the lower leaf side. But it is unlikely that the behaviour of *T. brassicae* is a result of co-evolution with *O. nubilalis,* since it is a generalist parasitoid. Landing distribution and movement patterns of *T. brassicae* have probably evolved to provide an efficient way to search many different plant species for eggs of a variety of host species.

T. brassicae, like many *Trichogramma* species, reacts to host cues. Scales of *O. nubilalis* elicit an arrestment response (Bieri *et al*., 1990). However, based on the results presented in this paper, it is difficult to conclude whether scales of *O. nubilalis* can be used by the parasitoid to find egg masses more efficiently. Therefore, we developed an individual based Monte Carlo simulation model which, together with validation experiments, showed that presence of scale patches on the same leaf as an egg mass and even when they are not close to the egg mass, increase the encounter probability with host eggs (Suverkropp, 1997).

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