THE ROLE OF ANTENNAE, TARSI, LABELLUM, AND OVIPOSITOR
IN FACE FLY OVIPOSITION

by

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INTRODUCTION AND LITERATURE REVIEW

Ovipositional behavior of insects can be summarized into two
major divisions. The first involves the attraction of the insect to
the oviposition site and the second is concerned with behavior that
leads to oviposition (Barton-Browne, 1960). Since these behaviors
are adjusted to the specific requirements and living conditions of the
larvae, their detection of ovipositional sites are of utmost importance
to the insect's survival (Engelmann, 1970).

Olfaction is important in oviposition of _Phormia regina_. Barton-Browne
(1960) reported that the antennae and/or palps are the most important
olfactory receptors on _Phormia regina_. He also found that the antennae,
palps, and labellum are capable of olfactory discrimination and gave
circumstantial evidence that the ovipositor was also a discriminatory
organ involved with oviposition. Wallis (1962a) concluded that receptors
located on the antennae, labellum, and ovipositor of _Phormia regina_ are
involved with one of the fly's "instinctive behavioral repertoire-
oviposition."

The role contact chemoreceptors might play in causing oviposition
in insects has not been extensively studied. West (1951) describes
Kuzina's work in which Kuzina determined that taste was necessary for
Musca domestica oviposition, though olfaction was important for locating
the ovipositional site. Tarsal contact chemoreceptors of the mosquito
are important in oviposition (O'Gower, 1957). Barton-Browne (1962)
concluded that the presence of volatile oviposition stimulants and
tarsal contact with water increase the oviposition rate of the blow

fly <u>Lucilia</u> <u>cuprina</u>. The addition of NaCl or sucrose to the water did not influence the effect of the water as a stimulant.

Barton-Browne (1960) and Wallis (1962b) felt that mechanoreceptors on the ovipositor of <u>Phormia</u> <u>regina</u> were responsible for the final placement of the egg. Wallis (1962a) found through electrophysiological studies that the majority of hairs on the ovipositor of <u>Phormia</u> <u>regina</u> are mechanoreceptors that show peak sensitivities to deflections in certain directions and termed them 'position-sensitive' sensilla. He concluded that <u>Phormia</u> <u>regina</u>'s probing into crevices at the oviposition site is done in such a manner as to deflect the hairs in their most sensitive directions. This speculation was confirmed with behavioral studies on <u>Phormia</u> <u>regina</u> in which Wallis waxed the leaflets on the fly's ovipositor so as to interfere with the fly's perception of mechanical stimulation. This procedure interfered with normal egg deposition (Wallis, 1962b).

DeVaney et al. (1970) found a drastic drop in oviposition in the screw-worm fly on horse meat when the antennae and rostrum were removed. Forty-three percent of the flies without antennae and haustellum deposited eggs. Removal of the fifth tarsal segment of all legs did not effect egg deposition, either when the legs were cut off plus the antennae or rostrum. Removal of the antennae, hastellum, or antennae did not appear to affect the percentage of flies laying egg masses.

Research on oviposition stimuli and their detection in <u>Musca</u> <u>autumnalis</u> is limited. Attraction of the fly to bovine manure occurs shortly after it has been dropped in the field (Hammer, 1942). In laboratory experiments, oviposition was not initiated until about ten

minutes after the fly had alighted on the dung. During the intervening time it was reported that the fly spent the remainder of the time imbibing dung liquids. If the manure was old enough to form a crust, the fly sought out cracks or other soft areas of the manure in which to insert her ovipositor. Oviposition required a few seconds with eggs being laid singly. The female extended the terminal segment of her ovipositor each time an egg was laid. On fresh manure eggs were laid randomly (Wang, 1962). Dobson and Matthew (1960) never observed a female lay more than two or three eggs in one spot before moving on.

The face fly oviposits in manures from different animals. Of the manures tested, face flies preferred bison, sheep, pig, bovine, deer, and horse in that order (Bay et al., 1969b). It has also been found ovipositing on human feces in latrines (Kobayaski, 1919).

The chemical make up of the manure affects the adult face fly's oviposition. When fresh manure is compared to reconstituted manure, the fresh was preferred for oviposition. It is felt that unknown volatile factor(s) that are lost during the lyophilization could be responsible for the difference in choice (Bay et al., 1969a).

Various chemoreceptor sites have been morphologically defined on the face fly. The ovipositor's anal leaflets contain a three-dendrite thickwalled hair, a five-dendrite thickwalled hair, and pegs with pores (Hooper, 1971). Unpublished observations by Ms. Hooper defined chemoreceptor hairs on the tarsi, proboscis, and antennae. Thus, chemoreceptor organs have been morphologically defined on the face fly's ovipositor, labellum, antennae, and tarsi.

The question remains as to the function chemoreceptor organs play in relation to face fly oviposition. Benzocaine was used to desensitize the chemoreceptors and possibly mechanoreceptors. Blockage of the tarsi, antennae, labellum and ovipositor will provide information as to the role each of these play in face fly oviposition.

MATERIALS AND METHODS

Experimental flies were obtained from the Kansas State University Department of Entomology rearing room. The colony was maintained in screened cages at 26.7^{o} C and a relative humidity of 70%. Refer to Bay et al., 1969 for procedures used in rearing face flies.

Experimental flies were randomly selected from cages containing seven-day-old adults. Collection of flies for experimentation was made by rapidly moving a vacuum apparatus through the cage. The captured flies were immobilized by placing them in a freezer at -11° C for ten minutes. Females with expanded abdomens were transferred to a small beaker contained in an ice bath. Individuals for experimentation were obtained by "pouring" out the females as needed.

Americaine[R] Aerosol (Arnal-Stone Laboratories, Inc., Mount Prospect, Illinois 60056) containing 20% benzocaine and a 0.5% 8-hydroxyquiolene dissolved in a water dispersible polyethylene glycol-400 dilaurate base was used to block the chemoreceptor sites on the tarsi. Flies were suspended by beeswax from wooden sticks three hours before testing. This allowed for recuperation from the attaching procedure and physiologically prepared the flies to respond to the test solutions. The tarsi were immersed in the Americaine

solution for 15 seconds and were tested for their ability to detect
1 M. sucrose, manure juice, and distilled water. Proboscis extension
indicated the detection of the stimulating solution or not. This method
proved satisfactory and was used in subsequent experiments to desensitize
various chemoreceptor organs in order to determine their importance in
regard to face fly oviposition.

Oviposition tests were conducted in a clear plastic chamber con-
structed of two square 9.5 cm x 9.5 cm x 1.5 cm petri dishes. On one
surface of each pair was placed twelve centrally located holes covered
with fine copper screen. The petri dishes were inverted and fitted
together to form the test chamber. Baby food jar lids (5.5 cm in
diameter and 0.8 cm deep) filled with bovine manure served as the ovi-
position substrate.

The chemoreceptor sites on the tarsi, labellum, and ovipositor were
immersed in the Americaine solution for 15 seconds and then placed in
the test chamber. It was not possible to successfully apply the Americaine
solution to the antennae. Therefore, antennectomy of at least the third
antennal flagellar subsegment was necessary three hours before antennal
experiments were performed. Flies with chemoreceptor organs immersed in
the benzocaine solution were allowed to recuperate for 35 minutes and
then lids containing fresh bovine manure were introduced into the test
chamber. The experiments were concluded with the removal of the manure
after 40 minutes.

At the conclusion of each test period, eggs were counted in the
manure. The flies were dissected to determine the number of mature eggs

(eggs with masts) present. Those flies with eggs without masts were termed immature. Three such individuals in any test discounted the results of that particular experiment and it was rerun.

Observations were made on the behavior of the flies in the plexiglas test chambers. The thesis includes only observations on the groups of experimental flies that were pertinent in explaining significant results.

All tests were randomly performed four times using five flies in each replicate. The tests were performed under constant fluorescent lighting, at the same time of day, and a constant temperature of 24.4° C.

RESULTS

Effect of Benzocaine on Tarsal Chemoreceptors

When compared to the control flies, flies with their tarsi immersed in the benzocaine solution had an obvious reduction in proboscis extension when the tarsi were stimulated. At the end of 75 minutes, 6% of the treated flies exhibited proboscis extension when their tarsi were stimulated with manure, 4% responded to water, and 6% to 1 M. sucrose (Plate I, II, III). Therefore, it was concluded that benzocaine was able to desensitize the chemosensory hairs and that its effect will last for at least 75 minutes.

Comparison of the control percentage of eggs layed to each of the combinations of blocked chemoreceptor sites was made by using Dunnett's t. In all cases the benzocaine treatments caused a significant decrease in percent eggs layed (Table 1). Thus, the elimination of one chemoreceptor organ significantly interferes with oviposition.
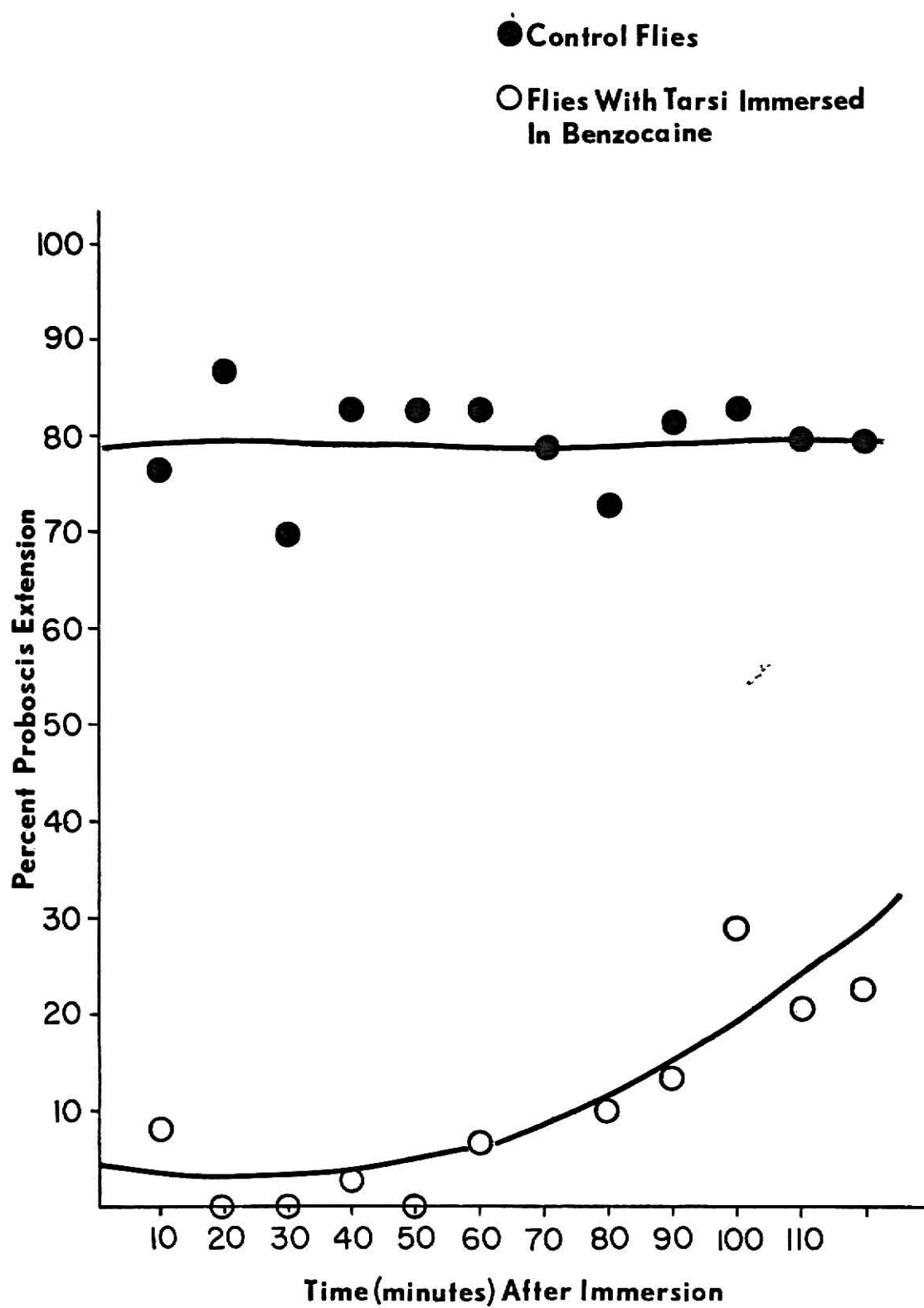
EXPLANATION OF PLATE I

Effect immersion of tarsi in benzocaine has on
proboscis extension when tarsi are stimulated
with manure.

THIS BOOK CONTAINS NUMEROUS PAGES WITH DIAGRAMS THAT ARE CROOKED COMPARED TO THE REST OF THE INFORMATION ON THE PAGE.

THIS IS AS RECEIVED FROM CUSTOMER.

PLATE I

● Control Flies

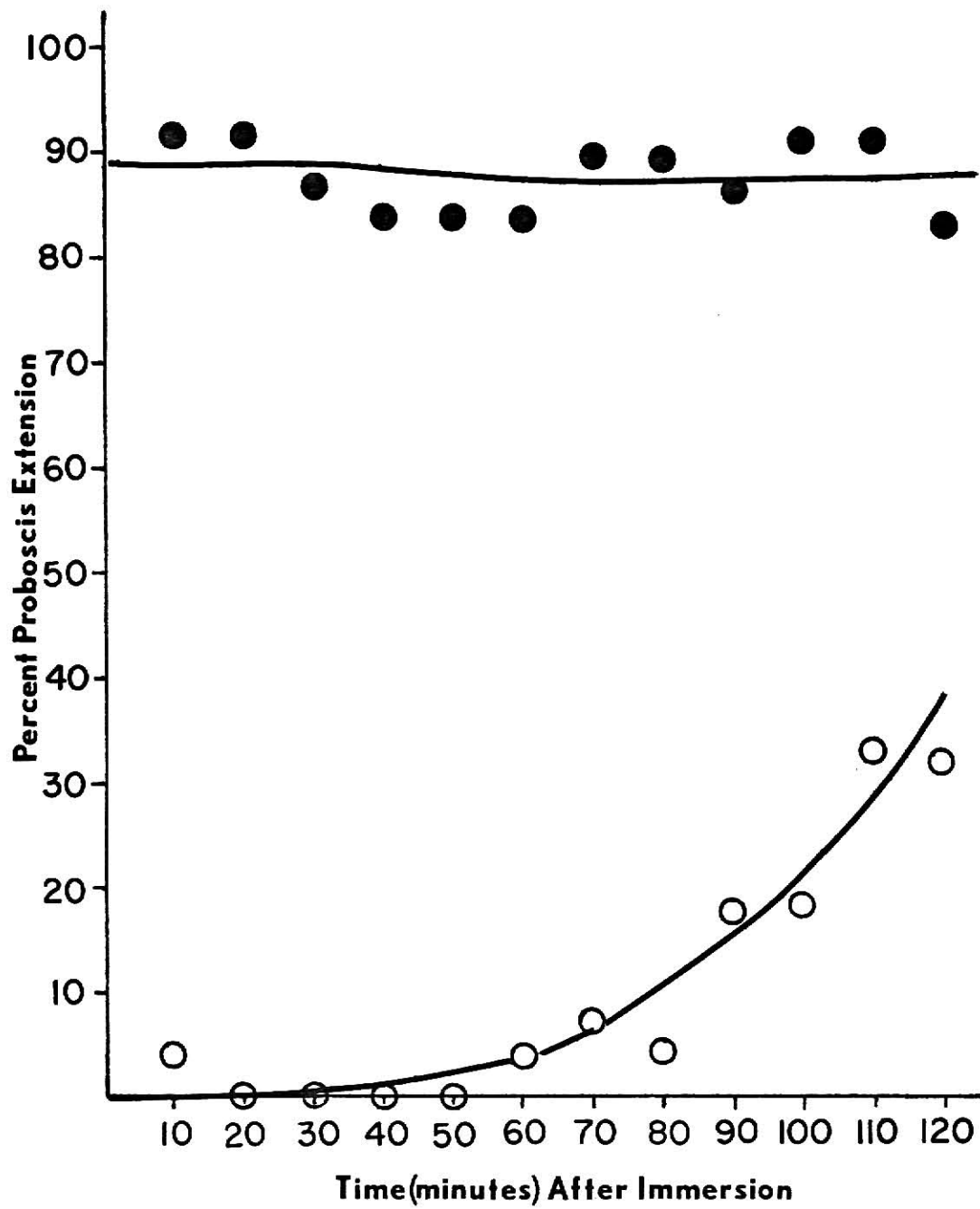○ Flies With Tarsi Immersed In Benzocaine

EXPLANATION OF PLATE II

Effect immersion of tarsi in benzocaine has on
proboscis extension when tarsi are stimulated
with distilled water.

PLATE II
● Control Flies
○ Flies With Tarsi Immersed In Benzocaine

EXPLANATION OF PLATE III

Effect immersion of tarsi in benzocaine has on

proboscis extension when tarsi are stimulated
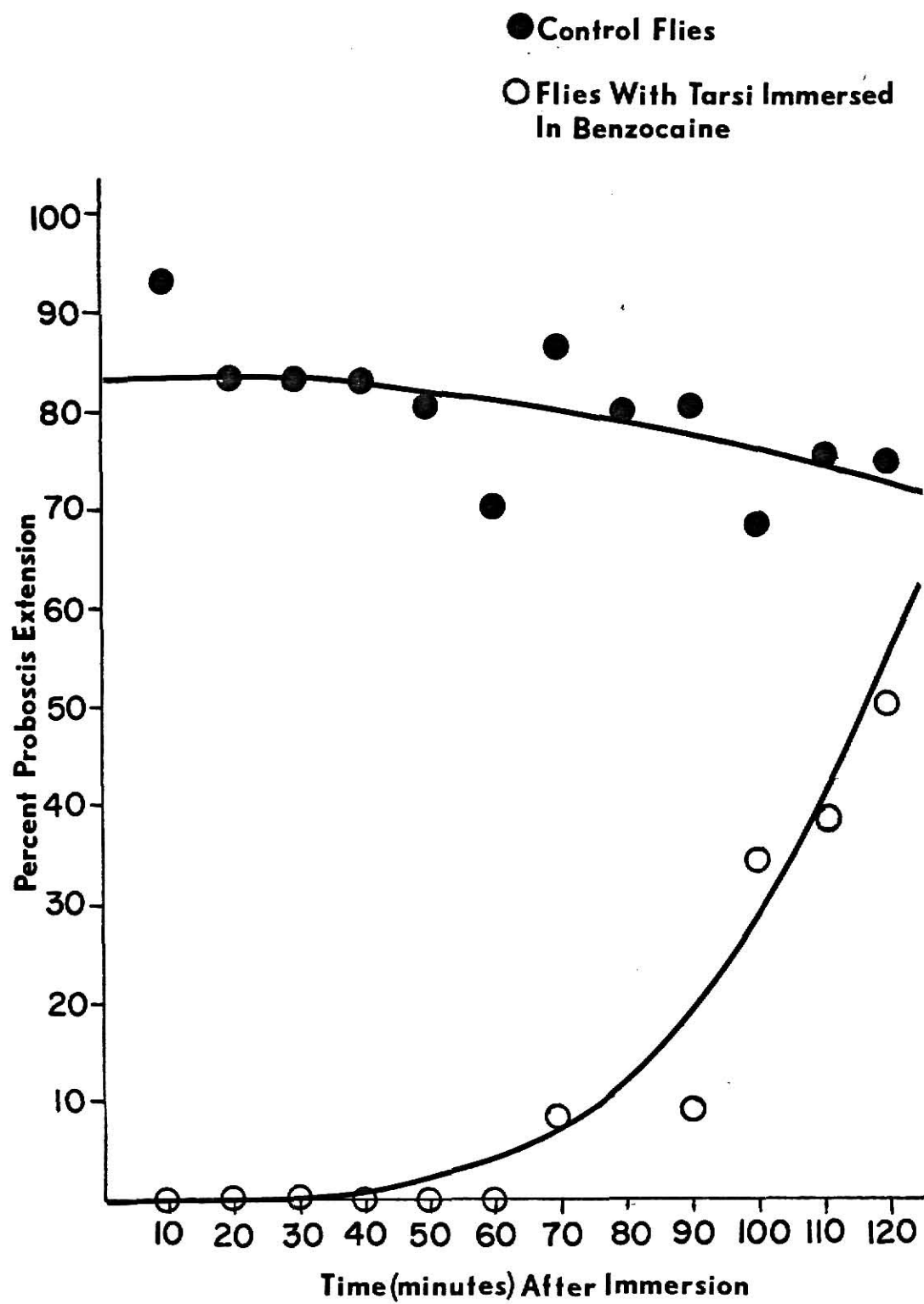
with 1 M. sucrose.

PLATE III

●Control Flies

○Flies With Tarsi Immersed
In Benzocaine

Percent Proboscis Extension

Time(minutes) After Immersion

Table 1. Effect blockage of various chemoreceptor organs has
on face fly oviposition.

Experimental flies with various blocked chemo-receptors	Mean percent eggs layed	Statistical significance as compared to control (p=0.05)
Antennae	14.3	Significant
Labellum	36.6	Significant
Ovipositor	59.1	Significant
Tarsi	23.5	Significant
Antennae-Labellum	7.9	Significant
Antennae-Ovipositor	14.1	Significant
Antennae-Tarsi	1.9	Significant
Labellum-Ovipositor	13.6	Significant
Labellum-Tarsi	18.8	Significant
Ovipositor-Tarsi	11.1	Significant
Labellum-Tarsi-Antennae	0.0	Significant
Antennae-Labellum-Ovipositor	4.9	Significant
Ovipositor-Tarsi-Labellum	1.2	Significant
Tarsi-Ovipositor-Antennae	0.0	Significant
Tarsi-Labellum-Antennae Ovipositor	0.0	Significant
Control	82.5	

These results are in conflict with DeVaney et al. (1970) work on the screw worm fly. These authors concluded that the removal of one chemoreceptor organ (the fifth tarsal subsegment, the antennae, hastellum or rostrum) did not drastically interfere with oviposition. A possible explanation of the difference could be that the chemoreceptor organs on the two species of flies are functionally different as a result of the chemical composition of their oviposition substrates.

Determination of the Relative Importance Chemosensory Organs Play in Face Fly Oviposition

To determine the relative importance of the various chemoreceptor organs in relation to oviposition, a transformation of the data was necessary. The transformation involved changing the percent eggs layed by the experimental flies to percent reduction of oviposition of experimental flies. The equation is a modification of Abbott's formula and is as follows:

$$\text{\% reduction of oviposition of experimental flies} = \frac{\text{\% of eggs layed by control} - \text{\% of eggs layed by experimentals}}{\text{\% of eggs layed by control}}$$

The data was then analyzed by using an analysis of variance and Duncan's NMRT with alpha equal to 0.05. These statistical tests made it possible to compare the relative importance blockage of various chemoreceptor organs might have on face fly oviposition.

Table 2 indicates that flies with desensitized ovipositor tips had the lowest mean percent reduction in eggs layed (27.8%). Blockage of the

Table 2. Comparison of percent reduction in oviposition of
          experimental flies with one chemoreceptor organ
          blocked.

Chemoreceptor organ blocked[1]	Mean percent reduction in oviposition
Antennae	82.3
Tarsi	70.9
Labellum	55.0
Ovipositor	27.8

[1]Lines connect blocked chemoreceptor organs that are not
significantly different (p=0.05).

labellum caused the flies to have the next to the lowest mean percent

reduction in oviposition (55.0%) as compared to flies with their

ovipositors desensitized and those without their antennae. Removal of

the antennae caused the highest percent reduction of eggs (82.3%) to be

layed when compared to flies with blocked ovipositor tips and labella.

Although flies with desensitized tarsi had the next to the highest percent

reduction in oviposition (70.9%), the data were not sufficient to statis-

tically determine if there was a difference in percent reduction in ovi-

position between flies with their tarsi or ovipositors desensitized. The

tarsi when functionally eliminated caused a greater reduction in oviposition

(70.9%) than those flies with blocked ovipositor tips (27.8%).

     It was not statistically possible to determine the relative importance

the blockage of two chemoreceptor organs has on oviposition (Table 3).

Table 3. Comparison of percent reduction in oviposition of
experimental flies with two chemoreceptor organs blocked.

Chemoreceptor organs blocked[1]	Mean percent reduction in oviposition
Antennae-Tarsi	100.0
Antennae-Labellum	90.6
Tarsi-Ovipositor	86.3
Labellum-Tarsi	83.7
Ovipositor-Antennae	82.8
Labellum-Tarsi	77.5

[1]Lines connect blocked chemoreceptor organs that are not
significantly different (p=0.05).

The only comparison that could be made indicates that the experimental
flies without antennae and their tarsi blocked caused the greatest
reduction in oviposition (100.0%) when compared to the flies with their
tarsi-ovipositor (86.3%), labellum-tarsi (83.7%), ovipositor-antennae
(82.8%), and labellum-tarsi (77.5%) combinations blocked.

Blockage of the antennae-labellum-ovipositor combination on
experimental flies caused the least percent reduction in oviposition
(94.0%). It was not statistically possible to separate out the means
for the various other mean percent reductions in oviposition (Table 4).

Table 5 shows that experimental flies with desensitized ovipositor
tips caused the least percent reduction in oviposition (27.8%). Flies
with desensitized labella had the second to the lowest mean percent
reduction in oviposition (55.0%). Blockage of the tarsi of experimental

Table 4.   Comparison of percent reduction in oviposition of experimental flies with three chemoreceptor organs blocked.

Chemoreceptor organs blocked[1]	Mean percent reduction in oviposition
Tarsi-Ovipositor-Antennae	100.0
Labellum-Tarsi-Antennae	100.0
Ovipositor-Tarsi-Labellum	98.4
Antennae-Labellum-Ovipositor	94.0

[1]Lines connect blocked chemoreceptor organs that are not significantly different (p=0.05).

Table 5.   Comparison of percent reduction in oviposition of all chemoreceptor organs to each other.

Chemoreceptor organ(s) blocked[1]	Mean percent reduction in oviposition
Antennae-Labellum-Tarsi-Ovipositor	100.0
Labellum-Tarsi-Antennae	100.0
Tarsi-Ovipositor-Antennae	100.0
Antennae-Tarsi	100.0
Ovipositor-Tarsi-Labellum	98.4
Antennae-Labellum-Ovipositor	94.0
Antennae-Labellum	90.6
Tarsi-Labellum	86.3
Labellum-Ovipositor	83.7
Ovipositor-Antennae	82.8
Antennae	82.3
Labellum-Tarsi	77.5
Tarsi	70.9
Labellum	55.0
Ovipositor	27.8

[1]Lines connect blocked chemoreceptor organ(s) that are not significantly different (p=0.05).

flies caused for the third to the lowest percent reduction (70.9%) in oviposition when compared to the blocked combinations consisting of the antennae-labellum (90.6%), antennae-labellum-ovipositor (94.0%), ovipositor-tarsi-labellum (98.4%), antennae-tarsi (100.0%), tarsi-ovipositor-antennae (100.0%), labellum-tarsi-antennae (100.0%), and antennae-labellum-tarsi-ovipositor (100.0%).

Experimental flies with their antennae removed had a greater reduction in oviposition (82.3%) when compared to flies with desensitized ovipositor tips (27.8%) and labella (54.6%). The flies without antennae did not have as great an effect in reducing oviposition as compared to flies with their ovipositor-tarsi-labellum (98.4%), antennae-tarsi (100.0%), labellum-tarsi-antennae (100.0%), and antennae-labellum-tarsi-ovipositor (100.0%) combinations blocked.

Flies with desensitized tarsi-ovipositor (86,3%), labellum-ovipositor (83.7%), and ovipositor-antennae (82.3%) combinations had a greater reduction of oviposition when only compared to the flies with desensitized ovipositor tips (27.8%) or labella (55.0%).

Blockage of the antennae-labella (90.6%) and antennae-labellum-ovipositor (94.0%) combinations caused a greater reduction in oviposition as compared to flies with desensitized tarsi (70.9%), labella (55.0%), and ovipositors (27.8%).

The last possible statistical comparison that can be made is that the functional elimination of the ovipositor-labellum-tarsal combination caused a greater reduction of oviposition (98.4%) than those flies with their labellum-tarsi (77.5%), tarsi (70.9%), labellum (55.0%), and ovipositor tips (27.8%) blocked.

The ovipositional behavior of control face flies and experimental flies with one chemoreceptor organ removed or desensitized were made. This provided a better understanding of the effect desensitization of various chemoreceptor organs had on face fly oviposition behavior.

Control Face Fly Oviposition Behavior

The majority of the control flies made contact with the manure after being in the test chamber for two minutes. The behavior of the flies on the manure was varied. Some would immediately extend their proboscises after walking onto the manure. Others would walk a short distance across the manure, stop, and then extend their proboscises to the manure's surface. The flies were observed to continue extending their proboscises while walking on the manure. Others after making initial proboscis contact, would move to another area on the manure and re-extend their proboscises. All proboscis activity at this initial stage was repeated and vigorous.

After approximately 9 minutes in the chamber, oviposition was observed. Oviposition was initiated with partial ovipositor extension in addition to walking and proboscis activity. The ovipositor continued to be extended while the fly was walking but was not fully extended until the fly stopped. At this time the ovipositor would be moved from side to side over the manure and then retracted partly back into the fly's abdomen. Then one of two things would happen. Either the ovipositor was re-extended and placed on the manure and egg laying would occur or the ovipositor tip was placed on the manure surface and the fly would walk about with it touching the manure. Proboscis extension could

occur during this particular walking procedure. The fly would stop and egg laying would proceed.

During the period when the flies were stationary and an egg was layed, proboscis extension did not occur. The hind tarsi usually were moved to straddle the egg's mast during the removal of the ovipositor from the manure. After egg laying, the fly would move a short distance (2 c.m. or less) with the ovipositor tip touching the manure and lay another egg or the ovipositor was partly retracted into its abdomen and the fly would move to another site.

Most of the oviposition was completed after 25 minutes. Some flies were observed ovipositing throughout the thirty-five minute test period.

Behavior of Experimental Face Flies

The behavior of flies with their tarsi immersed in benzocaine was similar to control flies. One obvious difference was that the initial proboscis extension was not frequent. Ovipositor extension occurred on a few flies after 20 minutes in the test chamber. Toward the end of the test period, those flies not ovipositing were completely off the manure and spent most of the remaining time walking around the test chamber. Occasionally these flies would walk across the manure and proboscis extension would occur.

Flies with their labella immersed in benzocaine also behaved like the control group. Ovipositor extension and oviposition was initiated after 19 minutes in the test chamber. Flies not ovipositing spent most of their time on the manure and frequently probed its surface with their labella.

The only difference between flies with their ovipositors blocked and control flies was that ovipositor extension and egg laying did not occur until 18 minutes in the test chamber. The behavior of flies that did not oviposit was similar to control flies except no ovipositor extension occurred.

A few of the flies without antennae reached the manure within 2 minutes. The majority of the flies remained around the periphery of the test chamber. Of those on the manure, a few started to extend their ovipositors and initiated oviposition 19 minutes after being introduced into the test chamber. The ovipositing behavior of these flies was similar to that already described for the control flies.

DISCUSSION

If a face fly is to reproduce maximally it must be able to select an ideal site for its larvae to develop. External chemoreceptor organs provide a means whereby a fly can sample its environment. Interference with any one of these organs (i.e., the tarsi, ovipositor, antennae, or labellum) could affect the fly's detection of the oviposition site.

The data analyzed by Dunnett's t indicated that blockage of the chemoreceptors on the tarsi, ovipositor, labellum or antennae and their various combinations caused a significant decrease in the percentage of eggs layed by a face fly (Table 1). Therefore, all chemoreceptor organs are necessary for a face fly to oviposit maximally. Since the blockage of the chemoreceptor organs and their combinations significantly reduced oviposition by varying amounts, it appears that some chemoreceptor organs are more important than others for oviposition. The remainder of the discussion will pursue this aspect more fully.

Blockage of the ovipositor receptors caused the lowest percent reduction in oviposition (27.8%, Table 5); therefore, it is the least important chemoreceptor organ. But the ovipositor possesses some discriminatory function since its blockage can significantly reduce oviposition when compared to control flies. As the ovipositor is the last chemoreceptor organ to contact the manure, the chemoreceptor sensilla located there could serve to position the ovipositor at a specific site located by the other three chemoreceptor organs.

Blockage of sensory receptors on the labellum of experimental flies caused next to the lowest percent reduction in oviposition (55.0%, Table 5). Observations of these flies indicated that the application of benzocaine to labella did not seriously affect its contact with the manure surface. Since the labellum was able to contact the manure and its blockage caused the next to the lowest percent reduction in oviposition, it can be theorized that the labellum is more important than the ovipositor in stimulating oviposition.

Greater percent reduction in oviposition (70.9%, Table 5) occurred when the tarsi were blocked as compared to flies with their labella (55.0%, Table 5) or ovipositors (27.8%, Table 5) desensitized. Since the blockage of the tarsi does affect proboscis extension and egg laying, their function, as the first chemoreceptor organ to contact the manure, could be to inform the fly that oviposition is possible.

The tarsi and the labellum are singly the most important contact chemoreceptor organs and therefore, it would seem that the elimination of the two should significantly reduce oviposition when compared to flies with just one of these chemoreceptor organs blocked. This was

not entirely the case. The flies with their labella and tarsi blocked caused a significantly greater reduction in oviposition (77.5%, Table 5) than flies with desensitized labella (55.0%, Table 5). However, the flies with desensitized tarsi were not significantly different (70.9%, Table 5) from those with blocked tarsi and labella (77.5%, Table 5). In this particular set of data statistical significance occurred only when the tarsi were not desensitized. This supports the previous conclusion that the tarsi are involved with informing the fly that oviposition is possible.

The antennae are more important than the ovipositor or the proboscis in causing oviposition. The majority of antennectomized flies were observed to remain off the manure. Thus, it seems reasonable to conclude that the antennae are necessary for helping the insect locate the manure.

Since flies without antennae had the greatest percent reduction in oviposition among flies with one chemoreceptor organ blocked, it is possible that the antennae along with the tarsi could be involved with a process that signals the fly that oviposition is possible. In fact, the importance of the antennae and tarsi in signaling the fly of the possibility of oviposition is illustrated by the fact that their blockage completely eliminates oviposition.

Using the previous conclusions it is possible to describe an ovipositional sequence used by a gravid face fly (Fig. 1). The antennae are concerned with the detection of odors from the manure. The perception of these odors stimulates the central nervous system (CNS) and produces the initial attraction to the manure. Utilizing manure

EXPLANATION OF FIGURE 1

Proposed oviposition sequence used by a gravid face
fly. Arrows coming from and into the various chemo-
receptor organs represent information these organs
supply to the CNS and where this information is
relayed. Solid and dotted lines represent olfactory
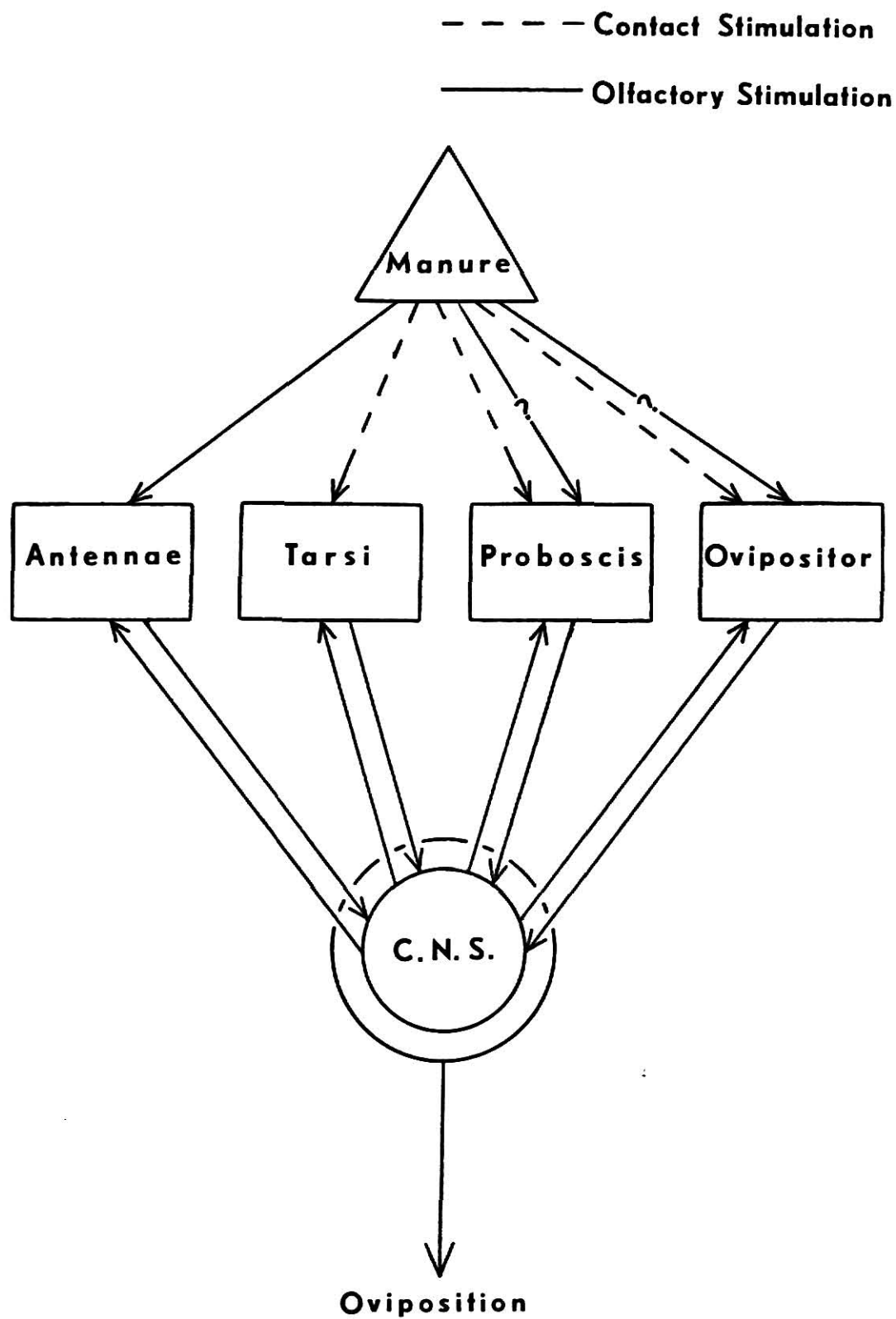and contact chemical stimulation, respectively.

Fig. 1

odors and possibly other factors, the fly is able to land on the manure.

Upon landing on the manure, the tarsal chemoreceptors signal the CNS that the manure could be a suitable substrate. Stimulation of tarsal chemoreceptors by the manure causes the CNS to initiate proboscis extension. The chemoreceptors on the tarsi and labellum sample the manure and this information is used by the CNS to determine if oviposition can occur. The antennae are probably involved with this sampling process since antennectomized flies generally do not remain on the manure even after contacting it.

Once the fly has located an oviposition site, utilizing information supplied by the labellum, tarsi, antennae, the CNS signals for extension of the ovipositor. Lateral movements of the fly's ovipositor over the manure bring the olfactory receptors on the anal leaflets in a position to be maximally stimulated. As oviposition occurs shortly after this time, the olfactory receptors on the leaflets help to further localize the oviposition site on the manure. The CNS now signals the fly to lower its ovipositor. The mechanoreceptors and chemoreceptors on the leaflets are then responsible for finding a protective crevice in the manure for the fly's eggs to be layed into. When this site has been found, the CNS is signalled and egg laying proceeds.

SUMMARY AND CONCLUSIONS

Benzocaine was found to desensitize chemoreceptors on the face
fly's tarsi for a period of approximately 75 minutes. It could not
be determined if the mechanoreceptors located there were also blocked.
Accordingly, the chemoreceptors on the antennae, tarsi, labellum, and
ovipositor were blocked singly and in various combinations in order to
determine their role in oviposition.

Removal of the antennae or the desensitization of the labellum,
tarsi, or ovipositor and their combinations significantly reduced
oviposition as compared to control flies. Depending on the chemo-
receptor organ(s) blocked, oviposition was reduced by varying amounts.
Blockage of the ovipositor's chemoreceptors caused the least percent
reduction in oviposition (27.8%, Table 5) and therefore, the ovipositor
is the least important chemoreceptor organ necessary for oviposition.
Desensitization of the chemoreceptors on the labellum caused the next
to the lowest percent reduction in oviposition (55.0%, Table 5) and is
the second to the least important chemosensory organ. The antennae and
tarsi were more important in reducing oviposition (82.3% and 70.0%, re-
spectively, Table 5) than the proboscis (55.0%, Table 5) and the ovi-
positor (27.8%, Table 5). Therefore, the chemoreceptors on the antennae
and tarsi are more important in reducing oviposition than those on the
ovipositor or the labellum.

The data and observations on gravid face flies allow one to
propose a tentative sequence of events used by the face fly in ovi-
position. The antennae are probably concerned with the detection of
manure odors. Perception of the odors stimulates the CNS and produces

the initial attraction to the manure. Upon landing on the manure, the
tarsi inform the CNS and cause the proboscis to be extended. The chemo-
receptors on the tarsi, labellum, and possibly the antennae and ovipositor
are involved with a sampling process that determines if oviposition can
occur. Once a site has been located, the CNS signals for the extension
of the ovipositor. The chemoreceptors and mechanoreceptors on the
ovipositor's anal leaflets are responsible for the final site selection
on the manure for the egg. When this site has been found, the CNS is
signalled and egg laying proceeds.

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THE ROLE OF ANTENNAE, TARSI, LABELLUM, AND OVIPOSITOR
IN FACE FLY OVIPOSITION

by

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Experiments were conducted to determine the role chemoreceptors, located on the tarsi, labellum, ovipositor and antennae, play in face fly (<u>Musca</u> <u>autumnalis</u>) oviposition. Benzocaine was used to desensitize the chemoreceptors on the tarsi, labellum and ovipositor; the antennae were amputated.

When tarsi were immersed in a 20% benzocaine solution for 15 seconds, proboscis extension was greatly reduced when the tarsi were stimulated with distilled water, manure juice and 1 M. sucrose. After 75 minutes, 6% of the treated flies exhibited proboscis extension when tarsi were stimulated with manure, 4% responded to water, and 6% to 1 M. sucrose. It could not be determined if the mechanoreceptors located there were also blocked.

Oviposition tests were made to determine the effect blockage of the chemoreceptors on the tarsi, antennae, ovipositor or labellum and their various combinations had, on reducing face fly oviposition. These tests were randomly performed four times, using 5 flies in each replicate.

Removal of antennae or desensitization of the labellum, tarsi, or ovipositor and their combinations, significantly reduced oviposition as compared to control flies. Depending on the chemoreceptor organ(s) blocked, oviposition was reduced by varying amounts. Blockage of the ovipositor's chemoreceptors caused the least percent reduction in oviposition while desensitization of the labellum caused the next to the lowest percent reduction of 27.8% and 55.0%, respectively. Therefore, the labellum is more important than the ovipositor in reducing oviposition. The antennal and tarsal chemoreceptors, when blocked,

were more important in reducing oviposition (82.3% and 70.0%, respectively) than receptors on the labellum (55.0%) or ovipositor (27.8%). The antennae and tarsi, hence, are more important in reducing oviposition than those on the ovipositor or the proboscis.

The data and observations on gravid females allow one to propose a tentative sequence of events used by the fly in oviposition. The antennae are concerned with the detection of manure odors and this perception stimulates the CNS and produces the initial attraction to the manure. Upon landing on the manure, the tarsi stimulate the CNS which causes the proboscis to be extended. The chemoreceptors on the tarsi, labellum, and possibly the chemoreceptors on the antennae, and oviposition are involved with a sampling process that determines if oviposition can occur. Once a site has been located, the CNS signals for the extension of the ovipositor. The chemoreceptors and mechano-receptors on the ovipositor's anal leaflets are responsible for the final site selection on the manure for the egg. When this site has been found, the CNS is signalled and egg laying proceeds.