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Effects of Host Quality on Female Locomotor Activity in the Parasitic

Wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae)

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Abstract

Upon encountering a poor quality host, a female parasitoid may need to disperse in order to find a host suitable for oviposition. The effect of host quality on locomotor activity was examined for females of the parasitoid wasp *Nasonia vitripennis* (Walker) using a natural host, *Calliphora vomitoria*. In the first experiment, females were exposed to either poor hosts (freeze-killed and stored at room temperature) or good hosts (fresh) hosts for three hours. Then, their activity was recorded for ten minutes. Females given poor quality hosts were more active than those exposed to good quality hosts. In the second experiment, females were either exposed to good hosts, larval stage hosts, or poor hosts (freeze-killed and kept frozen until used) for three hours. The activity level of these females was also recorded for ten minutes. There was no significant difference among females given good hosts, females given larvae and females given freeze-killed-moist hosts.

Introduction

Due to the large number of adverse effects produced by chemical pesticides, scientists have focused on natural enemies, such as parasitoids, as an alternative method for the biological control of pests (APSS, 1998). *Nasonia vitripennis*, also known as the jewel wasp, is one of several species, belonging to the superfamily Chalcidoidea, that is mass cultured and sold for control of filth-fly pests (Morgan, 1986).

N. vitripennis may be effective in certain fly pest situations because females oviposit on the fly pupa (Carolina Arthropods, 1995). Hosts of *N. vitripennis* include flies found on carcasses and manure, such as *Calliphora vomitoria* (Rueda & Axtell, 1985). The female pierces the fly pupa's shell (the puparium) and lays about 10-30 eggs on each host. After oviposition the female may also feed on the host; the host's fluids are vital for the fast production of eggs (Edwards, 1954).

The parasitoid larvae feed on the pupa, preventing the fly's development into an adult. The adult (reproductively mature) jewel wasp emerges from the host about two weeks after oviposition. Upon emergence, females mate with males from their own and neighboring hosts (Bontje et. al. 1998). Since males do not fly, it is important that females remain at the site of emergence until they have mated (King, unpublished). After mating, females must leave to find fresh host for oviposition.

An individual's fitness is often measured by its ability to survive and reproduce. In order to reproduce, a female of this species needs to find a quality

host. Although *N. vitripennis* is not a species known to migrate long distances, "oviposition sites may be well dispersed" (King, 1993). Flight and locomotor activity may thus play a very important role in reproduction. Understanding what affects locomotor activity is also important to the use of *N. vitripennis* in biological control because activity level may directly reflect on the wasp's ability to disperse and find a new host, upon encountering one not suitable for oviposition.

This study focuses on the effect host quality has on locomotor activity of females of *N. vitripennis*. The first experiment compared activity levels of females exposed to poor quality hosts (freeze-killed and stored at room temperature) vs. females exposed to good host (fresh). I hypothesized that females exposed to poor quality hosts would show greater locomotor activity than those given good hosts. Such greater activity might result in their leaving and subsequently finding a site with better quality hosts.

For the second experiment, I predicted that the activity level of females exposed to freeze-killed-moist hosts would be higher than that of females exposed to good hosts or hosts in the larval stage. Although larvae are unsuitable for oviposition, they may still be considered potentially good future hosts. Freeze-killed-moist hosts, on the other hand, may be considered poor host because they may begin to decompose and dry out during the parasitoid larval stage.

Numerous studies have addressed aspects of the host-parasitoid relationship. The species *N. vitripennis* has been found to respond to variations

in host size, distribution, quantity, and quality among other things (e.g., King, 1994; King, 1997; Roth, 1991).

A host may have certain typical traits that are essential in making it suitable for oviposition. The absence or presence of certain characteristics in a host seems to have an effect, not only on oviposition itself, but also on other behaviors of the parasitoid. For instance, size, shape and moisture each seem to affect whether a female explores and/or drills a host (Edwards, 1954).

The host's fluids are important for both feeding and oviposition. There must be a certain level of fluids, neither too high nor too low. When these fluids are not longer present, the pupa is an unsuitable source of nutrition for the liquid feeder *N. vitripennis* (Gerling and Legner, 1968). However, if the host is too damp, it may also be rejected by the parasitoid (Edwards, 1954).

Host age also affects both feeding and oviposition. Older hosts are a less suitable source of food for the female, perhaps because they have lower moisture levels (King, 1997). Hosts that are too young may also be considered unsuitable. Females of *N. vitripennis* "do not attack larvae of their hosts;" however, they will attack as soon as pupation starts (Edwards, 1954). This attack is not followed by oviposition, but by feeding on the host's fluids. *N. vitripennis* oviposits in the space between the pupa and the puparium. This space is not present when the puparium is first formed.

The present experiments 1) test the effect of good hosts vs. poor hosts on the locomotor activity of females, 2) assess whether a female parasitoid considers a larval stage host as a poor host or as a potentially good host, 3)

examines the extent of damage necessary for a host to be considered unsuitable for oviposition, 4) examines the importance of moisture as trait used by the parasitoid to determine host suitability. By studying the behaviors of females after they have left the host, the females' ability to parasitize more than one host can be assessed.

Materials and Methods

General methods

N. vitripennis used in this experiment were from a laboratory colony. They were reared in small test tubes by placing five to six fly pupae with one to two females. The females were kept in the test tube for 24 hours and then removed to minimize superparasitism. The established colonies were kept in an incubator at 25°C-26°C to minimize temperature and humidity fluctuations. The hosts were pupae of the fly *Calliphora vomitoria* obtained as larvae from a commercial supplier. The larvae were allowed to pupate and then stored in the refrigerator at 11°C to arrest their development and prevent their emergence. Upon emergence, the parasitoids were fed by smearing a small amount of honey on the side of the test tube. This was done to increase their longevity.

During the first, after a few weeks of rearing *N. vitripennis* in small test tubes, shorter than expected lifespan was observed on newly emerged offspring. Large and small petri dishes were then used for rearing. A small drop of water was also added every two days, in order to counterbalance low humidity levels caused by fans in the incubator. Both of these new measures seemed to increase the number of wasps reared, as well as their longevity. This difficulty was not encountered in experiment II.

Only females less than 14 days old (timed from emergence as adult) were used in each experiment. To avoid any significant difference in age, females of the same test tube were used for a given replicate. Since males and females

were not separated prior to or after emergence, females were assumed to have mated; however, mating was not observed.

Preparation for testing involved placing a single adult female in a small test tube with a host (good, poor or larval; see below) for three hours. After this three-hour exposure, the female was gently tapped into a glass terrarium (51 cm long x 26 cm wide x 31 cm high). Activity was then recorded for 10 minutes. Activity was defined not only as walking, but also flying and hopping as well. When a wasp showed flight activity, the approximate distance traveled was used to place the movement in one of three categories. These three classifications were: hops (distances < 2 cm), short flights (distances of about 2-4 cm), and long flights (distances > 4 cm). Temperature and humidity were also recorded at the beginning of each treatment in order to keep track of any environmental difference between treatments or replicates.

The data obtained were analyzed by using Statistical Package for the Social Sciences (SPSS).

Good vs. Freeze-killed host

Good hosts were obtained from the refrigerator kept stock about five minutes before they were given to the females. Poor hosts were generated by putting fresh pupae in the freezer for 48 hours. After freezing, the pupae were kept at room temperature until used (about 1 – 4 weeks). Females exposed to previously frozen hosts were designated “P” (poor); females exposed to fresh hosts kept in the refrigerator were designated “G” (good).

Good vs. larval vs. freeze-killed-moist host

In this experiment, as in the previous one, the good hosts were obtained from the refrigerator kept stock (11°C). These hosts were taken out of the refrigerator about five minutes before they were to be given to the females. Freeze-killed-moist hosts were generated by putting fresh hosts in the freezer. These pupae were kept frozen until an hour before their use. The hosts were kept in the freezer (up to 60 days) to avoid the loss of moisture that occurs that occurs when they are left at room temperature. They were removed from the freezer an hour before testing to ensure the host was not frozen when given to the female parasitoids.

The larvae were obtained from the same commercial supplier, but they were stored in the refrigerator at 11°C before pupation. These temperatures kept them in the larval stage for several days. The larvae were removed from the refrigerator within 5 minutes of when they were to be given to the females.

Results

Good vs. freeze-killed host

A large degree of variation in activity was observed, not only among wasps in different categories (P and G), but also among wasps within the same category (see below and Tables 1 and 2). The absence of skewness and kurtosis suggests that the total activity time for each type of wasp was normally distributed ($p > .001$, $p > .001$); consequently a parametric test was done. On account of not substantial correlation being found by a two-tailed probability test between P and G ($r = .002$, $n = 30$, $2tp = .99$), an independent t-test was chosen to analyze the data. The assumption of equal variance needed for the parametric test was also met. Testing temperature and relative humidity ranges were 21°C - 24°C and 22 – 55 %.

Females exposed to poor quality hosts were considerably more active than females given good hosts (278.99 ± 17.20 sec, 133.07 – 474.24 vs. 177.55 ± 19.87 sec, 21.8 – 434.79; $t = 3.86$, $df = 58$, $2tp < .0005$).

Good vs. larval vs. freeze-killed-moist host

There was no skewness or kurtosis found in the distribution of the data. This suggested that the total activity time for each group were normally distributed. A two-tailed probability test found no correlation between the activity levels of females given good host and either, females given larvae ($r = .159$, $n = 30$, $2tp = .403$) or females given freeze-killed-moist hosts ($r = .218$, $n = 30$, $2tp = .246$). There was also no correlation in the activity levels of females exposed to larval hosts and females exposed to freeze-killed-moist hosts ($r = .120$, $n = 30$, $2tp = .529$).

The testing temperature and relative humidity ranges were 22°C – 27°C and 20 – 46 %. No significant difference was found in the activity levels of females exposed to, good, larval, or freeze-killed-moist hosts (see Table I).

	N	Mean	Std. Deviation	Range
Good host	30	307.4913	186.2791	0 – 582.05
Larval host	30	338.7810	160.4190	89.03 – 583.30
Freeze-killed host	30	354.6207	169.9966	0 – 573.16
Total	90	333.6310	171.7448	0 – 583.30

Table I. Mean, standard deviation and range for the total active time (in seconds) of females given good hosts, larvae or freeze-killed hosts.

	N	Mean	Std. Deviation	Range
Good host I	30	177.5493	94.2170	133.07 – 474.25
Good host II	30	307.4913	126.2791	0 – 582.05

Table II. Comparison of the total active time (in seconds) of females given good hosts in experiment I vs. females given good hosts in experiment II.

Discussion

Good vs. freeze-killed host

The results obtained in this experiment are consistent with the hypothesis that a female of *N. vitripennis* given a poor host will show higher locomotor activity than a female given a good host.

Female *N. vitripennis* not to perceive external changes, if any exist, in hosts that have been freeze-killed. The internal host changes caused by freeze killing and/or subsequent loss of fluids in the hosts stored at room temperature may be significant enough to be detected by the female upon insertion of her ovipositor. State of decomposition and the presence of bacteria may also be detected by females in a dead rotting pupa. This may be facilitated by the presence of chemo-receptors or mechano-receptors found on the ovipositor (Edwards, 1954).

By finding a suitable host, a female parasitoid not only enhances her own probability of survival, she may also increase the chances of reproduction of her progeny (Legner & Gerling, 1967). For example, younger hosts tend to result in larger parasitoid offspring (King, 1997). Larger females have larger reproductive organs, which means more eggs for oviposition or for reabsorption in the absence of nourishment (King & King, 1994).

The higher locomotor activity expressed by females given a poor quality pupa may be an indication of search for a suitable host. Females of *N. vitripennis* use volatile chemicals found at the site of emergence as a guide in their search for hosts (Hastings & Godfray, 1998). A search may be necessary

because the natal site hosts that were not parasitized may be fully developed flies by the time the next generation of parasitoids emerges (Bontje et al., 1998).

In past, some scientists seemed to be skeptical about the exploratory abilities of the parasitoid. It was even suggested that due to the "dispersal of young fertile females" from every emergence site, hosts may be found by chance (Edwards, 1954).

To find out whether a female's search for a host is guided or not may require further evaluation. However, the findings in this experiment suggest that an exploratory urge (expressed in the form of increased locomotor activity) may arise in a female *N. vitripennis* upon encountering a poor quality host.

Good vs. larval host

Since there was no significant difference in the activity level of females given good hosts and females given larval hosts, it is likely that females may be accepting the larvae as potentially suitable hosts.

Females *N. vitripennis* feed on the host as soon as pupation begins and the puparium is hard enough (Edwards, 1954). Upon encountering a host in the larval stage, a female may wait until it pupates in order to feed and again some nutrients to produce more eggs or prevent the reabsorption of existing ones. After or instead of feeding, a female may wait until host pupation is complete. It takes about 24 hours for a space to form between the pupa and the puparium, which is necessary for *N. vitripennis* females to lay their eggs (Wylie, 1958).

Since *N. vitripennis* attacks a host as soon as pupation starts, the darkening and/or hardening of the puparium may be factors that help the female

assess host suitability. However, the presence of these characteristics does not guarantee that the host will be used. Chemicals present on the puparium may also serve as host-finding and host-acceptance cues (Godfray, 1993). Which factors the female uses may depend on availability of light for seeing.

If a female accepts a larva as a potentially good host even before pupation, it is likely that the larva possesses certain characteristics, which allow its recognition as a larva of a preferred host species. The cues used by the female are likely to be olfactory (Wylie, 1970). However, once a female contacts a host, nonvolatile chemicals present on the host's cuticle may also help the parasitoid identify the larval stage of a potentially suitable host.

Numerous experiments have studied the mechanism by which parasitoids assess host quality. It would be interesting to study whether a female can assess the potential suitability of a larva. Many of the behaviors displayed by the female during host inspection cannot be performed on a larval-stage host. For instance, often females of *N. vitripennis* do not reject a host until after insertion of the ovipositor (Edwards, 1954). Females can distinguish between live and dead pupal hosts after ovipositor insertion. Can they also differentiate between live larvae and dead larvae? This is important because if a female cannot do this, she may find herself waiting for the pupation of a larva which is not to occur, if the larva is dead. Since pupae do not move, movement cannot be the external or visual cue used by females to determine the suitability of a host (Rivers et al., 1992). Nevertheless, movement may sometimes be used as an internal cue. When a host is too old to serve as nutrition for parasitoid offspring, the movement

of the almost developed fly may serve as an indication for the female to reject this host (Godfray, 1993). Further review of this matter is required in order to understand the mechanism used by the female, if it assesses the potential suitability of a larva.

Waiting for the larva to pupate may prove more beneficial for the female parasitoid than searching for a pupal host she may or may not find, especially since by feeding on a recently pupated host, the female does not kill it. The pupa will continue its natural development into a suitable host for her offspring (Edwards, 1954; Wylie, 1958).

Good vs. freeze-killed-moist host

There was no evidence found to support the hypothesis that a female given a good host will display less activity than a female given a freeze-killed-moist host. These results suggest that the activity levels of females may not be largely affected unless the factors or factors which make a host poor quality are very significant. These findings may also serve as evidence of the importance of moisture for a female's determination of host suitability.

One difference between the freeze-killed hosts used in experiment I and freeze-killed hosts in experiment II was the amount of fluid present in each. Also, while no offspring emerged from freeze-killed hosts in experiment I, offspring emerged from freeze-killed-moist host in the second experiment. This observation contradicts earlier studies, which reported that females did not lay any eggs in freeze-killed pupae (Edwards, 1954; Wylie, 1958).

However, these studies did not specify if the pupae were stored at room temperature or kept frozen until used.

Numerous studies of *N. vitripennis* have suggested that the host must be alive in order to be considered suitable for oviposition. It has been suggested that the heartbeat of a healthy host is very important for the host to be considered suitable (Fischer, 1971 in Godfray, 1996). However, a study using artificial hosts filled with different types of fluids was able to get some parasitoids to oviposit in false hosts containing hemolymph (Godfray, 1993).

Although the present results suggest that there is no significant difference in activity of females given good hosts vs. freeze-killed-moist hosts, the number of offspring obtained from good hosts was larger than the number of offspring obtained from freeze-killed-moist hosts. Thus these pupae should be classified not as good or poor hosts, but as intermediate quality hosts. One of the measures taken by a female *N. vitripennis* when a host is of intermediate quality is to adjust brood size (Rivers, 1996). In this case the female may lay fewer eggs because after oviposition the moisture levels of a freeze-killed-moist host decrease faster than the moisture of a good host.

Even if the female were to oviposit the same number of eggs in each host, a dead host may not be able to support the same number of parasitoid larvae as a fresh host. By weighing a dead host every day for three days, it was determined that the mass of a dead host declines. In contrast, with live hosts, the venom of *N. vitripennis* has a preventive effect, retarding so that the host

does not die until 12 days after envenomation (Rivers et al., 1993). This preventive effect of venom however, may not occur with a dead host.

Although moisture within the host seems to be a very important aspect of host suitability, prior experience may also have contributed to the effect of freeze-killed-moist hosts on females. Host acceptance may be influenced by the quality of other hosts present in the environment (Godfray, 1994). The females used in this experiment did not have prior experience ovipositing in a good host. The hosts present in their natal vials were mostly empty pupariums. This may contribute to the female accepting the freeze-killed-moist host as a suitable host when compared to those in their natal colonies. Parasitoids have been observed parasitizing unsuitable hosts in the laboratory when a suitable host is not present (Godfray, 1994). Replicating this experiment using females that have previous exposure to suitable hosts could test the effect of prior experience on host acceptance.

Good hosts in experiment I vs. experiment II

Although measures were taken to prevent any significant differences between the good host treatments in the first and second experiment, differences were observed between the activity levels of these females (Table II). The exact factors causing this difference in activity levels can only be speculated upon, however, they should be addressed.

Due to improved methods employed for rearing parasitoids, larger females were obtained during experiment II. As stated before, larger females have larger reproductive organs, and therefore, more eggs (Edwards, 1954). It is likely that

these larger females used in experiment II had more mature eggs available for oviposition than the smaller females used in experiment I. The internal state of a female affects her response to host quality (Odendaal and Rausher, 1989). A female with a larger egg load is expected to search more intensely than one with a small load. Since not all the mature eggs in the ovaries are deposited at one time (Edwards, 1954), the larger females are expected to have more eggs remaining in their ovaries, and therefore, to be more active than the smaller females after exposure to a host. However, activity is unaffected by female size (as measured by head width) (King et al. 2000).

Furthermore, since environmental conditions also affect egg development, as well as the availability of suitable hosts, egg load may form a "mechanistic link" between the environment and the female's behavior (Odendaal and Rausher, 1989). If the female is able to perceive the time of the year (by using temperature, relative humidity, day length, etc.), it may change her searching behavior (Godfray, 1994). Although the vials containing the parasitoids were maintained in an environmental chamber for both experiments, the three-hour exposure to a host was done at room temperature. Perhaps the combination of temperatures and relative humidity created different environmental conditions during the three-hour exposure for females in experiment I vs. females in experiment II. The difference in the environmental conditions may have also been enhanced by the fact that the two experiments were carried out during different seasons (experiment I during fall-winter; experiment II during winter-spring). By measuring the activity levels of females exposed to hosts at different

temperatures, relative humidity or day length, one can assess if and how females detect time of the year, and how the females' behavior is adjusted.

By being able to distinguish between a good and poor quality host, as well as by increasing search intensity upon encountering an unsuitable host, a female *N. vitripennis* presumably increases her host finding rate and her chances to lay eggs. This may be an indispensable skill for the parasitoid to kill numerous hosts, and therefore, be better biological control for pests hosts.

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