

BEHAVIORAL RESPONSE OF THE PARASITOID CARDIOCHILES

NIGRICEPS TO KAIROMONES

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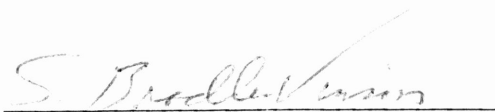
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A handwritten signature in cursive script, reading "S. Bradleigh Vinson", is written over a horizontal line.

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ABSTRACT. The response of the parasitoid Cardiochiles nigriceps (Hymenoptera: Braconidae) to the contact chemical of its host, Heliothis virescens (Lepidoptera: Noctuidae) is investigated in the following study. In response to an encounter with the host kairomone, C. nigriceps exhibits a kinetic response within the confines of the chemical patch involving increased turning and increased speed over unit time. When the parasitoid encountered a patch edge, it exhibited a klinotactic response which directed the parasitoid back to the interior of the patch. This orientation occurs because of the insect turning an average angle of 143° relative to its orientation at the time of the stimulus. Such an action greatly increases the time spent by C. nigriceps on a patch. Oviposition has the effect of significantly reducing the time spent by C. nigriceps on a patch. The nature of the distribution of H. virescens may be the cause for the observed reduction in patch time as a result of oviposition. Experience of the parasitoid also appears to be a factor in the host location process.

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BEHAVIORAL RESPONSE OF THE PARASITOID CARDIOCHILES

NIGRICEPS TO KAIROMONES

Introduction

Within the orders Hymenoptera and Diptera are a diverse collection of insects termed parasitoids. By definition, parasitoids are insects which develop as larvae in or on the tissues of their insect hosts. There has been increasing interest in recent years in the manipulation of the behavior of natural enemies, such as parasitoids, to control pest species of man. However, such manipulation requires a complete understanding of the biology and behavior of the natural enemy. Various aspects of host finding behavior have been summarized in several current reviews (Matthews, 1974; Vinson, 1976; Weseloh, 1976). Even though many stimuli involved in host finding have been identified, the precise reaction of parasitoids to these stimuli remains poorly studied.

Most parasitoids appear to locate their hosts through a sequence of responses rather than by random encounter or a single stimulus. Salt (1935) and Flanders (1953) separated host selection by parasitoids into three steps: 1) host habitat location, 2) host location, and 3) host acceptance. During each level of the host selection process, two types of stimuli are in effect. "Attractant" stimuli orient the parasitoid to areas containing hosts, and "arrestment" stimuli cause a decrease in the area covered by the parasitoid per unit time (Waage, 1978). Once a parasitoid has been attracted to a given host area, the parasitoid may then respond to further attractant and arrestment stimuli which tend to restrict

its movements to ever smaller units of possible host distribution, until ultimately, a host is located. If, during any part of this host searching process, the parasitoid fails to locate the proper stimulus, it will abandon the search.

The attractant and arrestant stimuli implicated in host selection are quite diverse. Attractant stimuli can be of two types, those produced by the host and those produced by the environment of the host. Arrestment stimuli are of similar origin. Although such factors as sound, color, and shape of the host or the host's environment have been implicated in the host selection process (Vinson, 1976), chemical stimuli appear to be the major determinant of parasitoid behavior during host selection.

Chemicals, in association with visual stimuli, play an important role in host habitat location. The evidence for such chemical attractants lies in the fact that many parasitoids are attracted to a habitat regardless of the presence or absence of hosts. Vinson (1975) found that the parasitoid Cardiochiles nigriceps was attracted to and searched tobacco in the absence of insect hosts, and Tayler (1932) found that the parasitoid Microbracon brevicornis Wesm only attacked Heliothis armigera (Hubner) when it fed on Anterrhinum sps. even though H. armigera feeds on numerous different plants. Such evidence suggests that a plant factor is involved in long range orientation of some parasitoids. Although the existence of such chemicals has been mentioned in the literature numerous times, only a select few have been isolated and identified (Read et al., 1970; Camors and Payne, 1972).

During host location, chemical stimuli of host origin often serve as the stimulus. Of notable exception are those stimuli, usually chemical which are produced by an action of the host on its environment. For example,

feeding by hosts often results in the release of chemicals from the plant which act as stimuli for the parasitoid (Bragg, 1974; Camors and Payne, 1972). Those chemicals which are produced by a given host, and which act as a parasitoid attracting or arresting stimuli are called kairomones. As defined by Brown et al. (1970), kairomones are chemical messengers released by an individual of one species that induce a behavioral or physiological response in an individual of another species, and this second species derives some benefit from the response. Parasitoids derive an adaptive benefit by responding to attracting and arresting stimuli produced by their hosts. Kairomones implicated in host selection include substances released from the host's cuticle, frass, hemolymph, and glandular secretions (see Table 1). Compounds which orient parasitoids to their hosts would superficially appear disadvantageous to the host; however, these kairomones also serve as pheromones or other chemicals vital to the host's physiology (Vinson, 1977).

Many of the kairomones involved in host location result in the arrestment of the parasitoid. These chemicals are deposited by the parasitoid's host on the substrate. Such stimuli have been termed as contact chemicals by Vinson (1976). The behavioral response of parasitoids to contact chemicals varies among species (see Table 1). Typically, contact chemicals appear to elicit a marked decrease in walking and an increase in turning, coupled with frequent antennation. Whether the parasitoid is exhibiting a random orientation through such action or a search for the source of the arrestment stimuli is currently not known, even though the results of Waage (1978) and Lewis et al. (1975) suggest the latter. By and large, the movements of most parasitoids in response to contact chemicals have been described in the literature with such commonly used words as "search", "examination",

and "investigation", but these words are rather vague in a behavioral sense and convey little useful information. Thus, the purpose of the present study is to better characterize the behavior of a parasitoid to the contact chemical of its host.

The parasitoid/host relationship to be investigated is between the braconid wasp Cardiochiles nigriceps and its host Heliothis virescens, better known as the tobacco budworm. Heliothis virescens is a well known pest of tobacco and cotton in the southern portion of the United States. The source of the contact chemical in this parasitoid/host relationship is the secretion of the mandibular gland of the Heliothis virescens larvae. The active components of the gland secretions have been identified as three long chain hydrocarbons (see Table 1) (Vinson et al., 1975). The contact chemical is deposited on the surface that H. virescens feeds and crawls upon (Vinson, 1968). In general terms, Cardiochiles nigriceps appears to be arrested along with increased turning and antennation when in contact with the kairomone.

Methods and Materials

In order to observe the locomotory response of C. nigriceps when exposed to the mandibular gland secretions of H. virescens, the following apparatus was constructed. A 20 x 20 cm. glass box was constructed and placed 3 cm. above an overhead projector (see Fig. 1). Light from a projector would pass through the glass box, through the prism, where the image was reflected from a mirror to the surface of a table. From the image reproduced on the table, a tracing could be made of the parasitoid's movement without the possibility of disturbing the insect as might occur if its movement was traced directly above the surface of the glass box. A voltage regulator was used in association with the overhead projector in order to lessen the intensity of the light which is normally emitted. In order to

be able to time the parasitoid's movement, a tape recorder was used with taps recorded on the tape at five second intervals. Through the combination of the overhead projector and the tape recorder, both the movement and the time involved in the parasitoid's behavior could be recorded. In the middle of the glass box was placed an 8 x 8 cm. piece of weighing paper. Within the piece of weighing paper was drawn a 2 cm. diameter circle. This circle will be referred to in the future as a patch. The arrestment kairomone of H.virescens was placed on the patch area by restricting the host larvae to the patch for a period of six hours prior to any trial. With the following setup, three experiments were undertaken.

Experiment One: Effect of a patch encounter on the behavior of C. nigriceps

The filter paper patch was covered by the secretion of five hosts for a period of six hours. A female wasp was then released into the glass chamber. The movements of the wasp was traced with a pencil on a peice of paper from the image that was produced by the prism and mirror. In addition, small marks were made down the length of the trail of the parasitoid at every five second interval as indicated by the tape recorder. The experiment was undertaken in a ventilated room at a temperature of 25⁰C.

Ten wasps were tested, and from these tests two measurements were made. The first measurement was the distance travelled by C. nigriceps prior, during, and after a patch visit per five seconds unit time. These measurements were calculated in centimeters by use of a planometer. Along with the distance moved per unit time, measurements were also made of the frequency of turning by the measurement of angles when on and off of the patch surface.

Experiment Two: Effect of oviposition on patch time

As in the first experiment, a patch contaminated by the secretions of five larvae for six hours was used to test the effect that oviposition had on the time spent by a female parasitoid searching a patch. Patch

times were recorded, using a stop watch. Times were recorded for female parasitoids searching a patch without any host larvae present. These times were compared with times recorded for female parasitoids that were allowed to parasitize one host. Immediately after the parasitism, the host was removed from the chamber. Besides a comparison between patch times with or without the presence of a host, a comparison was also made on the patch times of experienced and inexperienced female parasitoids when encountering unparasitized hosts. Female parasitoids were classified as inexperienced if they were newly fertilized and had never encountered a host or the arrestment kairomone of the the host. Likewise, experienced females were those parasitoids which had previously encountered numerous hosts and host secretions.

Experiment Three: Effect of experience on the degree of searching and arrestment response to host contact chemical

Experienced and inexperienced females were compared on the degree of movement within the experimental chamber and the frequency of arrestment if the kairomone patch was encountered. The basis for this experiment was largely based on previous observation. It had been noticed that inexperienced females appeared to be more lethargic and inactive than experienced females. In addition, experienced females appeared to be more sensitive to the contact chemical of H. virescens than did inexperienced females. Measurements were made of the frequency of encounter and arrestment to the patch between the two groups.

The measurements made and the data collected in the previously described experiments were statistically analyzed for significance. Statistical populations were determined for the three experiments on the following basis: For experiment one, ten trials were run with the first five distances

per five seconds being measured for each situation (before, during, and after a patch visit), for an n=50, and an n=40 for the first four angles turned in each situation: For experiment two, mean patch times were calculated from the number of trials run for experienced females without hosts, experienced females with hosts, experienced females without kairomone on the patch or hosts, and inexperienced females with hosts: For experiment three, differences in frequency of patch finding and patch arrestment were gathered solely based upon response and number of trials.

Results

Experiment One: Effect of contact chemical on the locomotory response of C. nigriceps

Typically, when C. nigriceps was walking across the chamber floor, its path was more or less straight, with limited turning except when one of the box's walls were encountered. However, when the edge of the host contaminated patch was encountered, the following general behavioral changes occurred. Upon contacting the edge of the patch, the parasitoid stopped, began to antennate the patch surface, and then entered the patch. The insect's movement was then accelerated, with a much greater frequency of turning. The insect would often spread its wings while it moved, but it did not attempt to fly. When the wasp encountered the edge of the patch it usually turned sharply back into the direction of the host contaminated patch. Figure 2 is a diagrammatic representation of C. nigriceps movement when in contact with the host contact chemical.

On a more quantitative level, the following data was compiled concerning the observations described previously. In Table Two, it can be seen that the distance travelled per five seconds was significantly different

for C. nigriceps when off the patch than when on the patch. There was no apparent difference in the speed of the insect prior to and directly after a patch encounter (see Table 3). Coupled with an increase in movement was a marked increase in the angles turned when off and on the patch (see Table 4). While within the patch, turns were essentially random with turns ($\bar{x} = 69.9^{\circ}$) being to the right and left 53% and 47% respectively. However, the mean turn when encountering the patch edge was 143.4° with a range of from 107° to 173° . This turn directed the insect back toward the source of the stimulus and could be considered a klinotactic or directed response on the part of the parasitoid.

From this data several conclusions can be drawn. First, the movement of C. nigriceps is essentially random with very little turning movement while off the patch. While on the patch locomotory action is nearly doubled with a great increase in turning. And while direction of turning appears totally kinetic within the confines of the patch, there seems to be a tactic response to the edge of the patch. Thus, C. nigriceps moves at a much greater rate of speed within the patch, but is restricted in the area covered while moving by the response to the patch edge. Presumably, the parasitoid eventually abandons the patch due to a waning of the response received at the patch edge.

Experiment Two: Effects of oviposition on patch time of C. nigriceps

Patch times were measured for experienced females with kairomone present and a host present or absent, and for inexperienced females with kairomone and a host present. A patch visit was based partially on arbitrary observation. If a parasitoid failed to reenter a patch after leaving for the duration of 15 seconds, it was constituted as the termination of a visit. Such a time interval was needed to differentiate actual leaving by the parasitoid from those situations in which the momentum of the insect carried it beyond the patch boundary, stopped, groomed briefly, and then reentered the patch.

Before beginning this experiment, a certain type of result was expected. With only the kairomone present and no hosts, ten wasps were tested and it was found that the mean searching time for the patch was six minutes. This, together with the previously described searching movement, tended to indicate that oviposition would in some way lengthen search time. Many of the parasitoids which are arrested by a host stimuli and which exhibit searching behavior have demonstrated increased searching time after an encounter with a host. This type of behavior is known as success motivated searching and has been described by, among others, Edwards (1954), Chabora (1967), and Gross et al. (1975). Waage (1978) found, while investigating the searching behavior of the parasitoid Nemeritis canescens, that oviposition in its host Plodia interpunctata did not cause success motivated searching, but did cause a decrease in the decay of the klinotactic response of N. canescens to the loss of host stimulus at the patch edge.

Table 5 summarizes the data collected for Experiment Two. In C. nigriceps, oviposition appears to produce a marked decrease in the duration of a patch visit. Observationally, the parasitoid would initially enter the patch and begin searching in the same manner as it would if no host was present. Upon finding a host the female would parasitize and then immediately fly from the patch. Once off the patch the female would groom and rest for several seconds. Such behavior was consistent throughout all trials. No female tested would stay on the patch and continue searching after oviposition.

As a further test of how oviposition terminated searching, larvae were introduced after the parasitoid had begun searching the patch. A host was introduced in different trials at 30, 45, and 60 seconds after the parasitoid had been on the patch searching. In each case, parasitism of the host resulted in the immediate departure of the female. Such a consistent result to oviposition, regardless of when during the searching process a host was

located, tends to indicate that such behavior is a locomotory response to an encounter and parasitism of the host, rather than parasitism causing a more rapid decay of the host searching stimulus.

Most parasitoids which exhibit nonrandom searching have hosts which aggregate into clumps on particular species of plants. Contrastingly, parasitoids whose hosts feed on a variety of plants often forage more or less randomly (Van Lenteren et. al., 1976). Hosts of nonrandom searching parasitoids also tend to usually spatially orient within a group of host plants. Thus, one often finds hosts concentrated in one area of a field of host plants and also on a particular portion of the host plant (terminal leaves, flowers, fruit, etc.). In such a situation, host motivated searching would be an adaptive advantage and would seem to be a reasonable strategy since the finding of one host often means the finding of several hosts.

However, it has been observed that C. nigriceps does not forage randomly at either the host habitat stage (Vinson, 1975) or at the host location stage. H. virescens has a rather specific host range and it is reasonable that C. nigriceps searches nonrandomly for host plants of H. virescens. C. nigriceps most definitely does not exhibit host motivated searching even though it is definitely arrested by host produced kairomone. The reason for the observed behavior of leaving a patch after parasitism may be because of certain aspects of H. virescens biology. H. virescens is a cannibalistic species and the larger the larvae become the greater their dispersion. Quantitatively, Pieters and Sterling (1974) determined egg aggregation to be much greater than that of late instar larvae (see Table 6). Aggregation is represented in Table 6 by the exponent K of the negative binomial distribution. A value of zero for K represents extreme aggregation and a value of infinity for K represents a totally random distribution. Since C. nigriceps prefers late instar larvae for parasitism (Vinson, 1975), it is reasonable

for the parasitoid to leave a searched patch after location and parasitism of a host since the chance of encountering a second host on the same patch is very small.

Experiment Three: Effect of experience on the degree of searching and arrestment response to host contact chemical

It had been noticed that inexperienced C. nigriceps females were more lethargic and less prone toward movement than experienced females (Vinson, personal communication). Populations of inexperienced and experienced females were compared on patch finding ability (see Table 7). Statistically, the difference between experienced and inexperienced females was not significant ($\chi^2 = 3.69$), but this may have been due to too small a population since $\chi^2 = 3.69$ is very close to significance at the 95% confidence interval.

Of those females, both experienced and inexperienced, that found the patch, there was a significant difference in arrestment to the patch (see Table 8). All experienced females which found the patch were arrested by the contact chemical; however, 40% of the inexperienced females tested failed to show any signs of recognition to the kairomone. In all trials, kairomone concentration was approximately the same (five larvae per patch for six hours). Such a difference in arrestment response could be due to an experience factor. It was found that experience played a significant part in discrimination between parasitized and unparasitized hosts of the parasitoid Pseudeucoila bochei (Van Lenteren and Bakker, 1975). Only after exposure to several hosts could inexperienced females learn to discriminate between a parasitized and unparasitized host. A similar situation could exist in the case of arrestment to contact chemical by C. nigriceps. It would be worthwhile to test such a hypothesis by testing inexperienced females' response to host kairomone, allow these same females to be exposed to the host chemical, and then reperform the same arrestment test to see if these

females had become able to recognize the host kairomone. As stated in Experiment Two, there was no significant difference in the behavior of inexperienced and experienced females once a host had been encountered. Such an encounter led to immediate abandonment of the patch after parasitism in all females.

Discussion

The response of a female Cardiochiles nigriceps to the contact chemical of its host Heliothis virescens can be characterized as a combination of kinetic movement within a patch combined with a klinotactic response to the patch border. Such behavior is similar to that observed for several other parasitoids in response to contact chemicals (Waage, 1978; Vinson, 1976; Lewis et al., 1975). Eventual abandonment of the patch appears due to a gradual habituation to the odor at the patch edge and waning of the klinotactic response.

The immediate abandonment of a patch after parasitization was atypical of most documented descriptions of nonrandomly searching parasitoids. Such behavior appeared to be a locomotory response to host contact since patch abandonment was immediate with no further patch searching occurring after host parasitism. This behavior further suggests an adaptive response by C. nigriceps to the spatial distribution of late instar H. virescens larvae in the field. Such leaving behavior also raises potential questions concerning an observed host marking potential for C. nigriceps (Vinson and Guillot, 1972).

Experience appears to play a factor in host searching and responsiveness to host contact chemical. Inexperienced females were significantly less sensitive to host contact chemical. This lack of sensitivity may be due to an experience factor, and may partially account for an observed difference in host location ability between older and younger C.nigriceps

females. There did not appear to be any difference in the leaving behavior of experienced and inexperienced females after parasitism. Many more experiments could be performed to better understand the response of C. nigriceps to host contact chemicals, such as the effects of concentration, patch distribution, host marking, and encounters with parasitized and unparasitized hosts.

More precise characterization of the response of parasitoids to host chemicals is needed if such compounds are to be used to increase the efficiency of the host selection process. Without a complete understanding of the parasitoid/host relationship, and the possible effects various stimuli have on this relationship, potential problems could be encountered when various manipulatory practices are attempted on a large scale in a practical situation.

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Species and Family	Host	Source of Chemical	Chemical	Described Behavior	Reference
				Precontact Postcontact	
<u>Microplites croceipes</u> (Cresson) Braconidae	<u>Heliothis zea</u> (Boddie)	Host frass	13-methylhentriacontane	Walking Hesitation, stopping, antennal examination	Jones et al. (1971). Lewis and Jones (1971)
<u>Cardiochiles nigriceps</u> Vierick Braconidae	<u>Heliothis virescens</u> (Boddie)	Mandibular gland	11-methylhentriacontane 16-methyldotriacontane 13-methyltriacontane	Walking Excitement hyperactivity, antennal rubbing, rapid turning	Vinson et al. (1975).
<u>Campolitis sonorensis</u> (Cameron) Ichneumonidae	<u>Heliothis zea</u> (Boddie)	Cuticle	Hexane	Walking Antennal tapping, probing	Wilson et al. (1974).
<u>Trichogramma evanescens</u> Westwood Trichogrammatidae	Eggs of wide range of lepidopterous hosts	Female moth scales	Tricosane	Rapid Movement Intense search	Jones et al. (1973).
<u>Orgilus lepidus</u> Braconidae	<u>Phthorimaea operculella</u>	Host frass	Heptanoic acid	Walking Intense search, antennal tapping, probing	Hendry et al. (1973)

Table 1. Parasitoids and their hosts for which chemicals have been involved in some aspect of host selection and associated behavioral responses.

Table 2.

COMPARISON OF DISTANCE TRAVELLED BY CARDIOCHILES NIGRICEPS (cm/sec)

Means designated by the same letter are not significantly different

<u>Group</u>	<u>N</u>	<u>Mean*</u>	<u>Standard Deviation</u>	<u>Duncan</u>	<u>Multiple</u>	<u>Range</u>	<u>Grouping</u>
Distance travelled before patch encounter	50	2.898	1.71				A
Distance travelled during patch encounter	50	5.839	2.58				B
Distance travelled after patch encounter	50	3.098	1.83				A

*F 2,148 = 32.61; $R^2 = .31$; $p < .0001$

Table 3.

MEAN ANGLE TURNED BY CARDIOCHILES NIGRICEPS (degrees)

Means designated by the same letter are not significantly different

<u>Group</u>	<u>N</u>	<u>Mean*</u>	<u>Standard Deviation</u>	<u>Duncan Multiple Range Grouping</u>
Angle turned before patch encounter	40	49.889	26.68	A
Angle turned within patch	40	69.900	29.90	B
Angle turned when patch edge encountered	40	143.378	20.02	C

*F 2,110 = 133.49; R² = .71; p < .0001

Table 4.

EFFECTS OF OVIPOSITION[†] ON PATCH TIMES (sec) FOR CARDIOCHILES NIGRICEPS

Means designated by the same letter are not significantly different

<u>Group</u>	<u>N</u>	<u>Mean*</u>	<u>Standard Deviation</u>	<u>Duncan Multiple Range Grouping</u>
Alpha Level=.05				
Kairomone present No host Experienced females	9	360.667	375.80	A
Kairomone present Host present Experienced females	10	20.000	15.76	B
Kairomone present Host present Inexperienced females	11	12.636	15.64	B
Kairomone absent Host absent Experienced females	11	3.727	1.49	B

[†]First visit only*F 4,44 = 7.87; R² = .42; p < .0001

Table 5.

DISPERSION OF <u>HELIOTHIS</u> SPECIES		
[Adopted from Pieters and Sterling, (1974)]		
<u>Group</u>	<u>N</u>	<u>K</u>
<u>Heliothis</u> spp. eggs	35	.36
<u>Heliothis</u> spp. larvae (all)	17	.98
<u>Heliothis</u> spp. (small)	12	.88
<u>Heliothis</u> spp. (large)	10	.62

Table 6.

COMPARISON OF PATCH FINDING IN CARDIOCHILES NIGRICEPS
BASED UPON EXPERIENCE

	Located Patch*	Failed to Locate Patch*
Number of Observations = 41		
Experienced Females	11	2
Inexperienced Females	15	13

*Time limit of 15 minutes per observation

df = 1

$\chi^2 = 3.69$

Not significant at 95% confidence level

Table 7.

COMPARISON OF ARRESTMENT OF
CARDIOCHILES NIGRICEPS TO CHEMICAL STIMULUS

	<u>Arrested</u>	<u>Not Arrested</u>
Number of Observations = 25		
Experienced Females	10	0
Inexperienced Females	9	6

df = 1

 $\chi^2 = 5.26$

Significant at 95% confidence level

Figure 1.

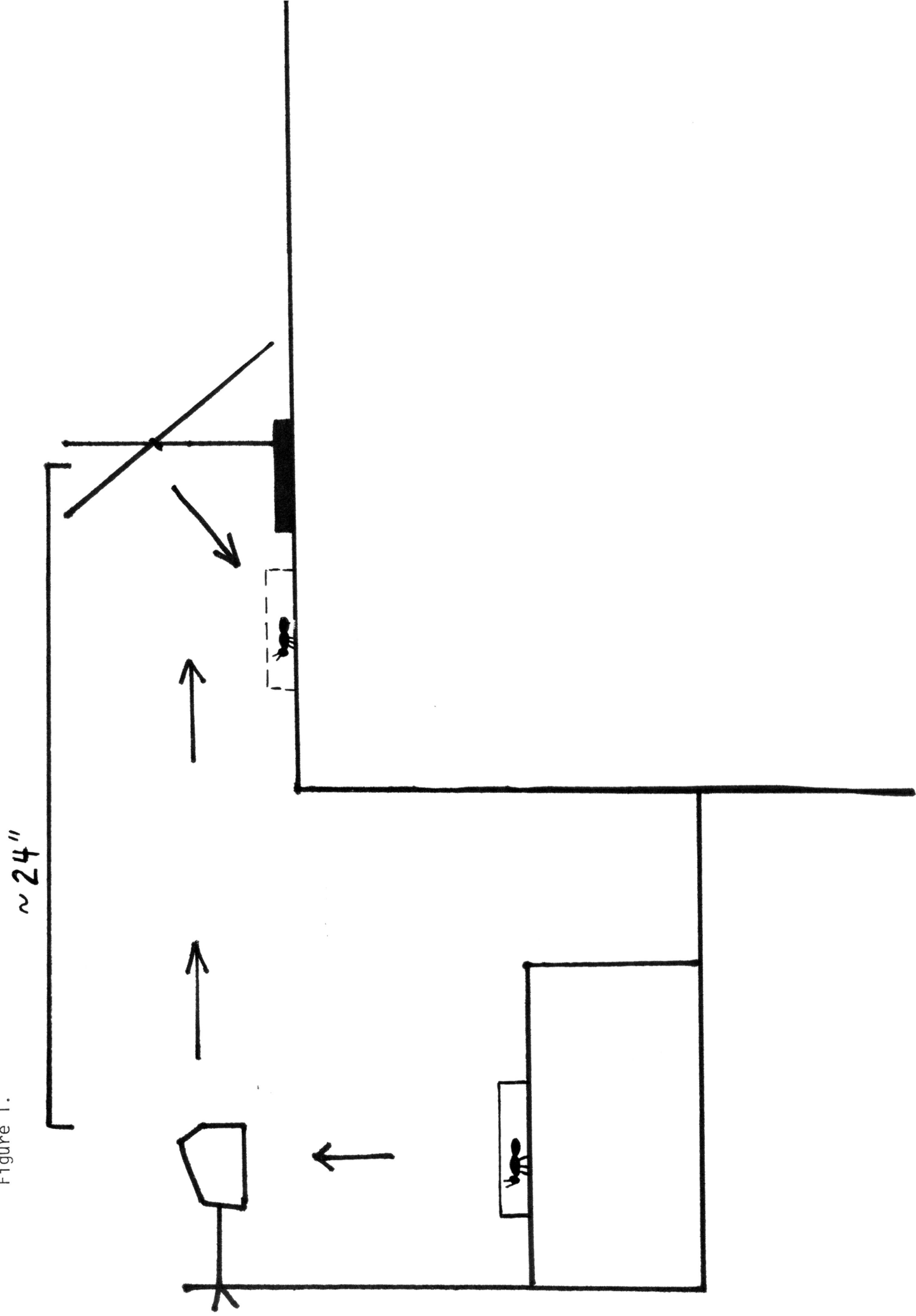
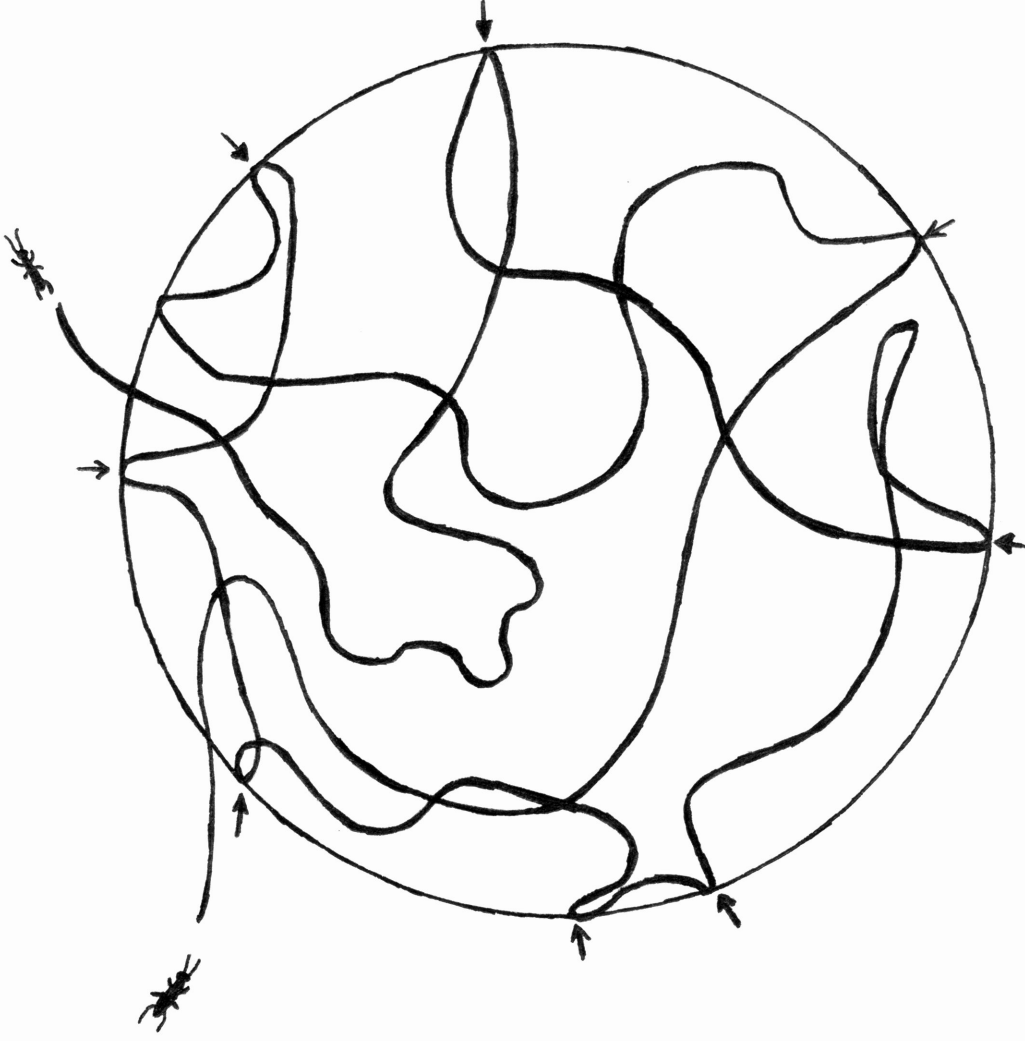


Figure 2.



Path of Cardiochiles nigriceps on a patch bearing arrestment kairomone. Arrows mark turns made at patch edge.