

ROLES OF VISION AND OLFACTION IN HOST PLANT SELECTION

BY CHELINIDEA VITTIGER UHLER (HEMIPTERA: COREIDAE)

by

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ABSTRACT

The means by which Chelinidea vittiger Uhler (Hemiptera: Coreidae) initiates host plant selection for Opuntia was investigated. Methods of testing vision and olfaction by means of ethological experimentation were developed and utilized. Experimental units were treated with independent and combined visual and olfactory stimuli from unburned host plants. Olfaction was determined to be the significant selection mechanism, and its use with vision was further determined to not be physiologically additive. Host plant selection for fire-damaged cactus pads was found to be significant over that for unburned pads. Influencing biological control by cactus bugs and other insects through use of prescribed burning may be of interest to ranchers and others desiring greater control of prickly pear cactus in range management.

Key Terms: biological control, cactus bugs, Chelinidea vittiger Uhler, host plant selection, olfaction, Opuntia, prescribed burning, prickly pear cactus, range management, vision.

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CHAPTER I
INTRODUCTION

Chelinidea vittiger Uhler (Hemiptera: Coreidae) has long been regarded as one of the more injurious insects attacking prickly pear cacti, Opuntia spp., in its native habitats (Hunter et al., 1912; Johnston and Tryon, 1914). Chelinidea vittiger has a natural range extending from northern Florida and Virginia west through California and southwestern Canada, and south into northern Mexico (Hamlin, 1924, 1932; Dodd, 1940; Mann, 1969; Herring, 1980). Due to the widespread occurrence and often undesirable presence of its host, C. vittiger (figure 1) has been examined as a potential biological control agent against prickly pear (Sickerman and Wangberg, 1983).

Prescribed burning is used as a control method against prickly pear (Wright and Bailey, 1980, 1982). Periodic burning of some ecosystems has historically acted as a factor in maintenance of vegetation levels and species rather than being solely destructive (Schowalter et al., 1981). Prescribed burning is now used by some ranchers in their range management to meet a number of goals. These



Figure 1--Adult cactus bugs, Chelinidea vittiger
Uhler, on prickly pear cactus.

goals may include control of other noxious brush and weeds as well as prickly pear. Unlike most other range plants, prickly pear may survive a burn because of its thick moisture-retaining character (Bunting et al., 1980).

Past research (Sickerman and Wangberg, 1983) has shown that C. vittiger prefers fire-damaged cactus. In light of this, it would be of added value to understand the mechanisms by which cactus bugs select host plants, and thereby clarify the relationship of cactus bugs to fire-damaged hosts.

Objectives

The purpose of this research was to determine the roles vision and olfaction play in host plant selection by C. vittiger and to test cactus bug selection for burned host plants. The following questions were addressed:

- 1) What is the significance of vision in host plant selection for: a) the nearby cactus surface and b) the cactus pad profile?
- 2) What is the significance of olfaction in host plant selection?

- 3) What is the combined significance of vision and olfaction in host plant selection?

- 4) What is the effect of treating (burning) the host plant on selection by cactus bugs? Do the results support preferential selection for fire-damaged cactus?

CHAPTER II
LITERATURE REVIEW

Chelinidea vittiger

Chelinidea is a Nearctic genus consisting of five species (Herring, 1980). Keys to the species in Chelinidea have been provided by several authors, including Hamlin (1924), de la Torre-Bueno (1941), and Herring (1980). The history and synonymy of cactus bugs have been provided by Burmeister (1834), Uhler (1863), Stål (1867), McAtee (1919), Hamlin (1923, 1924), and Herring (1980).

The biology of cactus bugs has been provided by Hunter et al. (1912), Hamlin (1924), Mann (1969), and DeVol and Goeden (1973). Chelinidea vittiger has a paurometabolous life cycle, consisting of egg, nymph, and adult (DeVol and Goeden, 1973). Mann (1969) and DeVol and Goeden (1973) report C. vittiger is univoltine in some parts of its range, and bivoltine in other parts. Egg incubation averages 13 days (DeVol and Goeden, 1973). The nymphs go through five instars averaging a total of 53 days (Mann, 1969). The adults are very hardy and long-lived, the longevity record being 542 days (Dodd, 1940).

Carroll and Wangberg (1981) determined temperature to be significant in nymphal development and found 31°C to be near optimal for development and reproduction. Throughout development, nymphs are gregarious which may lead to mass attack on one pad of a plant after which they move to another pad (Dodd, 1940). Adults are much less gregarious (Dodd, 1940). DeVol and Goeden (1973) and Sickerman and Wangberg (1983) found the sex ratio to be 1:1.

Feeding produces characteristic chlorotic lesions around each puncture. These spots merge when feeding is extensive (Mann, 1969). When C. vittiger is abundant, attack may be so severe that young growth, flower buds, and green fruit wither and abscise (Dodd, 1940). It feeds on most, if not all, Opuntia spp. growing within its range (Dodd, 1940; Mann, 1969).

Feeding may produce indirect effects as well. Hunter et al. (1912) reported cactus pads which survived limited feeding were often killed by frosts which did not affect normal pads. They also noted the presence of a fungus associated with cactus bug feeding, implying a possible vector relationship.

Chelinidea vittiger has a generally semi-sedentary character (DeVol and Goeden, 1973). This is perhaps

partially because of its long association with its protective host plant (Hamlin, 1924). Its character would require a number of years under favorable conditions to build up from introduction levels to the point of being capable of effecting an important role in biological control (Dodd, 1940).

Alexander (1925) and Dodd (1940) noted that Chelinidea adults are quite capable of flight, but seldom take wing, although they have been observed to occasionally take flight in large groups for distances of several miles (Dodd, 1940). Dodd used the term "swarm" for these groups, though no mating activity was mentioned.

Host Plant and Control

Australia

Prickly pear cacti, Opuntia spp., were spread to Australia and around the world by human activities largely for two reasons. The cacti were used as host plants for Dactylopius spp. (Homoptera: Dactylopiidae, sometimes Coccidae) in the production of cochineal dye (carminic acid) (Eisner et al., 1980). This purpose became outdated by the availability of aniline dyes. They were also used

as ornamental plants, and to a lesser extent, as food for human consumption. In Australia, prickly pear came to be an important pest and occupied much valuable rangeland until cacti populations were decimated in a spectacularly successful biological control program (Dodd, 1940, 1959).

The introduction of prickly pear to Australia eventually led to 24,300,000 hectares (60,000,000 acres) affected, half of which were rendered useless (Dodd, 1940). The primary species were Opuntia stricta Haworth and Opuntia inermis Decandolle. The cost of control by chemical and mechanical means was estimated to be much greater than the value of the land. Therefore, a biological control program was initiated as an alternative. Several insect species, including the cactus bugs, C. vittiger, C. tabulata (Burmeister), and C. canyona Hamlin were tested and released as a control measure, but it was the Argentine moth, Cactoblastis cactorum Berg (Lepidoptera: Pyralidae) which significantly reduced the cactus population.

Starvation feeding tests on economically important plants were made using C. vittiger, C. tabulata, and C. canyona during evaluation of potential biological control agents (Dodd, 1940). Adults and first instars were supplied with 40 to 50 different kinds of plants. In all

cases, the nymphs failed to survive past the first instar. Adults punctured various plants, but only survived on peaches and figs for any length of time. They sustained themselves for a shorter time on garden peas. Results of these tests were considered satisfactory and all three species were released.

A few years later, C. tabulata was found feeding in the field on grapes and young fruit of nectarine and apricot trees. Renewed tests on economically important plants were performed, and it was determined that C. tabulata's life cycle could not be completed on any plant tested. Fullaway (1954) reported that in tests for prickly pear control in Hawaii, starved C. vittiger fed on pineapple, resulting in rejection for introduction.

Goeden et al. (1967), DeVol and Goeden (1973), and Herring (1980) all incorrectly cited Dodd (1940) as having reported C. vittiger to be of little value in Australia. They also incorrectly cited Dodd as having reported C. vittiger would stay on its food supply after destruction by C. cactorum and often starve to death. Dodd made this statement about C. tabulata. It should be noted that this starving occurred in the presence of immediate catastrophic destruction of the host plant over many square kilometers.

Dodd cited other cases where C. tabulata adults flew out of destroyed areas in very large numbers. The case referred to by Dodd of the Queensland Prickly Pear Commission collecting and redistributing 12,500,000 cactus bugs would not have occurred if they had not demonstrated their value.

The effect of Cactoblastis cactorum on prickly pear was so dramatic that the effects of other insects have been practically ignored. Introduced Olycella (Lepidoptera: Pyralidae), Chelinidea, and Dactylopius all gave promising results (Dodd, 1940). Following the loss of host plants to Cactoblastis, all cactus-feeders were reduced, but C. vittiger is now well established in Australia. Cactoblastis destroyed most of the cactus before the full effect of other cactus insects could be determined. Australian researchers considered the introductions of C. vittiger and C. tabulata to be successfully established in Australia (Dodd, 1940). They were credited with roles in decreasing densities of heavy stands of cactus prior to the introduction of Cactoblastis. Their value in the control of prickly pear was considered to be increasing, but C. canyona was considered to be of little or no value against the prickly pear species in Australia.

Santa Cruz Island

Introductions of small numbers of C. vittiger and C. tabulata were considered to be of little value in controlling prickly pear on Santa Cruz Island, California, while Dactylopius was considered to be very valuable (Goeden et al., 1967; DeVol and Goeden, 1973). The prickly pear species on Santa Cruz Island were O. littoralis (Engelmann) Cockerell and O. oricola Philbrik and their hybrids (Goeden et al., 1967).

Devol and Goeden (1973) calculated a host plant acceptability index for 30 species or varieties of Opuntia using O. vaseyi (Coulter) as a standard. Goeden et al. (1967) misidentified O. vaseyi as O. occidentalis Engelmann and Bigelow. Opuntia stricta and O. inermis were not indexed. DeVol and Goeden (1973) cited differences in host plant suitability between Texas and southern California C. vittiger. Texas C. vittiger were released on Santa Cruz Island in 1945 (Goeden et al., 1967). Host plant suitability differences were attributed by DeVol and Goeden (1973) to be a major reason for their failure to become established. This appears to have been the case in Australia with C. canyona as indicated in the breeding work conducted there and by the failure of the single release (Dodd, 1940).

Cactus bugs released on Santa Cruz Island in 1961-62 were derived from O. vaseyi at Riverside, California. Their numbers dwindled and by 1966 could only be located at two of six former colonies (DeVol and Goeden, 1973). Only one colony was located in 1969 just 24 m (78.7') from the plant upon which it was last released in 1962. DeVol and Goeden (1973) interpreted the original plant to have been destroyed by Dactylopius. Apparently, they did not consider the presence of cactus bugs on that plant until it died may have been an important contributing factor to its weakening and susceptibility to destruction by Dactylopius.

Prescribed Burning

In North America, where cactus populations are generally kept in check by an assortment of natural enemies, some ranchers prefer to keep moderate amounts of prickly pear for use by cattle as an emergency forage and moisture reserve, and as a supplemental fiber source for winter (Hoffman et al., n.d.). In these cases, the spines are burned off before the cattle are allowed to feed on the cactus. This practice sometimes leads to certain cattle becoming "pear eaters" once they have tried the usually unappealing prickly pear. These cattle then consume

unburned cactus, often resulting in certain mouth and tongue problems, which in turn affect appetite and health. While some ranchers desire a moderate cactus density, other ranchers may attempt to eradicate prickly pear from their ranch, employing chemical, mechanical, and other means to do so (Costello, 1941; Hoffman et al., n.d.; Wright and Bailey, 1982).

In addition to the above use, prescribed burning is used to help get rid of prickly pear infestations (Wright and Bailey, 1980, 1982). Depending on the amount of combustible material surrounding the cactus, and other burn factors, a burn may kill many cacti or weaken them in varying degrees (Bunting et al., 1980; Wright and Bailey, 1980, 1982). A burn may be used against cactus while simultaneously achieving other range management goals (Wright and Bailey, 1982).

With the recognition of naturally occurring fires as a valid historical factor in the maintenance of certain ecosystems, prescribed burning has been developing into a complex science (Wright, 1974; Wright and Bailey, 1982). The effects of fire on desert grass-shrub range has been studied by Humphrey and Everson (1951), and Reynolds and Bohning (1956). The use of fire in sagebrush-grass and

pinyon-juniper areas has been reviewed by Wright et al. (1979). Wright (1978) reviewed fire effects in ponderosa pine forests. Wright and Bailey (1982) have written a review of prescribed burning and fire ecology.

Fire-Insect Interactions

The relationship between burning and insect populations has been researched by a number of authors. Interactions in both forests and grasslands have been studied. Whelan and Main (1979) concluded fire-insect interactions are not a major succession-initiating disturbance because of the evolution of specific survival and recruitment strategies.

Schowalter et al. (1981) proposed that the southern pine beetle, Dendroctonus frontalis Zimmermann (Coleoptera: Scolytidae) and naturally occurring fires interacted historically to maintain the pine forests of southeastern United States. Buffington (1967) regarded the New Jersey pine barrens as a fire-maintained subclimax. Soil arthropods one year after a fire were still at lower levels than those in unburned areas, except for two species of ants. In a five year study with forest floor litter, Pearse (1943) found that although burned areas had less than half as many soil-dwelling insects and animals as

unburned areas, they had more than those areas where raking was used to remove litter.

Bulan and Barrett (1971) evaluated the effects of mowing and burning on grassland arthropod populations. They found biomass, species/area diversity, and primary consumer species diversity to be the best indicators for measuring effects of a burn. They considered Coleoptera responses to be representative of the arthropod community as a whole.

Rice (1932) found a general decrease in insect populations following a prairie grassland burn, but for certain insects, a delayed increase above that of control populations due to fresh growth of appropriate plants was noted. Cancelado and Yonke (1970) found that spring burning of prairie produced immediate decreases in insect populations which later in the year were not apparent. Herbivorous insect biomass was found by Nagel (1973) to be significantly greater on burned than on unburned prairie sites. No significant differences were observed in non-herbivore biomass. Morris (1975) found significantly higher numbers of Hemiptera species and greater species-diversity in unburned than in burned areas of limestone grassland.

Wright and Bailey (1980) reported 70-80% of Opuntia plants are dead two to three years after a prescribed burn and attributed it to fire-insect interactions. Experimental data was not published to support this. Sickerman and Wangberg (1983) found that C. vittiger preferred burned over unburned cactus as a host in laboratory experiments. Further evidence has suggested other cactus-feeding insects prefer burned hosts (Sickerman, 1982).

Some insects are attracted to fire-damaged host plants and even to fires in progress. Several species of Melanophila (Coleoptera: Buprestidae) are attracted to forest fires and oviposit in scorched coniferous wood (Hunter et al., 1912). They are also attracted to tar extraction plants, oil fires, sugar mills, burning sawdust and slash, smelter plants, and cement plants (Linsley, 1943; Evans, 1962). Linsley (1943) cites the case of Melanophila consputa Leconte swarming at a 750,000 barrel oil fire in an arid region over 50 miles from the nearest coniferous forest. They are reported to run over very hot soil and fly through smoke in forest fires (Linsley, 1943).

Another beetle, Dendroctonus brevicomis Leconte (Coleoptera: Scolytidae) is attracted to lightning-struck

ponderosa pine trees (Johnson, 1966). Neuenschwander and Alexandrakis (1982) found that freshly emerged females of Phloeotribus scarabaeoides (Bern.) (Coleoptera: Scolytidae) were repelled by smoke of the olive tree host plant and the non-host cypress tree. After two weeks had passed, they were attracted to smoke from burning olive wood, while smoke from cypress wood still repelled them as at first. The siricid wood wasps (Hymenoptera: Siricidae) usually leave healthy standing trees alone, but are attracted to fire-damaged, diseased, or otherwise injured trees as well as to forest fires in progress (Hanson, 1939; Middlekauff, 1960).

Visual and Olfactory Perception

A gap has existed for some time in the literature on the behavior and mechanisms of host plant perception and selection by insects, notably Hemiptera and Homoptera (Kareiva, 1983). The behavior and sensory mechanisms of herbivorous insects has been reviewed primarily using research on Coleoptera and Lepidoptera (Ahmad, 1983). Vision and olfaction in insects has been studied for some time. Original or foundational articles are cited where possible in the following review.

Vision

Insects may visually perceive ultraviolet radiation and most wavelenghts of visible light (Chapman, 1982). Lovell (1910) and others have studied color perception in honey bees. They are red-green color-blind, but differentiate other colors quite well (Abbott, 1936). Honey bees also use ultraviolet in selecting flowers (Chapman, 1982) and to perceive the sun through clouds (von Frisch, 1958). They make visual use of the sun's position, polarized light, and landmarks in orientation during flight (von Frisch and Lindauer, 1954).

Many other insects use polarized light to navigate, especially ultraviolet which is less subject to atmospheric disturbance. Parallel arrangement of rhodopsin molecules in ommatidial microvilli maximizes absorption and sensitivity to polarized light (Duelli, 1975; Wehner, 1976). In bees, the rhabdom portion resulting from non-twisted or less-twisted visual cells may be used in selective polarization detection (Wehner, et al., 1975). As C. vittiger does not usually migrate or use navigation in locating food, it may not use polarization, but this has not been researched.

Many examples of insect attraction to colors are known. Kelsheimer (1932) found leafhopper response to colored lights greatest for ivory, moderate for green, brown and buff, and lowest for red and blue. Other examples for other orders were given by Packard (1903). Attraction to wavelength differs in many insects. Weiss et al. (1941a, b) found blue wavelengths to be very attractive to 22 species (mostly Coleoptera) tested.

Colors are not necessarily influential. For example, ovipositional behavior in Diatraea grandiosella Dyar was not affected by the substrate colors tested by Poston et al. (1979).

In addition to wavelength, there is the factor of intensity. In studying the Oriental peach moth and codling moth, Peterson and Haeussler (1928) found intensity to influence reactions to different light wavelengths. Intermittent light was found by Dolley (1930) to have more effect than the same intensity of continuous light on Eristalis tenax (Diptera: Syrphidae). Dolley (1932) confirmed the importance of both intensity and flash interval in studies using intermittent light to stimulate flies.

Olfaction

Insects often use olfaction to sense pheromones, food sources, etc. (Chapman, 1982). Many insects possess olfactory organs in the antennae (Abbott, 1936). Olfactory organs discovered elsewhere and an overlap with the function of gustatory mechanisms have combined to make some olfactory experimentation with insects difficult to interpret. Cockroaches (Glaser, 1927) and water beetles (Schaller, 1926) have olfactory organs on their palpi. Organs morphologically classified as gustatory have been shown to possess strong olfactory functions (Stadler and Hanson, 1975).

McIndoo (1914a, b, 1915) found olfactory organs to be located on the bases of the legs and wings of bees, and even believed antennae to not possess them. He found bees responded to essential oils with antennae removed. Snodgrass (1925) described bees as possessing olfactory organs in these areas, but included antennae, saying they were for different purposes. In later research, McIndoo (1933) found that when antennae were removed from Calliphora erythrocephala and Phormia regina (Diptera: Calliphoridae), they still responded to food odors as well as intact specimens. Abbott (1932) found that detached

heads of Cynomyia cadaverina (Diptera: Calliphoridae) responded to food and other odors. Even when antennae were coated with shellac, odors produced responses. The sensitivity of blowfly gustatory chemoreceptors to vapors has been confirmed (Dethier, 1972).

The exact mechanisms of olfaction have not been determined and specialists disagree on how olfaction works (Callahan, 1975). There are three main theories: 1) Classical olfaction theory (molecular shape). This theory is contact-dependent. 2) Dyson-Wright theory (high-frequency vibration). This theory is contact-dependent. 3) Callahan theory (electromagnetic waves). This theory is largely contact-independent, but also accounts for the collection of scent molecules by the antennae.

Callahan's theory is unique in that it offers new concepts resulting in the existence of a grey area in which the functions and sensory perceptions of vision and olfaction overlap. Callahan (1975) summarized evidence that insects smell by means of reception of electromagnetic transmissions mostly in the infrared wavelengths from scent molecules. Additionally, he gave evidence of direct reception of signals from host plants and mates.

Many different infrared-sensitive sensilla have been discovered on both nocturnal and diurnal insects (Callahan, 1965, 1966a, b, c, 1967, 1970, 1971). The infrared sensitive sensilla on insects are postulated to be operative largely in the far IR and possibly microwave wavelengths (Callahan, 1975). Many sensilla may be operative in the near IR and even visible light wavelengths. The only known dielectric waveguides, natural or otherwise, sensitive to visible light wavelengths were discovered by Callahan (1968) on nocturnal insects. The known function of the directional waveguides is as a safety mechanism, keeping nocturnal flyers from flying in daylight where they would be easy prey. Other functions may exist. It is unknown whether C. vittiger may possess any comparable mechanism.

The means by which Melanophila beetles may sense fires or air-borne fire products was described by Evans (1964, 1966, 1975) as specialized mesothoracic organs adjacent to the coxal cavities which detect infrared radiation. Callahan (1975) discusses Haller's organ, but the relationship of the organ on Melanophila to the Callahan theory of olfaction remains undetermined.

CHAPTER III
METHODS AND MATERIALS

Experimental Population

Cactus bug nymphs and adults were collected as needed from the Griffis Ranch, 3 miles southeast of Justiceberg, Garza County, Texas, during spring and summer, 1983. Cactus and cactus bugs were brought back to the laboratory for establishment of a population reservoir. The population was kept at 29-31°C using a 12:12 photoperiod. A reservoir of potted cactus plants was maintained in a greenhouse, from which cacti were taken to maintain the cactus bug population.

Experimental Design

Apparatus and Conditions

The roles of vision and olfaction in host plant selection were determined utilizing trials in which behavioral responses to choices were enumerated. Preliminary tests affirmed that cactus bugs would move in tunnels and suggested appropriate tunnel size range.

Handedness, ambient light wavelengths, and the construction materials used were not observed to influence cactus bugs in other preliminary trials.

The experiments utilized Y-shaped tunnels in which the insects, after being released in one end, could move freely toward either choice presented. A single design was employed for Y-tunnels while modifying choices outside the tunnel to achieve the desired stimuli. This eliminated introduction of possible experimental error factors from use of different tunnel designs and allowed the insects to remain in as normal a condition as possible. A five-level construction was used for the tunnels to allow five independent trials to be made simultaneously.

The Y-tunnels were constructed of brown corrugated cardboard after prototypes were tested using different materials. Steel pins were used to fasten the parts together. No glues were used, and tape was used almost exclusively on the outside and kept to a minimum to avoid possible olfactory influence. The ends were closed off by screens cut to fit tightly. They were hinged with tape and held in place with pins to allow easy opening.

The internal diameter or opening size of each of the five Y-tunnels was 3.8 x 2.3 cm. This size was large

enough for ease of movement and allowed for retrieval of the insects with instruments when necessary. The length of the base portion of the Y-tunnel was 22 cm. The branch length was 13 cm, which was short enough to allow the cactus bugs to perceive choices from the Y-tunnel junction, and yet long enough to act as receptacles to encourage retention until data tabulation. A junction angle of 120° was employed.

A small fan was used to draw air through the tunnels from the choice locations. Airflow was accommodated by the insertion of the release end or base of the five-level Y-tunnel into a cylindrical fan housing as illustrated in figure 2. The fan housing was 50 cm high with an internal diameter of 13 cm. The Y-tunnel was supported by a pedestal and the release end was tightly inserted 5.5 cm deep into a vertically oriented 4.5 x 13 cm opening beginning 11 cm from the base of the fan housing. The space inside the fan housing acted as an equalizing buffer zone modulating airflow through the tunnels. The fan was mounted in the housing 6.5 cm above the top of the inserted Y-tunnel. A 1.5-6 volt DC motor was paired with a 1.4 volt DC power source to provide an even gentle airflow.



Figure 2--Apparatus used in testing behavioral responses of Chelinidea vittiger to treatment by visual, olfactory, and combined stimuli.

Cactus bugs of both sexes were placed in all tunnel openings before using the Y-tunnel in experiments, and the branch sides were randomized by inverting the Y-tunnel on the pedestal. These two factors and the presence of airflow served to counteract possible build-up of residual cactus bug odors as a potential source of experimental error.

Sensory stimuli from the choices were selectively allowed to the cactus bugs through the use of physical barriers. A large glass jar was inverted over the cactus to block olfactory stimuli but not interrupt visual stimuli. Visual stimuli were blocked with white cardboard while olfactory stimuli were carried around it by the airflow provided by the small fan. Thin transparent polyethylene film was draped over the choices and Y-tunnel branch openings to force air to flow past the choices and pick up scent. Airflow was present during all experiments to guard against possible experimental error.

The choices were positioned outside the openings of the two branches using a platform and supports such that the choices were approximately 10 cm from the tunnel openings. The sides for choice location were randomized. To avoid introduction of another possible olfactory influence, brown

corrugated cardboard of the same type used to construct the tunnels was used to make the supports and platform. To test selection for visual stimuli from the cactus pad profile, choices were set up on a neutral brown cardboard surface against a white posterboard background 2.5 m from the tunnel openings. Light intensity was measured from the tunnel openings using a directional photometer and was equalized by light source adjustment. Choice distances remained the same.

Opuntia polyacantha Haworth was used as a host plant. All cactus pads used in experiments were removed from plants showing evidence of previous C. vittiger feeding, indicating acceptability. All pads were washed with water and suberized. Treated pads were removed from the same plant and burned for five seconds in flames from a fire made from dry sticks. In the profile experiment, a single large pad served as the positive profile choice. A larger pad was cut into a square of approximately the same surface area to serve as the negative choice.

Adult cactus bugs were used for experimentation. The population reservoir sex ratio was 1:1. Equal numbers of both sexes were used up to trial number 45, in which sex was randomized. They were starved for 48 hours before

experimentation to induce host plant seeking. During trials, each cactus bug was given two hours to make a choice. Data was tabulated at 15, 30, 60, and 120 minute intervals. After experimentation, a period of two days in the population reservoir was assigned to normalize cactus bugs.

Each experiment was performed in the form of a series of Bernouli trials. The first side in which a cactus bug was recorded was considered to be the choice. A positive choice was tabulated when the cactus bug was anywhere in the tunnel section leading from the junction to the appropriate choice. Trials in which the insects did not move into either side were recorded as negative responses to yield fixed column marginals, allowing independence of cell proportions to be tested beyond the application of testing classification independence only.

The enumeration data resulting from the Bernouli trials was analyzed by χ^2 . The Fisher (1922, 1923, 1924) modification of the Pearson (1900) χ^2 was used for analysis. As ϵ is not dealt with quantitatively in χ^2 , potential factors were addressed in the experimental design. The number of replications was chosen to keep N greater than recommended application limits for

χ'^2 using Yates' (1934) χ^2 continuity correction term. Experimental results were monitored to ensure that sufficient replications were performed to yield an estimated expected value of each cell exceeding five counts, following the recommendations of Cochran (1954).

The first three experiments were designed for maximum counts. Instead of using cactus-related stimuli as a negative choice, a white blank was used. This ensured that cactus bugs which otherwise might have chosen a more attractive cactus stimuli did not have the choice overruled. This allowed the highest cell value for the treatment tested to be reached under the given conditions. Treatment replication numbers were kept equal in the first three experiments to enable use of the χ^2 additive property.

Experimentation

The first three experiments were those dealing with cactus bug selection for the untreated host plant. Each experiment used 45 replications. In the first experiment (figure 3), the cactus bugs were treated with visual stimuli from the nearby host plant surface. In the second experiment (figure 4), they were treated with olfactory

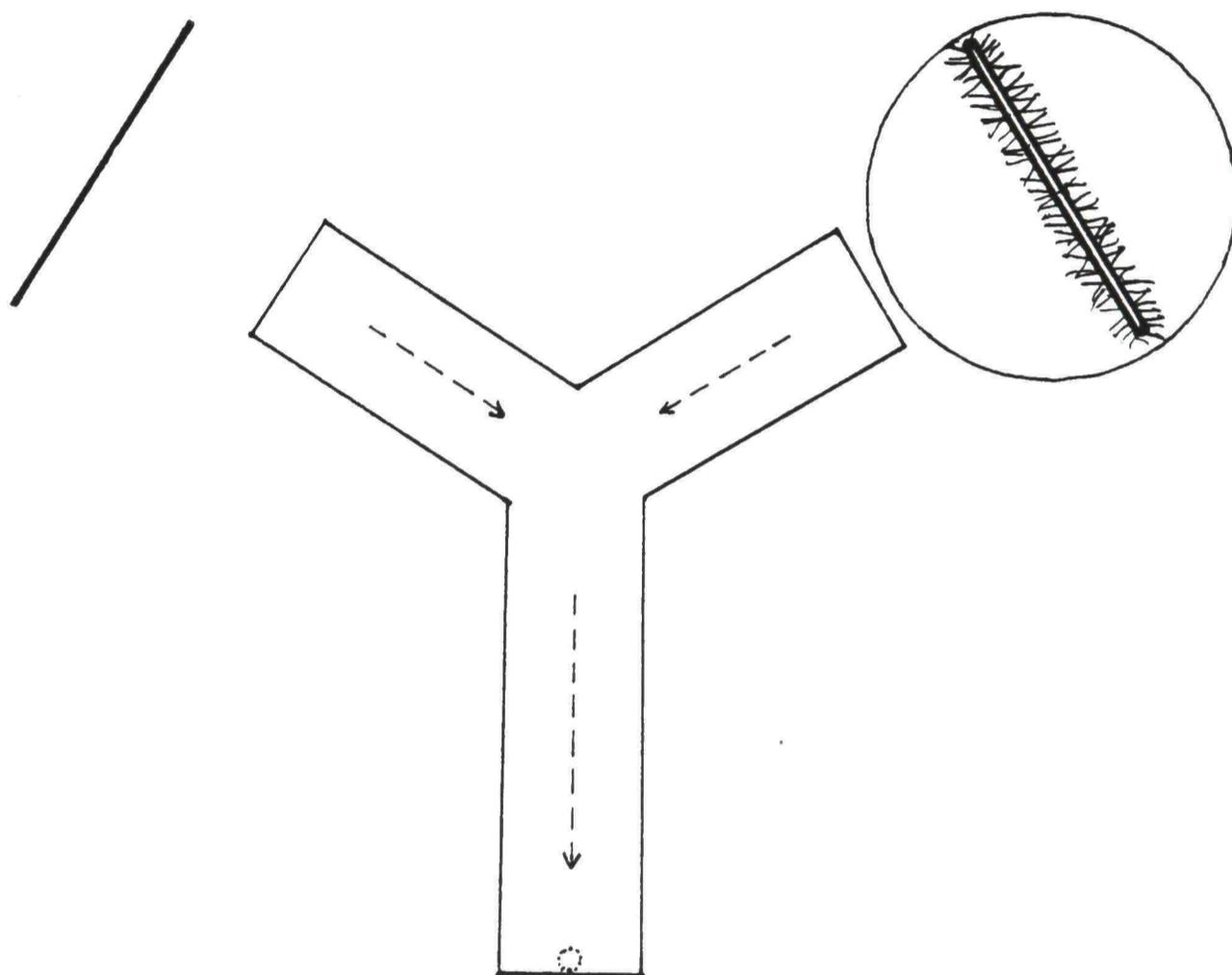


Figure 3--Schema for experiment testing effect of visual stimuli while disallowing olfactory stimuli to experimental units. Definitions: solid circle, olfactory barrier; solid line, white blank; broken line, direction of airflow; dotted circle, release point.

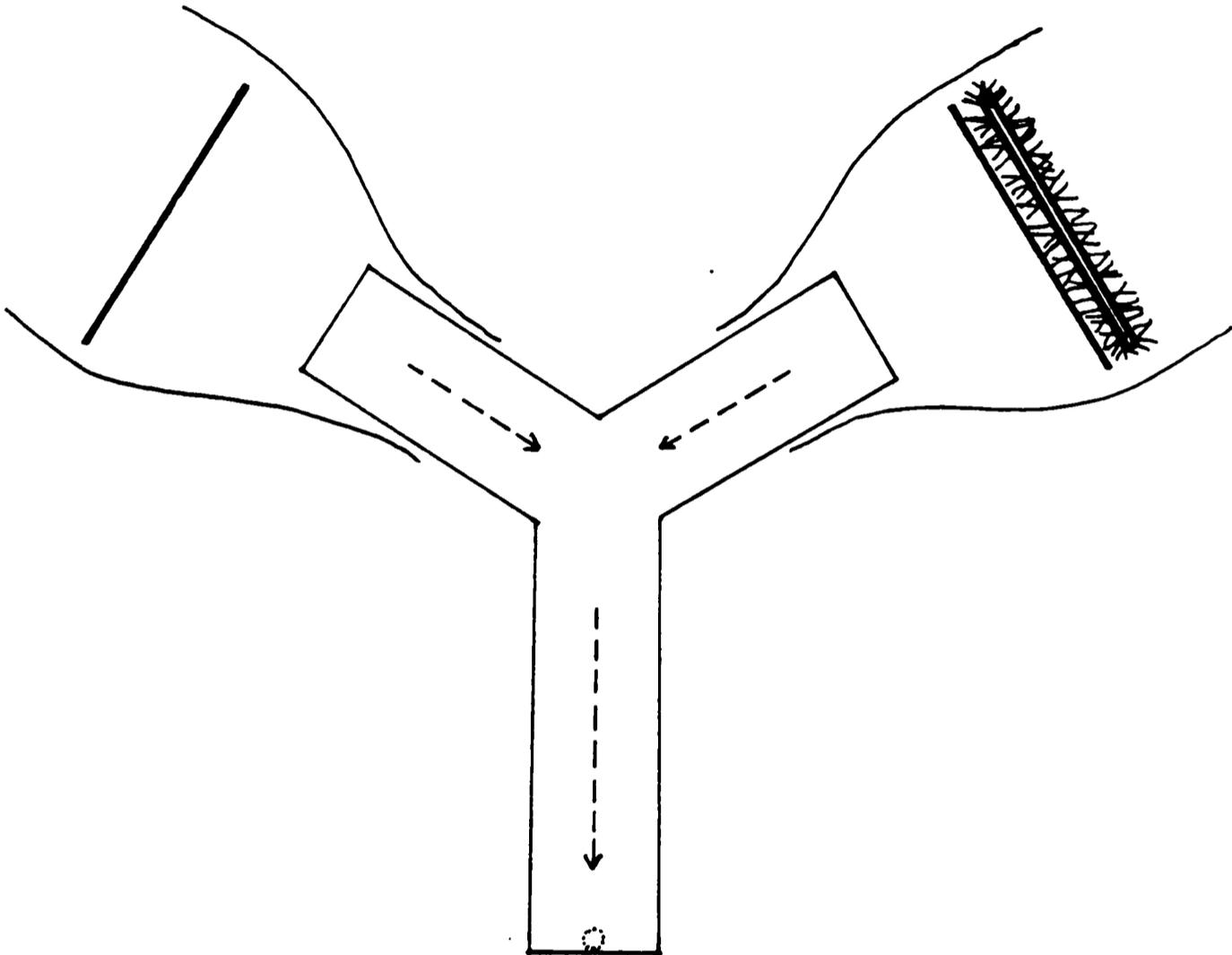


Figure 4--Schema for experiment testing effect of olfactory stimuli while disallowing visual stimuli to experimental units. Definitions: curved lines, polyethylene film; single straight solid lines, white blanks; broken line, direction of airflow; dotted circle, release point.

stimuli from the host plant. The third experiment treated them with combined visual and olfactory stimuli. All results were tabulated for analysis.

Following these experiments, pooling was used to analyze the data. Each experiment was then analyzed individually. Results of the individual analyses were used to determine the next research step. They indicated pooling to be used to analyze two of the experiments.

The experiment testing selection by C. vittiger for host plants treated by burning versus untreated host plants was performed next. Experimentation using only fire-damaged hosts and analysis using data from the third experiment above by the χ^2 additive property was not done, as the resulting maximum values would not reflect a true choice between the two treatments. Cactus bugs were allowed combined visual and olfactory stimuli from both sources simultaneously, using a total of 45 replications. The positive choice was defined as treated cactus pads.

The last experiment tested host plant selection by treating cactus bugs using the profile of the cactus pad as the distinguishing visual stimuli, using 40 replications. The results are discussed with those from the non-profile visual experiment.

CHAPTER IV
RESULTS AND DISCUSSION

Data from the first three experiments were pooled for χ^2 analysis to test for the presence of independence in 2x3 contingency format. The analysis is provided in table 1. H_0 was accepted, establishing independence. Differences in the host plant selection mechanisms were found to be significant ($p < .05$) under the experimental conditions.

Visual Role

In the first experiment, H_1 was accepted, indicating the role of vision in host plant selection to be not significant ($p > .05$) under the experimental conditions. The experimental data and analysis are included in table 2.

Some behaviors are known to be visually oriented, such as avoidance responses. The tunnels provided conditions very different from field conditions in which C. vittiger might make use of its flight ability, in which vision may be important.

Table 1--Contingency table for pooled enumeration data from experiments testing host plant selection by Chelinidea vittiger for treatment by visual, olfactory, and combined stimuli from unburned Opuntia polyacantha.

Response	Treatment			Total
	Visual Stimuli	Olfactory Stimuli	Combined Stimuli	
Positive a_i	27 (33.000)	35 (33.000)	37 (33.000)	99
Negative	18 (12.000)	10 (12.000)	8 (12.000)	36
Total	45	45	45	135

$$p_i = \begin{matrix} .6000 & .7777 & .8222 \end{matrix} \quad \bar{p} = .7333$$

$$\chi^2 = 6.36 * (df = 2)$$

Table 2--One-dimensional count data analysis series for experiments testing host plant selection by Chelinidea vittiger for Opuntia polyacantha. Top four rows present results for treatment using nearby visual cactus surface, more distant visual cactus profile, olfactory, and combined nearby visual and olfactory stimuli from unburned hosts. Bottom row presents results for treatment using fire-damaged (burned) vs. unburned hosts.

Trt	df	#Toward		Tot	Pi+	χ^2
		Pos	Neg			
Vis	1	27	18	45	.6000	1.80 ns
Pro	1	17	23	40	.4250	0.90 ns
Olf	1	35	10	45	.7777	13.88 **
Com	1	37	8	45	.8222	18.68 **
Brn	1	31	14	45	.6888	6.42 *

Definitions: Brn, Burned; Com, Combined; Neg, Negative; Olf, Olfactory; Pos, Positive; Pro, Profile; Tot, Total; Trt, Treatment; Vis, Visual (non-profile).

In the experiment testing selection by C. vittiger for visual treatment by profile, H_1 was accepted. Host plant selection using visual perception of the cactus pad profile was not significant ($p > .05$) under the experimental conditions. The results are included in table 2.

Olfactory Role

In the experiment testing the role of olfaction alone in host plant selection by C. vittiger, H_0 was accepted. The role of olfaction was found to be significant ($p < .01$) under the experimental conditions. The results are included in table 2.

The experiments testing olfactory and combined stimuli were designed for contact of airborne host plant scent molecules with the olfactory sensory organs of C. vittiger. Classical and Dyson-Wright olfaction were therefore accommodated by the experimental design.

In light of the theory of olfaction developed by Callahan (1975), the following considerations should be made in interpreting the significance of the experiment. While the general electromagnetic wavelength filtration characteristics of the olfactory barrier were taken into

account during experimental design, host plant emission, scent molecule emission, and glass transmission spectra were not available. As many different infrared-sensitive sensilla have been discovered on both nocturnal and diurnal insects, the possibility can not be ruled out that such sensilla may play a role in sensory abilities of C. vittiger.

The p_i for cactus bugs responding positively to visual host plant stimuli was .6000. Whether this value was due to a visual response or the weak dielectric reception of possible host plant or scent molecule emissions is untestable from the present experiments. Therefore, the visual experiment should not be used in conjunction with the olfaction experiment to test the Callahan theory of olfaction. The experimental design effectively separated visual and olfactory stimuli as conventionally understood, allowing meaningful χ^2 tests and interpretations to be made.

Combined Role

In the experiment testing the effect of combined visual and olfactory stimuli, H_0 was accepted. The combined

stimuli were found to be significant ($p < .01$) in host plant selection under the experimental conditions. The results and analyses are included in table 2.

Olfactory vs. Combined Roles

Data from the olfactory and combined stimuli experiments were analyzed by pooling, resulting in the acceptance of H_1 . Olfactory and combined roles were not significantly different ($p > .05$). Olfaction was therefore interpreted to be the significant host plant selection means. A 2x2 contingency format is used to give the results and analysis in table 3.

Beyond the evaluation of independence of classifications, fixed marginals provided for cell proportion independence to be tested. Independence of proportionality was not significant ($p > .05$), indicating the combined effect of visual and olfactory sensory means did not have a physiologically additive relationship under the conditions tested.

Table 3--Contingency table using pooled values to test host plant selection by Chelinidea vittiger for olfactory and combined stimuli from unburned Opuntia polyacantha.

Response	Treatment		Total
	Olfactory Stimuli	Combined Stimuli	
Positive a_i	35 (36.000)	37 (36.000)	72
Negative	10 (9.000)	8 (9.000)	18
Total	45	45	90
$p_i =$.7777	.8222	$\bar{p} = .8000$

$$\chi^2 = 0.27 \text{ ns } (p > .05) \text{ (df = 1)}$$

Treated vs. Untreated Host Plants

The results of the experiment testing selection by cactus bugs for hosts treated by burning are included in table 2. H_0 was accepted, indicating host plant selection for treated cactus pads to be significant ($p < .05$) over that for untreated pads under the experimental conditions. This supports Sickerman and Wangberg's (1983) conclusion that C. vittiger prefers fire-damaged cactus as a host.

CHAPTER V
SUMMARY AND CONCLUSIONS

The cactus bug, Chelinidea vittiger Uhler, was investigated in several experiments for its use of vision and olfaction in host plant selection. Another experiment tested selection for fire-damaged versus unburned host plants. Each experiment utilized a series of trials to determine behavioral responses to choices.

Olfaction was found to be the significant ($p < .01$) sensory means of host plant selection under the experimental conditions. The use of vision along with olfaction raised responses slightly, but the effect was not significant ($p > .05$). The combined use of vision and olfaction was further determined to not be physiologically additive. Visual roles in host plant selection for the nearby cactus surface and more distant cactus pad profile were found to be not significant ($p > .05$).

Preference for fire-damaged pads was significant ($p < .05$) over that for unburned cactus, thus providing confirmation of previous research (Sickerman and Wangberg,

1983). Chelinidea vittiger is a limiting factor of prickly pear within its indigenous range, acting in alliance with other insects and environmental factors to inhibit cactus growth, reproduction, and vitality. Prescribed burning may enhance the impact of C. vittiger on prickly pear, and therefore, the role of biological control by insects may be of practical importance to ranchers and others desiring greater control of prickly pear.

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