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Manuscripts from *all* areas of the discipline of entomology are accepted for consideration. At least one author must be a member of the Florida Entomological Society. Please consult "Instructions to Authors" on the inside back cover. Submit the *original manuscript, original figures and tables, and 3 copies* of the entire paper. Include an abstract in Spanish, if possible. Upon receipt, a manuscript is acknowledged by the Editor and assigned to an Associate Editor who sends it out for review by at least 3 knowledgeable peers. Reviewers are sought with regard only for their expertise; Society membership plays no role in their selection. Page charges are assessed for printed articles.

Manuscripts and other editorial matter should be sent to the Editor, JOHN R. McLAUGHLIN, 4628 NW 40th Street, Gainesville, FL 32606.

This issue mailed December 30, 1988

THE 72nd ANNUAL MEETING OF THE FLORIDA ENTOMOLOGICAL SOCIETY

The 72nd annual meeting of the Florida Entomological Society will be held August 7-10, 1989 at the Daytona Beach Hilton, 2637 So. Atlantic Ave., Daytona Beach, FL 32018; telephone (904)-767-7350. Registration forms and information will be mailed to members and will appear in the Newsletter and the March, 1989 Florida Entomologist.

Notice of Change of Deadline for Submission of Papers

The deadline for submission of papers and posters for the 72nd annual meeting of the Florida Entomological Society will be May 1, 1989. The meeting format will be much the same as in the past with eight minutes allotted for presentation of oral papers (with 2 minutes for discussion) and separate sessions for members who elect to present a Project (or Poster) Exhibit. The three oral student papers and the three student Project Exhibits judged to be the best on content and delivery will be awarded monetary prizes during the meeting. Student participants in the judged sessions must be Florida Entomological Society Members and must be registered for the meeting.

James R. Price, Chairman
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5007 60th Street East
Bradenton, FL 34203
(813)-755-1568

National Center for Physical Acoustics
NATIONAL AGROACOUSTICS SYMPOSIUM

PREFACE

As part of its broad research effort in agroacoustics, The National Center for Physical Acoustics (NCPA) was pleased to sponsor the first National Agroacoustics Symposium in Jackson, Mississippi on April 26-27, 1988. *Florida Entomologist* has provided a forum to the participants of that symposium by the dedication of this issue to agroacoustics. We gratefully acknowledge the assistance of J. C. Webb and Carrol O. Calkins with reviewing and editing the papers.

Agroacoustics is a developing discipline which blends the detailed and systematic observational techniques of the biological scientist with the ever increasing technical sophistication of physical science and engineering. As this field grows, and more biological scientists utilize acoustics instrumentation to acquire additional information about the behavior of an individual organism, an increased need will develop for specialized devices that are adapted to a specific insect or data acquisition modality. The NCPA wishes to help scientists meet their individual and group research needs. We can participate in joint research efforts, provide technical advice on available equipment and, in certain instances, develop specialized instrumentation.

The recent development of the discipline of agroacoustics is evidenced by the following milestones: The first acoustics session of the Entomological Society of America meeting was held in 1987; a National Agroacoustic Symposium was organized in 1988; this agroacoustics issue of *Florida Entomologist* in 1988 continues the exciting progress. The National Center for Physical Acoustics is pleased to see this progress and hopes that it can assist existing programs and participate in the development of additional efforts that would result in benefit to this discipline and to the country at large.

It is our sincere hope that others find the meeting and its proceedings as profitable as we have.

Dr. Ralph R. Goodman
Laboratory Director
Oxford, Mississippi

Dr. Robert T. Walden
Chairman of Symposium
Oxford, Mississippi

HOW DO ACOUSTIC INPUTS TO THE CENTRAL NERVOUS SYSTEM OF THE BOLLWORM MOTH CONTROL ITS BEHAVIOR?

HERNDON R. AGEE

Insect Attractants, Behavior, and Basic Biology Research Laboratory,
Agricultural Research Service, U.S. Department of Agriculture,
Gainesville, Florida 32604.

ABSTRACT

The nervous system of the bollworm moth, *Heliothis zea* (Boddie), a noctuid moth that is a major pest of cotton, corn, and tomatoes, is served by two pairs of acoustic sense cells. The moths use the acoustic receptors to detect the ultrasonic cries of predatory bats that feed on these moths. Bats use pulsed high frequency sounds to echolocate and capture moths for food. The moths have developed an avoidance behavioral reaction that protects them from predatory bat capture when they detect the echolocating cries of the bats.

A pair of acoustic receptors are located in each tympanic organ located on the lateral wall of the metathorax on each side of the moth. A1 receptor, the most sensitive unit, can detect 20 kilohertz frequencies at sound pressure levels of 35 dB (0 dB re 20 μ Pa). The A2 receptor is about 20 dB less sensitive and is also tuned to be most sensitive to 20 kHz sounds. Pulse rates of 10/sec and pulse durations of 10 msec were most effective for eliciting evasive reactions in the bollworm moth.

In field and laboratory behavior tests, we have determined that the moths can detect 85 dB pulses of ultrasound (20 kHz) at a distance of 50-80 feet from the moth and after detection the moths make evasive reactions.

My recent research has focused on identification of the neural circuits from the acoustic receptors *to* and *through* the central nervous system (meso- metathoracic ganglia and prothoracic ganglion and brain) to the motor nerves responsible for executing the evasive reactions. The structure of the various parts of the circuits responsible for the behavioral reactions have been identified using histochemical techniques (cobalt chloride and lucifer yellow) that mark only the axons carrying the acoustic information (action potentials) and the motor nerve commands from these nerves to the muscles responsible for directed flight.

Electrophysiological techniques were used to monitor the information flow in the acoustic axons that feed the moth coded information on the high frequency sounds in its environment. If the information is from the A1 receptor, it is processed in the brain to produce behavior commands that are transmitted by the motor nerves to generate a behavioral reactions that produce turn reactions. The information from the A2 receptor is transmitted to neurons in the mesothoracic ganglion directly and produce rapid unpredictable evasive reactions (spirals, dives, and cessation of flight) and do not require "brain" processing. The anatomical circuits, behavioral reaction times, and electrophysiological monitoring of neural activities confirm these findings. These and other studies have demonstrated that the behavior of the moth is influenced or controlled by sensory inputs that can have positive and negative effects on the moth behavior. When the flying moth is attracted to an ultraviolet light and a sound source at the light source generates a pulses of high frequency sound, the moth will make an evasive reaction to the sound stimuli in preference to the continued attraction to the visual stimuli. In other instances, another nocturnal moth species that is attracted to a sex pheromone (an olfactory attractant) can be terminated (behavior turned off) if the trap containing the pheromone is constructed of specific colors that cause an avoidance reaction to the visual stimuli that are dominant over the attractive odor.

These model acoustic studies are establishing the boundaries and conditions that must be met in the neural circuits of the central nervous system of the moth for specific sensory stimuli to be functionally effective. Normal or usual behaviors can be turned

on and off when the proper sensory stimuli are presented according to specific "criterion" conditions. To obtain maximum benefits from the use of non-insecticidal technologies to control insects, a full understanding of the levels of neural processing of sensory stimuli is needed, as is an understanding of the spheres and levels of dominance that specific sensory stimuli exert in the control of the behavior of the insect pest.

RESUMEN

El sistema nervioso de *Heliothis zea* (Boddie), que es una alevilla noctuida y una plaga mayor del algodón, maíz y tomates, es asistido por un par de células del sentido acústico. Las alevillas usan los receptores acústicos para detectar el grito ultrasónico de los murciélagos predadores de estas alevillas. Los murciélagos usan pulsaciones de sonido de alta frecuencia para localizar por el eco y capturar las alevillas como comida. Las alevillas han desarrollado una reacción en su comportamiento donde evitan la captura cuando detectan el grito localizador de ecos de los murciélagos.

Un par de receptores acústicos están localizados en cada órgano timpánico que se encuentran en la pared lateral del metatórax a cada lado de la alevilla. El receptor A1 que es la unidad más sensitiva, puede detectar frecuencias de 20 kilohertz a niveles de presión de sonido de 35 dB (0 dB re 20 μ Pa). El receptor A2 es como 20 dB menos sensitivo y también es el más afinado y sensitivo a los sonidos de 20 kHz. Pulsaciones a razón de 10/segundo y pulsaciones durando 10 megasegundos fueron los más efectivos en educir reacciones evasivas en las alevillas.

Hemos determinado en pruebas de comportamiento en el campo y en el laboratorio, que las alevillas pueden detectar pulsaciones de 85 dB de ultrasonidos (20 kHz) a una distancia de 50-80 pies, y que después de detectados, las alevillas reaccionan evasivamente.

Mis investigaciones reciente se han enfocado en la identificación de los circuitos neurales de los receptores acústicos *hacia y a través de* del sistema nervioso central (ganglio meso-metatorácico y ganglio protorácico y el cerebro).

The nervous system of the bollworm moth, *Heliothis zea* (Boddie), a noctuid moth that is a major pest of cotton, corn, and tomatoes, is served by two pair of acoustic sense cells (Agee 1967, Roeder & Treat 1957). The moths use the acoustic receptors to detect the ultrasonic cries of predatory bats that feed on these moths (Agee 1969a). The bats use pulsed high frequency sounds to echolocate and capture moths for food. The moths have developed an avoidance behavioral reaction which protects them from predatory bat capture when they detect the echolocating cries of the bats.

A pair of acoustic receptors is located in each tympanic organ located on the lateral wall of the metathorax on each side of the moth. The A1 receptor, the most sensitive unit, can detect 20 kilohertz frequencies at sound pressure levels of 35 dB (Agee 1967). The A2 receptor is about 20 dB less sensitive than the A1 receptor and is most sensitive at 20 kHz. Pulse rates of 10/sec and pulse durations of 10 msec were most effective for eliciting evasive reactions in the bollworm moth (Agee 1969a, 1969b, Agee & Webb 1969). In response to bat cries or electronically generated pulses of ultrasound, the acoustic receptors generate action potentials that are transmitted to the central nervous system. In the flying moths, this information causes evasive reactions that include directed turns, unpredictable dives, and falls to the ground. The behavior of non-flying moths is less affected by pulses of ultrasound (Agee 1969b).

In field and laboratory behavior tests, we have determined that the moths can detect ultrasounds at an SPL of 85 dB at a distance of 50-80 feet and make evasive reactions (Agee 1969a,b) after detecting this sound.

Recent research has focused on identification of the neural circuits from the acoustic receptors to and through the central nervous system (meso- metathoracic ganglia and

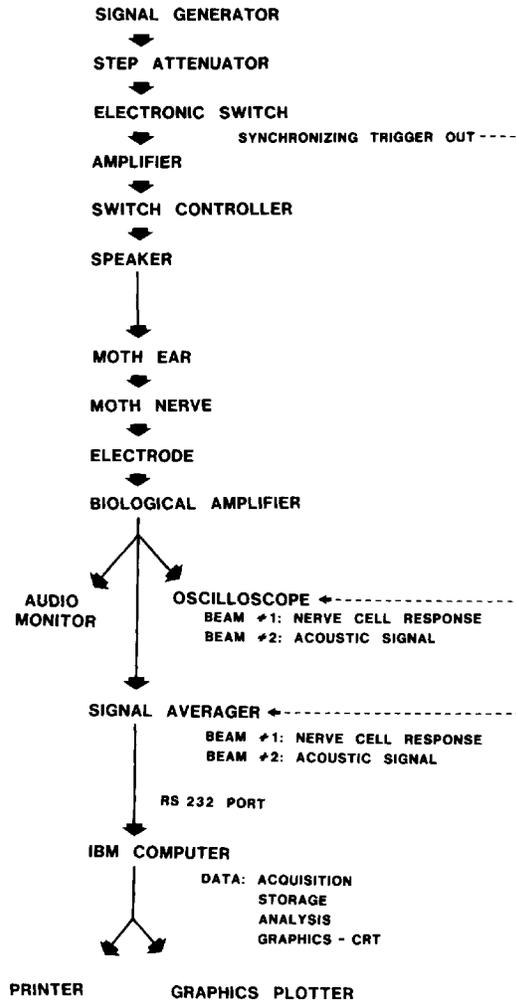
ACQUISITION AND ANALYSIS
OF NEUROBIOLOGICAL DATA

Fig. 1. Flow diagram of data acquisition and analysis system for neurobiological studies.

prothoracic ganglion and brain) to the motor nerves responsible of executing the evasive reactions.

A special electronic data acquisition and analysis system was developed to selectively record and analyze the electronic events occurring in the central nervous system in response to pulsed ultrasound (Agee 1985a) (Fig. 1).

The action potential caused by the stimulation of ultrasound can be tracked from the tympanic nerve through the central nervous system using special electrodes. Figure 2 compares the action potentials from the tympanic nerve, the axon in the ganglion, the coded information on a pulse of sound identified as an action potential from a pulse marker neuron and the action potential produced by the non-acoustic B cell in the central nervous system as shown in Figure 1.

The structure of the various parts of the sensory input and motor nerve output circuits responsible for behavioral reactions have been identified using histochemical

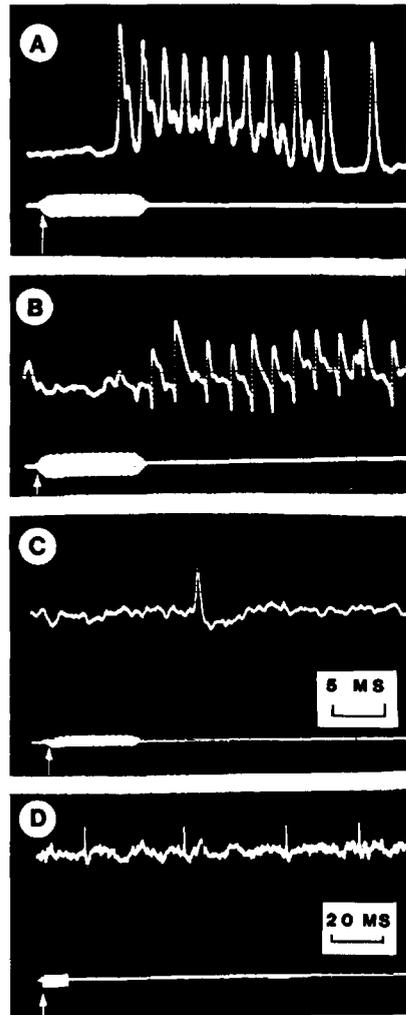


Fig. 2. Examples of acoustic responses recorded at (A) the tympanic nerve, (B) repeater neuron in the mesothorax, (C) pulse marker neuron in the prothoracic ganglion, and (D) B cell recorded from position 3 in the prothoracic ganglion. Time scale for A, B, and C indicated on C.

techniques (cobalt chloride and lucifer yellow) that mark only the axons carrying the acoustic information (action potentials) and the motor nerve commands from these nerves to the muscles responsible for directed flight (Fig. 3) (Paul 1973, Orona & Agee 1987a,b, Tyrer & Altman 1974).

Electrophysiological techniques were used to monitor information flow in the acoustic axons that feed the moth coded information on the high frequency sounds in its environment (Agee 1985a). If the information is from the A1 receptor, it is processed in the brain to produce behavior commands that are transmitted by the motor nerves to generate behavioral reactions that produce coordinated turning. The information from the A2 receptor is transmitted to neurons in the mesothoracic ganglion directly and produce rapid unpredictable evasive reactions (spirals, dives, and cessation of flight) that do not require "brain" processing. The anatomical circuits, behavioral reaction times, and electrophysiological monitoring of neural activities confirm these findings. These and other studies have demonstrated that the behavior of the moth is influenced or controlled by sensory inputs that can have positive and negative effects on the moth

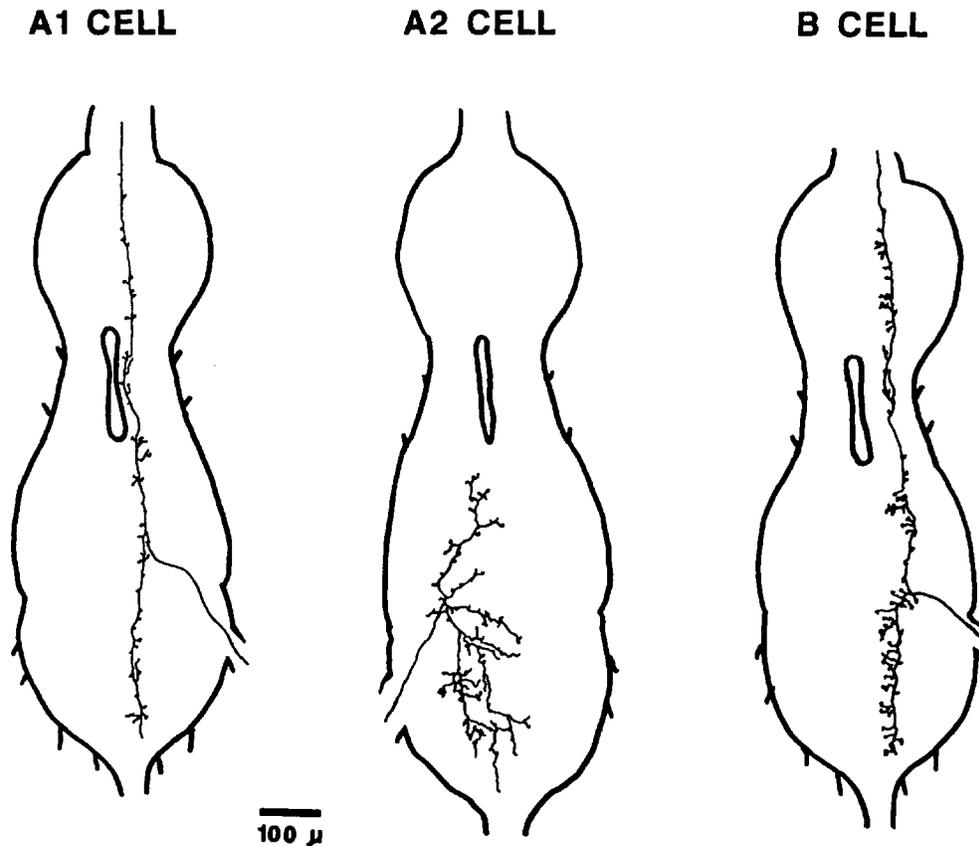


Fig. 3. Representative camera lucida reconstructions of the cells labeled following cobalt infiltration of the tympanic nerves. The A1 and B cells have synaptic terminals scattered throughout the thoracic ganglia. The axonal terminations of the A2 cell are confined to the meso-metathoracic ganglia.

behavior. For example, when the flying moth is attracted to an ultraviolet light and a sound source at the light source generates pulses of high frequency sound, the moth will make an evasive reaction to the sound stimuli in preference to the continued attraction to the visual stimuli (Agee & Webb 1969). In other instances, a nocturnal moth species that is attracted to a sex pheromone (an olfactory attractant) can be terminated (behavior turned off) if the trap containing the pheromone is constructed of specific colors that cause an avoidance reaction. Visual stimuli are dominant over the attractive odor (Mitchell et al., unpublished data). If an olfactory attractant, i.e., sex pheromone, is presented to the moths without a repellent visual or acoustic stimulus the olfactory attractant is effective. Figure 4 illustrates these events graphically.

Figure 5 shows what we have learned to date regarding the flow of information in the acoustic network from the receptors through the tympanic nerve, meso-metathoracic ganglia, prothoracic ganglion and brain to the motor nerves that control flight of the moth. As mentioned before, there are two networks that function in the moth to avoid bat predators. In the rapid reaction network the acoustic inputs from the A2 receptor cause the motor nerves to operate directly and provides for the quickest reaction possible to protect the moth. In the slow reaction network, acoustic information that arrives in the central nervous system is transmitted to the prothoracic ganglion and brain and receives some coding, such as the pulse marker neuron; a longer and slower route for the information to travel before a behavior can be executed. This produces

Effects of Sensory Stimuli on Moth Behavior

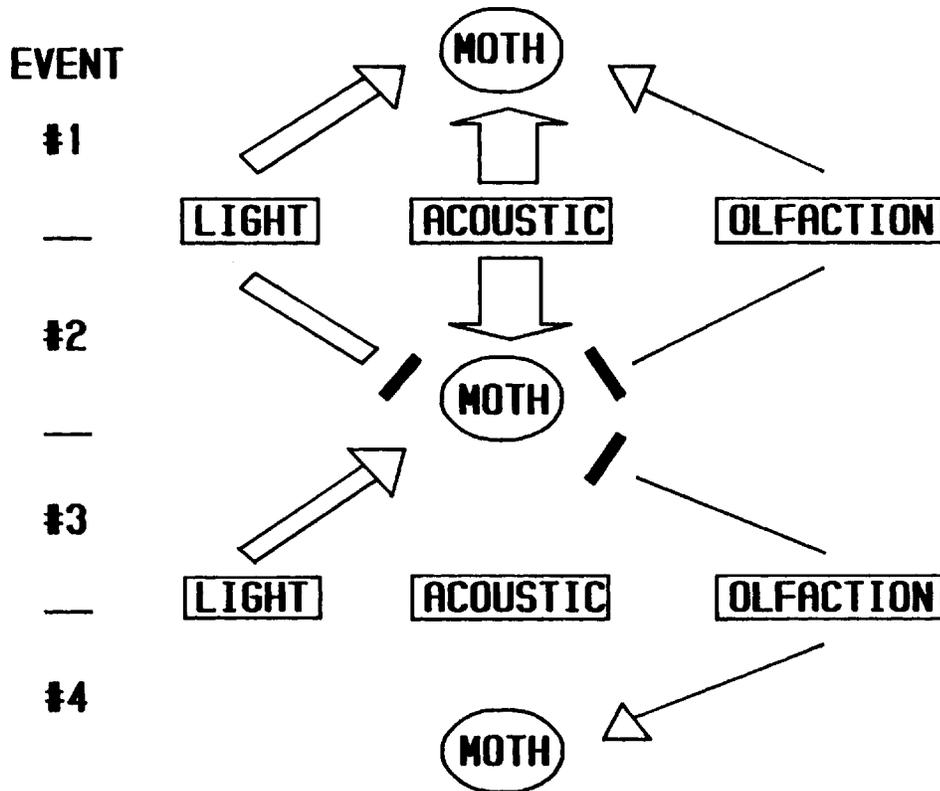


Fig. 4. Schematic diagram of the effects of sensory stimuli on the behavior of the bollworm moth. The width of the arrows indicate the relative influence of sensory input to the central nervous system of a flying moth. The bars indicate blockage of behaviors elicited by specific stimuli. In event #1, all three inputs affect behavior. Event #2, the attractant behavior induced by ultraviolet light or sex pheromones are blocked if a repellent acoustic stimuli is received. In event #3, the olfactory stimulus of a sex pheromone is blocked when it is being release from a color trap that is repellent. In event #4, an olfactory stimulus (a sex pheromone) is attractive when no repellent acoustic or visual stimuli are present.

a precise turn behavior that puts the maximum distance between the moth and the sound source.

These "model" acoustic studies are establishing the boundaries and conditions that must be met in the neural circuits of the central nervous system of the moth for specific sensory stimuli to be functionally effective in controlling of their behavior. Normal or usual behaviors can be turned on and off when the proper sensory stimuli are presented according to specific conditions. To obtain maximum benefits from the use of non-insecticidal technologies to control insects, a full understanding of the levels of neural processing of sensory stimuli is needed. We also need to know the spheres and levels of dominance that specific sensory stimuli exert in controlling the behavior of pest insects.

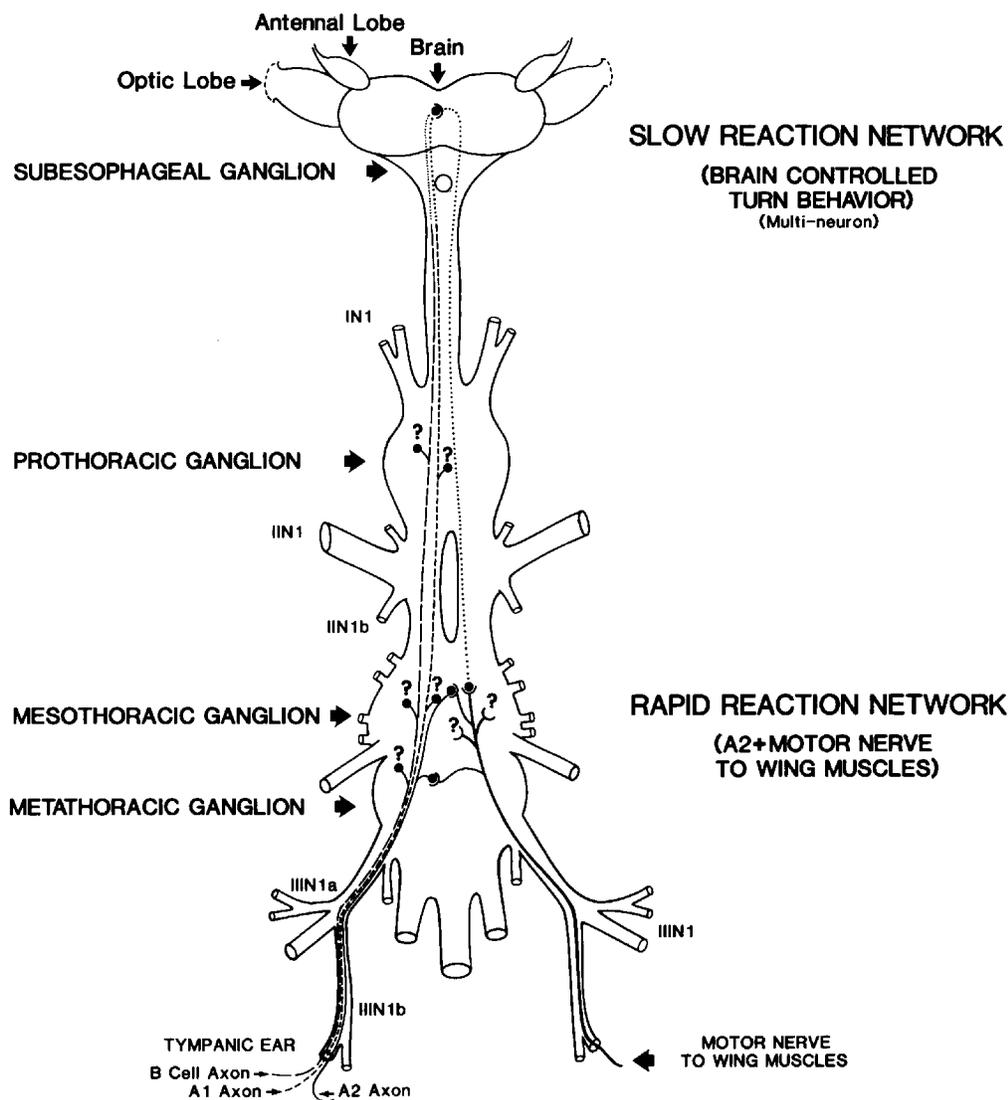


Fig. 5. Schematic diagram of the tympenic neurons and associated circuitry to the motoneurons involved in evasive flight behavior. Two behaviorally-relevant systems appear to be present. The A2 acoustic cell has direct monosynaptic connections to the motoneurons within the meso-metathoracic ganglia, forming a rapid reaction network. On the other hand, the A and B cells appear to be additionally linked to interneurons and the brain reflecting their involvement in a slower and directed reaction network.

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ACOUSTIC SIGNALS, ARMS RACES AND THE COSTS OF HONEST SIGNALLING

THEODORE BURK

Biology Department, Creighton University,
Omaha, Nebraska 68178-0103, U.S.A.

ABSTRACT

Animal signals evolve as adaptations to social as well as physical environments. Where the interests of signallers and responders differ, a coevolutionary "arms race" cycle of signal adoption, exaggeration, and devaluation may result. Stable, reliable signals evolve when costs of signalling constrain the evolution of bluff and exaggeration. Acoustic signals are especially costly, compared to other signal types, and are therefore especially likely to evolve as reliable signals in such "social competition" situations. Costs of acoustic signals include physiological costs of growth and signal production, probes by conspecific rivals and discriminating members of the other sex, and attacks by natural enemies such as predators and parasites.

RESUMEN

Señales dadas por los animales se han desarrollado como adaptaciones al medio ambiental físico así como al social. Donde el interés del que señala y del que responde difieren, pudiera entonces resultar en un ciclo coevolucionario de "carrera hacia las armas" en la señal de adaptación, exageración, y devaluación. Señales estables y confi-

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ABSTRACT

Animal signals evolve as adaptations to social as well as physical environments. Where the interests of signallers and responders differ, a coevolutionary "arms race" cycle of signal adoption, exaggeration, and devaluation may result. Stable, reliable signals evolve when costs of signalling constrain the evolution of bluff and exaggeration. Acoustic signals are especially costly, compared to other signal types, and are therefore especially likely to evolve as reliable signals in such "social competition" situations. Costs of acoustic signals include physiological costs of growth and signal production, probes by conspecific rivals and discriminating members of the other sex, and attacks by natural enemies such as predators and parasites.

RESUMEN

Señales dadas por los animales se han desarrollado como adaptaciones al medio ambiental físico así como al social. Donde el interés del que señala y del que responde difieren, pudiera entonces resultar en un ciclo coevolucionario de "carrera hacia las armas" en la señal de adaptación, exageración, y devaluación. Señales estables y confi-

ables se desarrollan cuando los costos de señal construyen la evolución de la decepción y la exageración. Las señales acústicas son específicamente costosas cuando se comparan con otros tipos de señales, y es muy posible que se desarrollen como señales confiables en situaciones de "competencia social". Los costos de señales acústicas incluyen el costo fisiológico de crecimiento y la producción de la señal, exploración por rivales con-específicos y miembros discriminantes del otro sexo, y ataques por enemigos naturales como predadores y parásitos.

COMMUNICATION ARMS RACES

Are the communication channels used by different animal species arbitrary? Or, does the variation among species in communication channels represent different adaptive solutions to varying ecological and social situations? To answer these questions, behavioral ecologists have recently begun to explore the mesh between communication channels and the environment (see discussion in Burk 1988). The approach has often been to take each type of signal in turn, and ask what its costs and benefits are, with the hope that knowing these will allow one to predict the kinds of environments in which it would be adaptive. For example, Alcock (1984) provides a table in which chemical, auditory, visual, and tactile channels are compared for ability to reach receivers, information available, and cost to sender. Acoustic (auditory) signals—my focus in this paper—are characterized as long range, with fast transmission rates, flowing around barriers, of use day or night, having fast fadeout time, being fairly easy to localize, having a medium risk of exploitation (visual signals considered to be of higher risk), and being of high broadcast expense (all other signals being characterized as of low or low-moderate expense).

Such assessments are of great value, but a slightly different perspective can greatly add to our understanding of the reasons for the frequent evolution of acoustic signalling in animals. This involves an appreciation of the dynamics of communication evolution. Communication necessarily involves two individuals, a signaller and a receiver, both subject to natural selection. Krebs & Dawkins (1984, see also Dawkins & Krebs 1978) have characterized these two parties as a "manipulator" and a "mind-reader", respectively. Manipulator-signallers are selected to produce signals that effectively elicit responses in receivers that are beneficial to the signaller. Mind-reader-receivers, on the other hand, are under selection only to respond in ways that are beneficial to themselves. Sometimes, the interests of signallers and receivers will lead to an "agreed" response. Under such circumstances, as in communication between close relatives or between mates involved in brood care, communication may evolve to be accurate & efficient. An excellent example is the waggle-dance foraging communication system of honeybees (Winston 1987). On the other hand, where the interests of the signaller and receiver do not necessarily coincide, as in intrasexual competition or intersexual mate choice situations, a complex co-evolutionary process is expected to be set in train. By analogy to human processes, Dawkins & Krebs (1979) called such dynamic coevolutionary events "arms races."

How will signalling systems evolve in such "social competition" arms races (West-Eberhard 1979)? A number of authors, for a number of contexts, have suggested that complex signal systems with multiple signals, each a rather weak predictor of subsequent behavior, will result (Barnard & Burk 1979: dominance hierarchies; Burk 1981: sexual signalling; Andersson 1980: threat signals generally). Andersson's (1980) paper, "Why are there so many threat displays?", presents the expected scenario clearly: In agonistic encounters, some incidental movement, such as baring the teeth, may be well correlated with likelihood of attack. Natural selection may favor a retreat response by opponents when such a movement occurs. However, once a response spreads, natural

selection favors "bluff" teeth-baring by individuals with lower likelihoods of attack. Now natural selection on responders will lower their likelihood of retreat; the original threat display, while not meaningless, has nevertheless become devalued. At this point, responders may be selected to use a second attack-associated movement as a cue along with teeth-baring. This second movement will then go through a similar cycle of ritualization and devaluation. The cycle may occur many times, leading to agonistic encounters consisting of a string of threat displays. A similar arms race scenario may occur in courtship: females look for indicators of male quality, these indicators become ritualized and elaborated, and ultimately females devalue them and evolve responses to additional indicator traits (West-Eberhard 1979, Burk 1981).

HONEST OR RELIABLE COMMUNICATION SYSTEMS

If such elaboration-devaluation arms races are common, why aren't agonistic or courtship encounters infinitely long? Does this simply reflect the possibility that we commonly see communication processes that are somewhere near the beginning of a coevolutionary spiral? Or is it rather due to the existence of some factor that can halt the arms race spiral and stabilize a communication system at a point where displays contain only slight elements of bluff and where there will be little selection for response devaluation? That the answer is likely to be the latter was suggested by Zahavi in an important paper in 1977 (Zahavi 1977). Zahavi argued that stable "honest" or "reliable" communication systems will evolve when responders only consider "... signals that are not easily open to cheating . . . a signal is reliable when the difficulty of its performance is related to its meaning . . ." Zahavi argued that "... cost is a necessary component of the signal; the more significant the signal, the higher the cost to the performer . . . characters important in determining quality should be affected adversely by the signal" (Zahavi 1977).

To state Zahavi's thesis more explicitly, some signals are costlier to produce than others. Only vigorous, healthy signallers will be able to develop the signal producing mechanisms these require, and/or to withstand the physiological burden of their production. When, in the course of communication coevolution such a signal is "chosen" by natural selection on responders, exaggeration and bluffing are constrained. Little devaluation of response evolves either; the communication system is stabilized when costly, and therefore "reliable", signals have evolved (see discussion in Wiley 1983).

TABLE 1. METABOLISM INCREASES IN CALLING ANIMALS.

Animal	Increase in Metabolism Over Resting Rate	Reference
<i>Euconocephalus nasutus</i> katydids	14.2X	Stephens & Josephson 1977
<i>Neoconocephalus robustus</i> katydids	15.3X	Stephens & Josephson 1977
<i>Teleogryllus commodus</i> crickets	3.9X	Kavanagh 1987
<i>Anurogryllus arboreus</i> crickets	10.0-15.8X	Prestwich & Walker 1981
<i>Oecanthus celerinictus</i> tree crickets	6.2-12.0X	Prestwich & Walker 1981
<i>O. quadripunctatus</i> tree crickets	6.5-8.0X	Prestwich & Walker 1981
<i>Gryllotalpa australis</i> mole crickets	13.4X	Kavanagh 1987
<i>Cystosoma saundersii</i> cicadas	18.4X	MacNally & Young 1981
<i>Physalaemus pustulosus</i> frogs	2.1-4.3X	Ryan 1985
<i>Hyla versicolor</i> tree frogs	5-22X (\bar{X} = 12.4X)	Taigen & Wells 1985
<i>H. crucifer</i> tree frogs	14.0X	Taigen et al. 1985

The thesis of this paper is that acoustic signals are particularly likely to be the stable end points of communication coevolutionary events. Paradoxically, acoustic signals will commonly act as honest or reliable cues because they are especially costly to produce, compared to other types of signals. I will argue that three types of costs maintain the reliability and thus stability of acoustic communication systems: (1) Acoustic signals are physiologically very expensive to produce; (2) Acoustic signals, because they are conspicuous, elicit probes of the signaller's vigor by conspecific social competitors (bluffs may be called!); (3) Acoustic signals, because they are conspicuous, attract natural enemies such as predators, parasitoids, and parasites.

In the remainder of this paper, I attempt to document the costliness of acoustic signals and the way in which they become reliable cues. To properly test my hypothesis, it would be preferable to compare the costs of acoustic signals with those of other signals, such as visual or pheromonal ones. However, a cursory glance at the literature suggests that few attempts to quantify the costs of signals other than acoustic ones have been made. I will therefore review only the information available on acoustic signals, in the hope that this may stimulate others to collect comparative data for other signals.

THE COSTS OF ACOUSTIC SIGNALS

PHYSIOLOGICAL COSTS

Some male frogs and insects are so highly motivated to produce acoustic signals that they will do so normally even when enclosed in a respirometer (Kavanagh 1987). Using this device, one can measure metabolic rates of calling animals and can compare them with metabolic rates at rest or when performing other behaviors such as walking or eating. A range of values from the literature is given in Table 1. On average, there is an increase in metabolism by calling animals of about an order of magnitude. Acoustic calling is usually one of the most energetically expensive things an animal does: the mass-specific rate of oxygen consumption by calling *Hyla versicolor* frogs is the highest measured for any ectothermic vertebrate (Given 1988), while only the demands of flight exceed those of calling in some insects (Prestwich & Walker 1981).

Knowing the energy cost of sound production, and measuring the sound energy levels in the acoustic field around a signaller, allows one to calculate the energetic efficiency of sound production. Values from the literature are given in Table 2. They are all very low, in no case more than a few percent. Earlier higher estimates, such as those of Bennet-Clark (1971) for mole crickets (35%) and Counter (1977) for katydids (26%), have been re-evaluated recently and lowered by an order of magnitude

TABLE 2. ENERGETIC EFFICIENCY OF ACOUSTIC SIGNALLING.

Animal	% Efficiency	Reference
<i>Cystosoma saundersii</i> cicadas	0.82	MacNally & Young 1981
<i>Neoconocephalus robustus</i> katydids	2.1	MacNally & Young 1981
<i>Gryllotalpa viniae</i> mole crickets	3.41	Kavanagh 1987
<i>G. gryllotalpa</i> mole crickets	0.5	Kavanagh 1987
<i>G. australis</i> mole crickets	1.05	Kavanagh 1987
<i>Teleogryllus commodus</i> crickets	0.05	Kavanagh 1987
<i>Anurogryllus arboreus</i> crickets	0.23	Kavanagh 1987
<i>Physalaemus pustulosus</i> frogs	0.05-1.2	Ryan 1985
<i>Gallus domesticus</i> cockerels	2.0	Brackenbury 1980

(Kavanagh 1987, MacNally & Young 1981). It is interesting that the one value for a bird is in the same range as those of anurans and insects.

In the absence of information on the metabolic cost and efficiency of other signal types, it is impossible to draw firm conclusions. It seems likely, however, that acoustic signals will turn out to be highest in cost and lowest in efficiency, because of their transitory nature (requiring their repetition), omnidirectionality, and the extensive muscle movements involved in their production—often a production mechanism involving substantial frictional forces.

SOCIAL COMPETITION COSTS

The above information, while striking, fails to give an adequate impression of signaling costs. The presence of “social competitors” (West-Eberhard 1979) such as rival males or discriminating females imposes certain physical signal forms and high signal rates on acoustic callers, so that total costs of signalling are multiplied, as the following discussion will show.

Sexually advertising males, for example, often call at high rates for hours a day, and for weeks or months during prolonged breeding seasons. Rates of acoustic display by a variety of animals are taken from the literature and presented in Table 3. In a variety of species, mate-choosing females have been shown to respond disproportionately often to males who call at the highest rates or for the longest durations (fruit flies: Sivinski et al. 1984; crickets: Hedrick 1986; frogs: Halliday 1987; sage grouse: Gibson & Bradbury 1986; red deer: McComb 1987). In many species, males greatly increase their calling rates when females are present (Sivinski & Webb 1986, Taigen & Wells 1985), or switch to a more energetically demanding call type (Ryan 1985).

The physical form of acoustic signal favored by choosing females is often demanding of male vigor. Females prefer loud calls (Forrest 1980, Halliday 1987), and measured intensity levels of male calls are often astounding. *Hyla versicolor* frog calls averaged 109 dB at 50 cm from the caller (Wells & Taigen 1986), *Scapteriscus acletus* mole cricket calls 91 dB at 15 cm (Forrest 1980), *Neoconocephalus robustus* katydid calls 116 dB at 1 cm (Counter 1977), and *Cystosoma saundersii* cicada calls 91 dB at 20 cm (MacNally & Young 1981). Females also prefer individual calls of long duration (Halliday 1987), calls with additional notes (Ryan 1985) and—very commonly—calls of low frequency that can be produced only by the largest males (Halliday 1987, Morton 1977, Webb et al. 1984, Latimer & Sippel 1987). [Anuran calls are longer in duration and lower in frequency at lower temperatures; it is possible that a small frog or toad could fake larger

TABLE 3. SOME EXAMPLES OF ACOUSTIC DISPLAY RATES.

Animal	Display Rate	Reference
<i>Neoconocephalus robustus</i> katydids	Wing closures during stridulation (25°C): 673,000/hr.	Stephens & Josephson 1977
<i>Cystosoma saundersii</i> cicadas	tymbal muscle “twitch” rate (21.5°C): 72,000/30 min. calling period	MacNally & Young 1981
<i>Hyla crucifer</i> tree frogs	call rate (16°C): 4500/hr.	Taigen et al. 1985
<i>Centrocercus urophasianus</i> sage grouse	“strut” vocalizations: 720-1080/2-3 hour display period	Krebs & Harvey 1988
<i>Cervus elephus</i> red deer	roaring rate during rut (31 days): 2.7/min.	Clutton-Brock et al. 1982

size by calling from colder sites in the water at a pond's edge. In Fowler's toad (*Bufo woodhousei fowleri*), Fairchild (1981) has shown that such cheating is prevented by male-male competition: large males occupy these pond-edge sites & displace small males onto the warmer pond bank. Thus males that already have long duration, low frequency calls exaggerate these traits even more. "To those that have shall be given . . ."] Comparative studies support the hypothesis that female choice leads to the evolution of especially low-pitched calls: female *Physalaemus pustulosus* frogs and *Tettigonia cantans* katydids have been shown to mate preferentially with males producing low-frequency calls, and each species has a much lower calling song fundamental frequency than would be expected for a species of that size in that taxonomic group (Ryan 1985, Latimer & Schatral 1986).

The costs of such strenuous & extended signalling can be seen in the weight loss experienced by breeding males. Some frogs lose over 1% per day (Halliday 1987), some orthopterans 2-3% in 1-2 h (Dodson et al. 1983), and red deer stags 20% in a month (Clutton-Brock et al. 1982). The males that were in the best physical condition at the beginning of the sexual display season may be able to sustain costly signalling in the face of such losses longer than less vigorous males. In a number of frogs, the best correlate of mating success is length of time spent at a mating site (Halliday 1987); this is probably true for many other animals with extended sexual advertisement seasons.

Effects of costly signalling extend beyond the immediate breeding season. With males putting as much as 86% of their energy assimilation into calling (*Ranidella* frogs: MacNally 1981), it is not surprising that there is often a negative relationship between reproductive activity and growth (frogs: Given 1988) or survival (ungulates: Clutton-Brock et al. 1982). Just to develop the sound producing structures may impose considerable costs on signallers, with effects on overall growth and mortality rates. In frogs, the trunk muscles used in vocalizations amount to as much as 15% of a male's body mass, compared to 3% of a female's (Taigen et al. 1985).

Production of conspicuous acoustic signals attracts another class of "social competitors", rival males. The songs that are favored by females have also been shown to attract rival males in animals as diverse as crickets (Cade 1979, Burk 1983), frogs (Given 1987), and cowbirds (West et al. 1981). The aggressive encounters that subsequently occur are frequently settled on the basis of qualities of acoustic signals that are unbluffable, such as low frequency—correlated with size (frogs & toads: Arak 1983, Given 1987; katydids: Latimer & Sippel 1987; birds & mammals: Morton 1977)—or high acoustic display rate—correlated with physical condition (red deer: Clutton-Brock et al. 1982). Small, subordinate, or out-of-condition males may not be able to bear the costs of such aggressive challenges and may opt for non-calling alternative strategies (Cade 1980), leaving acoustic signals as relatively reliable indications of the vigor, large size, or dominance of their producers (Burk 1983).

PREDATION COSTS

As we have seen, an acoustically-signalling animal may be heard by individuals other than its intended targets: a calling male attracts rivals as well as potential mates. Perhaps even more costly to signallers is another class of "eavesdroppers" (Alcock 1984): predators, parasitoids, and parasites may orient acoustically to calling hosts. The first demonstration of such acoustic orientation by natural enemies was by Walker (1964); the number of examples has steadily increased, as seen in Table 4. Mortality rates of callers from such eavesdroppers can be very high: 1% or more per hour calling in *Physalaemus pustulosus* frogs (Ryan 1985), over 90% per season for crickets & katydids (Cade 1979, Burk 1982). Noteworthy is the fact that the calls which are most attractive to females, such as loud, complex calls, are also typically more attractive to

TABLE 4. ACOUSTICALLY-ORIENTING NATURAL ENEMIES.

Prey	Predator/Parasite	Reference
Crickets	Cat	Walker 1964
Crickets	Ormiine Tachinid Flies	Cade 1975
Crickets	Hérons	Bell 1979
Crickets	Geckos	Sakaluk & Belwood 1984
Cicadas	Sarcophagid Flies	Soper et al. 1976
Katydids	Bats	Tuttle et al. 1985
Katydids	Ormine Tachinid Flies	Burk 1982
Frogs	Mosquitos	McKeever 1977
Frogs	Bats	Ryan 1985

natural enemies (Ryan 1985). The costs of conspicuous calling may be bearable for vigorous males that may be more able to escape predators or to compete successfully within the large choruses that evolve as anti-predation defenses (Ryan 1985), but these costs may lead to a loss of calling by less vigorous or less dominant individuals. Again, the cost of acoustic signalling tends to restrict the subset of individuals that sings, keeping the communication system more "honest" for conspecific responders.

RELEVANCE FOR AGRO-ACOUSTICS

Without making exaggerated claims, it seems to me that the view of the importance of acoustic signals presented above is relevant to applied entomologists for three reasons. First, and most generally, in order to design the most appropriate integrated pest management programs, one needs to know as much as possible about the ecology and behavior of the target species. Since development rates, relative development of different parts of the body, extent and type of sexual dimorphism, dispersion and dispersal characteristics, and many other features of a species' biology may be shaped by sexual selection involving acoustic display, one certainly needs to appreciate the importance of such signals. Second, for pest species producing conspicuous acoustic signals, the strong possibility exists that there are acoustically-orienting natural enemies. A systematic search for such species, especially dipteran parasites of pest orthopterans, would be justified (see Walker, this symposium, for one example). Third, I have argued that acoustic signalling is one of the most demanding activities animals engage in, one that only possessors of vigorous phenotypes can sustain for long. If so, then acoustic signals should be one of the first traits to change as laboratory populations undergo domestication. In mass rearing programs, as in applications of the sterile insect technique, quality control managers could use decrease in call rate or degradation of acoustic signal form as a "canary-in-a-coal-mine" early indicator of quality declines.

CONCLUSION

To understand the evolution of animal communication systems, one has to adopt a dynamic, coevolutionary perspective. Signals will evolve that reflect not only a fit to the physical environment, but also to the social situation involved. Stable communication systems, ones buffered against arms-race cycles of exaggeration and devaluation, will be ones in which signals remain reliable or honest because of their high costs to signalers. Because acoustic signals are particularly costly, they may frequently act as such reliable cues. As with other coevolutionary processes, the resultant communication systems may not be "optimal", but they will be "evolutionarily stable" (Dawkins 1980).

Note added in proof: Similar ideas about the evolution of acoustic signals have recently appeared in an article by M. J. Ryan (American Zool. 28: 885-898).

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TEMPORAL AND SEASONAL DIFFERENCES IN MOVEMENT OF THE CARIBBEAN FRUIT FLY LARVAE IN GRAPEFRUIT AND THE RELATIONSHIP TO DETECTION BY ACOUSTICS

C. O. CALKINS AND J. C. WEBB

Insect Attractants, Behavior, and Basic Biology Research Laboratory
Agriculture Research Service, U. S Department of Agriculture
Gainesville, Florida 32604

ABSTRACT

Larvae of the Caribbean fruit fly *Anastrepha suspensa* (Loew) can be detected by the sounds they make while feeding using an acoustical detection system. Efforts to improve and determine the efficiency of the system led to detailed studies of the feeding behavior of larvae in grapefruit. Movement, feeding and growth are related to the maturity of the fruit. As the fruit matured, it became more sweet and larvae fed more consistently and voraciously, moved into the pulp portion earlier, and developed more rapidly. Larvae were detected within hours after they hatched from eggs, when they are often too small to be seen in the fruit with the unaided eye. The efficiency of the system in detecting infested fruit has been demonstrated to be more efficient than the accepted method of cutting and visual examination.

RESUMEN

Larvas de la mosca de frutas del Caribe, *Anastrepha suspensa* (Loew), se pueden detectar por el sonido que hacen cuando comen usando un sistema de detección acústica.

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TEMPORAL AND SEASONAL DIFFERENCES IN MOVEMENT OF THE CARIBBEAN FRUIT FLY LARVAE IN GRAPEFRUIT AND THE RELATIONSHIP TO DETECTION BY ACOUSTICS

C. O. CALKINS AND J. C. WEBB

Insect Attractants, Behavior, and Basic Biology Research Laboratory
Agriculture Research Service, U. S Department of Agriculture
Gainesville, Florida 32604

ABSTRACT

Larvae of the Caribbean fruit fly *Anastrepha suspensa* (Loew) can be detected by the sounds they make while feeding using an acoustical detection system. Efforts to improve and determine the efficiency of the system led to detailed studies of the feeding behavior of larvae in grapefruit. Movement, feeding and growth are related to the maturity of the fruit. As the fruit matured, it became more sweet and larvae fed more consistently and voraciously, moved into the pulp portion earlier, and developed more rapidly. Larvae were detected within hours after they hatched from eggs, when they are often too small to be seen in the fruit with the unaided eye. The efficiency of the system in detecting infested fruit has been demonstrated to be more efficient than the accepted method of cutting and visual examination.

RESUMEN

Larvas de la mosca de frutas del Caribe, *Anastrepha suspensa* (Loew), se pueden detectar por el sonido que hacen cuando comen usando un sistema de detección acústica.

Esfuerzos para mejorar y determinar la eficiencia del sistema nos dirigió hacia estudios detallados del comportamiento de las larvas cuando comen toronjas. El movimiento, alimentación y crecimiento están relacionados con la madurez de la fruta. A medida que la fruta madura, se pone más dulce, y las larvas se alimentaron más consistente y vorazmente, se movieron hacia las porciones de pulpa más temprano, y se desarrollaron más rápidamente. Las larvas se detectaron a pocas horas de salir de los huevos cuando a menudo todavía eran muy pequeñas para verse a simple vista en la fruta. Se ha demostrado la eficiencia del sistema en detectar frutas infestadas y es más eficiente que el aceptado método de cortar y examinar visualmente.

The Caribbean fruit fly, *Anastrepha suspensa* (Loew) (caribfly), has inhabited Florida since 1966. Although most of its hosts are wild and dooryard fruits, it does occasionally infest citrus, particularly grapefruit and oranges (Swanson & Baranowski 1972). Although it has never been found to cause extensive damage in citrus groves, the threat of the presence of its larvae in citrus fruit being shipped to other tropical and subtropical areas has caused it to become subject to quarantine regulations. Florida citrus is now quarantined by Arizona, California, Hawaii, Texas and Japan.

Prior to 1983, fumigation by ethylene dibromide (EDB) successfully controlled eggs and larvae in fruit. However, after the withdrawal of this compound, citrus exporters were only able to use methyl bromide, cold treatment and shipment of fruit from fly-free areas as means of overcoming the quarantine restrictions. In all cases, because these methods are more complicated and less effective than EDB, a large sample of fruit must be examined by cutting to determine the presence or absence of caribfly larvae.

When it was discovered that sounds of feeding by larvae of the caribfly could be detected by use of an accelerometer (Webb & Landolt 1984), a new technology for the detection of fruit fly infested fruit was developed. Subsequent improvements in the system eliminated the accelerometer and the frequency of the feeding sounds produced were altered at the detector due to the physics of the system (Webb et al. 1988). To improve on the efficiency of the system and to help explain the variability in the sounds detected, it was necessary to determine the feeding behavior of the larvae in the target fruit. It also became necessary to determine patterns of movement in relation to age of larvae producing the audible signal and the maturity of the fruit so that standard comparisons could be made between different equipment modifications.

MATERIALS AND METHODS

Grapefruit in Central Florida blooms in March. The fruit picking starts in late October and extends to May of the following year. Grapefruit (var. Marsh White) used in this study were picked every four weeks from November, 1984 to April, 1985 from a grove maintained on Merritt Island, Florida. The fruits were transported to the Insect Attractants, Behavior and Basic Biology Research Laboratory in Gainesville where they were washed and infested with eggs from gravid female caribflies. Fruits were placed into cages containing large numbers of sexually mature flies and the females were observed for probing and oviposition activity. The fruits were exposed to the flies for 6 hours, then were removed from the cage and placed on trays and incubated for 3 days at 25 C. From each collection, 45 to 60 fruits were infested, 15 on each of 3 days.

After 3 days, the fruits were placed individually on the sound detector (Webb et al. 1988) to see if eggs had hatched and the larvae had begun feeding. Under ideal conditions in the laboratory at 25° C., eggs hatch in 3 days. If feeding sounds were detected, the date of detection was written on the fruit and the fruit was returned to the incubation tray. If no sound was heard, the fruits were examined acoustically each day thereafter until larval sounds were apparent.

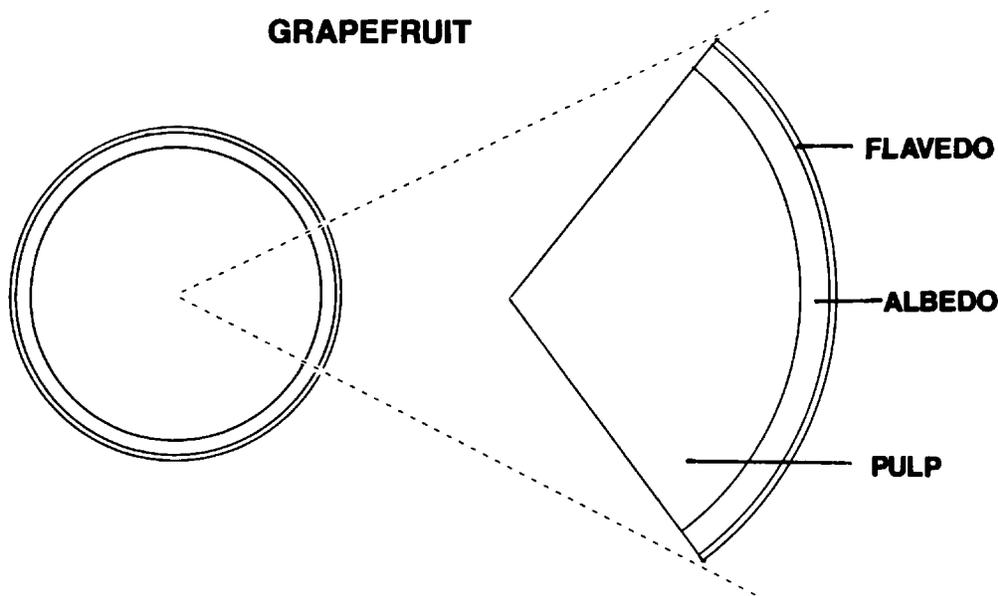


Fig. 1. The three major regions of a citrus fruit. Flavedo is the colored outside layer containing the oil glands. The albedo is the white fibrous inner layer. The pulp is the edible portion from which the juice is extracted.

The three main layers of fruit are illustrated in Figure 1. The flavedo is the yellow portion of the grapefruit peel. It contains most of the oils in the peel. The albedo is the white layer between the flavedo and the pulp and is made up mostly of pectin, but several chemicals including narangin and limonin also occur there (Greany et al. 1983, Kefford & Chandler 1970). The pulp is the yellow edible center portion of the fruit. Each of these portions of the fruit were dissected to locate larvae.

Three fruits were dissected to locate larvae at 2-day intervals after the first larval sounds were heard during the months of November through February. During March, dissections were made daily for 5 days because larval development and movement were so rapid. During dissections, the fruits were first cut in half and then into quarters. Then a cut was made to separate the albedo from the pulp. After each cut, the fruit portion was examined carefully with a 2X magnifier/lamp or with a 10X dissecting microscope for feeding trails or larvae. The flavedo and the albedo were carefully teased apart with forceps and probes. Neonate larvae are very small and identical in color to the albedo layer in grapefruit which makes them difficult to see. As they become larger, they and their feeding trails were more easily found. An example of a feeding trail is shown in Figure 2.

Data were recorded on a diagram of the fruit indicating where each larva was located. The distance that the larva moved from the outer perimeter of the fruit was measured with a direct line from the outer edge to the center. No attempt was made to determine lateral distances the larvae may have moved while feeding because of the great variations found and the difficulty in following the complete feeding route.

RESULTS

The average location of larvae and the number of days after acoustic detection for each month are shown in Figures 3 and 4 for each month from November through March. The lines on either side of the dot is the range of depths that larvae had pene-

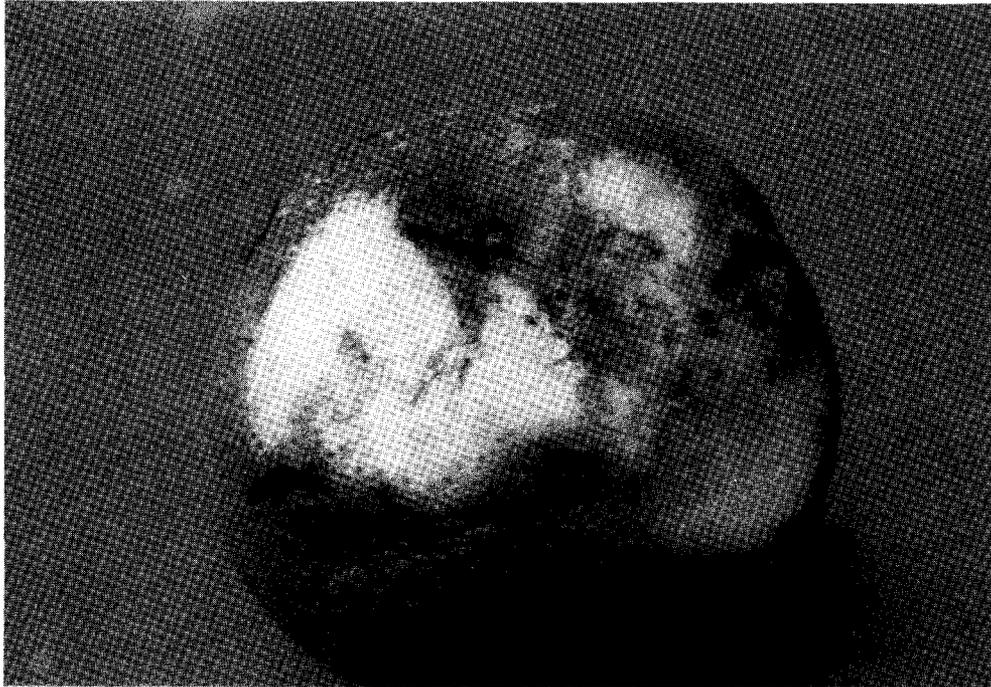


Fig. 2. An example of a feeding trail in the albedo of a grapefruit made by a Caribbean fruit fly larva.

trated by that day. Because growth and movement of larvae in November and December were slow, the figure only indicated locations at 4-day intervals.

Fruits picked in November were just beginning to turn yellow. The peel was still firm to the touch. In all cases when eggs were discovered, always in the flavedo, they were found to be laid singly rather than in aggregates. During the first 4 days after larval chewing was detected, the larvae were only found in the flavedo. By day 8, larvae were found in the albedo and in the outer regions of the pulp. On day 12, most of the larvae found were in the pulp with a few still in the albedo. On day 14, one mature larva left the fruit to pupate. By day 16, all of the larvae found were in the pulp. This was the last observation made because all of the infested fruit from the November picking date had been cut for examination. The number of larvae found on the days of examination ranged from 11 to 33, more larvae were found in the later examination periods as might be expected because they were larger in size and easier to see.

In December, larvae were recorded only in the flavedo on day zero. On day 4, they were found in both the flavedo and the albedo. On day 8, they were found in all 3 regions and by day 12 and 16 were found exclusively in the pulp (Figure 3). The first larva emerged from the fruit on day 13.

From January through March, fruits were collected every 2 weeks so that 60 fruits could be infested each week. They were examined every two days after larval sounds were detected. Five fruits per day were cut and examined. During the first 2 days after egg hatch, larvae were found exclusively in the flavedo. On day 4, most of the larvae were found in the albedo with a few still in the flavedo and 2 larvae were found at the border between the pulp and the albedo. By day 6, although most of the larvae were still in the albedo a few larvae had penetrated the pulp, one as deep as 26 mm. On day 8, most of the larvae were found in the pulp with a few still found at the border between the pulp and the albedo. The number of larvae found per fruit ranged from 14 to 44.

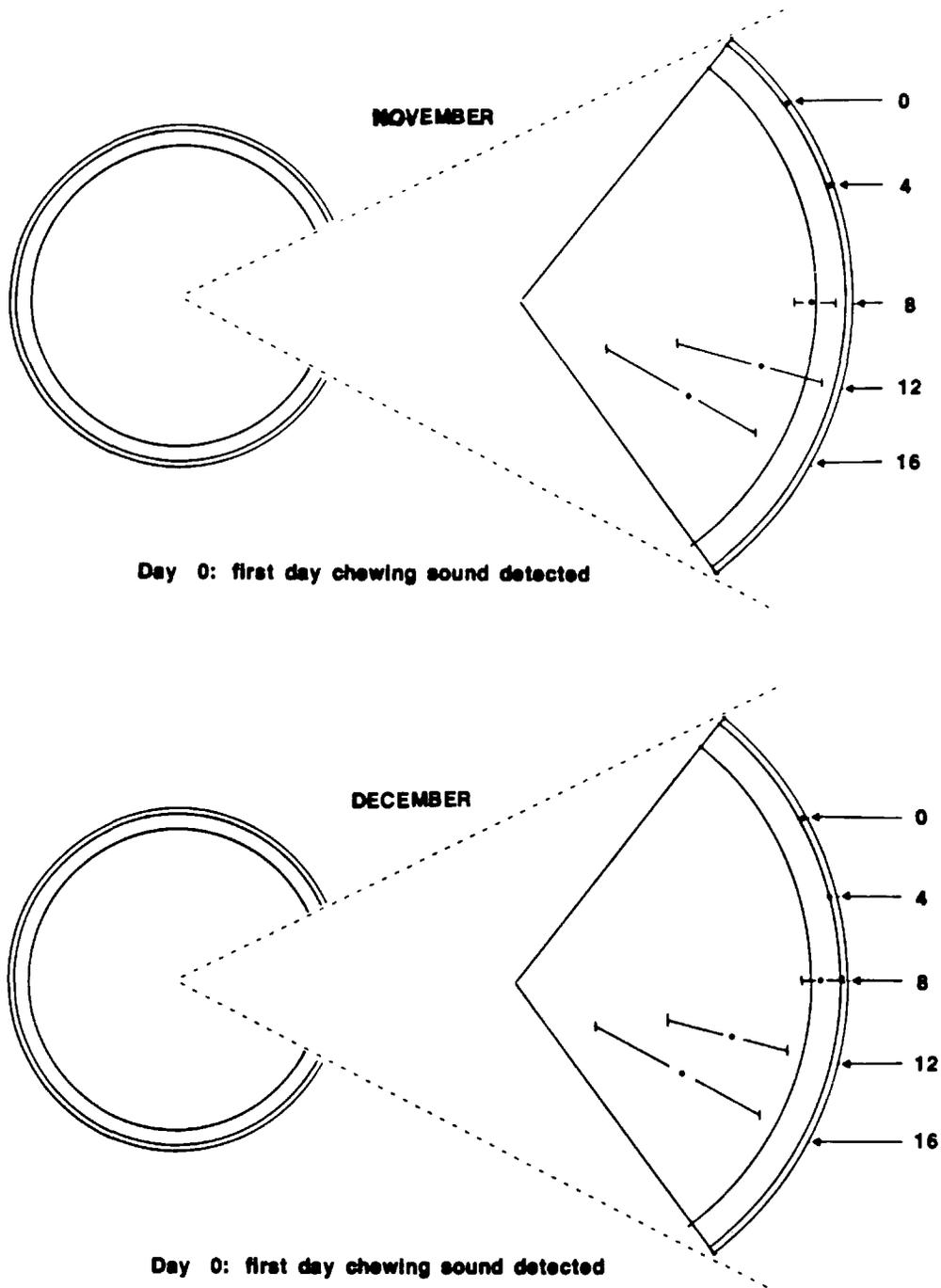


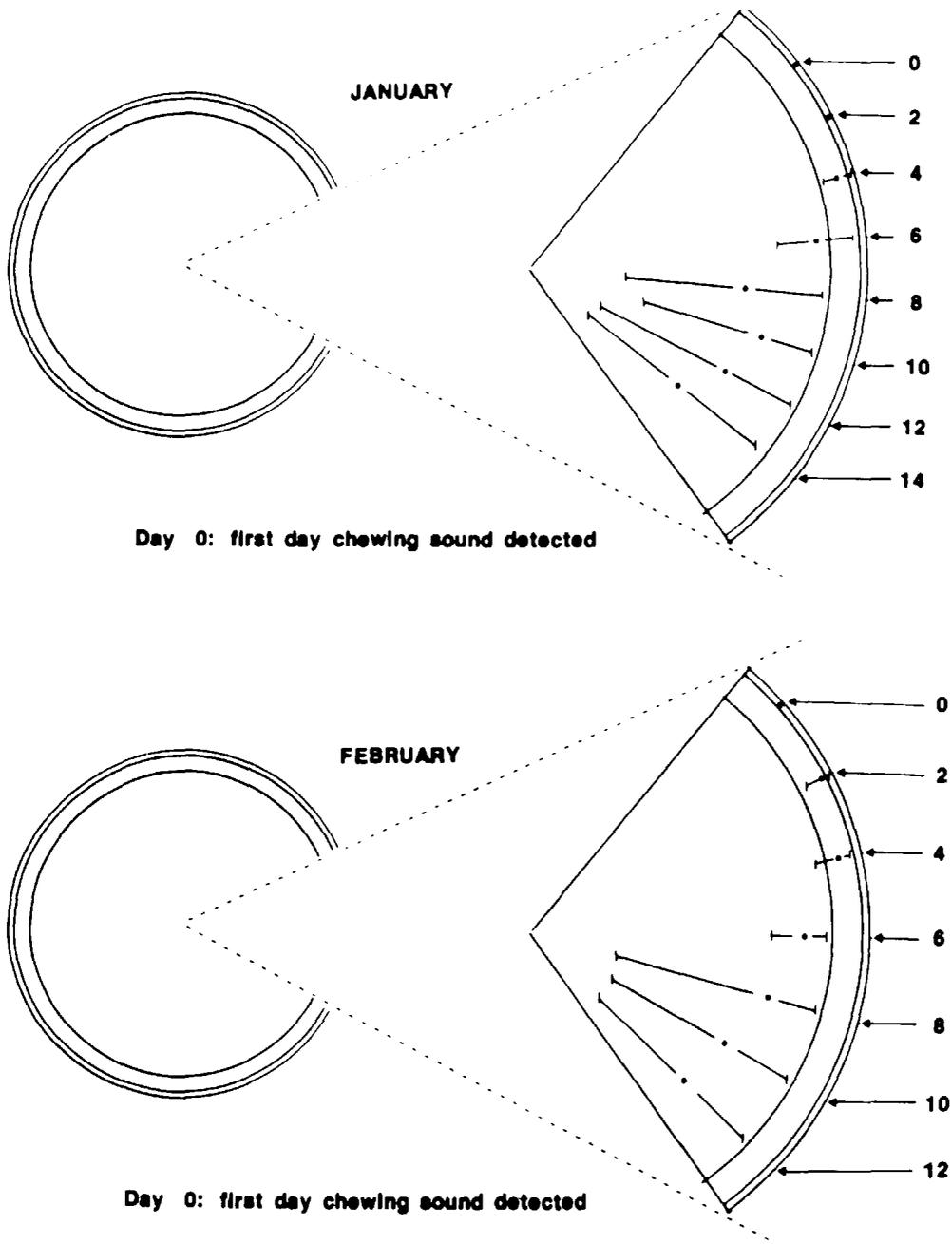
Fig. 3. The mean location of Caribbean fruit fly larvae in grapefruit picked during November and December at specified days after larval eclosion.

From day 10 on, almost all of the larvae were found in the pulp (Figure 4). The first larvae to emerge during the first week's infestation was on day 13. Later in the month, the first emergence of mature larvae occurred on days 12, 10 & 10 for the next 3 weeks, respectively. The number of larvae found ranged from 13 to 55/fruit.

In February, larvae were already found in the albedo on day 2 and one larvae was found in the pulp at the interface between the pulp and the albedo. By day 4, a few

larvae were moving into the pulp, one as deep as 5 mm while most were at the interface. By day 6, most of the larvae were in the pulp as deep as 26 mm (Figure 4). Most of the larvae had completed development and had exited the fruit before the 14th day. Unfortunately, the date of first emergence was not recorded.

During March, fruits were examined every day for 5 days. On day zero, the first day larval sounds were detected, all of the newly hatched larvae were still in the flavedo. On day 1, several had already migrated into the albedo. By day 2, most were found in the albedo. By day 3, although most were in the albedo, a few had already entered the pulp as deep as 2 mm. On days 4 and 5, the larvae were found both in the albedo and the pulp. The first larva began exiting the fruit on day 6 (Figure 4). Feeding



and growth were very rapid in fruit picked in March. The number of larvae found ranged from 16 to 81/fruit. The feeding passages were difficult to follow because there was such a large number of larvae in each fruit and the feeding was so extensive. The fruit also became infested with fungi and mold and broke down very quickly, partly as a consequence of the extensive larval feeding.

DISCUSSION

Results of this study indicate that the maturity of the fruit has a great influence on the development rate and movement of larvae within the fruit. The rate of egg hatch in November took from 6 to 12 days to hatch. In February, the egg hatch occurred within 4.6 days. An interesting side observation of this study was that about 50% of the eggs were found in the oil glands and about 50% between the oil glands in fruit from all picking dates. Greany et al. (1983) observed a high mortality of eggs and newly-hatched larvae that were inside of oil glands. The increase in development rate and movement of larvae into the pulp occurred earlier in consecutive months from November through March. The greatest increase occurred in March when complete larval development occurred as early as 5 days after egg hatch. During this month the fruit has reached a stage of maturity when grapefruit is truly susceptible to attack from the Caribfly. Feeding sounds of larvae are most easily detected by acoustical techniques when fruit is most mature because larvae feed almost continually at this stage (Webb, unpublished data). There are also several changes in the chemistry of the peel with maturity and, these appear to affect feeding and development rates early in the season. (Shaw & Calkins, unpublished).

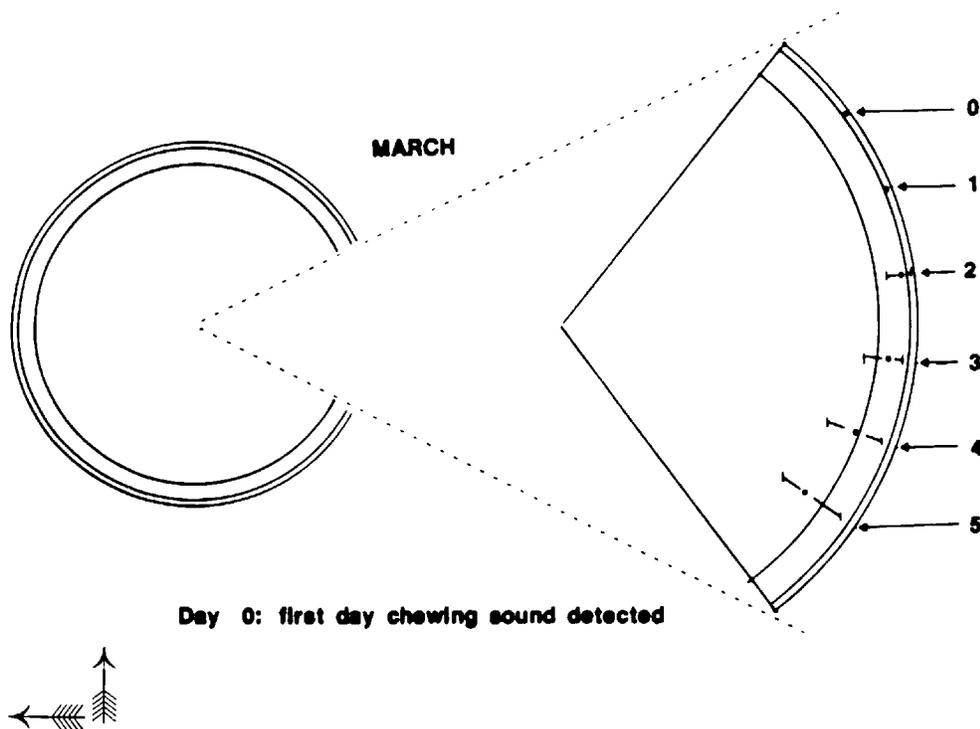


Fig. 4. The mean location of Caribbean fruit fly larvae in grapefruit picked during January, February and March at specified days after larval eclosion.

ACKNOWLEDGEMENTS

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USING INSECT SOUNDS TO ESTIMATE AND MONITOR THEIR POPULATIONS

T. G. FORREST

National Center for Physical Acoustics

P.O. Box 847

University, MS 38677

ABSTRACT

Accurate estimates of population size are needed to understand the population dynamics of any species. They are also needed to determine when to implement a specific control tactic, and to measure whether that control tactic has been effective. This paper discusses the use of acoustic signals produced by insects and the feasibility of using these signals to census populations.

Insect sounds are either incidental (produced as a by-product of some activity) or non-incidental (produced to cause a response in some other animal). Incidental sounds differ from non-incidental sounds with respect to several features that are important to using sound to census populations. These features include species specificity, frequency content, ease of localization, distance traveled, and the duration and timing of sound production.

Studies of crickets show that information about which individuals in a population are producing sound, when the individuals produce sound (seasonally and daily), and the probability that individuals produce sound during census periods must be known to accurately estimate the size of a population.

RESUMEN

Se necesitan estimados precisos del tamaño de la población para entender el dinamismo de la población de cualquier especie. También se necesitan para determinar



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RESUMEN

Se necesitan estimados precisos del tamaño de la población para entender el dinamismo de la población de cualquier especie. También se necesitan para determinar

cuándo es necesario implementar una táctica específica de control, y para medir la efectividad de dicha táctica. Se discute el uso de señales acústicas producidas por insectos y la posibilidad de usarlas en censos de poblaciones.

Los sonidos producidos por insectos son incidentales (producidos como producto secundario de otra actividad) o no incidentales (producidos para inducir una respuesta en otro animal). Los sonidos incidentales difieren de los no incidentales con respecto a algunas características que son importantes en el uso del sonido en el censo de poblaciones. Estas características incluyen especificidad de las especies, el contenido de la frecuencia, la facilidad en localizarla, distancia cubierta, y la duración y lo oportuno del sonido producido.

Estudios hechos con grillos muestran que se debe tener información sobre aquellos individuos que producen sonidos en la población, cuándo producen los sonidos (diariamente y estacionalmente), y la probabilidad que los individuos produzcan sonidos durante el censo para poder estimar con exactitud el tamaño de la población.

An often asked question of animal populations is 'Do individuals occur in a certain area?'. While knowing if they occur at a locality is necessary to study them, an even more important question is 'How many animals are there?' or 'What is the number of individuals in a certain area?'. One of the most important properties of any population is its size. Population size or density is information that is needed to understand the dynamics of a population, and it has import in all areas concerned with ecological modeling of populations.

Knowing the dynamics of pest populations is crucial in determining effective control tactics, when to initiate the tactics, and if the tactics, once implemented, are successful. Knowing how a population changes through time must be considered paramount in the management of a pest, and therefore, accurate and precise estimates of pest population density are needed.

For more than 20 years researchers have used sounds produced by insects to detect their presence (Adams et al. 1953, Wojcik 1968; see also Webb, Calkins, Wolfenbarger et al., Toba, Vick et al. this symposium). In contrast, few attempts have been made to use insect generated sound to estimate population size and density.

This paper will discuss the use of sounds produced by insects as a means of estimating their population size and in monitoring the population size over time.

CATEGORIES

In this paper the term "sound" is used in a broad sense: a vibration in some medium. By using this definition, all insects produce sounds during all stages of their lives. These sounds can be classified into two broad categories (Table 1). The first category contains sounds that are by-products of some activity of the animal. They are termed *incidental* sounds. In the second category are sounds that function to produce a particular response in another animal. These *non-incidental* sounds are termed *communication*. In most instances communication occurs between members of the same species, but interspecific communication also occurs, for instance in warning and anti-predator signals. Communication, as it is used here, includes deceptive or false signals (see Burk this symposium). An insect's activity can be monitored by listening for either incidental or non-incidental sounds, and therefore the sounds may be used to census insect populations.

Examples of the two categories of sounds produced by insects are shown in Table 1. The two categories differ in one fundamental aspect. Whereas, sounds used in communication are produced to be heard by another animal, incidental sounds are not.

TABLE 1. EXAMPLES OF SOUND GENERATED BY INSECTS AS BY-PRODUCTS OF SOME ACTIVITY (INCIDENTAL) OR DURING COMMUNICATION (NON-INCIDENTAL).

INCIDENTAL	COMMUNICATION
walking	mating signals
flying (adults)	courtship signals
chewing	territorial displays
swimming	social & subsocial signals
breathing	anti-predator signals
heartbeats	warning signals

CATEGORY DIFFERENCES

Whenever an insect produces sound, that sound is a potential cue that predators and parasites might use in locating prey or hosts (Burk 1982 and refs.). Selection will favor the production of sounds that avoid the attention of predators and parasites. Because communication signals and incidental sounds differ in the function for which they are produced, it might be expected that differences in certain characteristics will be reflected between the categories. Understanding these differences will be important if we are to use insect sounds to monitor and census individuals within a population (Table 2).

Species Specificity: One of the major differences to be expected between the two categories is whether the sound is specific to a particular species. Sounds produced as by-products of certain activities should not be as species specific as those used in communication, especially when the communication mediates sexual pair formation. Specificity is important in whether sounds are suitable to monitor a particular species. When more than one species in an area produce the same or similar sounds it will be difficult to estimate population size for the species of interest. Likewise, it will be difficult to accurately estimate a population size if different members of same population produce different sounds.

Frequency Content: Generally incidental sounds have a broader frequency range than sounds used in communication, and a spectral 'signature' of the sound produced by an insect may be important in its detection and identification. However, the spectrum (relative power at different frequencies) of a sound changes with distance from the source, and is influenced by the particular habitat over which the sound propagates (Marten & Marler 1977, Wiley & Richards 1978). Thus, sounds with a narrow frequency range (non-incidental or communication signals) will be more convenient to use to locate and count individuals in a population.

TABLE 2. GENERALIZED COMPARISON OF CHARACTERISTICS BETWEEN INCIDENTAL SOUNDS AND THOSE PRODUCED DURING COMMUNICATION.

	INCIDENTAL	COMMUNICATION
Species Specificity	low	high
Frequency Range	broad	narrow
Localization	difficult	easy
Distance Traveled	short	long
Duration	short	long
Timing	unpredictable	predictable

Ease of Localization, Distance Traveled and Duration Produced: Because sound may attract the attention of predators and parasites, selection should favor incidental sounds that are not easy to localize, do not travel far, and are produced for short durations and/or at unpredictable times. While sounds used in communication can also be used by predators and parasites, they have evolved to be heard by another animal. Therefore they should be easily localized and produced at a level and for a duration that will allow the intended receiver to detect and locate the sender from some distance. Being able to localize a sound source from a distance is an important consideration when using sound produced by insects to census their populations.

Device Design: The ease and success with which sound can be used in monitoring and estimating populations will depend upon the above characteristics and understanding the contexts in which the sounds are produced. The differences in the two categories of sound will also influence the design of listening devices. Development of listening devices for specific incidental sounds will be difficult and will require in-depth analysis of the sounds (Webb et al. 1988). One potential advantage to sounds that are produced for communication is that an efficient and effective device for listening to the particular sound in the specific environment in which it is produced has already been developed. Natural selection has shaped and modified the ears of the receiving animals to be effective in detecting the sounds. Investigating the properties of the ears of receiving animals may help develop transducers with similar properties. Perhaps the animals' own ear can be used as a 'biological microphone' or transducer (Rheinlaender & Romer 1986, Romer & Bailey 1986).

MONITORING POPULATIONS

Sexual and Life-Stage Differences in Sound Production: To accurately census populations it is necessary to know what individuals in the population are producing sound and how these relate numerically to the rest of the population. In insects that communicate via sound usually only one sex produces the sound. For crickets it is usually the adult male, and to estimate a population size by counting calling males one must know the proportion of adults in the population and the sex ratio of the adults.

Another important consideration for sound censusing is whether different individuals of a population produce different sounds. For example, the characteristics of the sounds produced by insects often depend upon the size of the structures that produce the sound. During the growth of an insect the size of the structures change, and thus, the characteristics of the sound change with the life stage of the insect.

Different life-stages of an insect often occur at the same time of the year. If only one stage produces a particular sound, then information about the life history and the proportion of individuals in each age class must be considered. When certain sounds are characteristic of each stage then the sounds can be used to estimate the number of individuals in each life stage class and will provide information about the distribution of age classes of a population.

Life table data for a hypothetical cricket population, *Gryllus hypotheticus* are shown in Table 3. This species has six life stages from egg to adult. The individuals in the population are distributed amongst the different age classes as shown in column p_x . During a census period 100 calling males are counted. Counting calling males gives a minimum size of the population, however this is far from a more accurate estimate ($N = 166$) calculated using life table statistics of the population. The number of individuals in each age class, n_x , can be estimated using the following equation:

$$n_x = (N \cdot p_x) / p_c \quad \text{Eq. 1}$$

where n_x is the estimate of the number of individuals in the x age class, N ($=100$) is

TABLE 3. LIFE TABLE STATISTICS AND POPULATION ESTIMATION BASED ON MALE CALLING IN A HYPOTHETICAL CRICKET, *GRYLLUS HYPOTHETICUS*.

Life Stage x	Prop. of Population p_x	Number Counted N	Estimate ¹ n_x
1	0.00		0
2	0.05		8
3	0.05		8
4	0.10		17
5	0.20		33
adult	0.60	100	100
TOTAL	1.00		166

¹The estimate for each age class, n_x , is calculated from Eq. 1 (see text).

the number of individuals counted producing sound, p_x is the proportion of the population in the x age class, and p_c (=0.60) is the proportion of individuals in the counted age class. This assumes that all individuals in the age class being counted are producing sound during the census. To make the equation more general the number counted must be divided by the proportion of individuals of the age class that are calling at the time of the census, r_c . The equation then becomes

$$n_x = (N \cdot p_x) / (p_c \cdot r_c). \quad \text{Eq. 2}$$

For instance, if all adult males are calling during the census and the adult population has a sex ratio of 50:50 (ie. $r_c = 0.50$), then the estimates of each class increase by a factor of 2. The total population is 332. As will be seen below, all males are not always calling during a census, and it becomes necessary to find out what proportion of the individuals are producing sound during a particular time to estimate the population.

Daily Periods of Sound Production: One of the problems with using sound to census populations is the lack of information about when to monitor. If reliable estimates of populations are to be made using the sound produced by insects, then all individuals in the population, or a constant proportion of those individuals, must produce sound at the time of censusing. Almost all activities of animals, especially those of insects, follow a circadian rhythm (Brady 1982). Much has been learned about physiological and environmental influences on these animal rhythms in the laboratory, but only recently have researchers looked at such rhythms with the animal's ecology in mind (Walker 1983). If insect sounds are to be used in estimation of population size, understanding these rhythms becomes necessary.

Species Differences in Rhythms: The periods of sound production are often very specific to a species and may be very different between closely related species. For a particular species these activities can be brief, lasting only a few minutes, or they may be spread throughout the day. For instance, each evening male mole crickets, *Scapteriscus acletus* and *S. vicinus*, begin calling shortly after sunset and continue to call for about an hour (Forrest 1983). This period also corresponds to female flight activity. Similarly, male *Anurogryllus arboreus*, a short-tailed cricket, call for about an hour shortly after sunset (Walker 1980a).

Males of other crickets call throughout the night and these species differ in the proportions of individuals calling at any one time. During an evening, about 25% of the *Anurogryllus muticus* in the population call at the same time (Walker & Whitesell 1982,

Walker 1983). About 50% of the total population of *Gryllodes supplicans* call simultaneously during an evening (Sakaluk 1987). The proportion of male field crickets (*Gryllus integer*, *G. veletis*, and *G. pennsylvanicus*) that call during an evening varies throughout the night and is dependent upon population density. Just after sunset 25-80% of the male population is calling, and there is an increase in calling activity at sunrise when almost 100% of the males are calling (Cade 1979, French & Cade 1987).

These daily calling periods may be changed by several environmental factors. For instance, calling may shift from predominantly nighttime to mostly daytime calling if nighttime temperatures are below those suitable for calling (Alexander & Meral 1967). Rain may also cause shifts in the calling period (Alexander & Meral 1967, Forrest 1983, Walker 1983, Walker & Whitesell 1982). Interaction with other species has also been found to cause shifts in the calling period of some katydids (Greenfield 1988, Latimer & Broughton 1984).

Characterizing the periods of sound production is useful in determining the proper times to census an insect population. Once this characterization has been made it becomes necessary to understand what the individuals in that population are doing during the periods of sound production. However, few data are available on sound production by individual insects under natural conditions.

Individual Differences in Rhythms Within Days: Calling periods sometimes vary between individuals within a population. Individual male mole crickets, *Scapteriscus acletus* and *S. vicinus*, have significantly different times that they begin their evening calling (Forrest 1983). Walker & Whitesell (1982) studied calling of individual male *A. muticus*. They found males that called near burrows generally called during the same period and for the same duration from night to night, but individuals differed in both respects. Some males were early evening callers while others called late in the evening. Other males that were not associated with burrows were more variable in their calling times and durations, often moving between census periods. One male moved more than 50 m during a night of singing.

Individuals Differences in Rhythms Between Days: Another important aspect of sound production is the variability in sound production from one day to the next. To reliably quantify population density using the sounds that are made by individuals in the population, the variation in sound production by individuals must be known. The probability of calling from night to night varied among individual male mole crickets monitored for periods of as long as a month (Fig. 1). One *S. vicinus* male called only 26% of the nights compared with other males that called as much as 79% of the nights during the same period. For all males combined, *S. acletus* males called an average of 78% of the suitable nights (>16°C and no rain) and *S. vicinus* males averaged 76%. All males were kept outdoors in 19-liter buckets of soil and were provided with enough food so as not to limit energy needed for calling (see below).

Effects of Density and Nutrition on Sound Production: If sounds are to be used to measure population size and density, the influence of population size or density on the production of sound must be known. This too will depend upon the context in which the sound is produced. For incidental sounds, the number of sounds detected should increase linearly with increasing density. In other contexts (eg. aggressive sounds), the proportion of the population producing sounds may be low under low density situations and may then increase dramatically (exponentially) as the population density increases. The reverse may be true for sounds such as the calling songs of crickets. In this case, the proportion of the population calling may decrease as the density increases because of an increase in attacks from neighbors (see Burk 1983 and this symposium), or because the sounds are energetically expensive to produce and the high density situation makes another strategy of finding mates more profitable.

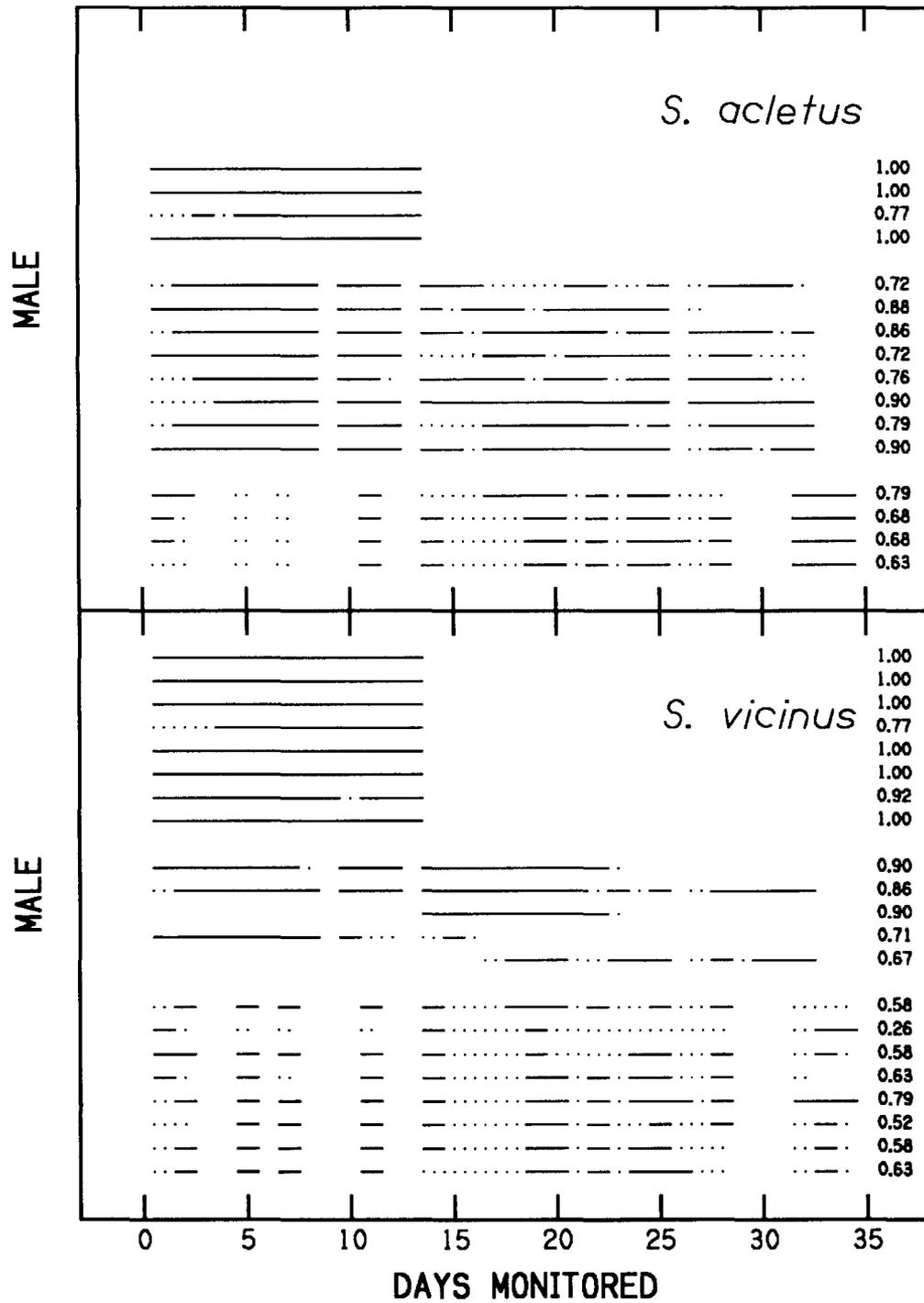


Fig. 1. Daily calling probabilities of individual male *Scapteriscus acletus* and *S. vicinus*. Each horizontal line represents data from a single male (N = 16 *S. acletus* = 21 *S. vicinus*). Solid lines are days males called, dotted lines represent days males did not call, and open area show days males were not monitored. Males are grouped according to dates monitored. Top 4 *S. acletus* and 8 *S. vicinus* were monitored 10-22 Apr 1979, middle 8 *S. acletus* and 5 *S. vicinus* were monitored 18 May-18 Jun 1979, and bottom 4 *S. acletus* and 8 *S. vicinus* were monitored 7 Mar-9 Apr 1980. Numbers at the right are the proportion of suitable (>16°C and no rain) nights that each individual called.

Data for calling in two mole crickets as a function of male density (Shaw 1981, personal communication) are shown in Figure 2. Male mole crickets were placed at various densities in 10 m² outdoor arenas. The number of individuals calling in the arenas was monitored on successive nights. The maximum percentage of males calling decreases exponentially with increasing density and reaches a constant level of about 10% calling at high densities (Fig. 2). These data can be fit with an exponential decay function of the form

$$P(x) = \alpha / (1 - e^{-x/\tau}), \quad \text{Eq. 3}$$

where $P(x)$ is the proportion of the total calling at density x , α is the asymptotic value of the function as x becomes large, and τ is the function's rate of decay. The dotted line in Figure 2 is the least-squares fit to all data using the above equation ($\alpha = 0.11$ and $\tau = 2.00$). Walker (1980b, personal communication) has shown that the presence of conspecific male and female mole crickets will decrease the proportion of nights individual males call by as much as 70%.

Nutrition will also influence sound production. If the sounds to be monitored are produced because of feeding activity, then abundant food supplies could cause a decrease in movement associated with acquiring food. Sound production caused by the movement of the insect would decrease. However, if the food has little nutritional value, then the individual must consume more and feed more often to make up for the low nutritional intake (Slansky 1982). Sound production would increase. If the sounds are energetically expensive to produce, poor nutrition may decrease the production of such sounds. Cal-

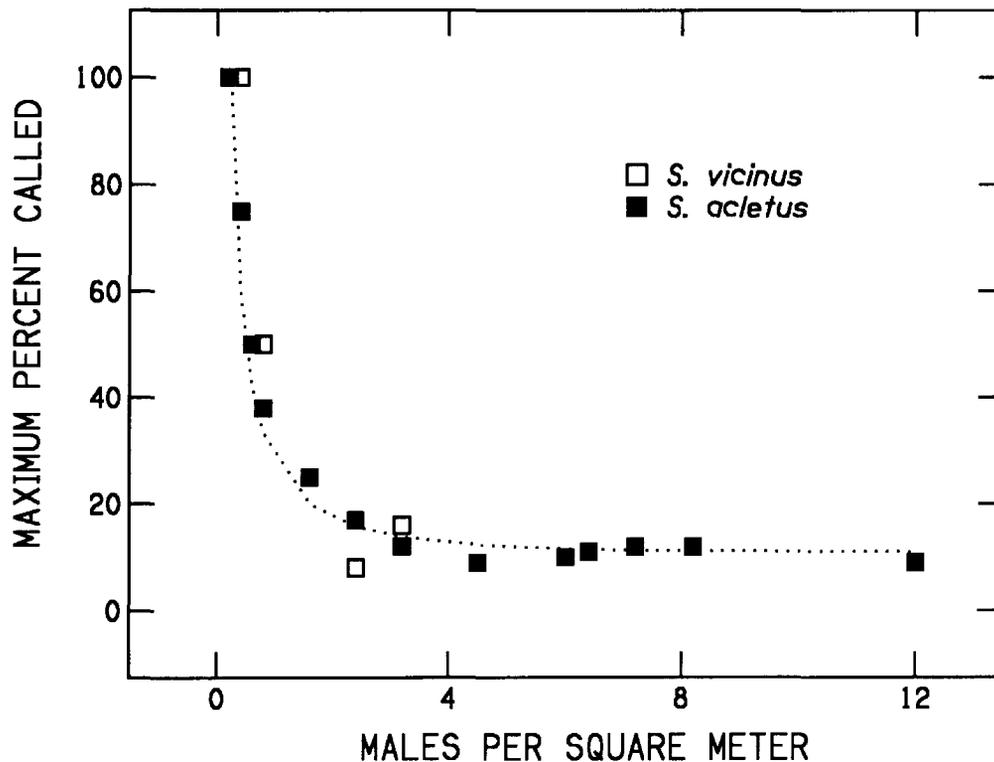


Fig. 2. Maximum percent of male mole crickets calling in 10 m² outdoor arenas plotted as a function of male density in the arena. Dotted line is a least-square fit to the data using $\alpha = 0.11$ and $\tau = 2.00$ as parameters of Eq. 3 (see text, Shaw 1981, personal communication).

ling male crickets use more than 10 times the energy used during resting (Prestwich & Walker 1981, Kavanagh 1987). Walker (1980b, personal communication) found that the proportion of nights that male mole crickets called decreased from about 80 to 30% when they were deprived of food (Fig. 3).

Seasonal Periods of Sound Production: Besides daily periods of sound production, animals very often have specific seasonal periods. This is especially true of insects where certain life stages are only present during specific times of the year. Crickets are a good example. It has become common practice to use counts of calling crickets to determine life cycles, seasonal maturation, and adult activity periods of crickets (Alexander 1962, Alexander & Meral 1967, Walker 1983). Because adult males are the only part of the population that produce calling songs, the season of sound production generally corresponds to the adult activity of the species. However, in some species males are rarely heard at certain times of the year even though adult males are abundant in the population. This may be caused by the abundance of acoustically orienting parasitoid flies present at this time of the year (Burk 1982 and refs.). The seasonal activity of sound production must be considered if acoustic signals are to be used to monitor populations.

Geographic Ranges and Population Spread: Two very practical uses of monitoring insect populations based upon the sounds produced are determining geographic ranges and measuring the spread of populations. The use of acoustic signals to determine population ranges and their spread have been used extensively in insects that use sound to com-

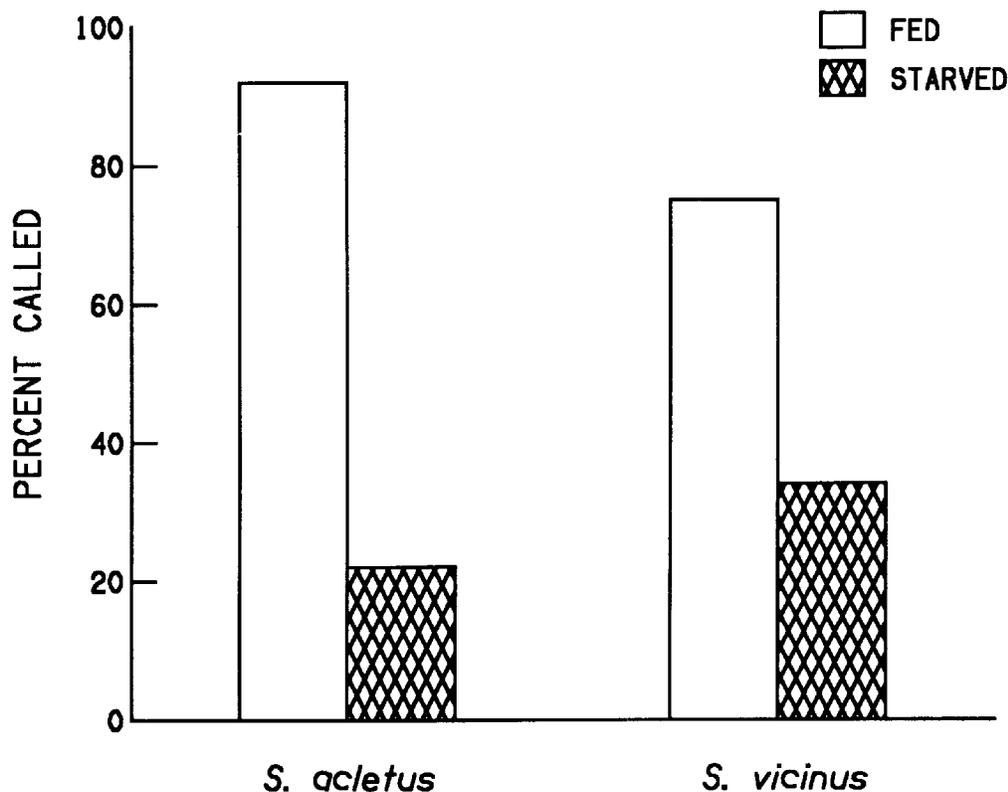


Fig. 3. Bars show how starving influences the nightly calling of male mole crickets. Percent of nights called is significantly decreased for males that are deprived of food (hatched bars) compared with males provided food (open bars) (Walker 1980b, personal communication).

municate over long distances (Alexander 1962). The signals of particular species are easily distinguished, and to determine a species geographic range it is a simple matter of cataloguing the localities where that species sound has been heard. This technique could also be used for incidental sounds, provided a suitable detection device can be produced. This application will increase our ability to monitor the spread of migratory species and pest species that have been introduced to new areas.

CONCLUSIONS

Monitoring and estimating populations is important in the management of any pest species. Because sound of one form or another is produced by all insects, a promising area of research is to use sound in detecting, censusing, and monitoring insect populations. An understanding of the sounds, knowing the contexts in which they are produced, and knowing how the production of sound relates to the ecology and biology of the animals will improve population estimation. In most instances, the population size will be underestimated. It is only when insects of different species produce indistinguishable sounds or when individuals are very mobile and are counted more than once that a population would be overestimated. Thus, the use of sound censusing provides baseline data for estimating population size. Where exact counts are not a necessity, monitoring the sounds of insects can provide much information about a species life history. Using sound should become an increasingly important tactic for monitoring population spread and has application in monitoring the movement of migratory pest species.

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ULTRASONIC ACOUSTICAL EMISSIONS FROM SAPWOOD
OF EASTERN WHITE PINE, NORTHERN RED OAK,
RED MAPLE, AND PAPER BIRCH: IMPLICATIONS
FOR BARK- AND WOOD-FEEDING INSECTS

ROBERT A. HAACK¹, RICHARD W. BLANK¹, FREDERICK T. FINK²,
AND WILLIAM J. MATTSON¹

¹North Central Forest Experiment Station, USDA Forest Service,
1407 S. Harrison Road, Room 220,
East Lansing, MI 48823

²Department of Metallurgy, Mechanics, and Materials Science,
College of Engineering, Michigan State University,
East Lansing, MI 48824

ABSTRACT

Ultrasonic acoustical emissions (AEs) were recorded from trunk samples of eastern white pine, *Pinus strobus* L., northern red oak, *Quercus rubra* L., paper birch, *Betula papyrifera* Marsh., and red maple, *Acer rubrum* L., that were cut in winter (February) and allowed to dry indoors. Emission rates were determined for waxed and unwaxed samples at weekly intervals throughout the drying period. Waveform parameters determined for each AE were duration, counts (oscillations above threshold), rise time, amplitude, energy, and average frequency (counts/duration). For all tree species, AE rates from unwaxed samples first increased and then decreased during drying, and they were several times greater than rates for waxed samples. For white pine, mean duration, counts, rise time, amplitude, and energy decreased over time while average frequency increased. Such patterns were often lacking among the three hardwood species. Average waveform parameters differed among species; AEs from white pine were strongest while those from red oak were weakest. Implications for bark- and wood-boring insects are discussed.

RESUMEN

Emisiones acústicas ultrasónicas (EAU) se registraron en muestras de troncos de pinos blancos del este, *Pinus strobus* L., robles rojos del norte, *Quercus rubra* L., abedul de papel, *Betula papyrifera* Marsh., y en el meple rojo, *Acer rubrum* L., que fueron cortados en el invierno (Febrero) y secados dentro de la casa. Se determinó la proporción de emisión de muestras enceradas y sin encerar a intervalos semanales durante el período que se secaban. Los parámetros determinados del tipo de onda para cada EAU fueron duración, conteo, (oscilación encima del umbral), tiempo en ascender, amplitud, energía, y el promedio de la frecuencia (conteo/ duración) Para todas las especies de árboles, la proporción de EAU de muestras sin cera primero aumentó y después disminuyó cuando se secaban y fueron varias veces mayor que la proporción de muestras enceradas. Para los pinos blancos, el intermedio de duración, conteo, tiempo en ascender, amplitud, y energía, disminuyó con el tiempo mientras que el promedio de la frecuencia aumentó. Tales patrones amenudo estaban ausentes entre las tres especies de madera dura. El promedio de los parámetros del tipo de onda diferió entre las especies; EAU del pino blanco fueron los más fuertes mientras que aquellos del roble rojo fueron los más débiles. Se discuten las implicaciones para insectos taladradores de la corteza y de la madera.

Water is conducted upwards in the xylem tissue of plants. To accomplish this, xylem functions at negative pressures, with water being held under tremendous tension

(Kramer 1983, Oertli 1971, Zimmermann 1983). This tension increases dramatically during drought and at some critical point the hydrogen bonds between the water molecules break or cavitate (Tyree & Dixon 1983). The breaking of individual water columns releases energy that results in acoustical emissions (AEs) primarily at ultrasonic frequencies (>20 kHz) (Sandford & Grace 1985, Tyree & Dixon 1983, Tyree et al. 1984b). Each AE is believed to result from cavitation of an individual water column within the conducting xylem. As drought stress intensifies, AE rate increases with the largest diameter xylem conduits tending to cavitate first (Sandford & Grace 1985, Tyree & Dixon 1986). The term conduit is used to include both the single-cell tracheids of conifers and the multi-cell vessels of hardwoods. Ultrasonic AEs from drought-stressed plants are a recent discovery, being first reported by Tyree & Dixon in 1983. AEs have since been recorded from a number of hardwood tree species (Jones & Peña 1986, Salleo & Lo Gullo 1986, Sandford & Grace 1985, Tyree & Dixon 1986), conifers (Dixon et al. 1984, Peña & Grace 1986, Sandford & Grace 1985, Tyree and Dixon 1983, 1986, Tyree et al. 1984a, 1984b), and herbaceous plants such as corn (Tyree et al. 1986). In the forest products industry, AEs have been reported to occur in drying lumber (Becker 1982, Honeycutt et al. 1985, Noguchi et al. 1980, 1983, 1985, Skaar et al. 1980).

Considering that many bark- and wood-boring insects preferentially attack drought-stressed trees (Mattson & Haack 1987), and that several insects from at least nine Orders can detect and/or produce ultrasound at similar frequencies (Lewis & Gower 1980, Sales & Pye 1974, Schwartzkopf 1974, Spangler 1988), Mattson & Haack (1987) hypothesized that some bark- and wood-boring species might perceive and utilize drought-induced acoustic signals during host colonization. One means to test this hypothesis requires characterization of the AE rate and waveform pattern from drought-stressed trees during the period of host colonization, and then testing the relative attractiveness of substrates pulsed with ultrasound to simulate drought-related AEs with that of similar nonpulsed substrates.

AEs are sensed by transducers affixed to the bark or wood (xylem) surface. Most researchers have used wideband transducers that are sensitive over the range 100-1000 kHz. The most commonly reported AE parameter has been emission rate. Besides simply counting AEs, technologies exist to determine several AE waveform parameters such as duration, counts, rise time, amplitude, and energy (see Fig. 1). Because (a) larger xylem conduits tend to cavitate first, (b) frequency is inversely proportional to conduit size, and (c) AE intensity is proportional to cell size, average frequency theoretically would increase while signal intensity would decrease during an extended period of drought. Moreover, because xylem cells vary among species in length, width, structure, and arrangement (Panshin & de Zeeuw 1980), it is possible that different species or genera of trees will produce unique AE signatures. In the present study, our objective was to describe emission rates and several AE waveform parameters during an extended period of dehydration for freshly cut trunk samples of eastern white pine, *Pinus strobus* L. northern red oak, *Quercus rubra* L., paper birch, *Betula papyrifera* Marsh., and red maple, *Acer rubrum* L. Such information will allow us to pulse substrates with ultrasound at meaningful levels.

In conifer xylem, the principal water-conducting units are single-celled tracheids. Conifers lack vessels. Hardwood xylem is more complex; vessels are the chief water-conducting components. Vessels are tubular structures, consisting of individual cells from which the end walls have disintegrated. Vessels are much larger than tracheids. The arrangement of vessels is variable among species, but fixed for a given species. Hardwoods are often classified as either ring porous or diffuse porous. In ring-porous species, earlywood vessels are much larger than latewood vessels, thus producing an abrupt and obvious transition between growth rings. In diffuse-porous species, there is little change in vessel size across the growth ring (Kramer & Kozlowski 1979). In the

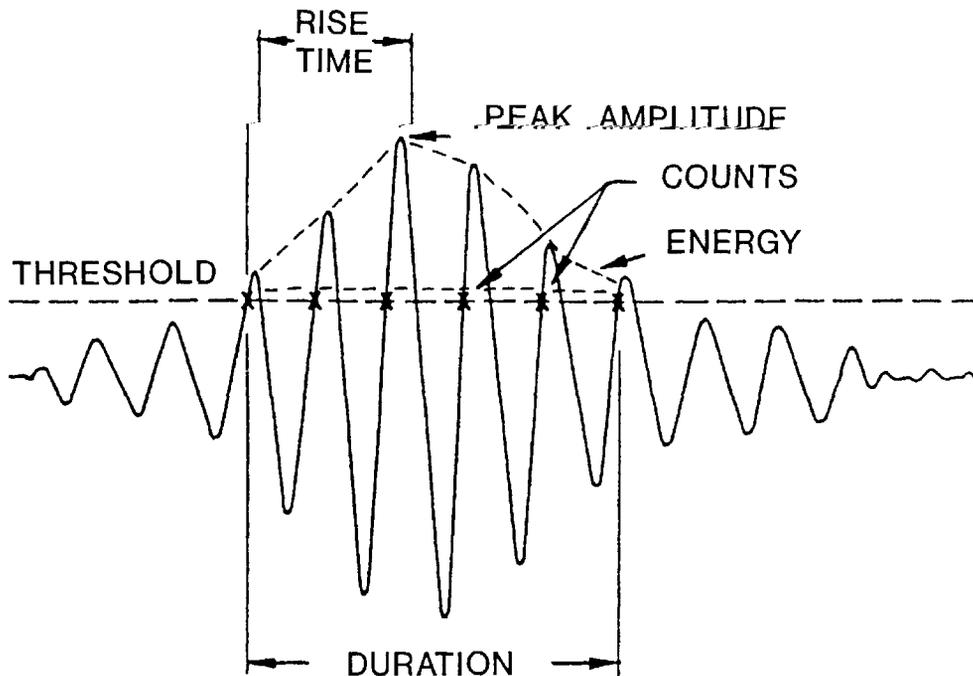


Fig. 1. Typical acoustical emission waveform showing parameters commonly measured above a preset threshold voltage: event duration (time between first and last threshold crossing), rise time (time from first threshold crossing to peak amplitude), peak amplitude (the peak voltage of the largest excursion attained by the signal waveform from an emission event), counts (number of times the signal passes above the threshold), and energy (total elastic energy released by an emission event; this parameter is calculated in various ways using the values for amplitude and duration).

present study, white pine is a conifer, red oak is a ring-porous hardwood, and paper birch and red maple are diffuse-porous hardwoods.

METHODS AND MATERIALS

Plant Material and Preparation

A small-diameter (6-10 cm) tree of each of the four test species was cut on February 22, 1988 in a forested area in southwestern Michigan. Six, branch-free, 40-cm long samples were cut from the trunk of each tree and immediately taken to the laboratory and weighed (Table 1). For each species, two samples were dried to determine initial moisture content (wet-weight basis), two were end-dipped in melted paraffin to slow dehydration, and two were left unwaxed. The waxed and unwaxed samples were used to simulate low and high levels of water stress, respectively. The samples were allowed to air-dry in the laboratory at room temperature; weight was recorded periodically during the drying period. At the end of the study, all samples were dried at 75°C and weighed.

To aid in transducer placement, we removed a small area (ca. 4 cm²) of bark near the center of each sample, shaved the exposed sapwood flat, affixed the transducer with couplant, and constructed a support cylinder around the transducer using a hot-melt adhesive. The support cylinder allowed for exact placement of the transducer on each sampling day. Any remaining exposed sapwood around the support was coated with petroleum grease to reduce local dehydration.

AE Monitoring

An acoustical emission is a phenomenon in which transient elastic waves are generated by the rapid release of energy from a localized source within a material. In our case, the energy released as a result of cavitation is believed to generate the elastic waves that we detected. Elastic waves propagate outward from their source and can be detected with the appropriate transducer as small displacements on the surface of the specimen. Transducers transform elastic waves into electrical signals that can be further amplified, filtered, and conditioned by other AE-detecting hardware.

We used AE equipment from Physical Acoustics Corporation (PAC) of Princeton, NJ. The sensors were 150 kHz resonant transducers (PAC model R15) of the ceramic piezoelectric type with -68 dB sensitivity. We used PAC model 1220A preamplifiers with 100-300 kHz bandpass filters and 40 dB gain (0 dB = 100 μ V; a decibel is 1/20 of a logarithmic unit; thus 20 dB is 10 times greater, 40 dB is 100 times, 60 dB is 1000 times, etc.). The AE processor was a PAC model 3000/3004, which was set for an additional gain of 32 dB. The total gain was thus 72 dB. An event was recorded when the resulting amplified signal was greater than a 0.3 V threshold voltage; considerable background noise was detected at 0.1 and 0.2 V. For comparison, others have used total gains of 67 to 82 dB and thresholds of 0.12 to 0.25 V (Jones & Peña 1986, Peña & Grace 1986, Sandford & Grace 1985, Tyree & Dixon 1983, 1986, Tyree et al. 1984a, 1984b, 1986). For each recorded AE, the PAC 3000/3004 measured waveform parameters such as duration (microseconds), counts (oscillations above threshold), rise time (microseconds), amplitude (dB), and energy (volt seconds). Given that frequency is defined as hertz (cycles per second), we estimated average frequency for each AE by dividing counts by duration. We realize that this method will not calculate the true frequency of a signal in most cases because (1) it assumes equal time intervals between oscillations, (2) it allows for only one frequency per signal, and (3) a resonant transducer was used which is most sensitive to its resonant frequency.

AEs were recorded three times weekly as the trunk samples dried. The base of the transducer was coated with couplant and affixed to each sample within the support cylinder. AEs were recorded for 5 minutes (or until at least 50 AEs had been recorded) per sample using the same transducer, preamplifier, and AE-processor channel throughout. Samples were tested until no AEs had been recorded for two successive sampling dates.

Statistical Analysis

The AE data were analyzed by using the general linear models procedures of the Statistical Analysis System (SAS Institute 1982). To keep the data set sizes manageable,

TABLE 1. SUMMARY DATA FOR SAMPLE MATERIAL FROM EASTERN WHITE PINE, NORTHERN RED OAK, RED MAPLE, AND PAPER BIRCH.

Species	Tree age (yr)	Sample		Moisture content (%)			Weeks of AE production (unwaxed only)	
		Lth (cm)	Diam (cm)	When cut	After 8 wks		First week	Last week
					waxed	unwaxed		
Pine	16	40	7.7	68	66	34	1	7
Oak	39	40	8.6	41	39	30	1	8
Maple	20	40	5.6	51	43	22	2	11
Birch	20	40	6.0	49	47	24	1	7

only the first 50 AEs were recorded from each 5-min sampling period. All recorded AEs were used in determination of AE rate and nearly all in conducting simple correlations among AE waveform parameters by species. However, in analyses of AE waveform parameters, only AEs with values of 1 or greater for duration, count, rise time, and amplitude were used, thus eliminating the weakest signals. Positive and negative linear trends in the weekly mean values for all AE parameters were tested for each species by using simple linear regression techniques. ANOVA and multiple range testing were used to determine significant ($P < 0.05$) differences among the four species for overall mean values for each AE parameter.

RESULTS

Moisture Content

At the time of felling, moisture content was highest in pine and lowest in oak (Table 1). For all species, replicate samples dried similarly, being within 1% moisture content on each sampling day. After 8 weeks of air drying, waxed samples had lost little moisture compared with unwaxed samples (Table 1) indicating that waxing the cut ends reduced dehydration. Unwaxed maple contained 16% moisture after 11 weeks, after which AE production stopped.

AE Rate

The rate of acoustic emissions was far greater in unwaxed than in waxed samples (Fig. 2; note differences in scale). In general, considering unwaxed samples only, AE rate increased rapidly at first, remained steady, and then slowly declined. AE rate was higher in pine than in any of the hardwood species. Unwaxed pine, oak, and birch samples produced AEs during the first week of drying, whereas none were detected from maple until week 2. Similarly, AE production ended in pine, oak, and birch samples during weeks 7 and 8; however, maple samples produced AEs through week 11 (Table 1).

Waxed pine and birch produced practically no AEs, whereas waxed oak and maple produced some (Fig. 2). Cracks in the wax coatings of the oak and maple samples were noted at the end of the study; it is possible that these cracks allowed water loss and thus AE production.

AE Waveform Characteristics

All correlations among the AE parameters were highly significant ($P < .001$), and in general, patterns were similar for each tree species (Table 2). Strong positive correlations existed among duration, count, energy counts, amplitude, and rise time. Weak, negative correlations were found for frequency with each of the other five AE parameters, indicating that signals of lower intensity were often of higher average frequency (as defined here).

Weekly mean values for duration, counts, rise time, amplitude, energy, and average frequency are presented by species for the unwaxed samples in Fig. 3. Data points represent an average of 55-255 individual AEs.

Mean duration tended to decrease during the drying cycle for pine, oak, and birch, whereas maple remained rather constant (Fig. 3; Table 3). The greatest decline occurred in pine. For all weeks combined, AEs from pine were the longest while those from oak were the shortest in duration (Table 4). Noguchi et al. (1985) recorded durations of 50-200 μsec for two hardwood species and one conifer.

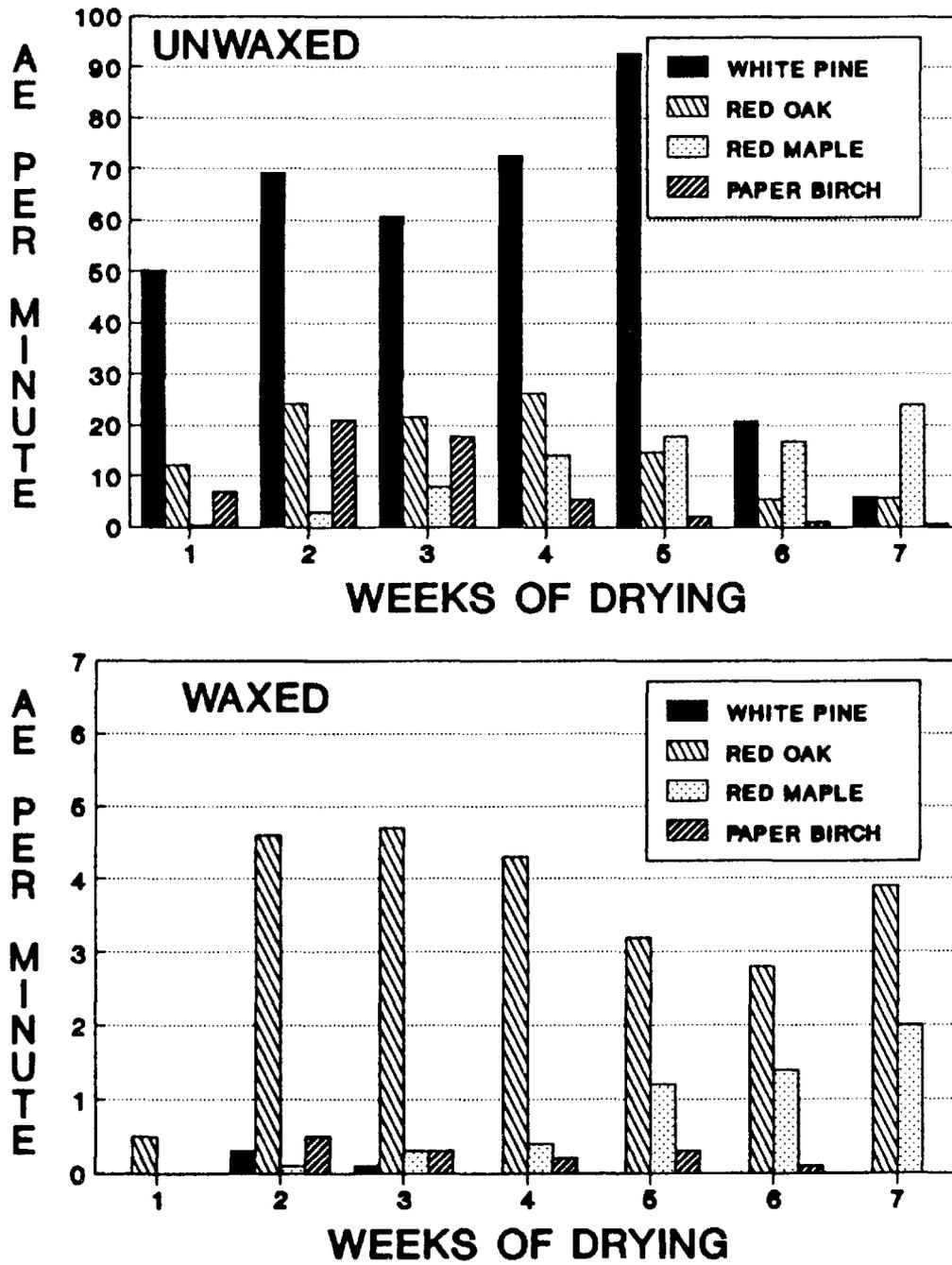


Fig. 2. AE rate (events/minute) recorded with a 150 kHz resonant transducer from unwaxed (top) and waxed (bottom) trunk samples cut from four tree species in February and allowed to dry indoors in a heated building: threshold voltage = 0.3 V, total system gain = 72 dB.

Mean counts per AE declined during the drying cycle for pine and oak, but no consistent linear pattern was found for either maple or birch (Fig. 3; Table 3). The most dramatic decline occurred in pine. For all weeks combined, AEs from pine had the most counts while those from oak had the fewest (Table 4).

TABLE 2. SIMPLE CORRELATIONS (r) AMONG AE WAVEFORM PARAMETERS BY SPECIES; BASED ON ALL AEs HAVING VALUES OF 1 μ SEC OR GREATER FOR DURATION; $P < .001$ FOR ALL VALUES BELOW.

	Duration	Counts	Rise time	Amplitude	Energy	Frequency
Eastern white pine (below right, N = 1645 AEs)						
Duration		.97	.66	.80	.87	-.26
Counts	.93		.63	.75	.84	-.15
Rise time	.67	.65		.48	.60	-.27
Amplitude	.72	.66	.49		.71	-.28
Energy counts	.84	.80	.68	.61		-.21
Frequency	-.31	-.14	-.33	-.31	-.27	
Northern red oak (above left, N = 1619 AEs)						
Red maple (below right, 2259 AEs)						
Duration		.97	.71	.72	.88	-.28
Counts	.97		.70	.66	.84	-.15
Rise time	.73	.71		.44	.66	-.28
Amplitude	.81	.76	.55		.60	-.32
Energy counts	.89	.86	.72	.69		-.25
Frequency	-.29	-.13	-.32	-.31	-.27	
Paper birch (above left, N = 655 AEs)						

A decline in mean rise time was noted for pine and maple but not for either oak or birch (Fig. 3; Table 3). Pine demonstrated the greatest decline in rise time. For all weeks combined, rise time was longest for pine and shortest for oak (Table 4).

Mean amplitude decreased over time in pine, oak, and birch, but not maple (Fig. 4; Table 3). Pine showed the steepest decline. For all weeks combined, pine and birch had the largest mean amplitude while oak and maple had the smallest (Table 4).

Mean energy tended to decrease during the drying cycle for pine and maple, but no such trend was observed for oak or birch (Fig. 4; Table 3). The greatest decline in energy occurred in pine. For all weeks combined, mean energy was highest in pine and lowest in oak (Table 4).

Mean average frequency tended to increase during the drying cycle in pine, but did not show a consistent pattern in oak, maple, or birch (Fig. 4; Table 3). For all weeks combined, average frequency was broadly similar in all species (Table 4), being close to the resonant frequency of the transducer used (i.e., 150 kHz).

DISCUSSION

Seasonal Changes in Xylem Moisture Content

The winter-time moisture contents reported here are typical of conifers and hardwoods in north-temperate forests. Moisture content of sapwood is generally higher in conifers than in hardwoods, reaching a maximum in winter and a minimum in mid-summer. In hardwoods, on the other hand, moisture content reaches a maximum in spring and a minimum in autumn or in mid-winter; it is lower in winter in ring-porous types than in diffuse-porous hardwoods (Clark & Gibbs 1957, Gibbs 1958). Therefore, the relative ranking of species by moisture content will vary depending on the season during which a study is conducted.

Variation in Xylem Conduit Size

There is much within-tree, between-tree, and between-species variation in size of xylem conduits. Three important trends in conduit size are (a) size decreases with

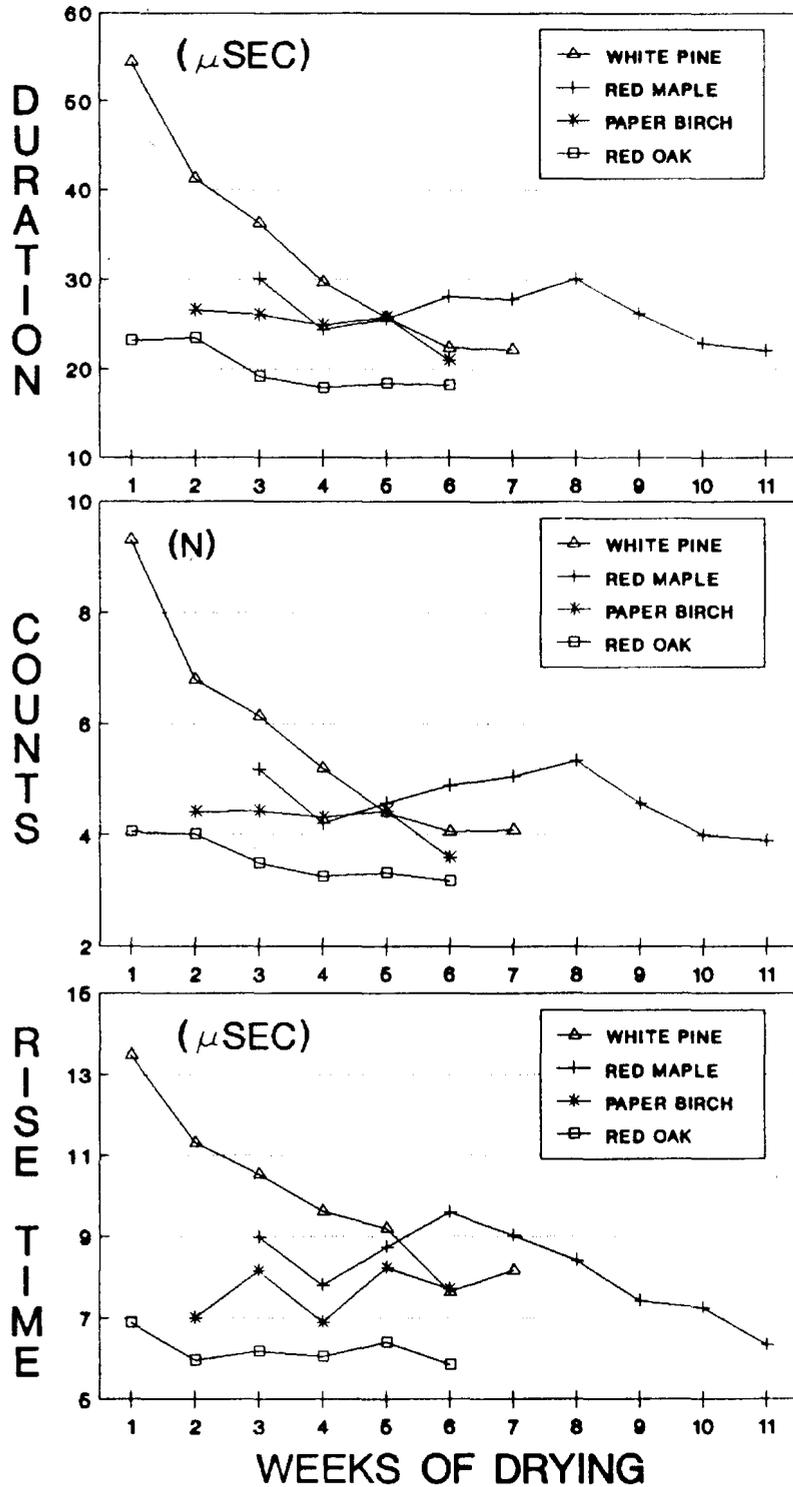


Fig. 3. Mean duration, counts, and rise time for AEs recorded with a 150 kHz resonant transducer from unwaxed trunk samples cut from four tree species in February and allowed to dry indoors in a heated building: threshold voltage = 0.3 V, total system gain = 72 dB, N = 1645 AEs for pine, 2259 for maple, 655 for birch, and 1619 for oak.

TABLE 3. ANOVA PROBABILITY (*P*) VALUES FOR VARIOUS AE WAVEFORM PARAMETERS TESTED AGAINST TIME (WEEKS OF DRYING) FOR TRUNK SAMPLES FROM EASTERN WHITE PINE, NORTHERN RED OAK, RED MAPLE, AND PAPER BIRCH.

Species	<i>P</i> <					
	Duration	Counts	Rise time	Amplitude	Energy	Frequency
Pine	0.001	0.002	0.001	0.001	0.001	0.010
Oak	0.028	0.008	0.245	0.047	0.069	0.283
Maple	0.147	0.208	0.035	0.378	0.021	0.801
Birch	0.100	0.183	0.536	0.035	0.435	0.826

increasing height within the tree, (b) the number of conduits per unit area (tangential section) increases with sampling height, and (c) average conduit length increases with tree age (Bailey 1958, Fegel 1941, Zimmermann 1978, Zimmermann & Potter 1982). Vessel length and diameter are positively correlated (Greenidge 1952, Zimmermann & Jeje 1981). Xylem conduits are shortest in conifers, relatively long in diffuse-porous hardwoods, and can be extremely long in ring-porous hardwoods. For example, white pine tracheids are up to 4-5 mm long (Bailey & Tupper 1918), whereas the longest vessels in maple, birch, and oak are typically 25-35 cm, 36-40 cm, and 10-11 m, respectively (Zimmermann & Jeje 1981). However, only a few vessels belong to the longest length class. In red maple, for example, although some vessels reached 42 cm in length, over 50% were in the 0-4 cm class (Zimmermann & Potter 1982). Therefore, in addition to season of year, AE studies will be influenced by sampling location within the tree, tree age, and sample length.

AE Rate

The higher AE rate in unwaxed versus waxed samples reflected the former's greater rate of water loss, given that the evaporated water resulted from cavitated xylem conduits. The differences in AE rates that we recorded between waxed and unwaxed specimens are similar to differences in AE patterns from well-watered and drought-

TABLE 4. MEAN AND RANGE VALUES FOR VARIOUS AE WAVEFORM PARAMETERS RECORDED FROM TRUNK SAMPLES OF EASTERN WHITE PINE, NORTHERN RED OAK, RED MAPLE, AND PAPER BIRCH.

Species	Duration (μ sec)	Counts (N)	Rise time (μ sec)	Amplitude ² (dB)	Energy (V sec)	Frequency ² (kHz)	AEs ³ (N)
Pine	43.6 a ¹ (8-187)	7.2 a (2-33)	13.3 a (1-95)	41.4 a (30-73)	3.0 a (1-30)	168 a (68-583)	1069
Oak	30.9 d (7-230)	5.2 d (2-36)	10.0 d (1-44)	39.6 b (30-66)	2.2 d (1-11)	171 a (27-444)	801
Maple	39.2 b (9-269)	6.6 b (2-42)	12.5 b (1-68)	40.0 b (25-79)	2.8 b (2-42)	172 a (30-500)	1264
Birch	35.1 c (8-172)	5.7 c (2-28)	10.8 c (1-42)	41.1 a (31-65)	2.5 c (1-13)	164 b (62-278)	382

¹Means followed by the same letter (within columns) are not significantly different at the $P < 0.05$ level (Duncan's multiple range test).

²For amplitude, 0 dB = 100 μ V; frequency was calculated as (counts)/(duration) for each AE.

³Data were provided across weeks of operation. Def. cells with values of 0 are greater for duration, counts, rise time, and amplitude were used. AEs were sensed with a 150 kHz resonant transducer.

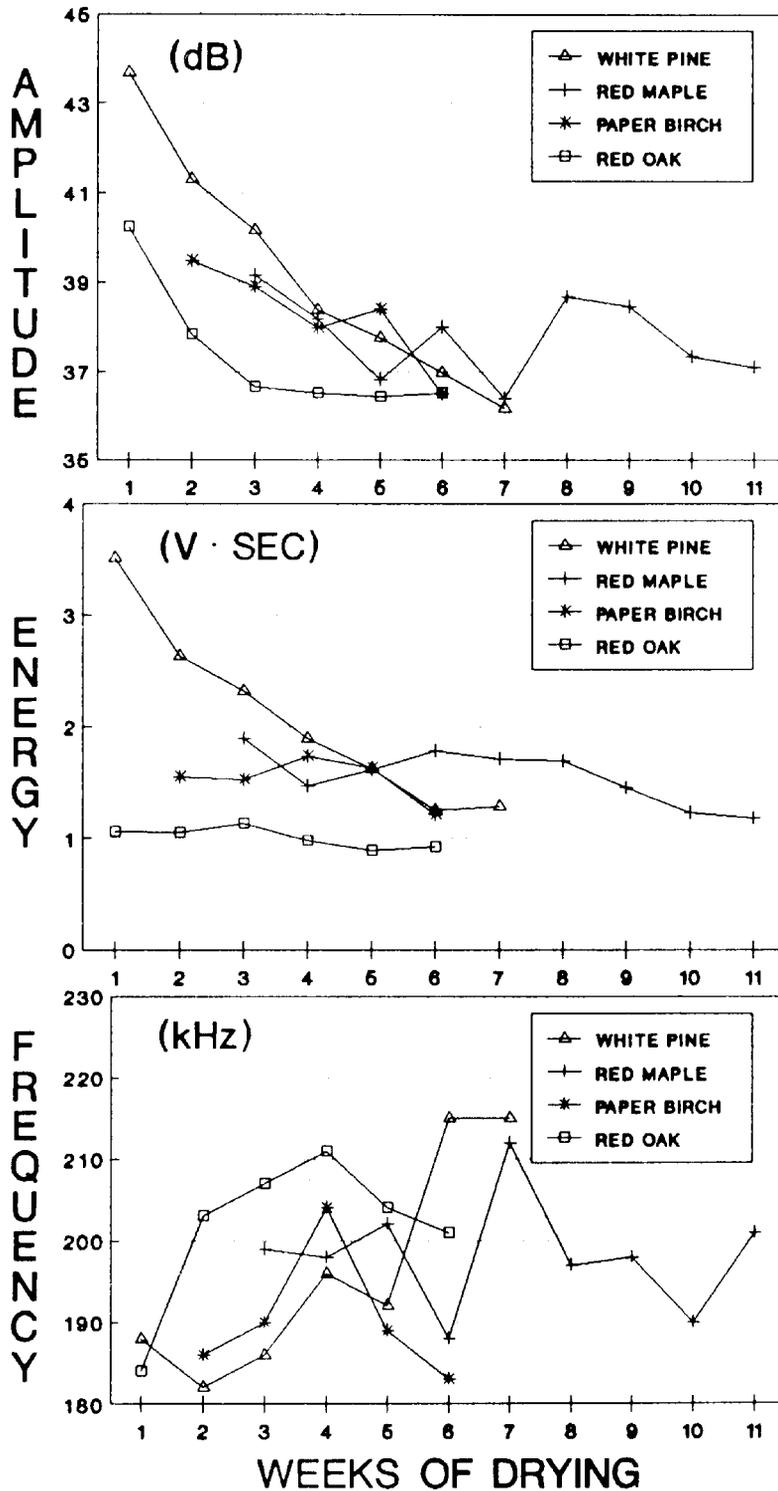


Fig. 4. Mean amplitude, energy, and average frequency for AEs recorded with a 150 kHz resonant transducer from unwaxed trunk samples cut from four tree species in February and allowed to dry indoors: threshold voltage = 0.3 V, total system gain = 72 dB, N = 1645 AEs for pine, 2259 for maple, 655 for birch, and 1619 for oak.

stressed conifers (Peña & Grace 1986) and hardwoods (Jones & Peña 1986). The increase and eventual decrease in AE rate noted here is similar to the AE rate recorded from drying lumber (Becker 1982, Honeycutt et al. 1985, Noguchi et al. 1980, 1983, 1985, Skaar et al. 1980).

AE rate and the time over which AEs are produced are known to increase with increasing specimen size (Becker 1982, Jones and Peña 1986). In our study, because specimen size was kept within a narrow range, we feel that differences in AE rate reflect primarily variation in conduit size and moisture content, i.e., more water-filled xylem conduits cavitated within the "listening" distance of the transducer in pine than in the hardwood samples. However, it is possible that many of the AEs produced by the hardwoods could have been above or below the bandwidth we examined (100-300 kHz). For example, Noguchi et al. (1985) reported that AE rate was greater in hardwoods than conifers but they recorded AEs between 50 and 150 kHz. Additionally, had testing been done during spring or summer, hardwood AE rate would probably have been higher because more cells would have been water-filled, and conversely pine AE rate may have been lower for similar reasons.

AE Waveform Parameters

Although most AE parameters varied among species, it is not known how similar the findings would be in another experiment if we sampled other trees of the same species, other tree locations, longer or shorter samples, during other seasons of the year, or used other transducers that were sensitive to different frequency bands. For example, given the above information on within-tree variation in xylem conduit size and that frequency is inversely correlated with conduit size, we hypothesized that the average frequency would increase with increasing within-tree sampling height and sample length as well as with lowered tree age.

Highest mean AE intensity (i.e., energy) was measured in pine. This may have occurred because pine had the highest moisture content and the smallest xylem conduits. That is, more conduits cavitated within the listening range of the transducer on pine than on any of the hardwoods. Sandford & Grace (1985) reported that the listening distance was greater on hardwoods than conifers. If true, this could also help explain lowered AE intensity on hardwoods because more distant AEs, which weaken as they propagate, would be averaged in the calculations. Average intensity is also known to decrease as sample diameter increases (Tyree et al. 1984b). As just mentioned, sound attenuates as it travels through wood. We do not know the distances that AEs traveled to reach the transducer in this study. Given two AEs of similar magnitude that occur at different distances from a transducer, the more distant signal will be sensed as weaker.

Only in pine was there a significant trend of increasing average frequency with drying time. Such evidence supports the contention that large conduits cavitate earlier than smaller ones (Tyree & Dixon 1986, Tyree et al. 1984b). The values we reported for average frequency are crude estimates based on counts and duration. Individual AEs may have more than one major frequency component (Noguchi et al. 1985, Tyree & Dixon 1983). Detailed spectrum analyses are needed to determine the actual frequency components produced by drought-stressed plants, and how these spectra change as drought intensifies.

Considering that oaks have the largest xylem conduits of the species tested, it is puzzling that average frequency was not substantially lower in oak. However, because the samples were only 40-cm long, more than 80% of the earlywood vessels may have been severed (see Fig. 12 in Zimmermann & Jeje 1981). Moreover, Zimmermann (1983) states that most earlywood vessels of ring-porous hardwoods cavitate during winter.

Because samples were collected in February, most earlywood vessels probably had already cavitated. Thus, the AEs recorded from our oak samples, most likely resulted from cavitations occurring in the much shorter (mostly <25 cm) latewood vessels (Zimmermann & Jeje 1981).

Implications for Bark- and Wood-Feeding Insects

Visual and olfactory cues are considered of primary importance in host finding by bark- and wood-feeding insects (Haack & Slansky 1987). It is well recognized, however, that ultrasound in the range 20-200 kHz is produced and/or detected by insects in diverse groups such as Diptera (Saini 1984), Lepidoptera (Spangler 1988), Neuroptera (Olesen & Miller 1979), Orthoptera (Silver et al. 1980), and Trichoptera (Silver & Halls 1980). Two species of *Ips* bark beetles (Scolytidae) are known to produce low-frequency ultrasound (Swaby & Rudinsky 1976, Wilkinson et al. 1967). We believe it highly plausible that some insects could detect and utilize drought-induced AEs during host finding and accepting. It is not known, however, to what distance ultrasound radiates from stressed trees into the surrounding air. If insects do utilize tree-produced AEs, we believe it is likely that they would sense them primarily after landing on the bark or after initiating boring. In support of such a scenario is evidence that mate calling by a species of pyralid moth involves using pheromones for long-range communication and ultrasonic pulses for short-range orientation (Spangler et al. 1984).

To be meaningful to insects, host-produced AEs should convey information that is consistent and specific. AEs are consistent in that they are associated with drought-stressed trees; AEs are typically lacking in well-watered trees and in dry host material. More specific information could be ascertained from AE waveform parameters such as intensity and frequency. Since these waveform parameters tend to change as drought intensifies, certain combinations of them could signify susceptibility. We are currently measuring a number of AE parameters on drought-stressed potted trees that are exposed to bark beetle attack. Our future studies will test whether substrates artificially pulsed with AEs that simulate the drought-stressed condition are any more attractive to bark beetles than are unpulsed controls. Besides visual, olfactory, and gustatory cues, it may be learned that certain insects utilize plant-produced vibrational cues in host recognition or acceptance. It is already known that certain Homoptera communicate by sending and perceiving vibrational signals through their host plants (Michelsen et al. 1982).

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ACOUSTICAL DETECTION AND ESTIMATION OF
RHYZOPERTHA DOMINICA (F.) LARVAL POPULATIONS
IN STORED WHEAT

D. W. HAGSTRUM

U.S. Department of Agriculture, Agricultural Research Service
U.S. Grain Marketing Research Laboratory
Manhattan, Kansas 66502

J. C. WEBB AND K. W. VICK

Insect Attractants, Behavior and Basic Biology Research Laboratory,
Agricultural Research Service, U.S. Department of Agriculture,
Gainesville, Florida 32604

ABSTRACT

The possibility of using insect-produced sounds to estimate insect populations without removing grain samples was investigated. The number of insect-produced sounds, heard with a piezoelectric microphone pushed into the grain, increased as the number of lesser grain borer, *Rhyzopertha dominica* (F.), larvae increased. The probabilities of detection and the accuracy of estimation of insect densities with the acoustical method were comparable to those obtained with a standard grain trier.

RESUMEN

Se investigó la posibilidad de usar sonidos producido por insectos para estimar las poblaciones de insecto sin tener que remover muestras de granos. El número de sonidos producido por insectos, oídos con un micrófono piezoeléctrico empujado dentro del grano, aumentó a medida que el número de larvas de *Rhyzopertha dominica* (F.), aumentó. Las probabilidades de detección y la exactitud del estimado de la densidad de insectos con el método acústico fue comparable a aquellos obtenidos en un probador patrón de grano.

Nondestructive methods of detecting insects feeding inside kernels of grain during storage include x-ray of insects within the grain (Milner et al. 1950), and measurement of insect-produced carbon dioxide (Bruce et al. 1982) or sounds (Vick et al. 1988). The initial cost of the x-ray machine and the ongoing cost of the x-ray film and chemicals to develop the x-ray film are high and examination of each of the individual grains on the x-ray film for insects is labor intensive. While the cost and labor might be lower for carbon dioxide and acoustical methods than for the x-ray method, x-ray has the added advantages of 1) detection of both live and dead insects (although live insects cannot be distinguished from dead insects) and 2) identification of the species and stage of insect detected. However, eggs and small larvae are generally difficult to distinguish from denser portions of the grain. Also, not all carbon dioxide or sound detected in grain are produced by insects. Adams et al. (1953) suggested that the acoustical method might be used to monitor “. . . grain within storage bins for infestation without sampling or removing the grain from the bins in much the same manner as permanent thermocouple systems are now used for checking the heating of grain in storage.” This potential for automation of insect monitoring with the acoustical method may be a major advantage over the carbon dioxide and x-ray methods.

We investigated whether the insect-produced sounds, heard with a piezoelectric microphone pushed into grain, can be used to detect insect infestations and to estimate insect densities as efficiently as other methods.

MATERIALS AND METHODS

The acoustical system shown in Figure 1 was used for discovery and estimation of the densities of lesser grain borer, *Rhyzopertha dominica* (F.), larvae detecting the feeding sounds they produce. The system was composed of a durable piezoelectric microphone (#9D0576 BNF Enterprises, Peabody, Mass.) mounted on the end of a probe which was pushed into the grain, a battery operated amplifier (Insecta-scope, Sound Technologies Inc., Kilgore, TX) and earphones for listening to insect-produced sounds. A Krohn-Hite model 3700 filter (not shown in Figure 1) was used between the amplifier and earphones to remove frequencies below 1000 hz and above 3000 hz. Feeding sounds were recorded on a Technics magnetic tape recorder, Model RS-B16, equipped with dBx. Magnetic tape recordings of these sounds were analyzed later with a Fast Fourier Transformation (FFT) instrument (Nicolet Model 660A) and a Hewlett Packard vectra computer to compare earphone with instrument counts. The FFT determined the frequency content of the sounds, whereas instrument counts with the Hewlett Packard Vectra computer coupled through a Hewlett Packard universal counter Model 5316A

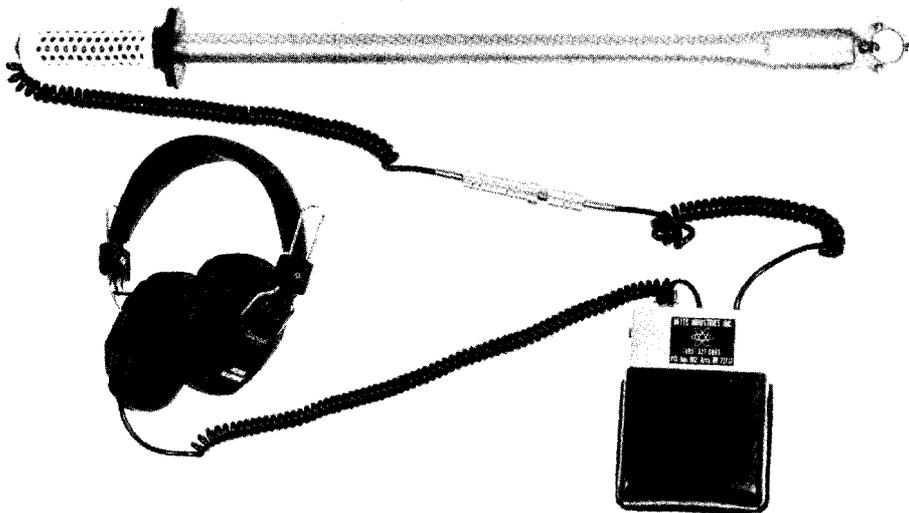


Fig. 1. Acoustical insect detection system including a probe with piezoelectric microphone (Top), battery operated amplifier (Bottom Right), and earphones (Bottom Left).

determined the number of voltage spikes in a predetermined time interval (Webb et al. 1988).

Insect populations of several densities were prepared by diluting lesser grain borer cultures with clean wheat. The actual densities and age structure of the lesser grain borer populations were determined at each density level by x-raying 90 ml samples of wheat. The acoustical system was used 1) to estimate insect densities by counting the number of sounds per unit of time produced by insects at each of nine locations during a one minute interval in a grain mass (10 cm deep by 14 cm diameter) in a four-liter jar or 2) to determine the probability of detection from the fraction of nine locations in a grain mass (10 cm deep by 30 cm diameter) in a 20-liter can at which sounds were heard during 20-s intervals. Both containers were set on 10 cm thick synthetic foam inside a 40 cm diam cylinder of 5 cm thick synthetic foam to dampen background sound. The acoustical probe was inserted 3 cm deep in the grain at the centers and at eight equidistant locations halfway between the centers and edges of the containers. A series of 1:1 dilutions was repeated four times in each size of container.

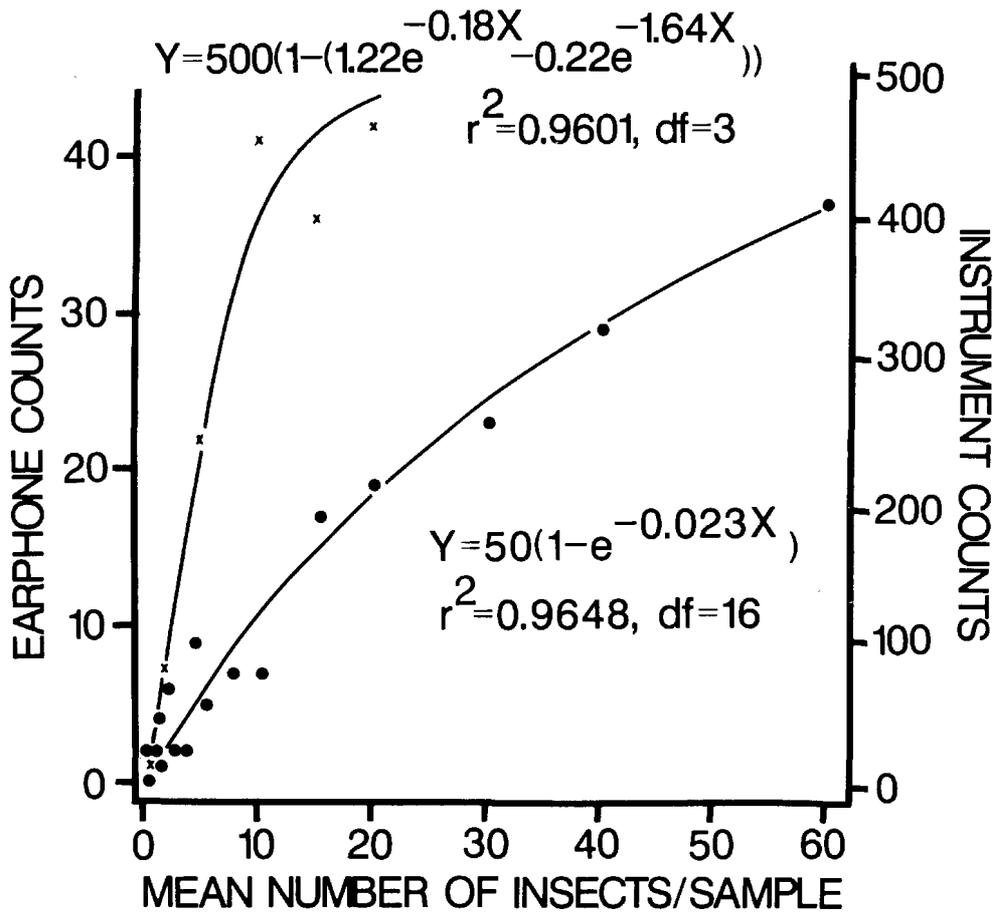


Fig. 2. Relationship between insect density and the number of insect-produced sounds counted with instrument (x) by Vick et al. (1988) or heard in the present study with earphones (.).

RESULTS AND DISCUSSION

The number of sounds heard with the piezoelectric microphone pushed into the grain increased as the density of lesser grain borer larvae increased (Fig. 2). This is consistent with the results of Vick et al. (1988) using an acoustical system which required that grain samples be taken. In both studies, the relationship between the number of sounds or voltage spikes counted and the number of lesser grain borer larvae present was not

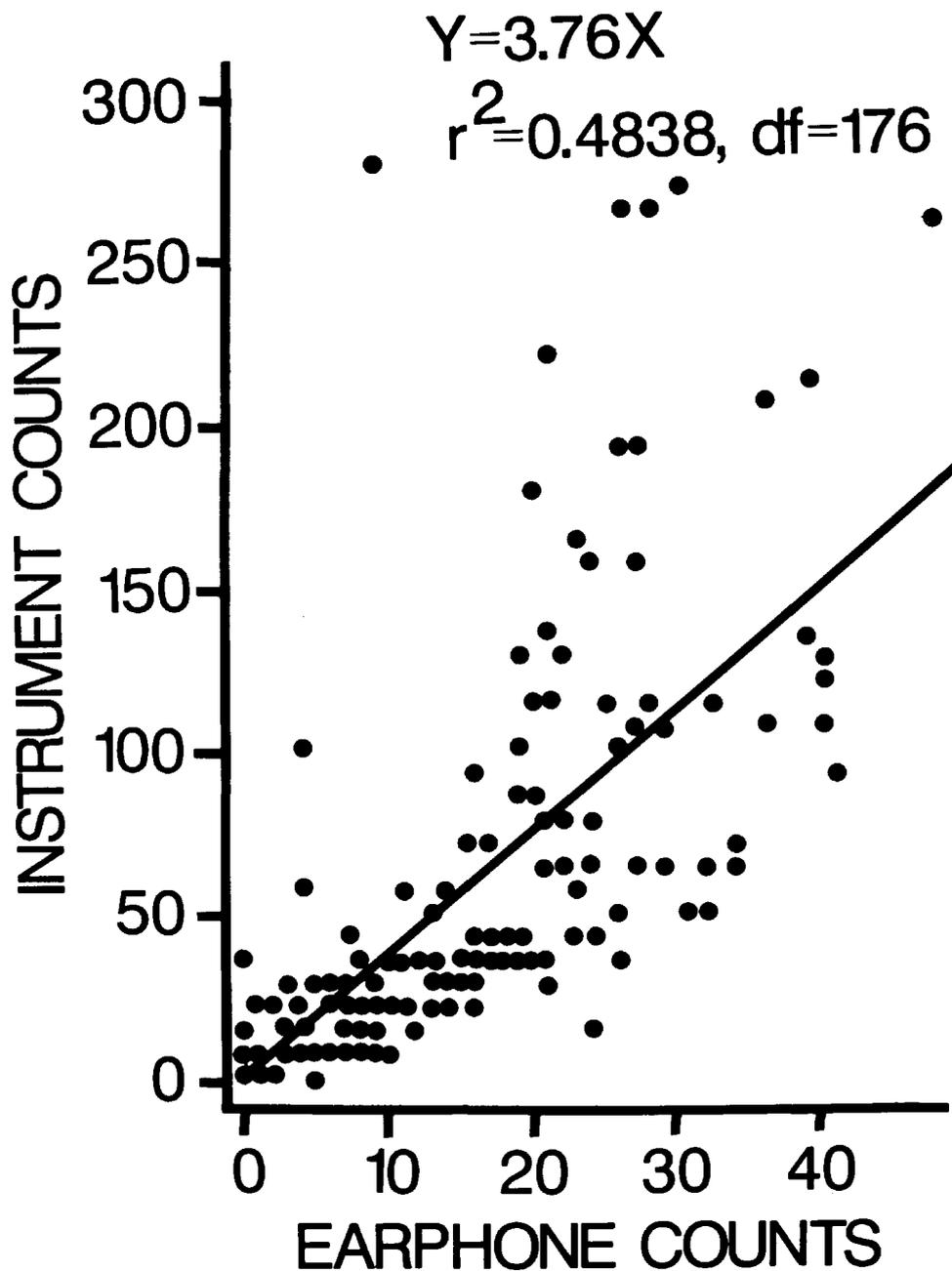


Fig. 3. Relationship between earphone counts of insect-produced sounds and instrument counts of insect-produced sounds in the present study.

linear. The nonlinear increase in insect-produced sounds is probably the results of an increased simultaneous occurrence of sounds of insects which cannot be distinguished as separate sounds.

In the present study, the positive correlation between the number of insect-produced sounds counted with earphones and the number counted with the instrument indicates that our use of earphones instead of instrumentation has not altered the relationship observed between insect sounds and insect density (Fig. 3). The slope of the regression indicates that each insect-produced sound counted with the earphones was actually composed of an average of 3.76 instrument counts. This means that the instrument counts from Vick et al. (1988) must be divided by 3.76 in comparing the two data sets. Even with this adjustment, the counts in this earlier study increased much more rapidly as insect density increased than in the present study. In Vick's earlier study, the number of counts per insect increased rapidly between 0 and 10 insects per 100 ml sample of wheat, but the counts increased more slowly as insect density increased from 10 to 20 insects per sample. Because we are estimating increases in the number of insects by increases in the number of sounds counted, insect densities are estimated

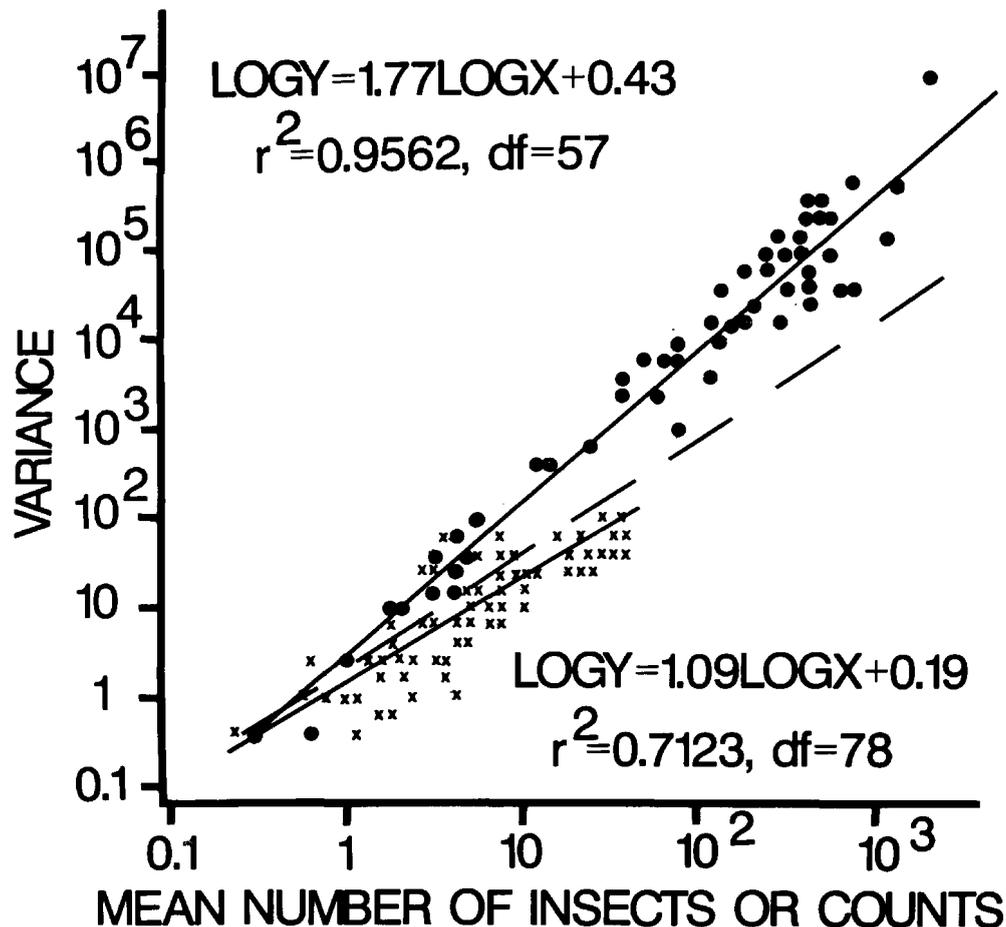


Fig. 4. Regressions of the logarithm of variance in the number of counts or insects (Y) against logarithm of mean (X) number of counts or insects are given for present study (.) and an earlier study (x) by Vick et al (1988). Regression line for other insect sampling methods from Hagstrum et al. (1988) is shown as dashed line for comparison.

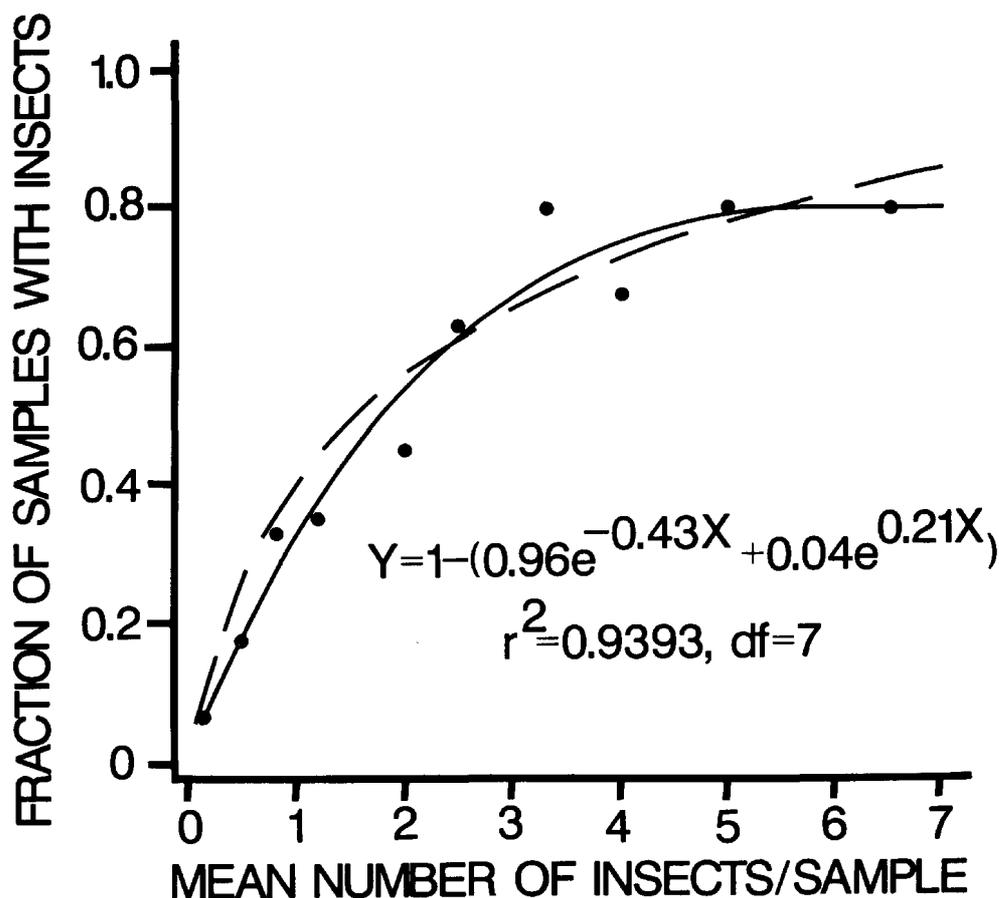


Fig. 5 Regression of the fraction of samples with insects or sounds against mean number of lesser grain borer larvae per sample. The regression line for other sampling methods from Hagstrum et al. (1988) is given as dashed line for comparison.

better between 1 and 10 insects per 100 ml sample of grain than at higher densities. In the present study, over a much broader range of 0 to 60 insects per 100 ml sample of grain, the rate of increase in counts for each increase in insect density was intermediate between rates observed for the 0 to 10 and 10 to 20 density ranges in the earlier study.

The relationship between the mean number of insects or insect-produced sounds per sample and the sample-to-sample variance (Fig. 4) provides a measure of insect distribution and a means of calculating the accuracy of estimation of insect populations (Hagstrum 1987). The relationship between the variance and mean for the acoustical method are very similar to the relationship between variance and mean for other insect sampling methods. Such similarities indicate that the accuracies of the acoustical method will be similar to accuracies for other methods.

We also determined the fraction of samples with insect-produced sounds because this represents the probability of detection. The increase in the fraction of samples with insect-produced sounds as insect density increased is described by the double logarithm model (Fig 5). The similarity of relationship between probability of detection and insect density for acoustical method to that for other insect sampling methods is also shown. Because it is simpler to record the number of locations at which insect-produced sounds are heard (presence or absence sampling) than to count the number of insect-produced sounds at each location, these curves may also be useful in estimating insect densities from the fraction of sample locations with insects.

These studies suggest that with further development the acoustical method might provide a quick and easy way of detecting and perhaps even estimating insect populations in stored grain. In our laboratory studies, the probability of detection and accuracy of estimation with an acoustical method appear to be quite similar to those for other methods.

END NOTE

Mention of a commercial or proprietary product in this paper does not constitute endorsement by the USDA.

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- WEBB, J. C., C. A. LITZKOW, AND D. C. SLAUGHTER. 1988. A computerized acoustical larval detection system. *Applied Engineering in Agriculture.* 4: 268-274.

 ACOUSTIC STUDIES OF *DENDROCTONUS* BARK BEETLES

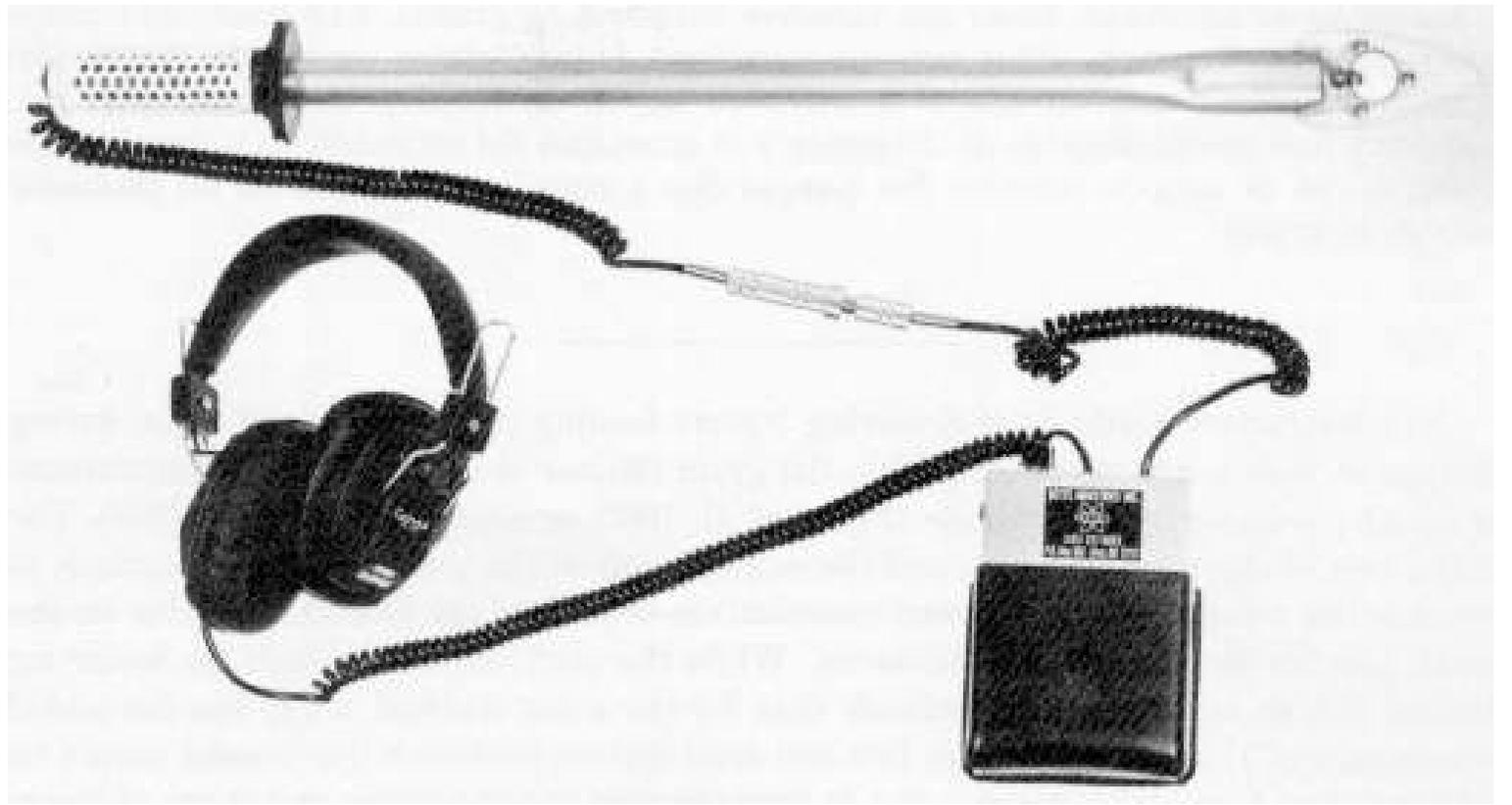
LEE C. RYKER
 478 Willow Street
 Ashland, Oregon 97520

ABSTRACT

The utility of recording, monitoring, and manipulating acoustic signals of destructive bark beetles and some methods of bioassay and analysis related to pheromone research are discussed. J. A. Rudinsky and his research group at Oregon State University utilized particular chirps of males and females to acoustically stimulate pheromone release, for bioassays of odors as possible pheromones, and as indicators of the behavior of beetles hidden under the bark. A summary of the acoustic signals of five species of *Dendroctonus*, *D. pseudotsugae*, *D. ponderosae*, *D. brevicornis*, *D. valens*, and *D. frontalis*, is presented.

RESUMEN

Se discuten la utilidad de grabar, chequear, y manipular las señales acústicas de escarabajos destructores de cortezas y algunos métodos de bio-ensayos y análisis re-



These studies suggest that with further development the acoustical method might provide a quick and easy way of detecting and perhaps even estimating insect populations in stored grain. In our laboratory studies, the probability of detection and accuracy of estimation with an acoustical method appear to be quite similar to those for other methods.

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RESUMEN

Se discuten la utilidad de grabar, chequear, y manipular las señales acústicas de escarabajos destructores de cortezas y algunos métodos de bio-ensayos y análisis re-

lacionados con investigaciones de feromonas. J. A. Rudinsky y su grupo investigador en la Universidad del Estado de Oregon utilizó chirridos particulares de machos y hembras para estimular acusticamente la liberación de feromonas, para bio-ensayos de olores como posible feromonas, y como indicadores del comportamiento de los escarabajos escondidos debajo de la corteza. Se presenta un sumario de las señales acústicas de cinco especies de *Dendroctonus*, *D. pseudotsugae*, *D. ponderosae*, *D. brevicomis*, *D. valens*, y *D. frontalis*.

In keeping with the purpose of this agroacoustic symposium, this paper considers the practical results obtained from the study of insect acoustics by J. A. Rudinsky and his co-workers at Oregon State University. It describes some of the laboratory methods developed to study destructive bark beetles and brings together and reviews the acoustic signals of five species of *Dendroctonus*. The signaling repertoire of several of these beetles has been obscured until now by non-uniform illustration and by being scattered piecemeal through several papers as different types of signals, i.e., stress, attractant, rivalry, territorial, and courtship signals, were described.

Virtually every important timber species of conifer in North America, excluding redwood and sequoia, are attacked by bark beetles, Family Scolytidae (Stark 1982). The economic impact of one species, the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, was \$1.5 million for the states of Oregon and Washington in a non-epidemic year, 1980; and the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, was responsible for over \$13 million of losses of pines the same year (Ruderman 1980). Four epidemics of the Douglas-fir beetle between 1950 and 1969 killed 7.4 billion boardfeet of prime timber valued at over \$3 billion (Furniss & Orr 1970). Losses of timber in the southern U.S. due to the depredations of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, reach similar proportions (Bronson 1986). Attempts to control infestations of bark beetles are made difficult because the insects are inaccessible except during a brief flight period, spending their lives under the bark of trees (Rudinsky 1962). Therefore, research focused upon pheromones as a possible means of control (Rudinsky 1963).

Stridulation by species of *Dendroctonus* was mentioned as early as 1909 (Hopkins 1909), and chirping was identified by Chapman (1955) as a characteristic of males. Allen et al. (1958) published oscillograms of a pair of *D. pseudotsugae* beetles chirping beneath the bark of a Douglas-fir tree. The elytra-abdominal stridulatory apparatus and method of sound production of several species of *Dendroctonus* was described and illustrated by scanning electron micrographs by Michael & Rudinsky (1972). Wilkinson et al. (1967) reported that females of *Ips calligraphus* (Germar) attracted to nuptial chambers chirp to polygynous males guarding the entry. Barr (1969) demonstrated similar behavior for *Ips paraconfusus* (LeConte). She proposed that the gender that invades the host is silent, and the gender that is attracted to the invader has well developed stridulation in sound producing species. Males of polygynous species colonize the trees, and females chirp at the entry; conversely, females of monogynous beetles, such as species of *Dendroctonus*, colonize and males chirp. Barr also described three different types of stridulatory organs occurring on numerous species of bark beetles.

Alexander et al. (1963) reported loud chirps coming from the burrow of a skin beetle, *Trox suberosus* Fabricius, and generalized that the chirps of most beetles would likely be of low intensity, close range sounds. The long range signals of beetles, analogous to the songs employed by crickets and other Orthoptera, were expected to be pheromones, chemical signals (Ryker 1975). With this expectation, the idea of studying acoustic signals of economically impacting species of bark beetles seemed unrewarding. However, the chemical communication system of the Douglas-fir beetle, our number one

target insect at Oregon State University in the 1970's, was so complex and difficult to analyze that it became apparent that an understanding of the acoustic signals might be useful in manipulating the beetle's signaling behavior for pheromone analysis (Rudinsky & Michael 1972).

Rudinsky (1968) made a discovery that underlined the importance of acoustic signals for understanding the behavior of the Douglas-fir beetle. He had attracted thousands of flying beetles to caged logs infested with female Douglas-fir beetles. After he placed a male with each female in her burrow (gallery), the attractiveness of the logs was completely extinguished within minutes. The effect was so dramatic that Rudinsky hypothesized the release of an antiaggregation pheromone, which he called "the mask." Further, he found that the male did not have to enter the female's burrow for the pheromone mask to be produced, but it did have to be able to chirp. Surgically silenced males had no effect, but normal males that chirped continually while on the screen over the entry triggered the masking effect (Rudinsky 1968, 1969, Rudinsky & Ryker 1977).

Acoustic signals still are not considered promising as population control tools, but they became invaluable for analysis of the various pheromone components. Indeed, the communication system of *Dendroctonus* bark beetles cannot be understood or explained without detailed knowledge of the acoustic signals. Acoustic signals were of value: 1) as stimuli to cause males or females to release pheromones for analysis; 2) as indicator responses of beetles during behavioral bioassays of possible chemical stimuli; 3) as indicators of the timing of release of pheromones during natural interaction between the male and female; 4) as indicators of passive vs aggressive behavior during natural beetle interactions; and 5) as releasing signals in the chain of stimuli and responses that allow destructive bark beetles to select host trees, to attack *en masse*, and to regulate the density of the attack, preventing overcrowding and subsequent starvation (Rudinsky 1968, Rudinsky & Ryker 1977, Alcock 1981, Ryker 1984). These studies have resulted in the patenting of methylcyclohexenone as a control pheromone for the Douglas-fir beetle (Rudinsky 1974) and the identification of *endo*-brevicomin and verbenone as anti-aggregation pheromones with potential as control substances for the mountain pine beetle (Ryker & Yandell 1983, Borden et al. 1987).

SOUND RECORDING METHODS

Test beetles were obtained each spring by cutting sections of logs from infested trees, holding them in the warmth of a greenhouse while the brood matured, and then storing the infested logs in walk-in coolers at 4°C until needed. All species of *Dendroctonus* can be sexed by the presence of a sclerotized plectrum on the seventh abdominal tergite only in males (Michael & Rudinsky 1972). Females were introduced into holes drilled into the bark of freshly cut logs and given 36 h to begin a burrow and produce attractive frass (bark shreds and fecal pellets containing tree odors and pheromones). At this point, a Hewlett-Packard 15119A condenser microphone was placed directly above the entry, leaving space for the tiny male to walk beneath it and enter the burrow (Fig. 1). The signal was amplified by a Princeton Applied Research 113 low noise preamplifier, and recorded on a Nagra 4.2L tape recorder at 38 cm/sec tape speed. Recording system components all showed an essentially flat response from about 0.02 to 22 kHz, and frequencies below 0.3 kHz were filtered by the preamplifier settings to minimize stray noise. Signals were monitored via earphones and an oscilloscope, and signal parameters were measured on a Tektronix 5103N storage oscilloscope. Stored tracings were photographed by a Polaroid® camera (Rudinsky & Ryker 1976).

ACOUSTIC STIMULATION METHOD FOR PHEROMONE RELEASE

Pheromone odors were trapped on Porapak-Q for gas chromatographic/mass spec-

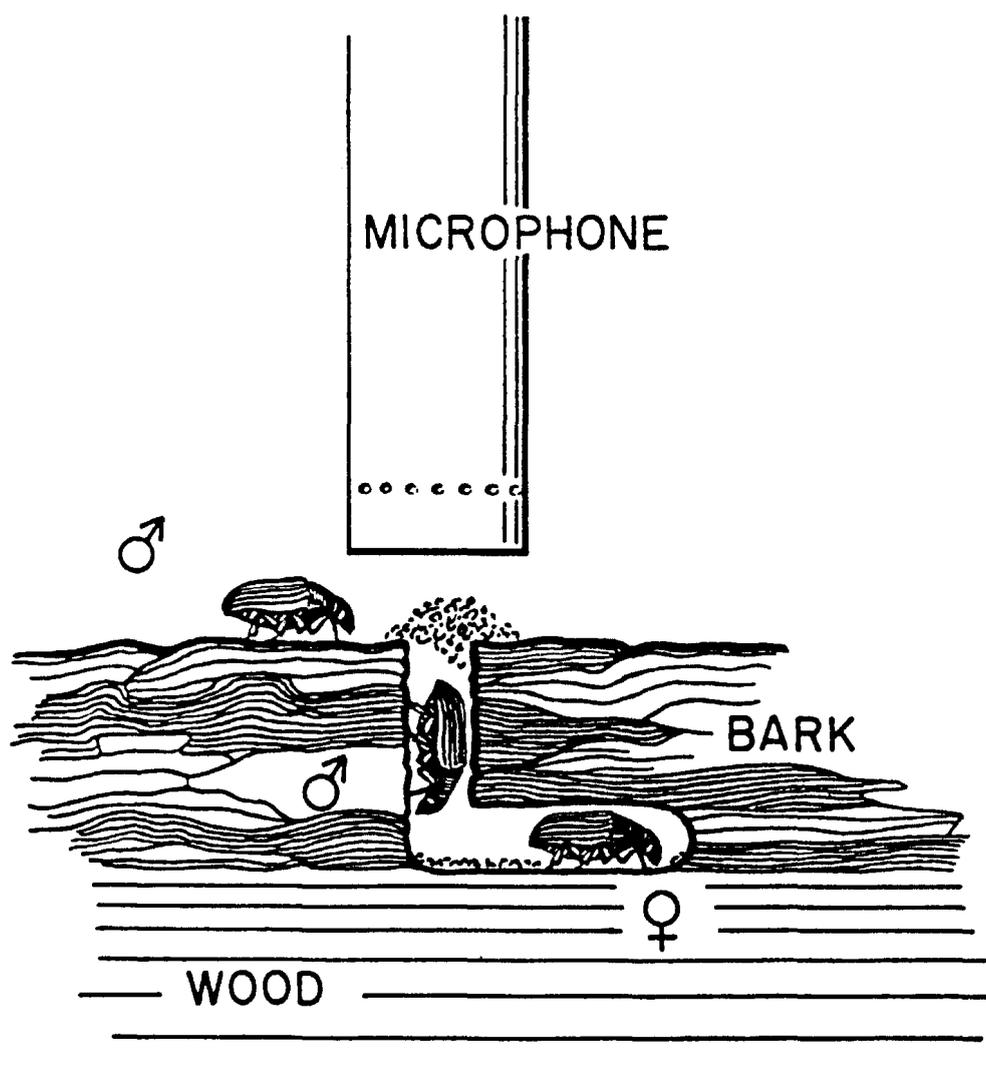


Fig. 1. Method of tape recording and monitoring acoustic signals of *Dendroctonus* bark beetles on a section of log.

trometric analysis easily by placing together a male and female Douglas-fir beetle in a short, paper-lined glass vial and trapping odors from purified air flowing over 30 to 50 such vials within a larger glass container. The male would chirp and jostle the female, and they would each release pheromones. Two males confined in a single vial would chirp and fight, and would also release pheromones. However, females would not release their pheromones if placed together. To trigger pheromone release by single females, Rudinsky stimulated them with recorded male attractant chirps played back through a piezoelectric ceramic disk. The disk was pressed to a silicone rubber gasket over an opening in the glass chamber facing the screened ends of the vials, where it acted as a transducer for recorded chirps (Rudinsky et al. 1973, Ryker et al. 1979) (Fig. 2). Only the chirp of males near the females' burrow successfully triggered females to release their pheromones (Rudinsky et al. 1973).

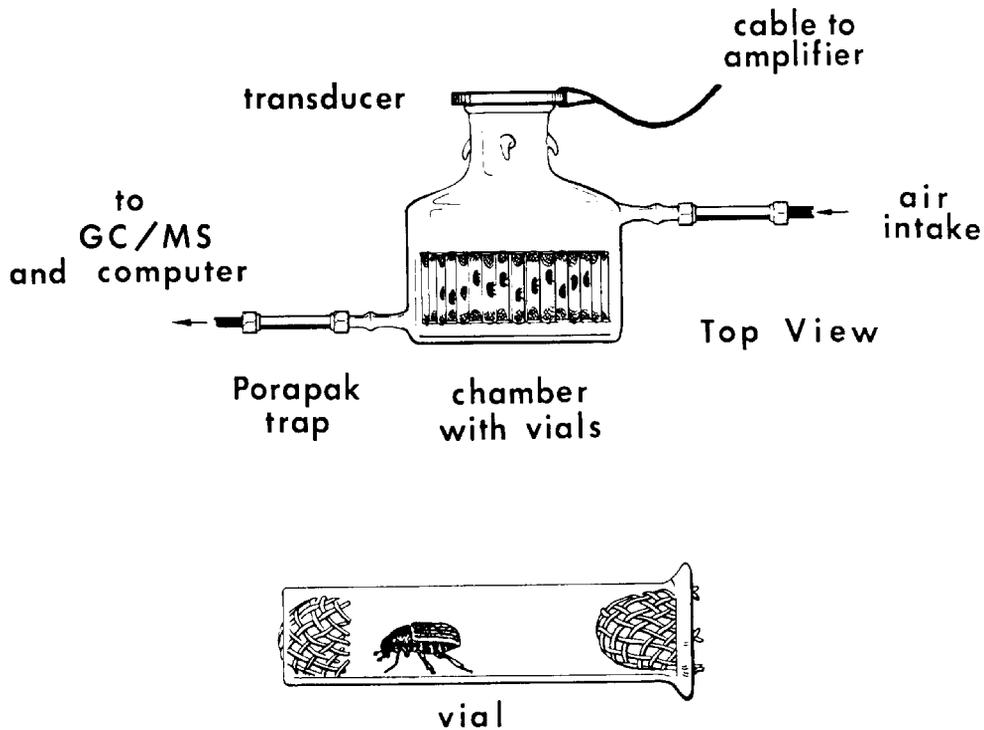


Fig. 2. Glass chamber used to trap pheromones via acoustic stimulation (Ryker et al. 1979) modified from earlier chamber (Rudinsky et al. 1973). The small vial shown has the paper removed from the inside; the wire mesh is stainless steel. A single female is in each vial in this example.

METHOD FOR BIOASSAY OF ODORS VIA CHIRPING RESPONSE

Jantz & Rudinsky (1965) tested the responses of male beetles walking on screening above a tiny vial containing either natural attractive frass or a dilute solution of synthesized chemical odors. Their technique was developed further to include monitoring of the presence or absence of chirping (Rudinsky & Michael 1972), and finally the identification of the type of chirp elicited (Rudinsky & Ryker 1976) (Fig. 3). This technique was very helpful in determining when the beetles switched from being attracted to being repelled as the concentration of certain pheromones increased. For example, the pheromone methylcyclohexenone at only 0.002% concentration in a solution of several other attractants (evaporating at about 1 ng/h) stimulated walking males to double their turning and digging behavior above the test vial, and to double their tendency to emit attractant chirps. Increasing the concentration (and evaporation rate) of methylcyclohexenone 100 times stimulated the male beetles to pass by the vial without stopping and to give aggressive (rivalry) chirps. Flying beetles showed a similar inhibition to attractive traps and logs in the forest in the presence of higher concentrations of this pheromone (Rudinsky & Ryker 1976, 1980). The chirping response of male beetles was similarly used to bioassay candidate odors and concentrations of synthesized pheromones with other species of *Dendroctonus* (Michael & Rudinsky 1972, Rudinsky & Ryker 1977, Rudinsky et al. 1974, Ryker & Yandell 1983).

ACOUSTIC SIGNALS OF *DENDROCTONUS* BARK BEETLES

The Douglas-fir beetle, *D. pseudotsugae* Hopkins, emits five known types of sounds (Fig. 4). Females click intermittently in their burrows in the bark. Clicks appear to be

Monitoring Equipment

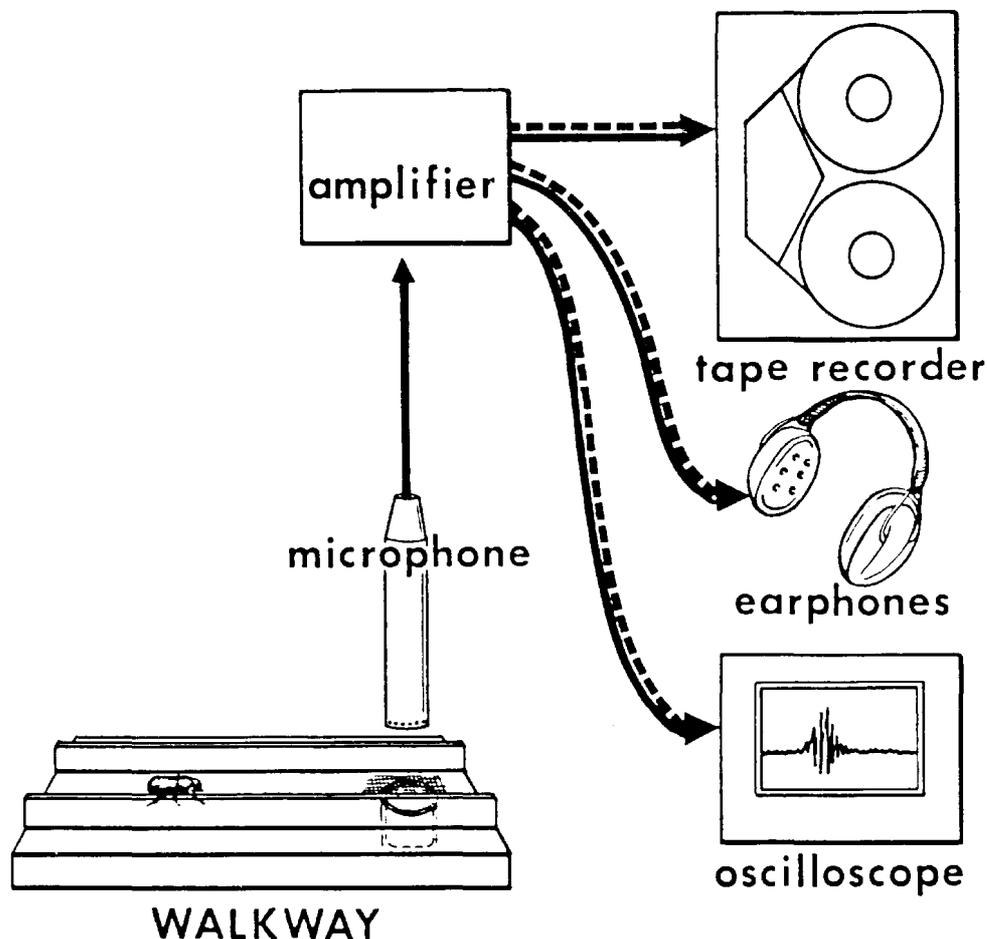
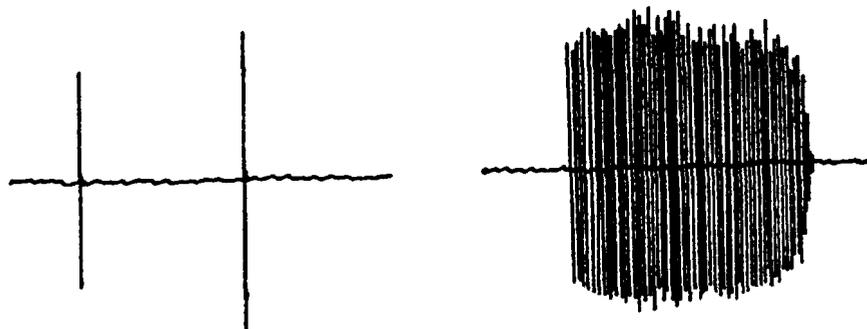


Fig. 3. Olfactory walkway for testing of various concentrations of candidate pheromones, modified for acoustic monitoring (Rudinsky & Ryker 1977).

territorial signals because other females turn away from established, clicking females as they select a place to cut an entry hole. When she is disturbed by digging or scratching sounds, a female increases the frequency of clicking (Rudinsky & Michael 1973). Thus she clicks when the male digs into the entry, causing him to release concentrated methylcyclohexenone as an antiaggregation pheromone (Rudinsky et al. 1976).

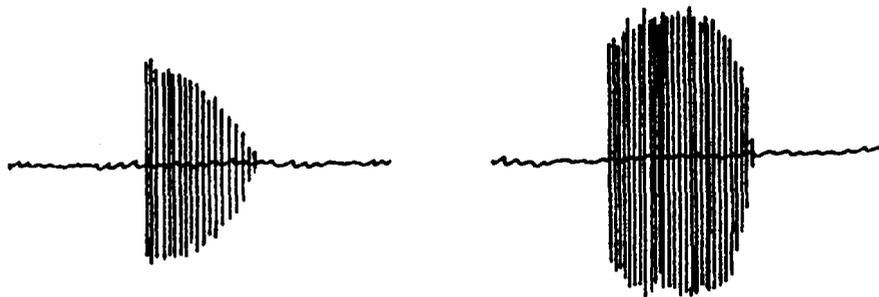
The male attractant chirp is produced by males responding to the pheromones in female frass at the burrow entry (Rudinsky & Michael 1972). A dilute solution of synthesized tree terpenes and pheromones, with methylcyclohexenone in trace amounts, duplicates the effect of frass (Rudinsky 1973, Rudinsky & Michael 1972, Rudinsky & Ryker 1976). This male chirp also signals the female to actively release additional pheromone, including concentrated methylcyclohexenone (Rudinsky et al. 1973), and to stridulate (clicking) loudly (Rudinsky & Michael 1973).

Male Douglas-fir beetles emit an interrupted chirp, the aggressive chirp (= rivalry chirp), when they meet another beetle in a burrow, on which occasion they invariably attack (Fig. 4). Males fight head to head. The female faces away from the male and pushes backward with the heavily armed posterior portion of her elytra, attempting to force the male out of her burrow (Rudinsky & Ryker 1976, Ryker 1984). This is aggres-



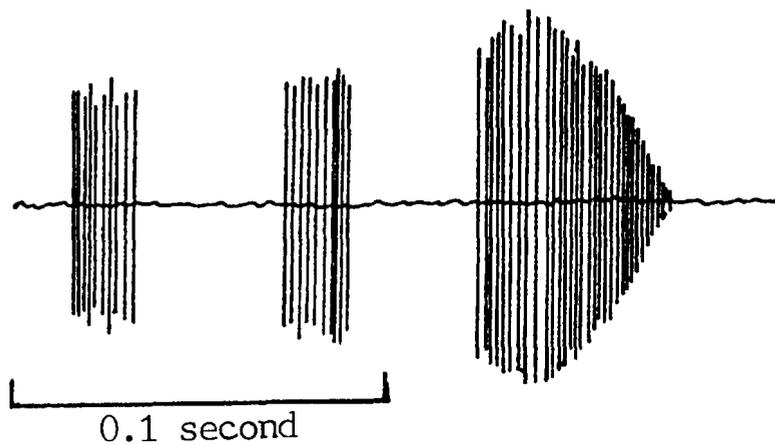
FEMALE CLICKS

MALE STRESS



MALE ATTRACTANT

MALE COURTSHIP



MALE AGGRESSIVE

Fig. 4. Drawings of oscillograms of stridulations of *Dendroctonus pseudotsugae*, the Douglas-fir beetle. All oscillograms in this paper are to the same time scale; the shortest tracings each have a 0.1 sec. sweep duration.

sive courtship. When unmated beetles or two males meet, both sexes release concentrated methylcyclohexenone. This pheromone, even in the absence of another beetle, stimulates males to give the aggressive chirp and to pass by rather than to stop and dig (Rudinsky & Ryker 1976).

The male Douglas-fir beetle courts the female aggressively, with much jostling, biting, and aggressive chirping for about an hour, after which he emits the courtship chirp (Fig. 4). While giving the courtship chirp, the male strokes the female gently. Copulation follows within minutes (Rudinsky & Ryker 1976). Males give the stress chirp when disturbed (Fig. 4) (Rudinsky & Michael 1972).

The mountain pine beetle, *D. ponderosae* Hopkins, males and females each emit two chirps (Fig. 5). Females click intermittently in their burrows in the bark; this is presumed to have a territorial function (Rudinsky & Michael 1973). The female produces a multi-impulse chirp when the entry is disturbed by digging or scratching, and when defending her burrow against intruders, a territorial function. She ceases to chirp only when touched by a chirping male (Ryker & Rudinsky 1976a). If the male beetle does not chirp correctly, the female attacks and repels him from her burrow if possible, chirping continually.

Male mountain pine beetles give the attractant chirp, an interrupted chirp, when stimulated by the odor of female frass or a synthetic pheromone mixture (Michael & Rudinsky 1972, Ryker & Yandell 1983, Yandell 1984). This chirp also accompanies aggressive behavior whenever unmated beetles meet or when rival males fight (Rudinsky et al. 1974). A male also gives this chirp while digging through frass to enter the female's burrow and while attacking his future mate; this aggressive phase of courtship lasts only a few minutes before mating (Ryker & Rudinsky 1976a).

Mountain pine beetle males produce the simple chirp both when disturbed (stress) and during courtship. Within five minutes of contacting the female, the male ceases to attack the female, begins to stroke her, and gives simple chirps. Copulation follows (Ryker & Rudinsky 1976a).

The western pine beetle, *D. brevicornis* LeConte, female has two and the male has three chirps (Fig. 6). Females click intermittently (about 8 clicks per minute) when alone in their burrows. When disturbed by other females boring nearby (Rudinsky & Michael 1973), or when a male enters her burrow, they give a multi-impulse chirp about twice per second.

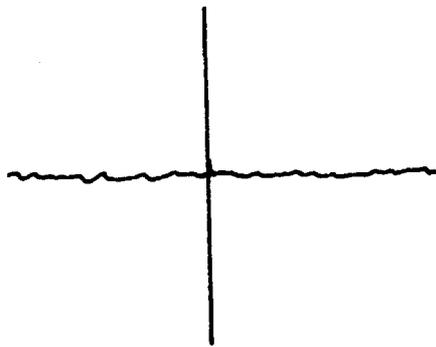
Males emit an interrupted chirp with two or three subchirps when attracted to female frass (attractant) (Rudinsky & Michael 1974) and when courting the female (Fig. 6).

The male rivalry chirp is an interrupted chirp with an average of about five subchirps (Fig. 6) and is given during fighting (Rudinsky & Michael 1974). Males also emit a simple stress chirp when disturbed.

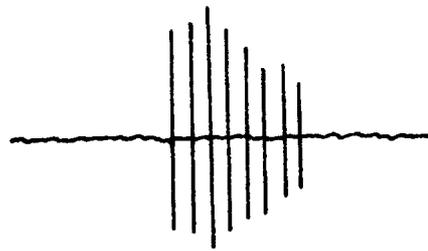
The red turpentine beetle, *D. valens* LeConte, male has two distinctive chirps and the female emits several rather variable sounds (Fig. 7). Males produce a simple chirp when attracted to female frass; the stress chirp given by the male when disturbed is not measurably different (Ryker & Rudinsky 1976b).

The "agreement" chirp is a grating sound emitted by a female when a male is digging and chirping in her entry. This is possibly a territorial signal. When first contacted by a male, females produce a much shorter and less variable chirp, the "greeting" chirp. Females also produced stress chirps, containing only about five pulses of sound (Fig. 7). This is the only species of *Dendroctonus* known to do so.

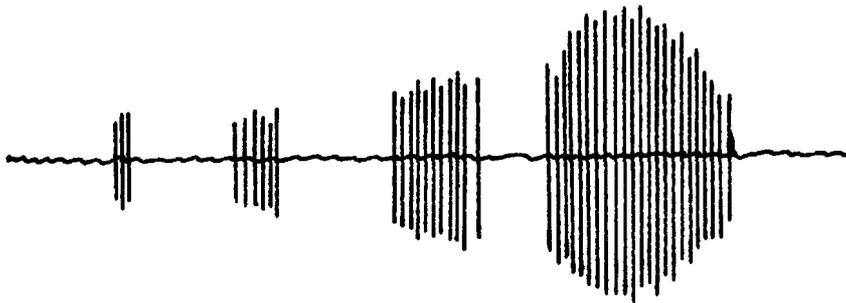
The rivalry or aggressive chirp of male beetles is produced during fighting, as well as during the first 30 seconds of courtship. The entire train of sounds is an interrupted chirp, made by a single motion of the abdomen (Ryker & Rudinsky 1976b).



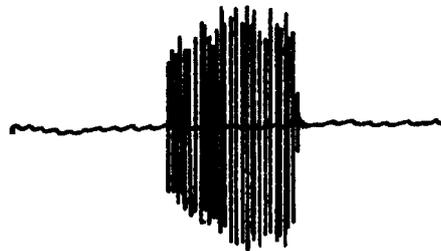
FEMALE CLICK



FEMALE CHIRP



MALE ATTRACTANT AND AGGRESSIVE



MALE SIMPLE CHIRP

Fig. 5. Drawings of oscillograms of stridulations of *Dendroctonus ponderosae*, the mountain pine beetle.

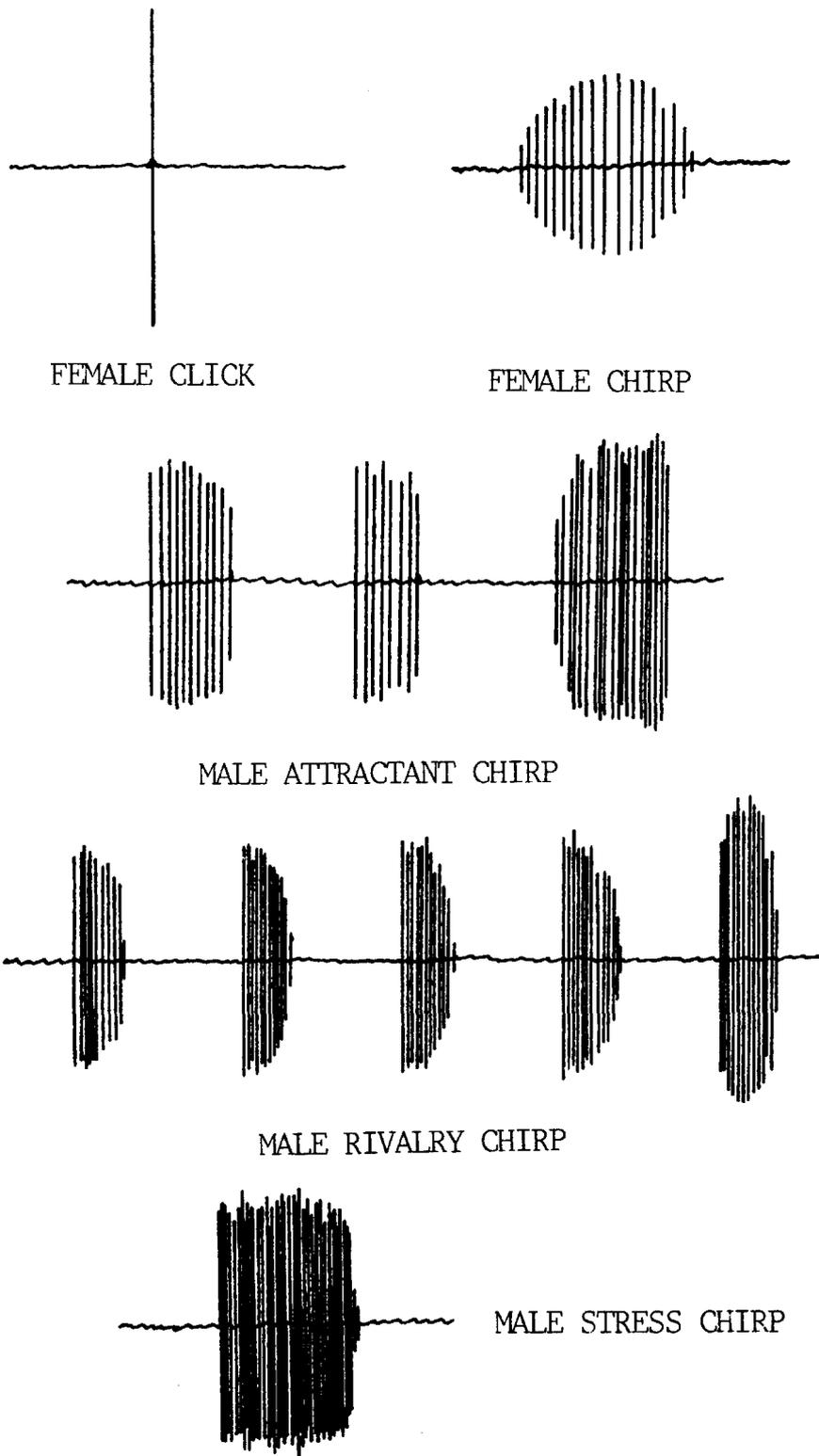


Fig. 6. Drawings of oscillograms of stridulations of *Dendroctonus brevicomis*, the western pine beetle.

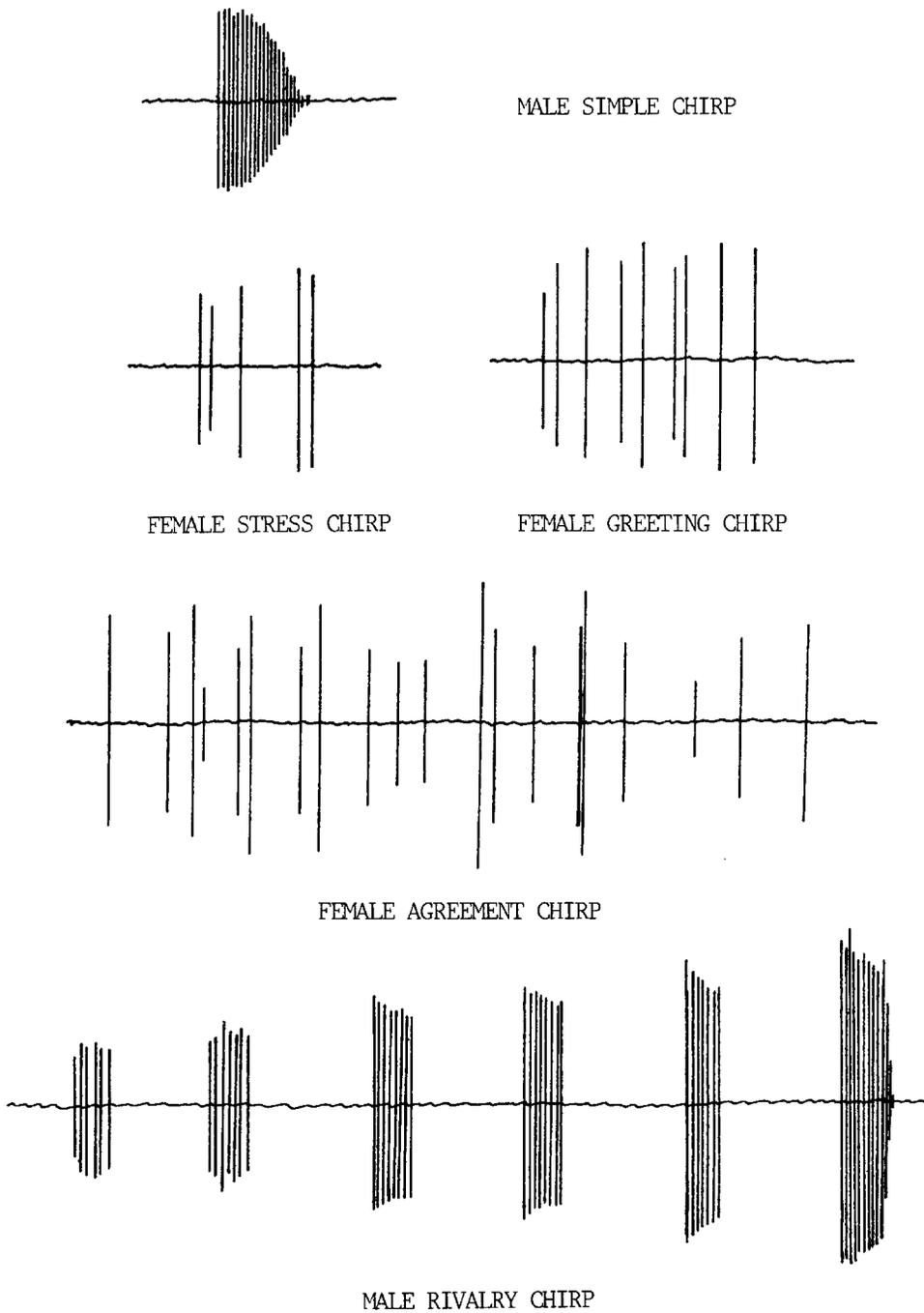


Fig. 7. Drawings of oscillograms of stridulations of *Dendroctonus valens*, the red turpentine beetle.

The southern pine beetle, *D. frontalis* Zimmermann, is diminutive compared to the other species of *Dendroctonus*, but it is a remarkable chirper. Males readily produce many stress chirps when disturbed (Fig. 8). The male attractant chirp is an interrupted chirp produced when the male is digging in the frass of a virgin female (Rudinsky & Michael 1974).

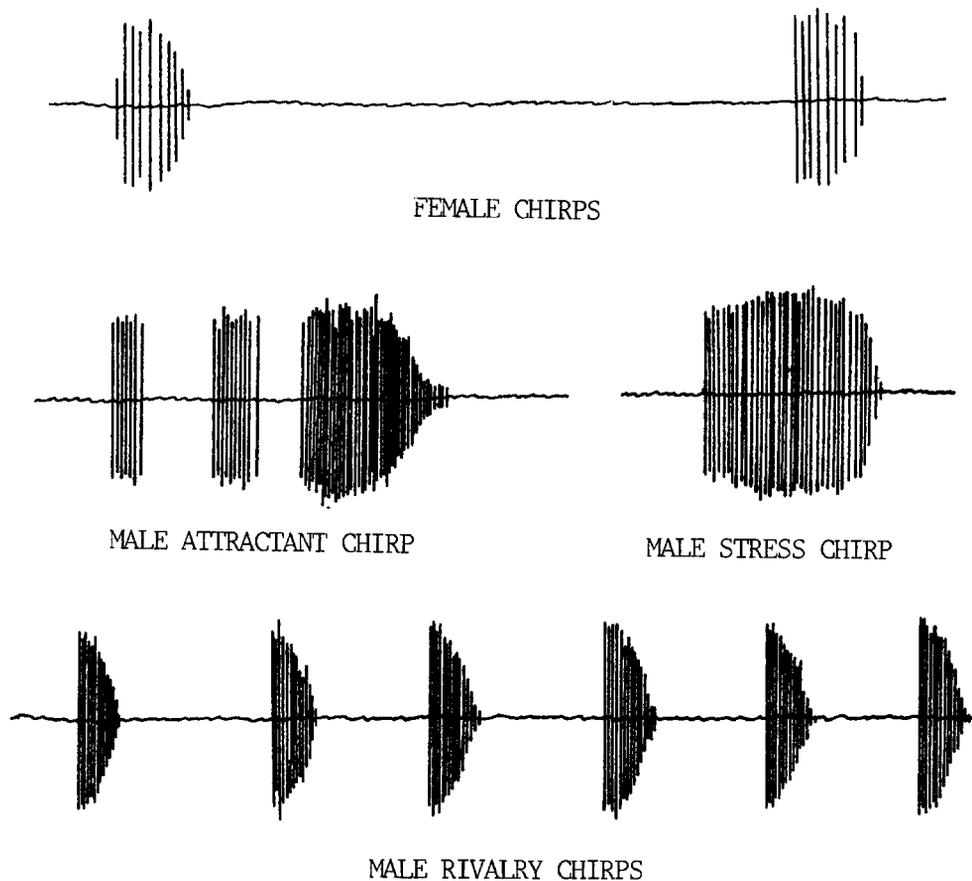


Fig. 8. Drawings of oscillograms of stridulations of *Dendroctonus frontalis*, the southern pine beetle.

A female produces a series of chirps (about eight per second) when a male enters her burrow. Female chirps are probably territorial signals (Rudinsky & Michael 1973).

Males defend their burrows, fighting other males and producing long, fast series of rivalry chirps (Fig. 8). These chirps are high-pitched, brief, and are delivered at a rate of about 16 per second (Rudinsky & Michael 1974, Rudinsky et al. 1974).

FUNCTIONS OF ACOUSTIC SIGNALS

All five species of *Dendroctonus* reviewed in this paper show aggressive behavior in both sexes. Colonizing females compete for limited and ephemeral host material, have territorial clicks or chirps, and attack strangers. Males both fight over control of a female's burrow and test the female for fitness by attacking her (Alcock 1981, Rudinsky & Ryker 1976, Ryker 1984). Specific chirps are associated with fighting; these signals either cease or are replaced by a distinctive courtship signal before mating. This suggests that aggressive chirps are important to the reproductive success of male *Dendroctonus*. Excluding *D. ponderosae*, these species of *Dendroctonus* also have a distinctive signal to the female as they locate the entry of her burrow (attractant chirp). This signal has been shown in two species to trigger an interaction between the female and the male that results in release of antiaggregation pheromones (Rudinsky et al. 1976), thus protecting their brood resources from pressure of over-population and warning

flying beetles to seek more sparsely settled trees. Alcock (1981) gives a convincing argument for individual selection *vs* signal selection for the benefit of the population. Such closely interlocked acoustic and chemical signals are most complex in species of *Dendroctonus* bark beetles that attack and overwhelm living trees *en masse*. Similarly complex development of acoustic and chemical signals, especially territorial and aggressive sounds, might be expected in other highly competitive species of bark beetles (Swedenborg et al. in press).

APPENDIX

A list of acoustic studies of bark beetles other than *Dendroctonus*, arranged by host tree, follows:

On pine: *Ips calligraphus* (Germar), Wilkinson et al. (1967); *Ips paraconfusus* (LeConte), Barr (1969); *Ips pini* (Say), Oester & Rudinsky (1975), Swaby & Rudinsky (1976).

On spruce: *Ips concinnus* (Mannerheim), Oester & Rudinsky (1975, 1979); *Ips plastographus* (LeConte), Oester & Rudinsky (1979); *Ips tridens* (Mannerheim), Oester and Rudinsky (1975, 1979); *Ips typographus* L., Rudinsky (1979); *Polygraphus rufipennis* Kirby, Rudinsky et al. (1978); *Hylurgops rugipennis* (Mannerheim), Oester et al. (1978).

On Douglas-fir: *Pseudohylesinus nebulosus* (LeConte), Oester et al. (1981).

On ash: *Hylesinus oleiperda* Fabricius, Rudinsky & Vallo (1979); *Leperisinus californicus* Swaine and *L. oregonus* Blackman, Vernoff & Rudinsky (1980); *Leperisinus fraxini* Panzer, Rudinsky & Vallo (1979).

On apple: *Scolytus mali* Bechst, Rudinsky et al. (1978b).

On elm: *Hylurgopinus rufipes* (Eichhoff), Swedenborg et al. (in press).

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WHAT DO FRUIT FLY SONGS MEAN?

JOHN SIVINSKI

Insect Attractants, Behavior, and Basic Biology Research Laboratory,
Agricultural Research Service, U.S. Department of Agriculture,
Gainesville, Florida 32604

ABSTRACT

Many flies, including tephritid fruit flies, produce acoustic courtship signals; however, the message these signals transmit is not always clear. Courtship in general is often considered to be a mechanism for species recognition and the prevention of hybridization. Such a proposition suffers from the rarity of sympatric character displacement, the complexity of displays in some species with few close sympatric relatives and the simplicity of courtships in other species with many close sympatric relatives. The theory that displays are sexually selected advertisements of male qualities that females prefer in a mate faces none of these objections. The acoustic signals of male Caribbean fruit flies can be examined from a sexual selection perspective. Females appear to prefer large mates. Both the "calling" and "precopulatory" songs have characteristics that are correlated to male size and females are more likely to react to songs typical of large males. Studies of fruit fly acoustics may serve agriculture either in the development of attractants or by providing criteria to monitor the sexual competitiveness of insects reared for sterile release programs.

RESUMEN

Muchas moscas, incluyendo moscas tefriticas, producen señales acústicas de cortejo; sin embargo, el mensaje transmitido por estas señales no es siempre claro. En general, el cortejo es a menudo considerado ser un mecanismo de reconocimiento de especies y para prevenir la hibridación. Tal proposición sufre de la rareza de la destitución de la característica simpátrica, lo complejo de la demostración de algunas especies con pocos parientes cercanos simpátricos, y la simplicidad de cortejos en otras especies con muchos parientes cercanos simpátricos. La teoría que demostraciones del macho son un anuncio de sus selectas cualidades sexuales que las hembras prefieren en su consorte presenta ninguna de esta objeciones. Las señales acústicas de machos de la mosca del Caribe pueden ser examinadas desde una perspectiva de selección sexual. Las hembras parecen preferir machos grandes. Cantos "llamantes" y "precopulatorios" tienen características que están correlacionadas al tamaño del macho y es más probable que las hembras reaccionen al canto típico de machos grandes. Estudios acústicos de las moscas de fruta pudieran servir a la agricultura ya sea en el desarrollo de atrayentes o proporcionando un criterio para chequear la competitividad sexual de insectos esteriles criados para programas de liberaciones.

Many male flies, including tephritid fruit flies, make sexual courtship sounds. The contexts in which these songs are produced are often well described, but the information being transmitted to listening flies is less well understood. Acoustic and other courtship displays, such as wing waving, colors, and scents, are sometimes considered species isolating mechanisms, i.e., means by which creatures of the same species and opposite sex recognize each other. Calls in translation might be nothing more than, "I am a male species A—I am a male species B," etc.

A model for the evolution of such a song in a fruit fly might start with allopatric speciation (see Mayr 1963). First, a population of flies becomes geographically divided. Suppose, for example, that a fly cannot cross a mountain which arises to bisect its

range. Environments and, hence, selection pressures on the two sides of the mountain may not be identical; perhaps one is warmer or wetter or contains a novel predator. In addition, different mutations might arise in the separated regions from alleles whose frequencies differed in the first place because of genetic bottlenecks so that the raw material of evolution is also different. Over time, the genomes of the two populations diverge. When erosion breeches the mountain and the flies from the two sides mingle there are reproductive consequences arising from their previous isolation—hybrids between the two types may be less fit than offspring produced by same-type parents. Thus flies that only mate with members of their own isolate are at a reproductive advantage and will eventually replace those that do not. After all, the latter are spending time and resources on offspring (should zygotes even develop) that will bear fewer or no grandchildren. Flies that are clearly of a particular type and those that prefer mates that are clearly of their own type can “collaborate” in evolving features, *de novo* or through exaggeration, whose role is to explicitly say “I am a species A.”

This model is appealing because the signals of so many species are recognizably different, even to humans. One can easily assume that these signals are different *because* species are different. However, the argument faces objections when applied to male-produced displays. First, it makes the largely unmet prediction of sympatric character displacement. That is, animals sometimes have similar signals in the parts of their ranges that do not overlap. Where the ranges do overlap, the need for species recognition should force the signals to diverge. Such cases of character displacement are rarely found (e.g. Walker 1974). Second, some of the most complex and elaborate courtships occur in species that have few close relatives and who would have little chance to err by choosing an almost, but not quite, proper mate (Otte 1972, Alcock & Pyle 1979, Thornhill & Alcock 1983, West-Eberhard 1984). A mirror image phenomenon can be observed by anyone watching the flies on a fresh pat of dung or other resource that concentrates insects. Closely related species can often be seen in great density on the fecal surface. The opportunity for error seems quite high, yet the courtship of these insects tends to be relatively simple. (see for example phoretic sphaerocerids of the genus *Borborillus*, Sivinski 1983, 1984, or many of the dung breeding Sarcophagidae, pers. obs.).

If it sometimes seems that species isolation is an insufficient explanation for the variety and complexity of male courtship, what does all its behavioral sound and fury signify? An alternative explanation arises from how much the sexes invest in their offspring. Females produce large gametes. The number of offspring they can have is largely limited by the number of eggs they can generate. Males make small, cheap gametes and the scope of their paternity is largely a function of how many females can be mounted and eggs fertilized. While number of matings is generally important to males, copulatory quantity is often of little concern to females. Rather, females can enhance their success at reproduction by choosing quality mates, i.e., by incorporating the best available genes into their offspring or by obtaining a valuable resource, such as ejaculate-borne proteins from the “wealthiest” male they encounter (Trivers 1972, Thornhill 1976, Sivinski & Smittle 1987).

Assume, then, that at least some courtship displays are advertisements that males produce to convince females that they have the qualities females prefer in a mate. One might imagine that females would be very discriminating, looking for relatively small differences among suitors. Species could be kept separate incidentally by females engaged in making minute distinctions among a subset of males of her own species. Hence the lack of large scale character displacement is less surprising. The elaborate courtship of isolated species poses no difficulty to the female choice/male advertisement model. If there were only one species in the world, it might still evolve complex communications between the sexes. The variety and species-uniqueness of signals may simply be due to

the improbability of selection ever repeating itself exactly during the evolution of independent displays.

There is profit in examining fruit fly songs as "intersexually selected" instruments of persuasion (Sivinski & Burk 1988). In the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Caribfly), there are two male sexual sounds, both produced by wing movement (Webb et al. 1976, Sivinski & Webb 1985a). The "calling song" is made up of repeated bursts (pulse trains). It is sung by males on the leaf territories they defend against interloping males and coincides with the release of pheromone from abdominal glands and everted anal membranes (Burk 1983, Nation 1972, Sivinski 1988, Chuman et al. 1988). Calling song may be sung in the absence of other flies, although it can be continued in the presence of a visiting fly. The "precopulatory song" is a continuous sound made as the male mounts the female and typically lasting until the male genitalia are completely threaded through the female ovipositor, a period averaging a minute and a half (Webb et al. 1984).

What qualities might such songs advertise? One trait that is preferred by females is large size (Burk & Webb 1983). Big males are more likely to mate than smaller rivals in many species of flies (e.g. Sivinski 1984). It is often unclear, however, if bulk wins out in competition with other males for access to females or if it is something favored by females or both. In Caribbean fruit flies the problem is simpler. Females go to males to initiate courtship and so must either prefer big males or be more likely to sense them.

Are there characteristics of the signals that are correlated to large size? In the calling song, the interval between pulse trains is such a correlate. Larger males tend to have shorter intervals (Burk and Webb 1983, see however Webb et al. 1984). The reason is unknown; perhaps with size come greater resources to sustain what must be a more expensive signal. The sound pressure level (SPL) of the precopulatory song is also related to male size, big males being louder (Webb et al. 1984).

Do females use these correlates when choosing a mate? Virgin females are more responsive (i.e., increase movement) to shorter pulse train interval songs. Their activity increases when a recording of a short, but not a long, pulse train interval song is broadcast into their cage (Sivinski et al. 1984). This increased movement is a plausible response to a sound heard at some distance that directs the hearer toward an attractive goal. It is interesting that the papaya fruit fly (*Toxotrypana curvicauda* [Gerstäcker]) sings only as it approaches nearby females. These sounds quiet the female (Sivinski & Webb 1985b). Perhaps these females become still in order to access their approaching suitors. Also of note is a sexual dimorphism in the response of Caribflies to calling sounds. Males become quiet in the presence of the shorter pulse train interval songs, while mated females are not affected by differences in pulse train intervals. This makes it less likely that virgin females are simply startled by the short interval sound and so become agitated. If short pulse train interval songs are both more effective and more energetically expensive, it might be predicted that pulse train intervals would decrease when a male was "certain" a female was observing. This is the case. An individual male will shorten his pulse train intervals in the presence of a female. When another male is close by, the pulse trains themselves are longer in time, and made at a higher frequency, suggesting a between-male communication role for calling song as well (Sivinski & Webb 1986).

The precopulatory song is also an important component of courtship. Its absence in muted (dealated) males leads to a greater number of rejections by females. A calling sound reproduced by a tape recorder at a SPL of 90 dB (OdB re 20 μ pac) broadcast increases female acceptance, but a broadcast at 50 dB does not (Sivinski et al. 1984). Thus, females make sexual decisions on the basis of precopulatory SPL and that SPL is positively correlated to male size.

What agricultural purpose is served by studies of fruit fly sex sounds and an appreciation that not all males and their displays are equally attractive? Studies of this type,

not only on sounds but also visual and pheromonal displays, have at least two potential applications. The first, which is arguably more important in studies of chemical cues, is the manufacture of attractants and more efficient traps, either to monitor pests or to control them. Caribbean fruit fly calling sounds are attractive in themselves. Traps baited only with recorded songs are more effective than silent controls (Webb et al. 1983). It remains to be demonstrated that sounds and pheromone together, for example, can be more attractive than a more conventional chemical cue alone or, if they are, whether it is economically feasible to produce such a trap. The second use is in the quality control of reared insects. A major concern of sterile release programs is that their reared insects be sexually competitive with the wild rivals they encounter in the agricultural arena. While sterile releases are often a very efficient means of fruit fly control, there have been some less spectacular efforts where overflooding ratios have reached thousands of reared for every wild fly and still not succeeded (Burk & Calkins 1982). A possible reason for these expensive failures (and perhaps some overly expensive successes) is the inadequate courtships of the reared flies. A first step in ensuring that competitive flies are released is a description of sexual behavior in a species followed by periodic comparison of factory reared stock wild flies in mating compatibility and competitive tests. In this way, waste can be minimized and the efficiency of programs be enhanced. It may concern *A. suspensa* breeders, for instance, that radiation can increase the calling pulse train interval of irradiated males (Webb et al. 1987). On the other hand, years of domestication in Central American stocks have not dramatically influenced the acoustical signals of the Mediterranean fruit fly *Ceratitidis capitata* (Wied.) (Sivinski et al. 1988).

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SOUND AND THE MOTHS THAT INFEST BEEHIVES

HAYWARD G. SPANGLER
U.S. Department of Agriculture
Agricultural Research Service
Carl Hayden Bee Research Center
2000 E. Allen Road
Tucson, AZ 85719

ABSTRACT

Both lesser wax moth, *Achroia grisella* (F.) and greater wax moth, *Galleria mellonella* L. males produce sounds using tymbals located on their tegulae. Wing movement twists one end of a tymbal causing it to buckle and produce an ultrasonic pulse. Both sexes are equipped with tympanic ears that hear the high-frequency sound. *A. grisella* females use the sound to locate males prior to copulation. In contrast, female *G. mellonella* respond to the sound with wing fanning. This wing fanning sets off a more complex, three-step behavioral sequence that allows the females to locate males by male-produced pheromone. Techniques that make use of the moth-produced sounds to detect and control these pests of bee products include locating calling males with electronic detectors and using acoustically-baited traps to capture receptive females.

RESUMEN

Ambos machos de los gusanos de cera, *Achroia grisella* (F.) y *Galleria mellonella* L., producen sonidos usando timbales localizados en su tégula. El movimiento del ala dobla una punta del timbal causando que se encorve y produzca una pulsación ultrasónica. Ambos sexos están equipados con oídos timpánicos que oyen el sonido de alta frecuencia. Hembras de *A. grisella* usan el sonido para encontrar al macho antes de copular. En contraste, hembras de *G. mellonella* responden al sonido abanicando con las alas. Abanicando con las alas produce una secuencia más compleja de tres etapas que le permite a las hembras encontrar los machos por feromonas producidas por los machos. La técnica que hace uso de los sonidos producidos por las alevillas para detectar y controlar estas plagas de productos de las abejas incluye el localizar a los machos que llaman usando detectores electrónicos y usando trampas de cebos acústicos para capturar las hembras receptoras.

Many insects possess organs that serve as receivers of airborne sounds. In Hemiptera, Orthoptera and Diptera these organs function primarily in intraspecific communication. In Lepidoptera, Neuroptera, Dictyoptera and Coleoptera the organs serve to warn the bearer of the potential threat of a predator. In both groups, however, some insects use their hearing ability for both communication and defense. For example, while some Orthoptera use hearing to warn them of approaching insectivorous bats (Moiseff et al. 1978), certain moths have acquired the additional ability to generate sounds for intraspecific communication.

Although acoustical communication for pair forming is probably uncommon among moths, recent research has exposed a number of demonstrated or suspected cases (See review by Spangler 1988). Most moths are equipped with tympanic ears, which apparently resulted from the selective pressure of echolocating insectivorous bats (Fenton & Fullard 1981). The location of ears, that varies with moth group, can be on the head, metathorax, first, second or seventh abdominal segment of the insect's body. These ears provide moths with the hearing ability needed for ultrasonic communication. Two

pyralid moths, the greater wax moth, *Galleria mellonella* L. and the lesser wax moth, *Achroia grisella* (F.), specifically consume the products of honey bees, *Apis mellifera* L. Both moths have ears which allow them to defend against bats (Spangler and Takesian 1983). Structurally similar to ears of other pyralid moths, these ears are located on the first abdominal sternum (Coro 1973, Coro & Fernandez 1972, Mullen & Tsao 1971a, b). They are sensitive to a wide range of sound frequencies from ca. 20 kHz to over 200 kHz (Spangler and Takesian 1983, Spangler 1984a). This hearing ability suggested that both moths were capable of developing acoustical communication systems. In fact, *A. grisella* was the first moth discovered to have such a system (Dahm et al. 1971, Spangler et al. 1984). However, acoustical communication is not unique to these was moths. Within the subfamily Galleriinae, to which both wax moths belong, acoustical communication may be widespread. Galleriinae is divided into three tribes: Galleriini, Megarthridiini and Tirathabini and contains about 55 genera and 250 species (Hampson 1917, Pajni & Rose 1977, Whalley 1964). Several members of this group which feed on agricultural products are of great economic importance. The rice moth, *Corcyra cephalonica* (Staint.) and *Paralypsa gularis* (Zeller) damage a variety of stored products (Hodges 1979, Smith 1957). Three well-known species consume the stored products of bees. Besides *A. grisella* and *G. mellonella*, *Aphomia sociella* (L.) feeds on the products of bumble bee nests. *Eldana saccharina* Walker, the sugar cane borer, is another well-known economic pest in this group (Sampson & Kumar 1983). In fact intraspecific acoustical communication also appears to occur in a number of distant or unrelated moth groups including Pyralidae, Agaristidae and Noctuidae (Gwynne and Edwards 1986, Bailey 1978, Surlykke & Gogala 1986).

Moths within the Galleriinae subfamily have different sound-producing structures. Although both *A. grisella* and *G. mellonella* have tymbals which produce single sound pulses per wing-stroke (Spangler et al. 1984, Spangler 1985a), *C. cephalonica* has tymbals with nine striations, which buckle in sequence to produce up to 36 pulses of sound per wingbeat (Spangler 1987b) (Fig. 1). *C. cephalonica* is in the tribe Tirathabini while *A. grisella* and *G. mellonella* are in the tribe Galleriini. *E. saccharina* and *A. sociella*, in the tribe Tirathabini, also have striated tymbals (Zagatti 1985). That tymbals or other sound producing mechanisms occur only in male insects, suggests that an intraspecific communication system is present. Only the males of most insects that communicate with sound face the increased risk of parasites or predators attacking the sound source (Burk 1982, Cade 1976).

Both *A. Grisella* and *G. mellonella* wax moths are distributed widely throughout the tropical and temperate regions of the world. Because the larger, faster growing *G. mellonella* seems to out-compete *A. grisella* in most areas of the United States, it causes more damage. But where *A. grisella* predominates, in the extreme Pacific Northwest and at higher elevations, it also causes considerable damage to stored bee comb. Initial studies on sound and wax moths involved attempts to prevent the females from ovipositing near bee colonies and stored bee equipment by triggering their defensive behavior with simulated cries of echolocating bats (Spangler 1984c). However, like similar previous studies on different moth species (Belton & Kempster 1962, Agee & Webb 1969), the moth populations were affected, but habituation to the sound prevented any efficacious control. More recent discoveries that these moths use ultrasound as a component of their mate-calling systems suggests new possibilities for detection and control. However, the role of sound in pair forming behavior is different in *A. grisella* and *G. mellonella*. *A. grisella* males use sound as the primary signal to call females. Male *G. mellonella*, in contrast, use sound to stimulate females to fan their wings, an action which in turn stimulates males to emit pheromone, the primary signal which attracts females (Spangler 1985a, 1987a).

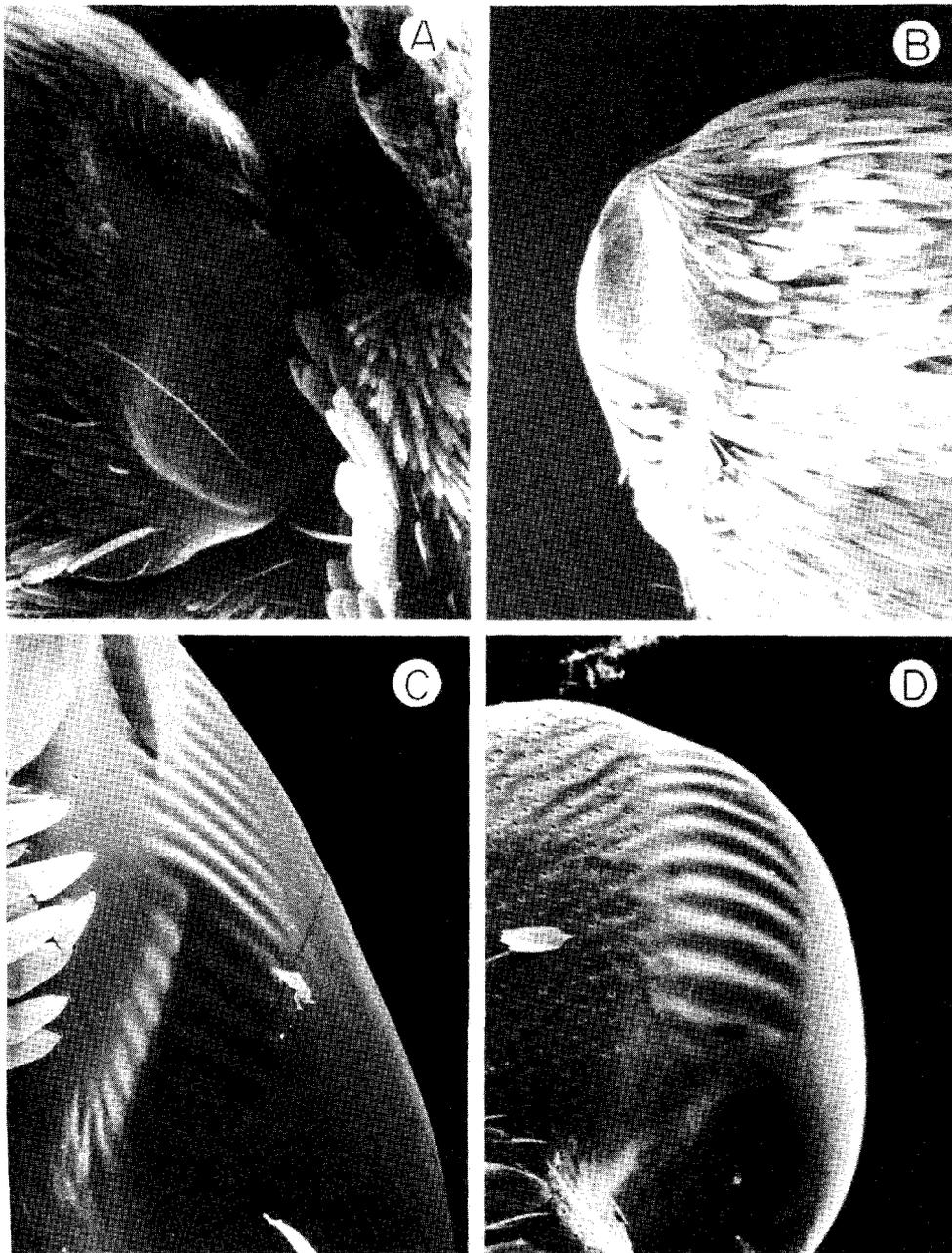


Fig. 1. Tymbals of four species of galleriine moths: A. *Achroia grisella* (by S. L. Buchmann); B. *Galleria mellonella*; C. *Aphomia sociella* (from Zagatti 1985); D. *Coryra cephalonica*.

Different Roles of Sound in the Pair-Forming Behavior of Two Wax Moth Species

Achroia grisella. Each tegula of male *A. grisella* bears an anteriorly situated tymbal (Fig. 1). The tegular-wing coupler, a blade like structure, attaches to the lower, distal order of the tegula, directly below the tymbal (Spangler et al. 1984). When pushed

down by the wing, the coupler causes the tymbal to snap inward (buckle), simultaneously producing an ultrasonic pulse (Spangler and Takessian 1986). Release of pressure on the coupler caused by the wing moving upward, allows the tymbal to snap outward producing a second ultrasonic pulse. Stroboscopic analysis not only confirmed that the tymbal snapped inward during the wing downstroke and outward during the upstroke, but also revealed that the snapping action of the tymbal produced sound about midway through the downstroke and upstroke (Spangler et al. 1984). Exactly how the insect accomplishes this precise timing is not known. It appears, however, that moths produce sound when they elevate the tegular process on the underside of the tegula with a structure referred to as the "striker" on the costal margin of the forewing (Spangler et al. 1984). An air chamber, enclosing not only the back side of the tymbal, but also most of the underside of the tegula, may play a role in the positioning of the striker, although its function is unknown.

Male *A. grisella* produce pulses of 100 kHz sound when calling, one pulse per upstroke and one pulse per downstroke. The wings, held posterior to the normal flying position and fanned through about a 45 degree arc, also release a pheromone (Dahm et al. 1971). The wing action produces a continuous series of sound pulses at a repetition rate of 80-90/sec (Fig. 2). Males prefer calling in subdued light or darkness, but may be found calling at any time under a variety of conditions.

The function of the sound is clearly to call potential mates. In tests using simulated male sound (short pulses of 72 kHz sound at 80/sec), 15 of 21 unmated females ran to the transducer; 13 fanned their wings. No females moved toward muted, pheromone-producing males at the opposite end of the arena. In another test, 16 of 20 unmated females arrived at the sound source plus females, while only one arrived at the muted males plus silent transducer. In a third test, simulated sound plus females was equally attractive to unmated females as sound plus muted males (Spangler et al. 1984). Additional tests over longer distances in greenhouses once again confirmed that simulated

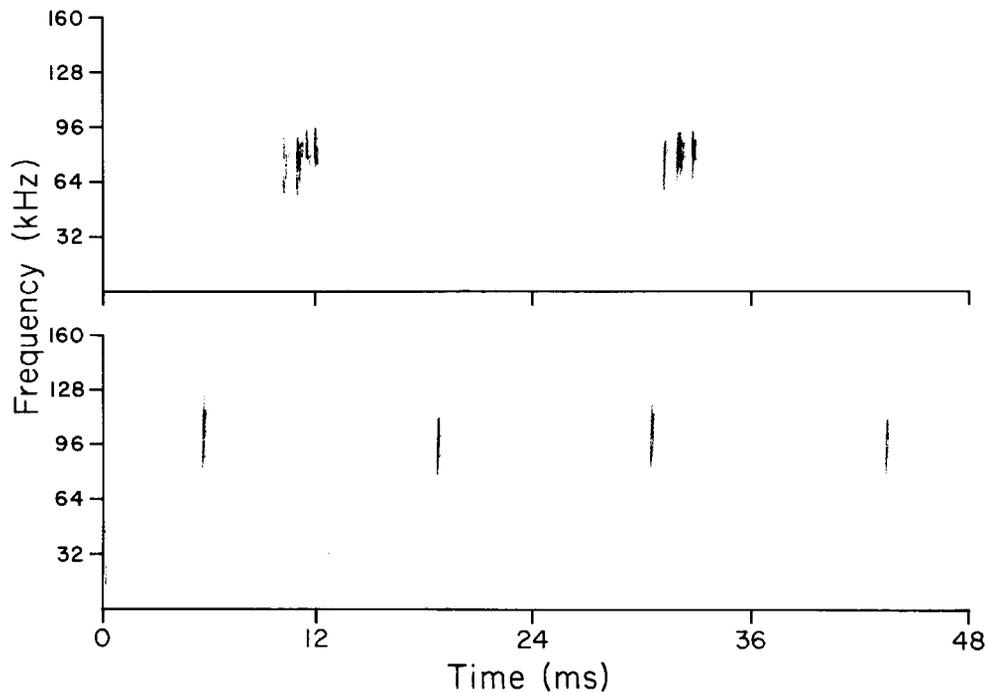


Fig. 2. Sonagram of sounds produced by two species of wax moths: upper trace = *Galleria mellonella*; lower trace = *Achroia grisella*.

sound alone attracted 32% of the females and was much more effective than male pheromone (6%) (Spangler 1984b).

Typically, *A. grisella* males assume calling positions near food (bee hive or stored comb) where emerging females are expected to arrive. They stay near the culture if no bees or only a few bees are present. However, if the bee colony is strong, both sexes run from the hive immediately after emerging, before their wings have expanded. Males outside the hive call from positions on the hive or on nearby vegetation (Greenfield & Coffelt, 1983). From either location, females, activated by male pheromone, search until they locate the sound of a male, then run or fly directly to him (Spangler, 1984b).

Galleria mellonella. Male *G. mellonella* also have sound-producing tymbals on their tegulae which are activated when their forewings push down on the tegular-wing coupler. The sound is released at the bottom of the wingstroke. As a downward moving wing approaches the end of the stroke, it exerts pressure on the tegular-wing coupler, which twists the distal area of the tegula and causes the tymbal to buckle in, producing an ultrasonic pulse. Just as the wing starts back up, the pressure is released, the tymbal snaps out, and a second pulse is produced. Since two tymbals buckle in and snap back out, a train of two, three or four pulses of ultrasound may be released for each wingbeat, depending on how synchronized the wings are in their movement (Spangler 1985a). These pulse trains are produced by subsequent wing beats to form a series or phrase. The number of pulse trains in a phrase ranged from 1 to 18 but averaged 4.03. When many males are inside an enclosure such as a hive containing comb, but few or no living bees, the ultrasonic pulses occur frequently. For example, in an abandoned outdoor bee hive infested with *G. mellonella*, ultrasound production began about 11 minutes after sunset and continued for 8 hours or more. Isolated males still remained silent because stimulation from other wax moths is required before they will produce sound (Spangler 1986a).

G. mellonella males do not fan their wings continuously while they are calling, as do *A. grisella* males. Instead, they extend their wings outward about 45 degrees from their bodies (Flint & Merkle 1983, Spangler 1985a). When wings are in this position, the upper wing surface is at the same height as the top of the moth's body. If no other male or female *G. mellonella* is nearby, a male remains stationary while releasing enough pheromone to attract females. However, if another male or female *G. mellonella* approach the calling male, it may flutter its wings briefly and emit pulses of 75 kHz sound.

The ultrasonic pulses produced by *G. mellonella* males are known to stimulate only wing fanning in unmated females (Spangler 1985a). Although a female may run about, she will not orient directly toward the sound source. Reactions of 100 virgin females in groups of 5 to bursts of 72-kHz sound at 5-second intervals were tested. Eight moths began wing fanning in response to the second sound burst at 5 seconds. Forty-five had responded by 35 seconds; 57 by 1 minute; 77 by 2 minutes; and 83 by 3 minutes. Seventeen moths did not respond within the 3-min test period. The average threshold intensity at which simulated male sounds caused virgin females to wing fan was 69 dB. The frequency within the pulses could be made to vary widely and still elicit virgin female response. Transducers resonating at 25 kHz and 150 kHz caused the females to wing fan and emit low frequency sound with energy peaks at about 40 and 80 Hz (Spangler 1985a).

Males in calling position are sensitive to low-frequency airborne sounds. A recent study showed calling males to be highly sensitive to sound and vibrations from 35 to 100 Hz, a range which includes most of the sound energy released by a wing-fanning female. When sound or vibration simulating the sound of a wing-fanning female was directed toward a male, it responded by increasing the quantities of pheromone it

released from wing glands (Spangler 1987a). Existence of a sexual pheromone in *G. mellonella*, known for some time (Leyrer & Monroe 1973), has been demonstrated to attract females (Finn & Payne 1977).

Males move about and produce ultrasound (Spangler 1986a) and pheromone within a cavity such as an abandoned bee hive. When a nearby female recognizes the sound signal, she fans her wings and produces a low-frequency sound which causes the male to sharply increase the release of pheromone so she can locate him. Outside of the hive, *G. mellonella* males are unlikely to produce sound. However, they release a low-level of pheromone probably sufficient to attract nearby females and they have been observed producing ultrasound only when two males approach each other closely. When a male hears the wingbeat sound of a nearby flying female he may flutter his wings to increase his pheromone dispersal (Spangler 1985a).

Hearing Adaptations and Communication

Whether *A. grisella* females exhibit behaviors either for defending themselves against insectivorous bats or responding to calling males depends, in part, on the pulse repetition rate of the sound they hear. Most females show a sexual attraction above 40 pulses/sec and apparent defensive response below 30 pulses/sec (Spangler et al. 1984). In contrast, while female *G. mellonella* wing fan in response to a single pulse and to repeated pulses with a repetition rate up to about 117/sec, this behavior normally takes place within the protection of the beehive (Spangler 1985a).

A. grisella females can orient, then run or fly to the sound of a calling male from distances of about 1 m (Spangler 1984b, Spangler et al. 1984). They lose ability to orient if one ear is deafened by tearing the tympanum (Spangler & Hippenmeyer 1988). Although they may run and circle in response to sound, they are unlikely to find the source. Although no mechanism for distinguishing sound frequencies, as in Orthoptera (Michelsen 1979), has been identified in any moth ear (Miller 1983, Roeder 1967). Some evidence indicates that *G. mellonella* can distinguish different frequencies because they do not appear to respond defensively when subjected to lower frequency ultrasound of moderate intensity. They do respond with typical defensive behavior at higher frequencies (Spangler 1984a). In contrast, simulations of the very short sound pulses used for *G. mellonella* sexual communication affect the female by causing her to wing fan at low intensities throughout her hearing range (Spangler 1985a).

The Acoustical Environment of Wax Moths

Wax moths of both species usually occur in situations where there are few or no honey bees (the colony has died, abandoned the hive or the comb has been removed from the hive). However the moths do emerge and exist in active bee colonies and females will enter colonies to oviposit. Bees defend their hives against the moths by evicting both larvae and adults in ways that suggest elaborations of existing cleaning behavior (Clark 1984).

Bees produce a wide variety of sounds, some of which are in the hearing range of wax moth ears. However, at the low end of the frequency spectrum there does not appear to be much opportunity for acoustical interactions (Fig. 3). Male greater wax moths respond to airborne sounds from a wing-fanning female at the 40 Hz wingbeat frequency and the second harmonic at 80 Hz (Spangler 1987a). However, they do not respond much at the lowest frequencies produced by wing-fanning bees. In fact, bees produce very little sound energy in the 30-100 Hz range which might interfere with the communication system of greater wax moths.

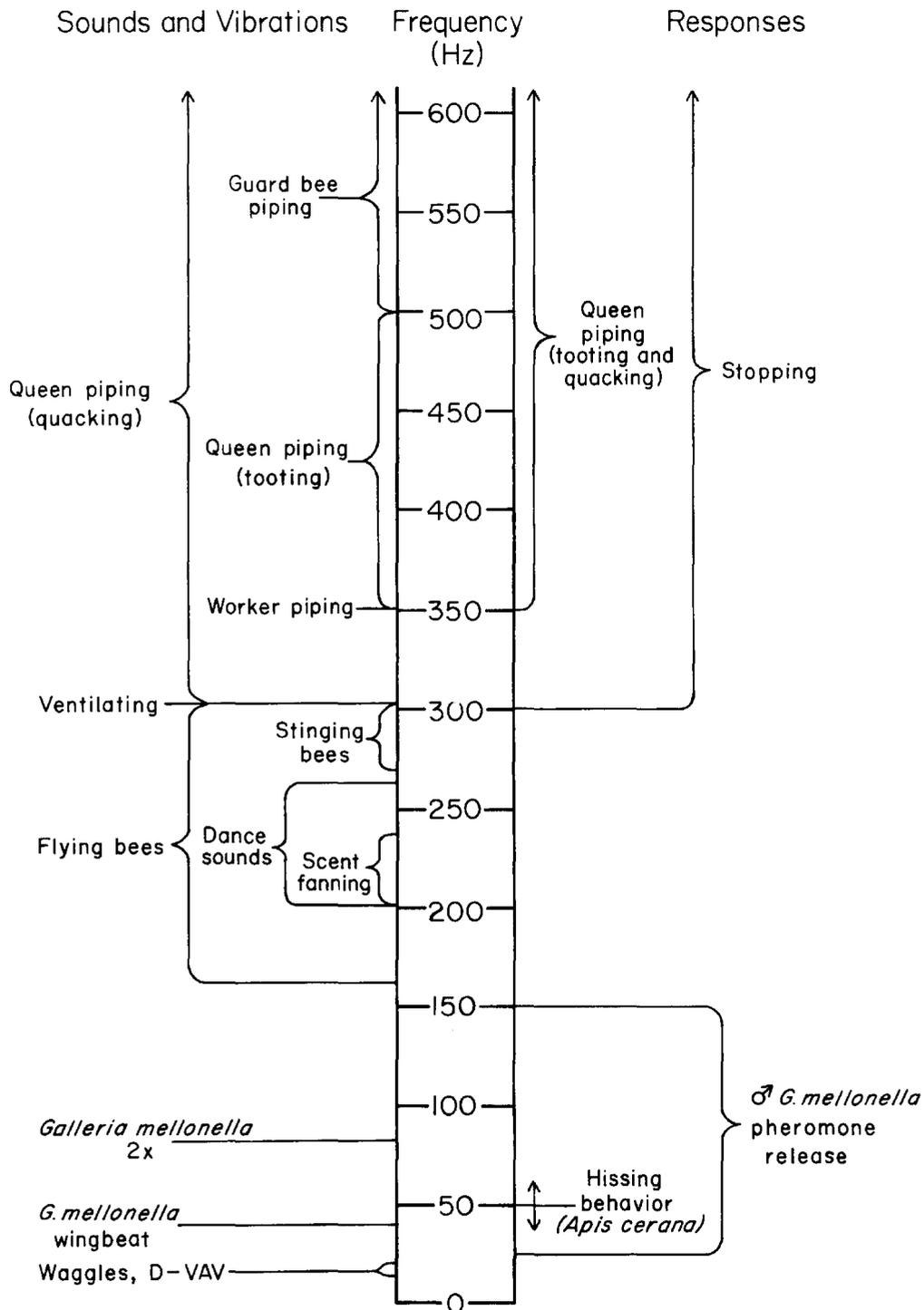


Fig. 3. The low-frequency sounds which occur around a bee colony, including those produced and received by the *Galleria mellonella*. Only ultrasound is important for the *Achroia grisella*.

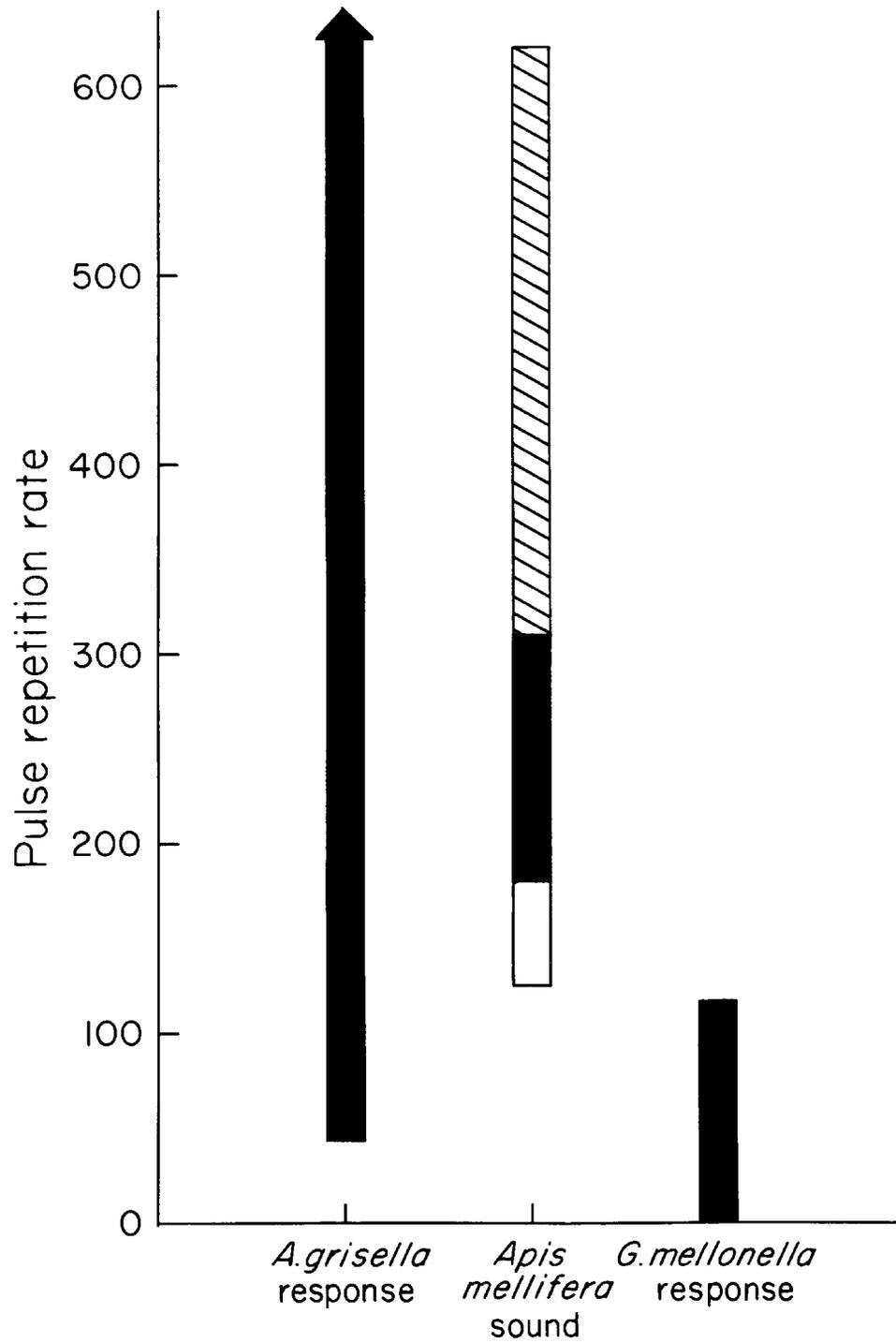


Fig. 4. The repetition rate of ultrasonic pulses produced by wing-fanning bees compared to the response range of two species of wax moths to similar pulses. The open area represents lower frequency wing-fanning by standing bees while the crosshatched area represents two pulses per wingbeat.

On the other hand bees do produce a broad range of ultrasonic frequencies (Spangler 1986b). This sound is in the form of pulses produced when bees fan their wings, either while stationary or when flying. The pulses have their highest intensity from about 25 to 50 kHz. Generally there is one loud pulse per wing beat, although sometimes there is a second pulse of lesser intensity. The pulse repetition rate is typically above the frequency that female greater wax moths responded to by fanning their wings (Fig. 4). However, it seems possible that wax moths obtain some information from the bee sound or respond to it defensively as if a bat were attacking. It is also possible that moths are able to use the ultrasound produced by wing-fanning bees in locating and/or assessing the condition of bee colonies to allow females to decide whether to enter the hive or to oviposit near an opening into the hive.

Although generally honey bees are not sensitive to most airborne sounds and are unlikely to hear any ultrasound, *Apis cerana* detect 50 Hz sound, probably from vibrations on the comb, then respond by hissing (Fuchs & Koeniger 1974). Bee hissing, produced by many bees fanning their wings, is rich in almost continuous ultrasound (Spangler 1986b). Thus, it would seem that bees, particularly when nesting outside of cavities, might be able to detect approaching wax moths and disrupt them by triggering their defensive responses. However, no conclusive evidence has established that the sound from hissing bees affects any insect (Fuchs & Koeniger 1974). Perhaps this is because *G. mellonella* has developed the ability to limit its defensive responses to bee-produced sound (Spangler 1984a).

CONCLUSION

Female *A. grisella* has a sophisticated system for determining the pulse repetition rate of incoming sound to distinguish male moths from bats. Pheromone released by the wing glands of calling males may cause females to search, although they are unlikely to find males without the acoustical signals.

Acoustical techniques have already proven useful in problem situations caused by *A. grisella*. Electronic devices designed to detect male sound allow quick inspection of comb storage facilities for the presence of adult moths (Spangler 1985b). Acoustically baited traps, designed to monitor for the presence of moths in apiaries or storage facilities, may also be possible (Spangler 1984b).

If the intensity of simulated male sound is increased above that of male-produced sound, these acoustically-baited traps might outcompete calling males in attracting enough unmated females from greater distances to reduce population levels.

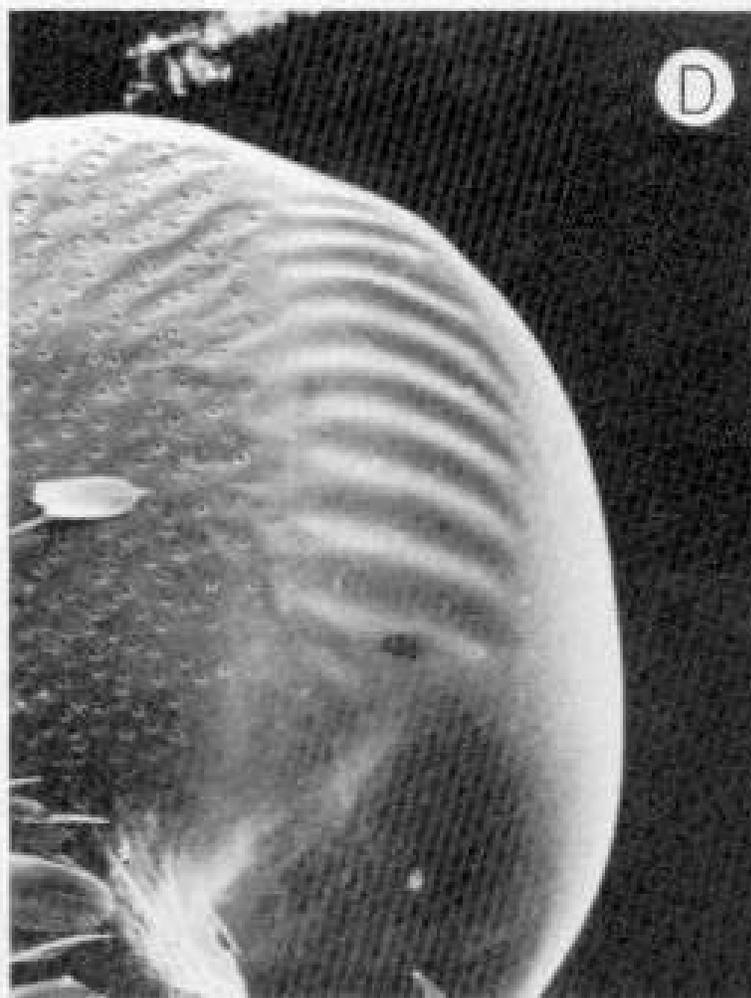
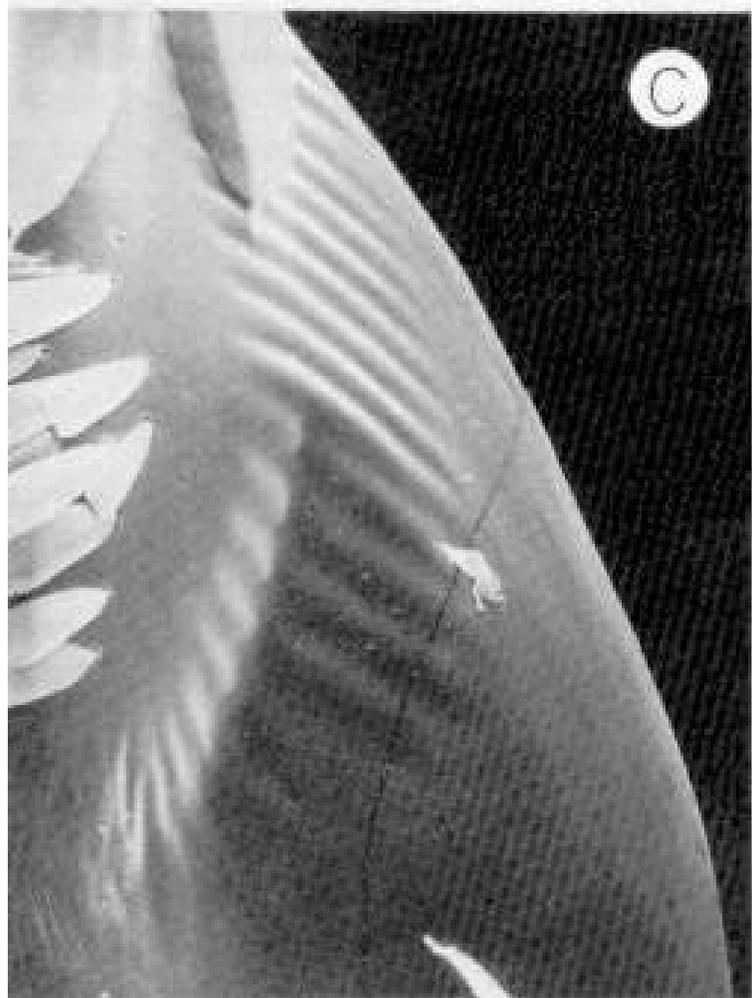
The sexual signalling system of *G. mellonella*, which includes chemical, ultrasonic and low-frequency sound signals, allows it to function efficiently both inside and outside enclosures. Because all of these signals seem to operate at a distance of less than one meter, *G. mellonella*'s communication system is short range. By concentrating their mating activities on or near bee hives, these moths have no need for a long-range sexual signalling system. Because *G. mellonella* produce sound sporadically, the techniques suggested for monitoring, detecting and controlling *A. grisella* males using acoustical equipment seem unlikely to work with *G. mellonella*. While it is possible to locate *A. grisella* males with an electronic detector, isolated male *G. mellonella*, which don't produce ultrasound, cannot be detected by sound until a number of males are present. By that time one can usually detect the odor of their pheromone.

Understanding the biology of these bee pests may lead to yet undiscovered control techniques. If, for example, the odor and/or acoustical signals that attract wax moths to bee colonies could be defined, then appropriate methods to lure the moths into traps could probably be devised.

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A SOUND-INSULATED ROOM SUITABLE FOR USE WITH
AN ACOUSTIC INSECT DETECTION SYSTEM AND
DESIGN PARAMETERS FOR A GRAIN SAMPLE
HOLDING CONTAINER

K. W. VICK¹, J. C. WEBB¹, D. W. HAGSTRUM²,

B. A. WEAVER¹, AND C. A. LITZKOW¹

¹Insect Attractants, Behavior, and Basic Biology

Research Laboratory, Agricultural Research Service,

U.S. Department of Agriculture, Gainesville, Florida 32604

²Grain Marketing Research Laboratory

Agricultural Research Service, U.S. Department of Agriculture

1515 College, Av., Manhattan, Kansas 66502

ABSTRACT

A small, easily constructed sound-insulated room suitable for use in acoustic detection of insect larvae in stored commodities is described. Sound measurements are presented to quantitate the reduction of exogenous noise. The directionality of the acoustical detector used for detection of *Sitophilus oryzae* larvae feeding inside kernels of grain was determined. "Dead spots" were located and suggestions for the design of a sample holder are given which will minimize this problem.

RESUMEN

Se describe un cuarto pequeño, insulado a prueba de ruido, y fácil de construir, para uso en la detección acústica de larvas de insectos en cultivos almacenados. Se presentan medidas del sonido para cuantificar la reducción de ruidos externos. Se determinó la direccionalidad del detector acústico usado para detectar larvas de *Sitophilus oryzae* comiendo dentro de los granos. Se localizaron "lugares muertos" y se hacen sugerencias para el diseño de un porta-muestra que reducirá el problema.

Recent interest in detecting internally feeding insects in kernels of grain has centered on the use of acoustical methods. Although the electronic filtering used by Webb et al. (1988), Vick et al. (1988) and Hagstrum et al. (1988) reduces the ambient and system noise to some extent, the high amplification required to detect the low-power sounds that feeding larvae produce requires that the grain sample be isolated from ambient noise. Although an anechoic chamber would be the ideal environment to use with these detector systems, this often is impractical given constraints of budget and space common at most laboratories. We describe a small sound-insulated room which is easily constructed, inexpensive and suitable for use for insect detection using acoustical methods.

The ideal acoustic detector should be one which detects sounds equally well from all directions. Our preliminary data indicated that our detectors had some degree of directionality. This problem of directionality and consequent dead space in the grain sample holder can be minimized with certain grain sample holder designs provided the directionality of the transducer is known. We present data on this directionality for one type of detector used in this laboratory and suggest a sample holder design to minimize directionality effects for this detector.

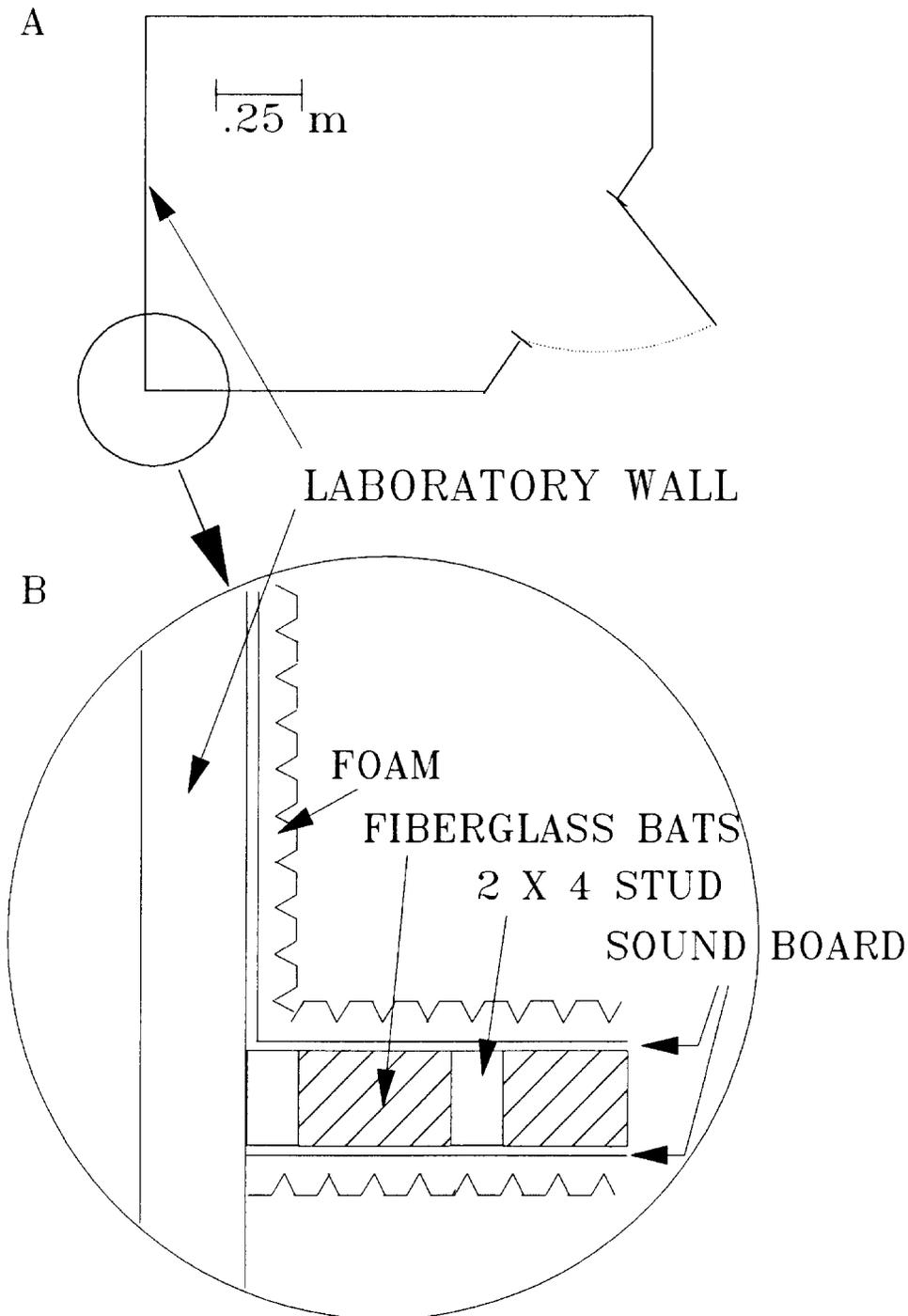


Fig. 1. A. Outline of sound-insulated room. B. Schematic representation of a wall section to show construction details.

METHODS AND MATERIALS

Sitophilus oryzae (L.), the rice weevil, (laboratory stock in culture at this laboratory for 19 years) was reared on wheat incubated at $25 \pm 1^\circ\text{C}$ and $65\% \text{ RH} \pm 5\%$ with a 14:10

(L:D) photoperiod. Adults were allowed to oviposit on uninfested wheat for 7 days and then were removed. Individual kernels were checked for sounds using the acoustical detector system described by Webb et al. (1988) to identify kernels containing larvae 17 days after the adults were removed.

The sound-insulated room was constructed in a corner of our laboratory (Fig. 1). Sound control board (1/2 inch thick, Cellotex Co.) was cut to the size and shape of the floor of the proposed room and laid directly on the concrete floor of the laboratory. A frame for the floor was constructed of pine 2-inch X 4-inch wood (ca. 4 cm X 9 cm) and laid on the sound control board. The floor of the room was constructed of 3/4-inch (ca. 1.8 cm) thick plywood attached to the upper side of the 2 inch X 4 inch frame with nails and glue. The sound-insulated room used 2 existing laboratory walls for its back and right side wall. To these, sound control board was attached with glue. The left side wall (LSW) as well as the front wall (FW) were framed with 2 inch X 4 inch lumber on 16 inch centers (40.5 cm) using standard construction techniques. Three-inch thick fiberglass bats were placed between the studs. The LSW and FW walls were faced inside and out with sound control board. The door was a 28-inch (71 cm), hollow-core veneered door typically used for interior doors in houses. The ceiling was constructed of a 2-inch X 4-inch lumber frame covered inside and out with sound control board. A medium length shag carpet was installed on the floor. The walls and ceiling and door were then covered inside and out with 3-inch thick (ca. 7.5 cm) Sonex acoustical foam (Illbruck Co., 3800 Washington Avenue No., Minneapolis, MN 55412) except that the 2 walls shared with the laboratory were covered only on the inside.

A work bench was constructed in the sound insulated room by stacking 6 standard concrete building blocks into two, three-block high columns (61 cm high) upon which was placed a concrete slab (66 X 40.5 X 5 cm thick) which served as the work surface. The slab was covered with medium length shag carpet. A sound insulated box, 56 cm deep X 54 cm wide X 64 cm tall, constructed of 3/4 inch plywood and lined with 3/4-inch sound control board was placed on the work surface. Access to the box was gained through a hinged door measuring 38 cm wide X 51 cm tall located on the side of the box. The entire box including the door was lined with sound insulation foam. The sample holder was suspended in this box by rubber bands to reduce transmission of building vibrations to the sample holder and microphone.

The sound detection and amplification system used here was described in Vick et al. (1988). The filter, signal processing, and computer system were located outside the sound-insulated room. The sound insulation qualities of the room were tested by feeding a 1 kHz signal from an oscillator into a speaker placed 2 meters in front of the room door at a height of 1.5 meters. The sound in the room was measured with a 1-inch condenser microphone, Bruel & Kjaer (B&K) model 4145, and a microphone amplifier, B&K model 2610. The grain sample holder was made from a copper pail (ca. 0.5 mm wall thickness) with the top slightly larger than the bottom and having the following dimensions: 11 X 9.5 X 13.5 cm, respectively for the diameter of the top and bottom and the height of the sides with the sides tapering towards the bottom. The angle formed by the meeting of the sides and bottom was 93 degrees. A 33-mm diam hole was bored at the center of the bottom of the grain sample holder into which was fitted the plastic diaphragm of the acoustic coupler.

Five wheat kernels, each infested with a 17-26 day-old rice weevil larvae, were placed in a small mesh pouch (ca. 1 X 1 cm with a thickness of one wheat kernel) which was used as the sound source for measuring the effect of distance and angle on sound detection. The same 5 kernels were used throughout the 3 days of testing. The bottom of the sample container was covered with a 1 cm layer of uninfested wheat. The sound source was placed in the middle of the container on top of the layer of wheat and the detectable sounds emanating from the sound source were counted for 2 minutes. The

sound source was moved to a position 2.4 cm from the center towards the edge of the container and the sounds counted as before. A third count was taken at a position 4.6 cm from the center. The counts thus were taken at the center of the container (immediately above the diaphragm) (position A), at a point ca. midway between the middle of the container (position B) and the edge and at a point near the edge (position C). These 3 counts were taken in random order. The voltage spike counts at the 3 horizontal locations were taken at 1, 2, 3, 4, and 5 cm depths, also, in random order. Measurements were replicated 8 times per position.

RESULTS AND DISCUSSION

The sound-insulated room, the sound-insulated box inside the room and even the grain in the grain holder are components of an exogenous noise reduction system. To determine the contributions of the various parts of this system to overall noise reduction, sound levels were measured at various locations inside and outside of the sound-insulated room (Fig. 2). The sound level at the front of the door leading into the sound-insulated room (2 meters from the sound generating oscillator) was 67 dB. The sound level at the microphone in a full grain holder inside the sound-insulated box positioned inside the sound-insulated room was 13 dB for a total reduction of 54 dB. Since each 6 dB reduction represents a 2X reduction in sound power (volume), the entire noise suppression system reduces exogenous noise to a level ca. 0.15% of its original power.

The exogenous noise suppression afforded by this room when used with a sound-insulated box and the present grain sample holder would be sufficient for most larval

COMPARISONS OF NOISE LEVELS

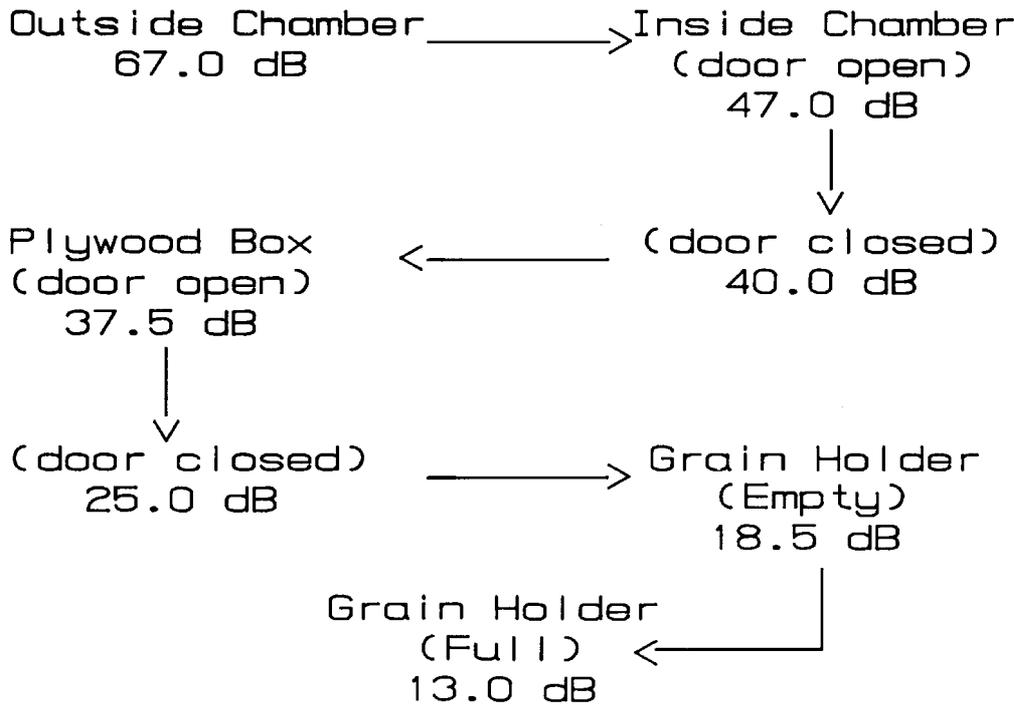


Fig. 2. Flow chart showing effect of each component of the exogenous noise reduction system on the reduction of background noise.

TABLE 1. NUMBER OF LARVAL SOUNDS DETECTED (S.D.) AS A FUNCTION OF HORIZONTAL AND VERTICAL DISTANCE FROM THE ACOUSTICAL DETECTOR.

Depth (cm)	Horizontal distance from center (cm)		
	0	2.4	4.6
1	4640 (1982) ¹	312 (474)	4 (7)
2	1635 (648)	180 (181)	7 (14)
3	1174 (1307)	101 (117)	7 (11)
4	814 (1022)	88 (105)	23 (28)
5	154 (174)	95 (114)	22 (27)

¹Number of larval sounds as determined by number of voltage spikes

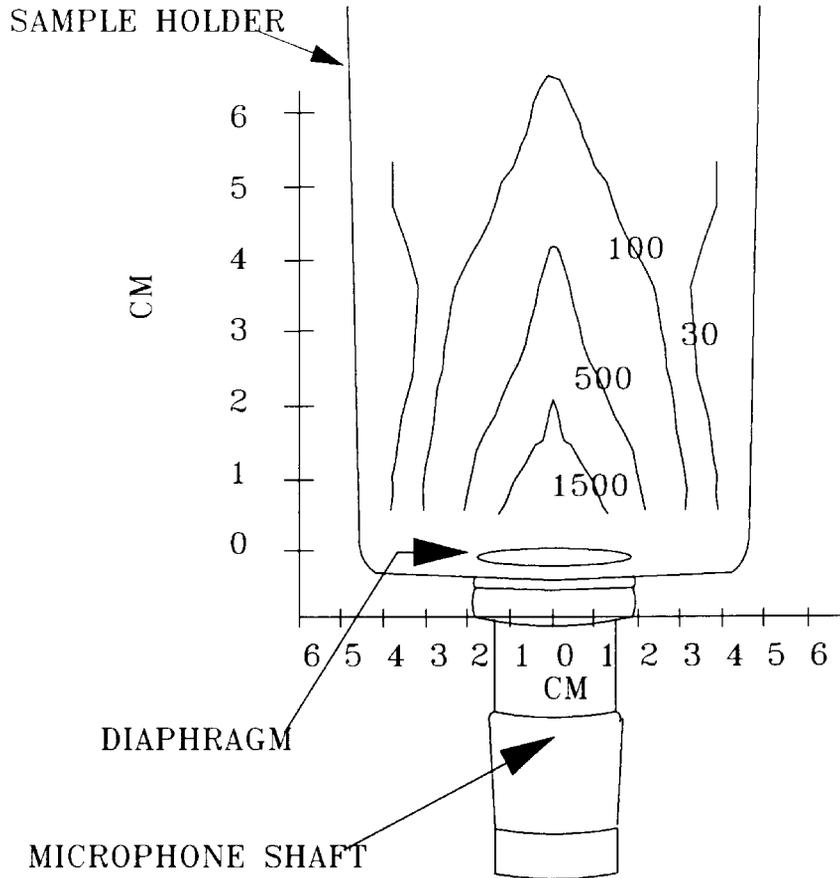
detection needs. Routine use of this room in our laboratory has shown that normal laboratory work, including the normal operation of laboratory equipment (refrigerators, freezers, etc.) and conversation, can be carried out in the laboratory without interfering with sound counts by the sound detection system in the insulated room. Problems might develop if the amplification had to be set at very high levels for some reason (i.e. to detect very young larvae). Extensive testing of the system with uninfested grain in the sample holder did yield rare spurious sound spikes which seemed to be attributable to building vibrations possibly made worse by the fact that this room is located on the second floor. In our situation these spurious sound spikes were sufficiently rare that they were easily identified as spurious sound spikes by the normal replication of the experiments. In cases where building vibrations are common enough to be troublesome, the problem might be solved by suspending the sound-insulated box from the ceiling of the sound-insulated room by elastic bands.

The extent that sounds could be detected was both a function of distance of the sound source from the diaphragm and angle of the sound source to a vertical perpendicular line in the center of the grain mass of the sample holder. Although the number of sounds detected decreased as the sound source was moved away from the acoustic coupler (Table 1), the distance of the sound source from the detector was not as important in this regard as the angle of the detector in relation to the sound source. The greatest sensitivity occurred when the sound source was at 0 degree incidence to the detector angle and decreased as the angle increased. This effect is especially apparent for the results at position C (4.6 cm, Table 1). As the depth increased from 1 to 5 cm, the distance from the sound source to the acoustic coupler increased but the angle decreased. The increase in sound counts with decreasing angle (even though the distance increased) indicates that in sample holder design, one of the top priorities should be the elimination of "dead spots", even if the design change would place some grain at a greater distance from the detector.

The log of the number of voltage spikes (Table 1) was plotted against the distance of the infested kernels from a zero degree incidence perpendicular line running from the detector up into the grain mass of the sample holder. Regression lines (not shown) were eye-fitted for grain depths of 1, 2, 3, 4, and 5 m. Thus from the resulting 5 regression lines one could estimate for each of the grain depths the number of sounds expected when the sound source was placed at positions A, B, or C (0, 2.4 and 4.6 cm, respectively, from Table 1) or at any position in between. Conversely, one could estimate at what point between position A and the sample holder wall that a given number of sounds would be detected.

Figure 3 illustrates the effect of detector directionality with "isobars" drawn for 1500, 1000, 100 and 30 counts expected from our standard insect sound source. A con-

INSECT DETECTOR FOR GRAIN



POINTS ON SAME LINE YIELD SAME NUMBER OF COUNTS

Fig. 3. Schematic diagram of the grain sample holder used in this study. A constant sound source when placed anywhere on each of the lines would yield sound counts equivalent to any other point on the same line.

stant sound source would give a constant number of voltage spike counts at any point on each of the lines shown. This figure dramatically illustrates the need to eliminate the "dead spot" formed at the angle where the bottom and sides of the container join. A more satisfactory shape for the sample holder would be a cone shaped vessel that eliminates the acute bottom to side angle, even if the total depth of the container had to be increased to hold the same quantity of grain sample.

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ACOUSTIC TRAPS FOR AGRICULTURALLY IMPORTANT INSECTS

THOMAS J. WALKER
University of Florida
Gainesville, Florida 32611-0143

ABSTRACT

Development of sound-baited traps for insects has lagged behind that of light- and chemical-baited traps. The principal successes for acoustic traps have been with mole crickets (Gryllotalpidae), field crickets (Gryllidae), and orniine flies (Tachinidae). The crickets are attracted to the conspecific calling song and the flies to the calling songs of their hosts. Electronic sound synthesizers facilitate routine operation of acoustic traps, and increasing the intensity of the sound far above the levels of the natural call greatly increases the numbers trapped. Acoustic traps are most likely to be useful for species that exhibit long-range phonotaxis under natural conditions. Acoustic traps are unlikely to be cost-effective for control but have proved valuable in studying behavior and ecology, collecting specimens, and monitoring populations.

RESUMEN

El desarrollo de trampas cebadas con sonido está más atrasado que trampas de luz o cebadas con productos químicos. El éxito principal de trampas acústicas ha sido con los topogrillos (Grillotalpida), grillos de campo (Grillida) y con moscas Taquínidas. Los grillos son atraídos a los cantos coespecíficos y las moscas al canto de su hospedero. Los sintetizadores electrónicos de sonido facilitan la rutina de la operación de trampas acústicas, y aumentan la intensidad del sonido mucho más que los niveles del llamado natural, aumentando el número de atrapados. Es más probable que trampas acústicas sean más útiles para especies que demuestren una fonotaxis de largo alcance bajo condiciones naturales. Es improbable que el costo de trampas acústicas valga la pena, pero han demostrado ser valiosas en estudios ecológicos y de comportamiento, en la colección de muestras, y en el chequeo de poblaciones.

Traps baited with lights or chemicals are widely used to collect insects and to monitor their populations. Light traps catch a wide variety of insects that generally are attracted in small numbers; why light attracts insects and from how far are poorly understood (but see Baker 1985). On the other hand, chemical traps generally trap one or a few

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Traps baited with lights or chemicals are widely used to collect insects and to monitor their populations. Light traps catch a wide variety of insects that generally are attracted in small numbers; why light attracts insects and from how far are poorly understood (but see Baker 1985). On the other hand, chemical traps generally trap one or a few

kinds of insects, frequently in large numbers; this is because chemical baits simulate specific sex pheromones or chemicals released by particular foods. Individuals are often attracted from 100 m or more. Acoustic traps are similar to chemical traps in that they generally catch one or a few species, often in large numbers. Acoustic baits simulate the mating call of the captured species or of the prey or host species.

In this paper I review the development and use of sound-baited insect traps, compare the principal components of successful traps, and consider potential uses and limitations of acoustic traps for agricultural insects.

A HISTORY OF SOUND TRAPS FOR INSECTS

Kahn & Offenhauser (1949; also Offenhauser & Kahn 1949) were apparently first to field test a sound-baited trap. In a swamp in Cuba, they used a recording of the flight sound of an *Anopheles albimanus* female to attract mosquitoes to a high-voltage electrified screen. Their equipment was crude by today's standards—they played a 78 rpm acetate disk on a record changer. Nonetheless, they killed more mosquitoes in the peak 10-minute interval of trapping than a nearby cattle-baited trap caught in a week. Because phonotaxis in mosquitoes is mainly a matter of males seeking a mate by homing on the female's flight sound, the mosquitoes Offenhauser & Kahn killed were principally males—rather than blood-seeking, disease-carrying, egg-laying females. In spite of this limitation, Belton (1967) and, more recently, Ikeshoji and co-workers (Ikeshoji et al. 1985, Ikeshoji 1986, Ikeshoji & Yap 1987) further developed and field-tested sound traps for mosquitoes. Such traps could reduce mosquito populations by reducing fertility of females, either by removing or chemically sterilizing attracted males.

The first acoustic traps developed for agricultural insects were for the mole crickets, *Scapteriscus acletus* and *S. vicinus*, which are important pests of pastures and crops in the southeastern United States (Ulagaraj & Walker 1973, Walker 1982). These traps (e.g., Fig. 1) broadcast the real or imitation calling song of the male and attract and catch flying mole crickets of both sexes. A standard trapping station, consisting of one *S. acletus* trap and one *S. vicinus* trap, generally yields thousands of mole crickets in a year; catches of hundreds during one evening are not uncommon. The record catch of *S. acletus* for one station in one night is 3,297; for *S. vicinus*, 2,174 (Walker 1982, and unpublished). Forrest (1983a) and Chukanov & Zhantiev (1987) trapped mole crickets of other species (*Scapteriscus* spp. and *Gryllotalpa* spp.) that flew or walked to reproductions of their calling songs.

A major use of acoustic traps for mole crickets has been to acquire living material for research. Adult mole crickets are exceedingly difficult to collect by other means, and large-scale laboratory rearing has thus far proved impractical. Sound trapping has made possible much of the research on the biology and on chemical and biological control of *Scapteriscus acletus* and *S. vicinus* (Walker 1984).

Field crickets are a second group of agriculturally important insects that have been caught with sound-baited traps. Campbell & Shipp (1974, 1979) and Campbell (ms. in review) developed traps for *Teleogryllus commodus*, an important pest of pastures in Australia and New Zealand. As in mole crickets, the bait was the natural or synthesized male calling song, and both males and females flew or walked into the trap. In North America, field crickets of the genus *Gryllus* have been acoustically trapped by Cade (1979, 1981) and Walker (1986). Sound trapping field crickets has contributed to studies of their migratory and mating behaviors (Campbell & Shipp 1979, Cade 1981, Walker 1987). It can also provide a ready source of live crickets for laboratory studies or for feeding animals: for three years, a trap broadcasting *G. rubens* song at Gainesville, Florida, caught hundreds of *G. rubens* most months and an annual average of 8,209 (Walker 1986).

A third group of insects successfully trapped acoustically are tachinid flies of the tribe Ormiini. These flies are parasitoids of crickets and katydids, and females find their hosts by homing on the hosts' calling songs. Cade (1975, 1981) trapped gravid females of *Euphasiopteryx ochracea* at broadcasts of the recorded song of *Gryllus integer*, and Mangold (1978) trapped it at the song of *Scapteriscus acletus*. In three trap-years Walker (1986, 1989) trapped 3,583 *E. ochracea* at synthesized *Gryllus rubens* song. A South American species of *Euphasiopteryx*, *E. depleta*, is important as a potential biological control agent for *Scapteriscus* mole crickets that became major pests when accidentally introduced into the southeastern United States (Fowler & Garcia 1987). Fowler (1988) devised sound traps to capture gravid *E. depleta* females for biological studies and for shipment to the United States.

Sound traps have been used for other insects with less success and/or on a more modest scale. For example, Webb et al. (1983) caught female Caribbean fruit flies (*Anastrepha suspensa*) using sound-baited traps within field-caged guava trees; Silveira-Guido & Fowler (1988) caught *Megacephala fulgida*, a tiger beetle predator of mole crickets, at mole cricket sound traps; and Walker (1979) and Zuk (1987) suspended gryllid males (*Anurogryllus arboreus* and *Gryllus veletis* and *G. pennsylvanicus*) over pitfalls to study what mates or enemies particular males attract.

COMPONENTS OF SOUND TRAPS

The principal parts of a sound trap are a sound source, a controller, and a catching device.

Sound source

Sounds used to attract insects to sound traps are, thus far, natural sounds or electronic imitations of natural sounds. Natural calls of insects can be used directly (e.g., Campbell & Shipp 1974, Forrest 1983b); they can be captured by microphone, amplified, and broadcast in real time; or they can be recorded for later broadcast (e.g., Ulagaraj & Walker 1973, Cade 1979). The first method changes no feature of the natural call. The second method keeps the timing and quality of the sound natural while permitting it to be amplified and broadcast from one or more speakers. The third allows a selected natural sound (the recording) to be produced on a predetermined schedule at a predetermined intensity. The third method can be adapted to routine operation of sound traps, but automated playback of recorded sounds requires expensive equipment not easily adapted to field use.

Using sound synthesizers as sound sources greatly simplifies automatic sound trapping (Walker 1982, Campbell & Forest 1987). Except for speaker diaphragms, electronic sound synthesizers have no moving parts to wear or bind, and they can be built or programmed to produce precisely the sound that is wanted. Under field conditions they reliably produce the specified song for weeks or longer; those incorporating a digital microprocessor may retain their calibration indefinitely.

Synthesizers are either line operated (e.g., 110 volt AC) or battery operated (e.g., 12 volt DC). Once lines are run to a trapping site, line power is economical and requires little routine maintenance. The virtues of battery power are that it can be used at any trapping site and is not disrupted by line power failures.

A bag made of 3 mil black polyethylene is an easy way to weatherproof a sound synthesizer (Fig. 1). The sound is attenuated 8 dB by the bag, but quality is not affected.

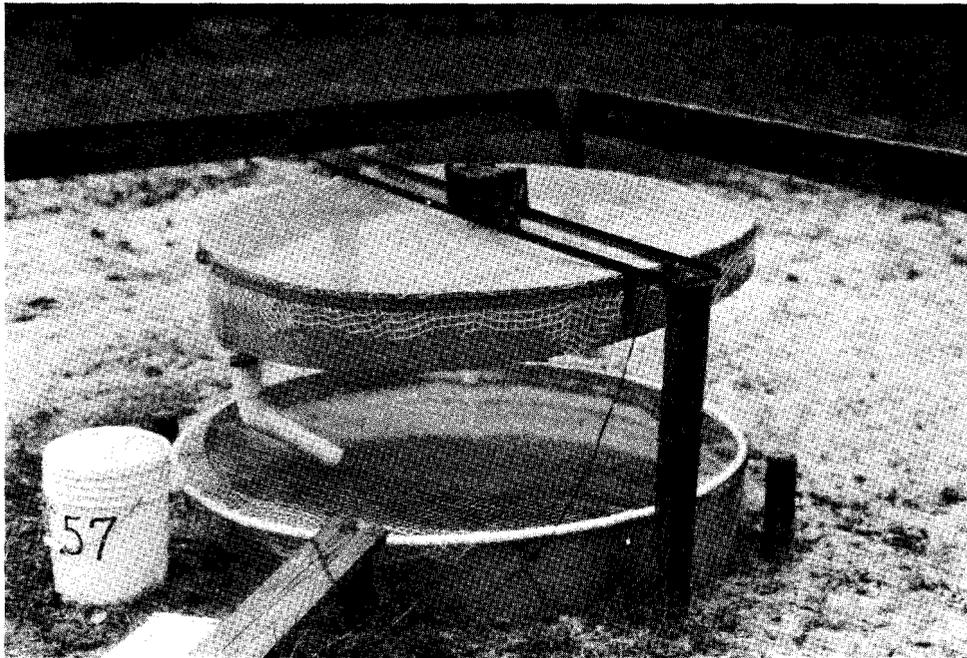


Fig. 1. Mole cricket sound trap. Sound synthesizer in black plastic bag produces calling song of *Scapteriscus* sp. Attracted mole crickets land on coarse net and crawl or fall into shallow, obliquely truncated, wirecloth-bottomed cylinder. Net prevents crickets from flying out as they work to low point of cylinder and fall into pipe. Outlet of pipe can be directed either into pool (as shown), where crickets swim until collected, or into bucket, where they find soil (for live collections), or preservative. Time clock (lower left) switches synthesizer on at sunset and off two hours later, when the flight period is over.

Controller

Unless a human operator is always available or the sound is to be broadcast continuously, routinely operated sound traps need a device that switches the sound on and off at appropriate times. Reliable, economical timer-controlled switches are commercially available for line-operated sound sources. For battery operated sound sources, commercial timers are difficult to find and expensive—e.g., the Paragon EC72D 12-volt DC timer costs ca. \$170.

Catching devices

In some cases, it is important that the insects caught at a sound trap be kept healthy for later use. In other cases, dead specimens are all that are needed. Lethal traps may use an electrified grid, sticky material (e.g., Tack Trap®), or insecticides. Catching devices for live traps are sometimes difficult to devise. For mole crickets and field crickets, sheet-metal funnels will direct those that land within its diameter to a holding container (Fig. 2) (Walker 1982, 1986). For mole crickets, an obliquely truncated sheet metal cylinder with a wire mesh bottom works like a funnel but does not direct rain

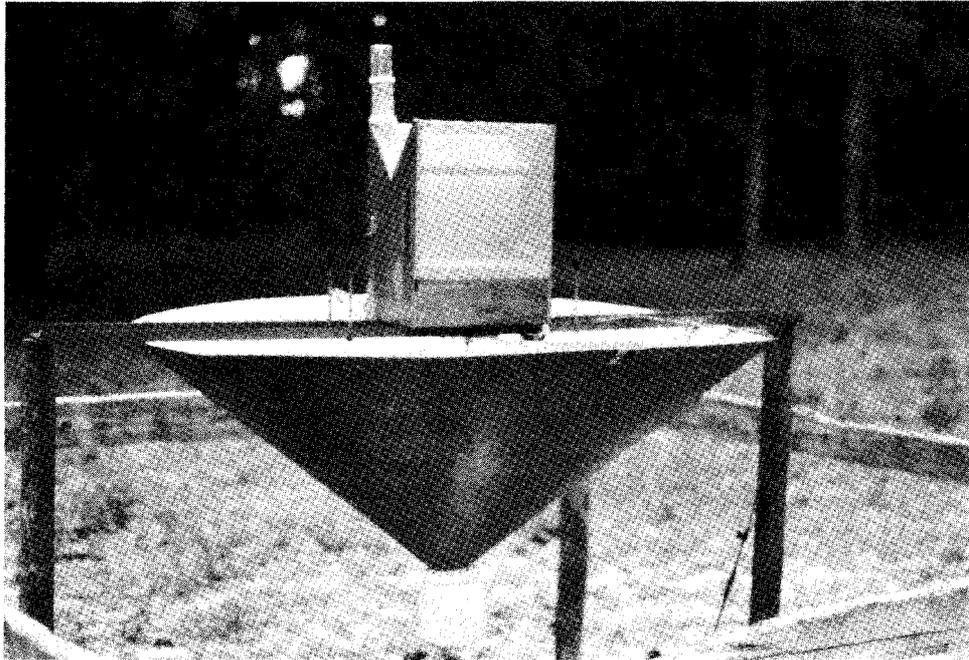


Fig. 2. Field cricket and fly sound trap. Sound synthesizer (concealed beneath screen cage) produces calling song of *Gryllus rubens*. Attracted field crickets that land in funnel slide into removable 2-liter plastic jar (which has a screen bottom to prevent flooding). Attracted flies (*Euphasiopteryx ochracea*) that land on top of cage run toward sound and pass into cage through 1-cm-wide slit at bottom of notch. They later fly upward and are trapped in removable collecting vial (on cage at upper left).

water into the holding container (Fig. 1). A cheaper, easier to transport device for mole crickets is a foldable child's wading pool (Fig. 1) (Walker 1982). Mole crickets landing on water are bouyed by their hydrofuge pile and swim or float for 12-24 hours until collected.

A serious problem with catching mole crickets that land at sound traps is that many alight meters from the sound source. Matheny et al. (1983) found that only 8% of *S. vicinus* and 36% of *S. acletus* landed within the 1.5-m-diameter funnel or pool of a standard mole cricket trap. Increasing the diameter of the catching area to 4.6 m increased the potential catch of the two species to 30% for *S. vicinus* and 75% for *S. acletus*.

The efficacy of catching devices for ormiine tachinids has also been a problem. Fowler (1988) and Walker (1989), who developed live traps for *Euphasiopteryx depleta* and *E. ochracea*, respectively, noted that attracted flies often did not find their way into the holding cage and thus escaped. However, the *E. ochracea* trap (Fig. 2) caught approximately as many flies as a concurrently operated sticky trap (Walker 1989).

SOUND LEVEL

Most acoustic traps have amplifiers and therefore can be operated at any of a wide range of sound levels. If the sound level matches that of the natural sound (e.g., a calling male), the number of insects attracted should approximate the number that would come to the natural sound. In most cases though, the goal of sound trapping is either to catch as many target insects as possible or to catch large samples. Sounds louder than natural,

generally, perhaps invariably, attract more target insects than sounds of natural intensity. This is in keeping with Burk's (1988) contention that intensity indicates fitness and cannot be counterfeited. It is also in keeping with the physics of competing sound fields (Forrest, personal communication).

The exact effects of intensity on the performance of acoustic traps are poorly known. Cade (1979) found that taped *integer* calling songs attracted significantly more *E. ochracea* and *G. integer* females when amplified ca. 10 dB above the natural sound level. Ulagaraj & Walker (1975) reported that at sound pressure levels (SPL's) between 70 and 106 dB (re 20 μ Pa, measured at 15 cm) catches of *S. acletus* approximately doubled with each 6 dB increase. Forrest (1980), using improved equipment and more replication, found that between 101 and 111 dB, catches of *S. acletus* averaged 5.7 times greater for the louder of two groups of traps differing in acoustic output by 6 dB. The 95% confidence limits for the 5.7 ratio were 5.2 and 6.3. Walker & Forrest (unpublished) ran further tests with *S. acletus*, increasing the range of sound levels tested to 128 dB. For traps differing by 12 dB, the louder traps caught 2.5 to 10.9 times as many *S. acletus* as the softer traps.

DISCUSSION

Limitations to acoustic trapping

The most fundamental limitation to using acoustic traps is that few insect species are attracted to sound. Those that are attracted come to natural sounds or their imitations. Nothing presently suggests that long-range acoustical communication is as common as long-range chemical communication or that yet-to-be-discovered acoustical signals will prove remarkably attractive to many insect species (cf. UV light for light traps).

Not only are few species attracted to sound, but within a species, attraction is usually restricted to one or a few classes of individuals. For example, in *Euphasiopteryx* spp. the only flies that come to broadcasts of the host's calling song are gravid females. In this case it is evident that individuals attracted are those that, under normal circumstances, would benefit from coming to the sound. The attraction of male crickets to calling songs of males is harder to explain—e.g., 44% of sound-trapped *G. rubens* were males (Walker 1986). It may be a matter of males landing near calling males for the opportunity to intercept attracted females (Cade 1979) or of their using conspecific calls to locate habitat, with calling sites and potential mates. The latter accords with the finding of Matheny et al. (1983) that the sex ratio of sound-attracted *Scapteriscus* spp. becomes less female biased as landing distance from the sound source increases.

Yet another limitation to acoustic trapping is its high cost—for purchase, operation, and maintenance of sound synthesizers, controllers, and catching devices. Unlike chemical traps, sound traps that do not use live insects to produce the attractant require batteries or line current for power and an amplifier and speaker for propagation. Improved electronic technology may lower the costs of acoustic trapping, but sound traps will likely remain many times as expensive as chemical traps.

Uses of sound traps

Sound traps have already proved their usefulness for studying behavior and ecology, collecting specimens, and monitoring populations. For example, Forrest (1983b) used male-baited traps to study phonotaxis, song and flight periodicity, and mate choice in mole crickets. Mole crickets attracted to amplified synthetic calls have been used to test pesticides, chemical attractants, and feeding stimulants in the laboratory; to test and

to rear biocontrol agents; and to study damage to grass cultivars (Walker 1984). By running sound trapping stations throughout peninsular Florida, Walker et al. (1983) revealed population trends, seasonal distribution, and life cycles. By trapping simultaneously in habitats suitable and unsuitable for mole crickets, Walker & Fritz (1983) estimated prevalence of interhabitat flights.

Sound traps are potentially important in establishing mole cricket biological control agents and in monitoring their spread. Mole crickets attracted to a sound trap can be automatically infected with an agent and released. Some will fly away the next evening (Ngo & Beck 1982), dispersing the agent. Sound traps can also be used to collect biological control agents for satellite releases and to collect samples of hosts for assay.

Crickets caught in sound traps could be used (or sold) for fish bait or animal food. Sound synthesizers, programmed to produce the most effective cricket call for the time and season, could be suspended over ponds to help feed fish.

Prospects are not good for using sound traps to control the attracted insects by directly reducing their populations. The attracted individuals may be impressively numerous but they are not likely to be a major portion of the local population, most of which may not be attracted. Indeed, the insects that are attracted may be chiefly migrating individuals that might not have stopped except for the supernormal stimulus of the trap's broadcast. Of those that do land, a small portion may be caught (Matheny et al. 1983)—though by poisoning the area around the trap or by placing the trap over a large fish-filled pond, those landing far away could be prevented from augmenting the local population. Sound traps are too expensive to use to blanket large areas—as has been done with chemical traps (e.g., >400,000 boll weevil traps were used in 1985: Dickerson 1986). For sound traps to be effective and competitive with other methods of control, an array of variables would have to coincide in favoring the method. That seems less likely to happen for sound than for chemical traps, and chemical traps have proved useful for control in few instances (Lanier 1989).

A final caveat: devices that attract and destroy large numbers of insects hold a fascination for the general public, and some farmers, out of proportion to the good they do—as witnessed by the popularity of UV-baited electric “bug zappers.” Some entrepreneur may very well make and market sound traps to control mole crickets or some other insect pest. Even if the traps do not provide control, their catches may be impressive enough to ensure their commercial success.

ENDNOTE

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ACOUSTICAL SYSTEM TO DETECT LARVAE IN INFESTED COMMODITIES

J. C. WEBB, D. C. SLAUGHTER AND C. A. LITZKOW
Insect Attractants, Behavior, and Basic Biology Research Laboratory,
Agricultural Research Service, U.S. Department of Agriculture,
Gainesville, Florida 32604

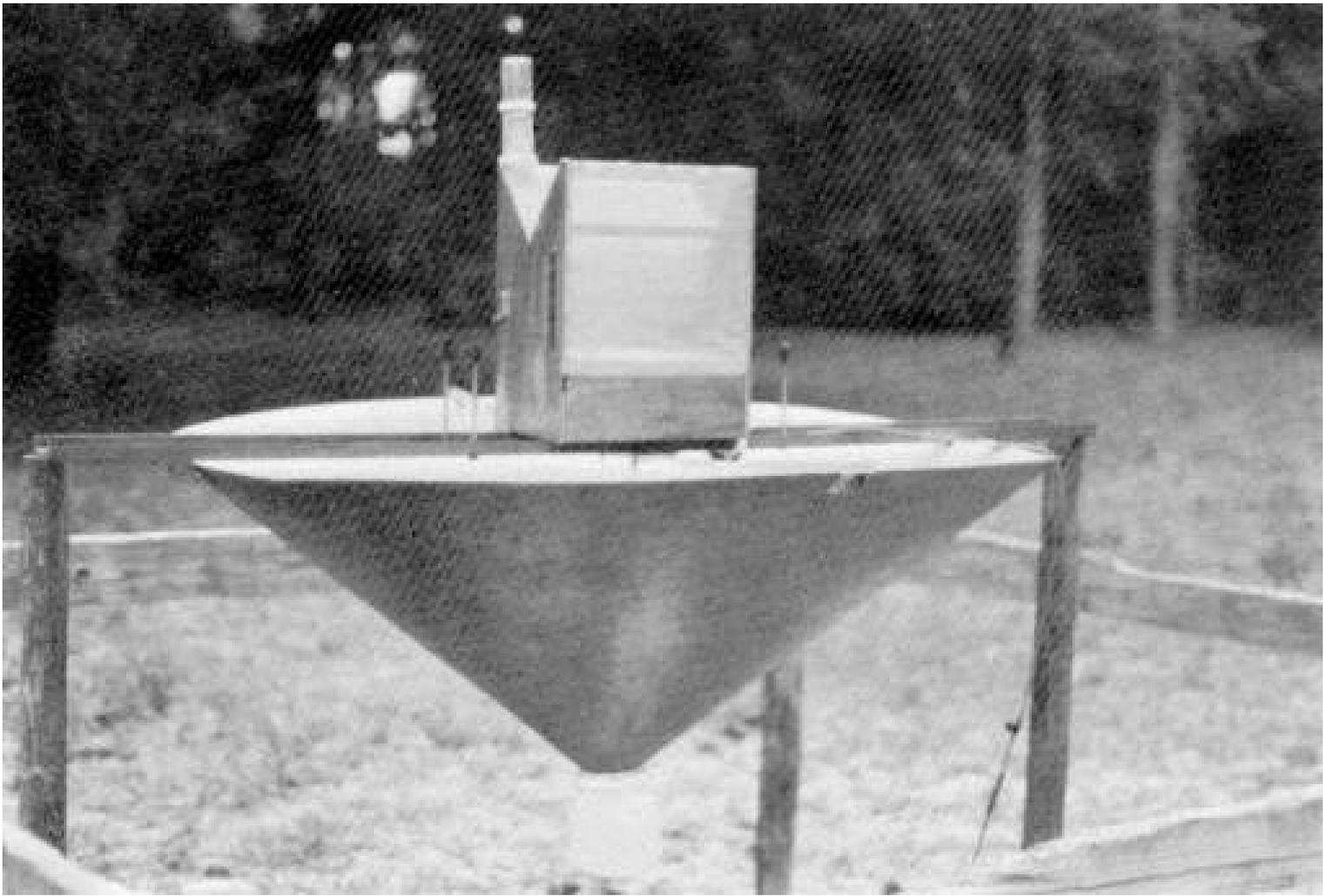
ABSTRACT

An acoustical system to detect larvae in post-harvest commodities is described. The system can detect one-day old fruit fly larvae in grapefruit, mangoes, and other similar fruit and lepidopterous and coleopteran larvae in individual kernels as well as bulk grain. The detectors have been modified so that they can be adjusted to accept fruit of various sizes and shapes. A computer system and software has been developed to monitor the feeding activity of the immature insect for its complete life cycle. The signal is amplified approximately 90 dB and then filtered through appropriate bandpass filters. The variables (trigger levels, time intervals of data collections, and sample rates) are controlled by the computer software. The computer also stores and analyzes the data.

RESUMEN

Se describe un sistema acústico para detectar larvas en productos después de cosechados. El sistema puede detectar larvas de moscas de las frutas de un día de nacida en toronjas, mangos y otras frutas similares, y larvas lepidópteras y coleópteras en granos individuales así como al granel. El detector se ha modificado para que se pueda adaptar para que acepte frutas de varios tamaños y formas. Se ha desarrollado un





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Insect Attractants, Behavior, and Basic Biology Research Laboratory,
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Se describe un sistema acústico para detectar larvas en productos después de cosechados. El sistema puede detectar larvas de moscas de las frutas de un día de nacida en toronjas, mangos y otras frutas similares, y larvas lepidópteras y coleópteras en granos individuales así como al granel. El detector se ha modificado para que se pueda adaptar para que acepte frutas de varios tamaños y formas. Se ha desarrollado un

sistema de computadoras y de programas para chequear la actividad de cómo comen los insectos inmaduros durante su ciclo de vida. La señal es amplificada aproximadamente 90 dB y filtrada a través de los filtros apropiados de paso-de-bandas. Las variables (niveles disparadores, intervalo de tiempo en la colecta de datos, y la proporción de muestras) son controladas por la computadora. La computadora también guarda y analiza los datos.

Post-harvest commodities are frequently infested with insect larvae, adults or both. As a result of such infestations, enormous quantities of food are lost or rendered unusable each year. Also, because of the quarantine restrictions imposed by many countries against certain insect pests, treatments or detection methods must assure that the affected commodities are insect free. Since the Environmental Protection Agency halted the use of ethylene dibromide (EDB) fumigation as a treatment for many of these commodities, it has been necessary to develop new treatments for the export market. Some of the more common treatments now being studied for fruit are other fumigants, cold treatment, vapor heat treatment, and irradiation. It also has been necessary to develop new detection methods, especially in fruit, to determine the presence of a quarantine pest.

The most common method used to determine the presence of larvae in perishable fruit, (i.e., citrus and mango) and thus to determine the effectiveness of the treatments is to cut the fruit and look for larvae. This method is very labor intensive when large numbers of fruit are involved, and inaccurate especially in detecting first and second instar larvae. The cutting of such fruit also renders it useless.

Several detection methods and devices are currently in use to detect adults and feeding (external and internal) larvae in storage grain. The two most common methods are X-ray (Milner et al. 1950, Ficus 1972), and carbon dioxide gas analysis (Bruce et al. 1982). Some of the techniques used to detect adult weevils in grain are described by Barak & Hariem (1982) and Barak & Burkholder (1985). Also, adult weevils in grain are detected by sieving the grain through hardware cloth.

Brain (1924) was one of the early scientists to publish on detecting the chewing and moving sounds of insect larvae in agricultural commodities with electromechanical devices. He reported that he could detect apple and quince borers in apple stems and weevils inside grain. Since Brain's work, many scientists have researched this area and each has made major contributions (Adams et al. 1953, Bailey & McCabe 1965, Street 1971, Webb & Landolt 1984, Webb et al. 1988). Unfortunately, early work was plagued by inadequate sensor sensitivity, sensor noise, ambient noise and equipment noise which resulted in poor signal to noise ratio. With the advent of microelectronic equipment, electronic noise and the signal amplification are no longer limiting factors. As in most systems the sensors or detectors are the limiting components.

The objectives of this research were to upgrade and modify the acoustical detection system reported by Webb et al. (1988). These include the development of an adjustable acoustical coupler that can be used on fruit of different size and shape, development of calibration curves for the system and the development of software that can monitor the feeding sounds over the life span of the larvae.

METHODS

ACOUSTICAL DETECTORS

The basic acoustical coupler with one detector is shown in Figure 1. The detector is composed of a 2.54 cm i.d. polyvinylchloride (PVC) pipe with a thin diaphragm mounted

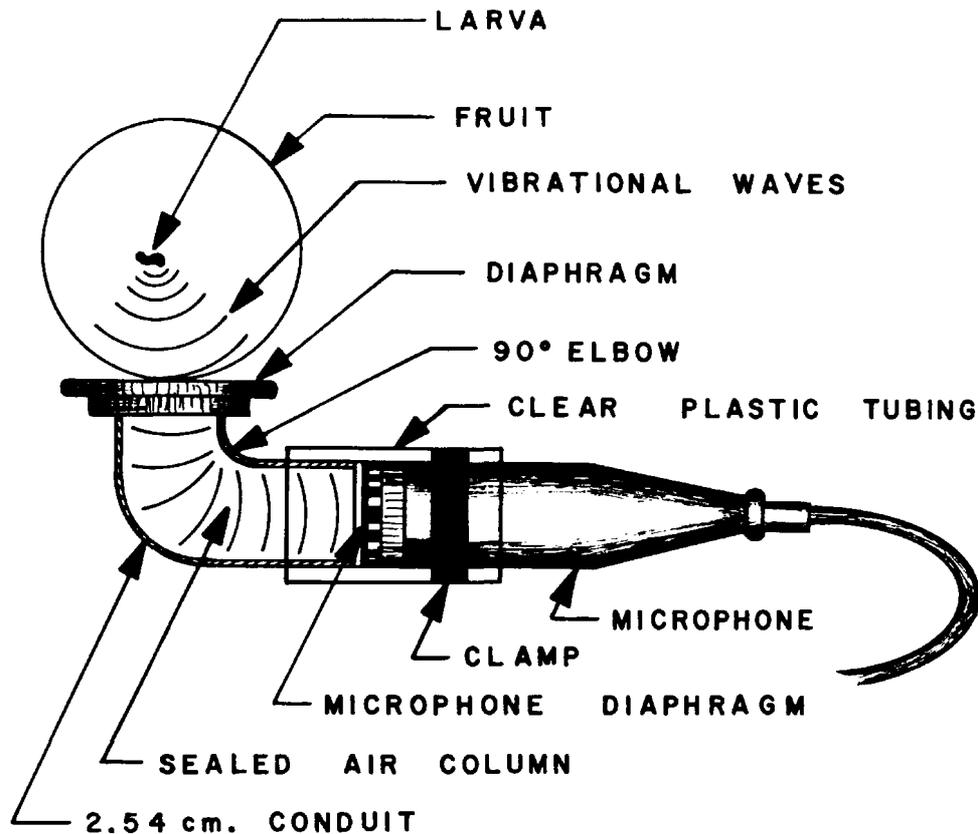


Fig. 1. The basic acoustical coupler with a single diaphragm illustrating the various components

on one end and a microphone on the other. The microphone is inserted into a 2.54 cm flexible plastic tubing that is attached to one end of the pipe and clamped to assure an air-tight seal. The vibrations on the surface of the fruit caused by the feeding larvae are transmitted to the plastic diaphragm causing the diaphragm to vibrate and create standing waves in the PVC pipe (Webb et al. (1988). To maximize the signal from the detector, the microphone must be tuned to the standing waves. This can be accomplished by carefully sliding the microphone in the pipe until a maximum amplitude is reached. The maximum signal normally consists of a very high amplitude narrow band frequency range when compared to a broad band signal for an untuned system (Figure 2). This basic design of the acoustical coupler can be modified to accommodate more than one diaphragm, thereby, allowing more than one contact point with the commodity which increases the probability of detecting the smaller larvae. An acoustical coupler is defined in this paper as a tuned airtight chamber with one or more plastic diaphragms that can be physically and acoustically coupled to a microphone. A typical acoustical coupler used for round fruit i.e., grapefruit and oranges, is shown in Figure 3 and an acoustical coupler for irregular type fruit i.e., mangoes and papaya, is shown in Figure 4. Ball type swivel sockets have been installed in most acoustical couplers just below the diaphragm to accommodate fruits of different sizes and shapes. The acoustical coupler can be modified to detect larvae in stored grain as shown in Figure 5 (Vick et al 1988). The detector and microphone must be in a relatively quiet environment for most studies; therefore, a lead chamber with a hinged lid was used to house the detector and microphone when additional sound attenuation is needed.

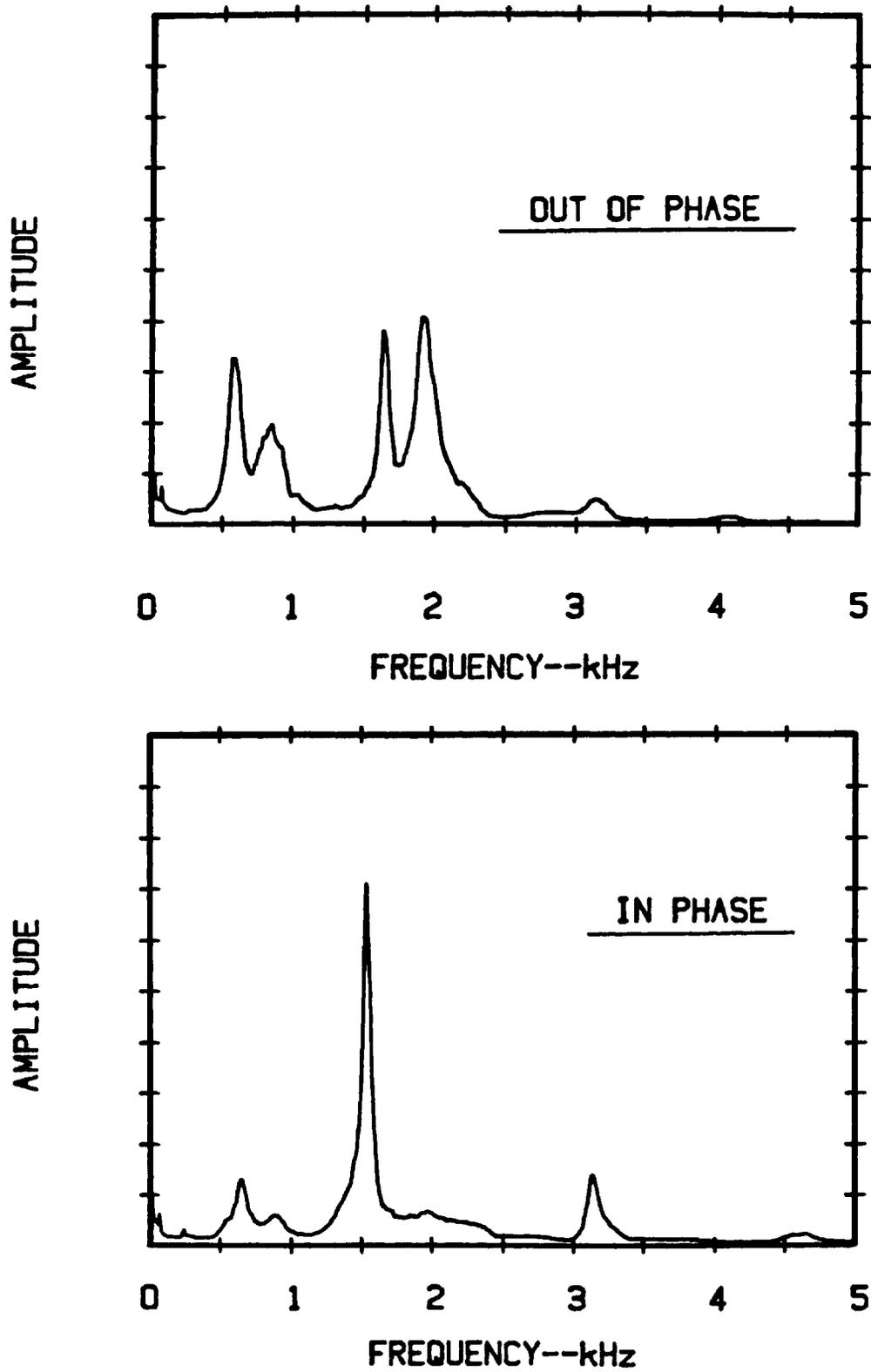


Fig. 2. The output of the system with the signal in phase and out of phase.

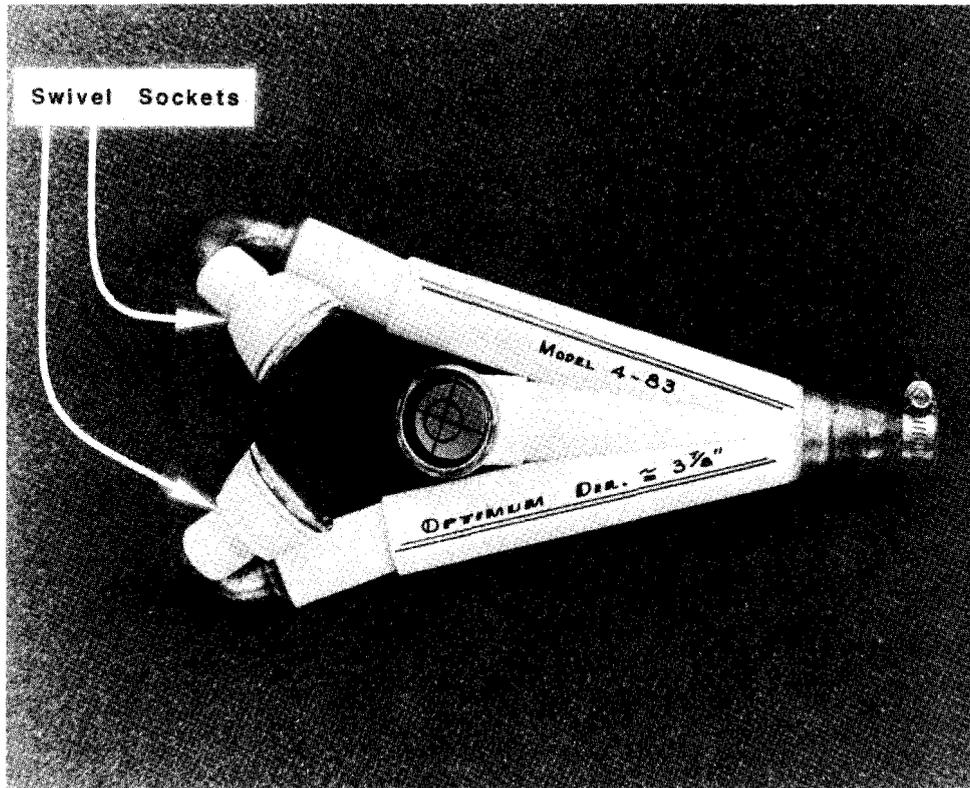


Fig. 3. An acoustical coupler with three adjustable detectors used mainly for round fruit i.e., grapefruit, oranges and apples. Note the swivels are located just under the vertical detectors.

SIGNAL PROCESSING SYSTEM

The equipment used to detect, condition the signal, and monitor the larval sounds are shown in Figure 6. The detection system consists of a sound insulating chamber (to insulate the detector and the commodity being tested from ambient noise), an acoustical coupler and the transducer. The sound insulating chamber can be anything from a commercially available anechoic chamber to a simple plywood box lined with acoustical insulation. The sound insulated chamber is often used in conjunction with a lead cylinder 42 cm long and 25 cm in diameter with a hinged lid located on the side of the cylinder. The lead chamber filters out many of the sounds that are common in the laboratory. A Model 4145 Bruel and Kjaer* (B&K) low noise 2.54 cm diameter condenser microphone was used as the transducer in the acoustic coupler.

The signal processing system is equipped with an 8 channel B&K model 2811 multiplexer for simultaneous monitoring of up to 8 inputs. The multiplexer is equipped with a HP-IB interface bus that makes it possible to be controlled by any IBM compatible computer equipped with an HP-IB interface card. We have written appropriate software for the multiplexer. The signal from the microphone or multiplexer is amplified by a low-noise, high-gain Model 2610 B&K amplifier. The signal amplification ranges from 70 to 90 dB depending upon the signal strength generated by the larvae. The amplifier also provides for subsonic filtering of frequencies below 22.4 Hz and for "A weight" filtering. These filters eliminate extremely low and high frequency noise. A Model 3700 Krohn-Hite* bandpass filter was used to provide additional filtering as well

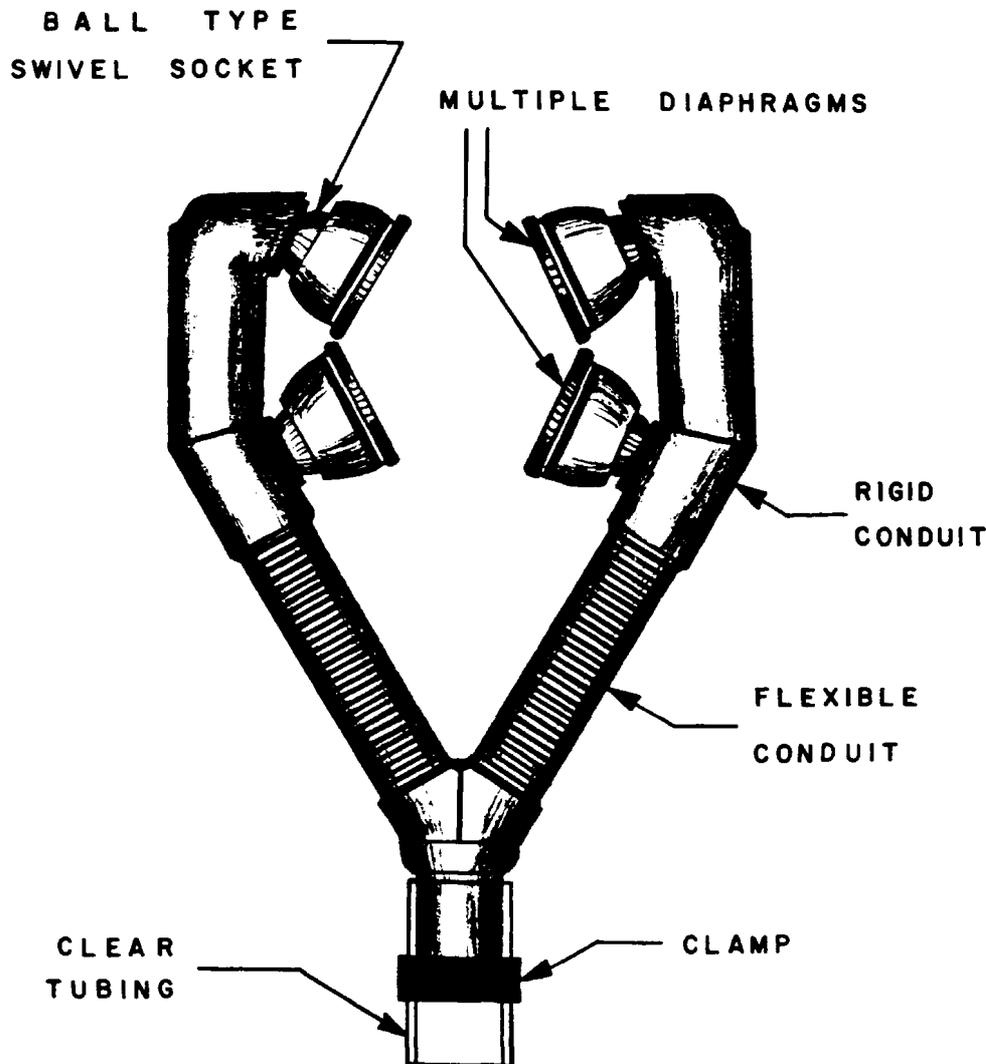


Fig. 4. An acoustical coupler constructed of flexible conduit and four sensors mounted to swivel. This acoustical coupler was designed for irregular fruit i.e., mango and papaya.

as an additional 20 dB gain. The filtered signal is then fed into a general purpose audio amplifier equipped with headphones for audio monitoring, a Model 5111A Tektronix* oscilloscope for visual monitoring and a computer system which controls the A/D converter and counter, collects, stores and analyzes the data. Much of the equipment after the bandpass filter is optional and will depend upon the nature of the measurements desired. For example, only an audio amplifier and earphones are required to detect the presence of larvae, but some type of computer system or data logger is required to monitor the activities over longer periods of time.

COMPUTER SYSTEM

The primary purpose of the computer system is to provide an efficient means of recording, displaying and analyzing the acoustical signals sensed by the detector. This gives, for the first time, a means of continuously monitoring an insect larva's feeding

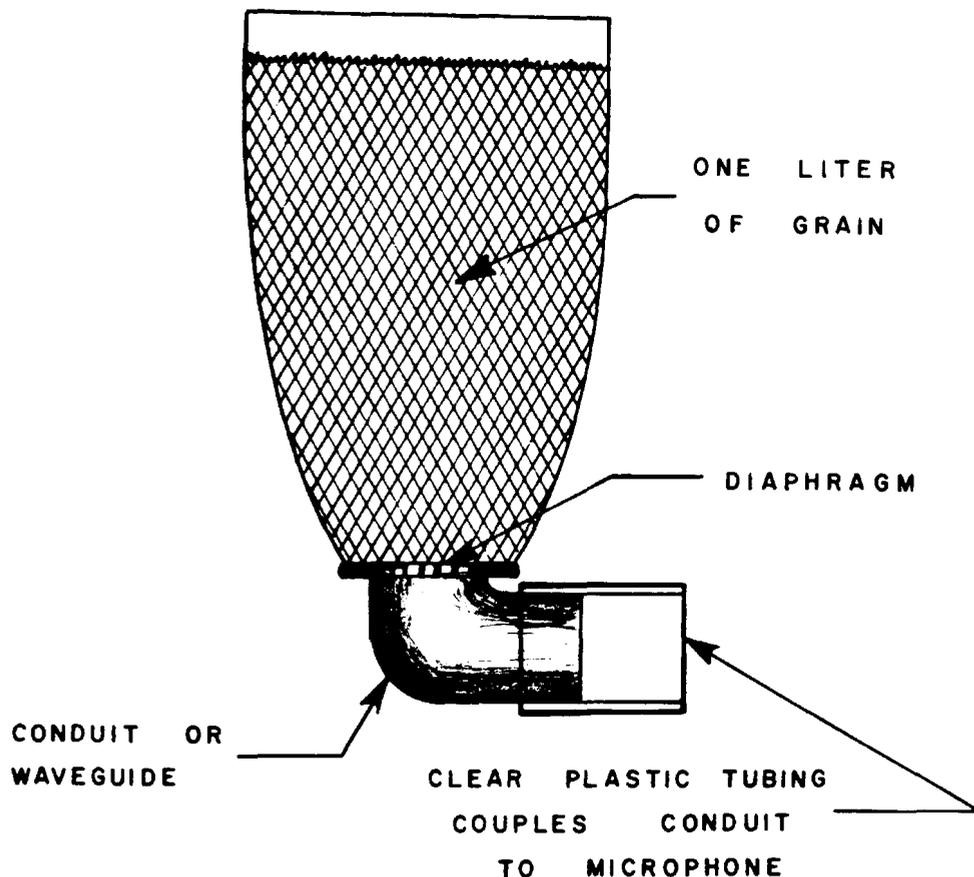


Fig. 5. Acoustical coupler and sample holder for detecting larvae in bulk samples of stored grain. The diaphragm is located in the bottom of the sample holder.

activity throughout its life cycle undisturbed in its natural habitat. The computer system consists of three main components: 1) a personal computer (PC) with at least 640 K bytes to 2.6 M bytes of dynamic random access memory (RAM) (the higher the RAM, the longer the data collection period can be) and a high speed interface bus, such as the IEEE 488-1978 system; 2) an A/D converter and a programmable universal counter with a frequency range of 0 to 10 MHz; and 3) a mass storage device (hard disk).

Specifically this system in our laboratory consists of a Model 3437A Hewlett-Packard (HP) voltmeter (analog to digital, A/D converter) a Model 5316 HP universal counter, and a HP Vectra (IBM compatible) computer with 20 M byte hard disk and a graphics printer (Figure 6). Computer software was developed to control both the A/D converter and the universal counter. The A/D converter was used primarily to measure the amplitude of the voltage when determining the trigger levels of the system and when calibrating the filters. The counter was used to monitor the larval feeding activities by counting the number of voltage spikes in a predetermined time period.

The purpose of the A/D system was to analyze insect activity using sound in the 100 Hz frequency region. The Nyquist sampling theorem requires that the computer sample an A/D converter at more than 200 samples/second to guarantee detection of 100 Hz sounds. This high sampling rate soon creates a data storage problem. For example, if a computer monitored an A/D converter at 200 Hz for a 48-h period, 34.6 million samples would be collected, which far exceeds the capacity of the PC memory. The universal counter was used in place of an A/D converter to alleviate this problem because of its natural data compression capability.

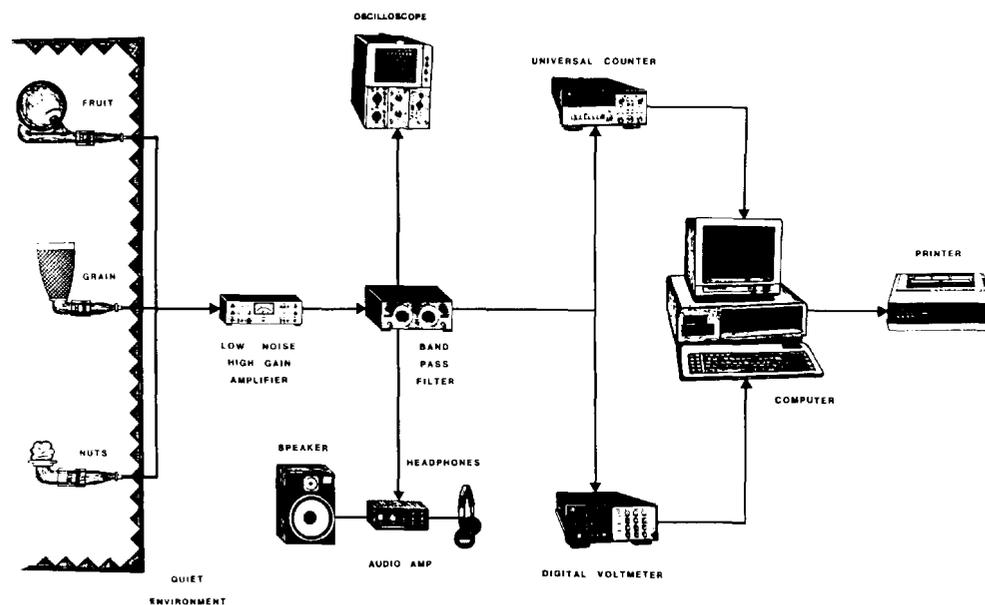


Fig. 6. Pictorial diagram of larval detector and signal processing system.

The function of the programmable universal counter is to monitor continuously an input signal and keep track of the number of times the voltage level exceeds a predetermined threshold level. By substituting a universal counter for the A/D converter the sampling interval can be reduced to a window of time dependent upon the experimental considerations rather than the frequency of the sound emitted by the insect larvae. In comparison, if a particular experiment only required information at a 1-sec resolution over a 48-h period, the computer could sample the counter at 1 Hz (independent of the frequency of sound emitted by the insect larvae) requiring 172.8 thousand samples. The use of a programmable universal counter thus provides a considerable reduction of data (over two orders of magnitude in this example), which not only reduces the storage requirements but reduces the analysis time as well. The primary disadvantage of using a universal counter in place of an A/D converter is that the actual voltage levels (or sound amplitudes in this case) are not recorded. We only know how many times the sound level exceeded the threshold during the selected window of time.

The system's software was developed using the Microsoft QuickBasic language. Basic was chosen as a developmental language because of its ease of use, reduced development time and the availability of a software library for instrument control. The scope of the software was two-fold, first to provide a routine that controlled the universal counter and voltmeter and second, to display data (both in tabular and plotted form) and calculate pertinent statistics.

The software that controls the universal counter permits data to be collected at a resolution ranging from 150 ms to 1 h and to store it in Lotus a 1-2-3 readable format. At a resolution of 150 ms the system can monitor signals "continuously" for 7.86 h and at a resolution of 10 seconds, monitoring can be conducted for over 21 days. The term "continuous monitoring" should be tempered with the understanding that between counter measurements the system requires a period of approximately 17 ms to store the measurement in RAM as well as to read and store the time of the measurement and reset the counter. Therefore at a 150 ms resolution, the system is "continuously" monitoring only 90% of the time, but at a 1-sec resolution this increases to 98%.

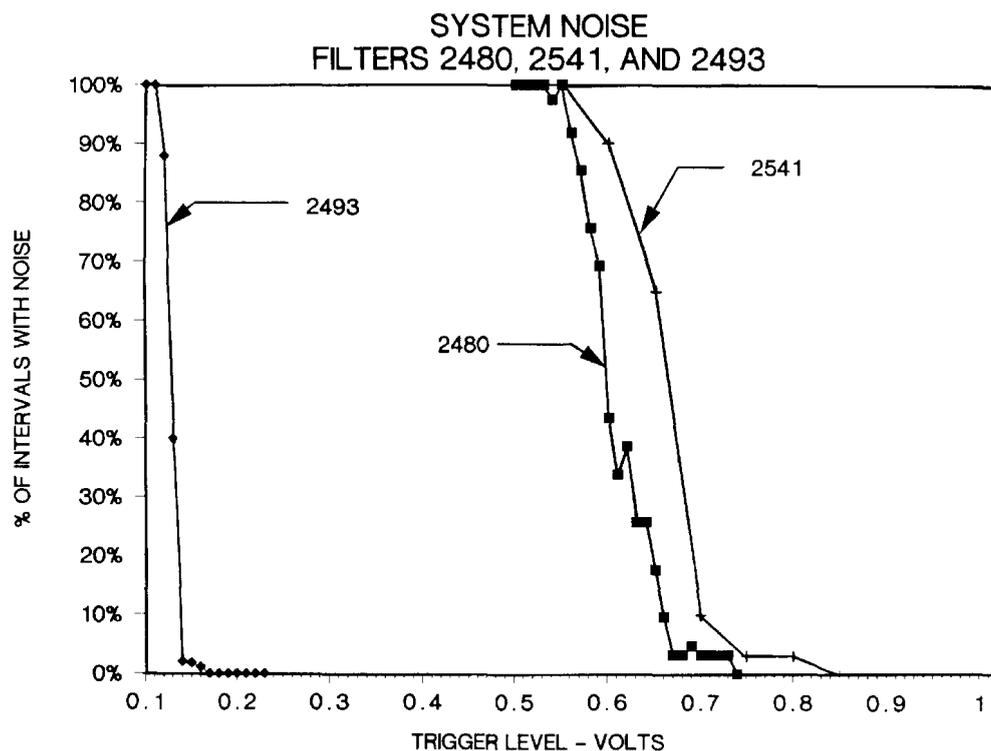


Fig. 7. The performance curves of three Krohn-Hite filters. These filters are identified by serial numbers and the graph shows the percent of system noise voltage spikes generated for a given trigger level.

RESULTS AND DISCUSSION

This detection system can be used to test a variety of commodities for hidden insects. However, one requirement is that the test be conducted in a relatively quiet environment such as an acoustically insulated room or a room with the walls lined with standard acoustical tile or acoustical foam to reduce the ambient noise level. The ambient and the inherent system noise must be determined in order to select the appropriate threshold settings for the counter. It was determined that all components of the various systems in operation could be used interchangeably without effecting the trigger level except the Krohn-Hite filter. The gain varied between filters and this had to be taken into consideration when a system with a different filter was used. Therefore, a calibration curve to determine the trigger level for each filter was developed using the universal counter. The curves were determined by placing a rubber ball filled with water, to simulate the size and weight of a grapefruit, on the detector and monitoring the output of the system. Since the counter was used to collect data for most experiments, the counter was used to collect data for the calibration curves. The counter was set at a gate time of 10 seconds with a total collection time of 1-h, this gave 360 intervals per hour. The minimum trigger level was selected by insuring that each of the 360 intervals contain voltage spikes generated from either ambient or system noise. Then the trigger level was increased in increments of 100 mV until none of the intervals contained spikes. This was the trigger level that was considered to be above the system and ambient noise for a time period of one hour or less. The results from three Kron-Hite filters are shown in Figure 7.

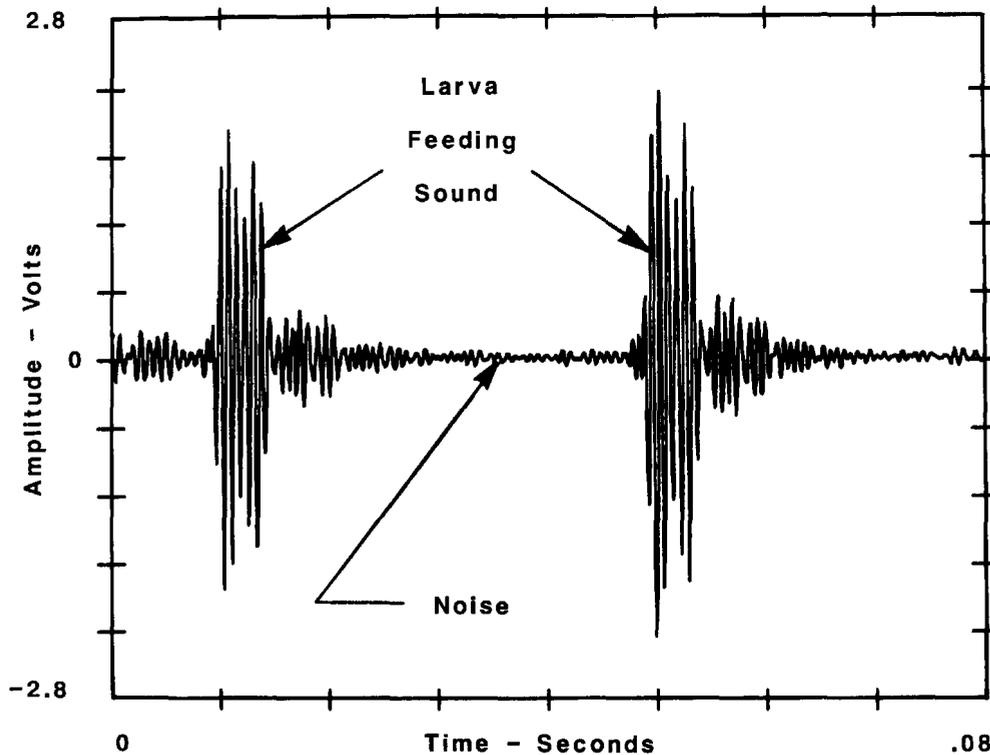


Fig. 8. The amplified and filtered signal of a 2-day-old Caribbean fruit fly larval feeding sound feeding in grapefruit vs background noise.

The trigger level of the A/D converter can be set so that only the voltage of those biologically generated spikes above a predetermined value will be recorded and those below this value will not be measured. Likewise, the trigger level of the counter can be set so that only those spikes that are above a preset voltage level will be counted. Therefore, it is important to know the ambient and system noise level before beginning the measurement of insect feeding sound. A typical example of a filtered and amplified analog signal fed into the A/D converter and the counter from a 2-day-old Caribbean fruit fly (*Anastrepha suspensa* (Loew)) larva in grapefruit is shown in Figure 8. As seen from this figure there is a large signal to noise ratio, therefore, a relatively high trigger level could be selected and still guarantee detection of the feeding sound generated by the larvae. However, as in most biological material not all signals are this large. The peak voltage of the spikes from a one day old larva may range from noise level to several times noise level. But when the larvae reaches 3 to 4 days old, the signal is normally of the magnitude of that shown in Figure 8. Therefore, in order to count the small signals the trigger level may have to be set just above noise level.

The universal counter totals the number of voltage spikes above the threshold level in a given time interval and sends this information to the computer. An example of the summary of the data taken with the counter is shown in Table 1, using a noninfested grapefruit and a grapefruit with one 2-day-old Caribbean fruit fly larva. The data was stored in a Lotus readable format and a plot for both sets of data is shown in Figure 9. Both tests were run for approximately 14-h with a gate time of 10 sec and a trigger level of 0.15 volts. As can be seen from the summary data in Table 1, there were some intervals that contained one or more spikes. If the trigger level were set at a higher value, these spikes could be eliminated. Graphically, these random noise spikes from

TABLE 1. AN EXAMPLE OF THE SUMMARY OF THE DATA SHOWN IN FIGURE 9, COLLECTED WITH THE UNIVERSAL COUNTER.

<u>A noninfested grapefruit</u>	
ID: NONINFESTED GF 2610 30-40 FIL 20DB	1.2-1.7 SOUND HEARD 1-12-87
FILE NAME: A:D701	DATE: 01-21-86 TIME OF TEST: 04-00-PM
GATE TIME: 10000 msec	TRIGGER LEVEL: .15 volts
MEAN SPIKE/SEC: .0072	STANDARD DEVIATION: .2561 sec
TOTAL SPIKES: 35	TOTAL COLLECTION TIME: 49961 sec
MAXIMUM PERIOD WITHOUT NOISE: 10259.00 sec	
PERIOD OCCURRED AT INTERVAL: 31551.00-41810.00	
MAXIMUM PERIOD WITH NOISE: 1.00 sec	
PERIOD OCCURRED AT INTERVAL: 10550.00-10551.00	
NUMBER OF INTERVALS WITHOUT NOISE: 1846	
NUMBER OF INTERVALS WITH NOISE: 15	
<u>A grapefruit containing one 2-day-old Caribbean fruit fly larva</u>	
ID: INFESTED GF 2610 30-40 FIL 20DB	1.2-1.7 SOUND HEARD 1-12-87
FILE NAME: A:D701	DATE: 01-22-87 TIME OF TEST: 04-10-PM
GATE TIME : 10000 msec	TRIGGER LEVEL: .15 Volts
STATISTICS FOR DATA BETWEEN 5.15-49966.00 sec	
MEAN SPIKE/SEC: 704.6153	STANDARD DEVIATION: 526.6220 sec
TOTAL SPIKES: 3.42SE+006	TOTAL COLLECTION TIME: 49966 sec
MAXIMUM PERIOD WITHOUT NOISE: 0.00 sec	
PERIOD OCCURRED AT INTERVAL: 0.00-0.00	
MAXIMUM PERIOD WITH NOISE: 49960.85 sec	
PERIOD OCCURRED AT INTERVAL: 5.15-49966.00	
NUMBER OF INTERVALS WITHOUT NOISE: 0	
NUMBER OF INTERVALS WITH NOISE: 4861	

noninfested fruit (9a) are insignificant compared to the number of intervals showing feeding activity in the grapefruit (9b) with only one 2-day-old Caribbean fruit fly larva presented graphically in Figure 9.

The examples shown here are typical of the feeding sounds of the aribbean fruit fly larvae. It must be emphasized that care should be used to determine the correct threshold level of the system before each test, because proper selection depends upon the gain of the amplifier, the bandpass filter setting and ambient noise level. If the threshold level was set too low, then there is a good chance of detecting false signals, but if the threshold level was set too high, some of the larval sounds may be missed.

When using the A/D converter in measuring the noise or signal voltage it is recommended to use a sampling rate as high as possible, the computer system and software allows a simple rate of up to 500 samples per second. In addition, the noise level calibration must be repeated whenever the detection environment changes.

CONCLUSIONS

In summary, an acoustical sensing system was developed that is capable of detecting the feeding and moving sounds made by early instar larvae in fruit, nuts and grain. The acoustical couplers were modified so they could be adjusted to accept different size and shape fruit. Electronic amplification, filtering, computer monitoring and data analysis

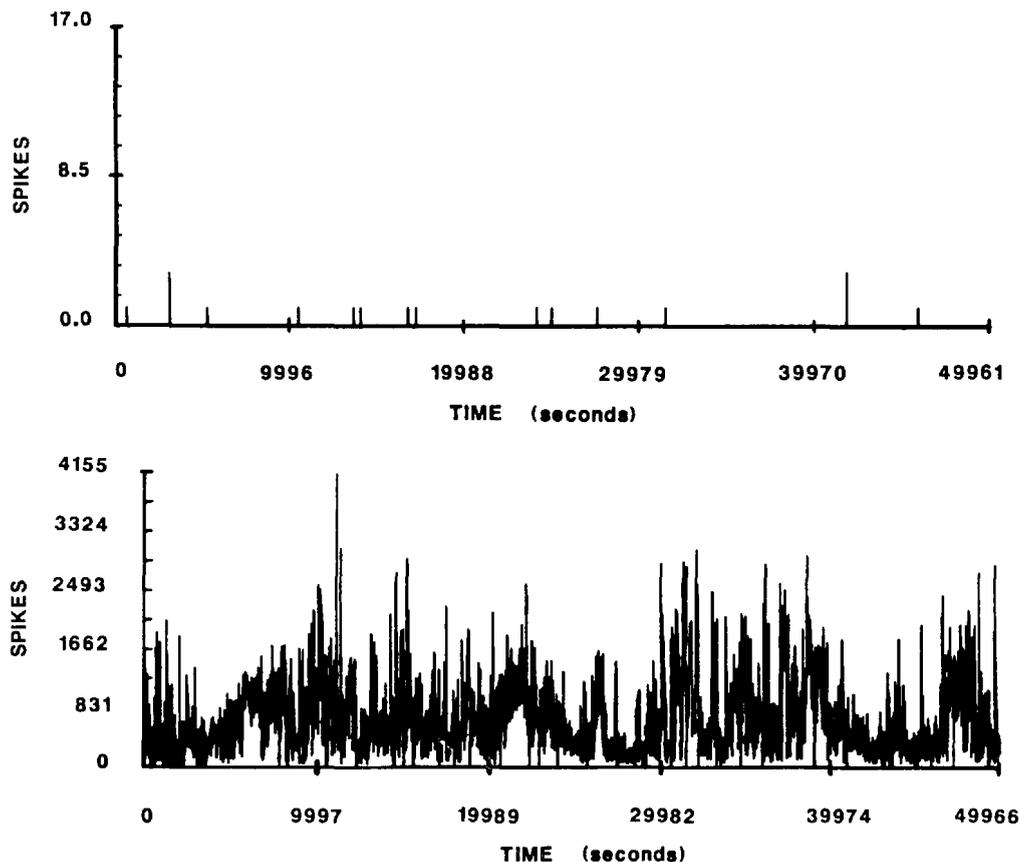


Fig. 9. (a) An example of data taken with the universal counter of a noninfested grapefruit. The vertical lines are noise spikes above background noise, and (b) a grapefruit with one 2-day-old Caribbean fruit fly larvae.

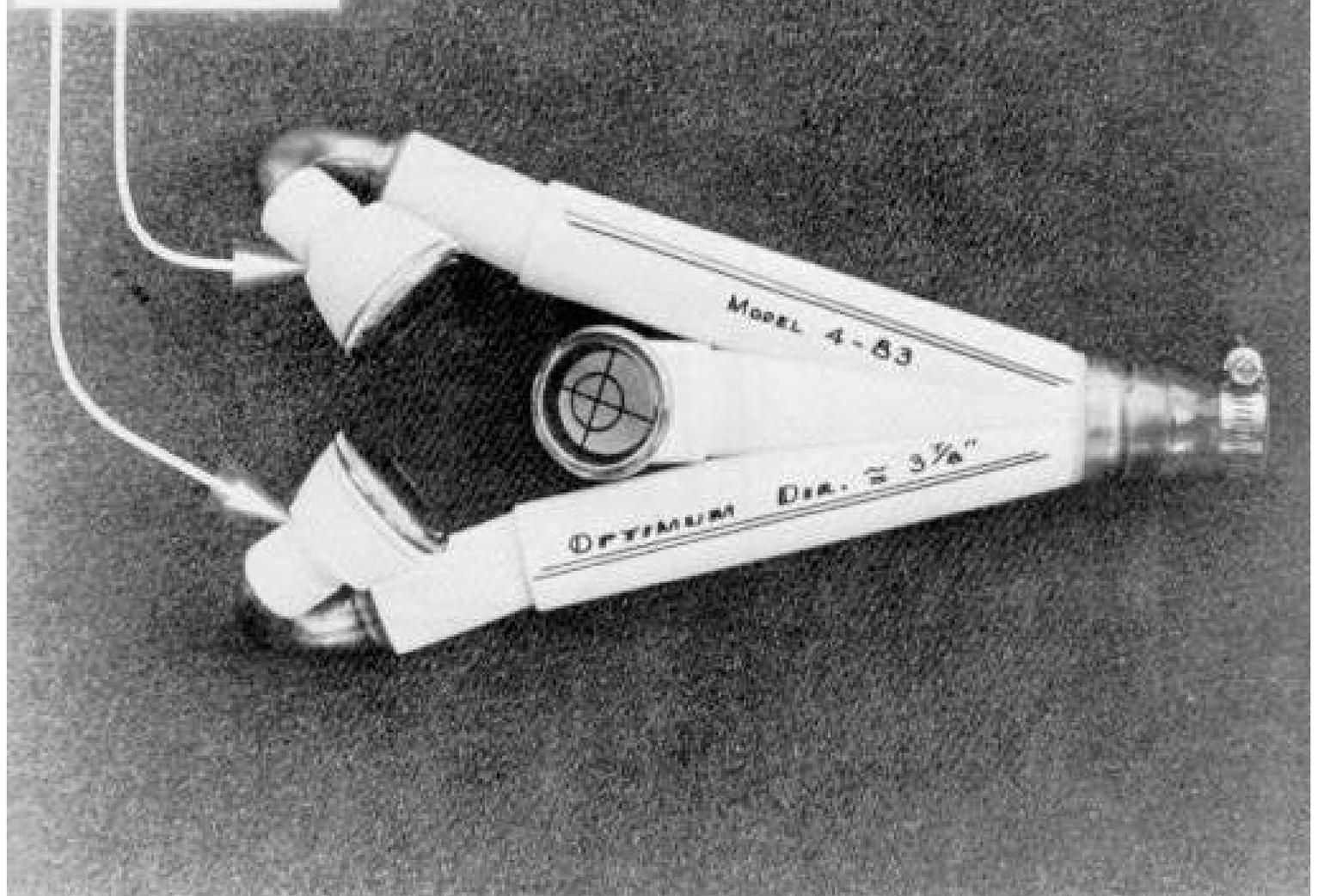
software were developed to process the acoustical signals generated by the feeding sounds of insect larvae. The system has potential in at least two areas. The first is to obtain basic biological information on larval behavioral activities such as time and frequency of feeding, and also the growth rate of insect larvae inside various commodities. Methods to obtain these data were unavailable previously. This information must be known before the detection system can be used effectively in most inspection programs. Therefore, research is being conducted at several USDA research installations across the country to obtain these data and to determine which agricultural commodities and which insects are suited to this method of detection. The system also has great potential for reducing the labor-intensive and destructive task of manually cutting and visually inspecting fruit, which is currently used by USDA commodity inspectors. Research is also under way to determine probability of error in detecting one insect larva in a single grapefruit or orange using a listening time of only 10 sec per fruit.

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Swivel Sockets



STUDENT SYMPOSIUM:
ALTERNATIVES TO CHEMICAL CONTROL OF INSECTS

PREFACE

Insecticides are currently our primary means of controlling damaging insect populations. However, a number of factors place restrictions on their use. Tightening government regulations, economic constraints, environmental concerns, and pest resistance to insecticides have all contributed to an increased awareness and interest in alternative management tactics. The fourth annual Student Symposium held 27 January, 1988 in conjunction with the annual meeting of the Southeastern Branch of the Entomological Society of America dealt with some of the alternatives to chemical control of insects.

In the development of biological control programs, valuable groups of natural enemies may be overlooked because information on them is not readily available. Presentations in the symposium reviewed the biology, history of use, and potential utility of two hymenopteran parasitoid families, the Scelionidae and the Eucharitidae. Additionally, the current status of attempts to biologically control mosquitoes was reviewed. Although the use of insect-resistant plant varieties presents several economic and environmental advantages over insecticides, the number of such varieties currently in use in agricultural systems is relatively low. The reasons for this lack of utilization were included in a discussion of the problems faced in the development of host plant resistance. An understanding of the biology and ecology of pest insects and often their natural enemies is crucial to the development of any pest management strategy. Radio-tracer methodology was described in the symposium as an often overlooked but very effective tool which can be used to gain such information.

The following series of manuscripts address in greater depth some of the alternatives to chemical control of insects which were presented at the 1988 Student Symposium.

DAVID B. ORR

SCELIONID WASPS AS BIOLOGICAL CONTROL AGENTS: A REVIEW

DAVID B. ORR¹

Department of Entomology, Louisiana Agricultural Experiment Station,
Louisiana State University Agricultural Center, Baton Rouge, 70803

ABSTRACT

The Scelionidae is a large family of parasitic Hymenoptera whose members specialize in egg parasitism of insects and arachnids. Many of the characteristics considered most desirable in a natural enemy can be found within members of this family. Species have been studied which demonstrate high searching abilities and reproductive rates, lack of hyperparasitoids, have synchrony with host populations, have positive host-density responsiveness, have simple adult diets, and can be reared easily. The advancements made in rearing techniques for these natural enemies should prove valuable in the future both in classical biological control and in augmentative efforts. Research which has been done indicates that a variety of approaches are possible for augmenting scelionid populations. These range from simple inundative releases to manipulation of preferred nectar-bearing plants. Although fewer than 30 species have been used in classical biological control attempts, several of these have produced excellent results. The interaction of scelionid wasps with various insect management tactics is discussed. In general, scelionids interact well with insecticide applications due to the protective nature of host egg choria. The number of known scelionid species represents only a fraction of those estimated to be in existence. The results of biological control efforts undertaken with known species suggests that much potential exists within the Scelionidae.

RESUMEN

La Scelionida es una familia grande de parásitos Himenópteros cuyos miembros se especializan en parasitar huevos de insectos y arañas. Muchas de las características consideradas deseables en un enemigo natural se pueden encontrar en miembros de esta familia. Se han estudiado especies que han demostrado una gran habilidad de búsqueda y proporción de reproducción, falta de hiperparasitoides, que tienen sincronía con poblaciones hospederas, responden positivamente a la densidad del hospedero, tienen una dieta simple como adultos, y pueden ser criadas fácilmente. Los avances que se han hecho en técnicas de cría de estos enemigos naturales debe de ser de valor en el futuro, tanto en control biológico clásico como en esfuerzos de aumentación. Investigación que se ha hecho indica que es posible una variedad de métodos para aumentar la población de Scelionida. Estos varían de liberaciones inundativas simple, a la manipulación de las plantas preferidas con néctar. Aunque menos de 30 especies se han usado atentando un control biológico clásico, algunas de estas han producido un resultado excelente. Se discute la interacción de avispas scelionidas con varias tácticas de administración de plagas. En general, scelionidas entreactúan bien con la aplicación de insecticidas debido a la protección natural de la coria del huevo del hospedero. El número de especies de scelionidas representa solo una fracción de las que se estima que existen. Los resultados de esfuerzos llevados a cabo en control biológico con especies conocidas sugiere que existe un gran potencial dentro de la Scelionida.

The Scelionidae is a very large, diverse hymenopteran family which includes 94 genera worldwide (Masner 1976). Most scelionids are solitary, and all are egg parasitoids which utilize the eggs of a wide variety of insects and some arachnids (Krombein et al.

¹Present address: Dept. of Entomology, Iowa State University, Ames, IA 50011.

1979). Because of the role they play in natural control of a number of insect populations, including some important pests, these parasitoids have received a certain amount of attention as useful or potentially useful biological control agents.

One major stumbling block to a fuller exploitation of this group has been the lack of a solid systematic base. However, numerous recent contributions have helped to improve this situation (Galloway & Austin 1984, Johnson 1984, Johnson 1985a, b, Johnson 1987, Johnson & Masner 1985, Kozlov 1967, Masner 1976, 1980, 1983, Ryu & Hirashima 1984, 1985a, b). Even with improvements in the systematics of known species, it remains that many species have yet to be discovered and described. In the subfamily Telenominae, for example, the total of over 600 species which have been described represents only 10-25% of the estimated total number of existing species (Bin & Johnson 1982a). The potential, therefore, of finding valuable new species is great.

Although numerous papers have been published which deal with scelionids, many of these simply contain reports of parasitism, often included as small notes within manuscripts. In this review, I will not attempt to summarize all the available literature dealing with this group of parasitoids. Rather, I will present that information most relevant to applied biological control utilizing scelionid wasps.

BIOLOGICAL AND ECOLOGICAL ATTRIBUTES OF SCELIONIDS

Although it is generally impossible to predict the effectiveness of a natural enemy prior to its introduction, it is useful to have some understanding of the enemies' biological and ecological characteristics (DeBach 1964). Several attributes which are generally considered desirable for a natural enemy to possess have been summarized by Coppel & Mertins (1977). Below I present available information under each of these categories to illustrate attributes which various members of the family Scelionidae possess.

Searching Capacity

Little work has been done to directly examine the host searching ability of scelionid wasps. One notable exception has been the work of Nakasuji et al. (1966) who compared the relative egg mass locating abilities of *Trissolcus (Asolcus) mitsukurii* Ashmead and *Telenomus nakagawai* Watanabe in potatoes and rice. The latter species was considered the superior searcher, with peak numbers finding host egg masses 1-2 days after masses were artificially placed in fields. Turner (1983) examined the rate of movement of *Trissolcus basalis* (Wollaston) on leaf surfaces of a variety of different crop plants, and found that parasitoids moved three times as slowly on soybeans as on the others. Parasitism of *Nezara viridula* (L.) eggs in field cage studies by the same author was lower on soybeans leading him to conclude that the trichomes on soybean leaves inhibit parasitoid movement and thus their effectiveness on this crop.

Debach (1964) states that, in lieu of direct empirical information, one can get an indication of host searching ability by the ease with which a natural enemy can be found at low host densities. This type of evidence has been presented by Hirose (1986) who concluded that *Telenomus dendrolimi* (Matsumura) had a greater searching ability than *Trichogramma dendrolimi* Matsumura. Hirose (1986) believed his work supported the contention that most *Telenomus* species have a searching ability superior to *Trichogramma* species. Other indirect evidence comes from an applied biological control program against *N. viridula* in Hawaii. The imported parasitoid *Tr. basalis* rapidly effected a level of parasitism greater than 90%, which was maintained in the years following introduction even though host egg masses became scarce (Clausen 1978). This evidence indicates a high searching ability on the part of *Tr. basalis*. Although the number of studies addressing searching ability of scelionids is small, the work which has been done indicates that these parasitoids are good searchers.

Reproductive Potential

Generally, it is considered desirable for a natural enemy to possess a high reproductive potential as well as high searching ability. Although a number of studies have examined the reproductive biology of scelionid wasps, few quantitative estimates of the reproductive potential of scelionids are available. The values which have been obtained are presented in Table 1 for comparison with available values for other hymenopteran families which specialize in egg parasitism. Although the values for scelionids are not as high as for some trichogrammatids, they are relatively high when compared to values for other parasitoid taxa, such as those presented by Force (1974). Also, it should be noted that while members of the Trichogrammatidae often produce multiple progeny from individual host eggs, scelionids are mostly solitary (Clausen 1940). Therefore, scelionids have the potential to inflict greater mortality on host populations for a given reproductive rate, if all other biological attributes are assumed equal.

Ecological Compatibility

When introducing natural enemies to control a pest insect it is desirable to have one or more species which will exert control throughout the ecological range of the pest (see for example the California red scale project discussed by DeBach 1974). This can be an important consideration since parasitoids are often more sensitive to environmental conditions than their hosts (Coppel & Mertins 1977).

TABLE 1. COMPARISON OF THE REPRODUCTIVE POTENTIAL OF SEVERAL SCELIONID SPECIES TO MEMBERS OF OTHER HYMENOPTERAN FAMILIES WHICH SPECIALIZE IN EGG PARASITISM.

Parasitoid taxon	Reproductive potential: r_m or r_c (temperature)	Reference
Scelionidae		
<i>Trissolcus basalis</i> (Wollaston)	0.315 (27°C)	Orr et al. 1986a
<i>Telenomus calvus</i> Johnson	0.149 (27°C)	Orr et al. 1986a
<i>T. cristatus</i> Johnson	0.217 (27°C)	D. B. Orr and D. J. Boethel, unpublished data
<i>T. dendrolimi</i> (Matsumura)	0.296 (30°C) ^a	Hirose 1986
<i>T. podisi</i> Ashmead	0.308 (27°C)	Orr and Boethel 1986
Trichogrammatidae		
<i>Trichogramma brevicapillum</i> Pinto & Platner	0.330 (25°C)	Pak and Oatman 1982
<i>T. dendrolimi</i> Matsumura	0.604 (30°C) ^a	Hirose 1986
<i>T. minutum</i> Riley	0.433 (27°C)	Manweiler 1986
<i>T. platneri</i> Nagarkatti	0.368 (27°C)	Manweiler 1986
<i>T. pretiosum</i> Riley	0.318 (25°C)	Orphanides & Gonzalez 1971
	0.340 (25°C)	Pak and Oatman 1982
<i>T. retorridum</i> Girault	0.277 (25°C)	Orphanides & Gonzalez 1971
Mymaridae		
<i>Anagrus epos</i> Girault	0.165 (28°C)	Williams 1984

^avalue presented is 'capacity for increase' (r_c); all others are 'intrinsic rate of increase' (r_m).

The ability of an individual scelionid species to suppress its host over a range of ecological situations has been demonstrated with the case of *Tr. basalis*. This parasitoid has been widely distributed, particularly in the South Pacific region (Luck 1981). The success of this parasitoid in Australia, where it exerts control over *N. viridula* in both the moist coastal regions and the dryer inland regions, has been attributed to the variety of imported strains from regions of differing climatic conditions (Ratcliffe 1965). Support for this conclusion comes from research demonstrating biological differences between *Tr. basalis* strains (Powell & Shepard 1982).

Siddiqui et al. (1986) indicated that *Scelio* spp., important natural enemies of acridids, are habitat specific, and species from this genus have been reported from a wide variety of climates. From their list of parasitoids with recorded hosts and geographical distribution, these authors suggest that species of *Scelio* from ecologically homologous areas could be introduced for the biological control of grasshoppers throughout many regions of the world.

Host-Specificity and Compatibility

Most of the natural enemies involved in successful biological control programs have been somewhat host-specific, and therefore this characteristic is desirable in potential biological control agents (DeBach 1974). Although the host ranges of scelionids vary widely, most species are considered monophagous or oligophagous (Krombein et al. 1979). However, the apparent host-specificity in this group may simply reflect a lack of collecting effort or host range testing (see for example Fedde 1977). It is interesting to note that two species with wide host ranges, namely *Telenomus alsophilae* Viereck (17 host genera; Fedde 1977, Johnson 1984) and *Tr. basalis* (14 host genera; Buschman & Whitcomb 1980, Corrêa-Ferreira 1980, Cumber 1964, Jones 1979, Orr et al. 1986b, Thomas 1972), were utilized for the two most spectacular classical biological control successes involving scelionids (Clausen 1978, Drooz et al. 1977).

However, the wide host ranges of these species may represent the ability to use alternative hosts when a preferred host is unavailable, which seems to be the case with *T. basalis* (see above references). Alternate hosts can be important in biological control (DeBach 1964), and this has been found in the field with scelionids. Yasumatsu (1983) noted that eggs of *Sepedon* and *Tabanu* spp. played an important role in Thailand rice fields by providing alternative hosts for *Telenomus* and *Trichogramma* spp. to maintain their populations during periods when eggs of stem borers were absent. Barrion & Litsinger (1984) reported similar findings in the Philippines.

Temporal Synchronization

Synchronization of field activity and life cycles of natural enemies with that of their hosts can be very important in determining the enemies' effectiveness (Coppel & Mertins 1977). Several studies have addressed this characteristic in scelionids.

Baker et al. (1985) examined the seasonal phenology of six species of *Scelio* and their acridid hosts over a range of latitudes in southeastern Australia. These authors reported that, in general, host insects entered diapause at higher temperatures than parasitoids and that the parasitoids were therefore able to attack diapausing host eggs.

Ticehurst & Allan (1973) reported that the maximum activity by adults of *Telenomus coelodasidis* Ashmead and peak oviposition by its host *Heterocampa guttivita* (Walker) occurred at approximately the same time. Romanova (1954) noted that development of egg parasitoids (including *Telenomus laeviusculus* Ratzeburg and *Telenomus terebrans* Ratzeburg) was well synchronized with that of their host *Malacosoma neustrium* L. Rauschenberger & Talerico (1967) found that *Tel. alsophilae* began ovipositing in host

eggs soon after the beginning of the oviposition period of *Alsophila pometaria* (Harris) in November or December.

Several studies have examined the synchronization of egg parasitoids with *Eurygaster integriceps* Put., a major pest of cereals in Eurasia. Kamenkova (1958) reported that overwintered egg parasitoids (including *Trissolcus* (*Microphanurus*) *vassilievi* (Mayr), *Telenomus chloropus* Thomson (= *T. sokolovi* Mayr), *Gryon* (*Hadronotus*) *afanassievi* Meyer, and *Trissolcus* (*Dissolcus*) *rufiventris* Mayr, but predominated by *Trissolcus* (*Microphanurus*) *semistriatus* (Nees)) emerged prior to *E. integriceps*, and thus could effect a high rate of parasitism of eggs from the beginning of the host ovipositional period. However, Popov & Paulian (1971) reported that scelionids in Romania had a threshold for activity 7-8°C lower than *Eurygaster* spp. and appeared in the field 2-3 weeks earlier than this pest. As a result, the parasitoids suffered a high mortality rate unless alternative hosts were available. Zatyamina et al. (1976) reported that telenomines moved into winter wheat in greatest numbers during the oviposition of *E. integriceps*. Popov (1981) indicated that even though the overwintered generation of *Trissolcus grandis* (Thomson) and *T. chloropus* were well synchronized with the ovipositional period of *E. integriceps*, the first generation was not. Talhouk (1977) reported that early-season egg masses produced by *E. integriceps* in Lebanon escaped parasitism by *Tr. grandis*, although late in the season parasitism rates reached 98%.

Grijpma (1984, 1986) found that adults of *Telenomus nitidulus* (Thomson) were able to survive for 12 months in the field, thus covering the period from one generation of their host, *Leucoma salicis* L. to the next. Torgersen & Ryan (1981) concluded that although *Telenomus californicus* Ashmead was univoltine, the long life of overwintered females allowed them to parasitize more than 80% of *Orgyia pseudotsugata* (McDunnough) eggs. Hirose (1969) noted that *Tel. dendrolimi* adults have a sufficient longevity to survive from the first to the second generation of their host, *Dendrolimus spectabilis* (Butler). However, Learmonth (1981) reported that a major factor limiting the effectiveness of *Telenomus rowani* (Gahan) in controlling *Scirpophaga innotata* (Wlk.) was the long resting stage of the pest.

Although there is some variation, populations of scelionids which have been studied generally appear well synchronized with their hosts. Reproductively active scelionids often appear in the field at the same time as the susceptible host stage appears. In addition, some scelionids can live for a very long period of time in the field, allowing them to survive host-free periods and remain in synchrony with host populations.

Dispersal Capacity

Based on the studies which have been done, scelionid wasps appear to be capable of dispersing well. A number of species of Scelionidae have been reported to be phoretic on their hosts (Bin & Johnson 1982b, Buschman & Whitcomb 1980, Clausen 1976, Learmonth 1981). Phoresy would allow these parasitoids to move to new habitats with their hosts, an adaptation which may be particularly important for species with migratory hosts. Scelionids apparently are also capable of weather-associated long-range dispersal. They have been collected on ocean-going ship traps and in aircraft-mounted sampling nets (Holzapfel & Harrell 1968, White 1970). Farrow (1981) indicated that *Scelio fulgidis* Crawford, an economically important parasitoid of the Australian plague locust, may be capable of dispersing up to 300 km daily on prevailing winds. Both Thomas (1972) and Lee (1979) reported that the dispersal of laboratory-reared *Tr. basalis* in soybean fields following mass-releases was uniform within their experimental areas of ca. 400 and 1600 m², respectively.

Density Responsiveness

In most cases where this characteristic has been studied, scelionids appear to respond in a positive manner to increases in host density, often through numerical responses. Agudelo-Silva (1980) reported that *Telenomus sphingis* (Ashmead) responded well to increases in egg density of its host *Erinnyis ello* (L.). During one year of this study, no time lag was noted between intense host oviposition and parasitoid action, and as a result a large host population buildup was prevented. Parasitism of *Parnara guttata* (Bremer & Grey) eggs, predominantly by *Telenomus* sp., was in a host density-dependent manner (Nakasuji 1982). Kokubo (1975) found that parasitism of *D. spectabilis* by *Tel. dendrolimi* tended toward density dependence. Nef (1976) found that *Tel. nitidulus* responded well to increases in populations of *L. salicis*. Rothschild (1970) reported that an increase in parasitism of *Leptocorisa oratoria* (F.) eggs by *Gryon flavipes* (Ashmead) on rice in Sarawak appeared to be density-dependent. Metcalfe & van Whervin (1967) found that parasitism by *Telenomus alecto* Crawford as well as *Trichogramma minutum* Riley was significantly related to *Diatraea* spp. egg density. In contrast, Hikim (1979) noted that parasitism of *Scirpophaga incertulas* (Wlk.) by egg parasitoids, including *Telenomus dignus* (Gahan) and *Tel. rowani*, may not have been density-dependent in rice. Owusu-Manu (1976) also noted that parasitism by *Trissolcus* spp. appeared to be independent of the density of their host, *Bathycoelia thalassina* (Herrich-Schaeffer).

Functional responses to changes in host density also have been noted in scelionids. Umeh & Ofoegbu (1983) found that *Gryon gnidus* Nixon displayed a Type 2 (C. S. Holling) functional response to changing densities of *Clavigralla tomentosicollis* Stål eggs. Buleza (1985) found that the functional response of *Tr. grandis* was more dependent on concentration of host-seeking kairomone than on host density.

Overall, it appears that scelionids have a positive density responsiveness. Of the 11 species or species groups examined, 8 displayed a host density-related response.

Food Requirements and Habits

Scelionids, in general, do not require a specialized diet such as host-feeding, etc. prior to egg maturation and/or oviposition. Exceptions are the two phoretic egg parasitoids of mantids, *Mantibaria seefelderiana* (De Stef.-Per.) and *Mantibaria (Rielia) manticida* Kieffer, which feed on the body fluids of adult mantids while waiting for host eggs to be deposited (Bin 1985, Clausen 1940). However, many scelionids appear to be proovigenic and require only a carbohydrate source and water to live for a relatively long period of time (ca. 8-70 days) in the laboratory (Hidaka 1958, Hirose 1986, Hokyo et al. 1966, Orr & Boethel 1986, Orr et al. 1985, Orr et al. 1986a, Powell & Shepard 1982, Schwartz & Gerling 1974, Yeargan 1982). Their simple diet makes these parasitoids more amenable to laboratory rearing.

In the field and laboratory, these parasitoids have been reported to feed on nectar and aphid honeydew (Grijpma 1986, Hidaka 1958, Safavi 1968, Zatyamina & Burakova 1980, Zatyamina et al. 1976). These carbohydrates, along with water from dew, precipitation, etc. should allow these parasitoids to survive long periods in the absence of hosts. In fact, Hidaka (1958) demonstrated that *Telenomus gifuensis* Ashmead adults fed aphid honeydew survived more than twice as long as those fed honey.

Hyperparasitism

To date there has been only one confirmed report of hyperparasitism of a scelionid species. Strand & Vinson (1984) reported that *Trichogramma pretiosum* Riley was a

facultative hyperparasitoid of *Telenomus heliothidis* Ashmead. In general, however, scelionids lack known hyperparasitoids or primary pathogens. Because of this, rearing and quarantine operations have been simplified, and as far as is known, effectiveness of these parasitoids is not reduced in the field as a result of secondary parasitism.

Culturability

Inherent characteristics such as simple adult diet, lack of hyperparasitoids and pathogens, good reproductive capability, small size (and therefore low space requirements), and often the ability to use alternate hosts, make scelionids very amenable to rearing. Mass-rearing methods have been developed for a number of different species and their hosts (Boardman 1977, Bustillo 1978, Conlong et al. 1984, Cumber 1951, Davis 1964, Gupta & Pawar 1985, Gusev & Shmettser 1975, Ji 1985, Korneeva et al. 1981, Kulshreshtha et al. 1967, Kumar et al. 1986, Orr 1985, Owusu-Manu 1976, Pemberton 1948, Romanova 1954, Safavi 1968, Suntsova & Shirinyan 1974, Thobbi et al. 1976). In addition, research conducted on a variety of topics outlined below may prove useful in enhancing rearing operations.

A difficulty often faced in mass-rearing operations is obtaining large quantities of suitable host material at times when they are needed. Several host storage or stock-piling methods, including the use of infertile eggs or freezer storage, have been examined for use with scelionid wasps.

A number of authors have looked at freezer storage and have indicated that, in general, it appears to be a viable method for rearing scelionids. Genduso (1979) demonstrated that the eggs of several species of Heteroptera could be stored for up to three years in liquid nitrogen and still be utilized normally by species of *Gryon* and *Trissolcus*. Gennadiev & Khlistovskii (1980) further demonstrated the utility of this method by showing that the eggs of *Graphosoma lineatum* (L.) could be stored for five years in liquid nitrogen for the mass-rearing of *Trissolcus simoni* (Mayr). Powell & Shepard (1982) found that emergence of *T. basalis* was not reduced in freezer-stored *N. viridula* eggs, and that eggs could be successfully stored for seven months. In addition, when eggs were removed from freezer storage they were suitable for a longer period of time than were fresh eggs (Powell & Shepard 1982). Infertile eggs of *Dendrolimus pini* (L.) kept in cold storage remained suitable for up to seven months, although the rate of successful parasitism by *Telenomus tetratomus* Thomson (= *T. verticillatus* Kieffer) declined with time (Korneeva et al 1981). Popov (1974) reported that neither *T. grandis* or *Tr. vassilievi* showed a preference for fresh eggs of several pentatomid species over those which had been stored at -20°C for up to 270 days, however, a decrease in successful parasitism was noted in eggs after 180 days of storage. Not all scelionids tested will develop in dead host eggs. Ryan et al. (1981) found that while *Tel. californicus* could successfully develop in *O. pseudotsugata* eggs which had been stored at 5°C, the parasitoid developed poorly in eggs which had been killed by freezing. Similarly, *G. gnidus* would not develop in freezer-killed eggs of *Acanthomia tomentosicollis* (Stål) (Egwuatua & Taylor 1977).

The cold storage of both parasitized eggs and adult parasitoids also has been studied. Kumar et al (1984) found that host eggs parasitized by *Telenomus remus* Nixon could be held at 5°C for two weeks before parasitoids died, regardless of developmental stage. Both male and female *Tel. remus* adults were safely stored at 5°C for three days, and parasitized eggs (6-7 days following parasitism) could be stored at 10°C for a week without affecting the efficacy of parasitoids (Gautam 1986a). Bakasova (1975) reported that the storage of telenomines at low temperatures did not reduce their ability to attack host eggs for up to six months.

Irradiation has also been studied as a possible tool for increasing the 'shelf-life' of host eggs for parasitism by scelionids. Nordlund et al. (1983) successfully adapted a *Trichogramma*-rearing technique for *Tel. remus* which involved irradiating (with ^{60}Co) *Heliothis zea* (Boddie) eggs prior to exposure to parasitoids. In contrast, Egwuatu & Taylor (1977) found that *G. gnidus* would not develop in eggs of *A. tomentosicollis* which had been killed by gamma-irradiation.

The use of infertile host eggs as a means of augmenting host storage capabilities in mass-rearing operations has met with some degree of success. Several authors have successfully reared scelionid wasps in infertile host eggs (Artem'ev et al. 1971, Pelley 1979, Phalek & Raodeo 1967, Schneider, 1940, Tadic 1972, Ticehurst & Allen 1973). Although parasitoid survival of *Tel. alsophilae* in infertile eggs of several lepidopteran hosts is reduced by about one half (Fedde 1977), these eggs remain attractive to parasitoids and can be successfully parasitized for about twice as long a time period as fertile eggs (Bustillo & Drooz 1977). However, parasitoids reared in infertile eggs may face possible changes in vigor and/or biology as a result of nutritional changes in their hosts. Gautam (1986b) found that infertile eggs of *Spodoptera litura* (F.) had amino acid deficiencies. Even changes in the diet of host insects have been implicated in reduced fecundity and survival of scelionids, possibly mediated through changes in the quality of host eggs (Orr & Boethel 1986, Orr et al. 1985).

Scelionid species have been successfully reared in the laboratory on factitious hosts. Pelley (1979) found that the eggs of *Agonoscelis versicolor* (F.) were very satisfactory hosts for *Gryon antestiae* (Dodd) in the laboratory but not in the field. Fedde et al. (1982) presented guidelines for selection of factitious hosts for the rearing of parasitic Hymenoptera based on their own successful experiences with *Tel. alsophilae*. These included: 1) Consider all 'surrogate' host options, 2) favor the use of artificial media for host rearing, when possible, and 3) Consider quality control of hosts. Although problems with reduced size, fecundity, longevity and vigor have been previously noted with *Trichogramma* spp. reared on factitious hosts, Fedde et al. (1982) suggested that this should not be assumed to be a problem with egg parasitoids.

Both the existence and characterization of kairomones involved in host-location and selection by scelionids have been documented by a number of authors (Aldrich et al. 1984, Bin & Vinson 1985, Buleza 1985, Buleza & Mikheev 1979, Cave et al. 1987, Lewis & Nordlund 1984, Nordlund et al. 1987, Sales 1979, Sales et al. 1978, Strand & Vinson 1982a, b, 1983a, b, Viktorov et al. 1975). There may be several potential uses for these compounds in scelionid rearing. Strand & Vinson (1982b) have demonstrated that *Tel. heliothidis* will develop successfully in the laboratory on non-host eggs to which kairomones have been applied. This technique may be very helpful in situations where the usual host insect of a parasitoid is difficult to rear in the laboratory but an easily reared potential host may be available. Another possibly useful application of kairomones was noted by Buleza (1979) who found that host-seeking kairomones from the frass and cuticle of *E. integriceps* increased both the longevity and fecundity of *Tr. grandis* in the laboratory.

AUGMENTATION

A number of attempts have been made to increase or help synchronize scelionid populations through periodic mass-releases. Mineo & Lucido (1976) found that releases of *Gryon muscaeformis* (Nees) in hazel resulted in higher rates of parasitism of *Gonocerus acuteangulatus* (Goeze), however, the same was not true for *Trissolcus flavipes* (Thomson). Both Thomas (1972) and Lee (1979) reported that mass-releases of native *Tr. basalis* into soybean fields resulted in significant increases in percent parasitism of *Nezara viridula* (L.). Early season releases of *Tel. gifuensis* against

Scotinophara lurida Burmeister were effective, resulting in much higher rates of parasitism than natural populations (Hidaka 1958). Martin et al. (1969) found that augmentative releases of *Tr. grandis* and *Tr. semistriatus* in Iran gave satisfactory results against *E. integriceps*. However, Kartavtsev et al. (1974) reported that seasonal releases of telenomines against *E. integriceps* were hampered by the wasp's behavior. Most of the parasitoids did not remain at the release sites, and levels of parasitism which did occur were strongly influenced by weather conditions.

Weekly mass-releases of large numbers of *Tel. remus* into cauliflower resulted in 60% parasitism of *S. litura*, however, releases into tobacco did not result in any parasitism of the pest (Patel et al. 1979). This parasitoid, although exotic, had first been introduced into India eight years prior to this test (Luck 1981). Krishnamoorthy & Mani (1985) used field cages to determine the optimal parasite-to-host egg ratio for releases of *Tel. remus* against *S. litura* in cabbage fields in India. Cochereau (1980) reported that *Telenomus* sp. nr. *dignus* was being released to attempt control of *Eldana saccharina* Walker on the Ivory Coast of Africa. Large-scale releases of *T. laeviusculus* and *T. terebrans* were made from 1950 through 1960 within the Soviet Union in attempts to control *M. neustrium* and *Dendrolimus sibiricus* Tschtv., respectively (see Kozlov 1967).

Parman (1928) reported on attempts to augment egg parasitism of tabanid flies in Texas by the field-collection of large quantities of naturally-parasitized eggs, and the subsequent placement of these eggs in containers along stream banks to allow emergence of *Telenomus olsenni* Johnson (*Phanurus emersoni* Girault) but prevent escape of hatched host larvae. The author concluded that this was a viable method of tabanid control, however, Anderson (1985) indicated that the reported 50% reduction of tabanid populations may have been as much a result of the removal of 20-25 million fly eggs from the study area as the dissemination of parasitoids.

Semiochemicals may also prove useful in augmentation efforts involving scelionids. As mentioned above, semiochemicals involved in host selection by several scelionids have been identified. Kairomones which stimulate host-seeking can be used to reduce or eliminate the escape response displayed by adult parasitoids when released into an area, thus increasing their effectiveness (Lewis & Nordlund 1984). These semiochemicals may also be used to attract and retain natural populations of parasitoids.

Environmental manipulation or modification can be helpful in increasing the effectiveness of natural enemies (DeBach 1964). Several studies have examined the value of this method for use with scelionid wasps. The influence of surrounding plant communities or agroecosystems on parasitism was discussed by Fed'ko (1982). The latter author reported dramatic increases in parasitism of *E. integriceps* by telenomines when winter wheat fields were located near buckwheat or nectar-bearing plants. Zatyamina & Burakova (1980) demonstrated that *T. grandis* will feed on the nectar of a variety of flowers, the type of which had an important influence on both the fecundity and longevity of these parasitoids. This work raises the interesting possibility of augmentation of scelionid populations by selective planting or encouragement of species preferred by scelionids. This approach has been suggested by Romanova (1951) as part of a biological control program against *M. neustrium* L. in the USSR.

Nagarkatti (1973) reported that *Agrius convolvuli* (L.), an occasional pest of *Phaseolus* spp. and sweet potatoes, will also frequently oviposit on the flowering shrub *Clerodendron fragrans* var. *pleniflorum* (which does not sustain any feeding damage by the pest) where eggs are parasitized by several egg parasites including a species of *Telenomus*. The latter author suggested either leaving or planting this shrub near fields to provide reservoirs of parasitoids.

Both Areshnikov et al. (1987) and Morales-Agacino (1972) found that irrigation of cereal crops increased the rate of *E. integriceps* egg parasitism by scelionids 2- to 4-fold

the rate in dry conditions. The latter author also presents an entire management scheme recommended for *E. integriceps* control on cereals in Iran based on conservation and encouragement of scelionids. Suggested practices included the provision of trees for overwintering sites, refuges for parasitoid populations, and insecticide applications only in host aestivation areas to avoid adverse effects on parasitoids in fields.

Ever since industrial melanism was first demonstrated in Great Britain, entomologists have been aware that industry can have an important impact on insect populations (Kettlewell 1961). An interesting example of how industrial pollution might affect a biological control agent was recorded in Finland. Heliövaara et al. (1982) found that the percentage of *Aradus cinnamomeus* Panzer eggs parasitized by *Telenomus aradi* Kozlov decreased significantly with proximity to an iron factory and concluded that the scelionid wasps did poorly in polluted conditions.

Two unusual approaches to augmentation of egg parasitoid (including *Telenomus* spp.) populations involved supplementing host egg masses in the field. Peng et al. (1984) found that by setting out cards with attached *Dendrolimus punctatus* Walker eggs into forest situations they could produce an increase in parasitism by the endemic egg parasitoid guild of 5.5-16.2 times the natural rate. Miah et al. (1984) reported that when "parasite boosters" (hollow bamboo stakes containing naturally-parasitized egg masses) were placed in sugarcane fields, infestations of sugarcane topshoot borer were reduced by 20%.

Augmentation of scelionid populations has also been attempted through the release of sterile adult female hosts. Artem'ev et al. (1971) reported that the field release of sterilized *E. integriceps* females resulted in a 16% increase in egg parasitism by *Tr. grandis* since the parasitoids' development and survival was not affected in infertile host eggs.

CLASSICAL BIOLOGICAL CONTROL

Scelionids have been used with a certain amount of success in classical biological control programs, although the number of programs in which they have been employed is relatively small. Luck (1981) recently tabulated the cases in which parasitoids have been introduced in classical biological control programs throughout the world. A total of 20 scelionid species were listed.

One of these species, *Tr. basalis* had been introduced into a number of different countries to control *N. viridula*, with repeated success (Clausen 1978, Luck 1981). Since that time, *T. basalis* has been further introduced into Argentina (Crouzel & Saini 1983), the Philippines (M. Shepard, D. B. Orr, and D. J. Boethel unpublished data), and Taiwan (Su & Tseng 1984). *Telenomus remus* also has been introduced against noctuid pests in many more countries including Antigua (Irving 1978), Australia (Michael et al. 1984), Barbados (Alam 1978, 1981), Guyana (Sinha 1982), New Zealand (Rep. Dept. Sci. Ind. Res. 1977), Suriname (Segeren & Sharma 1981), Trinidad (Yaseen 1981), and the United States (Earl & Graham 1984, Waddill & Whitcomb 1982, Wojcik et al. 1976).

An additional 16 scelionid species plus *Tr. basalis* were imported into the USSR from Morocco to be evaluated as control agents of *E. integriceps* (Shapiro et al. 1975, Voronin & Dzyuba 1971). Three of these, namely *Tr. semistriatus*, *Tr. basalis*, and *Trissolcus nigribasalis* Voegelé, were subsequently mass-released, with mixed results. Gusev (1970) reported that pentatomid population reductions of 25-50% resulted from releases, however, Kartavtsev et al. (1974) were not successful at increasing parasitism rates.

Biological control attempts have been made with several other scelionid species since Luck's (1981) review. *Tr. mitsukurii* was released in Brazil in attempts to control the guild of pentatomids occurring in soybeans (Kobayashi & Cosenza 1987). *Telenomus*

chloropus has been introduced into the U.S. and the Philippines against *N. viridula* and *Scotinophara coarctata* (F.), respectively (Orr 1985; M. Shepard, D. B. Orr, & D. J. Boethel unpublished data). Both *Telenomus cyrus* Nixon and *Psix lacunatus* Johnson & Masner were released on the island of Palawan in the Philippines in an effort to control *S. coarctata* (Annual Report 1984). The former species had not been previously recorded from Palawan where *S. coarctata* is a pest. *Telenomus proditor* Nixon has been further mass-released in India against *Achaea janata* (L.) (Thobbi et al. 1976). Conlong et al. (1984) and Carnegie et al. (1985) reported that *Telenomus applanatus* Bin & Johnson had been imported from West Africa and released in South Africa sugarcane against *E. saccharina*. Rees (1985) evaluated four Pakistani scelionids against North American grasshopper species, but found them to be unpromising as biological control agents.

Possibly the most outstanding example of classical biological control involving scelionids utilized an egg parasitoid of a forest pest. Bustillo & Drooz (1977), and Drooz et al. (1977) reported that *Tel. alsophilae*, a parasitoid of *A. pometaria* in North America, was imported to Colombia, South America, where it successfully controlled an outbreak of *Oxydia trychiata* (Guenée). The results supported Pimentel's (1963) hypothesis that biological control programs could be more successful if they utilized parasitoids which attack allied species and genera to control pest insects.

Overall, scelionids have been used quite successfully in classical biological control programs. Greathead (1986) reported that 12 scelionid species had become established following release against 11 target pest species. On 6 of the 23 separate occasions on which establishment of these parasitoids was reported, the target species was effectively controlled (Greathead 1986).

INTERACTIONS WITH OTHER MANAGEMENT TACTICS

Because scelionids parasitize the eggs of a number of predatory insects as well as those of phytophagous insects (Krombein et al. 1979), they might be expected to hamper predatory insect introduction efforts and also reduce the effectiveness of native predators. This has been shown to be the case with chrysopids and berothids for example (see Johnson & Bin 1982). However, this is not always so. Izhevskii et al. (1980) reported that the predatory pentatomid *Podisus maculiventris* (Say), imported into the USSR from the USA, was less preferred than native hosts of the indigenous scelionid guild and thus escaped high rates of parasitism. In the USA this predator is often heavily parasitized (Buschman & Whitcomb 1980, Yeargan 1979, Orr et al. 1986b). On the other hand, predation of parasitized eggs by non-discriminating egg predators may result in a further conflict between biological control programs utilizing these two types of natural enemies (see for example Krishnamoorthy & Mani 1985).

As mentioned previously, scelionids are not known to be attacked by any primary pathogens, and therefore should be expected to interact well with microbial control programs. Phadke & Rao (1978) and Kamat et al. (1978) demonstrated that *Tel. proditor* was not affected by the fungus *Nomuraea rileyi* (Farlow) Samson, and they concluded that the two natural enemies could be successfully used together to control the castor pest *A. janata*. Kaya & Dunbar (1972) reported that the immature stages of *Tel. alsophilae* in eggs of *Ennomus subsignarius* (Hübner) in apple orchards were unaffected by field applications of *Bacillus thuringiensis* (Berliner).

While much work has been done to illuminate the influence of host plant resistance on beneficial insects (see Boethel & Eikenbary 1986 for a recent review of this subject), it appears that a generalized statement cannot be made concerning the outcome of these interactions. Rather, it appears to depend on the particular system and its components. Several studies have been done to determine effects of insect-resistant plants on

scelionid wasps. Rabb & Bradley (1968) noted that *Tel. sphingis* parasitism of *Manduca sexta* (Johannson) eggs was reduced on resistant tobacco cultivars with glandular pubescence. Orr et al. (1985) and Orr & Boethel (1986) demonstrated further that soybean antibiosis, mediated through host insects over three and four trophic levels, had an adverse effect on the biology of both *Tel. chloropus* and *Telenomus podisi* Ashmead.

Biological control provided by scelionid wasps may interact well with pest management programs involving semiochemicals. Egg parasitism by *Tel. californicus* was unaffected by aerial application of synthetic sex pheromone for mating disruption of the host *O. pseudotsugata* (Sower and Torgersen 1979). Nordlund et al. (1983) reported that components of the sex pheromone of *Spodoptera frugiperda* (J. E. Smith) also stimulate host-seeking activity by *Tel. remus*, and suggested that the parasitoid could be used in conjunction with mating disruption programs against *S. frugiperda*.

The sterile-male technique can be a valuable management tool for some insect populations (Knipling 1979). While evaluating the release of sterile *E. integriceps* males, Tadic (1972) concluded that the effectiveness of *Telenomus* and *Trissolcus* populations would not be reduced because the parasitoids could successfully develop in infertile host eggs.

Insecticides remain the most important control measure we have against many pest insects. Therefore, workers in biological control must often integrate natural enemies into an existing pest management program based mainly on insecticides, even if their goal may be the eventual reduction of chemical controls. It is therefore of paramount importance to have an understanding of how natural enemies are affected by insecticides throughout their various life stages. A number of laboratory bioassay studies have addressed the contact toxicity of a variety of insecticides to adult scelionids. However, several other studies have a more direct application to field situations.

Kolomiets & Kovalenok (1958) noted that aerial application of insecticides did not reduce parasitism rates by *T. /* (= *T. gracilis* Mayr) because this parasitoid is phoretic and is recolonized along with its host *D. sibiricus* Tschetv. Kamenkova (1971) noted that if insecticide applications were made against first generation *E. integriceps* nymphs rather than overwintered adults, the scelionid fauna would be virtually unaffected, since they had already oviposited into host eggs produced by the overwintered bugs. Zaeva (1969) reported that insecticide treatment of wheat fields for control of *E. integriceps* in spring in the USSR resulted in reduced overall control when compared with the natural control provided by beneficial insects, particularly *Trissolcus* and *Telenomus* species.

While insecticides generally are toxic to adult scelionids, it appears that preimaginal parasitoids within host eggs are protected and thus can often escape high mortality in the field and replenish reduced adult populations (Joshi et al. 1982, Malysheva & Kartavtsev 1975, Nadejde & Teodorescu 1982, Niemczyk et al. 1979, Orr et al. 1988, Patnaik & Satpathy 1984, Rosca & Popov 1983). This phenomenon has also been seen with insect growth regulators. Leuschner (1975) reported that the development of *Trissolcus seychellensis* (Kieffer) was virtually unaffected by treatment of *Antestiopsis* spp. eggs with juvenile hormone analogs.

The reason for this 'protection' appears to be differential penetration through the chorion of host eggs. Novozhilov et al. (1973) found that the penetration of chlorophos through the chorion of *E. integriceps* eggs varied with developmental stage of *Tr. grandis*, but that most of the insecticide remained adsorbed to host egg choria. Parasitoids were least vulnerable in the egg and larval stages, and penetration was highest in the pupal stage, resulting in increased parasitoid mortality and number of malformed individuals. Two other studies have presented evidence to the contrary, indicating that scelionid emergence was greatly reduced by insecticides both in the field and in the laboratory (Sales 1978, Xie et al. 1984).

CONCLUDING REMARKS

Of the 63 scelionid species or groups of species discussed in this review, many have exhibited characteristics which make them worthy of consideration as candidates for biological control programs directed toward a variety of arthropod pests. Certainly, applied work has demonstrated a wide range of possibilities for the utility of this group of parasitic wasps, in both augmentative and classical approaches to biological control. Although major improvements have begun in the systematics of scelionids, most of the existing species within this taxon apparently await discovery. This information, combined with the results obtained both in basic research and practical applications involving known species, suggests that scelionid wasps hold much promise in the future as biological control agents.

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EUCHARITIDAE (HYMENOPTERA: CHALCIDOIDEA): BIOLOGY AND POTENTIAL FOR BIOLOGICAL CONTROL

D. W. JOHNSON
Department of Entomology and Nematology,
University of Florida,
Gainesville, Florida 32611

ABSTRACT

The biology of Eucharitidae is summarized, and the potential for biological control of ant pests using members of this family is reviewed. The morphology, habits, and life histories of these wasps are described. Their associations with thrips, and with plants during oviposition, are considered. The need for comparing infested and uninfested host colonies in a controlled setting is stressed. Aspects of eucharitid biology that may affect their use in biocontrol are examined, including dispersal, levels of parasitism, and possible synergistic effects with other natural enemies. Possible conflicts of interest in the use of these wasps for biocontrol are considered.

RESUMEN

Se sumaria la biología de Eucharitidae y se revisa el potencial del control biológico de plagas de hormigas usando miembros de esta familia. Se describe la morfología, hábitos, y la historia de la vida de estas avispas. Se consideran sus asociaciones con tisanópteros y con plantas durante la oviposición. Se acentúa la necesidad de comparar colonias infestadas y no infestadas en un ambiente controlado. Se examinan aspectos de la biología de eucaritidos que pueden afectar su uso en control biológico, incluyendo dispersión, niveles de parasitismo, y posible efectos sinérgicos con otros enemigos naturales. Se consideran posibles conflictos de interés en el uso de estas avispas como control biológico.

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The family Eucharitidae consists of small wasps (Hymenoptera) of the superfamily Chalcidoidea. The type genus is *Eucharis* Latreille (1802). Now 44 genera and over 300 species are recognized (Heraty 1985). Although the distribution of eucharitids is nearly world-wide, their diversity is greatest in tropical regions. The group is treated here as distinct from the related Perilampidae and Pteromalidae, in accordance with the findings of Heraty & Darling (1984) and Heraty (1985). In this communication, aspects of the biology of eucharitids are surveyed, and an evaluation is made of the potential for using them in biocontrol of their ant hosts.

SUMMARY OF EUCHARITID BIOLOGY

The life histories of these wasps are known from observation of a small number of species. It can be surmised that all are parasites of ants (Hymenoptera: Formicidae), although the full range of hosts utilized by eucharitids (as a group or even within a single species) is uncertain. Table 1 shows the known host associations for eucharitids. The taxonomically limited host preference of eucharitids as a group stands in contrast to the wider host ranges in related chalcidoid families such as Perilampidae (Iwata 1976).

TABLE 1. HOST ASSOCIATIONS OF EUCHARITIDS^a.

Eucharitid Genus	Ant Genus
<i>Chalcura</i>	<i>Formica</i> (12)
	<i>Odontomachus</i> (4,5)
<i>Epimetagea</i>	<i>Myrmecia</i> (5,12)
<i>Eucharis</i>	<i>Cataglyphis</i> (12)
	<i>Formica</i> (4,10)
	<i>Messor</i> (10,12)
	<i>Myrmecia</i> (12)
	<i>Myrmecocystus</i> (10)
<i>Eucharomorpha</i>	<i>Pheidole</i> (12)
<i>Isomerala</i>	<i>Ectatomma</i> (12)
<i>Kapala</i>	<i>Camponotus</i> (5,12)
	<i>Odontomachus</i> (3)
	<i>Pachycondyla</i> (12)
<i>Orasema</i>	<i>Pheidole</i> (4,6,8,12,13)
	<i>Solenopsis</i> (6,13)
	<i>Wasmannia</i> (4,9,12)
<i>Pseudochalcura</i>	<i>Camponotus</i> (7,12)
<i>Pseudometagea</i>	<i>Lasius</i> (1,6)
<i>Psilogaster</i>	<i>Pheidole</i> (12)
<i>Rhipipallus</i>	<i>Myrmecia</i> (5,12)
	<i>Odontomachus</i> (5,12)
<i>Schizaspidia</i>	<i>Calomyrmex</i> (5,12)
	<i>Camponotus</i> (2,12)
	<i>Odontomachus</i> (3,4,5)
<i>Stilbula</i>	<i>Camponotus</i> (3,4,5,10)
	<i>Polyrhachis</i> (5,11,12)
<i>Tricoryna</i>	<i>Chalcoponera</i> (12)
	<i>Ectatomma</i> (12)

^aReferences: (1) Ayre, 1962, (2) Clausen, 1923, (3) Clausen, 1941, (4) Gahan, 1940, (5) Hedqvist, 1978, (6) Heraty, 1985, (7) Heraty, 1986, (8) Mann, 1914, (9) Mann, 1989, (10) Ruschka, 1924, (11) Wheeler & Wheeler, 1924, (12) Wheeler & Wheeler, 1937, (13) Williams & Whitcomb, 1973.

The appearance of these wasps is varied and often bizarre. In adult eucharitids, the head is small and the mandibles are falcate. In some, the head is triangular in frontal view and thin along the antero-posterior axis. The thorax of many forms is robust, and often sculptured distinctively. The scutellum in many species is modified, sometimes with a bifurcate process extending posteriorly beyond the tip of the abdomen (Clausen 1940a). The abdomen is petiolate, and in some forms the exposed portions of the terminal segments are small. This gives the appearance of compression or telescoping of the terminal abdominal segments (Ashmead 1897, Clausen 1940b).

The first-instar larva of the eucharitids is termed a planidium. The tergites of this legless larva are highly sclerotized and are mostly ring-shaped. Thus, they do not surround the body completely. The tergites allow some flexibility at the intersegmental membranes and telescoping of the segments (Clausen 1940b,c, Tripp 1961). Although Malyshev (1966) considered Eucharitidae and Perilampidae to represent the so-called intermediate parasitic phase in the evolution of the Terebrantia (parasitic Hymenoptera in the wide sense, as opposed to the Aculeata), it has become evident through comparative morphological and systematic studies (Heraty & Darling 1984) that the planidium is a derived larval form within the Terebrantia.

Planidial larvae are known from two other hymenopteran families, namely the Ichneumonidae (subfamily Eucerotinae; Tripp 1961) and Perilampidae (Smith 1912, Heraty & Darling 1984). Within the dipteran families Acroceridae, Tachinidae, and Sarcophagidae (Wilson & Cooley 1972), and in the lepidopteran family Epipyropidae (Kirkpatrick 1957) are species with legless first-instar larvae that search actively for a host. These larvae are sometimes called planidia, but possess a different morphology than the hymenopteran planidia.

The eucharitid planidium hatches from eggs deposited usually in or on plants (Clausen 1941). A caudal sucker and in some cases stout spines are used by the planidium to assume an upright position when waiting for a host (Clausen 1940c). The method of movement or transport of the planidium to the host brood has not been studied in detail, but it is thought generally that it may attach to an adult foraging ant, and be carried back into the nest. Here it develops as a parasite of an immature ant (Clausen 1941). In several cases studied, the planidium remains attached to the ant larva until the host begins to pupate, the parasite feeding comparatively little through one or more puncture(s) made in the integument. In some cases the planidium feeds with most of its body inside the host, with the caudal end emerging from the wound site. Tracheal breathing has not been demonstrated in the planidia, but the small size of these larvae would allow respiration by diffusion through the body surface. Indeed, the absence of spiracles in planidia is seen as a derived trait in this group by Heraty & Darling (1984).

Once the host enters the pupal stage, feeding by the eucharitid is intensified. The parasite completes its development swiftly, and adults emerge within the ant nest (Heraty 1985). Some eucharitids consume the majority of the host pupae before beginning their own pupation (Ayre 1962), while others cause characteristic deformations of the host pupae (Wheeler 1907) which involves arrested development and eventual death. Moving out from the host colony, the adult parasites usually mate soon (within several hours) after emergence. In some cases females have been found to oviposit close to the host colony from which they emerged. Observations indicate that adults of some species do not feed (Clausen 1941).

Poor dispersal, as well as the specificity for particular host plants for oviposition, are among the factors thought to contribute to the seeming rarity of some eucharitids (Ayre 1962, Clausen 1941). However, some eucharitids are very good fliers (J. M. Heraty, Texas A&M University, College Station, TX, personal communication). Also, the known oviposition plants for some species are weeds throughout much of the ranges of the host ants, and the presumed specificity in oviposition plants may be an artifact of the limited data available.

The adult female eucharitid carries an abundance of eggs. These are minute, about 0.1 to 0.2 mm long, and stalked (Clausen 1940c). Dissections of females of *Pseudometagea schwarzii* (Ashmead) before and after oviposition (Ayre 1962) indicated that the full complement of approximately 450 eggs was deposited by a female during her life. The eggs are fully developed upon emergence of the adults from the nest. Individual females of some species of eucharitids may deposit as many as 10,000 to 15,000 eggs (Clausen 1940a) during their lives.

Eucharitid eggs are laid on or in the tissues of plants, but the exact site of oviposition on the plant, as well as the typical number of eggs laid per oviposition event, varies among different species. Eggs overwinter in some species (Clausen 1940a). They may be laid in overwintering leaf buds of mulberry, chestnut, oak, or birch; on expanding leaf and flower buds; or in leaf tissue incisions (Clausen 1940a,b). Some forms which oviposit into the surface tissues of leaves may deposit the eggs in characteristic designs or patterns. Some oviposit into seed receptacles, where the eggs may be dispersed on wind-borne seeds (Parker 1937).

The apparent specificity of oviposition sites chosen by eucharitids has been deduced from records based on field observations. These indicate that a given eucharitid oviposits on one or a few types of plant soon after emerging from the host colony (Clausen 1940a). Thus, the range of possible oviposition plants for a given species is uncertain. *P. schwarzii* is known to utilize several different plant species for oviposition, but it is not clear how this broad preference may affect dispersal of the parasite. It may limit distribution of the parasite (Ayre 1962) by allowing suitable oviposition sites to be found close to the nest from which the female just emerged. Or it may promote dispersal if, for example, a mated female is swept by winds away from the ant nest from which it emerged, and finds suitable oviposition sites near another host colony.

Some eucharitids oviposit at sites of prior oviposition by thrips. The eucharitid larva then attaches to the larval thrips, and may consume a portion of the hemolymph of the thrips. Probable feeding of *Orasema* sp. on nymphal *Sericothrips* sp. was noted by Johnson et al. (1986), who suggested that thrips may serve as a facultative alternate host until the suitable ant host was found. Females of the eucharitid *Psilogaster antennatus* Gahan will only deposit their eggs in close association with the eggs of *Selenothrips rubrocinctus* (Giard) (Clausen 1940a). In these types of interactions, it has been suggested that the planidium, in a phoretic relationship with the thrips, is transferred eventually to the ant host (Clausen 1940a). However, with at least one species of *Orasema* in Florida (L. Davis, USDA, ARS, Gainesville, FL, personal communication), and with *P. antennatus* (Clausen 1940a), the thrips involved are not tended regularly by ants. In the case of the *Orasema* in Florida (L. Davis, personal communication), as well as the eucharitid associated with the thrips *Frankliniella occidentalis* (Pergande) (Wilson & Cooley 1972), planidia were found imbedded partially in the body of a thrips in a manner similar to that in which they are found in ant larvae. However, no eucharitids are known to complete their development on thrips; therefore, the latter should not be considered alternate hosts. The thrips are at this time considered to be carriers or accidental hosts (J. M. Heraty, personal communication). The role of thrips in the life cycle of any eucharitid thus remains unclear.

In the case of *P. schwarzii*, development proceeds through three instars prior to pupation (Ayre 1962). During the first instar, the planidium, developing inside the ant larva, increases greatly in size. Development proceeds quickly, pupation occurring only four to five days after the first molt. The parasite is shed, prior to its own pupation, at the host's prepupal molt. At this point the wasp becomes an ectoparasite and consumes more or less the entire host (leaving only the integument). Preoral digestion, perhaps by regurgitation of enzymatic alimentary secretions, may facilitate such a complete consumption of the host. This possibility is supported by the observation in thin sections of destruction of host epithelial tissue at the locus of feeding of the first instar parasite.

A switchover from endoparasitism to ectoparasitism is not limited to a single eucharitid species. Development of an *Orasema* sp. on fire ant (*Solenopsis* sp.) brood in Brazil is also known to involve such a change in the ontogeny of the parasite (D. P. Wojcik, USDA, ARS, Gainesville, FL, personal communication).

After consuming the host, *P. schwarzii* pupates, and the worker ants sometimes assist in the emergence of the adult from the pupal skin. In some cases the workers carry the adults away from the nest, in a behavior that appears similar to that used for refuse disposal. Hostile behavior was not observed to be directed toward the parasites (Ayre 1962). In disturbed fire ant nests in Brazil, the worker ants rescue *Orasema* pupae and adults before they rescue ant brood (D. P. Wojcik, personal communication).

Thus, the eucharitids are a group with varied habits. Species exhibit differences in fecundity, oviposition behavior, developmental times, stage morphology, and host preference.

POTENTIAL FOR USING EUCHARITIDS IN BIOLOGICAL CONTROL OF ANT PESTS

Many ant species have been considered pests (Table 2). Some of these, such as species of *Solenopsis* and *Pheidole*, are known to be hosts of eucharitids. The assessment of the potential of these wasps in biological control of pest ants is made difficult by the paucity of information on the factors affecting levels of parasitism and colony vigor. It is also hindered by a scarcity of biological and systematic information for the eucharitids. Since ant colonies may be maintained in the laboratory, studies should be instigated in controlled conditions in which uninfested (control) ant colonies are compared to colonies infested with eucharitids.

Laboratory studies conducted with different ant-eucharitid combinations would allow an assessment of the impact of variations in abiotic factors such as temperature and humidity on levels of parasitism. These studies would suggest which eucharitids might best be used to induce mortality in a given environment. Biotic factors affecting mortality induced by eucharitids could also be investigated if colony size and composition were varied in the laboratory, and the level of parasitism could be varied in different

TABLE 2. SOME ANT GENERA WITH SPECIES CONSIDERED TO BE PESTS.

Ant Genus	Reference(s) ^a
<i>Atta</i>	1,5,6
<i>Camponotus</i>	1,2,3,4,5,6
<i>Crematogaster</i>	6
<i>Formica</i>	1,3
<i>Iridomyrmex</i>	1,2,5,6
<i>Lasius</i>	3,5,6
<i>Monomorium</i>	2,5,6
<i>Myrmecia</i>	2
<i>Pheidole</i>	2,6
<i>Pogonomyrmex</i>	3
<i>Polyrhachis</i>	7
<i>Solenopsis</i>	6
<i>Tapinoma</i>	2,5,6
<i>Technomyrmex</i>	2
<i>Tetramorium</i>	5,6

^aReferences: (1) Baker 1972, (2) Britton et al. 1970, (3) Furniss & Carolin 1977, (4) Hansen & Akre 1985, (5) Metcalf et al. 1951, (6) Smith 1965, (7) Wheeler & Wheeler 1924.

experiments by altering the ratios of wasps to ants. Analyzing the mortality induced by eucharitids in a quantitative and rigorous fashion may allow a reliable assessment to be made of the potential for using the wasps in applied biocontrol.

In evaluating the potential for using eucharitids in biocontrol of ant pests, it is useful to consider aspects of (1) dispersal, (2) levels of parasitism, (3) habits of the host that may affect parasitism, and (4) the effect of these and other factors on the survival and vitality of the host colony. In order to evaluate the potential for biocontrol of a given eucharitid, we must have information on these factors, as well as an understanding of the dynamics of the choice of the host species and oviposition site. The host range as well as the range of suitable oviposition sites should be known before a eucharitid is used in a biocontrol project, in order that beneficial ant fauna and flora are not affected adversely.

In a given area there may be found infested and uninfested colonies of a given host ant species. Dispersal of these parasites may be affected by the flight ability of the adults, and by the area controlled by the host colony. These parameters vary widely among different species within the respective groups. Although it has been thought (Clausen 1941, Ayre 1962) that the area monopolized by the hosts tends to limit dispersal of the parasites, this has not been proven. The short life spans of some adult eucharitids, requirements for certain oviposition plants, and abiotic factors such as wind may also affect dispersal.

Poor dispersal may hinder the establishment of an introduced biocontrol agent, but establishment may not be required in some control programs. The provision of plants to promote oviposition by the adult parasites may be accomplished in the field by setting out potted plants close to an infested colony. If the plants are monitored for the presence of eucharitid eggs, they could be moved at appropriate times to facilitate distribution of the parasites to other (uninfested) colonies.

The factors influencing the level of parasitism in a colony are not well understood. Parasitism of larvae of the ant *Lasius neoniger* Emery by *P. schwarzii* was found by Ayre (1962) to exceed 90% in some colonies. The levels of parasitism dropped with increasing distance from centers of infestation. In one instance collection data indicated a drop to 30% parasitism at a distance of 120 feet from the center of infestation. Parasitism of *Camponotus* sp. by *Stilbula tenuicornis* (Ashmead) was reported to be 47% by Clausen (1941), but the next year the level declined to 16%.

It is not clear how levels of parasitism within a colony affect colony vitality and longevity. Temporal determinants of parasite development may interact with seasonal patterns of development of host brood. As noted by Ayre (1962), an important factor may be the impact of parasitism on the worker:brood ratio.

Ants are not known to exhibit any behavior intended to harm or to prevent parasitism by a eucharitid. The behaviors which appear to aid the parasite, such as helping an emerging adult eucharitid out of the host cocoon and the transporting of adults away from the center of the colony, may be normal behavior patterns of the workers. However, it should be noted that interactions between the parasites and their hosts within the nest have been observed for a very limited range of species. There has been no rigorous study of these interactions for any eucharitid-plus-host system.

One approach to measuring the success of a biocontrol project involving eucharitids would be to determine the effects of parasitism on colony longevity or vitality. Colony vitality may be measured as the number of reproductive forms (or the ratio of these to workers in the colony) produced during the regular season of production of such forms. Vigorous biotypes of the parasites could be screened and selected in the laboratory using artificial colonies. Such studies might yield data that suggest other control practices that act to enhance the level of parasitism within an infested colony. The problem of providing the correct conditions in the laboratory to approximate those occurring in

the field is not trivial, but such an approach would surely yield insights into the interrelations between abiotic factors, parasitism, and other biotic factors influencing total mortality of the host brood.

Experimentation may reveal a synergistic action of eucharitids with other natural enemies of ants. As with any endeavor to achieve biological control, preliminary investigation must be directed toward the discovery and characterization of natural enemies of the pest.

The possibilities for achieving increased host mortality using more than one natural enemy of ants should be investigated. For example, fire ants may be parasitized by phorid flies (Williams & Whitcomb 1973, Williams 1980, Borgmeier 1963), and colonies may be weakened by social parasites (Bruch 1930, Silveira-Guido et al. 1973). There is evidence that a virus infects fire ants (Avery et al. 1977), and eucharitids may be able to spread these pathogens through a colony. Natural enemies of ants, including fungi, nematodes, and strepsipterans (Britton et al. 1970), may act synergistically in the control of their hosts.

An issue important in applied biocontrol projects is the potential for conflict of interest between the goals of the project and the interests of others. There are two possibilities in the ant-eucharitid system as regards conflict of interest. First, the wasps are known to cause damage to the tissues of plants during oviposition. This may result in economic damage to crops, as noted, for example, in tea (Das 1954, 1963, Kerrich 1963) and bananas (Kerrich 1963). This type of damage must be considered in biocontrol projects involving eucharitids. It could be prevented or minimized by proper choice of locations chosen for dispersal of the eucharitids, as well as the choice of a eucharitid species which is known not to oviposit on the types of crop plants being grown in the vicinity.

The other form of possible conflict of interest may occur where ants are considered beneficial in some circumstances but pests in other contexts. The fire ants provide an example of this type of conflict, as they have been considered to be beneficial as predators of crop pests in certain agroecosystems (see for example, Table 8.2 in Lofgren 1986). In many situations, however, fire ants are considered a direct threat to human welfare (they sting, and some people are allergic to their venom; Baer et al. 1979). In addition, they are also known to reduce the yield or quality of certain crops (Adams et al. 1976, Adams et al. 1983, Smittle et al. 1983, Glancey et al. 1979). In view of the possible types of conflict of interest in controlling ants, a limited dispersal of eucharitids may be a valuable trait. It would provide localized control while allowing the beneficial presence of the host ant in nearby areas to continue.

There are no known natural enemies of eucharitids, but the unknown degree of host specificity of these parasites is a hindrance to their effective use as control agents. There is much potential in their use in the control of ant pests, but much work needs to be done in assessing their effect on ant brood mortality. This may be done initially in the laboratory, and subsequently in field tests. The influence of other biocontrol organisms that may act synergistically with eucharitids to debilitate the hosts should be investigated. In addition, the oviposition habits of eucharitids used as biocontrol agents must be defined in order to allow optimization of the control of host numbers, and to avoid conflicts of interest.

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CURRENT STATUS OF THE USE OF
PREDATORS, PATHOGENS AND PARASITES
FOR THE CONTROL OF MOSQUITOES

ALAN R. HOLCK
Department of Entomology
Louisiana Agricultural Experiment Station
Louisiana State University Agricultural Center
Louisiana State University
Baton Rouge, La. 70803

ABSTRACT

The control of mosquito populations with predators, pathogens and parasites is discussed. Fish and canabalistic mosquitoes offer the greatest potential as mosquito predators. Bacterial pathogens such as *Bacillus thuringiensis* var *israelensis* and *B. sphaericus* along with the fungal pathogens *Coelomomyces* spp., *Culicinomyces clavosporus*, and *Lagenidium giganteum* are also discussed. The parasites of mosquitoes are limited, but the parasitic nematode *Romanomermis culicivorax* is discussed.

RESUMEN

Se discute el control de la población de mosquitos con predadores, patógenos y parásitos. Peces y mosquitos caníbales ofrecen el mayor potencial como predadores de mosquitos. También se discuten los patógenos bacteriales como *Bacillus thuringiensis* var *israelensis* y *B. sphaericus*, junto con los patógenos fungosos *Coelomomyces* spp., *Culicinomyces clavosporus*, y *Lagenidium giganteum*. Los parásitos de los mosquitos son limitados, pero se discute el parásito nemátodo *Romanomermis culicivorax*.

Mosquitoes (Diptera: Culicidae) provide a major threat to human health and well-being. Diseases vectored by mosquitoes include malaria, yellow fever, dengue, encephalitis and filariasis. Harwood & James (1979) report that approximately 300 million people world-wide suffer from mosquito borne diseases, primarily malaria and filariasis. The livestock industry also suffers economic losses from mosquitoes. Steelman (1976) estimates a loss of 10 million dollars annually in the dairy industry alone can be attributed to mosquitoes. Mosquitoes also are an important nuisance in many parts of the

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United States. Mosquito abatement districts (MAD's) often operate in such areas to keep mosquito populations below pestiferous levels.

The mosquitoes belong to the suborder Nematocera, the gnat-like flies. Approximately 3500 morphologically distinct species have been described (Knight & Stone 1977). All species undergo complete metamorphosis, with the larval and pupal stages being aquatic. Mosquitoes can be classified into two general categories based upon the aquatic habitats the larvae occupy: permanent water mosquitoes and floodwater mosquitoes. Permanent water mosquitoes complete their larval development in aquatic habitats that are permanent or semi-permanent in nature. These habitats include swamps, bogs, marshes, flooded rice fields and some roadside ditches. Floodwater species develop in more transient types of aquatic habitats, including ground pools, cattle hoofprints, treeholes and discarded containers. After adult eclosion, mating, and possibly blood host seeking, egg development begins. Not all mosquito species require a blood meal to complete development, but the majority do (Harwood & James 1979). Some species will only take blood from a particular class of vertebrate host, while for others almost any type of blood will suffice. Eggs are deposited by the female in an appropriate larval habitat for the species. Permanent water mosquitoes lay their eggs on the water surface, whereas floodwater species oviposit in an area likely to become flooded in the future. The seasonal histories displayed by mosquitoes are also very diverse. Some species (ex. *Aedes impiger* (Walker)) are univoltine, with only one generation per year. Other species (ex. *Ae. aegypti* (L.)) are polyvoltine, breeding year-round in tropical climates. Most species of concern in the temperate regions may be termed facultatively polyvoltine, with several generations occurring in the summer months with overwintering occurring in an inactive state.

Both larval habitat and life strategy must be taken into consideration when devising control measures for a particular species, especially when biological control is being considered. Biological control programs are most successful when several life stages of the pest are present at all times. This paper reports on the use of predators, pathogens and parasites in mosquito control and discusses the future of the biological control of mosquitoes.

BIOLOGICAL CONTROL USING PREDATORS

The use of predators for the control of mosquito populations has been tried often in the past. Koebele in 1898 attempted, with limited success, to import large numbers of the western salamander, *Diemyctylus tortosus* (Eschscholtz), from California to Hawaii for the control of larval mosquitoes breeding in small pools and taro fields (Howard et al. 1912). Herms & Gray (1940) state that for some time it was hoped that by the establishment of large bat (Mammalia: Chiroptera) colonies, control of adult mosquito populations would follow. An added side benefit of this type of control was that the large amount of bat guano produced could be sold to orchid growers at a large profit. Birds have also been suggested as potential biological control agents, but huge populations are required for adequate control (Gillett 1972). Unfortunately, all attempts to date using birds has failed.

By far the most widespread and successfully used predators for the biological control of mosquitoes are fish. These predators are most successful against permanent water species. Howard et al. (1912) report several cases where the introduction of insectivorous fish into larval habitats resulted in significant reduction of the pest population. Bates (1949) states that in North America fish of the genus *Gambusia* have received considerable attention as biological control agents. More recently, Gerberich & Laird (1984) state that while over 250 different species of fish have been studied for use in mosquito biological control programs, the mosquitofish, *Gambusia affinis* (Baird &

Girard), is by far the most successful. This species has been introduced into over 50 countries and is responsible for the majority of successful projects involving the control of mosquitoes with fish (Haas & Pal 1984). Gerberich & Laird (1984) also discuss various adaptations of *G. affinis* that make it such a good predator on mosquito larvae. Hoy & Dahlsten (1983), Gall & Campton (1983) and Beesley et al. (1985) discuss the mass production of *G. affinis* and its implementation into large scale mosquito control programs. However, the use of *G. affinis* does have some limitations. Schaefer et al. (1981) report that insecticide treatment of rice fields containing both mosquito and *G. affinis* populations killed a large portion of the fish population, which could not resurge in time to control a large mosquito population which had recovered much faster. Myers (1965) reports that many commercial fish producers view *G. affinis* as a pest that devours the young of several commercially grown species. In fact, the literature has shown that *G. affinis* may be responsible for the local extinction of several fish species (Meisch 1985).

Other fish species also have received attention as potential control agents of mosquito populations. Cech et al. (1985) report that the Sacramento blackfish, *Orthodon microlepidotus* (Ayres), is a biological control agent of considerable potential in California. Sasa & Kurihara (1981) discuss the use of the guppy, *Poecilia reticulata* (Peters), as a species that possesses much potential in controlling permanent water *Culex* sp. breeding in sewage pits where *Gambusia* cannot survive. Some success with this species has already been achieved in India (Sasa et al. 1965). Haas & Pal (1984) report on the use of *Nothobranchius* sp. in areas with a long dry season. Members of this genus are highly predacious on mosquito larvae and are able to withstand desiccation for many months, making them useful as predators of floodwater univoltine and facultatively polyvoltine mosquitoes.

Another predator that also has received attention as a potential biological control agent of mosquitoes are the predatory mosquitoes of the genus *Toxorhynchites*. Females of this species do not require a blood meal for egg development. Eggs are laid in treeholes and other small natural and artificial containers where certain species of floodwater mosquitoes develop. Gerberg (1985) reviews the utilization of these predators and details a method where *Tx. brevialpis* Theobald eggs are sequentially released for the control of the yellow fever mosquito *Ae. aegypti*. Although in the laboratory *Toxorhynchites* will consume many species of mosquitoes, in practice its use is restricted to treehole and container breeding mosquitoes. The New Orleans Mosquito Control Board rears two species of *Toxorhynchites* (*Tx. amboinensis* (Doleschall) and *Tx. splendens* (Wiedemann)) for mass release to control *Ae. aegypti* and *Ae. albopictus* (Skuse), both which breed in treeholes and small containers including discarded tires. Limitations concerning the use of *Toxorhynchites* are given by Service (1983) and include non-overlap of temporal and spatial distributions with prey, length of life cycle and cost of mass rearing. The larvae of several other mosquito species, notably *Psorophora ciliata* (F.) and *Ps. howardii* (Coquillett) are also known to be predacious. The adults of these species require blood meals and thus are often pests themselves.

Other invertebrate predators of mosquitoes have been considered for use in biological control programs, usually with little or limited success. Phantom midges (Diptera: Chaoboridae) may be useful as predators and are tolerant of cold temperatures. The flatworm, *Dugesia dorotocephala* (Wordworth) (Platyhelminthes), is an effective predator of mosquito larvae, but problems exist with mass culture (Service 1983). Hydrazoa (Hydrozoa) suffer the same problem. Mullen (1975b) reports on cases where mites (Acari) have been observed preying upon mosquito eggs and larvae. Although several orders of insects contain species predacious on mosquitoes (Coleoptera, Hemiptera, Odonata), large scale mass production to date has not been proven economically feasible. This is not to say that predators are unimportant in mosquito control. Andis & Meek

(1985) report that only 2.6% of the dark rice field mosquito *Ps. columbiae* (Dyar and Knab), larvae in a Louisiana rice field survived to the pupal stage when predators were present, compared to 53.3% survivorship in predator free situations. These data indicate that predators play a major role in the natural regulation of mosquito populations.

BIOLOGICAL CONTROL USING PATHOGENS

Pathogens, although they have not been historically manipulated by man for the control of mosquitoes, nonetheless provide one of the most promising methods of biorational mosquito control for the future. A survey of the older literature on mosquito control makes no mention of the use of pathogens (Howard et al. 1912, Herms & Gray 1940, Symes et al. 1962). In 1976, a mosquito-killing strain of the well known insect pathogen *Bacillus thuringiensis* (Berliner) was isolated from a ground pool filled with dead mosquito larvae located in Israel (Margalit & Dean 1985). The discovery of this pathogen, subsequently termed *B. t. var. israelensis* has prompted many scientists to search for other mosquito pathogens.

Bacillus thuringiensis israelensis (Bti) is a pathogen with great potential for use in mosquito biological control programs. It has been developed to the point that several companies now produce and market 'insecticides' with Bti cell walls, spores, crystals and live cells as the active ingredient. This pathogen is highly specific to mosquito larvae, with little or no danger to other aquatic organisms (Service 1983, Mulla et al. 1982, Holck 1986) except blackflies (Diptera: Simuliidae), which also happen to be an important group of vectors in many parts of the world (Lacy & Heitzman 1985). This pathogen has been used against mosquito larvae developing in a wide range of habitats including irrigated pastures and rice fields (Mulla et al. 1985), and marshes (Sjogren et al. 1986). The exact mode of action is not entirely clear, but involves sloughing of the peritrophic membrane upon ingestion. Qiu & Lei (1986) and Walther et al. (1986) further discuss the pathogenicity of Bti to mosquito larvae. When using Bti to control disease vectors it is important to use the maximum labeled rate. Sublethal exposure of larval mosquitoes to Bti results in small adults that are more competent vectors of the pathogens (Hare & Nasci 1986). Recent studies indicate that Bti may be particularly effective when applied with other biorational insecticides such as monomolecular surface films (Perich et al. 1987). However, Bti does possess some limitations. Drawbacks include lack of recycling making frequent re-treatments necessary; limited activity in polluted water; and difficulty of application on habitats with thick vegetation (Service 1983). There is hope that formulation chemistry can overcome at least some of these shortcomings. Although no cases of resistance to Bti have yet been reported, it too remains a possibility if mosquito larvae are exposed to high toxin concentrations over time.

Bacillus sphaericus Neide is another mosquito pathogen that has received considerable attention in recent years. Kellen et al. (1965) reported a strain from California that was slightly pathogenic to mosquito larvae, but it was not until Singer (1973) isolated a strain (SSII-1) from India 10,000 more times potent than Kellen's strain that serious development began. To date, more than 30 strains have been isolated from 11 countries, with strain 1593 from India being the most promising (Davidson 1985). The exact means of pathogenicity is again unknown, but the midgut appears to be the primary target organ (Davidson 1979, 1981). A main advantage *B. sphaericus* holds over Bti is its ability to recycle in the environment, eliminating the need for costly re-treatment (Service 1983). Several MAD's in Florida produce *B. sphaericus* on a small scale for their own use, and commercially available products are currently being evaluated by several universities and MAD'S.

Fungal pathogens also have aroused interest over the years, particularly those in the genus *Coelomomyces*, which contains approximately 70 species. The majority of

these species have been observed developing in larval mosquitoes (Lucarotti et al. 1985). At first, these organisms were thought to be of limited practical use because a complete recycling of the fungus would not occur under laboratory conditions. A breakthrough occurred when Whistler et al. (1974, 1975) reported that a copepod (Arthropoda: Copepoda) or ostrocod (Arthropoda: Ostrocooda) intermediate host was required for completion of the life cycle. The life cycle of *Coelomomyces* is rather complex, involving both sexual and asexual stages. The mosquito host range for most *Coelomomyces* sp. is considered wide, but it is not known how wide the range of alternate hosts is for this fungus (Lucarotti et al. 1985). The percentage of infected mosquito larvae in localized populations is variable, but can be high. Muspratt (1963) reported almost 100% infection of *Anopheles* larvae in Rhodesia (now Zimbabwe) by *Coelomomyces* species. However, in other studies the percentage of infected mosquitoes has been lower (Service 1977, Shemananchuk 1959). Nnakumusana (1986) reports that adult female mosquitoes surviving *Coelomomyces* infections exhibit lower fecundity. An advantage of this pathogen is its ability to withstand desiccation, but some field trials with *Coelomomyces* have not been as thought through as one would hope. Lucarotti et al. (1985) state that while infected mosquito larvae have been released on several occasions, the presence or absence of the proper intermediate host was only considered in one instance.

The fungus *Culicinomyces clavosporus* Couch, Romney, and Row first isolated from Australia in 1972, is also pathogenic to mosquito larvae (Sweeny 1981, 1985). A second strain, indigenous to North America, was reported in 1974 from North Carolina in *An. quadrimaculatus* Say (Couch et al. 1974). The host range of this pathogen seems to be very wide. Russel et al. (1983) infected 36 species of mosquitoes in 6 genera with the Australian strain. Sweeny (1975, 1969) states that this organism is pathogenic to other aquatic Diptera but pathogenicity is probably restricted to larvae of the Culicimorpha. Advantages include the ability to recycle, lack of alternate hosts and ease of production albeit at a low yield; major drawbacks are a short shelf life and an intolerance to desiccation (Sweeny 1985).

Lagenidium giganteum Couch is another fungus that has received attention as a control agent for larval mosquitoes (Lacey & Undeen 1986). Kerwin & Washino (1987) discuss the use of *L. giganteum* in the Central Valley of California including application technology necessary for use of this pathogen. Further formulation strategies are discussed by Axtell and Guzman (1987). Washino (1981) discusses the recycling of this species in California rice fields. Guzman & Axtell (1987) report on the use of *L. giganteum* in stagnant water pools. Pools treated at the beginning of the mosquito season produced 82% fewer adult when *Culex quinquefasciatus* Say over the 38 day mosquito season.

A wide variety of other fungi have also been evaluated as biological control agents of mosquitoes. However, most have problems of one sort or another (ie. recycling, temperature intolerance, etc.) which must be remedied before they can be useful for the control of mosquito problems.

BIOLOGICAL CONTROL USING PARASITES

The parasites of mosquitoes are very limited in number. Infestations of mites on adult mosquitoes have been reported for years (Howard et al. 1912), but effect little or no mortality (Mullen 1975a). Beier & Craig (1985) discuss the effects of gregarine protozoal parasites on mosquitoes and conclude that mortality attributable to these parasites is nil, and that they offer little control potential. On the other hand, certain species of nematodes that are parasitic on larval mosquitoes have shown great potential as biological control agents against mosquitoes.

Nematodes of the genus *Romanomermis* (Nematoda: Mermithidae) have been extensively studied and developed for use in mosquito control (Petersen et al. 1968). *Romanomermis culicivorax* Ross and Smith (= *Reesimermis nielseni*) has received particular attention. Petersen & Willis (1972) released preparasites of *R. culicivorax* in Louisiana with some of success. Westerdahl et al. (1979, 1982) observed recycling and overwintering of this species in California rice fields. Walker et al. (1985) successfully established *R. culicivorax* in Louisiana rice fields. Levy and Miller (1977) used *R. culicivorax* to control larval *Cx. quinquefasciatus* in sewage tanks in Florida. Advantages of this species include cold hardiness and recycling ability, but initial applications must be carefully timed to insure effective colonization Petersen (1985). Resistance also has been reported to have developed in a laboratory colony of *Cx. quinquefasciatus* after exposure to the nematode for 300 generations. (Petersen 1978). Products containing *R. culicivorax* are now marketed for use against mosquito populations (Coppel & Mertens 1977) but are not widely used by mosquito control agencies (Finney-Crawley 1985) presumably due to high cost.

CONCLUSIONS

Biological control provides many new possibilities for the control of mosquito populations. Predators, pathogens and parasites are now available that are highly effective against mosquitoes. Unfortunately, most mosquito control agencies in the United States do not take advantage of these new methods. Chemical control is still the most widely used means of mosquito control in the United States, followed by water management. However, problems with insecticide resistance as well as environmental concerns may cause a change in attitude over the next few years. The real potential of biological control of mosquito populations is being realized outside the United States. Mosquito integrated pest management programs in many countries rely to a large extent on biological control. Larval *Ae. aegypti* control in Thailand rests almost solely with the predator *Toxorhynchites splendens* (Mathis 1983). Fish, *Toxorhynchites*, Bti and nematodes are used in China (Pao 1981). In the Soviet Union, pathogens, nematodes and predators are manipulated as a facet of integrated control (Dubitski 1985). Israel now relies heavily on Bti for larval control (Margalit et al. 1985). While chemical insecticides will remain an important tool of mosquito control agencies in the United States for some time, it is hoped that mosquito abatement districts will begin to 'see the light' and incorporate more biological control aspects into their programs.

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RESISTANT PLANTS AS AN ALTERNATIVE TO CHEMICAL CONTROL OF INSECTS: PITFALLS TO PROGRESS

C. A. COOK¹ AND C. M. SMITH²

Louisiana Agricultural Experiment Station,
Louisiana State University Agricultural Center,
Baton Rouge, Louisiana 70803

¹Dept. Entomology, Louisiana State University, Baton Rouge, LA 70803.

²Dept. of Plant, Soil and Entomological Science, University of Idaho,
Moscow, Idaho 83843.

ABSTRACT

A possible alternative to chemical control of insect pests may be plant resistance to insects (PRI). Although PRI usually integrates well with other pest management strategies, its use has been limited. Progress in PRI is influenced by variation in plants, insects, and the environment. This review is intended to illustrate some of the factors that affect the expression of resistance.

RESUMEN

Una posible alternativa al control químico de insectos pudiera ser la resistencia de plantas hacia insectos (RPI). Aunque RPI usualmente se integra bien con otras estrategias de administración de plagas, su uso ha sido limitado. El progreso de RPI es influenciado por variaciones en las plantas, insectos, y en el medio ambiente. La interacción de este repaso es ilustrar algunos de los factores que afectan la expresión de resistencia.

Man has attempted to control insect populations for centuries. Since World War II, the use of insecticides has been the major control tactic employed. Rachel Carson's book, *Silent Spring*, caused people to become aware of, and concerned with, the hazards of chemicals. As the number of cases of insecticide resistance continues to grow, it becomes apparent that alternate control tactics must be developed and integrated with insecticides in a pest management context. Plant resistance to insects (PRI) is a tactic

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A possible alternative to chemical control of insect pests may be plant resistance to insects (PRI). Although PRI usually integrates well with other pest management strategies, its use has been limited. Progress in PRI is influenced by variation in plants, insects, and the environment. This review is intended to illustrate some of the factors that affect the expression of resistance.

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Una posible alternativa al control químico de insectos pudiera ser la resistencia de plantas hacia insectos (RPI). Aunque RPI usualmente se integra bien con otras estrategias de administración de plagas, su uso ha sido limitado. El progreso de RPI es influenciado por variaciones en las plantas, insectos, y en el medio ambiente. La interacción de este repaso es ilustrar algunos de los factores que afectan la expresión de resistencia.

Man has attempted to control insect populations for centuries. Since World War II, the use of insecticides has been the major control tactic employed. Rachel Carson's book, *Silent Spring*, caused people to become aware of, and concerned with, the hazards of chemicals. As the number of cases of insecticide resistance continues to grow, it becomes apparent that alternate control tactics must be developed and integrated with insecticides in a pest management context. Plant resistance to insects (PRI) is a tactic

that can successfully be integrated with other tactics. Use of resistant plants has reduced the amount of pesticides by one-third.

There are several advantages of PRI: (1) there is no additional pest control cost to the grower; (2) it operates at all levels of insect incidence; (3) it cumulatively reduces the insect population; (4) it avoids toxic residues and environmental pollution; (5) it usually interacts well with the other integrated pest management (IPM) strategies. Despite these advantages, the number of resistant varieties currently in use in agricultural systems (Fig. 1) is rather low.

This trend may be attributed to the disadvantages of PRI: (1) it requires several years of plant breeding to develop a resistant variety; (2) resistance is often found in taxonomically unrelated plants of poor agronomic quality; (3) PRI may encourage the development of insect biotypes; (4) different geographic regions require different varieties.

The ultimate goal of PRI is insect pest population control without induction of genetic counter-resistance in the insect (Fig. 2). The categories of plant resistance, antixenosis, antibiosis, and tolerance, are the different means by which PRI is expressed and serve as building blocks. Between the goal and the building blocks are barriers to progress in the form of variables in both plant and insect age, health, level of incidence, and genetics. All of these factors are influenced by the abiotic environment. These barriers prevent or affect the expression of resistance. As students of entomology, we often cite intrinsic and extrinsic factors as reasons for discrepancies in our data. Yet, it is a rare occurrence when we can actually identify the specific factors and their actual impact upon an experiment. This paper will attempt to expose some of the factors that affect the expression of resistance.

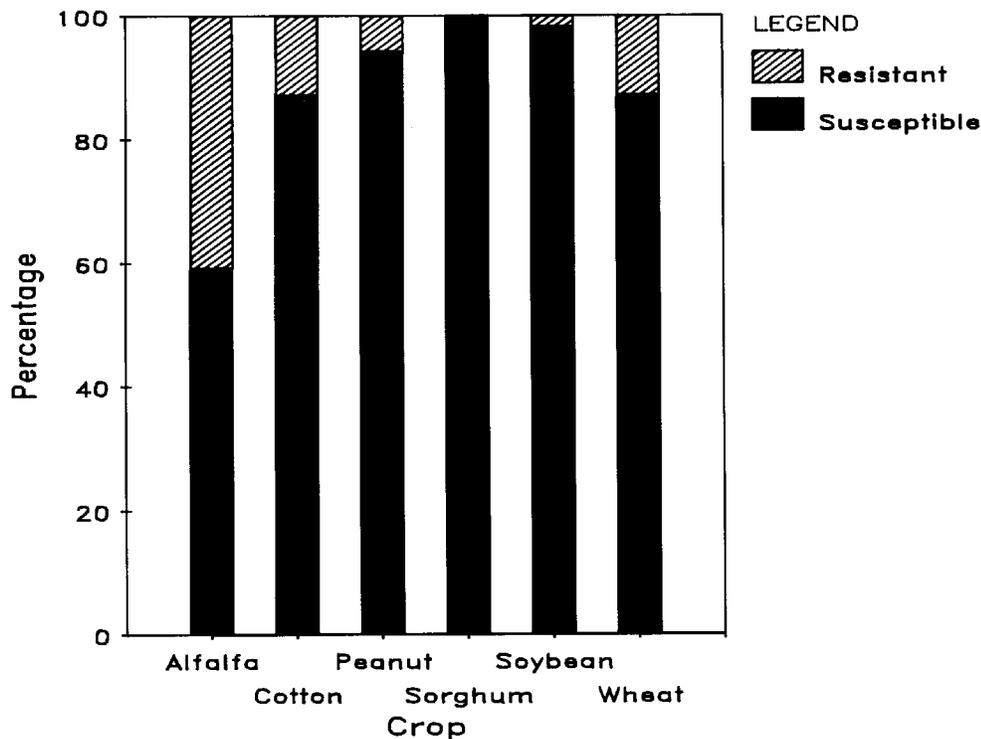


Fig. 1. The percentage of cereal grain crop cultivars, registered with Crop Science, with plant resistance to insects developed in the last 15 years.

ANTIXENOSIS

Antixenosis is the property of a plant that results in a negative response by an insect to that plant (Kogan & Ortman 1978). Some plant characteristics that may cause such a negative response include color, pubescence, wax, and trichome length (Tingey & Singh 1980).

Plant Characters

Plant density can influence antixenosis. Fery & Cuthbert (1974) determined that the damage by *Heliothis zea* (Boddie) larvae was directly proportional to the density of three tomato cultivars. Damage increased 31 to 67% by increasing plant density from one to 16 plants per 3 m row.

Plant height also affects the preference of insects, but there is no definitive rule. Western Lygus bugs, *Lygus hesperus* Knight, prefer taller cotton plants for oviposition (Tingey & Leigh 1974). However, when the height of the cotton plants was adjusted for uniformity, the taller plants that had been preferred were chosen less often for oviposition. But some insects prefer shorter plant cultivars. Dwarf rice varieties support larger populations of the least skipper, *Ancyloxypha numitor* (F.), and sustain a greater amount of defoliation (Smith & Robinson 1983).

Plant age also affects antixenosis. Surface wax in sorghum is a deterrent to the desert locust, *Locusta migratoria*, and its concentration varies considerably between cultivars (Woodhead 1982). Wax concentration decreases as plants mature. Therefore, deterrent amounts are only present in the early stages of sorghum growth leading to an increase in foliage palatability with plant age. Conversely, as the rice plant ages, resistance to the yellow stem borer, *Scirpophaga incertulas* (Walker), increases (Viajante & Heinrichs 1987). The greatest amount of plant damage and yield loss occurs when the yellow stem borer larvae attack the tillering and flowering stages; damage is lowest when the plants are at panicle initiation stage of growth (Viajante & Heinrichs 1987).

In cotton, tannin quality and quantity increase gradually from cotyledonary stage to peak in late bloom. At the 1/3-grown square stage a sudden drop in tannin quality and quantity occurs, followed by rapid recovery (Zummo et al. 1984). Fruit damage by *Heliothis zea* (Boddie) at the 1/3-grown square stage is highly negatively correlated with tannin quality (Zummo et al. 1984).

Insect characters

The age of the insect is an important aspect to consider in testing for plant antixenosis. Barnes & Ratcliffe (1967) determined that although adult alfalfa weevils, *Hypera postica* (Gyllenhal), feed on alfalfa directly in proportion to their body size, freshly emerged weevils consume 5-6 times more leaf material than 4-5 week old adults; the feeding rate between large and small weevils was similar. Smith et al. (1979) noted that 14-day old female Mexican bean beetles, *Epilachna varivestis* (Mulsant), cause more defoliation of soybean foliage than do younger (3-day) or older (35-day) females. Schalk & Stoner (1976) showed that adult Colorado potato beetles, *Leptinotarsa decemlineata* Say, feeding on tomato foliage reduce consumption as they age, but the larvae feed more than either the young or old adults.

In some instances, insect sex also may affect the outcome of an experiment. Female Mexican bean beetles and Colorado potato beetles both feed more than males (Smith et al. 1979, Schalk & Stoner 1976), but female alfalfa weevils do not (Barnes & Ratcliffe 1967).

Environment

In work involving the Colorado potato beetle on tomato, Schalk & Stoner (1976) demonstrated that moisture levels had no effect on larval feeding but that adults prefer low humidity conditions. Adult Colorado potato beetles feed on both juvenile and senescing foliage, whereas, the larvae prefer the senescing foliage of the resistant variety of tomato. At two temperature regimes, the preference for the susceptible tomato variety remained the same for both larvae and adults (Schalk & Stoner 1976).

The spatial arrangement of the test plants may also influence preferences of insects. Colorado potato beetle larvae are not affected by spatial arrangement, but adults feed equally on both the susceptible and resistant tomato lines when plants are in an alternate array (Schalk & Stoner 1976).

ANTIBIOSIS

Antibiosis refers to a plant's ability to adversely affect the biology of the insect (Painter 1951). Its expression is governed by biotic and abiotic parameters.

Plant Characters

Like antixenosis, antibiosis varies with plant age. In grasses, antibiosis to the aphid, *Metopolophim festucae cerealium*, increases with plant age (Dent & Wratten 1986). Resistance is greater at stem elongation stages than at seedling stages. However, resistance in sweet corn to the corn earworm, *Heliothis zea* (Boddie), decreases as the plant develops. In resistant corn, mortality of corn earworm larvae is greatest at silking, but 7 days later, mortality of corn earworm is absent (Wann & Hills 1966).

Phenolic acids act as deterrents to the desert locust, *Locusta migratoria*, and other acridoids (Woodhead 1981). In sorghum, the levels of phenolic acids vary according to the cultivar and plant age. Phenol concentration and locust resistance both decrease as the sorghum plant ages.

The phenology of allelochemicals in cotton and cotton resistance to the bollworm, *Heliothis zea* (Boddie), is complex. Zummo et al. (1984) identified the effects of tannin (see antixenosis—plant characters) and terpenoid aldehyde quantity on *Heliothis zea*. The terpenoid aldehyde quantity is greatest at fruit initiation; thereafter, it drops significantly and remains fairly constant. Zummo et al. (1984) determined that bollworm damage at second week of bloom is due to the drop in terpenoid aldehyde quantity.

Wounding

Induced resistance in plants subjected to wounding has been documented. In the tomato and potato, proteinase inhibitors increase after wounding. Deciduous trees, grazed by insects, increase cyanide mustard oils and phenolic compounds (Edwards & Wratten 1983). Oak leaves produce wound-induced responses that affect the survivorship of a lepidopterous leaf miner, *Phyllonorycter harrisella* (L.) (West 1985). Nebeker & Hodges (1983) demonstrated that pines injured during thinning may have less bark beetle damage because of wound-induced responses. Mechanical abrasion of the leaves of a resistant soybean lowers the rate of larval growth of *Pseudoplusia includens* (Walker) (Reynolds & Smith 1985). Resistance to spider mites, *Tetranychus urticae* Koch, can be induced by abrading cotton cotyledons (Karban 1985). In sorghum, insect and pathogenic fungi attacks increase phenolic content (Woodhead 1981). Ryegrasses infested with endophytic fungi have lower numbers of stem weevil eggs and larvae and, therefore, less damage than ryegrasses without endophytic fungi (Gaynor & Hunt 1983).

In some plants, the induced resistance lasts only a few hours; in other plants it lasts for years.

Environment

Light intensity influences the production of many plant allelochemicals. Kennedy et al. (1981) found that the foliage of an insect-resistant wild tomato grown under a long-day regime causes greater mortality in *Manduca sexta* (L.) larvae than does plant foliage grown under a short-day regime. This phenomenon is directly correlated to the production of 2-tridecanone, a toxin to *M. sexta*, that is greater in long-day regimes. Light intensity does not directly affect 2-tridecanone levels; but, it does affect the density of the glandular trichomes that secrete the toxin (Kennedy et al. 1981).

Continuous high-intensity light (24L:0D) induces susceptibility in soybean plants normally resistant to the cabbage looper, *Trichoplusia ni* (Khan et al. 1986). The induced susceptibility is reversed by placing plants into 16:8 (L:D) for two weeks (Khan et al. 1986).

DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) concentration in corn decreases under high-intensity light regimes, as does leaf nitrogen concentration. Feeding of European corn borer, *Ostrinia nubilalis* Hubner, neonate larvae is greatest on foliage with less DIMBOA, in both light regimes (Manuwoto & Scriber 1985). Manuwoto & Scriber (1985), however, reported that feeding rates of European corn borer are greater under low-light intensity regimes, inferring that feeding rates are unlikely to be DIMBOA-related.

Temperature also affects antibiosis. High temperatures decrease the resistance in wheat varieties with the H3H3 and H5H5 gene pairs that are resistant to Hessian fly, *Mayetiola destructor* (Say), larvae biotypes B & D (Ratanatham & Gallun 1986). Wood & Starks (1972) found the opposite to be true with sorghum cultivars and the greenbug, *Schizaphis graminum* (Rondani) biotypes A, B, and C, where resistance increases as temperatures increase.

TOLERANCE

A plant's ability to withstand infestation and support an insect population that otherwise would severely damage susceptible plants is known as tolerance (Horber 1980). The same barriers influence the expression of tolerance as antixenosis and antibiosis.

Plant Characters

Plant age influences the level of tolerance. As rice plants age, they become more tolerant to brown planthopper and green leafhopper (Velusamy et al. 1986, Rapusas & Heinrichs 1987).

While determining the effects of temperature on resistance of sorghum to the greenbug, Schweissing & Wilde (1979) found that tolerance is greatly influenced by plant nutrition. Resistant sorghum plants grown in solutions with excess potassium achieved the greatest amount of resistance.

Environment

Schweissing & Wilde (1979) in studying the temperature effects on the resistance to the C-Biotypes of the greenbugs found that cool season grasses, rye, barley, and oats, increase resistance with lower temperatures. Sorghum, a warm season grass, increases resistance with an increase in temperature.

Resistance in alfalfa to the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), could be reduced when treated with deficient levels of calcium or potassium or excess of magnesium or nitrogen. Deficient levels of phosphorus increase resistance (Kindler & Staples 1970b).

UNCATEGORIZED

Guthrie et al. (1986) reported that maize cultivars that are almost immune to the European corn borer larvae in the field become susceptible under greenhouse conditions. In general, for four maize lines, the DIMBOA concentration in the leaves of plants in the greenhouse was higher than or the same as the leaves of plants in the field. However, the role of DIMBOA as a resistance factor was not clear as the higher concentration of DIMBOA did not prevent severe leaf-feeding damage by the ECB larvae (Guthrie et al. 1986).

In mature potato plants, a fluctuating temperature regime (25°/15°C) provided wider range of expression of resistance to potato leafhopper than did constant 25°C (van de Klashorst & Tingey 1979). Spotted alfalfa aphids are more fecund on susceptible alfalfa under fluctuating temperature regimes than with constant temperature (Kindler & Staples 1970a). Greenbugs are also able to recover and reproduce at a higher rate under a cycling temperature than at a constant temperature (Schweissing & Wilde 1979). Kindler & Staples (1970a) demonstrated that the mean of the fluctuating temperature did not govern resistance in alfalfa, and resistance in alfalfa to spotted alfalfa aphid is retained at low temperatures.

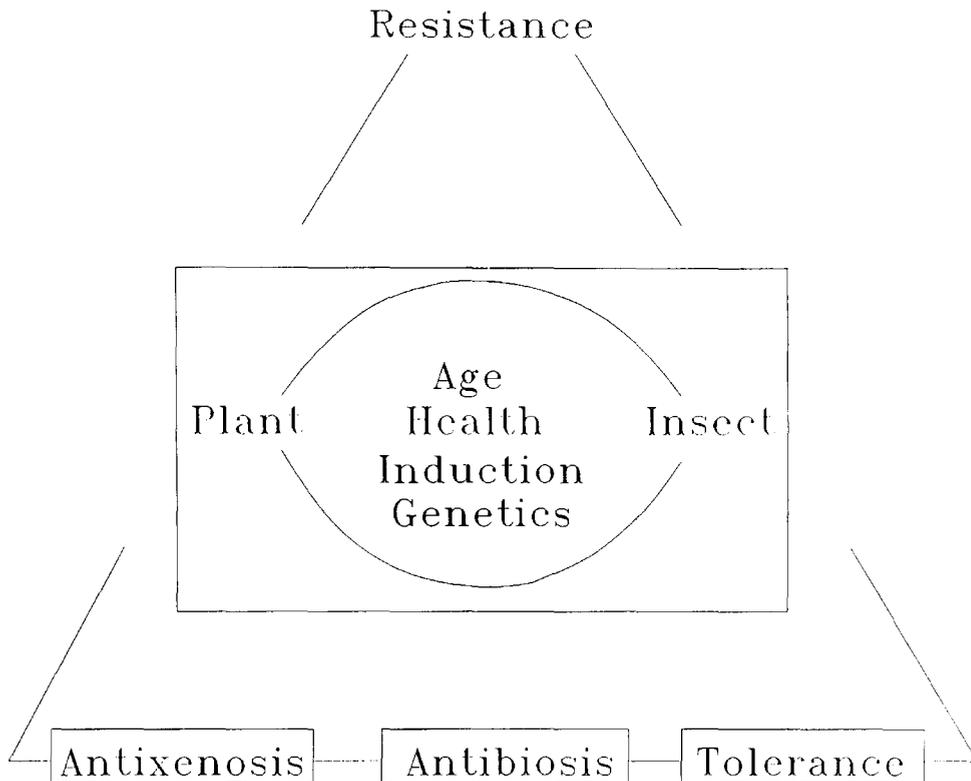


Fig. 2. Diagrammatic view of the components involved in plant resistance to insects.

CONCLUDING REMARKS

There are many factors to consider when testing plants for resistance to insects. In terms of the insects, their activity, infestation levels, and pre-conditioning before bioassay are very important. The plant tissue type—excised or intact, vegetative or senescing foliage—is important. The soil conditions, whether greenhouse-, laboratory-, or field-grown plants, and the agrochemicals present are vital to a study.

In spite of the numerous influences affecting plant-insect interactions, and subsequently PRI, only a few of these factors have been identified. To more effectively utilize PRI as a control tactic in the integrated management of insects, it is important that we develop a more comprehensive understanding of the factors that influence the expression of PRI and the myriad of interactions among these factors. As our knowledge expands, it is hoped that many of these factors will not only be identifiable but also controllable.

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THE VERSATILITY OF RADIOTRACER METHODS FOR STUDYING INSECT ETHOLOGY AND ECOLOGY

A. T. SHOWLER¹, R. M. KNAUS² AND T. E. REAGAN¹

¹Department of Entomology

Louisiana Agricultural Experiment Station

Louisiana State University Agricultural Center

Baton Rouge, LA 70803

²Nuclear Science Center

Louisiana State University

ABSTRACT

Isotope (nuclide) markers, tags, labels, or tracers can be radioactive or nonradioactive and include a wide diversity of nuclides that may be conservative (a mimic of biologically essential elements) or nonconservative. Detectable radiations include alpha or beta particles, or gamma or X-rays, or combinations thereof. Radiotracer half-lives range from hours to years, and stable-activable tracers can be permanent.

Modes of application to the organism of interest include injection, dipping, wire or disc attachments, paints, ingestion, trans-life-stage transmission, and water culture. Tags have been ingested from labeled baits, other insects, living plants with topically applied or translocated labels, blood, and living host animals. Radiolabels have been transferred to the insect life stage of interest by being retained through molts and metamorphic processes.

The unit labeled may range from selected individuals to entire populations and ecosystems. Communities studied have been aquatic, terrestrial, soil- or wood-limited, or combinations thereof. Radio- and stable-activable tracers have each been easily and rapidly applied to large insect populations.

It is possible to design experiments for studying each and combinations of the following behaviors and ecological interactions: Dispersal and movement patterns, territoriality, food handling and consumption, vector-parasite associations, and food chains and webs. Conservative isotopes can simultaneously be employed to study physiological aspects of each labeled organism.

Detectors for quantifying alpha, beta, gamma, X-ray, and Cerenkov radiations are available, and some are able to differentiate between several isotopes located within the same sample. Samples have been detected in the field or laboratory, manually or automatically, and with a wide range of detection methods that include portable ratemeters, Gieger-Muller tubes, liquid scintillation and solid scintillation crystals, semiconductor detectors, and autoradiographic emulsions. Samples can be analyzed while living, dead, or after conversion to any physical state. The versatility of radiotracers was shown to enhance their utility in research in contrast with conventional marking techniques.

RESUMEN

Marcadores, letreros, o rastreadores de isotopos (nuclide) pueden ser radioactivos o no e incluyen una gran diversidad de nuclides que pudieran ser conservadores (un mimico de elementos biológicos esenciales) o no conservadores. Radiaciones detectables incluyen particulas alfa o beta, o gama o rayos-X, o combinaciones de ellas. La media-vida de rastreadores radioactivos fluctúa de horas a años, y rastreadores activables-estables pueden ser permanentes.

Métodos de aplicación al organismo interesado incluyen inyección, inmersión, prendido a alambre o disco, pinturas, ingeridos, transmitido a través de las distintas etapas de vida, y por cultura de agua. Marcadores han sido ingeridos en cebos marcados, con otros insectos, de plantas vivas topicamente tratadas o con marcadores translocados, sangre, y con animales como hospederos vivos. Marcadores radioactivos han sido transferidos

a la interesada etapa de vida del insecto, reteniéndola a través de las distintas mudas y procesos metamórficos.

La unidad marcada puede variar de individuos selectos a poblaciones enteras y sistemas ecológicos. Las comunidades estudiadas han sido acuáticas, terrestres, limitadas al suelo o a la madera, o combinaciones de ellas. Rastreadores radio- y activable-estable han sido fácil y rápidamente aplicados a grande poblaciones de insectos.

Es posible diseñar experimentos para estudiar cada una y combinaciones de las siguientes interacciones ecológicas y de compartimiento: dispersión y patrones de movimiento, territorialidad, manejo de alimentos y consumo, asociación de vector-parásito, y la cadena y red de alimentos. Isotopos conservadores pueden ser simultáneamente usados para estudiar los aspectos fisiológicos de cada organismo marcado.

Hay detectores disponibles para cuantificar radiaciones de alfa, beta, gama, rayos-X y Cerenkov, y algunos pueden diferenciar entre varios isotopos dentro de la misma muestra. Se han detectado muestras en el campo o en el laboratorio, manual o automáticamente, y con un gran número de métodos detectores que incluyen medidores portátiles, tubos Gieger-Muller, titilación líquida y titilación sólida con cristales detectores semiconductores, y emulsiones autoradiográficas. Se pueden analizar muestras mientras vivas, muertas, o después de convertidas a cualquier estado físico. Se demostró que la versatilidad de rastreadores radioactivos aumenta su utilidad en investigaciones en contraste con técnicas convencionales de marcar.

Insect ethology and ecology studies often involve lengthy experiments in conditions that may preclude visual observations. To accurately assess insect behaviors such as dispersal, subterranean habits, feeding, and complex ecological relationships among diversified taxa, an efficient marker is desirable. Useful markers i) are easily applied to large populations, ii) involve minimal manipulation and trauma to the insect, iii) are detectable without destroying or killing the insect samples, iv) are persistent in the insect or community, and v) do not affect the physical or behavioral functions of the labeled organisms (Bugher & Taylor 1949). Our review of the literature has revealed an arsenal of marking techniques used by behavioral and ecological entomologists. While most markers were found to be effective for their respective purposes, the versatility of radiotracers (synonymous with radioactive markers, labels, and tags) enhance their potential use as a research tool in contrast to conventional labeling procedures.

CONVENTIONAL LABELING METHODS

Visual detection

Visually detected markers commonly suffer limitations. Mirenda & Vinson (1979) evaluated 3 methods for tagging the fire ant, *Solenopsis invicta* Buren: wire ties, paint, and clipped legs. Securely fastened wire ties were retained, but the process of attachment was laborious and required anaesthetization of the ants. Workers with excised legs were killed by their nestmates, and painted labels were scraped off. Fluorescent dye in noninjurious concentrations was retained by only 26-60 percent of treated hornflies, *Haemotobia irritans* L., and was frequently lethal (Chamberlain et al. 1977). Individually applied external labels inflict trauma upon the insect and are impractical in lieu of other options (Service 1976). Dusts and dyes have been used to easily label large numbers of insects (Dalmat 1950, Sheppard et al. 1973, Chamberlain et al. 1977). These labels, however, may be lost (Dow 1971, Chamberlain et al. 1977), are suitable only between molts (Arnason et al. 1950), and are not reliable for monitoring species with cryptic habits (Traniello et al. 1985). External markers, thus, are usually of little value for studying insect behavior over long periods of time, for researching trophallaxis (food exchange in social insects), and for unraveling food webs. Service (1976) suggested

that, in addition to affecting survival rates, paints and powders might make mosquitoes more susceptible to predation.

Internal labels such as dyes ingested by fire ants were used to monitor the intracolony exchange of oil, protein, and carbohydrate foods; however, detection of the label required the destruction of the insects while the dye was extracted, partitioned, and dried before light wavelength absorbance was measured (Vinson 1968). Wilson et al. (1971) tagged fire ants with ingested dyes and detection was only accomplished by crushing the ants on white paper. Brian & Abbott (1977) dissected ants, *Myrmica rubra* L., to detect dyes. It is difficult to detect dyes and vital stain indicators in small quantities (Hamilton 1935), whereas the sensitivity of radiation detection exceeds that of most chemical and physical methods (to illustrate, carrier-free tritium at 30 Ci per mmole can be diluted by a factor of 10^{12} without hindering detection) (Wang et al. 1975). Showler et al. (1988b) diluted 200 μ Ci Zn-65 in 20 ml molasses to label an entire fire ant colony. The tracer was easily detectable in the ants 6 months after the tagged bait was removed.

Rubidium

Stable (nonradioactive) rubidium (Rb) markers possess unique characteristics relative to visually detected labels. Rubidium can be ingested from labeled artificial diet (Stimmann et al. 1973, Graham & Wolfenbarger 1977), from Rb solutions sprayed onto host plants (Berry et al. 1972, Stimmann 1974, Shepard & Waddill 1976) and from host plants raised from Rb-treated seeds (Cheshire et al. 1987). Frazer & Raworth (1974) labeled pea aphids, *Acythosiphon pisum* Harris, that had fed on bean plants cultured in Rb-tagged nutrient solutions. Rubidium was detectable by atomic absorption spectroscopy in pea aphids for up to 4 days (77% was eliminated in 2 days) (Frazer & Raworth 1974) and up to 34 days in the adult Mexican bean beetle, *Epilachna varivestris* Mulsant (Shepard and Waddill 1976). Unlike visually detected markers, ingested Rb can be retained from larval to adult stages as has been demonstrated in the corn earworm, *Heliothis zea* Boddie (Graham et al. 1978a,b), tobacco budworm, *H. virescens* F. (Graham & Wolfenbarger 1977), fall armyworm, *Spodoptera frugiperda* J. E. Smith (Graham et al. 1978a,b), pink bollworm, *Pectinophora gossypiella* Saunders (Van Steenwyk et al. 1978a,b), cabbage looper, *Trichoplusia ni* Hubner (Berry et al. 1972, Stimmann et al. 1973), and the imported cabbage worm, *Pieris rapae* L. (Stimmann 1974); no toxic effects were observed. Stimmann et al. (1973) showed that ingested Rb concentrations of up to 28,000 ppm did not influence adult *T. ni* fecundity, fertility, longevity, mating behavior, and responses to sex pheromones. Rubidium labels have been successful in flight dispersal studies on the corn earworm, fall armyworm (Graham et al. 1978b), and pink bollworm (Van Steenwyk et al. 1978b), and to trace insect food chains (to primary predator level) on grain sorghum and cotton (Graham et al. 1978a). Despite these advantages, researchers frequently report equivocal results due to variation and detectable levels of naturally-occurring Rb in all samples (Stimmann 1974, Shepard & Waddill 1976, Graham et al. 1978b). Further, quantification of Rb requires the physical destruction of samples for the use of atomic absorption spectroscopy or flame emission spectrophotometry (Berry et al. 1972, Graham et al. 1978b, Van Steenwyk et al. 1978a).

RADIOTRACER METHODS

Selection of a radiotracer

A desirable marker i) provides analogs for biologically essential elements (examples: C-14, P-32, Fe-55 and H-3), ii) does not require the destruction of labeled samples, iii) persists in readily detectable quantities for long periods of time, iv) is easily applied to

large numbers of insects with minimal manipulation of the populations, and v) may permit detection in the field, even when tagged insects are located underground or within plant material. Unlike Rb, radioactive isotopes (radiotracers) provide analogs of biologically essential elements such as P-32 (Bugher & Taylor 1949, Yates et al. 1951, Radeleff et al. 1952), C-14 (Hilliard & Keeley 1984, Isaac & Rees 1985, Inagaki & Yamashita 1986), H-3 (Bermudez et al. 1985, Kappler et al. 1986, Whitehead et al. 1986), I-125 (Johnson et al. 1984, Ferkovich & Dillard 1986), S-35 (Ishikawa 1984, Wong & Ho 1986), and Ca-45 (Yagi 1958) that can be applied to study such physiological phenomena as reaction rates, metabolic pathways, and the distribution and incorporation of elements or compounds in biological systems (Wang et al. 1975). Radioactive analog or nonanalog nuclides can be administered to similarly monitor the behavioral and ecological dynamics of individuals, populations, and biotic communities (Odum & Golley 1961). Radiolabeled insects can be detected while living (Lambremont et al. 1977), dead but intact (Lindquist et al. 1951, Dietz & Lambremont 1970, Smittle et al. 1983), or while the insect is functioning in the environment (Rings & Layne 1953, Riegert et al. 1954, Green et al. 1957). Radiotracer techniques offer a wide arsenal of isotopes (Tables 1, 2, and 3) that can be administered and detected in a variety of ways (Table 1); Jenkins (1961) reported that about 44 different radionuclides were used in entomological studies. To select a radiotracer for labeling insects, several factors must be considered: i) the effective half-life of the isotope in the organism, ii) possible toxic effects to the insect, iii) the type of radiation emitted, iv) the energy of the radiation, v) the form or valence of the radionuclide, and vi) the ease of handling and detecting the label (Jenkins 1961).

The amount of a radioisotope retained by an insect after the administration of a single dose decreases exponentially through time because of biological elimination and radioactive decay. The time required for the amount of a particular internalized radiotracer to decrease by one-half in a given insect is termed the effective half-life (Table 2). DiGregorio et al. (1978) reviewed determinations of other effective half-lives in insects. Effective half-lives of radiotracers will decrease in response to excretion (Fuller et al. 1954, Rahalkar & Douth 1965), oviposition (Bugher & Taylor 1949, Rahalkar & Douth 1965), length of exposure to labeled bait (Sorenson et al. 1980), life stage (Mayer & Brazzel 1961, Crossley 1963) or caste (Spragg & Fox 1974) of the insect, and the nature of the labeled food ingested (oil, protein, carbohydrate) (Sorenson et al. 1980). Radioactivity can, however, be easily detected long after the isotope's effective half-life has elapsed (Radeleff et al. 1952, Fuller et al. 1954, Wang et al. 1975). To minimize loss of the radiotracers in individuals over time, the isotopes may be delivered to insects in a continuous infusion by providing a constant supply of radiolabeled food or water (Jenkins & Hassett 1951, Bachmann 1961, Showler et al. 1988b), or by using large, but nontoxic, doses of radionuclides in a single pulse application (Wang et al. 1975).

A radiolabel may prove detrimental to the inoculated system (and researcher) due to the nature of the emitted radiation (Wang et al. 1975). The biological hazards of radiation, although negligible in most radiotracer studies, have been magnified by the media; thus the decline in radioecology experiments after the early 1960's. Radiotracers have received wide application in the study of insect biochemistry and physiology (Odum & Golley 1961); it is known that various isotopes are selectively distributed within insect bodies (Yates et al. 1951, Grosch & Sullivan 1952, Yagi 1958). In the case of *Aedes aegypti* L., females were twice as radioactive as males (Bugher & Taylor 1949) such that radiotracers, in excessive quantities, can adversely affect each sex to different degrees within a species. Depending on the isotope, the dose of radiation delivered, the type of radiation, the insect species and life stage exposed, and the method of nuclide administration, radiation levels necessary to produce toxic effects may differ. Toxicity may also result from a species-dependent overdose of the stable element itself (Wang et al. 1975). Toxic levels of Ca-45, Fe-59, Ag-110, Cd-115, and I-131 in certain insect species have been documented (Jenkins 1961).

TABLE 1. RADIOTRACER USES IN INSECT ECOLOGY AND ETHOLOGY EXPERIMENTS CATEGORIZED BY THE TYPE OF STUDY (MARK-RECAPTURE POPULATION MEASUREMENTS, DISPERSAL AND MOVEMENT, FEEDING BEHAVIOR, VECTOR-PATHOGEN RELATIONSHIPS, AND FOOD CHAINS AND WEBS).

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stages ^a	Detector ^b	Reference
MARK-RECAPTURE						
POPULATION ESTIMATION						
Colony size	Termite <i>Mastotermes darwiniensis</i> Froggatt	La-140	ingested: bait	A/N; A/N	SS	Spragg & Paton 1950
Colony size	Formicid <i>Lasius flavus</i> F.	P-32	dipped	A; A	GM	Odum & Pontin 1961
Larval & pupal mortality	<i>Panaxia</i> sp.	S-35	ingested: labeled nettle	L; L/P	PRM	Cook & Kettlewell 1960
Population size	Mosquito <i>Culex pipiens</i> L.	P-32	water culture	L; A	GM	Lindquist et al. 1967
DISPERSAL/MOVEMENT						
Dispersal	Lone star tick <i>Amblyomma americanum</i> L.	Fe-59	dipping	A; A	—	Schmidt & Smith 1961
Dispersal	Acridid <i>Melanoplus mexicanus</i> Sauss	P-32	ingested: bran & molasses	N/A; N/A	GMB	Baldwin et al. 1958
Dispersal	Acridids <i>M. mexicanus</i> & <i>Camnula pellucida</i> Scudder	P-32	ingested: sprayed wheat seedlings	N/A; N/A	PRM	Riegert et al. 1954
Dispersal	Weevil <i>Conotrachelus nenuphar</i> Herbst	I-131, Co-60, Sr-89, Zn-65	ingested: water	A; A	GM & PRM	Rings & Layne 1953
Dispersal	S. pine beetle <i>Dendroctonus frontalis</i> Zimmermann	P-32	painted on tree boles	A; A	PRM	Moore et al. 1979

Dispersal	White pine beetle <i>Pissodes strobi</i> (Peck)	Co-60	painted on elytra	A; A	PRM	Sullivan 1953
Dispersal	Eur. pine shoot moth <i>Rhyacionia buoliana</i> Schiffermuller	Co-60	painted on abdomen	A; A	PRM	Green et al. 1957
Dispersal	Blackflies (Simuliidae)	P-32	water culture	L; A	AR	Baldwin et al. 1966
Dispersal	Blackflies	P-32	water culture	L; L & P	PRM	Fredeen et al. 1953
Dispersal	Mosquitoes <i>Aedes</i> <i>communis</i> DeGeer, <i>A. pionips</i> Dyar, <i>A. excrucians</i> Walker, <i>A. hexodontus</i> Dyar, <i>A. punctator</i> Kirby	P-32	water culture	L; A	PRM	Jenkins & Hassett 1951
Dispersal	Eyegnat <i>Hippolates</i> <i>pusio</i> Loew	P-32	ingested: honey	A; A	GM	Dow 1959
Dispersal	<i>Musca domestica</i> L.	P-32	ingested: milk	A; A	—	Schoof & Siverly 1954
Dispersal	<i>M. domestica</i>	P-32	ingested: milk	A; A	GM	Schoof et al. 1952
Dispersal	Flies <i>Phanencia</i> <i>sericata</i> Meigan, <i>Phormia regina</i> Meigan, <i>M. domestica</i>	P-32	ingested: aqueous diet	A; A	GM	Lindquist et al. 1951
Dispersal	Walnut husk fly <i>Rhagoletis completa</i> Cresson	P-32	labeled attractant on walnut branches	A; A	—	Barnes 1959
Dispersal	<i>Apis mellifera</i> L.	Au-198	—	A; A	—	Courtois & LeCompte 1963
Dispersal	<i>Apis mellifera</i> L.	P-32	ingestion: sugar water	A; A	GM & SS	Lee 1965
Colony location	Termite <i>Mastotermes</i> <i>darwiniensis</i> Froggatt	Sc-46, Au-198	ingested: bait	A; A	SS	Spragg & Fox 1974
Location in soil	<i>Phyllocnistis</i> sp.	P-32	ingested: sugar-water	A; A	—	Sunby 1958

TABLE 1 (Continued)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stages ^a	Detector ^b	Reference
Location in soil	<i>R. buoliana</i>	Co-60	painted on abdomen	A; A	PRM	Green et al. 1957
Movement in soil	Wireworm <i>Agriotes</i> sp.	Co-60	attached wire	L; L	—	Green & Spinks 1955
Movement in soil	Wireworm <i>Ctenicera destructor</i> Brown	Co-60	attached wire	L; L	GM	Arnason et al. 1950
Movement in soil	White grub sp.	Ta-182	inserted wire	L; L	—	Speers 1956
Movement in wood	Carpenter ants <i>Camponotus</i> sp.	I-131	ingested: diet	A; A	PRM	Riordan 1960
Crawling behavior	Coccinelid larvae	Ta-182	attached wire	L; L	PRM	Banks 1955
TERRITORIALITY						
territory	Formicid <i>Formica sanguinea puberula</i> Emery	P-32	injected thistle & ingested from herbivores	A; A	—	Pendleton & Grundmann 1954
territory	Formicid <i>Lasius minutus</i> Emery	P-32	ingested: honey	A; A	PRM	Kannowski 1959
territory	Formicid <i>Solenopsis invicta</i> Buren	Mn-54, Zn-65	ingested: molasses	A; A	SS	Showler et al. 1988b
FEEDING BEHAVIOR						
Amount royal jelly consumed	<i>A. mellifera</i>	P-32	ingested: royal jelly	L; L	LS	Dietz & Lambremont 1970
Amount foods consumed	<i>S. invicta</i>	I-125	ingested: protein, oil, sucrose	A; A	—	Howard & Tschinkel 1981b

Assess fire ant crop damage	<i>S. invicta</i>	P-32	ingested: injected crop plants	A; A	LS	Smittle et al. 1983
Feeding on cotton and <i>H. virescens</i> eggs	<i>Geocoris punctipoes</i> (Say)	C-14 P-32	ingested: cotton plants & <i>H. virescens</i> eggs	A; A	LS	Thead et al. 1985
Amount vegetation consumed by insects	Plants and insects: White Oak Lake bed ecosystem	Cs-137, Sr-90	radio-active waste disposal	PI & I PI & I	GS	Crossley 1961a
Feeding frequency & amount chemosterilant ingested	<i>A. aegypti</i>	P-32	ingested: honey + chemosterilant	A; A	—	Schmidt & Smith 1961
Feeding response to repellent	<i>A. aegypti</i>	P-32	ingested: blood + repellent	A; A	—	Bar-Zeev & Schmidt 1959
Feeding response to malathion bait	<i>M. domestica</i>	P-32	ingested: bait	A; A	GM	Schmidt & LaBrecque 1959
VECTOR-PATHOGEN RELATIONSHIPS						
Virus transmission to plants	Green peach aphid <i>Myzus persicae</i> Sulzer	Po	ingested: diet	N/A; N/A	GLE	Hamilton 1935
Virus transmission to plants	Pineapple mealybug <i>Pseudococcus brevipes</i> Cockerell	P-32	ingested: diet	N/A; N/A	AR	Carter 1945
Vector-pathogen relationship	Mosquito <i>Armigeres obturbans</i> Walker	P-32	water culture	L/A; <i>Setaria digitata</i> (filarial worm)	AR	Dissanaike et al. 1957a

TABLE 1 (Continued)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stages ^a	Detector ^b	Reference
Vector-pathogen relationship	Mosquito <i>Culex fatigans</i> Say	P-32	water culture	L/A; <i>Wucheria bancrofti</i> Cobbold	GM	Dissanaike et al. 1957b
FOOD CHAINS & WEBS						
Determine egg predators	Velvetbean caterpillar <i>Anticarsia gemmatalis</i> Hubner	P-32	ingested: honey; trans-ovarial passage	A to E; egg predators	GM & PRM	Buschman et al. 1977
Determine egg predators	<i>H. virescens</i> F.	P-32	injected adults: trans-ovarial passage to eggs	E; predators	GM	McDaniel & Sterling 1979
Determine egg & larval predators	<i>H. virescens</i>	P-32	ingested: adults to eggs and larvae	E & L; predators	—	Moore et al. 1974
Determine larval & pupal predators	Winter moth <i>Operopthera brumata</i> L.	C-14	ingested: sucrose solution	L & P; predators	GM	Frank 1967
Determine egg & larval predators	<i>Heliothis</i> spp., <i>Pseudoplusia includens</i> Walker, <i>A. gemmatalis</i>	P-32	injected adults: trans-ovarial passage to eggs & larvae	E, L; predators	AR	McCarty et al. 1980
Determine larval & pupal	<i>Aedes stimulans</i> Walker <i>A. trichurus</i> Dyar	P-32	water culture	L; aquatic predators	—	Baldwin et al. 1955

predators Determine predators	<i>Aedes communis</i> Degeer, <i>A. pionips</i> Dyar, <i>A. excrucians</i> Walker, <i>A. hexodontus</i> Dyar, <i>A. punctor</i> Kirby	P-32	water culture	A; predators	PRM	Jenkins & Hassett 1951
Determine larval predators	Blackflies (Simuliidae)	P-32	water culture	L; predators	PRM	Fredeen et al. 1953
Label internal parasites	<i>Pieris rapae</i> <i>crucivora</i> L.	Ca-45, P-32	ingested: cabbage	L; nematode & fungal parasites	—	Yagi 1958
Trophic chain	Balsam fir <i>Abies</i> <i>balsamea</i> L. → spruce budworm <i>Choristoneura</i> <i>fumiferana</i> Clemens larvae → predators	P-32	injected balsam fir roots	—	GQPD	Krall & Simmons 1977
Trophic web	Thistle <i>Cirsium</i> <i>undulatum</i> → herbivores → predators & symbiotes	P-32	injected thistle	—	—	Pendleton & Grundmann 1954
Trophic web	Insects on <i>Heterotheca</i> sp., <i>Rumex</i> sp., & <i>Sorghum halpense</i> L.	P-32	sprayed on foliage	—	GM	Odum & Kuenzler 1961
Trophic web	White Oak Lake bed ecosystem	Cs-137, Sr-90	radioactive waste disposal	—	GS	Crossley 1961b
Trophic web	Dow Run (stream)	Bi-214, Ac-228, Cs-137, Sr-90	radioactive waste disposal	—	SS	Minckley et al. 1961

TABLE 1 (Continued)

Type of study	Insect or community labeled	Isotope	Mode of application	Insect stages ^a	Detector ^b	Reference
Trophic web	West Branch of Sturgeon River	P-32	dripped in river	—	—	Ball 1961
Trophic web	Lake	Zn-65	sprayed on lake	—	SS & GM	Bachmann 1961

^aE = egg, N = nymph, L = larva, P = pupa, A = adult Pl = plant. Stage labeled; stage detected.

^bAR = autoradiography, GLE = gold leaf electroscope, GM = Gieger-Muller tube, GQPD = gas quenched proportional detector, LS = liquid scintillation detector, SS = solid scintillation detector, PRM = portable rate meter, — = detector not indicated in reference.

White pine weevils, *Pissodes strobi* (Peck), painted with 500 μCi Co-60 per individual did not suffer increased mortality for at least 2 months (Sullivan 1953), whereas boll weevil, *Anthonomus grandis* Boheman, mortality increased when P-32 concentrations exceeded 9.9 μCi per gram of labeled diet (Mayer & Brazzel 1961). Mortality studies on termites, *Reticulitermes flavipes* Kollar, revealed that while equivalent amounts of Mn-54, Sr-85, and Sr-85 + Co-60 produced lethal effects, Co-60, Cs-137, Sb-125, Mn-54 + Zn-65, Mn-54 + Se-75, Co-60 + Cs-137, and Cs-137 + Se-75 were benign (Traniello et al. 1985). In contrast, Grosch & Sullivan (1952) found that *Habrobracon juglandis* Ashmead developed "radioresistance"; P-32-treated adults survived as long or longer than controls. Sublethal doses of radiation have been shown to incur damage by reducing insect fecundity (Bugher & Taylor 1949, Blumel 1950). *H. juglandis* adults fed on less than 50 μCi P-32 per gram of labeled food displayed no ill-effects; 50-200 μCi resulted in decreased (ca. 26 percent) egg production, and 200 μCi halted the process entirely (Grosch & Sullivan 1952). Eggs produced from radiolabeled adults may also show increased mortality (Banks 1955, Babers et al. 1956) and offspring hatched from labeled eggs may be deformed or die soon after eclosion (Blumel 1950, Banks 1955). Mayer & Brazzel (1961) demonstrated, further, that *A. grandis* larvae raised on P-32-labeled diet developed into adults with adversely affected longevity, fecundity, and pre-oviposition and ovipositional periods when compared with adults fed on similarly tagged diet. Radiotracer levels, however, may not hinder longevity, fecundity, fertility, or egg eclosion as demonstrated by P-32 assays on the screw-worm fly, *Cochliomyia hominivorax* Coquerel (Radeleff et al. 1952). Thus the use of a fixed radionuclide dose may be suitable for one species but impractical for another (Jenkins 1961). If the nuclide is administered in a nontoxic dose, any species can be radiolabeled.

Those nuclides that dissipate energy as gamma photons possess advantages peculiar to the nature of gamma radiation. Gamma-emitting isotopes produce characteristic spectral emission "signatures" such that confusion between different radionuclides in the same insect or community is eliminated (Traniello et al. 1985, Showler et al. 1988b). Additionally, because gamma rays have negligible mass and are extremely energetic, gamma-emitting isotopes have been employed to locate cryptic insects through several cm of soil (Tomes & Brian 1946, Arnason et al. 1950) and up to 14 cm of wood (Riordan 1960).

Radiolabeling methods

There is a diversity of methods by which radiotracers have been introduced to insects (Jenkins 1961). Radiotracers can be applied as components of biologically essential compounds for biochemical research (Wang et al. 1975), and even radiolabeled insect sperm (*A. aegypti*) has been developed for mating studies (Schmidt & Smith 1961). Insect ethology and ecology research is less specific regarding the chemical form of the administered nuclide. The following labeling techniques have been used to tag individuals (Odum & Pontin 1961, Tomes & Brian 1946), populations (Spragg & Fox, 1974, Showler et al. 1988b), or entire biotic communities (Bachmann 1961, Crossley 1963):

A. Dipping and painting. Dipping insects in radioactive solutions has been successfully implemented to mark individuals. The lone star tick, *Amblyomma americanum* L., was dipped in an Fe-59 suspension to investigate dispersal in pastures (Schmidt & Smith 1961); I-131, Se-46, Ir-192 (Davis & Nagel 1956), and Co-60 (Sullivan 1953) dips for tracing Englemann spruce weevils, *P. strobi* (Davis & Nagel 1956); and Co-60 for labeling *A. grandis* (Babers et al. 1954). The addition of a detergent allowed a P-32-labeled water dip to penetrate the cuticle of the ant *Lasius flavus* F. for a retention time of 10 days (Odum & Pontin 1961). Phosphorus-32 dipping of the plum curculio, *Conotrachelus nenuphar* Herbst, was not effective (rate of success not given) despite

supplementation with wetting and sticking agents (Rings & Layne 1953). Phosphorus-32-glycerin suspensions painted onto the southern pine beetle, *Dendroctonus frontalis* Zimmermann, permitted the location of tagged beetles after dispersal by the presence of P-32 on host tree pitch tubes (Moore et al. 1979). *D. frontalis* adults were also labeled (100 percent effective) as they emerged from tree boles which had been painted with P-32 (Moore & Taylor 1976). Painted radiolabels, like many visual markers, can be chipped or washed off, and thus may give false indications of radioactivity in the environment (Green et al. 1957).

B. Disc and wire attachments. The movements of various subterranean beetle larvae have been monitored with external disc or wire attachments labeled with Ra-226 (Tomes & Brian 1946), Ta-182 (Speers 1956), and Co-60 (Green & Spinks 1955). Similarly, Ta-182 wire glued to coccinellid larvae was used to investigate crawling behavior on foliage (Banks 1955). Discs and wires glued or tied to the insect exoskeleton or inserted within the insect's body suffer the disadvantages previously described for some visually detected markers such as individual and manual tagging and subsequent trauma to the organism being studied.

C. Ingestion. Isotopes are effectively transferred to insects by ingestion of radiolabeled food; in this way, large numbers of marked insects can be reared simultaneously. See Table 1 for a representative list of various ingested radiolabeled materials. Tagged sugar and honey solutions (Grosch & Sullivan 1952, Baldwin et al. 1958), artificial diets (Babers et al. 1956, Mayer & Brazzell 1961, Traniello et al. 1985), royal jelly (Dietz & Lambremont 1970), milk (Babers et al. 1956), and living plants smeared or sprayed with radiotracers (Fuller et al. 1954, Crossley & Schnell 1961, Odum & Kuenzler 1961) have produced good results in a variety of insects. Labeled wood, blood, and living insect prey have been employed to tag termites (McMahan 1963), mosquitoes (Bar-Zeev & Schmidt 1959), and mantids (Jenkins & Hassett 1950), respectively.

A more refined radiolabeling technique involves rearing insects on plants cultured in radiotagged nutrient solutions (Cook & Kettlewell 1960) or plants injected with radioisotopes (Beckman & Kuntz 1951, Fraser & Mawson 1953, Graham 1954). Insect food webs on the thistle, *Cirsium undulatum* Nutt. (Pendleton & Grundmann 1954), and balsam fir, *Abies balsamea* L. (Krall & Simmons 1977), were determined by injecting these plants with P-32. Similarly, P-32 injected into living rats, rabbits, goats, sheep, and hamsters resulted in the tagging (exact rates not given) of *A. aegypti* (Jenkins & Hassett 1950), screw-worm flies (Radeleff et al. 1952), and Oriental rat fleas *Xenopsylla cheopis* Rothschild (Jenkins 1957), respectively.

Several food interaction studies have been conducted in the White Oak Lake bed, an area in South Carolina contaminated by Cs-137 and Sr-90 wastes that were subsequently translocated by the terrestrial plant community (Crossley 1961b, Crossley 1963). Naturally occurring U-238 and Th-232 fission-products bismuth-214 and actinium-228 were similarly used in a stream ecosystem (Minckley et al. 1961).

D. Water culture. Large quantities of aquatic insects such as mosquitoes and blackflies have been labeled through adulthood when the larvae were raised in P-32-tagged water (Yates et al. 1951, Fredeen et al. 1953, Baldwin et al. 1966); Yates et al. (1951) and Fredeen et al. (1953) reported that 100% of the adults acquired the P-32. In a large-scale application of this technique, Zn-65 was sprayed onto a lake (Bachmann 1961), and P-32 was systematically dripped into a stream (Ball 1961) to examine the trophic structure of each system.

E. Trans-life-stage transmission. Another illustration of the versatility of radiotracer application to insect populations involves transfer of radioisotopes through different life stages of the same insect. This phenomenon has been observed when the initially labeled insect stage obtained the tag by injection (McDaniel et al. 1978), ingestion (Kettlewell 1952, Moore et al. 1974), or radiolabeled water culture (Jenkins & Hassett 1951, Yates et al. 1951, Baldwin et al. 1966). Grasshoppers *Melanoplus mexicanus* Sauss and *Cam-*

al. (1973) found that first and second egg batches of *Culex pipiens* L. retained P-32 from individuals raised as larvae in a labeled water culture.

Methods of detection

Recognition of different methods for radiation detection adds another dimension to the versatility of radiotracer application. The detector of choice may depend upon the type of radiation to be measured, the physical state of the sample, and whether or not detection will occur in the laboratory or the field (Wang et al. 1975, Service 1976). Wang et al. (1975) described the different detectors available, of which the Gieger-Muller tube (Lindquist et al. 1951, Schoof et al. 1952, Dow 1959), liquid scintillation (LS) and (Auerbach et al. 1964, Dietz & Lambremont 1970) and solid scintillation (SS) detectors (Spragg & Paton 1980, Traniello et al. 1985, Showler et al. 1988b), autoradiography (Baldwin et al. 1966, Markin 1970), and portable rate meters (Fuller et al. 1954, Taylor & Moore 1978) have received greatest use in insect ethology and ecology studies. Portable rate meters are useful for the detection of labeled insects encountered in the environment and have been employed to locate P-32 (Riegert et al. 1954, Moore et al. 1979), Co-60 (Sullivan 1953, Green et al. 1957), I-131 (Rings & Layne 1953, Riordan 1960), Sr-89 and Zn-65 (Rings & Layne 1953), and Ta-182 (Banks 1955) in insects, some of which were located in soil (Tomes & Brian 1946, Arnason et al. 1950) or wood (Riordan 1960).

Cerenkov radiation (Wang et al. 1975) can be measured from within living insects placed in a liquid scintillation detector (Lambremont et al. 1977). See Table 1 for a more extensive review of detector types used to measure radioactivity in insect ethology and ecology experiments.

Fields of application

Odum & Golley (1961) listed areas of study within insect ecology and ethology to which radiotracer methods have been applied; these fields were population measurements, dispersal and movement, feeding behaviors, and food webs. In light of more recent applications, the above list should be amended to include territoriality and vector-parasite relationships. Representative implementations of radiotracer studies in ethological and ecological entomology are summarized in Tables 1 and 3.

A. Population measurements. Mark-recapture statistical methods (Southwood 1966, Steele & Torrie 1980) and radiolabeled population members have been used to estimate the numbers of ants, *Lasius flavus* F. (Odum & Pontin 1961), and termites, *Mastotermes darwiniensis* Froggatt (Spragg & Paton 1980), per colony. Lindquist et al. (1967) used P-32 to estimate the population size of *Culex pipiens* in Rangoon, Burma. Insects that exhibit trophallactic behavior distribute ingested labels among other individuals to render mark-recapture efforts invalid. Because a relatively large proportion of the studied population should be marked to obtain a high rate of recaptures (Mosby 1969, Seber 1973), radiotracers are suitable.

B. Dispersal and movement. Numerous researchers have investigated the dispersal of a variety of insects such as *D. frontalis* (Moore et al. 1979), blackflies (Fredeen et al. 1953, Baldwin et al. 1966), mosquitoes (Jenkins & Hassett 1951), *Musca domestica* L. (Schoof et al. 1952, Schoof & Siverly 1954), acridids (Riegert et al. 1954, Baldwin et al. 1958), weevils (Rings & Layne 1953, Sullivan 1953), honeybees (Courtois and LeCompte 1963), and moths (Green et al. 1957). A review of the literature revealed that the greatest weakness of dispersal experiments was in sampling for the insects after they had moved into the environment. More extensive reviews on mosquito (Jenkins 1954, Jenkins 1961, Service 1976) and housefly (Jenkins 1954) dispersal studies

demonstrate the successful application of radiotracers to such mobile and economically important insects. Insect movement patterns in soil (Green & Spinks 1955), wood (Riordan 1960), on foliage (Banks 1955) and termite colony location within earthen nesting structures (Holt & Easey 1985) have been investigated with radionuclides.

C. Territoriality. Social insects, such as ants, provide models for the study of territorial behavior. Pendleton & Grundmann (1954) injected a thistle, *C. undulatum*, with P-32; ants, *Formica sanguina puberula* Emery, acquired the label from the thistle by foraging on radioactive honeydew excreted by aphids. Because nearby *F. puberula* colonies remained unlabeled, intraspecific territorial behavior was suggested. Similarly, P-32-labeled *L. minutus* colonies were shown to be discrete from other colonies of the same species (Kannowski 1959). More direct evidence for territorial behavior was demonstrated by Showler et al. (1988b); two adjacent fire ant colonies, one labeled with Zn-65 and the other with Mn-54, were monitored. Territorial patterns were clearly delineated during 21 consecutive days.

D. Feeding behavior. Amounts of various food sources consumed by insects can be measured with radiotracers; examples include P-32-labeled royal jelly by honeybee larvae (Dietz & Lambremont 1970), and I-125-labeled protein, oil, and sucrose by fire ants (Howard & Tschinkel 1981a,b). Fire ant consumption of P-32-labeled corn, soybeans, and okra was assessed by analyzing the ants for radiation (Smittle et al. 1983). A complex application of this technique was undertaken by Crossley (1961a) to estimate the feeding rate of the herbivorous insect fauna in the Cs-137- and Sr-90-contaminated White Oak Lake bed ecosystem. Modification of such experiments permitted evaluation of *A. aegypti* feeding responses to chemically altered food sources such as repellents (Bar-Zeev & Schmidt 1959) and chemosterilants (Schmidt & Smith 1961) in blood, and houseflies to malathion baits (Schmidt & LaBrecque 1959).

The study of trophallaxis among social insects has largely relied upon radiotracer methods (Table 3). Naarmann (1963) used P-32 to show that formicid food secretions are primarily formed in the pharyngeal glands, stored in the crop, then regurgitated. Other radiotracer experiments revealed that food exchange rates may be governed by temperature, time, colony size, starvation (Kneitz 1963a,b, Gosswald & Kloft 1963, Howard & Tschinkel 1980), and the food type ingested (Markin 1970, Howard & Tschinkel 1981a,b). Different rates of food exchange were also observed between social castes (McMahan 1963; Sorenson et al. 1985) and life stages (Markin 1970, Howard & Tschinkel 1981a). Eisner & Wilson (1958) found that seed-eating *Pogonomyrmex badius* Latrille (a "primitive" myrmicine) exchanged I-125-labeled honey-water slowly (rate not given) while the more "specialized" aphid-tending *Solenopsis saevissima* Fr. Smith trophallactic rate was significantly higher: in 3 days 65% of a colony's adults were labeled. The "very specialized" aphid-tending *Crematogaster lineolata* Say transferred the tracer to 90% of its nestmates within 30 hr.

E. Vector-parasite relationships. The investigation of insect transmission of pathogenic organisms to plant and animal hosts has involved the use of radionuclides. The pineapple mealybug, *Pseudococcus brevipes* Cockerell (Carter 1945), and the green peach aphid, *Myzus persicae* Sulzer (Hamilton 1935), were portrayed as plant virus vectors using P-32 and polonium, respectively.

Jenkins (1954) indicated that several insect-vectored and medically important pathogens have been radiolabeled; examples include *Onchocerca volvulus* Leuckart with radioantimony; various protozoa with Fe-55, Fe-59, and P-32; and *Bacillus subtilis*, *B. coli*, *Escherichia coli*, a virus bacteriophage, and influenza virus with P-32. Moraczewski & Kelsey (1948) reported P-32-labeled *Trypanosoma* sp. Mosquitoes, *Armigeres obturbans* Walker and *Culex fatigans* Say, cultured in P-32-labeled water were found to transfer the tag to microfilarial *Setaria digitata* Railliet and Henry and *Wuchereria bancrofti* Cobbold (Dissanaike et al., 1957,a,b), which suggested that there was a trophic relationship between the insect vectors and the pathogens.

TABLE 3. TROPHALLAXIS RESEARCH ON TERMITES, ANTS, AND HONEYBEES USING RADIOTRACER TECHNIQUES.

Insect labeled	Radioisotope	Reference
ISOPTERA		
<i>Cryptotermes brevis</i> Walker	Co-57, Sr-85	McMahan 1963
<i>C. brevis</i>	Co-57	McMahan 1966
<i>C. brevis</i>	C-14	Beard 1974
<i>Kaloterme flavicollis</i> F.	P-32	Alibert 1959
<i>K. flavicollis</i>	I-131, P-32	Gosswald & Kloft 1963
<i>Mastotermes darwiniensis</i> Froggatt	Sc-46	Spragg & Fox 1974
<i>M. darwiniensis</i>	La-140	Spragg & Paton 1980
<i>Reticulotermes flavipes</i> (Kollar)	Co-60, Cs-137, Mn-54, Sb-124, Sb-125, Se-75, Zn-65	Traniello et al. 1985
<i>R. flavipes</i>	Co-60, Mn-54, Sb-125, Sc-46, Se-75, Sr-85, Zn-65	Rosengaus et al. 1986
HYMENOPTERA (Formicidae)		
<i>Formica integra</i> Nylander	P-32	Wilkinson et al. 1978
<i>F. rufa</i> L.	Au-198	Courtois & LeCompte 1963
<i>Formica</i> spp.	I-131, P-32	Gosswald & Kloft 1963
<i>Formica</i> spp.	P-32	Kneitz 1963a,b
<i>Iridomyrmex humilis</i> Mayr	P-32	Markin 1970
<i>Lasius niger</i> L.	P-32	Lenoir 1974
<i>Solenopsis invicta</i> Buren	I-131	Eisner & Wilson 1958
<i>S. invicta</i>	P-32	Gosswald & Kloft 1960
<i>S. invicta</i>	P-32	Naarman 1963
<i>S. invicta</i>	I-125	Howard & Tschinkel 1980
<i>S. invicta</i>	I-125	Sorenson et al. 1980
<i>S. invicta</i>	I-125	Howard & Tschinkel 1981a,b
<i>S. invicta</i>	I-125	Sorenson et al. 1985
<i>Crematogaster lineolata</i> Say	I-125	Eisner & Wilson 1958
<i>Formica fusca</i> L., <i>F. pallidefulva</i> Mayr, <i>Pogonomyrmex badius</i> (Latreille), and <i>Solenopsis saevissima</i> Fr. Smith		
<i>Pheidole dentata</i> Mayr, <i>Solenopsis geminata</i> F. and <i>S. invicta</i>	P-32	Bhatkar & Kloft 1977
<i>P. badius</i> and 2 <i>Formica</i> spp.	I-131	Wilson & Eisner 1957
HYMENOPTERA (Apidae)		
<i>Apis mellifera</i> L.	P-32	Nixon & Ribbands 1952
<i>A. mellifera</i>	C-14	Oertel et al. 1953
<i>A. mellifera</i>	Au-198, P-32	Courtois & LeCompte 1963
<i>A. mellifera</i>	I-131, P-32	Gosswald & Kloft 1963

F. Food chains and webs. Radiotracer methodology has enabled entomologists to identify predators of various economically important insects. Baldwin et al. (1955) produced tagged *Aedes stimulans* Walker and *A. trichurus* Dyar larvae from P-32-labeled water. After the larvae were transferred to ponds, predatory insect samples revealed that *Limnephilus indivisus* Walker, *Stagnicola palustris* Muller, *Gerris* spp., *Gyrinus lecontei* Fall, *Hydrophilus obtusatus* Say, *Glossiphonia fusca* Castle, *Belostoma fluminea* Say, *Ronatra fusca* Beauvoir, and *Callicorixa* sp. were radioactive. The amount of radiation per predator indicated the approximate numbers of culicid larvae consumed. Phosphorus-32-labeled *H. virescens* eggs were used to identify egg predators in cotton (Thead et al. 1987) such as *S. invicta*, *Orius insidiosus* Say, *Geocoris punctipes* Say, *G. uliginosus* Say, *Pseudatomoscelis seriatus* Ruter, *Hippodamia convergens* Guerin-Meneville, *Cycloneda sanguina* L., *Coleomegilla maculata* DeGeer, *Scymnus loewii* Mulsant, *Heliothis* spp. larvae, *Phidippus* spp., *Peucetia viridans* Hentz, *Oxyopes salticus* Hentz, and *Misumenops* spp. (McDaniel & Sterling 1979). Stam et al. (1987) identified 18 insect and six spider species as predators of *Nezara viridula* (L.) eggs and nymphs. Similarly, internal parasites of P-32-tagged *P. rapae* larvae, such as nematodes and fungi, obtained the label (Yagi 1958).

Radiotracers can be passed from injected plants to herbivores and on to predators (Krall & Simmons 1977, McCarty et al. 1980) and symbiotes (Pendleton & Grundmann 1954). Food webs in large-scale complex ecosystems have been untangled in areas where radiotracers have been introduced to areas where radioactive waste products have accumulated in the environment (Crossley 1961b, Minckley et al. 1961), or aquatic communities (Bachmann 1961, Ball 1961). Relative proportions of isotopes may differ from one organism to another because of dissimilarities in the chemical composition and physiological demands of the different taxa, different sorption characteristics, variation in moisture content between organisms, and relative position of the species on the food chain (Davis & Foster 1958).

NEUTRON ACTIVATION ANALYSIS

Due to public concern regarding the potential detrimental effects of ionizing radiation, some scientists have turned to neutron activation analysis (NAA) to provide an avenue to avoid this problem (Jenkins 1963) often without the sacrifice of radiotracer sensitivity (Wang et al. 1975). Wang et al. (1975) listed the large selection of available stable-activable markers. Rare earth elements, such as Sm and Dy, are good tracers but are not analogous to biochemically essential elements. Because NAA markers are made radioactive by exposing samples to specific thermal neutron fluxes in a nuclear reactor (Wang et al. 1975, Knaus & Curry 1979), the thermal neutron capture cross-section of the nuclide should be large (≥ 0.1 barn). The natural abundance of the stable tracer in the experimental system should be less than 10% of the applied dose to avoid equivocal results (Wang et al. 1975) such as those encountered with Rb labels. The NAA tracer for insect studies should be selected for a short half-life and readily detected radiations (preferably gamma rays) after the nuclide has been activated (Wang et al. 1975, Southwood 1978). NAA methods provide radio-safety in the environment, a diversity of nuclides from which to choose, and sensitivity of detection. The technique also permits long-term experiments without decay of the tracer, nondestructive sample analysis such that the same sample can be repeatedly activated and measured (Wang et al. 1975, Knaus & Curry 1979), and quantification of the label in each sample based upon the amount of radiation emitted (Knaus & Curry 1979). Drawbacks to NAA techniques include i) relatively long (≥ 1 day) analyses of samples (Wang et al. 1975, Knaus & Curry 1979), ii) persistence of the stable tracer in the environment which may render future experiments in the same area unreliable (Wang et al. 1975), and iii) "loss" of the

tracer in the experimental system until NAA is performed (Knaus & Curry 1979). The activated nuclide can be detected and quantified using the same diversity of methods available for conventional radiotracers (Wang et al. 1975).

While toxicity to the insect may result from stable-activable tracers, detectable nonlethal levels may be attained by experimentation (Curtis et al. 1973). Application of these nuclides to the insect has been achieved through ingestion (Richardson 1969, Richardson et al. 1971, Curtis et al. 1973) and by the absorption of cerium into the cuticle of palm weevils *Rhynchophorus* sp. (Rahalkar et al. 1971). White mustard, *Brassica hirta* Moench, and hairy vetch, *Vicia villosa* Roth, have been shown to translocate Dy and Eu from soil to leaves (Kloke & Riebartsch 1965); thus certain herbivorous insects may be labeled on tagged host plants, and, by extension, food webs could be examined using NAA techniques.

At present, NAA has not received great attention in entomology. Curtis et al. (1973) successfully tagged the tsetse fly, *Glossina morsitans* Westwood, with Eu-, Dy-, Au-, and Ir-labeled nutrient solutions. Dysprosium was shown to be a life-long marker in *Drosophila* spp. (Richardson et al. 1969) and was employed for dispersal studies (Richardson 1968). Manganese ingested by the Mediterranean fruit fly, *Ceratitis capitata* Wied, was detectable with NAA (Monro 1968). NAA allows the precise measurement of dispersal patterns that reveal behavioral parameters, ecological components, and rates and other characteristics of movement and reproduction with little disturbance to individual behaviors, population structures, and ecological systems (Gage et al. 1969). A more complex implementation of NAA involved Sm-labeled bait to tag fire ants in a Louisiana sugarcane field to observe the territorial areas of six colonies (Showler et al. 1988a).

Other activation analysis methods have been conducted with trace elements and compounds such as zirconium oxide, Bi, Pb, cerium oxide, Sn, and Se sprayed on mosquitoes then bombarded with alpha particles in a cyclotron to produce X-ray emissions (McClelland et al. 1973a). In a field trial, however, *Aedes nigromaculis* Ludlow adults did not retain detectable levels of the topically applied alpha-activable tracers (McClelland et al. 1973b). Service (1976) suggested the use of high energy X-rays to interact with natural trace elements in mosquitoes to elicit fluorescent X-rays that are proportional to the atomic weights of the "marker" trace elements in the sample.

CONCLUSIONS

Radiotracer methods provide researchers of insect ecology and ethology with versatile and sensitive tools relative to conventional labeling procedures. Applications of radioactive isotopes, when evaluated through the appropriate feasibility studies, can avoid the pitfalls of conventional labeling techniques. Radiotracers are easy to apply to large insect populations, minimize direct manipulation and trauma to individual insects, are detectable in the field or lab without killing or destroying the samples, can persist at detectable levels in the insect or community, and do not necessarily alter the physical or behavioral functions of the labeled organisms. Although conventional tagging methods have been shown to be effective for dispersal (Dalmat 1950), territorial (Wilson et al. 1971), and feeding (Berry et al. 1972, Frazer & Raworth 1974 experiments, Stimman 1974, Shepard & Waddill 1976), radiotracer labeling, as a single methodology, provides greater flexibility with regard to modes of application, detection, and the types of studies to be conducted. Judiciously employed combinations of available radiotracer techniques could reveal a wide spectrum of behavioral and ecological information unattainable with alternative methods. It is conceivable that a single, well-planned radiotracer and/or NAA experiment could provide information relevant to insect population structures, dispersal and movement, territoriality, feeding behaviors, reproductive

strategies, and various physiological phenomena. Prudent use of radiotracer and NAA technology could equip researchers with the capacity to expeditiously enhance current perceptions of insect interactions with man and the environment.

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ADOPTION OF NEWLY-MATED QUEENS:
A MECHANISM FOR PROLIFERATION AND PERPETUATION
OF POLYGYNOUS RED IMPORTED FIRE ANTS,
SOLENOPSIS INVICTA BUREN

B. MICHAEL GLANCEY AND CLIFFORD S. LOFGREN
Insects Affecting Man and Animals Research Laboratory
United States Department of Agriculture
Agricultural Research Service
Gainesville, FL 32604

ABSTRACT

The polygynous form of the red imported fire ant, *Solenopsis invicta* Buren was first reported from Mississippi in 1973; however, the source of the numerous fertile queens in polygynous colonies has remained an enigma. In 1987, 400 queens from a mating flight were marked with a durable paint and released in an area heavily populated with the polygynous form. None were recaptured after one week, but 9 months later, 4 clearly-marked queens were found in a nest 65 meters from their release point. This finding clearly points to adoption. About 5 weeks later, 37 of 107 fertile queens collected from 37 polygynous nests, were found to have partially histolyzed wing muscles and undeveloped ovaries. Mating flights had occurred a few days prior to the queen collections, thus it was apparent that these queens were newly adopted. This observation was verified following a second mating flight one week later. The results of our 3 studies clearly indicate that polygynous *S. invicta* can proliferate and perpetuate their colonies by queen adoption.

RESUMEN

La forma polígama de la hormiga roja importada, *Solenopsis invicta* Buren, fue reportada por primera vez en Mississippi en 1973; sin embargo, la fuente de numerosas reinas fértiles en colonias polígamas ha permanecido un enigma. En 1987, 400 reinas de un vuelo nupcial fueron marcadas con pintura duradera y liberadas en un área altamente poblada con la forma polígama. Ninguna fue recapturada después de una semana, pero 9 meses después, 4 reinas claramente marcadas fueron encontradas en un nido a 65 metros de donde fueron liberadas. Este descubrimiento claramente indica adopción. Como 5 semanas después, 37 de 107 reinas fértiles colectadas de 37 nidos polígamos, se encontraron tener histolizados los músculos del ala y ovarios sin desarrollar. Vuelos nupciales habían ocurrido varios días antes de que se colectaran las reinas, de aquí que es aparente que esas reinas fueron recientemente adoptadas. Esta observación fue verificada en el siguiente vuelo nupcial una semana más tarde. El resultado de nuestros 3 estudios indican claramente que *S. invicta* polígamas pueden proliferarse y perpetuar sus colonias adoptando reinas.

The increasing occurrence of populations of the polygynous form of the red imported fire ant, *Solenopsis invicta* Buren, has become a concern to those faced with controlling populations of this pest ant. Polygynous *S. invicta* tend to have high nest densities (up to 2,000/ha) and reproductive rates which cause greater economic, public health, and environmental problems. Populations of the polygynous form have been reported for all infested states except North and South Carolina and Puerto Rico; however, this probably reflects a lack of surveys for their detection rather than their absence (Glancey et al. 1973, Mirenda & Vinson 1982, Fletcher 1983, Lofgren & Williams 1984, Glancey et

al. 1987). The finding of polygynous colonies in Oklahoma in 1987 and in several isolated locations in west Texas (W. A. Banks, USDA, personal communication) suggests also that they may present a greater hazard of spread to uninfested locations.

While there has been speculation about the origin of polygyny in *S. invicta* there are no reports documenting the specific biological mechanism responsible for either the origin of these populations or the method by which they perpetuate themselves. Because a portion of our laboratory grounds is now infested with polygynous *S. invicta*, we were able to compare differences between monogyne and polygyne populations. Of particular interest was the possibility that the polygyne populations were being sustained through the adoption of newly-mated queens following mating flights. This adoption theory was proposed because orphaned *S. invicta* workers will accept new queens under certain laboratory conditions (Banks et al. 1981), particularly if the new queen is 10-14 days post-eclosion and producing the queen recognition pheromone (Glancey et al. 1981). Also, we have found that laboratory-reared polygynous colonies will often accept newly-mated queens (unpublished observations).

METHODS AND RESULTS

To test our theory of adoption, we collected about 800 newly-mated and dealate queens on the ground following a nuptial flight around a shopping area on June 15, 1987 near Ocala, Florida. We examined 200 of the queens for insemination and all contained sperm. We then painted 100 each with orange, white, blue and yellow and banded 100 with wire. The queens were painted by applying a small drop of Markal Ball Point Marker (Markal Co., 250 N. Washtenaw Ave., Chicago, Ill.) to the dorsal surface of their thorax and the gaster while they were anesthetized with CO₂. The banding was accomplished by tying fine copper wire around the petiole of the queen while she was inactivated by chilling (Mirenda & Vinson 1979). The queens were allowed to recover completely before they were returned to the field. The five groups of 100 queens were released on June 16, 1987 in pre-selected areas around our laboratory that had well defined populations of polygynous colonies. Seven days later, all mounds within 10 meters of each release site were dug up and placed in 5-gallon buckets. The ants were separated from soil by the drip-flotation method (Banks et al. 1981) and all queens examined for paint spots or bands. No marked queens were found. However, nine months later (March 30, 1988), during the sampling of polygynous nests in a nearby pasture area, we found 44 queens in one nest, 4 of which were marked. The nest was located 65 meters from the nearest release point (Fig 1 & 2). The queens were readily identified by bright orange spots on the dorsal side of their gaster and thorax. The means by which the released queens migrated to the nest in which they were captured, through an area highly populated with other polygyne *S. invicta* nests, is unknown. As far as we are aware, this represents the first time that adoption of queens by polygynous field colonies of *S. invicta* has been verified.

In early May, 1988, we collected queens from polygynous colonies in an adjacent area, about 75 m from the site where the marked queens were collected. A rain had occurred on May 13, and the ants had built up their mounds (15 cm or more) so they were easy to locate. Mating flights were noted on May 14 & 15 also. On May 17 we dug up 37 colonies, collected all the dealated females and dissected them to check for insemination and ovarian development. All of the queens were inseminated; however, it was evident that two types of queens were present: a) those that had well developed ovarioles containing 3-4 or more vitellogenic eggs in every ovariole and no fat body or alary muscles, and b) those that had a few ovarioles with 1 vitellogenic egg, but which had fat body and partially histolyzed alary muscles. It was apparent that these latter queens had mated recently and were in the initial stages of ovarian development and egg production. Queens were retrieved from 21 of the 37 nests. The data on the 107



Fig. 1. Photograph of pasture area in which marked queens or banded queens were released (rp = release point, cp = capture point).

queens collected are shown in Table 1. Ten of the 21 nests contained 1 to 8 newly-mated queens; 7 contained only newly-mated queens.

On May 20, another mating flight occurred the day after a rainfall. Six days later, we collected ants from two nests located at the base of oak trees about 100 meters from the location of the previous collection site. The data on queens from this collection also are presented in Table 1. In Nest 1, 52 of 72 (74%) of the queens were adopted, and in Nest 2, 12 of 22 (55%) were adopted. Observations of the wing muscles indicated various stages of histolysis. In neither nest did we find any males, alate females, or sex brood.

DISCUSSION AND CONCLUSIONS

In light of these observations, it is apparent that a principle method by which polygynous colonies of *S. invicta* perpetuate themselves is via adoption of newly-mated queens following their mating flights. However, we do not know the specific conditions which favor adoption, since it is obvious that not all queens are accepted. The possibility of intranidal mating as an alternative explanation for the 2 queen types does not seem logical since it would require a change in mating behavior of *S. invicta* for which there is no documented evidence. On the other hand, mating flights of males and females from polygynous colonies are documented (W. A. Banks, personal communication) and flights from nests in our test site were observed during May, 1988. The fact that the newly-mated queens were detected within 6 days of mating flights, and no sexual brood and/or alate males or females were present in the nests we excavated, clearly favors adoption of queens from local nuptial flights alighting near these nests rather than intranidal mating. There was no way for us to determine whether the new queens were from polygynous or monogynous colonies.

Another factor favoring adoption is the recent research of Morel et al. (In press) which demonstrates a lack of aggression between workers of polygynous colonies and

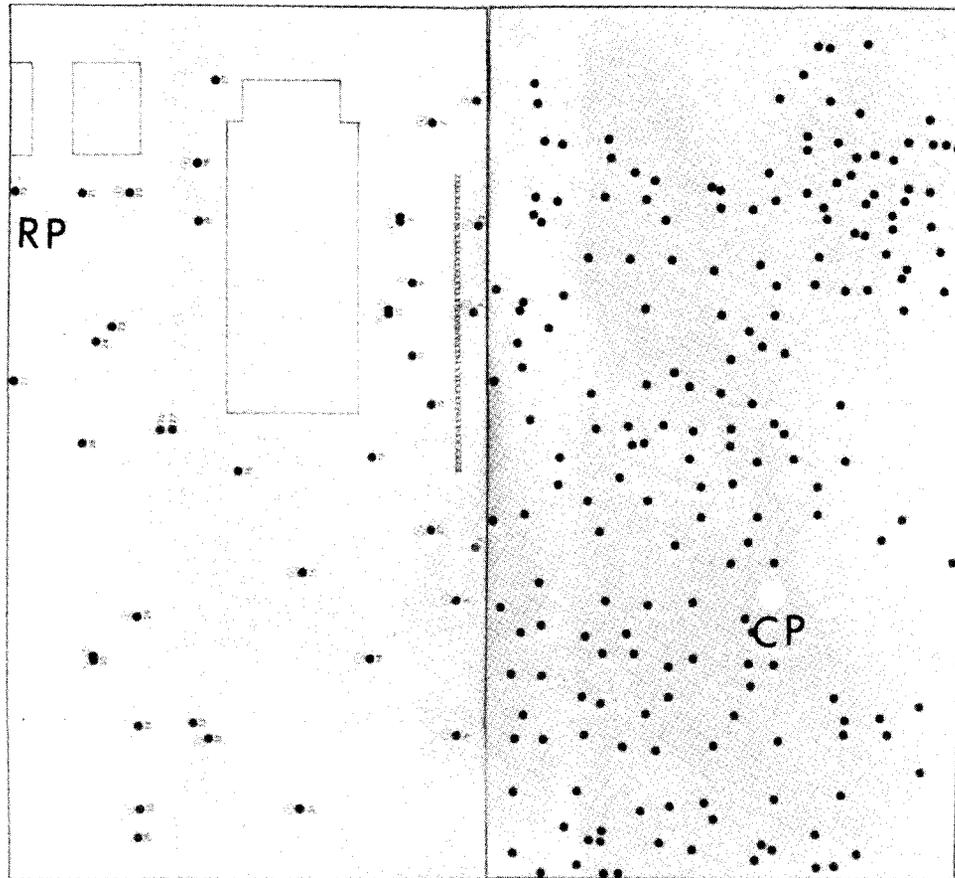


Fig. 2. Schematic map of pasture area showing location of multiple queen mounds and the release (rp) and capture (cp) locations (distance = 65m).

toward workers of monogynous colonies. The lowered aggression levels in polygynous populations are attributed to a greater variability in the polygyne template caused by highly variant discriminators derived from multiple matrilines, as well as exposure to a greater variety of environmental cues. From this evidence we infer that polygynous workers might be less hostile to newly-mated queens, thus allowing their adoption.

We conclude that polygynous *S. invicta* colonies are able to proliferate and perpetuate by adoption of newly-mated queens. While our observations indicate adoption immediately following the nuptial flight, we cannot rule out later adoption of claustral founding queens. Adoption of queens directly after a mating flight has been reported for *Formica ulkei* (Scherba 1958) and *Formica opaciventris* (Scherba 1961); however, in these instances the queens returned to the same cluster of nests from which they took flight.

Numerous other questions remain to be answered, particularly how individual polygynous populations originate. Ross & Fletcher (1985) speculate that they arise through kin selection and/or mutualism. It seems reasonable to us that both factors are involved. Tschinkel & Nierenberg (1983) discuss the importance of relatedness on the social biology of *S. invicta* in the United States. Because the original introduction of *S. invicta* into the Mobile, Alabama area between 1933 and 1940 involved only a small number of females, they suggested that relatedness could be associated with the development of polygyny. However, *S. invicta* queens were shipped from Mobile in nursery

TABLE 1. OVARIAN STAGE^a OF INSEMINNATED QUEENS COLLECTED FROM *S. INVICTA* POLYGNOUS FIELD COLONIES.

Mound No.	No. Queens	Ovarian Stage 1	Ovarian Stage 2	Mound No.	No. Queens	Ovarian Stage 1	Ovarian Stage 2
<u>Observation Area No. 1 (May 17, 1988)</u>							
1	13	0	3	12	4	4	0
2	1	0	1	13	8	8	0
3	17	0	17	14	1	0	1
4	1	0	1	15	3	3	0
5	7	0	7	16	2	2	0
6	4	0	4	17	7	4	3
7	7	1	6	18	4	4	0
8	2	0	2	19	2	0	2
9	20	9	11	20	1	0	1
10	1	1	0	21	1	0	1
11	1	1	0	Totals	107	37	70
<u>Observation Area No. 2 (May 26, 1988)</u>							
1	72	52	20				
2	22	12	10				
Totals	94	64	30				

^aStage 1 = some ovarioles with one vitellogenic egg, fat body present, wing muscles partially histolyzed.
 2 = all ovarioles with 3-4 vitellogenic eggs, no fat body or wing muscles.

stock to hundreds of other locations in the southern United States in the 1940's and 1950's (Culpepper 1953, Lofgren 1986). Most of the shipments probably involved only one or, at most, a few colonies. Tschinkel & Nierenberg (1983) state that these "outlier populations" could result in even higher degrees of relatedness associated with "second founder effects and higher inbreeding". Thus, it is easy to conceive of polygynous populations arising at various locations due to high genetic similarity in combination with pleometrotic colony founding. Once a polygynous founder colony becomes established, lowered worker aggression levels (Morel et al., In press), queen adoption and colony budding or fission (Vargo & Porter, in press) take over as the mechanisms by which polygynous colonies are populated and enlarged.

Adoption can have definite advantages for newly-mated queens by providing them with instant care. An example is provided by Ross & Fletcher (1986) who found that diploid male-producing queens could not establish colonies by themselves but did survive in polygynous colonies. This example can be extended to predict an overall increase in survival potential for queens. For example, in March 1988 we estimated through excavations and subsampling that the nests in the polygyne field populations at our laboratory harbored about 4,000 queens per acre. Glancey (1975) reported collection of over 4,000 queens in one year from 36 mounds along a ditch bank 45 m long by 1 m wide. If

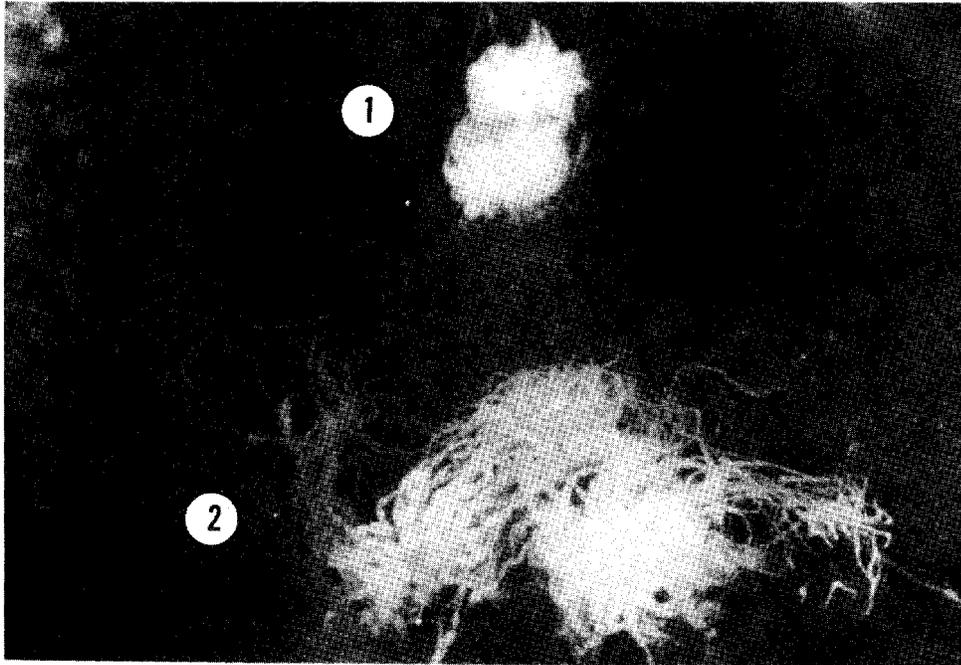


Fig. 3. Two types of ovaries found in queens from polygynous colonies. Class 1 queens had fat bodies, alary muscles, were inseminated and had only a few ovarioles with a single egg. Class 2 queens were inseminated also, but lacked fat body and alary muscles. Every ovariole possessed 3-4 vitellogenic eggs.

we assume the same number of newly-mated queens from nuptial flights alight in monogyne and polygyne populations, it follows that their chances for execution by the foraging monogyne workers will be much greater than by polygyne workers.

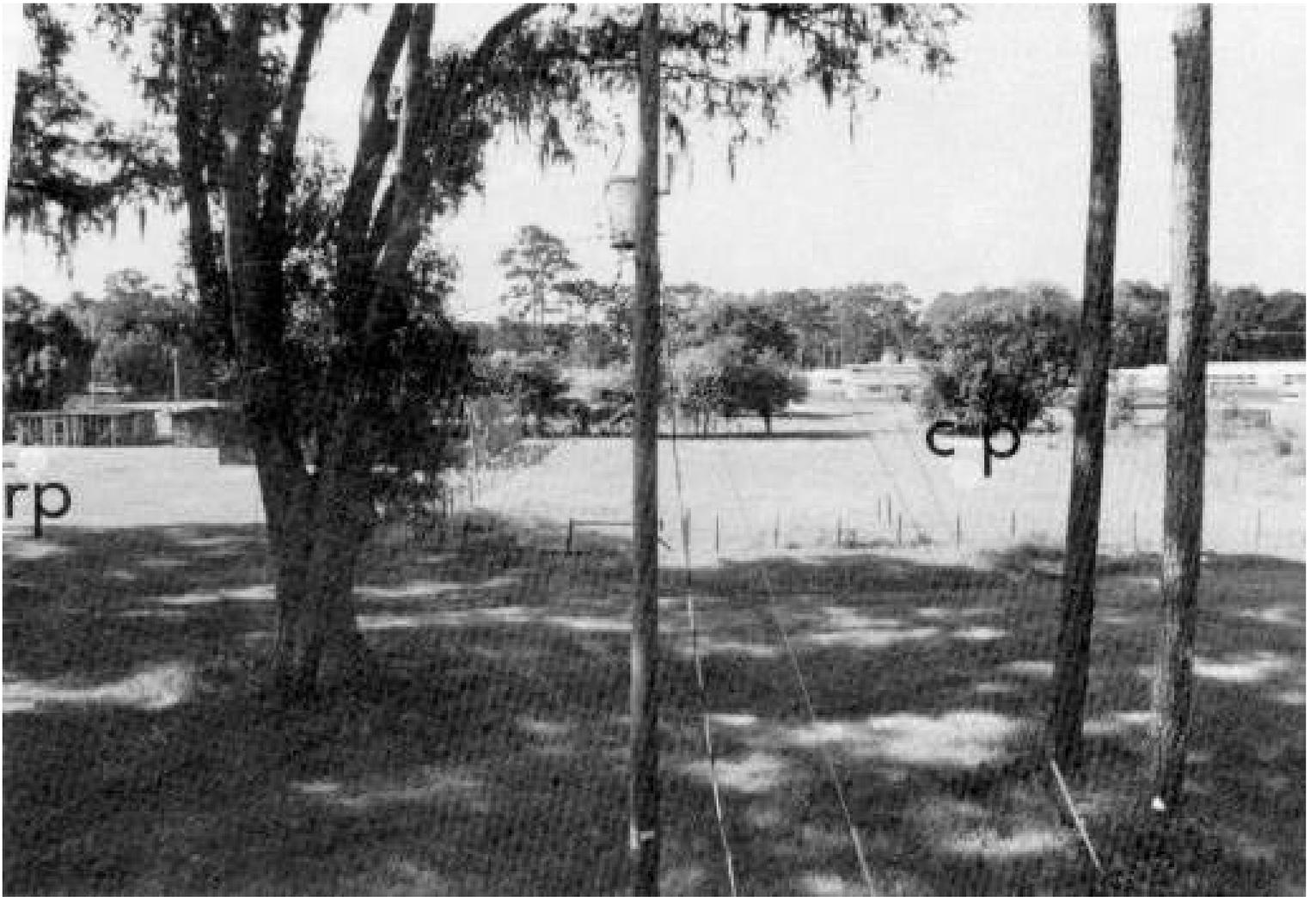
Disadvantages must also be associated with adoption. Lowered production of sexuals (Vargo & Fletcher 1987) indicates a decreased genetic input for each queen into future generations. The increased production of brood and workers causes an extreme foraging load and potential lack of food. This undoubtedly is reflected in the production of extremely small workers (Greenberg et al. 1985) and our personal observation that large numbers of dead worker "bone piles" are associated with polygynous populations.

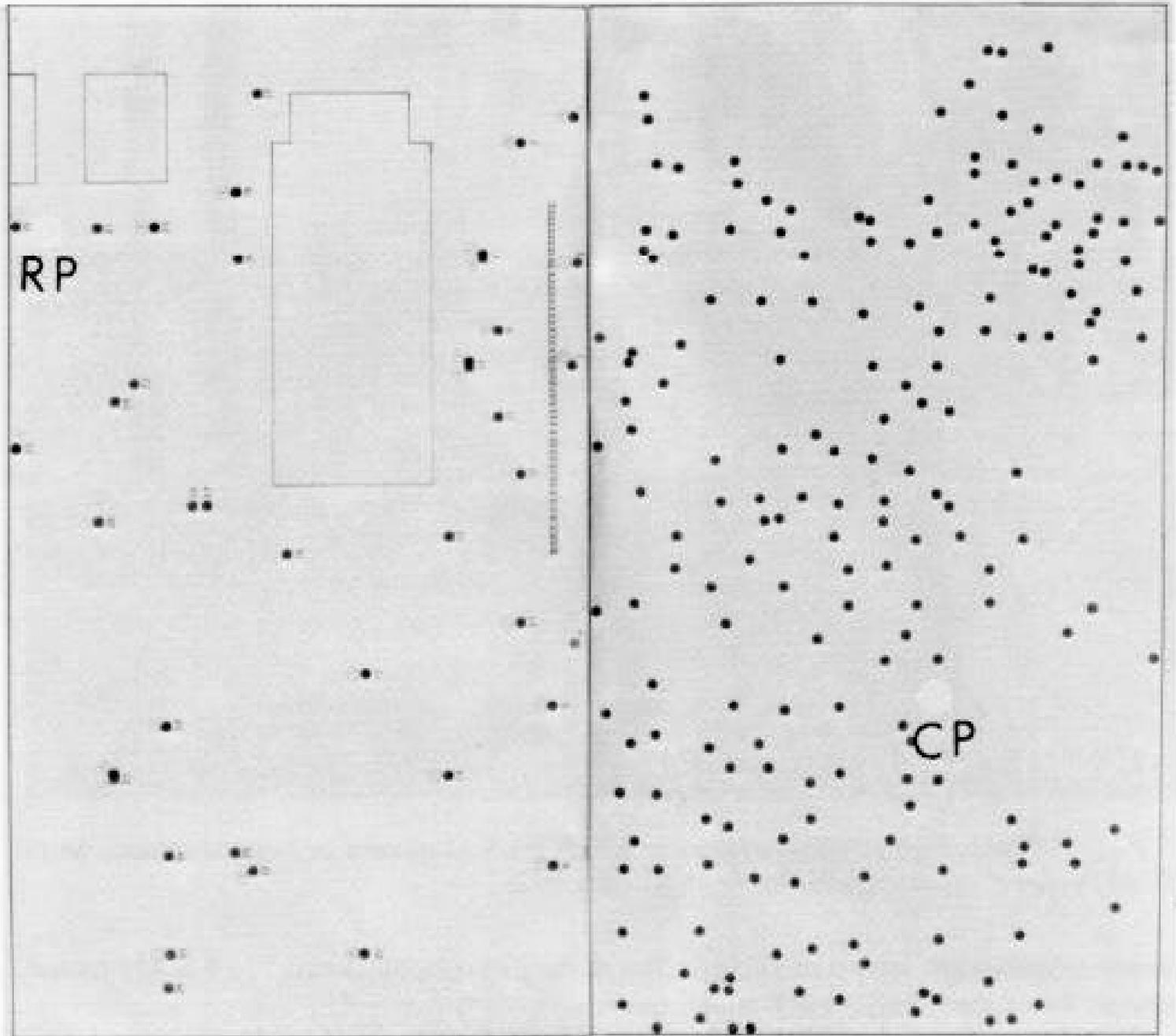
In the long term, it may be that negative aspects of polygyny will work against polygynous *S. invicta* populations. However, in the meantime, they pose a greater hazard to agriculture, public health and the environment (Lofgren 1986), especially to other ant species (Vargo & Porter, in press). Without a doubt, polygyny has added a new dimension to the fire ant problem.

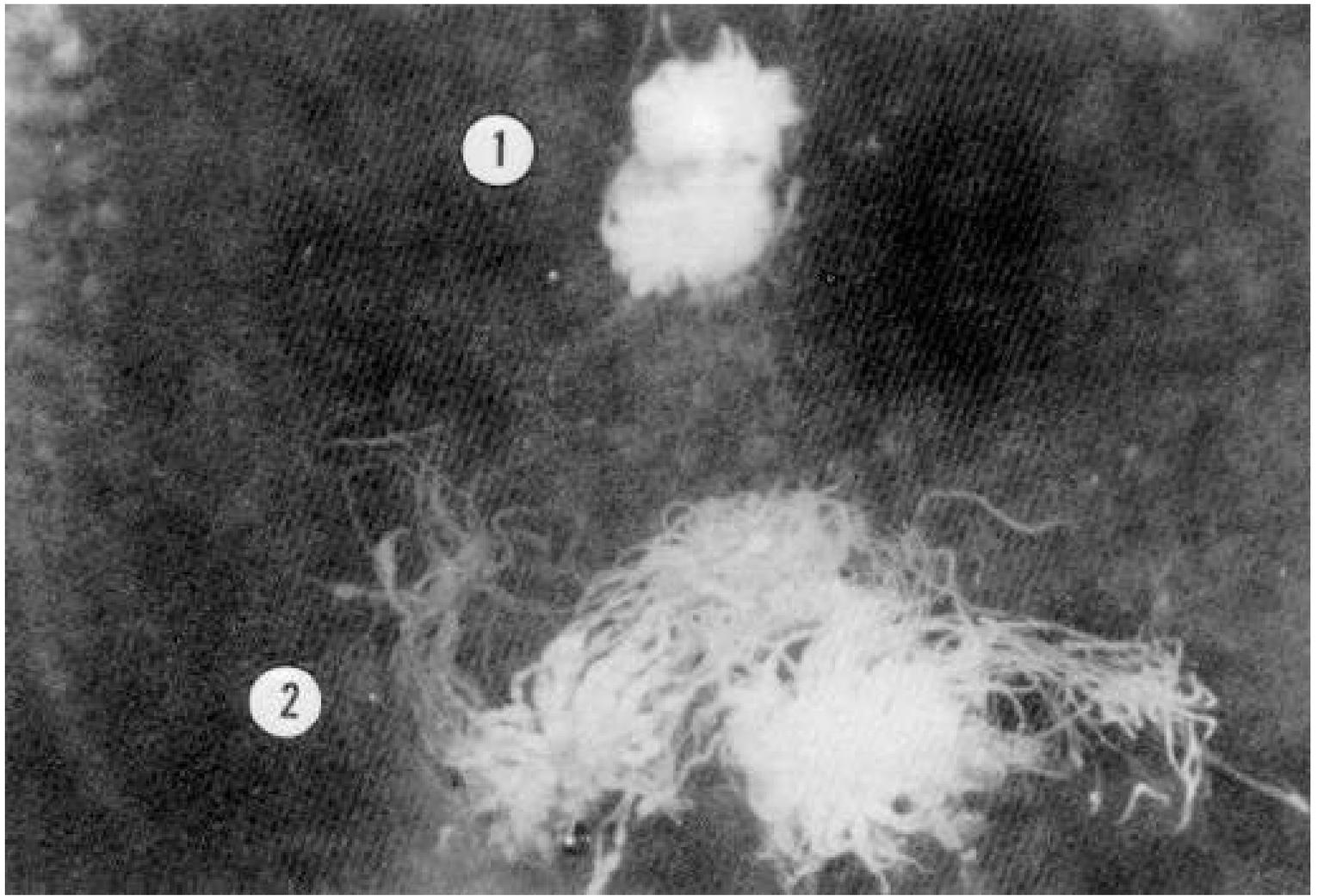
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NEARGYRACTIS SLOSSONALIS
(LEPIDOPTERA: PYRALIDAE, NYMPHULINAE):
LARVAL DESCRIPTION AND BIOLOGICAL NOTES

D. H. HABECK

Department of Entomology and Nematology
IFAS, University of Florida
Gainesville, Florida 32611

ABSTRACT

The mature larva of *Neargyractis slossonalis* (Dyar) is described and illustrated. Larvae of this southeastern United States species live among submerged roots of plants growing in or along streams and lakes. Larvae ingest young roots, but may also feed on periphyton. Pupation occurs under water among the roots.

RESUMEN

La larva madura de *Neargyractis slossonalis* (Dyar) es descrita e ilustrada. Las larvas del sudeste de los Estados Unidos viven en medio de las raíces sumergidas de plantas que crecen en o a lo largo de arroyos y lagos. Las larvas comen raíces jóvenes, pero también pueden alimentarse del periphyton. El estado de pupa también ocurre de bajo del agua en medio de las raíces.

Neargyractis slossonalis (Dyar) is a small pyralid moth with an aquatic larva. It occurs throughout Florida (Kimball 1965), in South Carolina (Herlong 1979), and probably occurs in Alabama and Georgia (Munroe 1972). Lange (1956) created the genus *Neargyractis* for the species Dyar had described in the genus *Elophila* (Dyar 1906). Kimball (1965) cited several Florida records for a second species, *N. moniligeralis* (Lederer) but Munroe (1972) believes this is a Caribbean species that does not occur in Florida. The immature stages of *N. slossonalis* have remained undescribed, and Lange (1956) speculated that the larvae should be rock inhabitants similar to *Petrophila* (= *Parargyractis*). Based on my unpublished report, Brigham & Herlong (1982) provided a brief description of the larva and habitat and included the genus in their key to pyralid larvae associated with aquatic plants. The present paper describes the larva in detail and summarizes known information on the biology of *N. slossonalis*.

Mature larva: Maximum length about 20 mm; creamy pale to light brown, densely covered with minute spinules. Head dark brown with creamy pale anteclypeal and stemmatal areas; prementum fuscous; mesal borders of maxillae and margins of hypostomal lobes of postgenae dark brown or black. Prothoracic shield yellowish brown to dark brown and darkly margined posterolaterally. Thoracic legs brown, posterior aspects of prothoracic coxae concolorous with prothoracic shield, meso- and metathoracic coxae unsclerotized posteriorly. Setal peritremes mostly concolorous with body, but peritremes of labral setae often lighter than body color; peritreme of SV setae on prothorax and the sclerotized band on dorsal surface of anal proleg darker than body color. Unbranched, brown filamentous gills located on distinct tubercles on mesothorax, metathorax and abdominal segments 1-9. Gill numbers variable (Table 1).

Head: (Figure 1, 2). Average width 0.53 mm (n = 10). Head circular in frontal view, hypognathous, and granulate. Adfrontals extending two-thirds distance to the vertical triangle, frontal suture about one and one-half times length of coronal suture. Labrum (Figure 3) with shallow, obtuse notch, setae M1 and M2 normal in a horizontal line. Seta

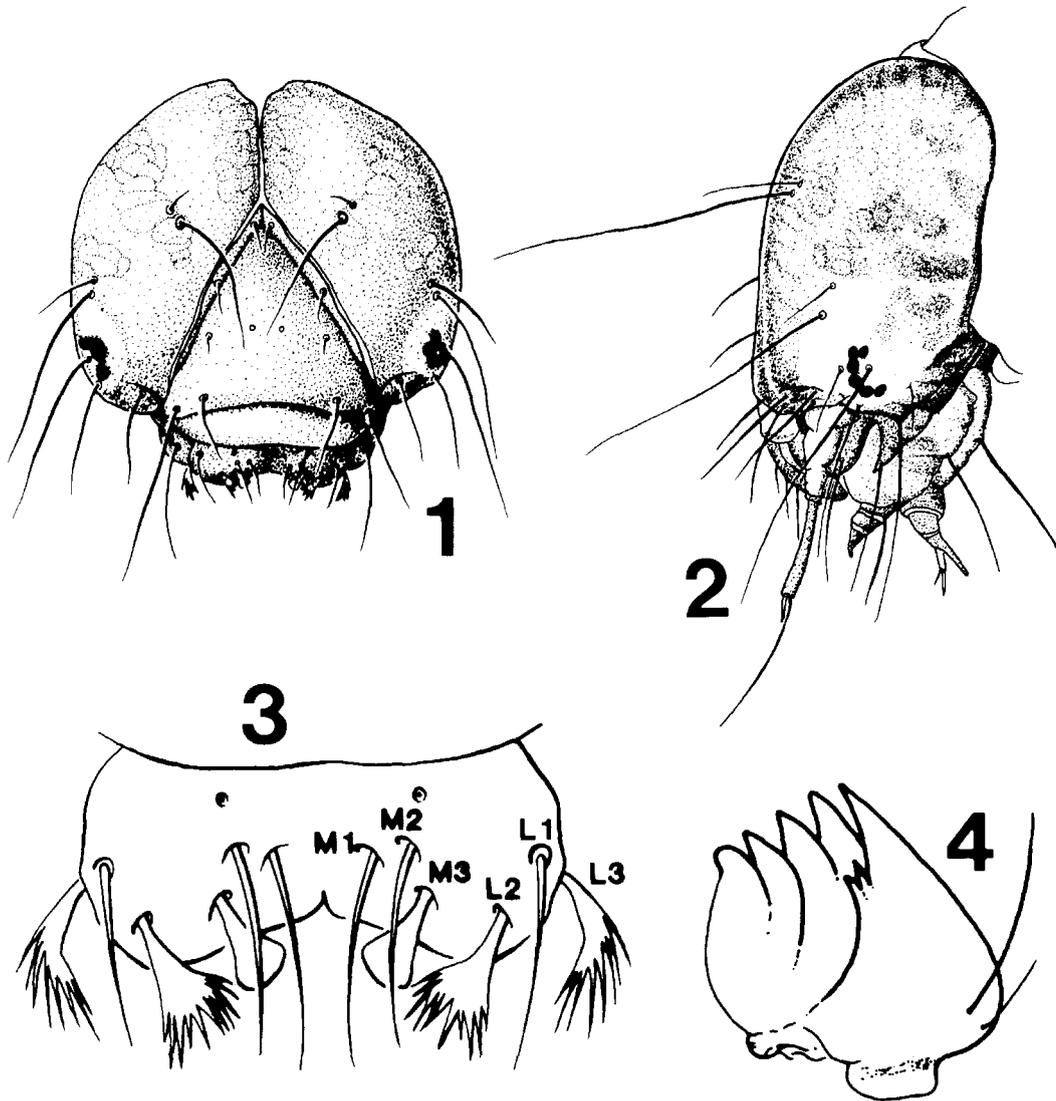
TABLE 1. MEDIAN NUMBER AND RANGE (IN PARENTHESIS) OF GILLS ON ABDOMINAL SEGMENTS 1-8 OF *NEARGYRACTIS SLOSSONALIS* LARVAE (N = 20).

Location	Abdominal Segment							
	1	2	3	4	5	6	7	8
Subdorsal anterior	4 (2-4)	4 (2-4)	4 (3-5)	4 (3-5)	4 (3-5)	4 (3-7)	4 (3-5)	4 (3-5)
Subdorsal posterior	4 (3-8)	4 (3-9)	4 (1-9)	4 (2-7)	4 (2-7)	4 (2-8)	4 (3-7)	3 (1-5)
Lateral anterior	2 (2-4)	2 (2-5)	3 (1-5)	2 (1-4)	2 (1-4)	2 (1-5)	2 (1-5)	3 (2-5)
Lateral posterior	2 (1-6)	2 (1-5)	2 (1-5)	2 (1-6)	2 (1-7)	1 (1-3)	1 (1-3)	1 (0-3)
Subventral anterior	1 (1-4)	2 (1-4)	2 (2-4)	2 (1-3)	2 (1-3)	2 (0-3)	1 (0-3)	1 (0-3)
Subventral posterior	3 (2-4)	3 (2-5)	3 (2-4)	2 (1-6)	3 (2-5)	3 (0-5)	3 (2-4)	2 (2-4)

L1 normal, slightly lower, setae L2, L3 brushlike, seta M3 spatulate. Mandible with two conspicuous inner ridges; teeth arranged in a semicircle (Figure 4). Spinneret slender, pointed apically and longer than labial palpi. Hypostomal lobes pointed mesally, gap between pointed ends less than or equal to that between postmental setae. Anteroventral region of the cranium with sclerotized projection extending forward near the base of the mandible. Cranium forming collarlike base around antenna. Distance between P1 and Adf2 setae two times greater than between P1 and P2. Seta Adf2 at or slightly below the level of the apex of the front; distances between setae Adf2, and P1 less than between Adf1 and P1. F1 at the same level or slightly above the punctures. Seta A2 closer to A1 than to A3; A1, A2, and A3 form an obtuse angle at A2. A3 and P1 setae more than two times longer than L1 and P2, respectively. Seta O2 very long. A3 and L1 setae as near or nearer to each other as P1 is to P2. Stemmata poorly developed, six pigmented areas generally visible, lenses obscure or absent.

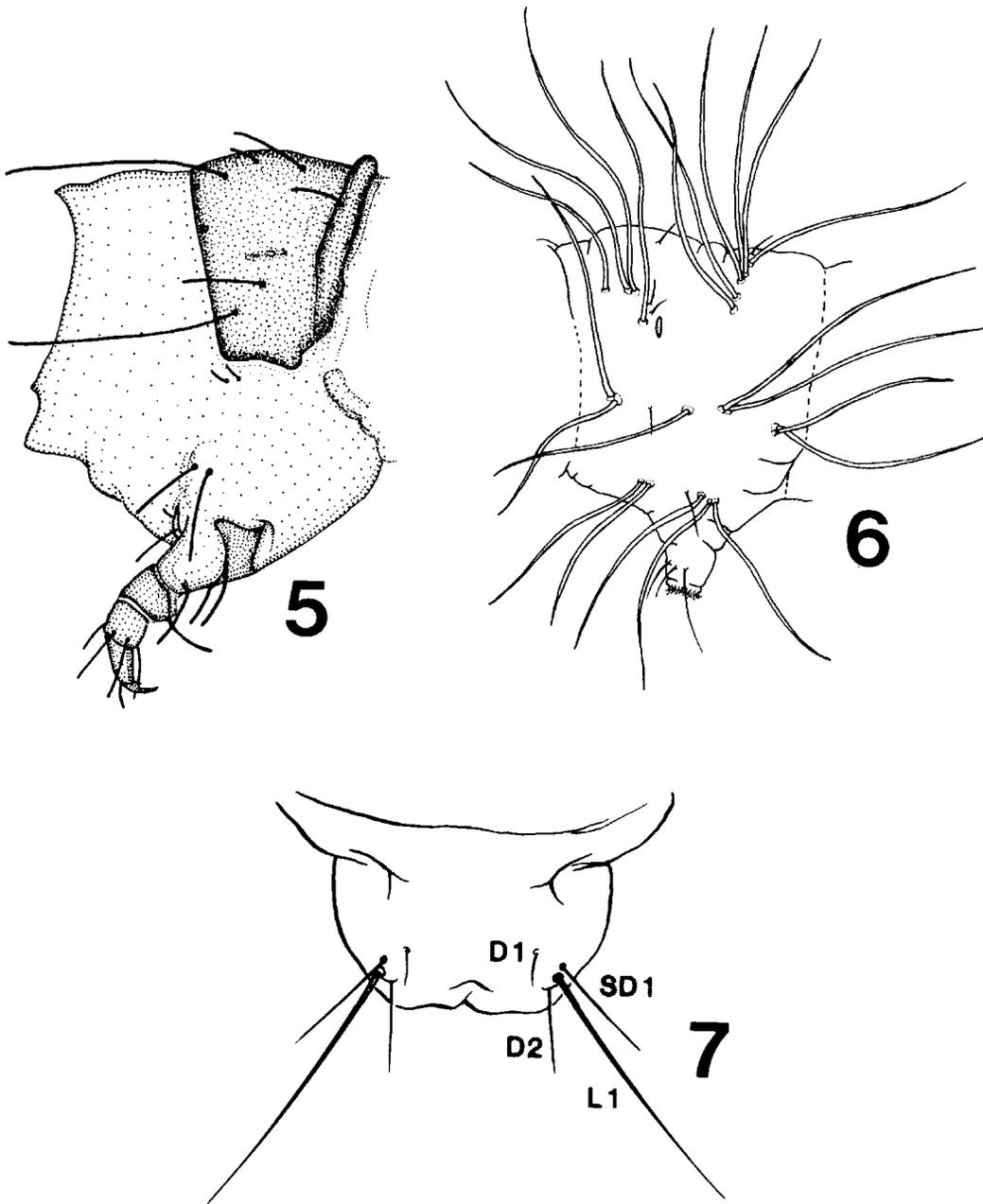
Thorax: Prothoracic shield, covering about one-half of prothorax dorso-laterally, rolled caudally (Figure 5). Seta XD1 anteroventrad of D1; D2 seta posteroventrad of D1 on prothorax. Prothoracic spiracle vestigial. Prothoracic coxae contiguous, gap between meso- and metathoracic coxae; tarsi longer and more slender on meso- and metathoracic legs than on prothoracic legs. Meso- and metathorax each with two pair of gill groups. Subdorsal gills adjacent and posterior to SD setae, subventral gills adjacent and ventral or posterior to SV setae. Usual number and range (in parenthesis) of subdorsal and subventral gills on meso- and metathorax are 3 (2-3), 2 (1-3); and 3 (2-5), 3 (2-4), respectively. D1 and D2 setae on meso- and metathorax fine and near each other. L group setae fine, short, distance from L2 to L3 about 4x L2 to L1. L3 just below subdorsal gills. SV group bisetose on prothorax, unisetose on meso- and metathorax.

Abdomen: Vestigial, slit-like spiracles on segments 1-8. Segments 1-8 each with 6 pairs of gill groups (Figure 6). No sclerotized band around ventral prolegs; 56-62 crochets in a biordinal circle on prolegs on segments 3-6. Anal shield (Figure 7) broad, truncate posteriorly, and unsclerotized; D1 seta on shield shorter than D2, L1 longer than SD1. V1 setae on segment 8 further apart than on segments 7 and 9. SV group unisetose on abdominal segments 1, 7-9. bisetose on 2, and trisetose on 3-6. L group unisetose on segment 9. Gills on segment 9 in 2 groups, subdorsal and subventral, the former with 2 or 3 gills, sometimes 4, the latter usually with 7 but ranging from 5 to 8.



Figs. 1-4. Mature larva of *Neargyractis slossonalis*: 1, head, frontal view; 2, head, side view; 3, labrum; 4, right mandible.

Most of the specimens examined were collected from clusters of living roots in the Santa Fe River in Alachua and Columbia Counties, Florida. Specimens were collected from submersed roots of grape, *Vitis* sp.; ash, *Fraxinus* sp.; cypress *Taxodium* sp.; and other unidentified roots. A single larva was also collected associated with stems of *Eleocharis elongata* Chapman in a small creek running out of Magnolia Lake in Clay County. Larvae of another aquatic pyralid *Eoparargyractis floridalis* Lange were frequently collected in the same habitat as *N. slossonalis*. Larvae are not confined to running water because a few specimens were collected associated with water hyacinth, *Eichhornia crassipes* (Mart.) (Solms-Laubach) roots in Lake Alice and Bivens Arm Lake (Alachua Co.) and in a roadside ditch near Melbourne (Brevard Co.). Larvae are apparently present year round since specimens were collected in January, March, May, June, October, and November. This coincides with Kimball's (1965) recording of adults throughout the year in Florida.



Figs. 5-7. Mature larva of *Neargyractis slossonalis*: 5, prothorax; 6, abdominal segment 4; 7, anal plate.

Dissections of freshly collected larvae indicated that the larvae were feeding on young white roots. Older brown roots were not found in the digestive tract. Injury to roots was never observed in the field although larvae confined in plastic cups in the laboratory fed on and scarified the older brown roots. The larvae of two related species, *Argyractis subornata* (Hampson) in Brazil (Forno 1983) and *Petrophila drumalis* (Dyar) in Florida (A. Dray, T. Center and D. Habeck, unpublished), consume roots of waterhyacinth and waterlettuce *Pistia stratiotes* L., respectively. Unlike *N. slossonalis*, larvae of these two species lack modified labral setae. The modified setae of *N. slossonalis* indicate that the larvae may also feed on periphyton as do *Petrophila*

santafealis (Heppner) and *Eoparargyractis floridalis* both of which have modified labral setae and apparently feed on periphyton.

Pupation takes place in a cocoon spun among the roots. Portions of the plant roots are incorporated into the cocoon. Adult moths were frequently observed on vegetation near the banks of streams and rivers and when disturbed flew a short distance before settling down again.

The number of gills varied from specimen to specimen and frequently from side to side in the same specimen. The anterior subdorsal gill group was considerably more ventral of the posterior subdorsal group and was often subdivided into 2 subgroups with a single gill located more ventrad of the other 2-4 gills. The lateral groups of gills are also less well defined with some gills apart from the group. The specialized, highly modified labral setae indicate the close relationship between *Neargyractis* and *Petrophila*. Superficially, the larvae of *Neargyractis* are very similar to those of *Oxyelophila*, but differ in not having dorsal gills.

ACKNOWLEDGEMENTS

Pat Travis, Jan Ondrovik, Judy Gillmore, John Watts and Debbie Matthews assisted in collecting and rearing. Mr. E. O. Ogunwolu made preliminary descriptions. The illustrations were prepared by Margot Kimball and funded thru the Center for Aquatic Weeds. Drs. Gary Buckingham and Kim Haag reviewed and improved the manuscript. Partial funding for this work was provided through a research grant from the Florida Department of Natural Resources. Florida Agricultural Experiment Station Journal Series No. 7847.

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A FOSSIL HORSEFLY (DIPTERA: TABANIDAE)
IN DOMINICAN AMBER

ROBERT S. LANE AND GEORGE O. POINAR, JR.
Department of Entomological Sciences, University of California
Berkeley, California 94720, USA

G. B. FAIRCHILD
Florida Department of Agriculture and Consumer Services
Gainesville, Florida 32602, USA

ABSTRACT

A fossil horsefly, *Stenotabanus brodzinskyi* n.sp., embedded in a piece of Dominican amber estimated to be 25 to 40 million years old is described and compared to extant members of the genus known from Hispaniola.

RESUMEN

Un tabánido fósil, *Stenotabanus brodzinskyi* n.sp., incrustado en una pieza de ámbar dominicano, cuya edad estimada es 25 a 40 millones de años, es descrito y comparado con congéneres vivientes conocidos en La Española.

Eight species and 1 infraspecific taxon of fossil Tabanidae (Diptera) representing 4 genera (*Chrysops*, *Haematopota*, *Silvius*, *Tabanus*) have been described worldwide (see review by Moucha 1972 and Stuckenberg 1975). These include 3 species (*Silvius*, 1; *Tabanus*, 2) from the New World that were obtained from Miocene deposits of Florissant, Colorado, U.S.A. (Cockerell 1909, 1917, Melander 1946). Here we describe from Dominican amber the first fossil member of the genus *Stenotabanus* and discuss its relationship to extant members of the genus from Hispaniola.

DESCRIPTION

The fly is embedded in a piece of amber approximately 15.1 mm x 9.3 mm x 8.8 mm. It is from an unspecified amber mine in the Cordillera Septentrional mountain range in northern Dominican Republic. Amber from several mines in this region have been estimated to be 25 to 40 million years old (Lambert et al. 1985) corresponding to early Miocene and late Eocene.

Important specific characters of Tabanidae include thoracic and abdominal ground colors and any overlying pubescent coloration. Since preservation of this fly in amber doubtless precluded accurate assessment of these character states, we present here as complete a description as possible with the caveat that the colors reported may not have reflected those of the fly in life. Indeed, most of the body of this specimen was colored various shades of orange-brown to dark brown with a golden tinge or metallic-like luster which seemed to reflect, at least in part, the orange color of the amber itself.

The format for the ensuing description follows that of Fairchild (1980), who described as new 3 species of *Stenotabanus* and 1 species of *Tabanus* from the Dominican Republic and presented a key to all 29 recognized Hispaniolan species. Terminology follows Fairchild (1980) and McAlpine (1981).

Stenotabanus brodzinskyi sp. nov.
(Figs. 1-4)

Diagnosis: A small orange-brown/brown species having hyaline wings, an unstriped mesonotum, and a narrow, convergent frons.

Female: Length of body 9.0 mm, of right wing 7.3 mm. Eyes bare, golden brown without evident banding. Postorbital hairs long, black medianly and shorter, pale submedianly and laterally. Frons narrowed below, ca. 5.4x taller than basal width, with index of divergence (width at vertex/width at base) 2.1, golden pollinose with scattered, long dark hairs throughout (absent on basal callus), these hairs somewhat denser toward vertex. Basal callus golden apically, brown basally, shape as in Fig. 2. Median callus golden, elongate, thin, reaching ca. 0.7 height of frons, connected to basal callus. Ocellar tubercle obscured by debris, dark brown; ocelli inconspicuous, only vestiges of anterior ocellus visible. Vertex (Fig. 2) poorly discernible. Subcallus brown, predominantly bare. Frontoclypeus brown with sparse, long dark hairs; genae slightly darker brown, partially covered with pale pollinosity, short, scattered dark hairs and long pale hairs, the latter readily discernible in photographs (Fig. 4) but not by microscopic examination. Antennae with scape, pedicel, and basal plate of 3rd segment dark orange-brown, the style dark brown; scape, pedicel and dorsal process of basal plate black-haired. Left antenna 1.32 mm long, with 3rd segment ca. 2.3x longer than length of scape and pedicel combined. Palpi orange-brown, slender, elongate, shape as in Fig. 4, with apical segment ca. 6x longer than greatest diameter in lateral view and beset with numerous black hairs on all surfaces; basal palpal segment clothed with numerous long, pale hairs and scattered, long black hairs. Proboscis orange-brown, length subequal to that of palpi but shorter than height of head.

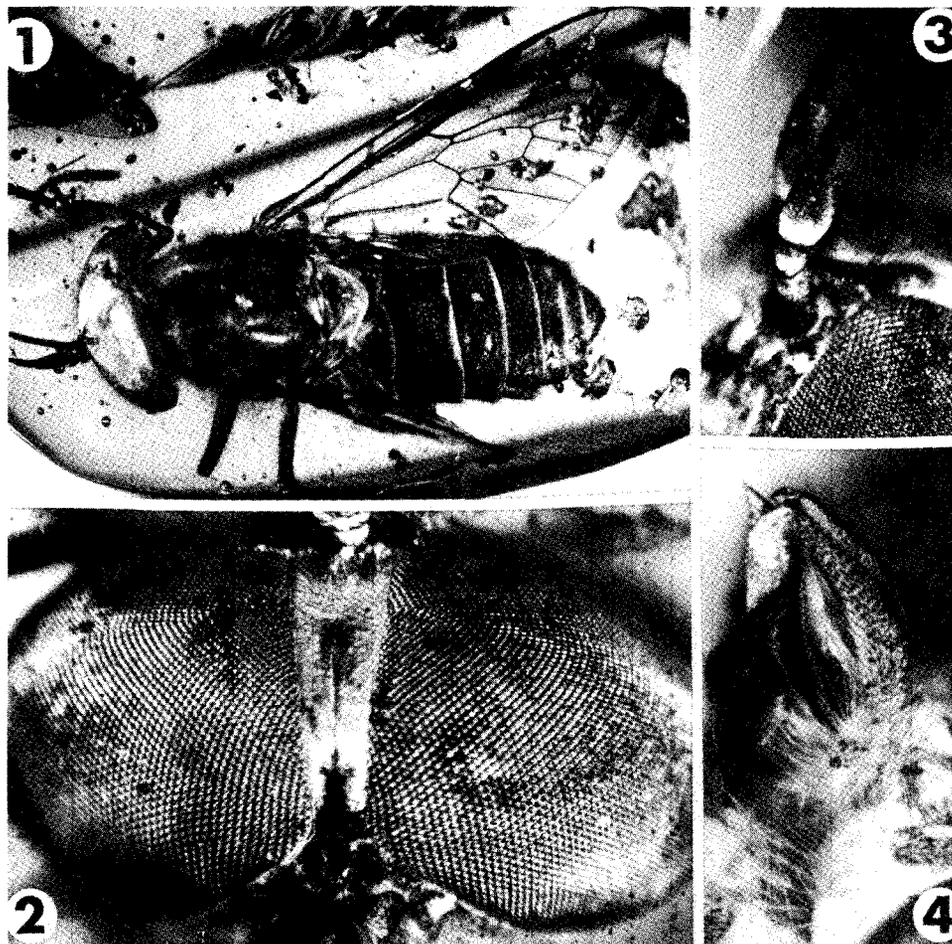
Mesonotum metallic orange-brown to golden without longitudinal stripes, moderately clothed with short, dark recumbent hairs medianly and scattered, longer erect dark hairs anteriorly, anterolaterally and laterally. Scutellum and prescutellum bare except for scattered long dark hairs laterally on former. Notopleuron heavily clothed with long dark hairs. Pleura ground color dark brown, covered in part by golden pollinosity appearing as a metallic sheen; sparsely pale-haired except for katatergite, the latter densely covered with long pale hairs. Knobs of halteres dark brown, the stems light brown. Right wing 7.3 mm long, hyaline except for a faint cloud apically at furcation (junction of R_4 and R_5 veins) that appears to be an artifact of preservation; venation normal, 1st posterior cell open widely, lacking appendix on 3rd vein; stigma dark brown; slightly more than apical 1/2 of left wing missing. Basicosta sharply pointed, bare apically, with sparse setulae basally. Costa, subcosta, and R_1 clothed with dark, robust, short setae. Coxae and femora brown, covered partly with golden pollinosity presenting as a metallic sheen, dark-haired with some pale hairs ventrally. Tibiae and tarsi orange-brown to dark brown, black-haired; fore- and hindtibiae without apical spurs, midtibiae with 2 strong spurs apically; tarsi with paired claws subequal in length.

Abdomen orange-brown to dark brown in ground color with posterior sternites and tergites darkest, predominantly dark-haired, lacking conspicuous pubescent color patterns.

Holotype female. The fly is named after its discoverer, J. Brodzinsky, of Santo Domingo, Dominican Republic. The piece of amber containing the fly described here is currently owned by J. Brodzinsky and is now being held in the amber collection of G. O. Poinar, Jr., at the University of California, Berkeley (accession number D-7-101).

DISCUSSION

The fossil *Stenotabanus* possesses characteristics of the subfamily Tabaninae and the tribe Diachlorini listed by Mackerras (1954). Additionally, it meets the generic



Figs. 1-4. Female *Stenotabanus brodzinskyi* n.sp. in Dominican amber: 1—Dorsolateral view of entire fly; 2—Anterior view of head showing details of eyes, subcallus, frons, and vertex in part; 3—Ventral view of antennae; 4—Ventrolateral view of head displaying palpus and proboscis.

criteria for *Stenotabanus* presented by Fairchild (1980, p. 168), which include the absence of strong setae on the basicosta and the presence of a tubercle at the vertex. Fairchild (1980) recognized 3 groups of Hispaniolan *Stenotabanus*, namely, the subgenus *Aegialomyia* and the *brunettii* and *fenestra* groups consisting of 2, 3, and 3 species, respectively. Of these 8 species, 7 are endemic to the Dominican Republic and 1 is widespread in the Greater Antilles.

The fly described here does not belong to the subgenus *Aegialomyia* because the height of the frons is ca. 5.4 times its basal width (vs. less than 4 times as high as basal width in *Aegialomyia*) and it has a prominent tubercle at the vertex (vs. small tubercle at vertex in *Aegialomyia*). On the other hand, its clear wings and seemingly unstriped mesonotum warrant tentative placement of this fly in the *fenestra* group which contains *S. fenestra* Williston, *S. marcanoi* Fairchild, and *S. hispaniolae* Bequaert. In Fairchild (1980), it keys out to *S. marcanoi* from which it differs by its smaller size (body 9 mm long vs. 11 mm in *marcanoi*); the apparent absence of white hairs on the frontoclypeus, legs and sternites; lack of a short appendix at the fork of the 3rd vein; and having palpi and proboscis subequal in length (vs. proboscis about twice the length of the palpi in *marcanoi*).

The published fossil record for Tabanidae reviewed by Moucha (1972) may be updated as follows: *Chrysops* is represented by 1 species from the Eocene of France; *Silvius* by 1 species from the Miocene of North America; *Tabanus* by 1 species from the upper Oligocene and 1 subspecies from the upper Pliocene of Germany, 2 species from the Miocene of North America, and probably 1 species from the Oligocene of the Isle of Wight; *Haematopota* by 1 species from upper Eocene Baltic amber; and *Stenotabanus* by 1 species from early Miocene-late Eocene Dominican amber (Stuckenberg 1975, present study). In addition the Baltic amber *Silvius laticornis*, though ostensibly a chrysopsine, was misplaced generically by Hennig (1967) and needs to be reevaluated (Stuckenberg 1975). Thus, the discovery of the Dominican amber *Stenotabanus* brings to 9 the number of fossil tabanid species reported in the literature. Moreover, this fly represents the first fossil member of the tribe Diachlorini and of the genus *Stenotabanus* to be described. Unfortunately, a clue to the probable feeding habits of this tabanid cannot be found among the 3 related Dominican species of *Stenotabanus* assigned to the *fenestra* group inasmuch as their biologies are unknown (Fairchild 1980).

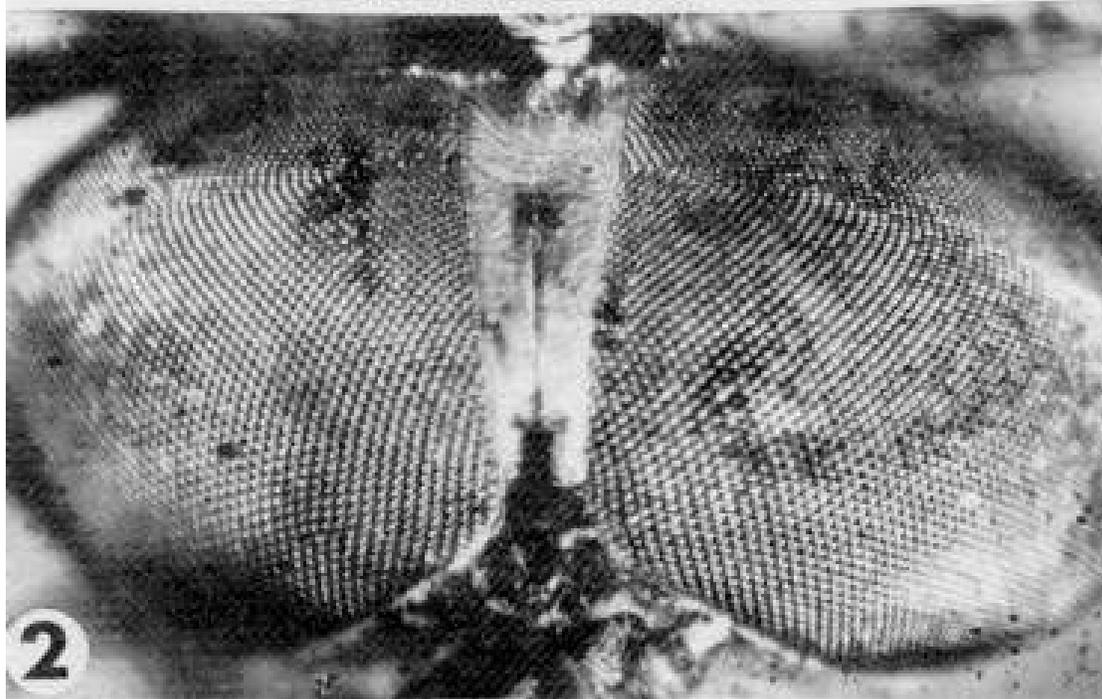
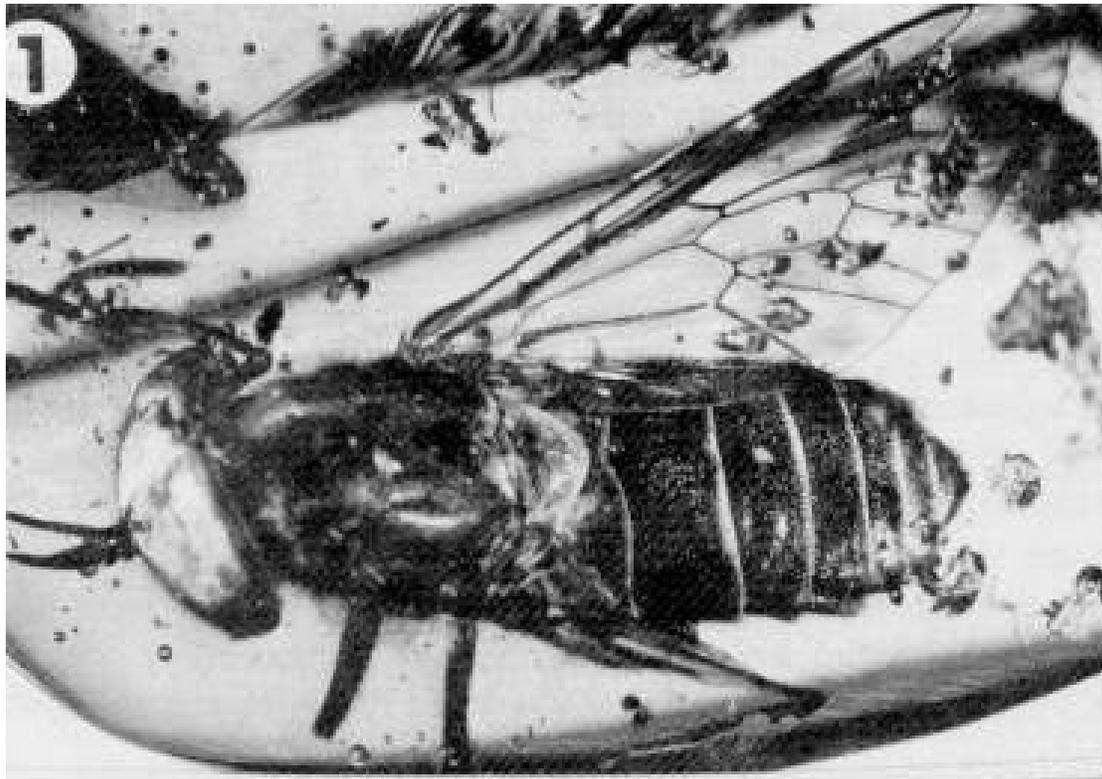
Two of us (G.B.F. and R.S.L.) are preparing for publication the description of another female *Stenotabanus* embedded in a piece of Dominican amber. This specimen, which was obtained from the same montane region as our fly, represents another undescribed species.

ACKNOWLEDGMENTS

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POLLEN-FEEDING IN *POECILOGNATHUS PUNCTIPENNIS*
(DIPTERA: BOMBYLIIDAE)

MARK A. DEYRUP
Archbold Biological Station
P. O. Box 2057
Lake Placid, FL 33852

ABSTRACT

Females of the bombyliid fly *Poecilognathus punctipennis* (Walker) feed avidly on pollen of *Commelina erecta* L. and *Tradescantia roseolens* Small (Commelinaceae). The front tarsi rapidly rake pollen from slits in the sides of the anther and transfer the pollen to the tip of the proboscis. Specialized tarsal hairs may assist in pollen collection. Pollen appears to be mixed with a liquid as it is transported the length of the proboscis. The stomach of pollen-collecting flies is distended with pollen. Pollen was also found in stomachs of females of *Geron* sp. Several types of evidence suggest that *P. punctipennis* females are specialized to exploit pollen of Commelinaceae, especially *T. roseolens*. There is no evidence that the plants have a coevolved symbiosis with the flies.

RESUMEN

Hembras de la mosca bombilid *Poecilognathus punctipennis* (Walker) comen ávidamente el polen de *Commelina erecta* L. y *Tradescantia roseolens* Small (Comelinaceae). El tarso frontal rápidamente rastrilla el polen en las rajadas a los lados del ánter y transfiere el polen a la punta de la probocis. Pelos tarsales especializados pudieran asistir en colectar el polen. El polen parece estar mezclado con un líquido cuando es transferido a lo largo del probocis. El estómago de las moscas colectoras de polen es distendido por el polen. También se encontró polen en los estómagos de hembras de la especie *Geron*. Varios tipos de evidencia sugieren que hembras de *P. punctipennis* están especializadas para explotar el polen de Commelinaceae, especialmente el de *T. roseolens*. No hay evidencia que las plantas tengan una simbiosis coevolucionaria con las moscas.

In the Sixth Century B.C., Aesop explored the problem of incompatible mouthparts: when the fox invited the stork to dinner, the soup was served in saucers; when the stork returned the invitation, the soup was served in narrow-mouthed urns. Nectivorous insects with elongate haustellate mouthparts adapted for probing deep within tubular flowers often face the stork's dilemma. These insects are usually in contact with a rich source of amino acids in the form of pollen, but it is mechanically difficult to ingest this food source. Several species have overcome this problem. *Heliconius* butterflies secrete a digestive fluid onto masses of pollen before imbibing (Gilbert 1972), and some swallowtails perhaps use a similar pollen-lubricating system (DeVries 1979). Certain syrphid flies have long been known to feed on pollen; species with a long proboscis accumulate pollen on the front tarsi, removing it with the labellum (Holloway 1976).

Many species of flower-frequenting bombyliid flies have a long proboscis for extracting nectar. It has often been assumed that nectar is the chief nutrient of these flies; various authors provide general discussions of bombyliid biology, mentioning only nectar as the food of the adult flies (Cole 1969, Curran 1934, Hall 1981). Oldroyd, in his excellent compendium of dipteran habits (1964), states that bombyliids differ trophically from other Asilomorpha in that protein-feeding has shifted to the larval stage. For some time, however, evidence has been accumulating that pollen is a major component of the

diet of adult bombyliids, especially the females. Graenicher (1910) noted that *Bombylius* sp. visits flowers that produce only pollen. Painter and Painter (1965) state that adult bombyliids feed on both nectar and pollen. Recent studies (Toft 1984a, 1984b, Grimaldi 1988) show that pollen-feeding is an important activity in certain bombyliids. According to bombyliid specialists pollen-feeding is virtually universal in female bombyliids, with the exception of species that lack functional mouthparts (personal correspondence: Neal Evenhuis, Jack Hall, John Neff).

Poecilognathus punctipennis (Walker) is a small bombyliid (length of wing 4-7 mm) in the subfamily Phthiriinae. It has been reported as widely distributed (Painter & Painter 1965), but now appears to be restricted to Florida and Georgia (Neal Evenhuis, personal communication). Some species of *Poecilognathus* have been recorded as predaceous on grasshopper egg pods (Hull 1973); the larval habits of *P. punctipennis* are unknown. In spring of 1988, Alan Herndon, a botanist visiting the Archbold Biological Station in south-central Florida, noticed a bombyliid manipulating the anthers of *Tradescantia roseolens* Small. Subsequent observations showed that these flies have a specialized pollen-gathering behavior. This behavior and associated morphological features are described below.

METHODS

All observations were made at the Archbold Biological Station (ABS), 10 km south of Lake Placid, Highlands Co., Florida. The ABS is on the the Lake Wales Ridge, whose well-drained sandy soils are suitable for a large variety of Bombyliidae. The observation sites were the edges of firelanes in scrubby flatwoods, where the host plants are common and easily observed. Field observations were made with a 10x hand lens, and photographed with a Nikon model F camera equipped with macro lens and extension ring. A few flies were willing to feed in the laboratory in plastic Petri dishes and could be observed with a dissecting microscope. The discussion of behavior in the field is based on observations of 542 flies, some of which might have been the same individuals seen on consecutive days. Pollen-feeding was studied 19 May-2 June 1988. Seasonal flight activity was monitored with 2 small Malaise traps operated continuously for 3 years in the same 2 sites along trails in mature sand pine scrub habitat. All insects and plants were identified by the author. Voucher specimens are in the collection of the ABS and in the Florida Collection of Arthropods (Gainesville, FL).

OBSERVATIONS AND DISCUSSION

The feeding behavior of *P. punctipennis* is easily observed, as the flies have a predictable schedule and are intent on their feeding. They assemble on newly opened flowers of *Tradescantia roseolens* (Fig. 1), *Cuthbertia rosea* Ventnat, and *Commelina erecta* Linnaeus (Fig. 2) around 7:00 AM, and begin avidly feeding on pollen. *T. roseolens* is the favored host; *C. erecta* has fewer fertile anthers, and *C. rosea* is relatively uncommon. Pollen is the only nutrient available to the flies, as these flowers, like all Commelinaceae, produce no nectar (Robert Faden, personal communication). The flies may be attracted by odor as well as by visual stimuli, as *T. roseolens* has scent-producing hairs on the stamens (Fig. 3). No odor was detected from the other host species. Artificial flowers of purple paper attracted flies, but these flies remained on the flowers for only a second or two. Once they begin to feed, the flies are not easily disturbed and can be observed with a hand lens. Photographic flashes did not appear to disrupt feeding. By 9:00 AM the anthers are senescing, and the flies disappear.

Several flies may feed simultaneously on a flower (Fig. 1), especially on *T. roseolens*, which has 6 pollen-bearing anthers. *C. erecta* has a single large, yellow, fertile anther

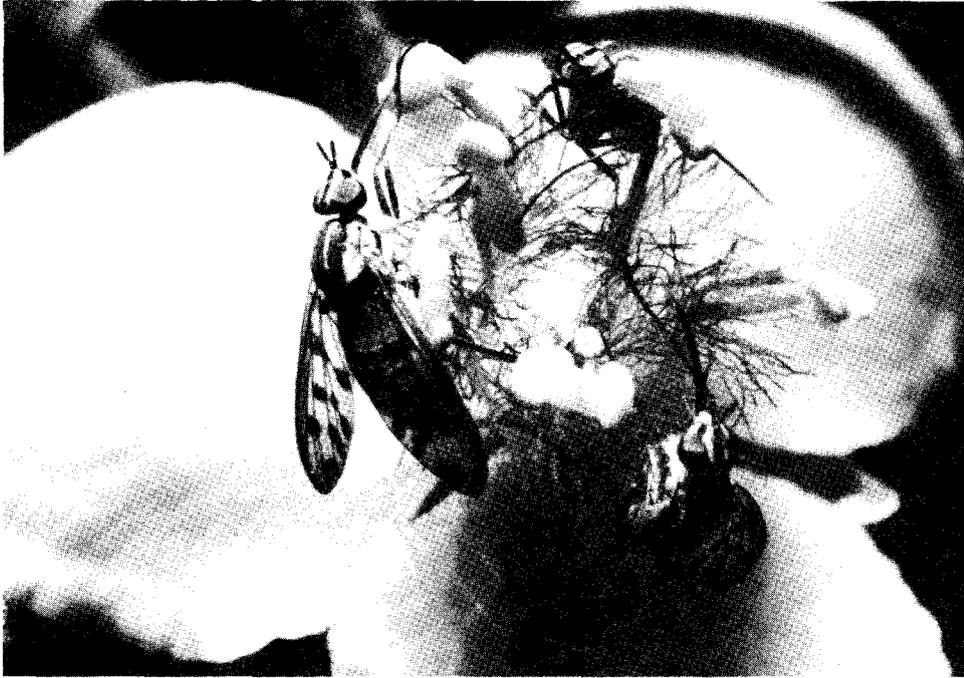


Fig. 1. *Poecilognathus punctipennis* feeding on anthers of *Tradescantia roseolens*.



Fig. 2. *P. punctipennis* feeding on fertile anthers of *Commelina erecta*.



Fig. 3. *P. punctipennis* removing pollen from anther of *T. roseolens*.

(similar to the anthers of *T. roseolens*), 3 sterile yellow anthers, and 2 inconspicuous fertile anthers (Fig. 2). No more than 3 flies can feed simultaneously on *C. erecta*, and usually there are only 1 or 2. The flies show no overt territorial behavior, such as that described by Evenhuis (1983). If a fly finds no unoccupied anther, it usually leaves. Since the extraction of pollen involves very rapid movements of the tarsi along the sides of the anther, it is impossible for 2 flies to work effectively on the same anther.

Pollen is collected by raking the front tarsi across the pollen-bearing surfaces of the anther. In *T. roseolens* pollen issues from the sides of the anther. The anther is on a highly flexible peduncle, and the fly rapidly bats the anther back and forth while scraping off the pollen. The fertile yellow anther of *C. erecta* is very similar to the anthers of *T. roseolens* and is treated similarly by the flies (Fig. 6). The 2 additional fertile anthers have pollen on the dorsal surface; the flies remove this pollen easily (Fig. 2). Pollen collection may be assisted by modified hairs on the bottom and sides of the last 4 tarsal segments. There are 2 subterminal ventral and 2 subterminal lateral hairs on segments 2 to 5, 3 to 5 lateroventral hairs along the inner sides of segments 3 to 5, and 1 or 2 lateroventral hairs along the outer sides of segments 3 to 5. In the laboratory the tips of these hairs adhere weakly to a fine human hair touched against them. The unmodified hairs of the tarsi have no adhesive properties. Such hairs are found in many other genera of Bombyliidae, and probably also serve in pollen collecting (John Neff, personal communication).

Pollen is transferred to the proboscis in a flicking motion that is almost too rapid to see (Figs. 3-5). The leg is raised and the tarsi quickly wiped across the tip of the proboscis, which is simultaneously lowered and retracted, with a retraction of the entire oral cone (See Lundbeck 1908 for a description of the mouthparts of *Poecilognathus*). The labellae spread and the labrum and/or hypopharynx protrude as the pollen is taken in. The wiping of the tarsi across the proboscis occurs at irregular intervals from less than a second to about 1.5 seconds apart. Both tarsi are used in transfer of pollen, but do not necessarily operate alternately. If only one tarsus is raking across an open pollen

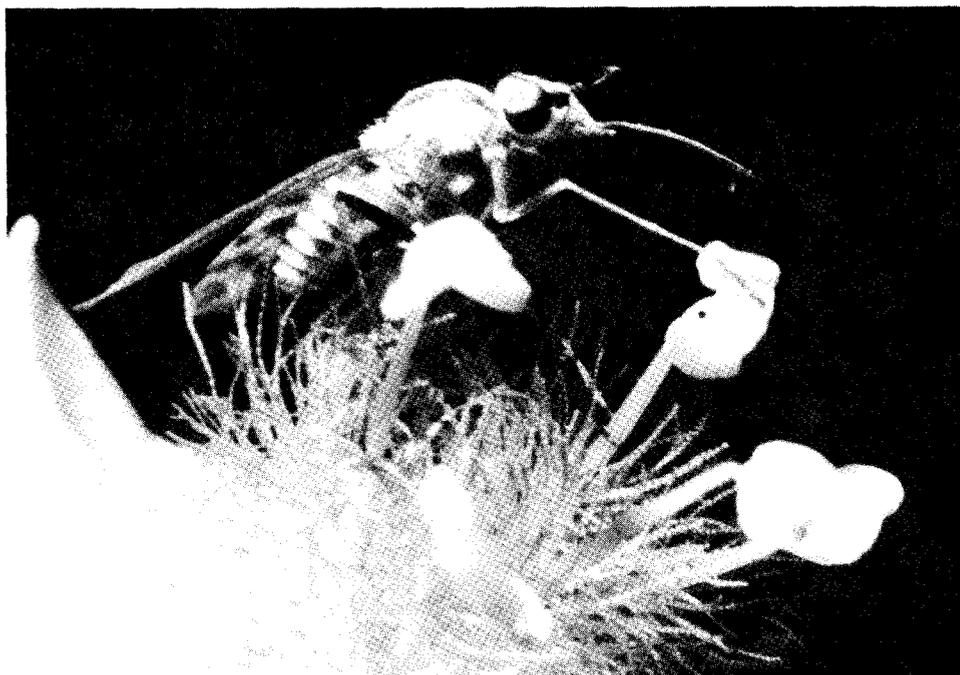


Fig. 4. Raising leg toward proboscis; proboscis beginning to deflect.

slit, only that tarsus flicks across the proboscis. If both are in contact with a pollen supply, they touch the proboscis more or less alternately. As a fly approaches a stamen, it makes rapid raking movements across the petals, glandular hairs, and other parts of the flower. During these exploratory movements the tarsi seldom touch the proboscis. This combination of behaviors suggests that the flies sense whether there is pollen adhering to a particular tarsus. Such a sensitivity should greatly increase the efficiency of pollen collecting.

The passage of pollen along the proboscis could not be observed directly, and the mechanism of propulsion remains unclear. The labrum can be seen moving rapidly back and forth along the trough of the labium while the fly is feeding. The hypopharynx and maxillae are about as long as the labrum and could also assist in pollen transport. A simple way to move pollen would be along a ratchet of backward-pointing ridges or hairs, but no such ratchet could be seen on any mouthparts. Pollen also could be transported in a slurry with liquid, and observations seem to support this. Under the microscope a droplet of liquid with pollen grains sometimes can be seen at the tip of the labella while the fly is feeding. On one occasion a feeding fly appeared to develop a blockage in the proboscis, and the labrum was raised partly out of the groove formed by the labium. There appeared to be a film of liquid, held by surface tension or viscosity, between the labrum and the labium. The stomachs of freshly killed flies contain relatively large amounts of pollen with relatively small amounts of liquid, and it may be that much of the liquid is strained out before it reaches the esophagus.

P. punctipennis is not the only pollen-feeding species of small bombyliid at the ABS. A series of 7 females and 8 males of *Geron* sp. nr. *vitripennis* Loew (Gerontinae) were captured in an open scrub area. All of the females and none of the males had pollen in their stomachs. Some specimens were taken on flowers of *Stipulicida setacea* Michaux, and the pollen in all the females was similar to the pollen of this plant. The anthers of this tiny (2 mm) flower are inside the corolla, and the flies are scarcer and more wary than *P. punctipennis*, making it difficult to observe pollen-feeding in this species of *Geron*.



Fig. 5. Leg wiping front tarsus on tip of proboscis; proboscis deflected, oral cone retracted.

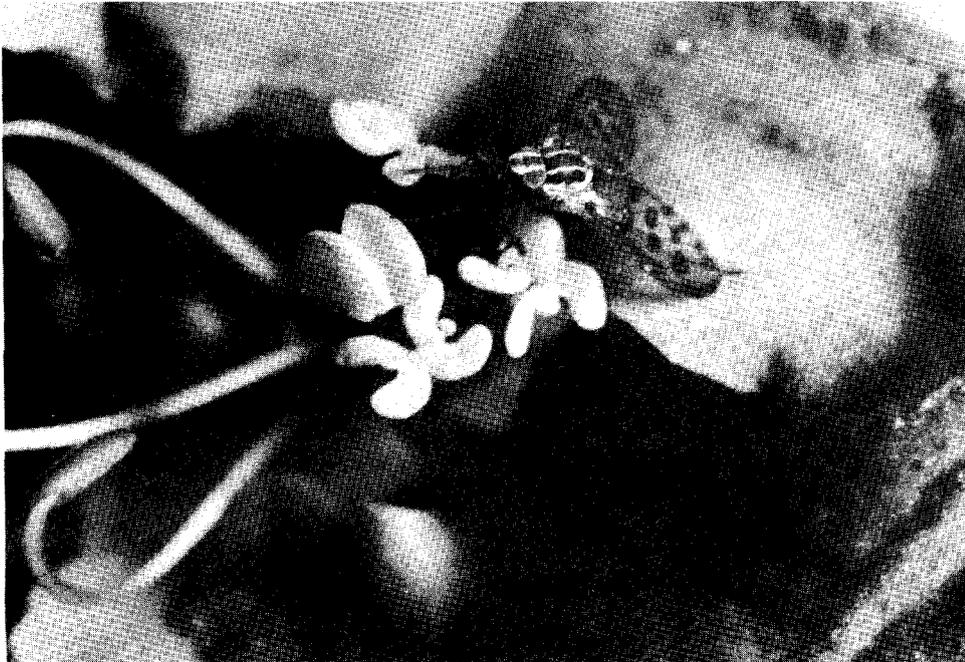


Fig. 6. *P. punctipennis* on central fertile anther of *C. erecta*.

Although nothing is known about pollen-gathering mechanisms in other species of *Poecilognathus* or in the Phthiriinae, it is possible to speculate in a general way about the evolution of pollen-feeding in *P. punctipennis*. Holloway (1976) has suggested that the transfer of pollen from the front tarsi to the mouthparts of the syrphid *Eristalis tenax* Linnaeus might have evolved from cleaning behavior, and a parallel evolution seems likely in *P. punctipennis* or its ancestral lineage. If pollen-feeding is widespread among species of Phthiriinae, as seems likely, it does not follow that the pollen-gathering mechanisms are uniform. The anthers of *T. roseolens* and the central fertile anther of *C. erecta*, with their pollen issuing from lateral grooves, could not be easily depollinated directly with the proboscis. The extreme wobbliness of the anther on its flexible peduncle would make direct removal of pollen even more difficult. The position of the anther on a highly flexible peduncle may be general adaptation that not only facilitates shedding of pollen, but also makes pollen more easily removed by insect legs (such as those of bees) than by mouthparts. Some anther configurations may allow or require direct feeding even by a species with a long proboscis. The *Geron* species mentioned above is not likely to use its feet to extract pollen from the corolla of *Stipulicida*, and *Bombylius* spp. appear to take pollen directly from flowers of *Hedyotis* (Grimaldi 1988).

Beyond the possibly specialized mechanism of pollen removal, there is some evidence that *P. punctipennis* has a specialized relationship with members of the Commelinaceae. *P. punctipennis* has never been seen to feed on a variety of plants that bloom in close proximity to its commelinaceous hosts. These flowers include *Befaria racemosa* Ventnat (Ericaceae), *Bidens pilosa* L., *Wedelia trilobata* (L.) (Asteraceae), *Bonamia villosa* (Nash) (Convolvulaceae), *Callicarpa americana* L., *Lantana camara* L. (Verbenaceae), *Cleome aldenella* Ernst (Capparaceae), *Licania michauxii* Prance (Rosaceae), *Serenoa repens* (Bartram) (Palmaceae), and *Ximenia americana* L. (Oleaceae).

Seasonal flight activity of *P. punctipennis* may be correlated with the principle blooming period of its floral hosts, especially *T. roseolens*. When the blooming period of *T. roseolens* ended in June of 1988, *P. punctipennis* disappeared, even though *C. erecta* flowers were still almost as abundant as earlier. Results of a 3-year survey of *P. punctipennis* taken in continuously operating Malaise traps showed a high correlation of bee fly activity with floral phenology. The total catches of *P. punctipennis* for the 3 years are: April:39, May:73, June:20, November:2, December:1. Like *P. punctipennis*, *T. roseolens* has previously been considered a widely distributed species, but recent evidence shows it to be restricted to Florida and Georgia (Robert Faden, personal communication).

During this study *P. punctipennis* was by far the most abundant insect on *T. roseolens* and *C. erecta*. Observations in the laboratory and field showed that *P. punctipennis* usually has small amounts of pollen adhering to its body (Fig. 2), and may transfer this pollen to the stigma. An individual fly, when given the opportunity, will go from one anther to another on the same flower until all the pollen is consumed, but in normal field conditions the flies are frequently forced to move from flower to flower because of crowding or because of disturbance by other insects. *P. punctipennis*, therefore, may cross-pollinate its floral hosts. However, the general impression is that relatively small numbers of bees and hairy syrphids, moving rapidly from flower to flower, are likely to be more important in cross-pollination than is *P. punctipennis*. Potential pollinators seen during this study are: on *T. roseolens*: *Bombus impatiens* Cresson (Apidae), *Dialictus placidensis* Mitchell, *D. suriana* Mitchell, *Augochloropsis sumptuosus* (Smith), *Augochlorella striata* (Provancher) (Halictidae), *Volucella nigra* Greene, *V. pusilla* Macquart (Syrphidae); on *C. erecta*: *D. placidensis*, *Volucella barei* Curran; on *C. rosea*: *A. striata*. There is no reason to suspect any coevolved symbiotic relationship between *P. punctipennis* and its floral hosts. If there has been coevolution, it may have been in the direction of making pollen more difficult to collect. In the case of *C. erecta*, it may be that the central *Tradescantia*-like fertile anther tends to distract the flies away from the inconspicuous pair of fertile anthers with their exposed pollen.

Predation may be a significant factor for both flies and flowers. There were 6 instances of flies captured by immature *Misumenops* sp. (Thonsidae) and a case of predation by *Vespula squamosa* (Drury). Flies on *C. erecta*, especially those on tall, exposed plants, were unusually wary and easily disturbed. Anthers were frequently eaten by the tettioniid *Odontoxiphidium apterum* Morse, the petals of *T. roseolens* were eaten by *Oulema laticollis* White, and the petals of *C. erecta* were eaten by *Lema cornuta* (Fabricius) (Chrysomelidae).

SUMMARY AND CONCLUSIONS

Pollen collecting appears to be an important activity of female *P. punctipennis*, presumably providing nutrients needed for egg production. There is evidence that this bombyliid is specialized in its use of Commelinaceae as floral hosts. Other small bombyliids could also be floral specialists, and there might be a whole array of interesting behavioral and ecological characters that could be used to clarify the taxonomy and evolution of this difficult group.

A more immediate question concerns the males of *P. punctipennis*: 542 females and no males were seen on the flowers. It is difficult to think of other cases among the insects in which females aggregate dependably and in large numbers on flowers, and no males exploit this aggregation for mating purposes. Any patch of flowers is likely to have a whole set of male flies, wasps, bees, and beetles cruising about waiting for females, even when there is no specific floral relationship, and the chances of finding a female are much less than in the situation of *P. punctipennis*. Males are still flying while females are feeding, as records of males (from Malaise traps) extend through early June. The simplest explanations would involve highly efficient mate-finding mechanisms prior to pollen-feeding, or a mechanism to prevent insemination once pollen-feeding begins. In either case, interesting behavioral problems remain for future studies of *P. punctipennis* and its congeners.

ACKNOWLEDGEMENTS

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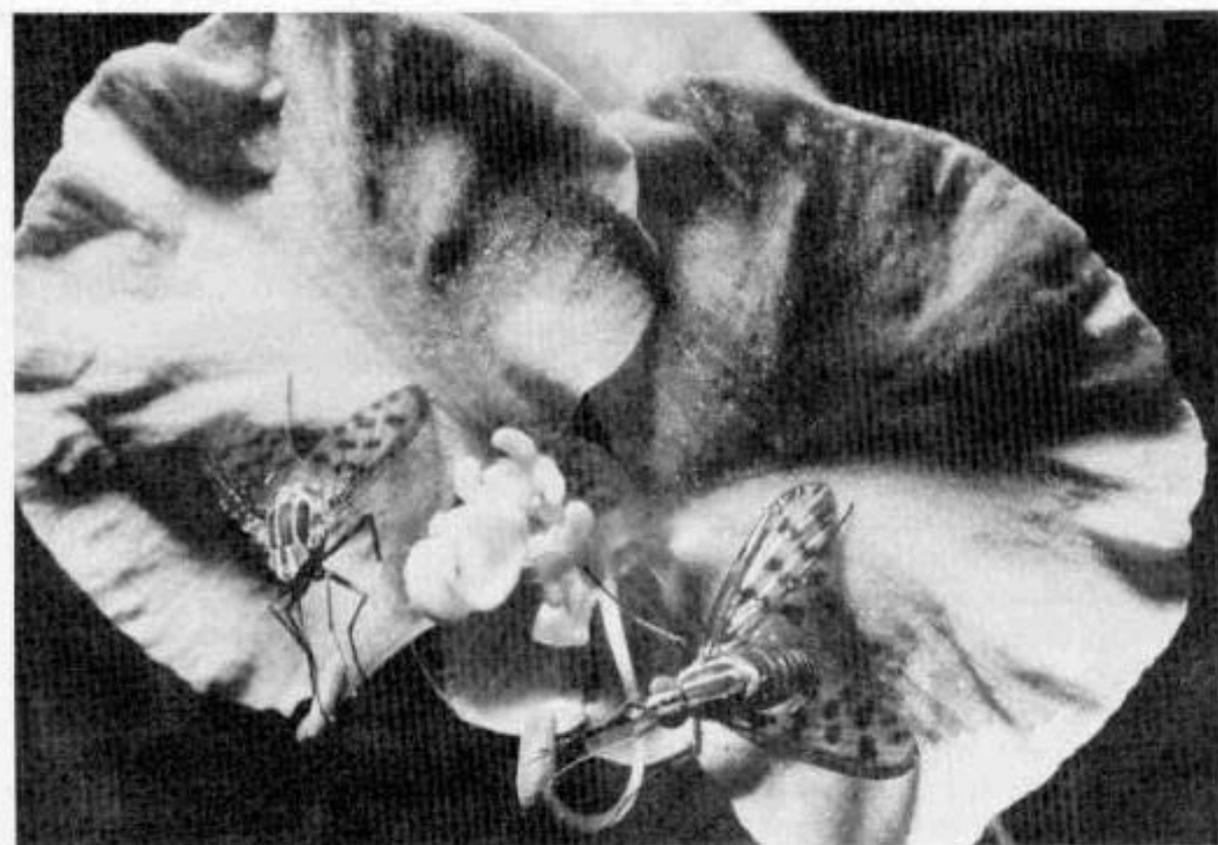
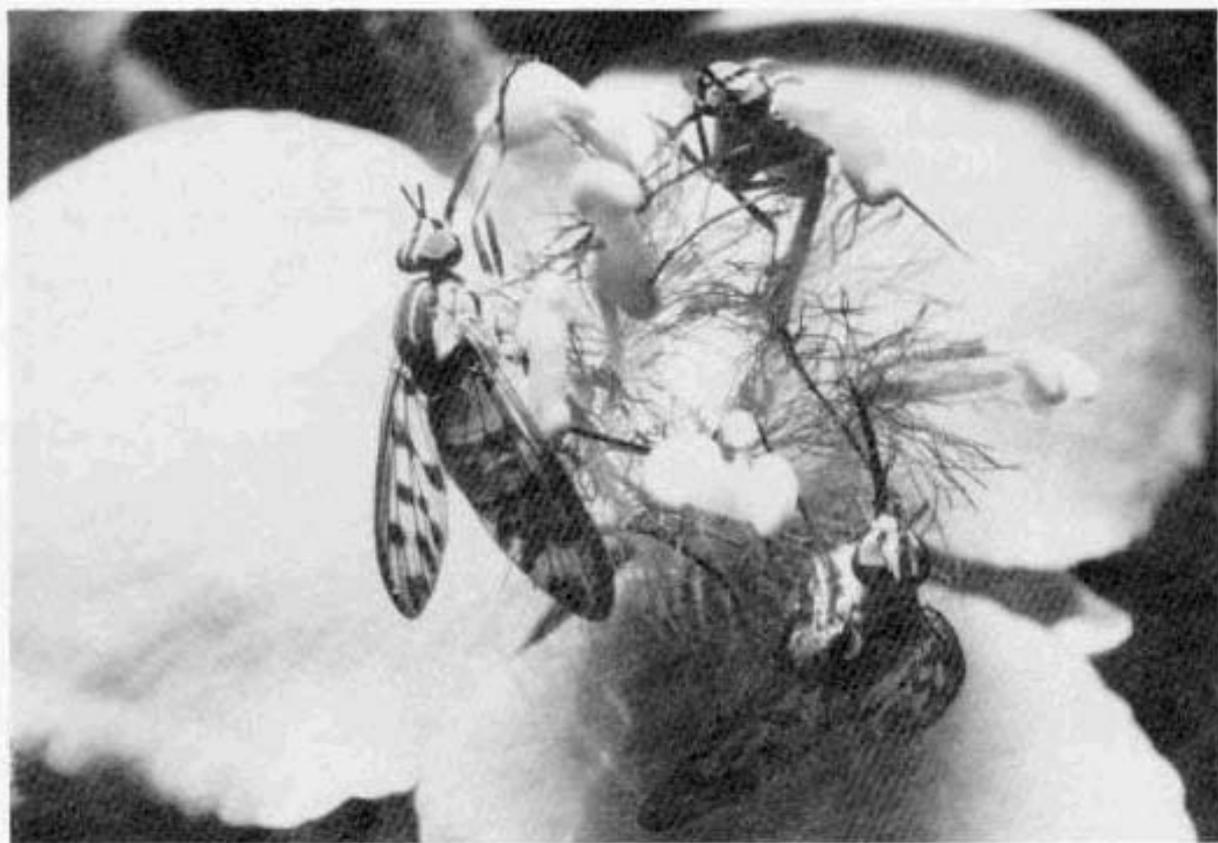
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POTENTIAL OF TEFLUBENZURON FOR DIAMONDBACK MOTH (LEPIDOPTERA: PLUTELLIDAE) MANAGEMENT ON CABBAGE IN SOUTHERN FLORIDA

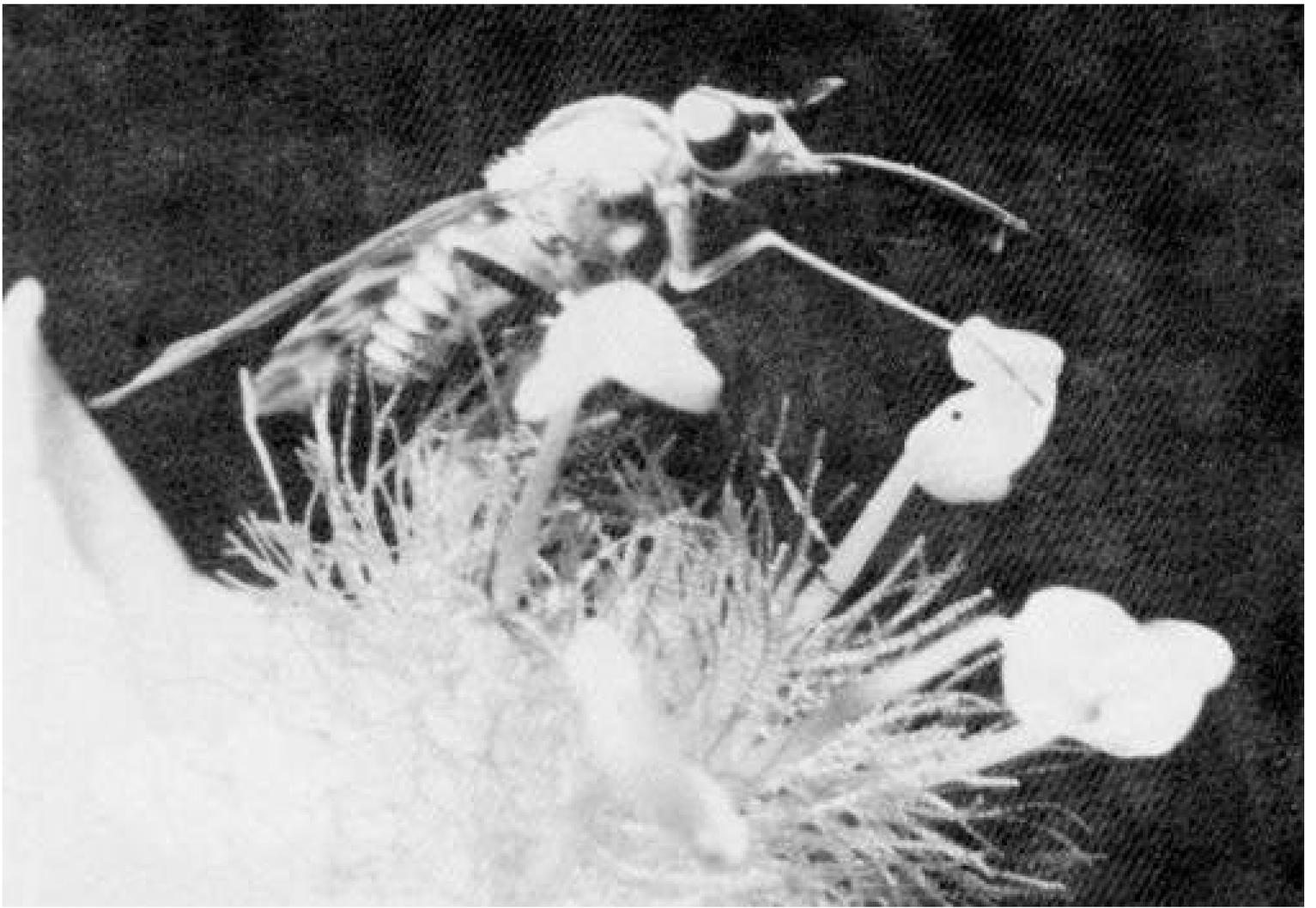
RICHARD K. JANSSON AND SCOTT H. LECRONE
University of Florida,
Institute of Food and Agricultural Sciences,
Tropical Research and Education Center,
18905 S. W. 280 Street
Homestead, Florida 33031

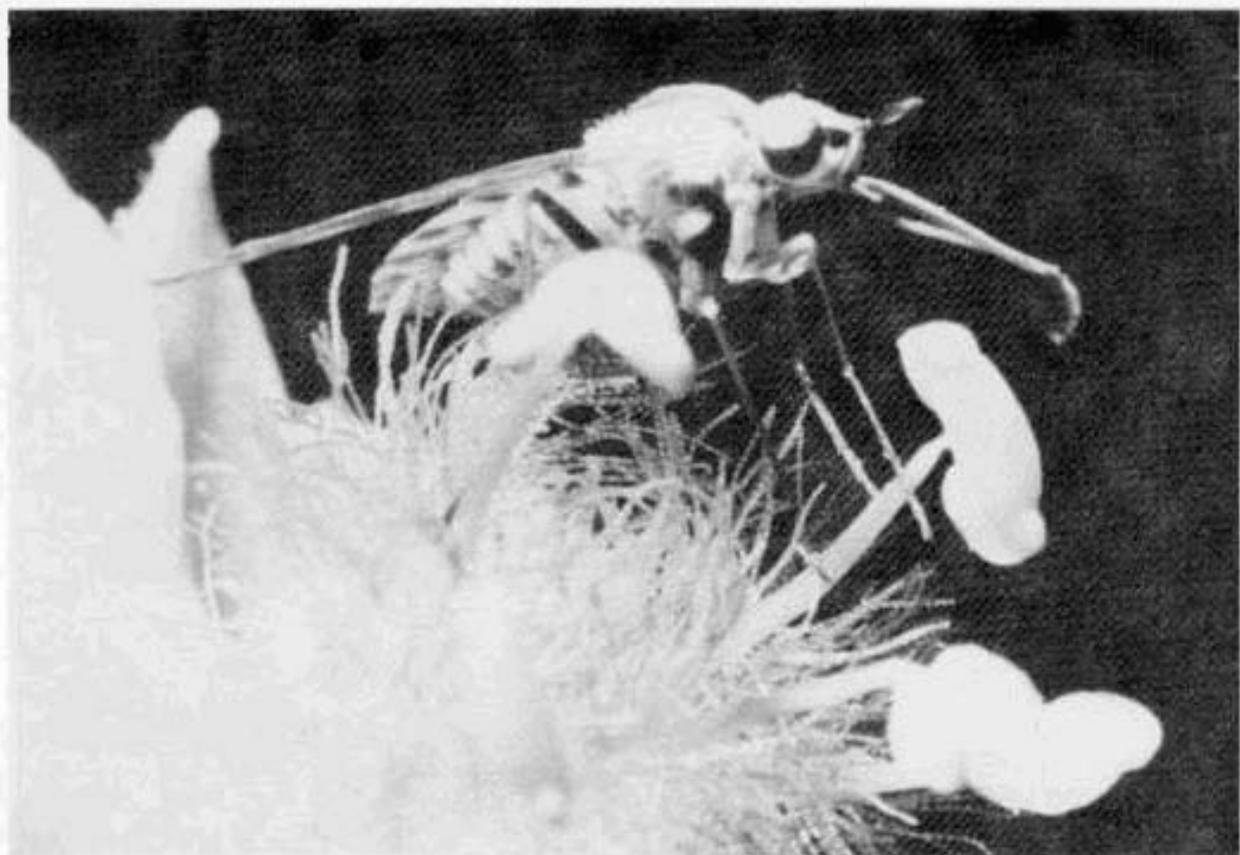
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The potential of the chitin synthesis inhibitor, teflubenzuron (CME 13406), for managing populations of diamondback moth (DBM), *Plutella xylostella* L., on cabbage was assessed during two consecutive growing seasons in southern Florida. In the first year, the effectiveness of two rates of teflubenzuron at managing DBM populations was compared with those of three commonly used insecticides, fenvalerate, methamidophos, and methomyl in combination with *Bacillus thuringiensis* var. *kurstaki*, applied at recommended rates. In the second year, the effects of different treatment intervals (7, 14 or 21 days) of teflubenzuron on DBM management were assessed. Teflubenzuron was more effective than other insecticides at suppressing DBM populations and protecting plants. The percentages of marketable cabbage heads were 98, 98, 83, 80, and 50% on plants treated with teflubenzuron at 0.022 and 0.044 kg ai/ha, methomyl in combination with *B. thuringiensis*, fenvalerate, and methamidophos, respectively, and was 17% in









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RICHARD K. JANSSON AND SCOTT H. LECRONE
University of Florida,
Institute of Food and Agricultural Sciences,
Tropical Research and Education Center,
18905 S. W. 280 Street
Homestead, Florida 33031

ABSTRACT

The potential of the chitin synthesis inhibitor, teflubenzuron (CME 13406), for managing populations of diamondback moth (DBM), *Plutella xylostella* L., on cabbage was assessed during two consecutive growing seasons in southern Florida. In the first year, the effectiveness of two rates of teflubenzuron at managing DBM populations was compared with those of three commonly used insecticides, fenvalerate, methamidophos, and methomyl in combination with *Bacillus thuringiensis* var. *kurstaki*, applied at recommended rates. In the second year, the effects of different treatment intervals (7, 14 or 21 days) of teflubenzuron on DBM management were assessed. Teflubenzuron was more effective than other insecticides at suppressing DBM populations and protecting plants. The percentages of marketable cabbage heads were 98, 98, 83, 80, and 50% on plants treated with teflubenzuron at 0.022 and 0.044 kg ai/ha, methomyl in combination with *B. thuringiensis*, fenvalerate, and methamidophos, respectively, and was 17% in

nontreated plots. In the second year, teflubenzuron (0.033 kg ai/ha) was consistently more effective than other insecticides at suppressing DBM populations. DBM populations and the percentages of marketable heads did not differ among plants treated with teflubenzuron at 7-, 14-, and 21-day intervals, suggesting that the negative effects of teflubenzuron on DBM were persistent. The potential importance of teflubenzuron in DBM management programs in Florida is discussed.

RESUMEN

El potencial del inhibidor de la síntesis de quitina, teflubenzuron (CME 13406), para administrar poblaciones de alevillas de *Plutella xylostella* L., fue evaluado durante dos temporadas del cultivo de repollo en el sur de la Florida. En el primer año se comparó la efectividad de dos proporciones de teflubenzuron en administrar poblaciones de *P. xylostella* con tres insecticidas comunmente usados, fenvalerate, metamidofos, y metomil en combinación con *Bacillus thuringiensis* var. *kurstaki*, aplicados a la proporción recomendada. Se evaluaron en el segundo año los efectos de diferentes intervalos de tratamiento (7, 14, o 21 días) de teflubenzuron en la administración de *P. xylostella*. Teflubenzuron fue más efectivo que otros insecticidas en suprimir poblaciones de *P. xylostella* y en proteger las plantas. El porcentaje de cabezas de repollos vendibles fue 98, 98, 83, 80, y 50% en plantas tratadas con teflubenzuron a 0.022 y 0.44 kg (ai)/ha, metomil en combinación con *B. thuringiensis*, fenvalerate, y metamidofos, respectivamente, y fue 17% en las parcelas no tratadas. En el segundo año, teflubenzuron (0.033 kg ai/ha) fue consistentemente más efectivo que otros insecticidas en suprimir poblaciones de *P. xylostella*. No hubo diferencia en poblaciones de *P. xylostella* y el porcentaje de cabezas vendibles entre plantas tratadas con teflubenzuron a intervalos de 7, 14, o 21 días, sugiriendo que los efectos negativos de teflubenzuron en *P. xylostella* fueron persistentes. Se discute el potencial de la importancia de teflubenzuron en programas de administración de *P. xylostella*.

The diamondback moth (DBM), *Plutella xylostella* L., is the most important insect pest of cole crops during the winter growing season in southern Florida (Jansson, personal observation). Current management programs rely on chemical and biological insecticides. Recently, several insecticides, including methamidophos and fenvalerate, were ineffective at managing DBM populations in certain commercial cabbage, *Brassicae oleracea* L., fields in southern Florida. Insecticide-resistant DBM populations are known to occur in many areas of the world (Sudderuddin & Kok 1978, Liu et al. 1981, Cheng 1986, Miyata et al. 1986, Sun et al. 1986, Tabashnik et al. 1987), including central Florida (G. L. Leibe, personal communication). For this reason, alternative tactics are needed to improve current DBM management programs in Florida.

One approach that has potential is the use of chitin synthesis inhibitors, benzoylphenyl ureas (e.g., teflubenzuron [CME 13406]), for DBM management. This group of compounds has been evaluated for its potential at managing insecticide-resistant DBM populations in several countries (Becker 1986, Kohyama 1986, Lim & Khoo 1986, Sagenmueller & Rose 1986). Currently, cross-resistance between conventional insecticides and these compounds has not been documented (Perng & Sun 1987). However, certain DBM populations in southeast Asia have developed resistance to benzoylphenyl ureas (Perng et al. 1988). The present study determined the effectiveness of teflubenzuron at managing DBM populations on cabbage in southern Florida, and determined the effects of different application intervals (7, 14, or 21 days) of teflubenzuron on DBM population suppression and corresponding field plant protection. This information will help develop an application strategy for teflubenzuron on cabbage in Florida and subsequently minimize the number of applications needed per growing season, delay teflubenzuron resistance, and reduce environmental contamination.

MATERIALS AND METHODS

Two experiments were conducted during the 1986-1987 and 1987-1988 growing seasons in southern Florida. Rockdale soil was fumigated with Terr-O-Gas (75% methyl bromide, 25% chloropicrin; 242 kg/ha) and covered with black (1986) or blue (1987) plastic mulch one to two weeks before planting; mulch was perforated on 17 November 1986 and 9 December 1987. Certified seeds of 'Rio Verde' cabbage were incorporated into a germination mix (Pro-Mix®) and direct seeded at the University of Florida's Tropical Research and Education Center on 18 November 1986 and 14 December 1987. Plants were spaced 0.3 m apart within each of two rows that were 0.76 m apart on 1.83-m center beds. In the 1986-1987 growing season, treatment plots were 2 rows (1 bed) wide by 10.7 m long. A 1.5 m buffer of nontreated plants separated treatment plots. In the 1987-1988 growing season, treatment plots were 4 rows (2 beds) wide by 12.2 m long. A 3 m buffer of nontreated plants separated each replicate and one nontreated bed and a 1.8 m alleyway separated treatment plots.

In the first year, 1,120 kg/ha of granular (6:12:12 [N:P₂O₅:K₂O]) and 672 kg/ha of liquid (7:16:8) fertilizer were applied; in the second year 1,680 kg/ha of granular (6:12:12) fertilizer were applied before planting. Plants were sprinkler irrigated (4.7-6.3 cm/ha/irrigation) twice per week. Maneb (Maneb 80) (Pennwalt Corp., Philadelphia, Pa.) was applied (3.36 kg ai/ha) weekly for routine management of various foliar plant pathogens.

Treatments were arranged in randomized complete blocks with four replications. In the 1986-1987 growing season, treatments evaluated were weekly applications of teflubenzuron (CME 13406, E. M. Industries, Hawthorne, N. Y.) (15 SC) (0.022 and 0.044 kg ai/ha), methomyl (Lannate 1.8L, E. I. du Pont Nemours & Co., Wilmington, Del.) (0.5 kg ai/ha) in combination with *Bacillus thuringiensis* var. *kurstaki* (Dipel 1X, Abbott Laboratories, North Chicago, Ill.) (0.28 kg/ha), methamidophos (Monitor 4L, Mobay Chemical Corp., Kansas City, Mo.) (0.56 kg ai/ha), fenvalerate (Pydrin 2.4EC, Shell Chemical Co., Houston, TX) (0.11 kg ai/ha), and a nontreated check. Since teflubenzuron was effective at suppressing DBM populations and protecting cabbage heads, in 1987-1988 we determined if the negative effects of teflubenzuron on DBM populations and on field plant protection were persistent. Treatments evaluated were teflubenzuron (CME 13406) (15 SC) (0.033 kg ai/ha) applied at 7-, 14-, and 21-day intervals, methomyl (Lannate 1.8L) (0.5 kg ai/ha) in combination with *B. thuringiensis* var. *kurstaki* (Dipel 2X) (0.28 kg/ha), fenvalerate (Pydrin 2.4EC) (0.11 kg ai/ha), and a nontreated check. An intermediate application rate (0.033 kg ai/ha) for teflubenzuron was selected because both the low (0.022 kg ai/ha) and high (0.044 kg ai/ha) rates used in the first year were equally effective at managing DBM populations. The methomyl in combination with *B. thuringiensis* and fenvalerate treatments were applied at 7-day intervals. In 1986-1987, treatments were applied on 7 dates: 8, 15, 22, and 29 January 5, 11, and 18 February 1987. In 1987-1988, teflubenzuron (7-day interval), methomyl in combination with *B. thuringiensis*, and fenvalerate were applied on 10 dates: 14, 21, and 27 January 3, 10, 17, and 24 February, and 2, 9, and 16 March 1988. Treatments of teflubenzuron at 14- and 21-day intervals were applied on 5 dates (21 January, 3 and 17 February, and 2 and 16 March) and 3 dates (21 January, 10 February, and 2 March), respectively. Treatments were applied with a tractor-mounted single-bed boom sprayer with two disc cone nozzles (D-4, no. 24) on each side of the bed and one nozzle over the center of each bed. The sprayer delivered 934.6 l/ha at 4.8 km/hr.

In 1986-1987, data were collected from the center 6 m of each treatment plot, and in 1987-1988 data were collected from the center 9 m of the two middle rows of each treatment plot. Numbers of DBM larvae and pupae, and other lepidopterous pests, including cabbage looper, *Trichoplusia ni* (Hubner), and cabbage budworm, *Hellula phidilealis* (Walker), were recorded on 8 plants per treatment plot on each of 8 dates in 1987 and 11 dates in 1988. In 1988, DBM larvae were categorized by size: small,

medium, or large. Foliar damage was rated visually on 24 plants per treatment plot on 26 February 1987, on 8 plants per treatment plot on 4 and 11 March 1988, and on 24 plants per treatment plot on 21 March 1988 using a scale from 1-6 as follows: 1, no apparent insect feeding; 2, minor feeding on wrapper or outer leaves, 0-1% leaf area eaten; 3, moderate insect feeding on wrapper or outer leaves with no head damage, 2-5% leaf area eaten; 4, moderate insect feeding on wrapper or outer leaves with minor feeding on head, 6-10% leaf area eaten; 5, moderate to heavy feeding on wrapper and head leaves and a moderate number of feeding scars on head, 11-30% of leaf area eaten; 6, considerable insect feeding on wrapper and head leaves with head having numerous feeding scars, over 30% of leaf area eaten (Greene et al. 1969). The percentage of marketable heads was determined on 26 February 1987 and 21 March 1988 by calculating the percentage of heads with ratings ≤ 3 .

Data were analyzed by the least-squares approach to analysis of variance (SAS Institute 1985b). Numbers of DBM larvae per plant and the percentage of marketable heads were transformed to $\ln(\text{DBM} + 1)$ and to the arcsin, respectively, to stabilize error variance. Normal probability plots and the Shapiro-Wilk statistic or the Kolomogorov D statistic were used to assess homogeneity of error variance (SAS Institute 1985a). The significance of differences among treatment means was assessed using the Waller-Duncan *K*-ratio *t*-test (SAS Institute 1985b). On several dates, the mean and variance for certain insecticide treatments of some insect counts were equal to 0. For this reason, these data could not be analyzed by least squares analysis of variance. These treatments were assumed to be significantly different from other treatments if 0 was outside the range of the 95% confidence interval of treatments with a mean > 0 . To further assess the effects of teflubenzuron on plant protection from DBM, square-root transformed damage ratings were regressed on the application interval of teflubenzuron for each of the three dates that damage was rated (SAS Institute 1985b). Also, the percentages of marketable heads per replicate at harvest were regressed on the corresponding teflubenzuron application interval.

RESULTS AND DISCUSSION

1986-1987 Growing Season

Abundance of DBM did not differ among most treatments on the first four sample dates; however, DBM were 1.5-26.0 times more abundant on nontreated plants than on plants treated with insecticides (Table 1). On the last four sample dates, DMB larvae were 2.3 to > 56.0 times more abundant on nontreated plants than on plants treated with insecticides. On 30 January and 9 February, fewer DBM larvae were found on plants treated with teflubenzuron (either 0.022 or 0.044 kg ai/ha) than on those treated with methomyl in combination with *B. thuringiensis*, fenvalerate, and methamidophos. On 16 and 23 February, DBM populations did not differ among most insecticide treatments; however, more DBM (although not consistently significant) were found on plants treated with methamidophos than on those treated with fenvalerate, methomyl in combination with *B. thuringiensis*, and teflubenzuron.

Damage ratings and corresponding percentages of marketable heads differed among most treatments (Table 1). Damage ratings of nontreated plants were 1.3-3.4 times greater than those of plants treated with insecticides. Plants treated with teflubenzuron (either 0.022 or 0.044 kg ai/ha) were least damaged. Damage ratings were 1.7, 1.8, and 2.6 times greater on plants treated with fenvalerate, methomyl in combination with *B. thuringiensis*, and methamidophos, respectively, than on those treated with teflubenzuron. Similarly, the percentage of marketable heads was 2.9-5.8 times greater on plants treated with insecticides than on nontreated plants. Teflubenzuron treatments resulted in the highest percentage of marketable heads (97.9%) followed in decreasing order by

TABLE 1. MEAN NUMBERS OF DBM LARVAE PER PLANT DURING THE GROWING SEASON, AND DAMAGE RATINGS AND PERCENTAGES OF MARKETABLE HEADS PRODUCED AT HARVEST FOR CABBAGE PLANTS TREATED WITH DIFFERENT INSECTICIDES AT HOME-STEAD, FLORIDA IN 1987.

Insecticide treatment	Rate, Kg ai/ha	Mean no. DBM per plant ^a								Damage rating ^b	% marketable heads ^c
		2 Jan.	11 Jan.	16 Jan.	26 Jan.	30 Jan.	9 Feb.	16 Feb.	23 Feb.		
Methomyl +	0.50										
<i>B. thuringiensis</i>	0.28	0.5a	0.9a	0.3b	0.4b	0.7c	0.4cd	0.6bc	0.1c	2.2c	83.3b
Methamidophos	0.56	0.8a	0.9ab	0.5b	0.8b	1.1b	2.4b	1.2b	0.9b	3.1b	50.0c
Fenvalerate	0.11	0.7a	0.6b	0.4b	0.9b	0.8bc	1.1c	0.4c	0.2bc	2.1c	80.2b
Teflubenzuron	0.022	0.6a	1.0b	0.5b	0.1b	0.2d	0.1d	0.1c	0.0c	1.2d	97.9a
Teflubenzuron	0.044	0.7a	0.5b	0.3b	0.5b	0.1d	0.0d	0.0c	0.0c	1.2d	97.9a
Nontreated check	—	0.2a	1.5a	1.7a	2.6a	3.4a	5.6a	3.9a	3.4a	4.1a	16.7d

^aData transformed to $\ln(\text{DBM} + 1)$ to reduce error variance. Nontransformed means are presented. Means in the same column followed by the same letter are not significantly different (K -ratio = 100; Waller-duncan K -ratio t -test).

^bFoliar damage was rated by the method described by Greene et al. (1969).

^cData transformed to the arcsin for analysis. Nontransformed means are presented.

TABLE 2. MEAN NUMBERS OF SMALL, MEDIUM, LARGE, AND TOTAL DBM LARVAE, AND DBM PUPAE DURING THE GROWING SEASON ON CABBAGE PLANTS TREATED WITH DIFFERENT INSECTICIDES AT DIFFERENT APPLICATION INTERVALS AT HOMESTEAD, FLORIDA IN 1988.

Insecticide Treatment	Rate, Kg ai/ha	Application interval, days	Mean no. of small DBM larvae per plant ^a										
			8 Jan.	15 Jan.	22 Jan.	29 Jan.	5 Feb.	12 Feb.	19 Feb.	26 Feb.	4 Mar.	11 Mar.	21 Mar.
Methomyl + <i>B. thuringiensis</i>	0.50 0.28	7	0.0a	0.1a	0.1a	0.1b	0.7b	0.1b	0.1b	0.1bc	0.1b	0.0b	0.0a
Fenvalerate	0.11	7	0.2a	0.0a	0.1a	0.1b	0.3bc	0.1b	0.2b	0.7b	0.6b	0.5ab	0.1a
Teflubenzuron	0.033	7	0.1a	0.0a	0.0a	0.0b	0.0c	0.0b	0.0b	0.0c	0.0b	0.0b	0.0a
Teflubenzuron	0.033	14	0.1a	0.2a	0.1a	0.2b	0.2c	0.0b	0.0b	0.0c	0.0b	0.0b	0.0a
Teflubenzuron	0.033	21	0.2a	0.2a	0.0a	0.1b	0.1c	0.1b	0.2b	0.1bc	0.1b	0.0b	0.0a
Nontreated check	—	—	0.1a	0.1a	0.1a	0.4a	1.7a	1.4a	3.5a	3.5a	4.5a	1.1a	0.0a
			Mean no. of medium DBM larvae per plant										
Methomyl + <i>B. thuringiensis</i>	0.50 0.28	7	0.1a	0.0a	0.0b	0.0b	0.2b	0.2b	0.1b	0.1b	0.0c	0.1c	0.1b
Fenvalerate	0.11	7	0.0a	0.1a	0.0b	0.1b	0.5b	0.1b	0.2b	0.4b	0.8b	1.0b	0.4a
Teflubenzuron	0.033	7	0.2a	0.0a	0.0ab	0.0b	0.0b	0.0b	0.0b	0.0b	0.0c	0.0c	0.0b
Teflubenzuron	0.033	14	0.1a	0.1a	0.0ab	0.0b	0.3b	0.0b	0.0b	0.0b	0.0c	0.1c	0.0b
Teflubenzuron	0.033	21	0.2a	0.1a	0.0ab	0.2ab	0.2b	0.1b	0.1b	0.1b	0.1c	0.0c	0.0b
Nontreated check	—	—	0.1a	0.1a	0.1a	0.4a	2.8a	1.1a	2.8a	3.7a	9.1a	3.7a	0.1b
			Mean no. of large DBM larvae per plant										
Methomyl + <i>B. thuringiensis</i>	0.50 0.28	7	0.1a	0.1a	0.0a	0.1a	0.1c	0.1b	0.1b	0.0b	0.0c	0.1c	0.0b
Fenvalerate	0.11	7	0.0a	0.0a	0.0a	0.0a	0.3bc	0.0b	0.0b	0.2b	0.7b	1.6b	0.4a
Teflubenzuron	0.033	7	0.1a	0.0a	0.0a	0.0a	0.0c	0.0b	0.0b	0.0b	0.0c	0.0c	0.0b
Teflubenzuron	0.033	14	0.1a	0.1a	0.0a	0.1a	0.5b	0.0b	0.0b	0.0b	0.0c	0.1c	0.0b
Teflubenzuron	0.033	21	0.1a	0.1a	0.0a	0.0a	0.1c	0.1b	0.0b	0.0b	0.1c	0.0c	0.0b
Nontreated check	—	—	0.1a	0.1a	0.1a	0.1a	0.9a	0.4a	1.8a	0.9a	5.3a	3.2a	0.2a
			Mean no. of total DBM larvae per plant										

Methomyl +	0.50												
<i>B. thuringiensis</i>	0.28	7	0.2a	0.2a	0.2ab	0.2bc	1.0b	0.4b	0.2b	0.2c	0.1c	0.2c	0.1bc
Fenvalerate	0.11	7	0.2a	0.1a	0.1ab	0.2bc	1.0b	0.2bc	0.4b	1.4b	2.2b	3.2b	0.8a
Teflubenzuron	0.033	7	0.5a	0.1a	0.0b	0.0c	0.0c	0.0d	0.0c	0.0c	0.0c	0.0c	0.0c
Teflubenzuron	0.033	14	0.4a	0.3a	0.2ab	0.2bc	1.0b	0.0cd	0.0bc	0.0c	0.0c	0.2c	0.1bc
Teflubenzuron	0.033	21	0.5a	0.3a	0.0b	0.3b	0.4bc	0.2b	0.2bc	0.1c	0.2c	0.0c	0.0c
Nontreated check	—	—	0.2a	0.3a	0.4a	0.9a	5.5a	2.9a	8.1a	8.1a	19.0a	8.0a	0.3b
Mean no. of DBM pupae per plant													
Methomyl +	0.50												
<i>B. thuringiensis</i>	0.28	7	0.0a	0.0a	0.1a	0.1a	0.2bc	0.1bc	0.1bc	0.1b	0.2b	0.2c	0.1a
Fenvalerate	0.11	7	0.0a	0.3a	0.0a	0.0a	0.2bc	0.3b	0.2bc	0.2b	0.4b	1.6b	0.6a
Teflubenzuron	0.033	7	0.0a	0.2a	0.1a	0.0a	0.0c	0.0c	0.0c	0.0b	0.0b	0.0c	0.0a
Teflubenzuron	0.033	14	0.0a	0.3a	0.1a	0.1a	0.6b	0.2bc	0.0c	0.1b	0.1b	0.0c	0.0a
Teflubenzuron	0.033	21	0.0a	0.2a	0.1a	0.0a	0.2bc	0.2bc	0.1b	0.1b	0.2b	0.4c	0.1a
Nontreated check	—	—	0.0a	0.1a	0.2a	0.1a	1.4a	1.0a	1.7a	1.6a	4.1a	3.3a	0.5a

³Data transformed to $\ln(\text{DBM} + 1)$ to reduce error variance. Nontransformed means are presented. Means for each life stage within each column followed by the same letter are not significantly different (K -ratio = 100; Waller-Duncan K -ratio t -test).

methomyl in combination with *B. thuringiensis* (83.3%), fenvalerate (80.2%), methamidophos (50%), and nontreated plants (16.7%).

1987-1988 Growing Season

Abundance of small, medium, large, total larvae, and DBM pupae did not differ among most insecticide treatments on most dates; however, DBM were consistently more abundant on nontreated plants than on plants treated with insecticides (Table 2). In general, DBM were most abundant on nontreated plants followed in decreasing order by plants treated with fenvalerate, methomyl in combination with *B. thuringiensis*, and teflubenzuron (either 21-, 14-, or 7-day application intervals). In general, teflubenzuron treatments were more effective than other insecticides at managing DBM populations. Interestingly, abundance of DBM larvae and pupae did not differ among plants treated with teflubenzuron at 7-, 14-, and 21-day intervals on most sample dates.

Although the numbers of other lepidopterous pests were recorded on plants, few were found. For this reason, we could not evaluate the effectiveness of teflubenzuron at managing other pests of cabbage.

Foliar damage ratings differed among most treatments on the three dates that damage was assessed (Table 3). Plants treated with teflubenzuron every 7 days were least damaged. On 4 March, damage ratings were 3.4, 1.9, 1.9, 1.8, and 1.8 times greater on nontreated plants and plants treated with fenvalerate, teflubenzuron every 21 days, methomyl in combination with *B. thuringiensis*, and teflubenzuron every 14 days, respectively, than on plants treated with teflubenzuron every 7 days. On 11 March, damage ratings were 3.2, 2.1, 2.0, 1.8, and 1.8 times greater on nontreated plants and plants treated with fenvalerate, teflubenzuron every 21 days, methomyl in combination with *B. thuringiensis*, and teflubenzuron every 14 days, respectively, than on plants treated with teflubenzuron every 7 days. At harvest (21 March), damage ratings were 2.9, 2.2, 2.0, 1.8, and 1.8 times greater on nontreated plants and plants treated with fenvalerate, teflubenzuron every 21 days, methomyl in combination with *B. thuringiensis*, and teflubenzuron every 14 days, respectively, than on plants treated with teflubenzuron every 7 days. Square-root transformed damage ratings were significantly positively correlated with the application interval of teflubenzuron on 4 ($F = 58.96$; $P = 0.0001$; $df = 1,94$; $r^2 = 0.38$; $Y = -0.27 + 0.20X$), 11 ($F = 53.09$; $P = 0.0001$; $df = 1,94$; $r^2 = 0.36$; $Y = 0.42 + 0.23X$), and 21 March ($F = 216.77$; $P = 0.0001$; $df = 1,286$; $r^2 = 0.43$; $Y = 0.99 + 0.03X$). Thus, longer application intervals of teflubenzuron resulted in more DBM damage to plants.

The percentage of marketable heads was 15.0-18.8 times greater on plants treated with insecticides than on nontreated plants (Table 3). Plants treated with teflubenzuron every 7 days produced the highest percentage of marketable heads (97.9%) followed in decreasing order by plants treated with teflubenzuron every 14 (93.7%) and 21 days (88.5%), methomyl in combination with *B. thuringiensis* (88.5%), fenvalerate (78.1%), and nontreated plants (5.2%). These data were similar to those from the first year. The percentage of marketable heads was not significantly correlated ($F = 4.08$; $P > 0.05$; $df = 1,10$; $r^2 = 0.30$; $Y = 1.028 - 0.007X$) with the application interval of teflubenzuron, suggesting that the negative effects of teflubenzuron on DBM populations were persistent.

In summary, this study showed that teflubenzuron was more effective than fenvalerate, methomyl in combination with *B. thuringiensis*, and methamidophos at managing DBM populations on cabbage and protecting cabbage heads from DBM damage. Cabbage yields were similar among plants treated with teflubenzuron at 7-, 14-, and 21-day intervals. Teflubenzuron appears to have considerable potential for managing DBM populations in Florida. Current label restrictions for teflubenzuron limit its use to 6

TABLE 3. FOLIAR DAMAGE RATINGS ON THREE DATES AND THE PERCENTAGES OF MARKETABLE HEADS AT HARVEST FOR CABBAGE PLANTS TREATED WITH DIFFERENT INSECTICIDES AT DIFFERENT APPLICATION INTERVALS AT HOMESTEAD, FLORIDA IN 1988.

Insecticide treatment	Rate, Kg ai/ha	Application interval, days	No. of applications	Damage rating ^a			% marketable heads ^b
				4 Mar.	11 Mar.	21 Mar.	
Methomyl +	0.50						
<i>B. thuringiensis</i>	0.28	7	10	2.2b	2.4c	2.6c	88.5ab
Fenvalerate	0.11	7	10	2.3b	2.8b	3.1b	78.1b
Teflubenzuron	0.033	7	10	1.2c	1.3d	1.4d	97.9a
Teflubenzuron	0.033	14	5	2.2b	2.4c	2.6c	93.7a
Teflubenzuron	0.033	21	3	2.3b	2.6bc	2.8bc	88.5ab
Nontreated check	—	—	0	4.1a	4.2a	4.1a	5.2c

^aAs in Table 1. Means followed by the same letter within the same column are not significantly different (K -ratio = 100; Waller-Duncan K -ratio t -test).

^bData transformed to the arcsin for analysis. Nontransformed means are presented.

applications per growing season. The present study indicates that adequate control of DBM may be possible with as few as 5 and perhaps even 3 applications of teflubenzuron per growing season. Future studies should develop an application schedule for teflubenzuron so that teflubenzuron selection pressure on DBM populations is minimized and DBM resistance to teflubenzuron is delayed.

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A SURVEY OF STRUCTURE-INFESTING TERMITES OF PENINSULAR FLORIDA

RUDOLF H. SCHEFFRAHN¹, JOHN R. MANGOLD², AND
NAN-YAO SU¹

¹Ft. Lauderdale Research and Education Center
University of Florida Institute of Food and Agricultural Sciences
3205 College Ave., Ft. Lauderdale, FL 33314

²The Terminix International Co. L.P.
2280 U.S. Highway 19 N., Suite 209
Clearwater, FL 34623

ABSTRACT

A total of 785 samples of termites was obtained from structures in central and southern Florida between February 1987 and March 1988. Eleven of the 15 termite species known from Florida were recorded including six drywood (Kalotermitidae) species and five subterranean (Rhinotermitidae) species. An unidentified species of Termitidae, new to Florida, was collected in St. Petersburg. The subterranean termites, *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks), accounted for 57% of the 716 survey samples identified to species, while the drywood termites, *Cryptotermes brevis* (Walker) and *Incisitermes snyderi* (Light), accounted for 36%. Flight seasons for various species were determined from alate collections. Fumigation for drywood termite control cost building owners in central and southern Florida ca. \$30 million in 1987.

RESUMEN

Se obtuvieron un total de 785 muestras de termites de edificios en el centro y el sur de la Florida durante el período febrero de 1987 hasta marzo de 1988. Se registraron 11 de las 15 especies conocidas para la Florida, incluyendo 6 especies de termites de madera seca (Kalotermitidae) y 5 especies de termites subterráneos (Rhinotermitidae). Se colectó en St. Petersburg una especie desconocida de Termitidae la cual es nueva para la Florida. De las 716 muestras identificadas al nivel de especie, 57% fueron termites subterráneos, *Reticulitermes flavipes* (Kollar) y *R. virginicus* (Banks), mientras las especies *Cryptotermes brevis* (Walker) y *Incisitermes snyderi* (Light) constituyeron la mayoría de los termites de madera seca y el 36% de los ejemplares. Se determinaron por ejemplares de termites aladas los vuelos estacionales de varias especies. La fumigación

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Clearwater, FL 34623

ABSTRACT

A total of 785 samples of termites was obtained from structures in central and southern Florida between February 1987 and March 1988. Eleven of the 15 termite species known from Florida were recorded including six drywood (Kalotermitidae) species and five subterranean (Rhinotermitidae) species. An unidentified species of Termitidae, new to Florida, was collected in St. Petersburg. The subterranean termites, *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks), accounted for 57% of the 716 survey samples identified to species, while the drywood termites, *Cryptotermes brevis* (Walker) and *Incisitermes snyderi* (Light), accounted for 36%. Flight seasons for various species were determined from alate collections. Fumigation for drywood termite control cost building owners in central and southern Florida ca. \$30 million in 1987.

RESUMEN

Se obtuvieron un total de 785 muestras de termites de edificios en el centro y el sur de la Florida durante el período febrero de 1987 hasta marzo de 1988. Se registraron 11 de las 15 especies conocidas para la Florida, incluyendo 6 especies de termites de madera seca (Kalotermitidae) y 5 especies de termites subterráneos (Rhinotermitidae). Se colectó en St. Petersburg una especie desconocida de Termitidae la cual es nueva para la Florida. De las 716 muestras identificadas al nivel de especie, 57% fueron termites subterráneos, *Reticulitermes flavipes* (Kollar) y *R. virginicus* (Banks), mientras las especies *Cryptotermes brevis* (Walker) y *Incisitermes snyderi* (Light) constituyeron la mayoría de los termites de madera seca y el 36% de los ejemplares. Se determinaron por ejemplares de termites aladas los vuelos estacionales de varias especies. La fumigación

para el control de los termites de madera seca les costó a los dueños de edificios en el centro y el sur de la Florida cerca de \$30 millones en 1987.

There are presently 42 described species of Isoptera in the continental United States of which 15 have been collected in Florida (Table 1). Eight of these species are known only from Florida and the northern Neotropics, especially the islands of the Bahamas and Antilles (Snyder 1956). As a result of their prodigious degradation of cellulose, termites serve an essential role in the detritivore cycle of many tropical and some temperate ecosystems (Wood & Sands 1978). A large majority of the ca. 2,000 described termite species do not feed on wood in structures, but rather attack live or decayed wood, foliage, grass, other plant material, fungi, and miscellaneous organic debris (Wood 1978, Edwards & Mill 1986). Edwards & Mill (1986) identified 21 pest genera of termites worldwide, and list approximately 150 species that cause at least minimal damage to buildings. Although all the described termites of Florida are wood feeders, no quantitative assessment has been made of their infestation frequency in structural lumber.

The descriptive foundation for the taxonomy, biology, and distribution of termites in Florida was published in a landmark study of Nearctic Isoptera by Banks & Snyder (1920). Later, Light (1934b), Snyder (1934a, 1954), Miller & Miller (1943), and Miller (1949) contributed additional field information, including notes on structural infestations and pest status of the Florida termite fauna. Snyder's (1949) world list of Isoptera and a generic revision of the Family Kalotermitidae by Krishna (1961) provide the present-day nomenclature applied to Florida species.

From February 1987 through March 1988, a survey of pestiferous termites of central and southern Florida was conducted through a joint effort of the University of Florida and The Terminix International Co., L.P., a large and long-established pest control

TABLE 1. SPECIES AND DISTRIBUTION OF FLORIDA TERMITES.

Species	Distribution in Florida
Family Kalotermitidae	
<i>Calcaritermes nearcticus</i> Snyder ^a	Clay Co. to Sebring
<i>Cryptotermes brevis</i> (Walker)	Widely introduced
<i>Cryptotermes cavifrons</i> Banks ^a	St. Johns Co. south
<i>Incisitermes milleri</i> (Emerson) ^{a,b}	Florida Keys
<i>Incisitermes schwarzi</i> (Banks) ^{a,b,c}	Mostly coastal south
<i>Incisitermes snyderi</i> (Light)	Statewide
<i>Kalotermes approximatus</i> (Snyder) ^b	Sarasota north
<i>Neotermes castaneus</i> (Burmeister) ^a	Lake Co. south
<i>Neotermes jouteli</i> (Banks) ^a	Fort Pierce south
<i>Neotermes luykxi</i> Nickle & Collins ^{a,b}	Broward, Monroe Cos.
Family Rhinotermitidae	
<i>Coptotermes formosanus</i> Shiraki	Isolated introductions ^d
<i>Prorhinotermes simplex</i> (Hagen) ^a	Coastal Broward, Dade Cos.
<i>Reticulitermes flavipes</i> (Kollar)	Statewide
<i>Reticulitermes hageni</i> Banks	Statewide, less common
<i>Reticulitermes virginicus</i> (Banks)	Statewide

^aNot known from other 49 states.

^bNot collected in present survey.

^cBanks and Snyder (1920 report *I. schwarzi* from Pensacola (Escambia Co.)

^dBroward, Dade, Escambia, Okaloosa, and Orange Cos.

firm. We herein report the findings of this survey, review the historical perspective of termite incidence in Florida, present additional information on the current status of the state's isopteran fauna, and summarize the frequency and cost of structural fumigations for termite control in and near the survey area.

MATERIALS AND METHODS

Field personnel from 15 Terminix offices participated in the survey. The service area of these offices roughly encompassed the three major population centers of central and southern Florida: greater Tampa Bay, the Orlando/Daytona region, and the coastal southeast including Miami, Ft. Lauderdale, and the Palm Beaches (Figure 1). Survey forms and collection vials were distributed to participants. Completed survey forms provided information including collection dates, locations, and specific evidence and conditions under which sample specimens were obtained. Termite specimens were preserved in the field in 7 ml glass vials filled with ethanol:water (85:15).

Terminix personnel, to perform service inspections, obtained unhindered access to infested structures, usually at the request of a property owner who suspected a termite infestation. The survey participants were instructed to collect soldiers and/or alate castes whenever possible to facilitate identification to species. Initials of participants followed by consecutive collection numbers (e.g. JRM-26) were used as unique codes to designate each sample. To avoid sample misidentity, a pencil-written code label was placed in each sample vial and inscribed on the accompanying survey form. Samples and completed forms were delivered to the laboratory for identification and cataloging of collection data.

All specimens in each sample were examined under a stereo dissecting microscope fitted with a 0.02 mm/div. (at 50X) eyepiece scale. Species determinations were based on descriptive material in Banks & Snyder (1920), Light (1934c), Emerson & Miller (1943), Miller (1949), Snyder (1954), Krishna (1961), and Weesner (1965). Identifications were supported by the collection information provided on the samples' survey forms. Only alates which were collected live or known to have swarmed on a specific date were included in the flight data summary (Table 3). Samples containing only workers were identified to family.

Notices of lawful intent to fumigate structures, submitted by commercial fumigators to the Florida Department of Health and Rehabilitative Services (FDHRS), Office of Entomology, were tabulated monthly by FDHRS regulatory inspectors. These data provide an accurate accounting of structural fumigations for the control of drywood termites in and near the survey area.

RESULTS AND DISCUSSION

General Findings

A total of 785 termite samples was collected; 716 samples were identified to species, and the remainder identified to family (Table 2). The samples represented 779 separate addresses. In six of these locations, two species were found. Sample vial contents ranged from a few wings, workers (includes larvae, pseudergates, and nymphs), or a single soldier or alate, to dozens of all three castes. Most alates were collected within structures immediately after dispersal flights. Soldiers, workers, and a few of the alate samples were extracted from either galleries in wood or from foraging tubes. No reproductively active kings or queens were taken.

Seven of eight genera, including 11 of the 15 species from the two families known to occur within the survey area were collected (Table 1). *Incisitermes milleri*, *I. schwarzi*, *Kalotermes approximatus*, and *Neotermes luykxi* were not collected. In

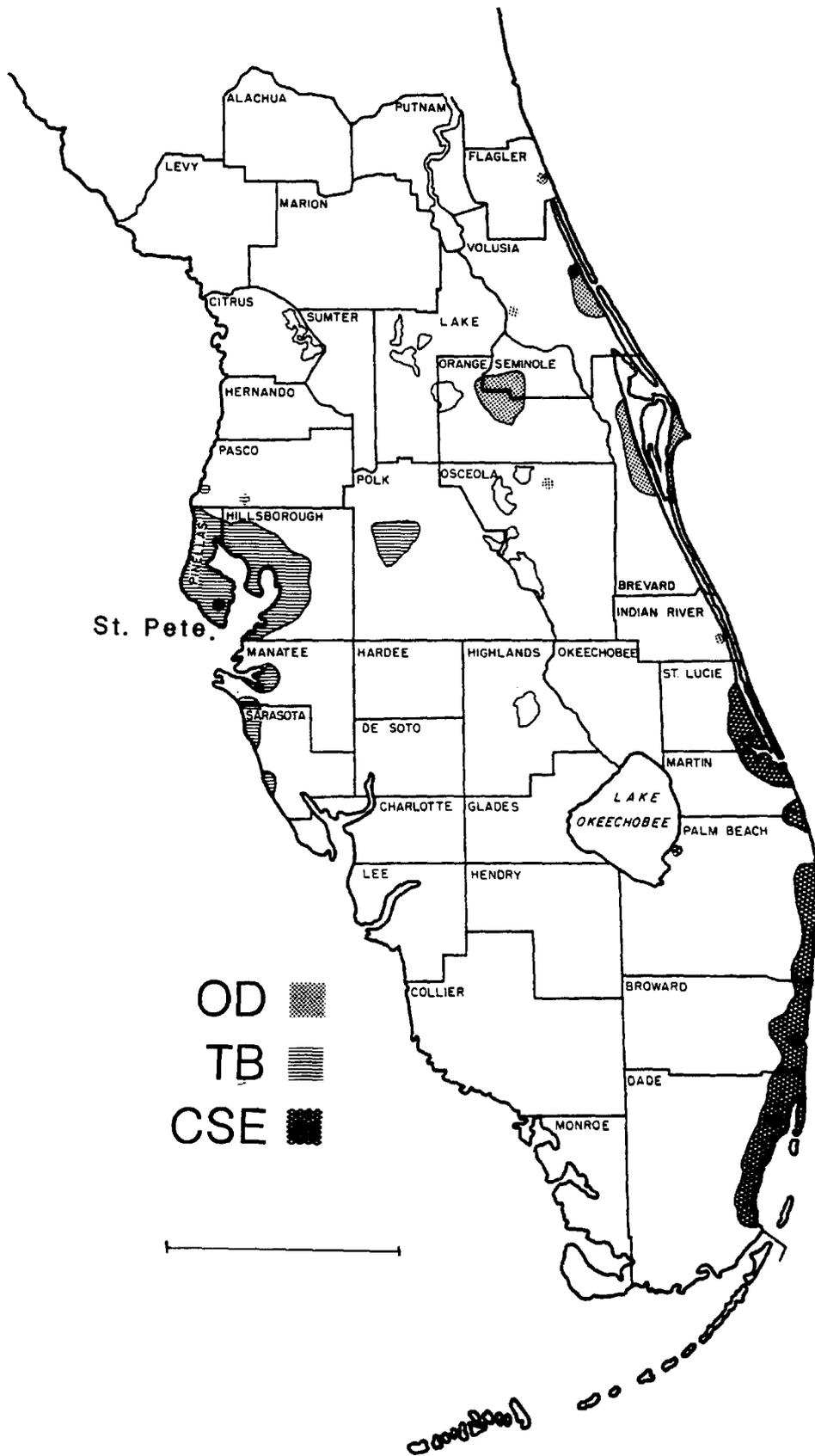


TABLE 2. TERMITE SPECIES, NUMBER OF SAMPLES COLLECTED FROM EACH SURVEY REGION, AND NUMBER OF SAMPLES CONTAINING SOLDIERS COLLECTED BETWEEN FEBRUARY 1987 AND MARCH 1988.

Species	No. samples by region			Total	No. samples with soldiers
	Greater Tampa Bay	Orlando/Daytona	Coastal Southeast		
KLOTERMITIDAE					
<i>C. nearcticus</i>	0	1	0	1	0
<i>C. brevis</i>	71	6	75	152	17
<i>C. cavifrons</i>	2	2	6	10	2
<i>I. snyderi</i>	44	7	53	104	16
<i>N. castaneus</i>	9	0	8	17	2
<i>N. jouteli</i>	0	0	8	8	6
Unidentified ^a	23	2	15	40	0
Total	149	18	165	332	43
RHINOTERMITIDAE					
<i>C. formosanus</i>	0	1	3	4	3
<i>P. simplex</i>	0	0	3	3	0
<i>R. flavipes</i>	152	44	52	248	85
<i>R. hageni</i> ^b	5	0	1	6	0
<i>R. virginicus</i> ^b	84	23	56	163	40
Unidentified ^a	18	4	6	28	0
Total	259	72	121	452	128
TERMITIDAE					
Unidentified ^c	1	0	0	1	0

^aSamples containing only workers.

^b*R. virginicus* and *R. hageni* soldiers not differentiated. See text.

^cFamily not previously known in Florida.

Florida, *I. milleri* is known only from the Florida Keys (Emerson 1943, Miller 1949). These islands were not included in the survey area. *I. milleri* has not been found in structural lumber (E. M. Miller, pers. comm.). *I. schwarzi*, although common in coastal mangroves and Everglades hammocks of southern Florida (Luykx 1986) and in native woods of the coastal southeast, did not, surprisingly, appear in our survey. Banks & Snyder (1920) considered *I. schwarzi* to be an abundant species in southern Florida, and it has been collected from wooden structures on the Yucatan peninsula of Mexico (Light 1934d), but has not been reported from lumber elsewhere in its Caribbean range. *K. approximatus* is common in central and northern Florida (Syren & Luykx 1981), often found in dead portions of trees (Hetrick 1961), but appears not to favor structural lumber. Snyder (1934a, 1954) reports that both *I. schwarzi* and *K. approximatus* have been taken from the woodwork of buildings. These were most likely rare infestations. *Neotermes luykxi* has recently been described as a new species (Nickle & Collins 1988) and is known, at present, only from coastal Broward and Monroe counties. Both soldiers and alates of *N. luykxi*, however, are very close in appearance to *N. jouteli* and the two species can only be distinguished tenuously on the basis of morphometrics. Discrimination of these two species can best be accomplished by elucidating chromosome number (Nickle & Collins 1988) from stained preparations of imago gonad tissue (Syren & Luykx



Fig. 1. Survey regions of peninsular Florida: greater Tampa Bay (TB), Orlando/Daytona (OD), and the coastal southeast (CSE). Patterned circles denote single outlying collections. Bar represents 100 km.

1977), or by electrophoresis studies of enzyme patterns (Luykx, et al., in prep.). Samples identified as *N. jouteli* in this study may, in fact, be *N. luykxi*.

The numbers of samples of each termite species collected from each of the three survey regions (Figure 1) are listed in Table 2. Of all samples submitted, 58% (452) were rhinotermitids, 42% (332) were kalotermitids, and one specimen was a termitid. On a regional basis, however, the ratio of rhinotermitids to kalotermitids varied substantially as follows: Orlando/Daytona region, 80:20; greater Tampa Bay, 63:37; and the coastal southeast, 42:58. These and related fumigation data (Table 4) suggest a trend for more drywood termite infestations in coastal and southern parts of the state. The eastern subterranean termite, *Reticulitermes flavipes*, was the most commonly encountered species during the survey, followed by *R. virginicus*. These two species alone accounted for 57% of the samples identified to species, in part because the survey period covered a portion of a second (i.e., spring 1988) flight season of *Reticulitermes* spp. The next two most abundant species, *Cryptotermes brevis* and the southeastern drywood termite, *Incisitermes snyderi*, constituted 21% and 15%, respectively. Thus, these four species comprised 93% of survey samples identified to species.

Seasonal flight patterns for *R. flavipes*, *R. virginicus*, *I. snyderi*, and *C. brevis* are listed by month and region in Table 3. During the survey period, the months of peak flight activity for *R. flavipes* were February and March with fewer samples submitted in January and April. Some swarming *R. flavipes* alates were taken in the summer and fall months. Peak collections of *R. virginicus* alates were made in April, especially in the Tampa Bay region, with additional flights occurring in May and June and a steady but lesser flight activity continuing throughout the year in all survey areas. *C. brevis* and *I. snyderi* alate collections peaked during June in Tampa Bay and Orlando/Daytona,

TABLE 3. ALATE FLIGHT PERIODS FOR FOUR MAJOR STRUCTURE-INFESTING SPECIES COLLECTED FROM EACH SURVEY REGION BETWEEN FEBRUARY 1987 AND MARCH 1988.

Species Region	No. samples by month													
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
<i>R. flavipes</i>														
Tampa Bay	20	30	4	1	0	1	0	2	0	1	1	8	14	10
Orl./Dat.	1	11	4	0	0	0	0	0	0	4	0	4	3	2
S.E. coast	1	13	2	0	0	1	0	0	0	0	0	0	7	10
Total	22	54	10	1	0	2	0	2	0	5	1	12	24	22
<i>R. virginicus</i>														
Tampa Bay	1	1	31	10	4	2	1	3	1	3	4	6	1	7
Orl./Dat.	0	0	9	6	1	0	0	2	1	1	1	1	0	1
S.E. coast	0	1	9	11	8	4	4	1	5	3	4	0	0	2
Total	1	2	49	27	13	6	5	6	7	7	9	7	1	10
<i>Cr. brevis</i>														
Tampa Bay	4	4	4	5	25	6	3	3	4	3	0	1	2	0
Orl./Dat.	0	0	0	0	4	0	1	0	0	0	0	0	0	0
S.E. coast	0	2	7	10	14	19	2	3	5	3	2	1	0	1
Total	4	6	11	15	43	25	6	6	9	6	2	2	2	1
<i>I. snyderi</i>														
Tampa Bay	0	2	2	5	22	5	1	0	1	0	0	0	0	0
Orl./Dat.	0	0	1	0	3	0	2	0	0	0	1	0	0	0
S.E. coast	1	3	3	4	6	9	6	6	5	0	1	1	1	1
Total	1	5	6	9	31	14	9	6	6	0	2	1	1	1

TABLE 4. STRUCTURAL FUMIGATIONS DURING 1987 FOR SELECTED COUNTY GROUPS IN FLORIDA AS REPORTED TO THE OFFICE OF ENTOMOLOGY, DEPT. OF HRS, BY PEST CONTROL COMPANIES.

Counties	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Citrus, Lake, Levy Hernando, Marion, Seminole, Sumter, Volusia, and six "panhandle" cos. ^b	— ^a	—	23	16	118	173	210	169	126	104	108	89
Hillsborough, Pasco, Pinellas, Polk	1101	1178	1146	1318	1145	2022	2041	1642	1211	1220	1110	765
Brevard, Indian River, Martin, Okeechobee, Orange, Osceola, St. Lucie	161	178	174	229	208	408	379	217	190	166	164	110
Charlotte, Collier, DeSoto, Glades, Hardee, Hendry, Highlands, Lee, Manatee, Sarasota	—	11	127	457	462	783	—	—	—	—	—	—
Broward, Dade ^c , Monroe, Palm Beach	1612	1908	1201	1783	1919	2603	2479	2730	2146	2188	2105	1489
Total	2874	3275	2671	3803	3852	5989	5109	4758	3673	3678	3487	2453

^aData unavailable^bDixie, Hamilton, Lafayette, Madison, Suwannee, and Taylor Cos.^cJanuary to June figures for south Dade Co. district are estimates based on north Dade and Broward Co. reports.

and July in the coastal southeast region. As with subterranean termites, elevated activities were tabulated in the months preceding and following peak months for drywood termite swarms with sporadic flights occurring during the remainder of the year.

In the following sections, survey results and previous findings will be reviewed in detail for each species.

Reticulitermes Spp.

R. flavipes is the most widespread and damaging subterranean species in eastern North America, and has been found from Toronto, Canada and Maine to Florida (Snyder 1954). Banks and Snyder (1920) collected *R. flavipes* throughout Florida (except the Florida Keys, as reiterated by Miller & Miller, 1943) and noted swarming records as early as February in the south and in May in northern Florida. Miller (1949) recorded flights of *R. flavipes* in Florida during February, March, April, and rarely, May. Weesner (1965) reports two flights in April 1965 from Orange Co., Florida. Our records of intermittent flights during May, July, September, November, December, and January may reflect deviations from "natural swarms" possibly as a result of colonies developing in temperature controlled and artificially lighted structures. Of the 46 samples of *R. flavipes* alates collected in February 1987 and 1988, 34 (74%) were from the Tampa Bay region. This compares to 40 (53%) of 76 March samples of *R. flavipes* from Tampa Bay, indicating earlier flight activity for this species in the Tampa Bay region than the other two survey regions.

Reticulitermes virginicus rivals *R. flavipes* for pest status in Florida. Miller & Miller (1943) first noted "extreme and consistent damage to human property" attributed to *R. virginicus*. The reason may be the higher tolerance to dry conditions by this species compared to *R. flavipes* as shown by Collins (1959). The sandy soils found in many areas of Florida have poor water holding capacity and can become dry, especially where the vegetative canopy is sparse. It is in these areas where *R. virginicus* appears to flourish more readily than *R. flavipes*. Miller & Miller (1943) also note the presence of *R. virginicus* in the arid oolitic soils of the lower Florida Keys.

Structural infestations of *R. virginicus* may be as severe as any noted for *R. flavipes* (Scheffrahn & Su, pers. obs.). Distinguishable by size, *R. virginicus* alates (and soldiers) are smaller than those of *R. flavipes* and their flights characteristically peak about one month after *R. flavipes* in a given area. According to records in Banks and Snyder (1920), the earliest swarm of *R. virginicus* in any year was on Feb. 21, 1919 in Labelle (Hendry Co.). Weesner (1965, 1970) recorded four *R. virginicus* flights in Orange Co. in April 1965, one swarm in March, and two in April in Tampa during 1967. Miller (1949) notes peak flight activity during March and April in southern Florida with additional swarms in May, October, and November. Dispersal flights of *R. virginicus* in our survey were most common during April in the Tampa Bay region, and remained elevated in May and June for the entire survey area with these three months accounting for 67% of the alate-containing samples collected in 1987. However, some flights of *R. virginicus* occurred in every month surveyed (Table 3). One massive swarm of *R. virginicus* in St. Cloud (Osceola Co.) on April 26, 1987 was estimated at nearly 33,000 based on a mean individual dry biomass of 0.769 mg from the 25.278 g of alates recovered from inside the home the day following the swarm. In another instance, a wooden interior door was severely damaged within several months from an *R. virginicus* infestation. Termites traveled freely between the door and frame even though the door was constantly opened, disrupting their only connection to the hinged door. There appear to be at least two distinct wing color forms of *R. virginicus* in Florida, a white-veined and a clear-veined type. Conclusions about these variants will require further investigation.

R. hageni, also a more xeric-adapted species (Collins 1959), is rare, based on our survey, compared to either of its congeners. Alates of *R. hageni* are similar in size to *R. virginicus* and may be distinguished by the former's light brown color and slender, cylindrical body form. Soldiers of these two species are morphologically indistinguishable. Banks (1946) found only that the curvature of the mandible tips of *R. hageni* were less pronounced than those of *R. virginicus* and Emerson & Miller (1943) noted a wider gula in *R. hageni*. Alate flights for *R. hageni* were recorded twice in March and December 1987, and once each in June 1987 and February 1988. Weesner (1970) reported a March 1966 flight in Leesburg (Lake Co.) and an April 1966 swarm in Tallahassee (Leon Co.), while Miller (1949) lists a fall and winter flight season with peak activity in January for this species in Florida. These observations suggest that *R. hageni* colonies have an asynchronous flight habit in Florida as was reported in southern Florida for the drywood species, *I. schwarzzi* (Luykx 1986).

Survey samples containing only soldiers of *Reticulitermes* spp. were identified on the basis of pronotum width: >0.81 mm = *R. flavipes*, <0.81 mm = *R. virginicus*. Banks (1946) found almost no overlap with this measurement. Because this parameter did not distinguish the two smaller congeners, a portion of the 40 *R. virginicus* samples containing only soldiers may actually have been of the much rarer (123:6 alates) *R. hageni*.

Coptotermes formosanus

The Formosan subterranean termite was identified in Hallandale (Broward Co.), Florida in 1980 (Koehler 1980). In 1984, *C. formosanus* was discovered infesting struc-

tures in Orlando (Orange Co.) and in the western panhandle communities of Gulfbreeze (Escambia Co.) and, in 1987, Ft. Walton Beach (Okaloosa Co.) (Su & Scheffrahn 1987a; R. Beal, pers. comm.). More recently, foragers of this introduced species have been collected in Hollywood (Broward Co.) and North Miami Beach (Dade Co.) (Su & Scheffrahn, unpublished). Unlike some *C. formosanus* colonies in southern Louisiana which occur in undisturbed native ecosystems (La Fage 1987), all known infestations of this termite in Florida are closely associated with human structures. Three survey samples of *C. formosanus* collected in Hallandale in May, July, and August 1987, all contained alates, soldiers, and workers. A single alate collected in Orlando in June 1987 confirms continued presence of this species in central Florida. Massive spring and summer swarms, beginning in April, are characteristic of this species in the Hallandale area. A single colony is known to have produced nearly 69,000 alates, all collected from a single flight staging area (Su & Scheffrahn 1987b). Recently, *C. formosanus* was twice discovered infesting private vessels on the southeastern coast of Florida. This implicates a maritime mode of introduction and dissemination of this threatening pest (Su & Scheffrahn 1987a). Considering its present distribution and affinity for structural lumber in coastal settings, *C. formosanus* has vast potential to establish in urban and resort locations along Florida's 13,547 km of tidal shoreline and connected inland waterways.

Prorhinotermes simplex

The "Florida dampwood termite", *P. simplex*, is found only in parts of extreme southeast Florida originating, most likely, from ancient dispersals from neighboring islands such as Cuba. In previous accounts (Banks & Snyder 1920, Miller 1949), this species was not known to forage in the soil, and its colonies appeared restricted to wet or decaying pieces of wood. However, more recent observations indicate some underground travel by *P. simplex*. A subterranean termite trap (Su & Scheffrahn 1986) infested by *R. flavipes* in early 1987 was found infested exclusively by several thousand *P. simplex* foragers when inspected at year's end at its Ft. Lauderdale location (Ban & Su, unpublished). The trap was not adjacent to wood, suggesting that the termites located it by soil exploration.

In our survey, we recorded three instances in southeastern Dade Co. of nocturnal *P. simplex* swarms in structures. Inspection of one home following a December 1987 flight revealed damage to outdoor wooden fencing and isolated damage to wooden molding in proximity to an interior expansion seam in the concrete slab which separated an adjoining foundation. It appeared that the termites had foraged a distance to reach the structure. In 1986, two Dade Co. infestations of homes by *P. simplex* yielded alates and foraging castes (J. Mangold, unpublished). In both later structures, no wood-to-ground contact was located. The other two infestations were discovered following alate flights in March of 1987 and 1988. Miller (1949) observed *P. simplex* flights in Dade Co. from October through January, apparently from colonies in native woodlands. He stated that this species has "considerable economic importance" in Dade County. Based on our survey results, we would rate *P. simplex* to be an infrequently encountered pest at this time and may be more of a nuisance from indoor alate swarms than from feeding damage.

Cryptotermes brevis

C. brevis was first discovered in Florida in 1918 infesting a building in Key West (Snyder 1934b). This drywood species, called the "powderpost" or "furniture" termite, is a pest throughout the tropics (Gay 1969) and has been collected, amazingly, only in structural lumber and furniture (Edwards & Mill 1986, Bacchus 1987). Miller (1949) observed an increase in *C. brevis* infestations over the twenty years leading to his publication, and by 1954, Snyder (1954) considered *C. brevis* a major drywood pest in

Florida. Our survey found *C. brevis* to infest structures in all regions, particularly in coastal urban centers of West Palm Beach/Ft. Lauderdale/Miami and St. Petersburg/Tampa. There is a tendency for *C. brevis* to be especially common in older, downtown buildings in these cities. A nocturnal swarmer, *C. brevis* can cause extensive damage, especially if left uncontrolled, as it will continuously reinfest a structure until structural framework and wooden contents are severely damaged by numerous colonies. Following a massive swarm in May 1987, the floor of a Hollywood (Broward Co.) roller rink was covered with more than 2,850,000 *C. brevis* wings based on a 1.428 gram sample (100 wings = 5 mg) estimated to represent less than 1% of the wings present in the building. The swarming of *C. brevis* alates was a chronic nuisance problem in a Tampa cookie factory (J. Mangold, unpubl.). The plant manager claimed alates swarmed throughout the year before a fumigation eradicated the infestation. Weesner (1970) recorded five flights of *C. brevis* in May and one each in June and July of 1967, all in Tampa. Miller (1949) has flight records for March through June in Florida.

Incisitermes snyderi

In addition to Florida, this drywood termite is found in Georgia, Louisiana, Mississippi, Alabama, South Carolina, and Texas (Light 1934b, Snyder 1954) making it the most widely distributed kalotermitid species in the eastern U.S. *I. snyderi*, originally confused with *Incisitermes marginipennis* (Latreille), was not collected in Florida by Banks and Snyder during their extensive collecting expeditions early in this century, but they reported an 1880 find in mangroves along the Indian River. Banks & Snyder (1920) noted that their Georgia collections proved this species was injurious to telegraph poles and the dry woodwork of buildings. By 1934, Snyder (1934a) recognized *I. snyderi* as the most injurious species of Eastern drywood termite. Miller & Miller (1943) stated that structures were "occasionally" infested by *I. snyderi* in Florida, and later, Miller (1949) noted that records of structural infestations were accumulating in the state. As of 1940, its pest status was on the increase in Miami (Snyder 1954). All these accounts suggest that, at least in Florida, *I. snyderi* has become increasingly prominent as a drywood pest by expanding its niche from native to "introduced" structural wood.

According to Krishna (1961), alates of *Incisitermes* are recognized from those of *Cryptotermes* by wing venation. In *Incisitermes* spp., the median vein runs to the tip of the wing, while in *Cryptotermes* spp., the median vein turns anteriorly to join the radial sector near the middle of the wing. This character has been used in all keys which include the Florida species. Banks & Snyder (1920) and Weesner (1965) specify that forewings be used for identification. Our examination of alates of *C. brevis* in samples submitted with soldiers (to verify species) revealed that the turn in the media is variable or entirely absent. This vein may extend to the wing tip in forewings (Figure 2) as well as hindwings. *I. snyderi* wings showed consistency in medial vein character; however, crossveins between the median vein and radial sector could be mistaken by a novice for upward branchings of the media. Head width with eyes (Miller 1949) is a consistent character to separate alates of *I. snyderi* (1.20-1.35 mm) from *C. brevis* (1.05-1.15 mm). Freshly killed, alcohol-preserved alates of *I. snyderi* are orange-brown, whereas *C. brevis* imagos are pigmented a darker green-brown. Future examination of imago fine-structure may yield more definitive morphological features to separate these two sympatric species. Weesner (1970) lists the following flight records of *I. snyderi* in Florida: August 1966 (Miami), December 1967 (Coral Gables, Dade Co.), and May 1967 (Hillsborough Co.). Miller (1949) records *I. snyderi* flights from May to November (except July) and an activity peak in March which we did not observe. This species typically swarms at night but may fly during the day in structures.

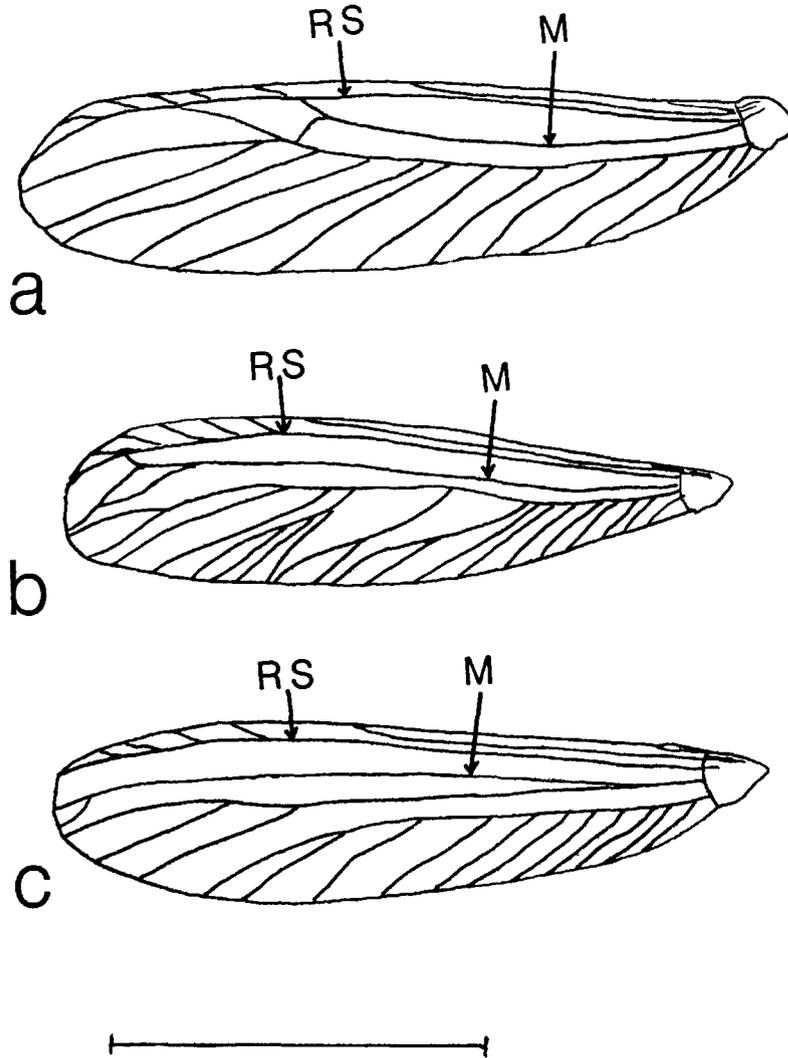


Fig. 2. Schematic drawings showing vein positions in forewings of *Cryptotermes brevis* collected during survey. Median vein (M) turning to radial sector (RS) near center of wing (a), near apex of wing (b), and extending to wing margin (c). Bar represents 5 mm.

Cryptotermes cavifrons

In our laboratory colonies, this small species requires higher humidity than either *C. brevis* or *I. snyderi*, which may account for its scarcity in interior structural lumber. As evidenced by our survey, development of a *C. cavifrons* colony in structural lumber requires that the wood be exposed to some periodic external moisture, such as landscape irrigation or rainfall. Outdoor moldings and wood sidings are examples of wood members from which *C. cavifrons* was collected in our survey. Miller (1949) reports a single house infested by *C. cavifrons* in Tampa but provides no details. Banks & Snyder (1920) found a colony in a porch sill in Palm Beach. Although this is a widespread (Table 1) and common species throughout the state, it is unlikely to become a serious pest.

Flights of *C. cavifrons* in structures in our survey were recorded three times in May, and once each in June, July, August, and December. Weesner (1970) received a

collection of alates from Tampa which had swarmed indoors in March 1967. Miller (1949) indicates peak flights of *C. cavifrons* in February and March. Unlike *C. brevis*, the smaller *C. cavifrons* alates have a consistently and clearly upcurved median vein in both the fore- and hindwings as illustrated by Krishna (1961).

Calcaritermes nearcticus

Next to *I. milleri*, *C. nearcticus* is probably the least encountered of the Florida termites. *C. nearcticus* and, with less certainty, *N. luykxi* are the only species which occur exclusively in Florida. Snyder (1933) described this species from three alates collected, one each in fruit fly traps located in Clay, Levy, and Orange Counties. In 1940, Miller (1943) collected the first soldiers and ergatoids of this species near Winter Park (Orange Co.). Subsequent collections of all castes from native wood were made in Bartow (Polk Co.) and near Jacksonville (Duval Co.) (Miller 1943) and from Sebring (Highlands Co.) (Miller 1949). Alate flights have been recorded in January and April (Snyder 1933) and March (Miller 1949). Alates were collected in Gainesville (Alachua Co.) during a swarm in April 1982 (Hetrick, unpublished). Our survey yielded a single collection of ten *C. nearcticus* alates from a group of several dozen swarming on May 13, 1987 in the early afternoon in a home in New Smyrna Beach (Volusia Co.). It was unclear if the termites emerged from structural lumber or from a live tree growing inside an enclosed porch.

Neotermes jouteli

All survey collections of *N. jouteli* were obtained in the coastal southeast region (Table 2). Two indoor collections of alates, one in June and one in October 1987, were recorded. Miller (1949) also reports of spring and fall swarms of this species. Two survey collections of *N. jouteli* from Ft. Pierce (St. Lucie Co.) mark its northern limits. Unverified accounts of *N. jouteli* occurring in the Tampa area (Miller 1949) may be from erroneous identifications of *N. castaneus*. When infesting structures, *N. jouteli* can penetrate into sound, dry wood but a moisture source must infuse at least some of the gallery network to support colony development. According to our survey and personal observations, *N. jouteli* colonies are associated with intermittently wetted exterior wood on porch sidings, fascia boards, and wood trim in structures in the Miami area.

Neotermes castaneus

N. castaneus is the largest termite species in Florida. Soldiers can be distinguished from those of the slightly smaller *N. jouteli* by their lack of pigmented eye spots. Unlike *N. jouteli*, this species occurs far inland. One survey sample of *N. castaneus* was obtained from Canal Point (Palm Beach Co.) ca. 60 km from the coastline. Moisture requirements and structural damage are similar to *N. jouteli*, however, *N. castaneus* may be common in the Tampa Bay region, where nine of the 17 collections were obtained. Survey records show one flight each in March, May, and July 1987, and January 1988; and four flights in October, two in November, and three in December 1987. Miller (1949) records flights in March, June, October, and November. Snyder & Banks (1920) report *N. castaneus* swarming in May. Weesner (1970) identified alates which had swarmed at night in October in Tampa and November in Sarasota (Sarasota Co.), both in 1967, and North Miami (Dade Co.) in August 1966.

Unidentified Termitid

In the course of termite investigations, we have received four separate collections of unusual alates from St. Petersburg (Pinellas Co.), one in 1986 and three in 1987 (one

specimen included in this survey) following July dispersal flights. Superficially, the unidentified alates resemble dark-winged *R. virginicus* alates. Their translucent black wings and midsummer flight season aroused the suspicion of experienced pest control personnel, who collected them. Examination of these partially damaged specimens revealed that these are in the family Termitidae, a taxon previously not known in Florida. Specimens had all the characteristics of termitid imagos as described by Light (1934a): short anterior wing scales (i.e., not overlapping hind wing scales), non-reticulate wing membrane, and hairy wing margins. Additional termitid characters include two protruding marginal teeth on the left mandible (Ahmad 1950), opaque wing membrane, and veins in the posterior wing portion which are pigmented and conspicuous throughout (Weesner 1965). The alates are ca. 8.2 mm in total length and are reminiscent of members of the genus *Amitermes*.

The habitat of this obscure native or introduced (unlikely) species has not been elucidated, and until colonies or foraging groups are collected, its identity will remain unknown. The nearest members of the Termitidae occur in Cuba, the Bahamas, and the Yucatan peninsula (Snyder 1956, Light 1934d). Most common Caribbean island species of Termitidae are in the subfamily Nasutitermitinae which have large alates (>12 mm) unlike those collected in St. Petersburg.

Incisitermes minor

Incisitermes minor (Hagen), the western drywood termite, is the principal drywood pest of the Pacific coast, especially California. Hicken (1971) witnessed the fumigation of a structure in Florida which was infested by *I. minor*, but gave no further details. Specimens from two Florida infestations have been recorded by the present authors. *I. minor* alates swarmed in a Pompano Beach (Broward Co.) home in June 1986. The colony was located in a chair moved from California. Another swarm occurred in September 1986 in Ft. Lauderdale, again from furniture originating in California. Although *I. minor* does not appear to be established in Florida, the potential for a permanent introduction exists.

Prominence of Drywood Termites in Florida

Florida's geographic position and the near-tropical climate of its southern expanse provide an ideal habitat for drywood termites. A useful indicator of drywood termite infestations is the number of structural fumigations which are performed in a given area. Florida statutes require that a notice of intent to fumigate be filed with state authorities before any such procedure is instituted. A summary of notices submitted during 1987 for the regions encompassing the survey is given in Table 4. Records for 45,622 notices were tabulated and an estimated 3,000 additional notices were written for fumigations in Sarasota and the surrounding southwestern Florida counties. Terminix records indicate that only a small percentage of their fumigation notices pertained either to cancelled or repeats of failed fumigations, or for pests other than drywood termites (three lyctid and two bostrichid beetle infestations were encountered during the entirety of this survey). Some fumigations may inadvertently not be reported by pest control companies. We conservatively estimate that ca. 40,000 fumigations were performed to control drywood termites in peninsular Florida in 1987 at an average cost to the consumer of \$750 per fumigation, or a total expense of \$30 million. The actual loss to drywood termites in this region is much higher when costs for other methods of control, damage repairs, and preventive measures are considered. Hamer (1985) estimates total losses from drywood termites in Florida at \$105 million for 1983.

The numbers in Table 4 indicate, as expected, that more fumigations take place in populated, coastal counties (i.e. Broward, Dade, Pinellas, and Hillsborough). Numbers

of structural fumigations in June 1987 showed a 55% increase over May which reflect the rise in swarming activity of *C. brevis* and *I. snyderi* observed from alate collections (Table 3). Terminix company records indicate that samples of drywood termites were under-represented in our survey as a result of heavy work loads and time constraints on field collectors to meet customer inquiries during months of peak drywood termite flight activity. Therefore, drywood termites may account for a greater percentage of infestations than this survey indicates.

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LATIN AMERICAN RESEARCH ON
SPODOPTERA FRUGIPERDA (LEPIDOPTERA: NOCTUIDAE)

KEITH L. ANDREWS
Department of Plant Protection
Escuela Agrícola Panamericana
Apartado Postal 93
Tegucigalpa, Honduras, Central America
and
Dept. of Entomology and Nematology
University of Florida
Gainesville, Florida 32611, USA

ABSTRACT

Recent Latin American literature concerning *Spodoptera frugiperda* (J. E. Smith) is reviewed. The pest's distribution, economic importance, seasonal abundance, host plants, life cycle and biology, as well as natural, cultural, genetic and chemical controls are discussed.

RESUMEN

Se revisa la literatura Latinoamericana que trata del gusano cogollero, *Spodoptera frugiperda* (J. E. Smith). Se resume la información disponible sobre su distribución, importancia económica, abundancia estacional, plantas hospederas, ciclo de vida, biología y control.

This literature review is an extension of that which was presented by Andrews (1980) and includes both previously unencountered pre-1980 publications and recent citations. This review includes many published summaries of papers presented at regional professional meetings. Most of these citations are not included in any entomological abstracting service. Brief, preliminary or even superficial, short publications have been included because they are oftentimes the only published information available on a particular subject. Moreover, each provides names and addresses which may help foreign researchers obtain further information through correspondence. For the most part, English-language references easily accessible to North American researchers through abstracting services are not included.

MORPHOLOGY

Angulo & Jana (1982) described the pupae of 4 species of *Spodoptera* encountered in northern Chile.

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KEITH L. ANDREWS
Department of Plant Protection
Escuela Agrícola Panamericana
Apartado Postal 93
Tegucigalpa, Honduras, Central America
and
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INTRACOUNTRY DISTRIBUTION

In Mexico, *Spodoptera frugiperda* (J. E. Smith) is a more serious pest in the coastal states and territories of Michoacan, Oaxaca, Quintana Roo, and Yucatan. It is also serious in Morelos state. It is of much less importance in highlands areas over 2000 mts in Puebla, Tlaxcala, Hidalgo, Guanajuato, Queretaro, and Mexico states (Sifuentes 1978). The pest is much more important in the coastal plain of Nicaragua than in interior areas. The heavy use of insecticides in cotton in the Pacific plain and subsequent destruction of natural enemies may cause this differential abundance (Van Huis 1981). Alternatively, the difference in populations in these areas may be a result of the higher biotic potential of the species where hot conditions and large monocultures predominate.

SEASONAL ABUNDANCE

Manrique et al. (1979) conducted a four-year study involving blacklight traps located at two sites in Durango and Chihuahua, Mexico. *S. frugiperda* moths were caught regularly between June and November but few were trapped from December through May. In Tamaulipas, Mexico, a three-year study involving staggered maize plantings from June to November revealed greatest damage in July and October; the least damage occurred in June and August (Alvarado & Carrillo 1981). Peralta (1980) reported little *S. frugiperda* damage in April and May in this same state.

In Rio Grande do Sul, Brazil, no *S. frugiperda* moths were caught in blacklight traps during August, September or October, and moths were most abundant in February, March and April (Silveira et al. 1979). In this state, *S. frugiperda* is most common in maize between December and April (Maia 1978). In Piracicaba, Brazil, Carvahlo et al. (1971) found highest adult populations between October and February; during this period, warm temperatures prevail and maize is growing. Lara et al. (1977) reported that *S. frugiperda* was collected in over 80% of the blacklight samples at 2 sites during 4 years. Lara & Silveira (1977) collected adults during the entire year in Sao Paulo with highest populations recorded between November and March.

Doreste (1975) reported the results of a 10-year study using light traps for collecting *S. frugiperda* in Venezuela. Few moths were caught during the dry season, November to April. Catches increased dramatically in June and July at the onset of the rainy season. Population crashes in August were due to the effects of *Beauvaria* sp. and other natural enemies. In dry years, the population peak was delayed until August. Clavijo (1981b) found similar results using data collected at 5 sites and over 12 years in Venezuela. He related abundance to rainfall. Silvain (1986) reported that highest larval and adult populations tended to occur around January and July in French Guiana.

Hichens & Mendoza (1976) reported that *S. frugiperda* was present in Chilean alfalfa throughout the year. According to van Huis (1981), in Nicaragua, second cycle maize (that which is planted in August or September) is more severely attacked than is maize which is planted in May or June at the beginning of the rainy season. Honduran data (Andrews et al., unpublished) contradict these findings. Adult populations are generally low throughout the second cycle growing season (August to December) and the dry season (January through May). Adult populations are very high during June, July and August. Larval populations are also highest during this period. Larval populations rapidly reach damaging levels in irrigated maize grown during the Central American dry season (Anon. 1984) indicating that lack of larval host plants, rather than mortality agents, normally maintain low adult populations during the dry season. Passoa (1983) collected *S. frugiperda* during every month in Honduras.

YIELD REDUCTIONS AND ECONOMICS OF *S. frugiperda* CONTROL

Just how important is *S. frugiperda* "south of the border"? Chemical control of *S.*

frugiperda on sorghum in Cuba was uneconomical (Ryder et al. 1968). In hybrid maize grown in Cuba for forage, Ryder (1968a) measured yield increases of 4.6-6.5 metric tons/ha due to whorlworm control and suggested that if 5% of the whorls are infested an application of insecticide might be economically justified.

Sifuentes (1978) reported that in areas in Mexico where the whorlworm is most damaging, yields are normally increased by an insecticide application. When 3 applications are made, yield increases of 2-2.5 metric tons are normal. Silva (1978) working in Oaxaca, Mexico, registered yield increases of 130 to 2000 kg/ha in maize which received 3 insecticide applications. Tello & Diaz (1982) reported yield increases in Sinaloa of 900 kg/ha through chemical control of whorl feeding *S. frugiperda*. These authors did not present compelling evidence that the reported losses were due only to *S. frugiperda* and not a combination of whorl and stem boring insects. Peairs & Saunders (1981) reported studies in Mexico involving a late maturing tropical white dent and an intermediate-maturing tropical yellow flint. They used controlled infestation methods developed in CIMMYT and an insecticide check. Yield reductions were significant only when considered over several growing cycles and averaged 13%. Maximum losses were 30%. Galt and Stanton (1979) reported average losses of 17% due to foliage-feeding insects in trials in Mexico carried out on experiment station grounds and on-farm.

Maize yields in Brazil were unaffected by *S. frugiperda* leaf feeding (Montenegro 1981). The same was true for maize in Venezuela (Clavijo 1984a,b).

In four unpublished theses based on work carried out in maize in Guatemala, whorlworm control was rarely associated with significantly reduced yields and was never justified economically (García de Dacarett 1975, Cabarrus 1977, Teos 1980, Pérez 1982). Dardón et al. (1983) registered yield increases of up to 15% due to control of foliage pests. In the Dominican Republic, Del Rosario et al. (1981) and Del Rosario & Dicio (1981) showed statistically insignificant yield increases of 8% when whorlworms were controlled chemically.

In Nicaragua, van Huis (1981) measured strong interactions between fertilizer use and whorl protection in studies involving a hybrid variety of maize. Use of fertilizer alone increased yields only 6%; use of insecticide increased yields by 24%. Use of both inputs increased yields by 60%. Because of this pronounced synergistic effect, the decision to control *S. frugiperda* and *D. lineolata* should precede a decision to use fertilizer. Ideally, however, credit facilities would enable use of both inputs. In another test, maize grain yields were not significantly less in plots where whorl protection started 7, 15 or 30 days after plant emergence as compared to plots which were always protected. Without whorl protection, yields were about the same for plants subjected to different degrees of water stress. With sufficient soil moisture, whorl protection increased yield by 50%, but under severe water stress, whorl protection did not increase yields. Whorl infestation was highest for maize which was deprived of irrigation for the longest period.

Based on artificial defoliation studies, van Huis (1981) contended that maize plants were more sensitive to late whorl than early whorl damage. Greatest yield reduction occurred after mid-whorl stage. With two open pollinated varieties, yields were reduced linearly as older plants were defoliated. With two hybrids, however, the greatest effect was registered when defoliation occurred immediately after mid-whorl with less effect on subsequent defoliation dates. Severe defoliation before mid-whorl caused moderate yield losses of 20-30%. This author concluded that the commonly recommended action threshold of 20% infested plants generally resulted in higher yields than did an action threshold of 50% and this was always better than an untreated check.

This species can be devastating as a cutworm. Shannon & Navarro (1983) included it as one of the three most serious pests of seedling maize in Panama. They estimated plant stand losses of 30%. León (1978) reported seedling losses of 60% in Sonora, Mexico. Rueda et al. (1985) argued that care must be taken to not attribute damage caused to maize seedlings by *Listronotus dietrichi* (Stockton) to *S. frugiperda*.

In Nicaragua, loss of maize grain yield due to ear feeding is negligible (van Huis 1981, Anon. 1984), but Sifuentes (1978) contended that this damage is important in Jalisco, Mexico.

Guiagossian et al. (1981) reported that yields of susceptible sorghum varieties were reduced 55-80% when subjected to heavy, artificially induced whorlworm attack. Losses in intermediately susceptible varieties were 35-50%. Carvalho et al. (1971) studied yield responses of one sorghum hybrid and found that severe damage resulted in 15% yield loss when compared to undamaged plants. Attacks at 64 days resulted in 34% yield reduction. Other varieties responded similarly, registering losses of 20-30% when serious versus light infestations were compared. In El Salvador, Hueso de Mira & Lainez (1980) found yield losses of 50% in 13- to 22-day old sorghum due to *S. frugiperda* acting as a cutworm. In 30- to 41-day old plantings the same pest population density resulted in 25% yield reductions; between 45 and 55 days, corresponding losses were 15%.

LIFE CYCLE AND BEHAVIORAL STUDIES

In Venezuela, Labrador (1967) found that *S. frugiperda* larvae passed through 6 or 7 instars when fed maize, and he presented detailed information regarding head capsule width. Nieto & Llanderal (1982) presented head capsule widths for a population of *S. frugiperda* in Mexico. Loya (1978) studied larval development on maize and sorghum in Mexico. Larval development took as little as 20 days in midsummer and as long as 35 days in September. Reproduction was greater and adults were longer lived when larvae were fed maize leaves. Most larvae passed through 7 instars. Another report from Mexico (Armenta 1971, cited in Sifuentes 1977) reported that larvae developed faster on sorghum than on maize (14 versus 19 days). Pierda (1974) found larval development times to be 17 and 15 days on sorghum and maize, respectively; this difference was not significant. Castro et al. (1987b) found no difference in development times when larvae were reared on these hosts, although adults reared on maize produced more eggs. Peña (1980b) reported that larval development took 13 days on maize and 22 days on an artificial diet. Nieto & Llanderal (1982) reported the larval development period to be 30 days, followed by a pupal period of 11 days; females laid 1,500 eggs. In Surinam, larval development typically is 15 days (van Dinther 1960) and 8-9 generations/year are expected. According to Doposto & Enkerlin (1964) larval and pupal stages are completed in 22 and 9 days, respectively. Estrada (1960, cited in van Huis 1981) reported that on maize, larval development took 9.6 to 20 days, the average being 11.1 days. In Peru (Campos n.d.), larval development on maize at 27°C was 18.9 days. Adults laid an average of over 1,600 eggs, with a mean oviposition period of 9.2 days. Bertels (1970) found that in Brazil egg and larval stages lasted 10 and 21-28 days, respectively. Pupae required 9 (Armenta 1971), 9-10 (van Dinther 1960), 8-9 (Piedra 1974), 8 (Peña 1980b), 10 (Loya 1978) or 10-30 days (Bertels 1970) to complete their development. Castro et al. (1987b) compared *S. frugiperda* development periods and other parameters of a Honduran colony with individuals collected in Mississippi.

Studies by Piedra (1971) in Cuba showed that 24 days were required for development from first instar larva to adult on maize. Corresponding times required on sorghum, *Stizolobium deeringianum* Bert. and *Pennisetum purpureum* Schumach. were 26, 28 and 29 days, respectively. In subsequent studies, she found that larval mortality was higher on *P. purpureum* than on maize, sorghum or *S. deeringianum*. In Colombia, Alvarez & Sánchez (1983) found that larvae fed on sorghum and nutsedge passed through 6-8 instars. Larvae fed on older sorghum leaves grew more slowly and molted more often than did larvae provided with young sorghum foliage.

According to Valerio & Combs (1980), adult *S. frugiperda* oviposit more readily on "callie" bermudagrass than on other varieties of *Cynodon dactylon* (L.) Pers. and the optimum temperatures for adults and larvae are 25 and 30°C, respectively. Sifuentes

(1977), van Huis (1981), and Alvarez & Sánchez (1982) observed that females laid more eggs on maize plants than on interplanted sorghum plants.

Fernandez (1971) caught twice as many *S. frugiperda* females as males in light traps in Venezuela over a 3-year period. Trevino (1980) captured more moths in light traps during new moon phase, at higher temperatures, and when there was less precipitation. Portilla et al. (1984) studied the sexual behavior of normal and allatectomized males.

Carvalho & Silveira (1971) found that in whorl stage sorghum in Brazil, the maximum size for coexisting large *S. frugiperda* larvae was 2.5 cm. However, in 74% of the whorls where they found a larva over 3.0 cm long, they also found small larvae. They often found small and medium sized larvae together in whorls; but, as they grew in size, the number of cohabitating larvae decreased. These authors considered this to be conclusive evidence for cannibalism. In the grain filling stage, 85% of the worms found were located in the basal part of the heads and only 15% in the upper half. Aguilera & Vargas (1970) found an average of 4.6 larvae/whorl but reported that large larvae do not cohabit a whorl.

S. frugiperda larvae collected by van Huis (1981) from *Digitaria* sp. did not show conditioning to that plant, but had a slight feeding preference for maize. The same author made several interesting observations on the biology of *S. frugiperda* on maize. All eggs laid on the early whorl stage were laid on the underside of the leaves, but by the late whorl and tasseling stages between 30-40% were laid on the upper side. Egg mass size increased linearly with maize plant growth; one week after plant emergence, masses averaged 80 eggs while at 50 days the typical mass contained more than 400 eggs. In 3 separate experiments van Huis (1981) measured peaks of oviposition activity in early whorl and tasseling stages; oviposition activity was low at mid-whorl stage (30 days after emergence).

HOST PLANTS

Brunner et al. (1975) listed 17 economically important plants attacked by *S. frugiperda* in Cuba, including peanut, pepper, papaya, garbanzo, gladiolus, rice, guinea grass, para grass, lima bean, verdulaga, sugarcane, Johnson grass, sorghum, maize, kudzu, pigeon pea and *Eucalyptus* sp. Van Huis (1981) reported sorghum, sesame, sugarcane, maize, rice, cotton, tobacco, potato, tomato, cucumber and cabbage as important crop hosts for this pest. Larvae were common on weeds, especially *Digitaria* sp. and *Eleusine indica* (L.) Gaertn. Passoa (1983) listed maize, rice, pepper, cabbage, tomato, sorghum, onion, bean, beets, lettuce, garlic and potato as important host plants in Honduras. Labrador (1967) listed 31 host plant species belonging to 21 families in Venezuela. Included in the list are 9 gramineaceous larval hosts and 3 fruit crops upon which eggs are laid. In Ecuador, the species is a problem on maize, cotton, tobacco, tomato, cucumber, rice, sugarcane, beans, soy beans, various grasses and forage legumes (Cevallos 1976).

According to Parasram (1976), larvae cause the most damage in cabbage by boring straight down into the head. In Brazil, De Moraes et al. (1974) reported that *S. frugiperda* caused considerable damage to buds on seedlings of *Eucalyptus wrophylla* S. T. Blake. In Chile, of 13 species of Noctuids which cause damage in alfalfa, *S. frugiperda* is the second most important, just behind *S. eridania* (Aguilera et al. 1971). In Brazil, Chandler (1984) and Calil et al. (1985) showed the importance of *S. frugiperda* as a pest of young dry beans. *S. frugiperda* is common on *Digitaria sanguinalis* (L.) Scop., *Digitaria eglumis* Peter, *Setaria geniculata* (Lam.) Beauv. and *S. viridis* Beauv. (Bertels 1970). Howell (1980) stressed the importance of *Digitaria* spp. as a host and source of migrating worms in Honduras. Alvarez & Sánchez (1983) cited *Cyperus rotundus* L. as an excellent, widespread host in hot areas of Colombia. Sinha (1982) reported

S. frugiperda as the key pest of blackeyed peas [*Vigna unguiculata* (L.) Walp.], maize and sorghum in Guyana. *S. frugiperda* is a key pest in soybeans in Columbia; it acts as a cutworm, leaf feeder, terminal borer and pod feeder (Hallman 1983).

ABIOTIC CONTROL

Van Huis (1981) showed that heavy rainfall a few days after first instar larvae were artificially infested into 8- and 18-day old maize plants resulted in a 20-30% reduction in intensity of damage in injured whorls. Light rains did not, however, kill significant numbers of larvae. The effect of rain was restricted to the early instars.

NATURAL ENEMIES

Parasitoids

Some of the parasitoids taken in Latin America and the Caribbean from *S. frugiperda* are listed in Table 1. Ashley (1979) listed others. Other species have been reported and distributions may be considerably wider than the limited information provided here would indicate.

Hexameris sp. is a commonly reported nematode parasitoid of whorlworm larvae. Nickle (1978) described the life cycle of *Hexameris*. Honduran data not yet published (M. Castro, H. Pitre, G. Wheeler & K. Andrews) indicate that this species occasions more mortality than any other larval parasitoid.

Van Huis (1981) reported 16 species of parasitoids and 3 entomopathogens which as a group accounted for an average 35% larval mortality. The most commonly recovered parasitoids were *Lespesia archippivora* (Riley) and the nematode *Hexameris* sp. Other important parasitoids were *Rogas laphygmae* Vier., *Chelonus insularis* Cresson, *Ophion* sp. and *Archytas narmoratus* (Tns.). *Hexameris* sp. is not common in coastal areas; the use of carbofuran as a soil treatment at planting probably destroys large numbers of this nematode. *L. archippivora* kill approximately 76% of the larvae recovered from weeds in maize field while larvae taken from whorls of maize in the same field were attacked at a much lower level. Weeds may be a significant source of this important parasitoid. Parasitism by *L. archippivora* was more important in the late whorl and tasseling stages than in young maize. The reverse was true for *R. laphygmae* which was frequent only in early growth stage maize. Intercropping of maize with beans decreased parasitism of *R. laphygmae*.

Teran (1974) listed 19 species of Diptera as parasitoids of *S. frugiperda* in Venezuela. Notz (1972) provided some biological data on 5 of these species and on 4 species of Hymenoptera. Campos (1965) found only 10% infestation by tachinids in Peru and provided some data on development for 3 species.

A number of *S. frugiperda* studies in Mexico may be cited. Laboratory and limited field tests with *Bracon kirkpatricki* Wilkenson were reported by Peña (1980a) and Moya (1980). Field test results were not impressive. Montoya (1979, 1980) reported that *Trichogramma* sp. and *Euplectrus* sp. caused 45-55% egg and 10-25% larval mortality in different years in Veracruz. In maize in Quintana Roo, average larval parasitism of 41% was caused by *Archytas* sp., *L. archippivora*, *Pristomerus spinator* (F.) and *Chelonus* sp. (Carrillo 1980). Loya (1978) attempted to control *S. frugiperda* with mass releases of an unspecified species of *Trichogramma* without success. Parasitism levels of 0.18% in fields where no liberations were made increased to only 0.56% in treated fields. *Chelonus* sp. parasitized 5% of the eggs. Another attempt to use mass liberations of *Trichogramma* spp. in Tamaulipas resulted in less than 15% average parasitism (Peralta et al. 1981). Castrejón (1981) conducted a laboratory study of oviposition behavior of *Telenomus remus* (Nixon).

TABLE 1. PUBLISHED REPORTS OF PARASITIDS OF *SPODOPTERA FRUGIPERDA* FROM VARIOUS LATIN AMERICAN AND CARIBBEAN COUNTRIES.

Parasites	Countries	Citation
DIPTERA		
SARCOPHAGIDAE		
<i>Sarcophaga lambens</i>	Lesser Antilles	Fennah 1947
<i>Sarcophaga</i> sp.	Venezuela	Terán 1974
TACHINIDAE		
<i>Acroglossa vetula</i>	Venezuela	Notz 1972
	Venezuela	Terán 1974
<i>Archytas analis</i>	Venezuela	Terán 1974
	Barbados	Alam 1978
<i>Archytas divisus</i>	Venezuela	Terán 1974
<i>Archytas incasana</i>	Chile	Etcheverry 1957
<i>Archytas incertus</i>	Chile	Etcheverry 1957
	Brazil	Lucchini & Almeida 1980
	Brazil	Patel & Habib 1984
<i>Archytas marmoratus</i> (= <i>A. piliventris</i>)	Lesser Antilles	Fennah 1947
	Venezuela	Notz 1972
	Venezuela	Terán 1974
	Chile	Valencia & Valdivia 1973
	Cuba	Brunner et al. 1975
	Nicaragua	van Huis 1981
	Barbados	Alam 1978
	Trinidad	Yaseen 1978
<i>Archytas</i> sp.	Mexico	Carrillo 1980
<i>Eucelatoria armigera</i> (= <i>Blondelia armigera</i>)	Cuba	Brunner et al. 1975
<i>Eucelatoria</i> sp.	Venezuela	Terán 1974
	Venezuela	Terán 1974
	Barbados	Alam 1978
<i>Euphorocera</i> sp.	Brazil	Goncalvez & Goncalvez 1973
<i>Gonia crassicornis</i>	Lesser Antilles	Fennah 1947
	Brazil	Goncalvez & Goncalvez 1973
	Venezuela	Terán 1974
<i>Gonia texensis</i>	Cuba	Brunner et al. 1975
<i>Lespesia archippivora</i>	Lesser Antilles	Fennah 1947
	Cuba	Ryder & Piedra 1968
	Venezuela	Notz 1972
	Cuba	Brunner et al. 1975
	Venezuela	Terán 1974
	Mexico	Carrillo 1980
	Nicaragua	van Huis 1981
	Brazil	Patel & Habib 1984
<i>Lespesia</i> sp.	Cuba	Ryder & Pulgar 1969
	Venezuela	Notz 1972
	Brazil	Goncalvez & Goncalvez 1973
	Venezuela	Terán 1974
	Brazil	Lucchini & Almeida 1980
	Colombia	Vargas & Sánchez 1983
<i>Linnaemya analis</i>	Venezuela	Terán 1977
<i>Patelloa similis</i>	Brazil	Patel & Habib 1984
<i>Peleteria robusta</i>	Chile	Etcheverry 1957
<i>Pronemorilla mimia</i>	Venezuela	Notz 1972

TABLE 1. (Continued)

Parasites	Countries	Citation
<i>Pseudokea</i> sp.	Venezuela	Terán 1974
<i>Spoggosia calaripennis</i>	Brazil	Costa Lima 1949
<i>Spoggosia floridensis</i>	Venezuela	Terán 1974
<i>Winthemia quadripustulata</i>	Venezuela	Terán 1974
<i>Withemi reliqua</i>	Venezuela	Terán 1974
<i>Withemia roblesi</i>	Chile	Valencia & Valdivia 1973
<i>Winthemia</i> sp.	Chile	Valencia & Valdivia 1973
	Lesser Antilles	Fennah 1947
	Chile	Etcheverry 1957
	Venezuela	Terán 1974
	Trinidad	Yaseen 1978
	Colombia	Vargas & Sánchez 1983
	Brazil	Patel & Habib 1984
HYMENOPTERA		
BRACONIDAE		
<i>Apanteles marginiventris</i>	Lesser Antilles	Fennah 1947
	Surinam	van Dinther 1960
	Venezuela	Notz 1972
	Brazil	Lucchini & Almeida 1980
	Nicaragua	van Huis 1981
	Brazil	Patel & Habib 1984
<i>Apanteles</i> sp.	Barbados	Alam 1978
(glomeratus group)	Trinidad	Yaseen 1978
<i>Aphanteles</i> sp.	Colombia	Vargas & Sánchez 1983
	Brazil	Patel & Habib 1984
<i>Bracon kirkpatricki</i>	Mexico	Peña 1980
	Mexico	Moya 1980
<i>Chelonus cautus</i>	Nicaragua	van Huis 1981
<i>Chelonus insularis</i>	Lesser Antilles	Fennah 1947
(= <i>C. antillarum</i> ,	Cuba	Ryder & Piedra 1968;
<i>C. texanus</i>)		Ryder & Pulgar 1969;
		Brunner et al. 1975
	Venezuela	Notz 1972
	Barbados	Alam 1978
	Trinidad	Yaseen et al. 1981
	Nicaragua	van Huis 1981
	Colombia	Vargas & Sánchez 1983
	Brazil	Patel & Habib 1984
<i>Chelonus</i> sp.	Mexico	Loya 1978
	Mexico	Carrillo 1980
	Brazil	Habib & Patel 1978
<i>Meteorus laphygmae</i>	Surinam	van Dinther 1960
	Venezuela	Notz 1972
	Colombia	Vargas & Sánchez 1983
<i>Palinzele</i> sp.	Trinidad	Yaseen 1978
<i>Rogas caphimal</i>	Nicaragua	Lacayo 1984
<i>Rogas laphygmae</i>	Nicaragua	van Huis 1981
<i>Rogas vaughani</i>	Nicaragua	van Huis 1981
	Honduras	Passoa 1983
<i>Rogas</i> sp.	Cuba	Ryder and Piedra 1968
	Cuba	Ryder & Pulgar 1969
	Honduras	Passoa 1983
<i>Zelee</i> sp. prob. <i>mellea</i>	Nicaragua	van Huis 1980

TABLE 1. (Continued)

Parasites	Countries	Citation
ICHNEUMONIDAE		
<i>Amblyteles</i> sp.	Brazil	Costa Lima 1949
<i>Campoletis flavicincta</i>	Nicaragua	van Huis 1981
	Uruguay	Yaseen et al. 1981
	Brazil	Patel & Habib 1984
<i>Campoletis groti</i>	Brazil	Lucchini & Almeida 1980
<i>Eiphosoma</i> nr. <i>annulatum</i>	Venezuela	Notz 1972
<i>Eiphosoma vitticolle</i>	Nicaragua	van Huis 1981
	Bolivia	Yaseen et al. 1981
	Brazil	Patel & Habib 1984
<i>Eiphosoma</i> sp.	Trinidad	Yaseen et al. 1981
<i>Enicospilus merdarius</i>	Cuba	Brunner et al. 1975
<i>Ophion flavidus</i>	Honduras	Passoa 1983
	Brazil	Patel & Habib 1984
<i>Ophion</i> sp.	Nicaragua	van Huis 1981
<i>Pristomerus spinator</i>	Nicaragua	van Huis 1981
	Brazil	Patel & Habib 1984
<i>Zenillia blanda</i>	Cuba	Brunner et al. 1975
TRICHOGRAMMATIDAE		
<i>Trichogramma exiguum</i> (= <i>T. fasciata</i>) (= <i>T. fasciatum</i>)	Barbados	Alam 1978
<i>Trichogramma</i> sp.	Mexico	Montoya 1979, 1980
	Nicaragua	van Huis 1981
<i>Trichogramma</i> sp. nov	Guadeloupe	Yaseen et al. 1981
EULOPHID		
<i>Euplectrus hircinus</i>	Panama	F. Bennett (pers. comm.)
<i>Euplectrus plathypenae</i>	Lesser Antilles	Fennah 1947
	Venezuela	Marin 1966
	Cuba	Ryder & Piedra 1968; Ryder & Pulgar 1969; Brunner et al. 1975
	Barbados	Alam 1978
	Trinidad	Yaseen 1978
	Colombia	Vargas & Sánchez 1983
<i>Euplectrus</i> nr. <i>insularis</i>	Nicaragua	van Huis 1981
<i>Euplectrus</i> sp. nov	Brazil	Lucchini & Almeida 1980
<i>Euplectrus</i> sp.	Mexico	Montoya 1979, 1980
	Nicaragua	van Huis 1981
SCELIONIDAE		
<i>Telenomus heliothidis</i>	Cuba	Brunner et al. 1975
<i>Telenomus minutissimus</i>	Dominican Republic	Yaseen et al. 1981
	Guadeloupe	Yaseen et al. 1981
<i>Telenomus remus</i>	Guadeloupe	Yaseen et al. 1981
	Dominican Republic	Yaseen et al. 1981

López (1981) reported that in Colombia *Meteorus laphygmae* Viereck is perhaps the most frequently encountered parasitoid of *S. frugiperda* and suggested that it is a good candidate for augmentative release. He provided laboratory-derived data on mass rearing and life cycle. In Córdova, Colombia, Cárdenas et al. (1982) and Valderrama & Tordecilla (1982) found low parasitism rates (1%) for *Euplectrus* sp. and *C. insularis* [= *C. texanus* (Cresson)], respectively. Landazabal et al. (1973) studied the effective-

ness of the nematode *Neoaplectana carpopocapsae* W. for control of *S. frugiperda* larvae in Colombia. Under humid field conditions, the nematode gave acceptable control when applied at 3000/plant. These authors gave details of rearing procedures and of laboratory studies.

Yaseen et al. (1981) reported that since 1976 the CIBC and cooperating agencies have made several introductions of exotic parasitoids of *S. frugiperda* involving at least 11 species in the Caribbean. Cock (1985) updated the report. *T. remus* exerts adequate control of the whorlworm in Barbados and may prove to be a valuable element in integrated control programs on other islands. This species may have been established in the Cauca Valley of Colombia. Ryder & Pulgar (1969) found that parasitism was low in maize in Cuba and associated phenological stage of the host plant to larval stage and rates of parasitism.

In São Paulo, Brazil, Patel & Habib (1984) collected over 2,500 *S. frugiperda* larvae during a 4-year period and found trimestral parasitism rates ranged from 9 to 35%. The most common parasites found were *Campoletis flavicincta* (Ashmead) and *Archytas incertus* (Macquart). Insecticide applications were reported to dramatically reduce levels of parasitism and three hyperparasites of *C. flavicincta* were observed. Fernández & Clavijo (1984) also reported that insecticides reduced effectiveness of certain Venezuelan parasitoids.

Pathogens

Van Huis (1981) concluded, as had previous Nicaraguan entomologists, that *Aspergillus flavus* Link and *Nomuraea rileyi* (Farlow) are both significant pathogens of *S. frugiperda* while *Entomophthora* sp. was unimportant. *Beauveria* sp. was reported to be of utmost importance in Venezuela as a regulating factor of whorlworm populations (Doreste 1975). Agudelo-Silva (1986) found five pathogens in collections made in Venezuela, including an NPV, a GV, *Erynia radicans* (Brefeld) Hunker, Ben-Ze'ev and Kenneth, and *N. rileyi*. As a complex, they killed 14% of the larvae collected. *Fusarium roseum* Link was reported by Fassiatiova et al. (1978) from Cuba. A detailed study of the histopathology and toxicology of an NPV was reported by Jiménez & Bustillo (1981). A Venezuelan strain of a nuclear polyhedrosis virus was studied by Agudelo et al. (1983). García et al. (1984) studied a Brazilian NPV in the laboratory. The factors which are responsible for susceptibility of *S. frugiperda* larvae to *Bacillus thuringiensis* were studied by García et al. (1982).

García & Habib (1978) reported that *Aspergillus parasiticus* Speare could kill adult *S. frugiperda*. Patel & Habib (1982) reported that wasp parasites were effective dispersal agents and inoculators of the fungus in larvae.

Predators

Predators must be of considerable importance in the tropics in control of *S. frugiperda* but researchers are only beginning to make the efforts necessary to appreciate their value. They are difficult to study.

Van Huis (1981) found that *Galerita* sp. and *Nerthra fuscipes* (Guérin-Méneville), two probable predators of the larvae, were more abundant in weedy fields than in clean cultivated plots. He identified 7 reduviids and 4 pentatomids as predators. Other general predators, such as *Nabis* sp., *Geocoris* sp. and *Chrysopa* sp., were also important. Loya (1978) also singled out *Chrysopa* as an important egg predator. Van Huis (1981) did not quantify the effect of predators because a methodology for sampling their populations accurately was not available. Labrador (1967) listed 6 species of predators of *S. frugiperda* from Venezuela. Native predators (e.g., *Polistes versicolor* Oliv. and *Col-*

emegilla sp.) were not effective in regulating whorlworm populations in Trinidad (Yaseen et al. 1981).

Van Dinther (1960) mentioned two birds, *Crotophaga ani* and *Pitangas sulphuratus sulphuratus*, as predators. He and van Huis (1981) reported vespid wasps of the genera *Polistes* and *Polybia* as important predators. Guagliumi (1972/1973) cited these same genera as predators of *S. frugiperda* in sugarcane in northeast Brazil. At the Panamerican Agricultural School and elsewhere in Honduras, *Polybia* spp. readily enter the whorls where they attack and kill larvae (Andrews, unpublished). Attempts to manipulate *Polybia* spp. have been unsuccessful. Gómez & Zapateiro (1982) concluded that 500 *Podisus nigrispinus* Dallas nymphs per hectare were capable of suppressing whorlworm larval infestations of up to 15% in maize.

Another predator which merits special attention is *Doru taeniata* (= *taeniatum*) (Dohrn). These earwigs are good fliers and hide deep in the whorl or behind sheath collars. Van Huis (1981) reported that more earwigs were found in maize intercropped with beans and in weedy maize than in monoculture or clean cultivation maize. In petri dish studies, van Huis (1981) showed that eggs and instars 1 through 3 were readily consumed while later instars were rejected. In field studies with one adult earwig per plant, an average of 57% of the whorlworm egg masses put on the plants were consumed. Varying the number of masses from 1-13/30 plants did not affect predation levels. Egg masses were either completely consumed or untouched. In other field cage studies with one adult *D. taenita* per plant, artificial larval infestation of 2 to 4/whorl were reduced by 50% within 6 days. The average damage level of injured plants was also reduced significantly. Earwig population densities are variable, but commonly reach 1 or more per plant by late whorl stage both in Nicaragua and Honduras (van Huis 1981). Unfortunately, the earwig does not usually colonize in high numbers during the first critical few weeks of plant growth. Farmers are rarely aware of the importance of *D. taeniata* and generally consider it to be a pest because it consumes pollen in rice, sorghum and maize. Jones et al. (in press) provided life table information for *D. taenita*.

In studies in Honduras (Andrews, unpublished), the most important egg predators were *D. taeniata*; a mirid, *Creontiades* sp. and 2 species belonging to the genus *Diabrotica*. The latter genus is normally considered to be strictly Phytophagus. During three 48 hour observation periods, 50-95% of the egg masses placed in the field were destroyed by predators.

Sequeira et al. (1986) reported that *Solenopsis* spp. were effective predators of both *S. frugiperda* and *Diatraea lineolata* (Wlk.) in seedling maize and sorghum. Little effect on yield was observed.

EFFECTS OF CULTURAL AND MECHANICAL PROCEDURES ON *S. frugiperda*

A major area of research which has to be addressed by neotropical entomologists is the effect of different cropping systems on pest densities and damage. This is certainly the case with *S. frugiperda*, where a number of experiments have indicated that low or no till agriculture and polycultures are less severely attacked by the pest than monocultures planted using conventional cultivation. One of the earliest tests involved the interplanting of sunflower and maize in Cuba (Ryder 1968b); interplanted maize was less severely attacked and yielded better than monoculture maize. Del Rosario et al. (1981) in the Dominican Republic showed that the use of no till techniques reduced whorlworm infestations by 30-60%. Yields were much higher in no till plots due to a number of factors, not just whorlworm attack. Studies carried out in Costa Rica (Shenk & Saunders 1981, Shenk et al. 1983, Saunders 1985) showed consistently lower whorlworm damage in no till plots as compared to conventional tillage. No tillage plots offer many other agronomic and economic advantages and merit considerably more attention by tropical researchers.

Van Huis (1981) studied several aspects of cultural control. He found significantly greater *S. frugiperda* damage in monoculture maize than in maize interplanted with beans. Damage reduction was generally on the order of 20-30%. The more complicated polycultural systems generally contained more predators, such as *Doru* sp., spiders, predatory ants and tachinids. However, van Huis concluded that the major reason for reduced infestations was less oviposition by moths and less successful dispersal by first instar larvae. More egg masses were found in monoculture maize than in maize intercropped with beans. It is not known if interplanted beans have any olfactory effect on *S. frugiperda* feeding in maize. Unfertilized maize received fewer eggs than fertilized, but whorl injury was not statistically different. No effect on oviposition was seen when distance between rows of maize was varied, nor were percentages of plants infested affected significantly by planting distance. Weeds present between rows of maize increased oviposition on the maize; very few egg masses were found on the weeds. Apparently, most larvae infesting the weeds originated from masses which were laid on maize plants. Farmers often report increased severity of whorlworm attack on maize shortly after they hand weed the crop; this is because many larvae move from the desiccating weeds to the maize. Increased attention to sampling is needed at this time. If weeding is required and chemical control is not possible, the severity of the attack may be reduced by leaving a thin strip of weeds in mid row.

In two experiments, applications of soil directly to the whorls provided no control of larvae in Nicaragua (van Huis 1981). Dardón et al. (1985) found that sand applied to maize whorls in Guatemala reduced larval infestations.

Clavijo (1981a) reported that planting density did not affect the percentage of plants infested by the whorlworm. In Venezuela, rice fields are commonly flooded until the plants are nearly covered in order to drown larvae (Labrador 1967) Castro et al. (1987a) observed no effect of pigeon pea on infestations of interplanted maize and sorghum plants.

DISPERSION, SAMPLING AND ACTION THRESHOLDS

Clavijo (1978a) reported that in Venezuela larval distributions were best described by a Poisson distribution; therefore, a random sampling allocation is appropriate. In a subsequent paper, Clavijo (1978b) estimated that between 122 and 190 plants had to be sampled to estimate the number of larvae/plant with 5% probability of error and precision levels of 20 to 5%. Barbosa & Perecin (1982) found that the number of larvae/10 plant samples was best described using the negative binomial model. The percent of plants infested in 10-plant samples adjusted best to the binomial distribution. Baez et al. (1980) found both aggregated and random dispersion patterns depending upon instar sampled and plant growth stage. Aguilera & Vargas (1970) reported that 0.45 larvae/whorl justified an insecticide application in Chilean maize. According to van Huis (1981), resource scarce farmers should count the number of injured whorls in 20 consecutive plants at 5 randomly selected sites. Carvalho & Silveira (1971) reported higher infestations in the edges of fields than in the center. Andrews (1984) provided detailed sampling recommendations for the pest in several crops grown in Honduras. Andrews et al. (1986) recommended sampling 20 plants in each of 5 sites and use of a 40% infestation rate in Honduran maize.

The use of sex attractant-baited sticky traps for predicting outbreaks of larvae was suggested by Ward et al. (1985). Herrera et al. (1982), Flores and Zapata (1982) and Izquierdo et al. (1983) reported the results of Mexican trials using various attractants and trap locations. Silvain & Hing (1985) and Silvain (1986) reviewed the programs developed in French Guiana to warn pasture managers of impending larval outbreaks on the basis of trap counts of male moths.

HOST PLANT RESISTANCE

Van Huis (1981) reported that a hybrid maize variety was significantly less severely infested by *S. frugiperda* than was a local variety, Tuza Morada, in the early weeks of development. Silva (1978) reported that 7 of 33 maize lines which he tested in Oaxaca, Mexico, were resistant or moderately resistant to *S. frugiperda*; all were susceptible to *Diatraea* spp. Peairs and Saunders (1981) suggested that yield reductions must be considered the most reliable indicator of resistance; damage estimates did not correlate well with yield reductions. Carvalho et al. (1971) working with maize in Brazil felt that the use of a 5 point foliar damage rating scheme was valuable; yield reductions were well correlated with foliar damage.

Carvalho & Rossetto (1971) tested sorghum varieties for resistance to *S. frugiperda* using the 5 point damage system. Other Brazilian sorghum trials were reported by Lordello et al. (1980) and Mesquita et al. (1980).

Guiragossian et al. (1981) reviewed progress made at CIMMYT on development of whorlworm resistant sorghum cultivars. There is no relationship between HCN content of sorghum and resistance to the pest. The resistance which has been observed must be due to other mechanisms, including tolerance. Tolerance was confirmed to be the principal mechanism involved (Guiragossian & Mihm 1985).

Castro et al. (1987c) reported that a Honduran dwarf sorghum showed antibiosis to *S. frugiperda*. Efficient mass rearing and infestation techniques to screen for host plant resistance to the whorlworm were summarized by Mihm (1983).

CHEMICAL CONTROL

Insecticides are widely used in Latin America for control of *S. frugiperda*. The following remarks supplement Pitre's (1986) review. Despite the recognized value of insecticides only certain farmers are capable of purchasing and applying them. For example, only 12% of Nicaraguan farmers use insecticides in maize; most applications were made against *S. frugiperda* (van Huis et al. 1982).

Soil applications of carbofuran and mefosalan at planting are increasingly common in Central America. Van Huis (1981) observed that they reduced larval populations significantly for about 15 days, but thereafter whorlworm populations were higher, often significantly so, when compared to check plots; he hypothesized that the insecticides impeded natural enemies, possibly the nematode *Hexameris* sp. However, soil treatments generally were associated with statistically significant yield increases. In Surinam, Segeren & Sharma (1978) found that carbofuran use resulted in higher yields as compared to check plots even when all known pests were present at very low levels. This compound provided effective control of *S. frugiperda*. Dardón et al. (1985) found that furathiocarb seed treatments protected seedling maize and increased yields in Guatemala. Trabanino et al. (1987) found that it gave better control than any other sorghum seed treatment.

Nakano & Zucchi (1971) cited the advantages of using vermiculite as a carrier in granular insecticides for use against *S. frugiperda*. Diazinon granules were effective in Cuban maize (Ryder 1967). Mixing of insecticides with sawdust and subsequent hand applications to whorls was effective in maize (Segeren & Sharma 1978). Sánchez & Gonzalez (1982) found granular formulations to be more effective than emulsifiable concentrate formulations of the same active ingredients. Cruz et al. (1983) described a tractor mounted apparatus used to apply granular insecticides directly to maize and sorghum whorls. A similar, hand-operated machine was reported by Cruz et al. (1984). Reyes et al. (1983) described a hand-held applicator for granular insecticides which can be made with local materials. Cevallos (1976) illustrated 5 application methods for granular formulations.

In Nicaragua, the selective application of granules only to those plants showing symptoms of whorlworm damage resulted in the same post-treatment infestation levels as with general applications. However, yields were higher in plots receiving the latter treatment. Savings in active ingredients on the order of 2/3 make selective applications attractive to resource limited farmer. The hand application of a chlorpyrifos and sawdust mixture can reduce use of active ingredients by 80% without sacrificing control (van Huis 1981). Selective applications were not effective in El Salvador (Reyes et al. 1983).

Several Brazilian references may be cited. Davidson (1966) reported that *S. frugiperda* was susceptible to carbaryl, but appeared to be resistant to certain organochlorines. Batagello & Monteiro (1970), Carvalho et al. (1971) and Gomes de Lima and Cola (1976) confirmed that carbaryl was effective in Brazil. In tests conducted in the same state, Waquil et al. (1982) found that diazinon worked well, but carbaryl was largely ineffective. However, Cruz et al. (1983) found that carbaryl controlled the pest well in Mato Grosso. Cruz and Pereira (1984) reported that trichlorfon and three other compounds gave adequate control in maize. According to Caetano & Schweder (1983) carbaryl and trichlorfon were recommended in Rio Grande do Sul, but they presented no efficacy data.

Few recent references from Andean countries were available. Casanova (1966) found that carbaryl granules gave adequate, but not excellent, control in Peru. Díaz & Flores (1969) found that carbaryl provided some protection to ears of maize against *S. frugiperda* and *Heliothis zea*; trichlorfon did not. Carbaryl was effective in Peru for whorl protection (Peña 1974). Carbaryl was recommended in Ecuador (Cevallos 1976). Campos (1982) provided toxicological data for larvae collected in Chilean alfalfa. Trichlorfon did not effectively kill larvae in the 1977 study reported by Clavijo (1984a), but diazinon functioned well in 1979 (Clavijo 1984b).

The work of Alvarado (1976) indicated that neither carbaryl nor trichlorfon was effective in Quintana Roo, Mexico. However, Sifuentes (1977) still recommended carbaryl for use in Mexican sorghum. This insecticide gave superior control in 1976 tests in Sonora (León 1978). López & León (1980) found carbaryl to be moderately effective in laboratory tests using larvae collected in northeast Mexico. In Tamaulipas, both carbaryl and trichlorfon were effective in suppression of *S. frugiperda* in maize (Charles et al. 1980). Tello & Díaz (1982) reported that in Sinaloa, use of carbaryl did not decrease foliar damage caused by *S. frugiperda* but did increase yields.

Based upon limited experimental data and considerable knowledge of pesticide use patterns, the following generalizations may be made regarding physiological resistance in *S. frugiperda* in Central America. Carbaryl is not effective and diazinon and trichlorfon are not reliable. Standard dosages of most pyrethroids give only sporadic control. Methyl parathion was not effective in the laboratory against third instar larvae from Honduras, but subsequent field tests against first instar larvae did not indicate resistance (Pitre 1987). Methomyl, chlorpyrifos and phoxim are the products of choice. Carbaryl was recommended in Nicaragua by Sequiera et al. (1979), but we have determined that it is of no value in the field in either El Salvador or Honduras (Andrews and Marengo, unpublished). Young (pers. comm.) reported that the Salvadorean strain he tested showed 400-fold resistance to carbaryl. Trichlorfon did not give satisfactory control under Nicaraguan conditions (van Huis 1981).

Hellpod & Mercado (1984) found that larval infestations and damage to maize in Nicaragua were reduced by application of a 0.2% neem extract to the whorls. Lagunes and coworkers (e.g., Lagunes et al. 1982) are actively screening extracts of Mexican plants for activity against *S. frugiperda*. Llanderal and Nieto (1982) reported results of laboratory studies of the effect of diflubenzuron on egg hatch and larval ecdysis. Cerecer et al. (1983) found triflumuron to be slow acting but selective in Mexican maize and sorghum.

CONCLUDING REMARKS

A sizable body of information concerning *S. frugiperda* in the neotropics has been developed by expatriate and Latin American scientists. Many comprehensive, careful studies were encountered; others were preliminary and of uneven quality. Seemingly contradictory findings may occasionally result from inadequate study or improper methods. More importantly, however, they reflect the geographic, ecological and agronomic heterogeneity of Latin America. Rather than trying to characterize the species throughout its nearly continental range, we should seek to study it in limited subregions. Moreover, the work of Pashley et al. (1985) compels us to rethink assumptions regarding the genetic homogeneity of the species.

It is ironic that most of the well financed research involving full-time, experienced, professional entomologists has been conducted in temperate zones (both the US and the southern cone of South America) where the pest's forays are seasonal. Many studies would be best carried out in the tropics where the species evolved and persists permanently. Long-term collaborative research projects located in the tropics can be expected to provide insights and information which are otherwise unattainable.

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SCIENTIFIC NOTES
TRAPS FOR COLLECTING LIVE
EUPHASIOPTERYX DEPLETA (DIPTERA: TACHINIDAE)
AT A SOUND SOURCE

H. G. FOWLER

Instituto de Biociencias, Universidade Estadual Paulista
UNESP, 13500 Rio Claro, S Paulo, Brazil, and (formerly)
Entomology & Nematology Department, 3103 McCarty Hall,
University of Florida, Gainesville, Florida 32611, U.S.A.

After Wolcott (1940) reported rearing the tachinid *Euphasiopteryx depleta* (Wied.) from a *Scapteriscus* mole cricket (Orthoptera: Gryllotalpidae), interest has been shown in using this fly in introductions for the biological control of *Scapteriscus*. Fowler and Kochalka (1985) reported attracting *E. depleta* to the synthesized broadcast calls of *S. acletus* Rehn & Hebard in Paraguay. Using similar synthesizers (Walker 1982), Fowler and Garcia (1987) reported additional captures of *E. depleta*, and of rearing it from *S. acletus*, *S. vicinus* Scudder and *S. abbreviatus* Scudder. In those studies, attracted female *E. depleta* were captured with an aerial net over the synthesizer and larvae taken from them were placed on mole crickets to achieve laboratory parasitism. Subsequently, aerial nets were replaced with a sheet of plastic covered with Tanglefoot®, and large numbers of female *E. depleta* were obtained. However, in the laboratory, often the Tanglefoot would interfere with obtaining larvae, as many were killed in the female's body through asphyxiation, or were gummed and died as they left the female's body. Also, for some laboratory studies, healthy, gravid females were needed, which could not be obtained by sticky trapping. Using flashlights and aerial nets to capture females at sound synthesizers was not highly productive, as *E. depleta* tended to avoid lighted areas.

To overcome these problems, two traps were designed and field tested (Fig. 1). Both traps were inexpensive, consisting of a wire frame, with muslin sides and funnels, which were used to direct flies into the trap. Cardboard baffles mounted on wire were used to hinder fly escape after capture (Fig. 1). The muslin base was built so that the trap could easily fit over a sound synthesizer (Walker 1982) or over a tape player.

Trap designs were evaluated by comparison of the numbers of flies caught in each with the numbers caught on sticky traps. In December 1984, three sound synthesizers broadcasting *S. vicinus* songs were placed in the field in Rio Claro, state of São Paulo, Brazil. One synthesizer was fitted with sticky plastic sheeting, and the other two with the two trap designs. After each night, the location of each was switched. Each synthesizer was separated by 30 m from its neighbor. The sticky trap caught 132 flies during 2 weeks of trapping. Trap B, fitted with 5 funnels, of which 4 were lateral, was about 2.5 times as efficient as design A, consisting of only 1 funnel (Fig. 1). Trap B was about a third as efficient as the sticky trap.

Field observations indicated that flies alighted on the muslin and walked extensively over the trap's external surface until they were channeled into its interior through the funnels. Many flies departed without ever reaching the trap's interior. This explains why the numbers of female *E. depleta* caught in the traps were much less than with sticky traps. If large numbers of flies are required, sticky traps should be used. If, however, viable healthy females are required, then trap design B should be used. Sticky traps are recommended for population monitoring.

I thank João Justi and Madelena Lima Costa for their assistance with the field portion of this project. This study was funded in part by a grant, USDA No. 83-CR-SR-2-

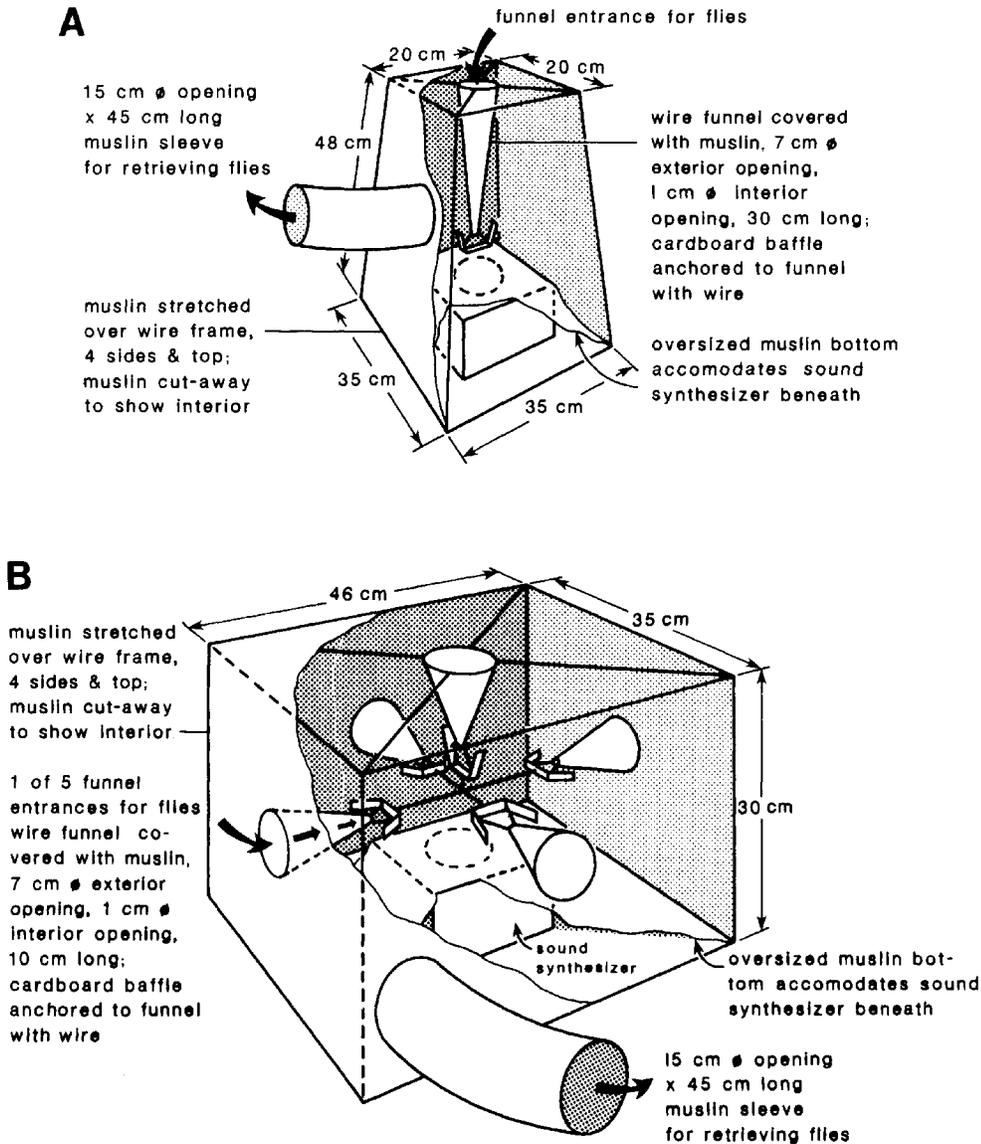


Fig. 1. Trap designs evaluated for live captures of healthy *E. depleta* females. Frames of both are of wire, and sides and funnels of muslin. Note how trap base sits over a sound trap. Baffles are made of cardboard and wire, and mounted over funnels.

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DIFFERENTIAL INJURY BY LESSER CORNSTALK BORER
(LEPIDOPTERA: PYRALIDAE)
IN SOYBEANS OF DIFFERENT GROWTH STAGES

L. B. BRAXTON

Senior Research Biologist Agricultural Products Department
Dow Chemical U.S.A., 5100 W. Kennedy Boulevard, Suite 450
Tampa, FL 33609 USA

AND

M. E. GILREATH

North Florida Research and Education Center
University of Florida, IFAS
Quincy, FL 32351 USA

The lesser cornstalk borer (LCB), *Elasmopalpus lignosellus* (Zeller), has been ranked one of the top four insect pests of soybean in Florida every year for the last four years, with crop losses estimated as high as \$1.7MM (Sprenkel 1984, 1985, 1986, 1987). Damage by LCB to soybeans is usually restricted to the period from plant emergence through the early vegetative stages (Todd & Suber 1988). Although other stages may be attacked, seedling soybeans are most susceptible to injury (Isley & Miner 1944). Our observations indicate a growth differential of only seven days can substantially affect the extent of damage incurred by lesser cornstalk borer larvae.

Observations were made in a 40-acre field of 'Centennial' soybeans in Jackson County, Florida. Approximately half the field had been planted June 19, 1987, and the other half June 26. Both plantings were adjacent to corn, which was nearing maturity about the time the soybeans were planted. Initial observations were made August 3. The younger side of the soybean field was noted to have a poor stand; many dead plants were present and several large LCB larvae were seen crawling on the soil surface near the plant bases. No larvae and few damaged plants were observed in the older soybeans. Numerous adults were flushed throughout the field.

Additional observations were made four days later. At that time, percent damaged plants was determined for each side of the field by sampling five adjacent plants at each of 20 randomly selected sites (100 total plants per side). Plants were unearthed with a trowel and inspected for larvae or characteristic LCB damage, as evidenced by visible stalk boring or stem feeding near the plant base, sometimes accompanied by a silken feeding tube. Slightly damaged plants exhibited varying degrees of stunting and chlorosis, while many heavily damaged plants were dead and had a characteristic brown teepee-shaped appearance (Herbert & Mack 1987).

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In the younger soybeans, 41% of the plants inspected showed evidence of LCB damage, and many of the damaged plants were dead or dying. In contrast, only 10% of the older plants sampled were damaged. Local areas in the field that showed apparent herbicide injury (crinkled, chlorotic leaves) or other physiological stress also had greater LCB damage.

While soybean planting date cannot be fully utilized as a LCB management tool until accurate methods of predicting LCB development are developed, these observations indicate that younger soybeans may be more susceptible to LCB injury and this consideration should be incorporated into LCB management strategies.

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THE FIRST RECORDS OF THE WHITEFRINGED BEETLE,
GRAPHOGNATHUS LEUCOLOMA (COLEOPTERA:
CURCULIONIDAE), IN NEW MEXICO AND TEXAS

R. W. SITES AND H. G. THORVILSON
Department of Agronomy, Horticulture, and Entomology
Texas Tech University
Lubbock, Texas 79409

Graphognathus leucoloma (Boheman) (Coleoptera: Curculionidae) is one of four species of this genus in the United States known as whitefringed beetles. This parthenogenic and flightless species is highly polyphagous and has been reported to feed on 385 species of plants (Young et al. 1950), many of which are crops. Adult beetles feed on leaves and usually cause only minor damage (Anon. 1972). Ottens & Todd (1980) showed that as many as 50 *G. leucoloma* adults per soybean plant were required to significantly reduce pod production. However, the primary damage is incurred through the feeding activity of the larvae on subterranean plant parts. Larvae typically feed on newly germinated seeds and roots, and tunnel through tubers. Damage by larvae is evidenced as chlorotic, wilted, or dead plants, and the damage in heavily infested fields usually progresses until the crop must be replaced (Gross & Harlan 1975). Populations of *G. leucoloma* reach

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peak levels in pure stands of legumes (including alfalfa) as compared with grasses (King & East 1979) and fecundity is highest among adults on legumes (East 1977). Many crops grown in the southwestern U.S., such as alfalfa and cotton, are recorded as host plants of this beetle (Anon. 1959). Records of this pest in South America indicate that it could become established in irrigated areas of the western U.S. (Anon. 1959).

Whitefringed beetles are native to Argentina, Brazil, Chile, and Uruguay (Young et al. 1950). In addition to South America, *G. leucoloma* is presently known to occur in southern Africa, southeastern Australia, New Zealand, and the southeastern United States (May 1975). Whitefringed beetles were first collected in the United States near Svea, Okaloosa Co., Florida in 1936 (Buchanan 1947). Buchanan (1947) discussed distribution and Warner (1975) provided maps that show the U.S. distribution of the four *Graphognathus* species. *G. leucoloma* occurs from the Florida panhandle north to Virginia and Kentucky, and west to central Arkansas and Louisiana.

Prior to this report, no specimens of *G. leucoloma* were known from New Mexico or Texas. We collected adult and larval specimens of *G. leucoloma* in an irrigated alfalfa field ca. 10 km north of Lovington, Lea Co., New Mexico on 25 September and 16 October 1987. This ca. 4.0 ha field was adjacent to State Highway 18. To estimate adult beetle density, we randomly placed 10, one-meter quadrats in a transect across this field and recorded 5.6 ± 2.0 ($\bar{x} \pm SE$) live and dead adult beetles/meter² on 25 September. Visual inspection for adult beetles in four other alfalfa fields within a ca. 8 km radius revealed very low infestation levels (<1 beetle/meter²) in two fields and no *G. leucoloma* in the other two. The Texas record is based on one adult specimen of *G. leucoloma* collected at Buffalo Springs Lake, Lubbock Co., Texas on 5 October 1986 by Mr. K. Stair.

These records represent a disjunct area of *G. leucoloma* occurrence ca. 1100 km west of the previously known range (Warner 1975). Voucher specimens from each collection locality and date are deposited in the Texas Tech University Entomological Collection.

The establishment of *Graphognathus leucoloma* in this area represents the addition of a significant pest because this species is both polyphagous and highly destructive. Alfalfa, cotton, and other crop host plants are grown extensively in eastern New Mexico and northwestern Texas and represent a vital part of the agricultural economy of these areas.

We would like to thank Mr. J. C. Snodgrass, Texas Tech University, for bringing the New Mexico situation to our attention; Dr. C. W. O'Brien, Florida A&M University, for identifying specimens; Dr. H. R. Burke, Texas A&M University, for searching that Collection for Texas records; and Ms. B. J. Nichols, Texas Tech University, for assistance with our field survey. We also thank Drs. L. Chandler, H. L. Schramm, and Mr. J. C. Cokendolpher, Texas Tech University, for critically reviewing this manuscript. Funding was provided by the State of Texas Line Item: Noxious Brush, Swine, and Vegetables. This is Contribution T-10-188, College of Agricultural Sciences, Texas Tech University, Lubbock, Texas, 79409.

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CENTIPEDES AND MILLIPEDES IN THREE CENTRAL FLORIDA PLANT COMMUNITIES (CHILOPODA AND DIPLOPODA)

DAVID T. COREY
Department of Biological Sciences
University of Central Florida
Orlando, FL 32816

The scorpion, pseudoscorpion, opilionid and ground surface spider faunas in pond pine, sand pine scrub, and flatwoods communities in central Florida were recently documented (Corey 1987, Corey & Taylor 1987). This study describes the composition and abundance of centipedes and millipedes in these communities.

The study sites were within natural areas of the University of Central Florida campus, located approximately 17km east of Orlando in Orange County (S10 R31E T22S). The three plant communities are described in Corey (1987) and Corey & Taylor (1987).

Pitfall traps as described by Corey & Taylor (1987) and Corey (1987) were the collecting device; they have been used to sample milliped populations (Fairhurst 1979).

Species composition and abundance for centipedes in the communities are presented in Table 1. Twenty-eight centipedes representing 4 families and 5 species were collected.

The most abundant centipede was *Neolithobius xenopus* (Bollman) and represented 50% of the total centipede population. Most centipedes were collected in July (39.3%) and September (21.4%).

Species composition and abundance of millipedes collected in the communities are listed in Table 2. Ninety-seven millipedes from 4 families and 5 species were collected.

Dicellarius okefenokensis (Chamberlin) was the only millipede found in all three communities. This is a new county record for *D. okefenokensis* in Florida. *Dicellarius okefenokensis* has been reported from beneath logs in moist hardwood habitats (Shelley 1984). The three communities examined in this study are pinelands and therefore this is a new habitat for *D. okefenokensis*. It appears to be active during cool weather with 14.7% collected in January and 85.3% collected in March. Of the 17 Florida records

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TABLE 1. CENTIPEDES COLLECTED IN PITFALL TRAPS IN POND PINE (PP), SAND PINE SCRUB (SPS), AND FLATWOODS (FW).

Species	May			July			September			November			January			March			Totals		
	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW
LITHOBIOMORPHA																					
Lithobiidae																					
<i>Neolithobius xenopus</i> (Bollman)				2	4		4		1			1			1			1	6	4	4
<i>Neolithobius</i> sp.															1				0	0	1
GEOPHILOMORPHA																					
Geophilidae																					
<i>Geophilus mordax</i> Meinert				2											1			1	2	0	2
SCOLOPENDROMORPHA																					
Cryptopidae																					
<i>Scolopocryptops sexspinosus</i> (Say)	3			3				1		1									7	1	0
Scolopendridae																					
<i>Scolopendra viridis</i> Say																		1	0	1	0
Total	3	0	0	7	4	0	4	1	1	1	0	1	0	0	3	0	1	2	15	6	7

TABLE 2. MILLIPEDES COLLECTED IN PITFALL TRAPS IN POND PINE (PP), SAND PINE SCRUB (SPS), AND FLATWOODS (FW).

Species	May			July			September			November			January			March			Totals		
	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW	PP	SPS	FW
JULIDA																					
Parajulidae																					
Species #1										3	2		4					0	7	2	
Species #2										42					4			4	0	46	0
SPIROBOLIDA																					
Spirobolidae																					
<i>Chicobolus spinigerus</i> (Wood)	2								1									2	0	1	
CALLIPODIDA																					
Casiopetalidae																					
<i>Abacion lactarium</i> (Say)							1			2					2			0	5	0	
POLYDESMIDA																					
Xystodesmidae																					
<i>Dicellarius okafenokensis</i> (Chamberlin)														1	4	14	5	10	14	6	14
Totals	2	0	0	0	0	0	0	1	1	0	47	2	0	5	4	14	11	10	16	64	17

Scientific Notes

reported by Shelley (1984) 15 were found from October through March, only 2 records were collected from warm weather (June) and this may be due to the method of collection.

Parajulidae is in need of revision and it is difficult to identify specimens below the family level. Two species are reported as Parajulidae species 1 and 2. Parajulidae sp. #2 was the most common millipede (47.4%) and was collected only in November (91.3%) and March (8.7%) in sand pine scrub.

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