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THE PERCEPTION OF INFRARED RADIATION BY THE

SPINY RAT MITE LAELAPS ECHIDNINA

(ACARI: LAELAPIDAE)

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree of Doctor of Philosophy in the Graduate
School of The Ohio State University

By

William Alvin Bruce, B.S., M.Sc.

* * * * *

The Ohio State University

1969

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FIELDS OF STUDY

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INTRODUCTION

Detection of hosts, prey, or others of the same species has been attributed to a variety of stimuli (Camin, 1950; Hodgson, 1956; Braken, et al., 1962; Brown, et al., 1964). However, surprisingly little is known regarding the sensory mechanisms involved (Burr and Catton, 1960; Acree, et al., 1968; Ash, 1968; Machan, 1968). One of the most intriguing theories purporting to explain the detection processes in arthropods is the infrared radiation (IR) theory of communication. It is made all the more interesting when one considers that the IR region is precisely that portion of the spectrum where a warm-blooded animal (300° K) would emit radiation. In addition, molecules are known to emit characteristic radiation due to various vibrational and rotational energies and, as a consequence, complex molecules such as pheromones might also be sensed using IR emissions (Wright, 1963; Moncrieff, 1967).

The theory is not new but is unique because it presupposes the organism has a wavelength discrimination capability and does not respond only to changes in intensity (cf. Bullock and Diecke, 1956; Humphries, 1968; Warren and Proske, 1968). This does not imply that wavelength discrimination is restricted exclusively to the IR range (McEnroe and Dronka, 1966) or that an organism could not utilize two

different portions (e.g., visible and IR) of the spectrum (Callahan, 1968).

If insects, which have been studied almost exclusively in regard to IR communication theory, can respond selectively to different wavelengths then it seems logical to assume that some kind(s) of receptor exists to receive the IR radiation. To test this assumption, Grant (1949) made actual measurements of insect spines and as a result suggested the dielectric antenna as a possible mechanism for an IR receptor. Since that time, Callahan (1965a,b,c) has expanded on the theory and this receptor mechanism, and has demonstrated electrophysiologically (Callahan, 1968) that at least some insect spines are capable of functioning as IR receptors.

Opposition to the radiation theory has usually centered around IR emission from molecular sources (i.e., pheromones). One example is in regard to the assembling of moths for the purpose of mating. Kettlewell (1961) has supported the olfaction-pheromone concept and has found Laithwaite's (1960) conclusions that IR radiation does play a role in moth behavior completely untenable. However, non-pheromone sources have been implicated in assembling in at least one insect. Congregation of a buprestid beetle, Melanophila acuminata De Geer, to recently burned forest areas is apparently accomplished by IR sensitive areas on the thorax capable of wavelength discrimination.

IR Communication

Electromagnetic waves are patterns of electric and magnetic fields oscillating in mutually perpendicular planes at right angles to the direction of movement. The electromagnetic spectrum consists of radiation ranging from high frequency ($\bar{\nu}$) gamma rays to low frequency radio waves. Traditionally the spectrum has been divided into several different regions. The portion of the electromagnetic spectrum extending from a wavelength (λ) of 0.75μ to $2,500 \mu$ comprises the infrared region. It is further divided into the near ($0.75 \mu - 2.5 \mu$), intermediate ($2.5 \mu - 25 \mu$), and far ($25 \mu - 2,500 \mu$) infrared (Vasko, 1968). A common feature is that all the radiation, in a vacuum, travels at the same speed ($C = 3 \times 10^8 \text{ m sec}^{-1}$) but differs in frequency and wavelength. These quantities are related by:

$$\lambda \bar{\nu} = C$$

Heat sources emit radiation because of increased temperature occurring in substances and the resulting emission is referred to as heat radiation. Solids and liquids emit continuous spectra whereas gases and vapors emit line or band spectra. Every body, then, with a temperature above absolute zero is capable of emitting radiation. The amount and spectral characteristics will depend on the absolute temperature of the object and upon its nature and surface finish. By definition a black body is any object which absorbs all radiation incident upon it and as a consequence will, at a given temperature, emit the maximum radiation possible. The emissivity factor, or radiating and absorbing efficiency, of a black body is unity. Most

objects, however, have an emissivity factor below unity and are termed gray bodies. As the temperature of a black body (or gray body) increases, the intensity of the radiation at all wavelengths increases rapidly. Wien's Displacement law states that as the temperature of a black body increases, the radiation peak shifts to shorter wavelengths:

$$\lambda_m T = K \quad (1)$$

where K is a constant with a numerical value of $2897.8 \mu^\circ \text{K}$.

Luminescent sources (Vasko, 1967) are those in which the emitted radiation is initiated by a means other than temperature increase. An example is the absorption of another radiation as in a laser. The laser (Light Amplification by Stimulated Emission of Radiation) produces radiation having several different characteristics from that produced by thermal sources.

Molecular sources, as in the case of a CO_2 gas laser, emit radiation when a transition is made between two vibrational or rotational energy levels (Pike, 1967). An electrical discharge causes collisions to occur between energetic electrons and CO_2 molecules. As a result, the molecules are excited to various vibrational levels. When more molecules exist in the upper laser level than in the ground state, a population inversion is said to have occurred. Lasing takes place during the de-excitation process as the molecule returns to a lower laser level. From the lower level the molecule returns to ground state. The efficiency of the CO_2 laser can be increased by:

1) maintaining a high population inversion and, 2) facilitating the

de-excitation process so that the molecules are again ready to be excited to the upper laser level (Patel, 1968). High population inversion is aided by vibrationally excited nitrogen molecules. Helium appears important in the two processes and both molecules are, consequently, added to the lasing medium. The resulting radiation emitted by the laser is predominately the 10.6μ wavelength.

Conventional light sources in which the photons or quanta are emitted in a random fashion are classed as incoherent radiators. As such, a mixture of frequencies in different phases is produced. In contrast, lasers produce coherent radiation. Coherency implies both temporal and spatial coherence.

Temporal coherence requires that each cycle of every wave takes the same amount of time to pass a given point. In essence, the frequency is the same and is termed monochromatic.

Spatial coherence necessitates having waves of the same frequency and in phase with each other in space (Pike, 1967). Coherency, therefore, implies both temporal and spatial coherence.

Transmission of electromagnetic radiation through the atmosphere is not always complete. Water vapor and carbon dioxide are the two most important attenuators or absorbers of radiation in the atmosphere (Hackforth, 1960). Various portions of the spectrum permit most or all radiation to pass through and are known as atmospheric transmission windows. One very large window in the intermediate infrared occurs between 7.5μ - 14μ . Curiously enough, this is precisely the range within which a warm-blooded animal could be expected to emit its peak

radiation according to equation 1 (i.e., at approximately 9.5μ). A parasite utilizing infrared radiation as a means of host detection might be expected to possess receptors which would be operable in this range.

A dielectric antenna or aerial has been suggested as a structure which could function to receive IR radiation. Kiely (1953) has provided a most comprehensive study of dielectric antennas and has defined them as primary radiators which employ a system of dielectric elements, as distinct from a system of conductors, to radiate electromagnetic energy or to collect radiated electromagnetic energy from one or more directions. It should be emphasized that all properties of transmitting antennas are also characteristic of receiving antennas even though the terminology used to describe these properties is conventionally that of a radiating antenna. If a dielectric antenna is expected to operate optimally it must possess certain structural as well as certain electrical properties. Most studies (Kiely, 1953; Griffith, 1968) have involved empirical measurements of actual models and the main emphasis here will be given to structural considerations of the hollow tube type of dielectric antenna.

Structurally, four properties describe a dielectric tubular antenna: dielectric constant (ϵ), diameter, length, and wall thickness. Since the inter-relationships of these properties have been thoroughly investigated (Kiely, 1953; Griffith, 1968) and adequately summarized (Callahan, 1967; Griffith, 1968) only a brief outline will be presented.

1. A high dielectric constant would require a tube with thinner

walls than a tube with a low dielectric constant because the electric path length in the wall would be greater in the latter case (Kiely, 1953).

2. Tapering the antenna adds greatly to its operating efficiency. Kiely (1953), using polystyrene rods ($\bar{\epsilon} = 2.5$) has provided appropriate formulae for the maximum and minimum diameter ($D_{\max}$, $D_{\min}$) necessary for this optimization:

$$D_{\max} = \lambda_0 / \sqrt{\pi(k-1)} \quad (2)$$

$$D_{\min} = \lambda_0 / \sqrt{2.5\pi(k-1)} \quad (3)$$

where λ_0 is the free space wavelength and k is the dielectric constant.

3. The directionality of a dielectric antenna is proportional to the length and at an optimum length the resulting radiation pattern will be found to have one dominating lobe (the main lobe) and several smaller lobes (side lobes) and, it is desirable to have as little energy as possible in the side lobes. Six wavelengths appears about the optimal length (Griffith, 1968).

4. If wall thickness of the tube is at a critical value, which is a small fraction of the wavelength, for a particular value of $\bar{\epsilon}$, then the radiation pattern will be essentially single lobed and the most likely mode, or pattern of oscillation, excited would be the hybrid HE_{11} mode (Kiely, 1953; Okress, 1965).

5. By combining a number of dielectric antennas the efficiency and performance of the detection system can be greatly increased. Such a set of antennas is called an array.

The Behavior of Laelaps echidnina

Laelaps echidnina Berlese, 1887 (Fig. 1) is a blood sucking ectoparasite of rats. Females are ovoviviparous. Instars include: larva, protonymph, deutonymph, and adult. All instars feed except the larva (Owen, 1956). Presumably, the entire life cycle is completed in the nesting material with host contact experienced only at times of feeding. Reynolds (1949) has indicated that mites exhibit a tendency to form aggregations and to become quiescent until disturbed by changes in light intensity, air currents, substrate vibrations, CO₂, and contact with moving objects. However, L. echidnina shows no response to gravity or directed light. Optimum temperature range for the mite appears to be 27 - 30° C. Recent water balance studies (Wharton and Kanungo, 1962; Knülle, 1967) have shown the critical equilibrium activity of water vapor in the ambient air (the lowest point at which the organism can gain water from unsaturated air) to be 90%.

MATERIALS AND METHODS

General Procedures

A stock culture of L. echidnina was housed at the Acarology Laboratory, from which adult female mites were removed and standardized (Cross, 1954; Kanungo, 1964) prior to experimentation.

In order to observe a behavioral response of the mites to IR it was necessary that they be in a quiescent state before exposure and, because of their size, that they be viewed under magnification. This necessitated suitable test chambers and a means of partially restricting movement so that the mite remained in the radiation beam.

A stopcock grease (Lubriseal), refrigerated at -2°C , had excellent adhesive properties and was apparently nontoxic to the test organisms. The adhesive was applied to the curled, pointed end of a minuten pin and the other end embedded into a cork. Individual mites were placed onto a cold stender dish cover and secured by the dorsal shield to the tip of the pin. The cork-pin assembly was then placed into one of two types of test chambers.

The test chamber used in conjunction with the monochromator consisted of a one-dram glass vial with a rectangular opening cut across the vial and covered with transparent polyethylene behind which the mite was situated. The type used with the CO_2 laser was a glass T-tube in which the inside diameter was approximately equal to the

diameter of the IR beam. The mite was suspended from the cork-pin assembly down the vertically positioned base of the "T" so that the mite was directed into the beam. A piece of transparent polyethylene was placed over each of the remaining ends of the tube.

The duration of radiation exposure was controlled with a Wollensak self-cocking, variable speed camera shutter. Exposure time, in all experiments, was restricted to 0.5 seconds with 60.0 second intervals between exposures or until the test animal again became quiescent.

In all experiments, except where noted, the procedure was to record the average percentage response of ten trials for each of ten individuals for each wavelength and intensity tested. The response of the mite to IR, observed with the aid of a dissecting microscope, consisted of extremely quick up and down movements of the legs immediately following exposure to IR. Responses of lesser magnitude were characterized by a distinct obliquely directed movement of one or both of the first pair of legs.

Illustrations which required the use of either a compound or dissection microscope were drawn with the aid of an ocular grid and ruled paper.

Photographs were taken with a Polaroid Land camera, model 250, using black and white 3,000 speed film and flash attachment.

Tarsus I

Removal of tarsus I. It has been demonstrated that tarsus I, in the Acari, has a sensory function (Farish and Axtell, 1966; Zolotarev and

Elizarov, 1963). To investigate this possibility in relation to IR reception by L. echidnina, a method of amputation was devised.

An adult female mite was first immobilized by attaching its dorsal shield to a piece of masking tape. Tarsal amputations were accomplished by cauterizing the intersegmental membrane just proximal to the tarsus by the application of a sharp pointed, electrically heated, nichrome wire and removing the tarsus with a scalpel blade. All mites were held for twenty-four hours to observe the effects of amputation before experimentation was begun. After an experiment each amputee was mounted in Berlese's fluid on a glass slide to verify the degree of amputation.

Setal measurements. Setal measurements on tarsus I were taken using an ocular micrometer and light microscopy. Specimens for study were mounted in Berlese's medium and were made to lie flat by applying slight pressure to the cover slip. Particular setae were measured from either the left or right tarsus, since the variation among individuals could be expected to be greater than that between left and right tarsi on a given individual. Measurements were taken whenever possible and the results are presented in Tables 2 and 3. In cases where data were insufficient for analysis, the individual measurements are given in parenthesis.

Electron Microscopy

Transmission electron microscopy. The preparation of material for study by transmission electron microscopy (TEM) followed standard

TEM techniques (Wharton, et al., 1968). Observations and photographs were made with an RCA EMU3H electron microscope.

Scanning electron microscopy. Mites were prepared for study by scanning electron microscopy (SEM) by two different methods. Specimens were affixed to a SEM observation stage by amyl acetate and coated by vacuum evaporation with 0.202 g of Au-Pb (4:6) alloy to give surface conductivity. It was subsequently found that the coating procedure was not necessary for proper study and was therefore discontinued. Observations and photographs, unless otherwise noted, were made with uncoated material on a Cambridge Scanning electron microscope.

Radiation Sources

Monochromator. A Perkin-Elmer, model 112G, fore prism monochromator (Fig. 2) with ballasted power supply was used to provide monochromatic light. The source of radiation consisted of an electrically heated siliconcarbide rod (Globar) enclosed in a water cooled jacket and controlled by means of a Variac. The radiation was reflected by mirrors through a calibrated, movable entrance slit and onto a KBr salt prism. Since the model 112G does not possess an exit slit, a portable slit was placed 8.0 cm from the fore prism component and was calibrated by attaching to it a microscope stage micrometer (Fig. 3). It was thus possible to control the intensity of radiation to which the test animals were exposed as well as the width of the radiation beam.

On the opposite side of the exit slit the test chamber and its holding apparatus were positioned directly in front of the slit opening (Fig. 4). Visible light from a low-pressure mercury vapor lamp was used to place the mite so that it would face directly into the IR beam.

Scanning the wavelengths from $1.0 \mu - 14.0 \mu$, at an arbitrary intensity of $0.25 \times 10^{-3} \text{ w cm}^{-2}$, revealed one wavelength (4.5μ) to which the mites were most sensitive. Intensities were measured with an Eppley thermopile and a Hewlett-Packard, model 425A, microvoltammeter and were subsequently controlled over the wavelength interval by opening or closing the entrance slit and setting the exit slit at 0.7 mm . To determine the test intensity (I_t), defined as the minimum intensity of radiation eliciting a 50% or greater response at the most sensitive wavelength, the intensity was changed appropriately and the percentage of response of the mites recorded.

Wavelength discrimination was determined by exposing individuals to specific wavelengths at I_t at an exit slit of 0.7 mm . The monochromator could not provide I_t at the longer wavelengths (i.e., $8.0 \mu - 14 \mu$) or at 1.0μ . The wavelengths tested were those having good transmitting windows (1.6μ , 2.2μ , 3.6μ , 4.5μ) and those having considerable attenuation (4.3μ , 5.0μ , 6.0μ , 7.0μ) caused mainly by carbon dioxide and/or water vapor. An experiment was designed which deviated somewhat from the normal testing procedure: each of three mites was subjected to a set of three, randomly arranged, wavelengths (3.6μ , 4.3μ , 4.5μ) such that each wavelength was tested ten times/mite.

CO₂ gas laser. A CO₂ gas laser (Figs. 5,6) provided a source of coherent radiation at a wavelength of 10.6 μ . The apparatus consisted of a water-cooled, low-pressure, gas filled tube located between two mirrors which form an optical cavity. The gas in the laser tube was a mixture of 10% CO₂, 10% N₂, and 80% He. Lasing action was initiated by applying an electrical discharge to the gas mixture. The pencil-size beam passed out the tube and through the partially reflecting mirror at one end. The camera shutter, polyethylene filter, and a test chamber were placed in sequence behind the mirror (Figs. 7,8). Detection of the beam for proper positioning of the mite was accomplished by means of UV light and special phosphor paper.

RESULTS

Electron Microscopy

TEM findings indicate the presence of thin-walled sense organs on tarsus I. Micrographs indicate definite pores or apertures in the wall and also suggest the presence of at least two morphologically distinct types of setae in regard to arrangement and distribution of pores. In Figure 9 the apertures are uniformly distributed but only along 180° of the wall and dendritic processes appear to fill the entire lumen. The dendritic branches or neurofibrils (Fig. 10) of the second type appear partially restricted to a vestibular cavity or chamber at the proximal end of a tubular canal. The distal end of the canal opens to the outside. The pore openings in Figure 10 seem to be confined to a much smaller proportion of the total circumference than the previous type.

SEM micrographs indicate a rather complex chaetotaxy (Figs. 11,12) on tarsus I. With few exceptions, however, the superficial design of the setae appears to be remarkably similar. The base of the seta is completely surrounded by a raised cuticular ring but is separated from the ring by a shallow depression (Fig. 13). The depression appears to be of a more flexible nature, indicated by the wrinkled appearance, than the ring. From the base, the setae taper uniformly to a finely pointed tip. Toward the distal end many of the setae are curved

anteriorly. The coated material (Fig. 18) more clearly indicates the presence of narrowly spaced, thin vertical ridges which exhibit a spiral pattern along the length of the seta.

The setae of the "dorsal complex" (Figs. 14,15) appear to lack the cuticular ring and depression and appear instead to be supported basally on a raised portion of the cuticle. Centrally located in the complex are three previously undescribed microsetae arranged in linear fashion and set in a deep depression. These microsetae are flanked laterally by three hollow, thin-walled setae anteriorly and by two more posteriorly. The latter form a side wall of the depression and are directed over the three microsetae in an anterior direction (Figs. 15,16).

A centrally located, sigmoid shaped seta also lacks the cuticular ring and depression and seems to fit flush with the tarsus. The bifurcate tip of the seta (Figs. 17, 18) is collared by a smooth, raised area which narrows anteriorly. The taper is not uniform and the outline appears triangular rather than circular.

Test Intensity

Preliminary scanning of the wavelengths from 1.0μ - 14μ at $0.25 \times 10^{-3} \text{ w cm}^{-2}$ indicated that at 4.5μ the percentage response was 96% and was the wavelength to which the mites were most sensitive. By decreasing the intensity over the next two lower intensities measured it was determined that the $I_T = 0.16 \times 10^{-3} \text{ w cm}^{-2}$. These results are presented in Table I.

TABLE I
DETERMINATION OF TEST INTENSITY

Test No.	No. Trials	Slit width (mm)		Intensity (mw cm ⁻²)	Percentage Response
		Entrance	Exit		
1	10	2.0	0.5	0.25	96
2	10	0.6	0.7	0.16	74
3	10	0.5	0.7	0.08	41

Wavelength Discrimination

Testing particular wavelengths at I_T revealed that the mites were able to discriminate among a number of different wavelengths (Fig. 19). The percentage of response to the two lowest wavelengths was negligible; 1% and 2% at 1.6 μ and 2.2 μ respectively. A marked increase in wavelength sensitivity in which responses were above 50% was demonstrated at wavelengths of 3.6 μ (60%), 4.5 μ (74%), and 5.0 μ (51%). At the remaining wavelengths of 4.3 μ , 6.0 μ , and 7.0 μ in which there is decreased atmospheric transmission there was also decreased wavelength sensitivity. The percentage of response of the mites at these wavelengths decreased to 26%, 30%, and 23% respectively.

The testing of one mite to three randomly arranged wavelengths resulted in percentages of response which were below those previously

established for 3.6 μ and 4.5 μ . These data are summarized here; 3.6 μ - 26%; 4.3 μ - 10%; 4.5 μ - 36%. Prior to experimentation the intensity at each wavelength was rechecked and, in addition, the original data does not suggest any procedural complications which might have been responsible for the lower percentages of response. Subsequent to this experiment, the wavelength 4.3 μ was tested singly under normal test procedure and the percentage of response was observed to be 26%. Comparison of the percentages from the set of three wavelengths with those in which these wavelengths were tested separately indicates that both are in approximately the same proportions (random set - 26%-10%-36%; individual expts. - 60%-26%-74%). This might suggest that some factor(s) (e.g., unclean prism, moisture) other than experimental design was the cause of the discrepancy.

Setal Measurements

Results of setal measurements are given in Tables 2 and 3. The setal numbers presented in column one of both tables refer to the setal numbers in Figure 20. Unfortunately, it was not possible to provide reliable wall thickness measurements. It is thought that the wall thickness of most of the hollow setae on tarsus I is probably less than 0.5 μ .

TABLE 2
 BASE DIAMETERS (μ) OF HOLLOW
 SETAE TARSUS I

Seta No.	$\bar{X}$ (μ)	$\pm$ SD	CV	Range (μ)	n
1	2.2	0.14	6.52	2.0 - 2.4	13
2	1.9	0.15	8.03	1.7 - 2.0	9
3	2.3	0.16	7.21	2.0 - 2.4	17
4	1.9	0.10	5.32	1.8 - 2.1	6
5	2.3	0.11	4.80	2.1 - 2.5	9
6	2.1	0.11	5.13	1.9 - 2.2	8
7	2.1	0.24	11.29	1.7 - 2.3	10
8	2.2	0.09	4.25	2.0 - 2.3	11
9	2.5	0.12	4.80	2.3 - 2.7	8
10	2.4	0.11	4.79	2.2 - 2.6	9
11	2.4	0.11	4.90	2.2 - 2.5	6
12	2.2	0.17	7.74	1.9 - 2.4	9
13	1.8	0.16	9.15	1.6 - 2.1	8
14	1.5	0.05	3.27	1.5 - 1.6	4
15	2.2	0.13	5.85	2.1 - 2.5	9
16	1.8	0.12	6.67	1.6 - 2.0	7
17	2.8	0.18	6.59	2.6 - 3.1	8
18	2.6	0.11	4.31	2.4 - 2.7	7
19	2.7	0.05	1.83	2.7 - 2.8	4

TABLE 3
LENGTH (μ) OF HOLLOW
SETAE TARSUS I

Seta No.	$\bar{X}$ (μ)	$\pm$ SD	CV	Range (μ)	n
1	55.5	2.40	0.43	53.9 - 60.0	6
2	20.6	0.38	1.84	20.2 - 21.0	7
3	33.5	1.03	0.31	31.6 - 34.6	14
4	22.5	1.30	0.56	20.5 - 23.9	5
5	31.3	1.11	0.35	30.0 - 33.1	6
6	26.9	1.30	0.48	25.4 - 28.7	6
7	26.9	1.74	0.65	24.3 - 28.9	7
8	32.6	0.94	2.88	31.5 - 33.8	6
9	35.7	1.98	0.55	34.5 - 37.9	3
10	36.1	2.00	0.56	33.8 - 37.6	3
11	33.1	0.18	0.54	33.0 - 33.3	3
12	33.0	0.83	2.52	31.8 - 34.1	8
13	15.7	0.57	3.65	15.0 - 16.0	3
14	(11.8)				1
15	32.1	0.48	1.49	31.6 - 32.7	4
16	(15.6, 14.6)				2
17	(65.0)				1
18	58.8	0.88	1.50	57.8 - 59.1	5
19	(60.0)				1

Coherent Radiation

The results of exposure to coherent radiation at 10.6μ and an intensity at $0.3 \times 10^{-3} \text{ w cm}^{-2}$ indicate a 79% kinetic response under normal testing procedure.

Receptor Location

A series of experiments using the monochromator at a wavelength of 4.5μ at $1+$ was designed to try to determine the location of the infrared receptor(s). Because of the unique chaetotaxy of tarsus I and the relative non-ambulatory nature of legs I, the hypothesis was established that IR receptors are present on tarsus I. In the first experiment the mite was positioned, in the test chamber, so that it was perpendicular to the IR beam with legs I, excluding segments proximal to the genu, completely out of the beam. Results (Fig. 21) indicated essentially no response. A second experiment involved removal of tarsus I and the placing of the mite directly into the beam. The results of three of the 14 mites tested were discarded since their percentage of response was higher than that of a normal individual (i.e., non amputee) at the most sensitive wavelength (4.5μ) at $1+$. Subsequent microscopic comparison of the discarded mites with those included in the results revealed no apparent differences in degree of amputation. To check the effects of amputation on the percentage of response, the tarsus of leg IV was removed and a third experiment conducted. Five mites were tested and no differences were noted in either the quality or magnitude of response, but the percentage of those responding showed a definite decrease over a normal individual at the 4.5μ at $1+$. A summary of these results is given in Figure 21.

DISCUSSION

Temperature (Peterson and Brown, 1951; Brown et al., 1964; Hodgson, 1956) or a change in background intensity (Humphreys, 1968, 1969) is at least in part responsible for a certain behavioral response in an organism. Other workers (Evans, 1966a,b; Callahan, 1965f, 1967, 1968; Griffith, 1968) have suggested that some organisms, notably insects, have the capability of wavelength discrimination in the IR region. If the data presented are to be interpreted on the basis of existing knowledge and theory of IR communication in insects (Callahan, 1968; Griffith, 1968) then definite criteria must be met. An effective communications system using incoherent radiation and operating in the near and intermediate IR region, necessitates the following: 1) the transmitting component (the rat) must have a temperature different from that of its surroundings, and 2) the temperature must provide an intensity at or above I_t to which the receiver (the mite) could respond.

It has been demonstrated (Bullock and Diecke, 1956) that the energy in calories emitted by a rat, 5 cm in radius, 50 cm from the receptor, and with a surface temperature 10°C above that of the receptor is $1.3 \times 10^{-5} \text{ cal cm}^{-2} \text{ sec}^{-1}$ or $0.5 \times 10^{-4} \text{ w cm}^{-2}$. The rat mite has been shown to respond to:

$$I_t = 1.6 \times 10^{-4} \text{ w cm}^{-2} \quad (4)$$

Comparison of intensity figures demonstrates that the intensity of the rat at 50 cm distance is well below that required. However, $0.5 \times 10^{-4} \text{ w cm}^{-2}$ represents the total intensity at all wavelengths emitted by the rat at a given distance. Equation 4, on the other hand, represents the intensity at I_t at a particular spectral bandwidth for all wavelengths tested. In other words, the intensity which the mite receives at a wavelength of 4.5μ must in fact be a small fraction of the total intensity emitted by the rat at a given distance.

The Stefan Boltzman law states that the total black body radiation measured in w cm^{-2} of the radiating surface is a function of the fourth power of the absolute temperature of the source ($W = \delta T^4$). For a gray body the equation must be amended to:

$$W = \epsilon \delta T^4$$

where ϵ is the emissivity factor of a gray body and $\delta = 5.673 \times 10^{-12} \text{ w (cm}^2 \text{ deg}^4)^{-1}$. Assuming an ϵ of 0.9 for the rat, the radiant emittance emitted by the rat is approximately $44.2 \times 10^{-3} \text{ w cm}^{-2}$. The fraction of the total intensity per unit wavelength interval at temperature T (305° K) was determined by Planck's law and was found to be 5.0×10^{-4} and $10.4 \times 10^{-4} \text{ w (cm}^2 \mu)^{-1}$ for the wavelengths 4.5μ and 5.0μ respectively. The actual wavelength interval or spectral bandwidth emitted at the exit slit (0.7 mm) of the monochromator was determined graphically (Perkin-Elmer Instruction Manual, 1952) to approximate 1.0μ (.966 μ). With the above information it is now possible to estimate the distances over which the mite detection system could operate at a given wavelength at I_t .

According to Lambert's law of cosines the amount of radiation from a radiating surface varies as the cosine of the angle between the detector and the normal to the surface. The distance that the detector is away from the source also influences the intensity received. The radiant intensity received at the detector is then:

$$J = \frac{W A}{2\pi d^2} \cos\theta \quad (5)$$

where W = total radiant emittance of the source; A = area of the source.

By the inverse square law the radiant intensity (J) varies inversely as the square of the distance between the source and the detector.

Thus, it is possible to estimate the distances over which L. echidnina could detect a rat at a particular wavelength interval. The value of W at 5.0μ is $10.4 \times 10^{-4} \text{ w cm}^{-2}$ and $J = 1_l$. The detection angle of the mite in relation to the rat is taken to be 30° . The distance, d , can be calculated by transposing equation 5 and substituting in the values: W at $5.0 \mu = 10.4 \times 10^{-4} \text{ w cm}^{-2}$, $J = 1_l$, θ (detection angle of the mite in relation to the rat) = 30° . The results indicate that at a wavelength of 5.0μ at 1_l detection is possible at 16 cm. At a wavelength of 4.5μ the distance decreases to approximately 12 cm.

From the data summarized in Figure 19 it appears that the spiny rat mite can discriminate among a number of different IR wavelengths. More importantly, it appears able to accomplish this at an intensity which corresponds well with the intensity data obtained from a rat and at what seems to be a realistic distance. If the mite does in fact have this differential capacity then it becomes of paramount interest to

provide a reasonable explanation as to the nature of the sensory apparatus.

Microscopic examination of the tarsal setae is one method or approach which can be used to determine, at least theoretically, whether or not the setae could function as IR receptors. Morphologically the setae would be required to meet certain structural requirements. Spatially, the arrangement and location of receptors could be expected to be on an area which would provide the most effective scanning of the environment.

SEM micrographs and light microscopy indicate that the hollow setae are tapered, curved toward the tip, and generally positioned in a forward direction which, as Callahan (1967) states, is another characteristic of a good dielectric antenna. Further analysis reveals a chaetotaxic arrangement which strongly suggests the possibility of arrays (e.g., setae 2 - 7, Fig. 20).

It is proposed that the hollow setae could function as hollow tubular dielectric waveguides operating in the infrared region of the electromagnetic spectrum. This assumption is based on the following setal characteristics:

1. The dielectric constant of insect cuticle is given by Callahan (1968) to be between 2.5 - 3.0. Based on the fact that insect and mite cuticle appear identical structurally (Wharton, et al., 1968), a similar dielectric constant will be assumed for L. echidnina.
2. The radiation pattern of a dielectric antenna is more directive when the tube is tapered toward the free end. The setae are tapered. Taper formulae demonstrate a good fit for optimal operation.

3. Length of the setae at a given wavelength closely approximates the operational optimum of six wavelengths.

The data given in Table 2 can now be applied to the appropriate structural design formulae. Formula 3 need not be considered since it represents the maximum minimum diameter necessary for optimal functioning of a dielectric antenna. In the case of the setae under consideration, the tip diameter approaches zero and therefore is well within design limits (Griffith, 1968). In equation 2 let $\bar{\Sigma}$ be approximately mid-way (2.8) between 2.5 - 3.0. Transposing equation 2 yields:

$$\lambda_o = D_{\max} \cdot \sqrt{\pi(k-1)}$$

By using the $\bar{\Sigma}$ value for a seta from Table 2, as the value of $D_{\max}$ in the above equation, the optimal operating wavelength can be estimated. For instance, setae 2 and 4 (Table 2; Fig. 20) have a $D_{\max}$ of 1.9 μ . Substituting this value into the equation, the wavelength is computed to be 4.51 μ . Therefore a seta having a diameter of 1.9 μ might be expected to function as a waveguide at an optimal wavelength of 4.5 μ . Table 4 lists the optimal wavelengths for all setae measured. Comparison of these data with the percentage response at various wavelengths from Figure 19 is extremely intriguing. Responses were observed at 3.6 μ , 4.3 μ , 4.5 μ , 5.0 μ , 6.0 μ , and 7.0 μ . To each of these wavelengths, with the exception of 7.0 μ , there is, in Table 4, a wavelength of close approximation at a particular setal diameter for a particular value of $\bar{\Sigma}$.

TABLE 4
WAVELENGTHS AT $D_{\max}$; $\bar{\Sigma} = 2.8$

$D_{\max}$ (μ)	Frequency of Seta Measured	Wavelength (μ)
1.5	1	3.56
1.8	2	4.27
1.9	2	4.51
2.1	2	4.99
2.2	4	5.23
2.3	1	5.46
2.4	2	5.70
2.5	1	5.94
2.6	1	6.18
2.7	1	6.41
2.8	1	6.65

The optimal operating setal length for a dielectric antenna is given by Griffith (1968) to be six wavelengths. Apparently, strict adherence to this value is not critical for the operation of a dielectric antenna. Klely (1953) states that as long as the ratio of antenna to wavelength is greater than 2.5 ($\bar{\Sigma} = 6.0$), the antenna will operate with reasonable efficiency. The data from Table 3 indicates that with the exception of one of nineteen setae measured, all are at least two and one half times the theoretical wavelengths given in

Table 4. The length of seven of the nineteen setae measured, with base diameters ($D_{\max}$) of $2.2 \mu - 2.5 \mu$, were very close to the optimum length of six wavelengths.

Three points should be borne in mind in discussing the CO_2 laser results. Firstly, a laser is inherently a source of coherent, monochromatic electromagnetic radiation. The experimental CO_2 laser emitted essentially one wavelength at 10.6μ . Secondly, the intensity was reduced to a level of $0.3 \times 10^{-3} \text{ w cm}^{-2}$ but was almost twice as high as the I_t established for L. echidnina. Thirdly, the response to the wavelength emitted by the laser may have absolutely no correlation with the fact that the mite exhibits a vigorous kinesis upon exposure to low concentrations of CO_2 gas.

Water vapor and carbon dioxide play an important role in the biology of the spiny rat mite. Unlike black body radiation, which produces an even distribution of wavelengths, these molecular sources produce characteristic absorption band spectral lines which are the result of vibrational stretching of the molecule.

The present investigation hints at possible mechanisms, other than traditional chemoreception, for the sensing of CO_2 by L. echidnina. Callahan (1968) has proposed that scent molecules may exhibit maser-like action at or near the receptor site. Presumably the energy necessary for this phenomenon to take place would come from the sun or the insect itself. Masing could take place in either the vestibular or tubular portions of the seta. Figure 10 indicates that there are present on tarsus I at least some setae having the appropriate configuration.

The second possibility (Griffith, 1968) presupposes that the mite is capable of sensing one or several of the CO₂ absorption bands. Sensory adaptation would enable the mite to become adapted to a particular level of background radiation. A further assumption is that the mite can detect a decrease in the background level at these wavelengths as the CO₂ content of the air is increased. This system is made more attractive because it requires no additional input of energy. Essentially the carbon dioxide molecule functions as a broad or narrow (depending on the absorption band) band filter. The percentage of response, or lack of it, (Fig. 19) at the center of a strong CO₂ absorption band at 4.3 μ may now have new significance. At a particular background intensity the mite could receive the wavelength of 4.3 μ and respond by becoming akinetic. As CO₂ is introduced into the environment by the rat there would be a decrease in background radiation at that wavelength. This system could account for the poor response observed at 4.3 μ .

Studies dealing with the sensory behavior of acarines have usually implicated leg I and specifically tarsus I as having a sensory function (Camin, 1950; Farish and Axtell, 1966; Zolotarev and Elizarov, 1963; Varcammen-Grandjean, 1965). The present study also seems to suggest that tarsus I indeed has a sensory function. The palps are also thought to play a chemosensory role in acarine behavior. Many of the palpal setae appear morphologically similar to the hollow type found on tarsus I. The results of the tarsal experiments (Fig. 21) would seem to indicate that in terms of the wavelengths

and intensity tested tarsi I possess the most effective IR receptors. However, it should be kept in mind that if the palps are IR receptors, different wavelengths and intensities might be involved.

Integration and interpretation of data and theory may become more meaningful if they are discussed in terms of the kinds of activities in which an ectoparasite must engage and the kinds of stimuli which confront it.

A rat can be considered a black body radiator or, more precisely, a gray body radiator. According to equation 1 at a body temperature of 305° K the wavelength of peak intensity would be 9.5 μ . This wavelength offers two distinct advantages for an organism using IR wavelengths to detect a warm-blooded host: 1) It is located in the center of a large atmospheric window, and 2) it is the wavelength of greatest intensity. Thus, it would seem rather puzzling for a host seeking organism to utilize shorter wavelengths at much lower intensities. However, it is proposed that this is apparently what the spiny rat mite has done. For the mite to detect long wavelengths in the 9.5 μ range, within the framework of the model presented, would require a seta having a base diameter approximately twice as large as any hollow seta present on tarsus I. In addition, the It at the short wavelengths has been previously demonstrated to be effective in eliciting a response.

Structural requirements and their relationship to receptor location may provide an additional clue as to why shorter wavelengths have been exploited. The first pair of legs are not involved continuously

in ambulatory activity. Much time is spent with the legs held slightly above the body with the distal segments positioned parallel to the substrate. The individual segments can only be moved in a vertical plane and the entire leg may be moved across a limited horizontal plane. The result appears to be a highly mobile platform upon which are located the sensing elements for scanning the environment. The advantages of doubling the setal diameters seem doubtful in terms of the spatial limitations of tarsus I and the possible resulting decrease in mobility.

The functioning of this detection system is undoubtedly related to the physiological state of the mite (e.g., fed or unfed) (cf. Camin, 1950; Wharton and Cross, 1957) and to the environmental conditions present just prior to detection. With these considerations in mind, a detection system such as the one described, if it operates at all, presumably does so with a reasonable degree of effectiveness. Since detection provides the parasite with information regarding the presence of a host it could be assumed that the distance interval between parasite and host would be the maximum possible for optimal detection. A distance of 12 - 16 cm hardly seems large enough to allow a parasite (rat mite) sufficient time for detection, appropriate taxic responses, and eventual host contact. Conversely, at greater distances the problem might be one of too much time. If the parasite could swiftly and accurately seek out the host perhaps a long range detection system would be quite effective. However, with long range detection coupled to a system in which chance plays a major role in eventual attachment, then prolonged precontact

activity by the parasite might be expected to result in an unnecessary expenditure of energy. Therefore, the rat mite detection system has probably evolved to operate at a distance which allows the host to be sufficiently close for directional precontact activity to occur and thus ensures a minimal expenditure of energy with a maximal chance of contact.

One measure of an IR host detection system might be the effectiveness of species discrimination. The spiny rat mite system appears to lack the essential characteristics for host specificity for the following reasons. The dielectric antenna is inherently a broad band device (Griffith, 1968), that is, it can operate over a number of frequencies other than the optimum. Certainly other rodents, likely to gain entry into the nest, would release CO₂, have a similar body temperature, and emit the same characteristic IR wavelengths as the normal host. From this standpoint, it does not seem likely that this particular system is very host specific. According to Strandtmann and Wharton (1958), L. echidnina has been recorded from at least six species of rats. The problem then is whether or not the "wrong" host enters the rat nest and, if so, how often. Such data was not found to be available but it would seem probable that the chances of wrong host entry are low. If most of the time the normal host enters the nest, then the detection system need only supply information relating to host presence and direction.

SUMMARY

Adult females of the spiny rat mite, Laelaps echidnina, are able to discriminate wavelengths of incoherent and coherent IR radiation. Using a monochromator as a source of incoherent radiation, eight wavelengths in a range from 1.6 μ - 7.0 μ were compared at a test intensity of $1.6 \times 10^{-4} \text{ w cm}^{-2}$. Kinetic responses of individuals which were above 50% were observed at wavelengths of 3.6 μ (60%), 4.5 μ (74%), and 5.0 μ (51%); below 50% were at wavelengths of 4.3 μ (26%), 6.0 μ (30%), and 7.0 μ (23%). Essentially no response was elicited at wavelengths of 1.6 μ and 2.2 μ .

A CO₂ gas laser provided a source of coherent IR radiation at a wavelength of 10.6 μ . A kinetic response of 79% was observed at an intensity of $3.0 \times 10^{-4} \text{ w cm}^{-2}$.

It was determined that the receptors which receive these wavelengths are located primarily on tarsus I. The basis for this conclusion is that if tarsus I were positioned out of the beam or if they were amputated, the percentage of response, at the most sensitive wavelength (4.5 μ) at 1+, decreased to 3% and 8% respectively.

It is proposed that the receptors of IR radiation are the hollow setae on tarsus I and that they function as dielectric antennas. This is supported by the close approximation of the expected characteristics, such as dielectric constant, base diameter, length, and

taper, of an optimally designed dielectric antenna with the observed characteristics of the hollow setae on tarsus I.

The fact that the spiny rat mite can detect and discriminate among different wavelengths of IR radiation in the laboratory becomes more significant when viewed in terms of the kinds of activities in which a host-seeking parasite must engage. One of the most important problems with which the mite must deal is how to detect and attach to the host with a minimum expenditure of energy. It is here suggested that while the lower wavelengths are not those of peak intensity, they do allow for smaller receptor dimensions to be utilized and at an intensity to which the spiny rat mite is able to respond.

Figure 1. Venter of the female of Laelaps echidnina
Berlese

Figure 2. Perkin-Elmer monochromator model 112G;
Globar source (left) and fore prism
component (right)

Figure 3. From left to right - Monochromator fore
prism component, camera shutter, exit
slit, and test chamber; viewed from above

Figure 4. Monochromator fore prism component,
camera shutter, exit slit, and test
chamber; observation microscope; viewed
in sequence from back to front

2

3

4

Figure 5. From left to right - CO₂ gas laser,
partially reflecting mirror, and testing
apparatus; lateral view

Figure 6. CO₂ gas laser tube; viewed from above

Figure 7. From left to right - Partially reflecting
mirror, camera shutter, polyethylene filter,
and test chamber; viewed from above

Figure 8. From left to right - Camera shutter,
polyethylene filter, and test chamber;
observation microscope; lateral view

5

6

7

8

Figure 9. Transmission electron micrograph; hollow seta; tarsus I; 12,000 X; Note distribution of apertures

Figure 10. Transmission electron micrograph; hollow seta; tarsus I; 12,000 X; Note distribution of apertures

9

10

Figure 11. Scanning electron micrograph; distal
portion of left tarsus I; en face view; 500 X

Figure 12. Scanning electron micrograph; distal
portion of left tarsus I; en face view; 1,000 X

11

12

Figure 13. Scanning electron micrographs; distal portion of left tarsus I; dorsal aspect; 2,000 X.
(To view micrographs in three-dimensions, hold a small mirror against the right side of the nose about six inches above the large dot. Focus the left eye on the left picture and adjust the mirror until the reflected image of the right picture merges with the left)

Figure 14. Dorsal complex; distal portion of
left tarsus I; dorsal aspect;
scale equals 5 μ

Figure 15. Scanning electron micrograph; distal portion of right tarsus I; dorsal aspect; 2,000 X

Figure 16. Scanning electron micrograph; microsetae of dorsal complex; distal portion of right tarsus I; dorsal aspect; 5,000 X

Figure 17. Scanning electron micrograph; sigmoid-shaped seta; distal portion of tarsus I; lateral aspect; 11,200 X

Figure 18. Scanning electron micrograph; sigmoid-shaped seta; distal portion of tarsus I; lateral aspect; gold coated; 18,000 X

15

16

17

18

Figure 19. Wavelength discrimination at I_+ ;
% response vs. λ

Figure 20. Tarsus I; diagrammatic; dorsal aspect;
numbers correspond to setae measured

- dorsal setae
- ventral setae

Figure 21. Infrared receptor location; wavelength -
4.5 at I_+ ; % response vs. type of mite

N = normal female

Tr₄ = tarsi IV removed

Tr₁ = tarsi I removed

P = normal female positioned

perpendicular to IR beam;

leg I not in beam

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