Ent. exp. & appl. 33 (1983) 179—187. *Ned. Entomol. Ver. Amsterdam*

THE ROLE OF SENSORY STRUCTURES AND PREOVIPOSITION BEHAVIOR IN OVIPOSITION BY THE PATCH BUTTERFLY, *CHLOSYNE LACINIA*

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The role of antennae and foretarsi in oviposition and host discrimination was investigated in *Chlosyne lacinia* Geyer (Nymphalidae, Lepidoptera) a cluster laying nymphalid butterfly which exhibits drumming and antennal dipping behavior prior to oviposition. Ablation of the entire antennae drastically reduced oviposition, while fractional antennectomy reduced it in proportion to the number of antennal receptors removed. Host/non-host ovipositional discrimination was not significantly affected by antennal ablations. Ablation of the foretarsi abolished discrimination in a controlled environment chamber, but did not affect it in outdoor cages or in a greenhouse. This difference was retrospectively associated with a diminished release of host volatiles due to cooler leaf surface temperatures in the environmental chamber or with continuous air turbulance caused by humidifier fans in the environmental chamber. Electrophysiological techniques were used to demonstrate chemosensory activity in setae located on the foretarsi. We conclude that foretarsal contact chemoreceptors employed during drumming are used for host verification in environmental conditions where olfaction is unreliable.

KEY WORDS: Oviposition — Host discrimination — Drumming behavior — Antennal receptors — Foretarsal receptors — *Chlosyne lacinia* — Nymphalidae.

The remarkable ability of butterflies to distinguish their host plants among the numerous plant species encountered while in search of oviposition sites has long been recognized (Brues, 1924). Monophagous and oligophagous insects are especially dependent on the ability of the ovipositing ♀ to find the correct plant since a mistake can greatly increase mortality by causing inanition of the larvae (Straatman, 1962; Berenbaum, 1981) or by forcing migration of the 1st. instar larvae to another plant (Dethier, 1959). In spite of widely publicized host specificity (Ehrlich & Raven, 1964) and the consequences of ovipositional mistakes, very little is known about the sensory receptors which mediate host finding or the behavioral mechanisms which utilize them.

Observations of the behavior of gravid female butterflies prior to oviposition provide a picture of behavioral patterns and involvement of various receptor groups in host-plant discrimination. Many butterfly species in several families rapidly tap the leaf surface with their foretarsi in a process which Ilse (1937) termed "drumming" (Calvert, 1975). Ilse (1956), Fox (1966), and Ichinose & Honda (1978) describe these behaviors for several species of nymphalid, pierid and papilionid butterflies. A more complicated behavior was described for the nymphalid *Chlosyne lacinia* (Calvert, 1974). Females alight on a candidate leaf and drum rapidly by tapping the leaf surface with their fortarsi, structures which are not used for ambulation but are normally held folded against the prothoracic sternum. Often during their drumming behavior they dip their antennae towards the leaf area which was drummed. This behavior is repeated several times and culminates in curling the abdomen over the edge of the leaf and ovipositing an egg mass on its underside. Unacceptable hosts are usually vacated after one or two taps of the forelegs. No ♂ of any species has ever been observed to drum.

These behavioral observations strongly imply that the sensory structures on the foretarsi and antennae participate in the selection of an oviposition site. Fox (1966) described clusters of hairs associated with long spines on the foretarsi of several butterfly species, and suggested

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that they might be sensilla. He proposed that in the process of drumming, the spines might abrade the leaf surface causing the release of essential oils which are detected by these sensila.

Similar structures located on the forelegs of *Chlosyne lacinia* have been described in detail using scanning electron micrographs (Calvert, 1974). In the ♀, four pairs of spines were found on the ventral aspect of the foretarsi, the distal pair of which project beyond the terminal tarsal subsegments. The ultimate and penultimate pairs of spines have small clusters of long, curved hairs closely associated with them in a manner which suggests their use in contact chemoreception of plant chemicals (Calvert, 1974). These hairs have a terminal pore similar to classical gustatory chemoreceptors.

In addition, the dorsal surface of the terminal tarsal segment harbors a pit containing setae (Calvert, 1974). Its location in a position where it cannot directly contact the leaf surface suggests it has an olfactory function. Male foretarsi lack all of the above described features. Other single, small hairs having the appearance of trichoid sensilla were found on the dorsalateral surfaces of the forelegs of both ♂♂ and ♀♀.

The foregoing behavioral and morphological data offer compelling evidence for the following model of host verification: drumming causes physical abrasion of the leaf surface by spines on the foretarsi with a subsequent release of plant chemicals. These chemicals are detected by the butterfly's foretarsal contact chemoreceptors and/or olfactory setae located in the dorsal foretarsal pits, palps, and antennae. On the basis of this sensory information, the animal accepts or rejects the leaf as a suitable oviposition site.

Some experimental evidence supporting this model has been obtained. Oviposition is quantitatively affected by ablation or acid treatment of the tarsi (Myers, 1969; Ma & Schoonhoven, 1973; G. de Boer, pers. comm., Ichinose & Honda, 1978). Furthermore, receptor sensitivity to plant chemicals was shown electrophysiologically (Ma & Schoonhoven, 1973; Behan & Schoonhoven, 1978). Several important questions, however, remain unanswered. The role of the tarsi in discrimination among plants for oviposition sites has not been assessed. The role of the antennae in oviposition needs clarification: some of the above research suggest that the antennae are not important for oviposition, whereas our work indicates that they are. Finally, no electrophysiological recordings have been obtained from the foretarsal receptors used by drumming nymphalids, the butterfly group showing the most pronounced drumming behavior.

We have undertaken the investigation of the mechanisms of host discrimination by ovipositing ♀ *Chlosyne lacinia* in an attempt to clarify the involvement of the drumming and antenna-dipping behaviors and of the implicated antennal, palpal, and foretarsal chemoreceptors.

MATERIALS AND METHODS

Oviposition choice tests. Adults of *C. lacinia* were reared from field-collected eggs or young larvae in ventilated plastic boxes or on cut plants whose turgor was maintained by pressurized water (Kendall, 1957). Adults captured in the field were also used when available.

Host plants for the choice tests depended upon seasonal availability. Whenever possible, we used the most commonly infested hosts, namely, *Helianthus annuus* L. (sunflower), *Ambrosia trifida* L. (ragweed), and *Verbesina encelioides* Gray. Other hosts were *Viguiera dentata* Cav, *Xanthium strumarium* L., and *Heterotheca latifolia* Buck. Non-host plants were *Phaseolus vulgaris* L. (bean) and *Lantana horrida* H.B.K.

The choice tests involved placing up to 5 gravid ♀♀ at a time into cages containing both host and non-host plants trimmed and arranged such that each plant occupied approximately the same space and presented similar physical profiles. The cages were made with plywood floors and wire mesh walls and tops and were 0.5 m in diam and 0.4 m high. Outdoor experiments required nylon netting on the cage walls and tops to keep out predaceous wasps; bird tanglefoot was applied to the supporting stands to prevent access by patrolling ants.

Choice tests were conducted in 3 experimental environments: an indoor chamber with controlled environment, a greenhouse, and outdoors. In the environmental chamber, natural lighting was approximated through the use of Plant-gro (Westinghouse Corp.) or Optima (Duro-test Corp.) fluorescent bulbs. Temperature was maintained at 29° ± 2.2°; humidity at 48% RH and daylength at 16 hr. In the greenhouse and outdoors, temperature, humidity and daylength fluctuated more widely depending on time of day and season. Outdoor work was restricted to April through September.

To compare the performance of varying numbers of experimental animals, the results of choice tests are expressed as discrimination indices:

$$\mathrm{DI} = \frac{\text{Number of egg masses laid on hosts}}{\text{Total number of egg masses laid}}$$

To meet the normality requirements of the t-tests employed in statistical analysis of these data, an arcsin transformation was applied to the indices (Sokal & Rohlf, 1969).

Electrophysiology. The method used to record electrical activity from the tarsal sensilla was similar to that described by Ma & Schoonhoven (1973). Female *C. lacinia* were prepared by removing the head, abdomen and hindwings, and scrambling the thoracic musculature and ganglia with an insect pin to prevent muscular movements (see Mitchell, 1972). The specimen was then mounted on a cork by its forewings; one tarsus was extended and held in position by insect pins. The reference electrode containing a 0.1 M NaCl solution was placed in the thoracic cavity, and the active electrode was maneuvered over a single foretarsal seta. Action potentials generated in the receptor cells of the sensillum were recorded via electrolytes present in the stimulating solution in contact with a silver-silver chloride surface in the electrode holder. The signal was fed into a Grass P15 high impedance preamplifier with a filter bandpass from 300 to 1300 Hz, displayed on an oscilloscope, and recorded on a FM magnetic tape recorder.

Plant hot water extractions. Soluble polar compounds were extracted by allowing 50 g wet wt. of leaves to stand 2 hr in 250 ml distilled water initially at 100°.

RESULTS

The role of the antennae in oviposition. To assess the role of the antennae in oviposition, antennectomized gravid ♀♀ were tested in three different environments (see Methods). The number of egg masses laid by antennectomized animals was reduced drastically from that of the controls in all three environmental conditions (Table I). The average number of masses/♀ for antennectomized animals was about 10% of controls. Host discrimination, however, remained at the same level as controls. Removal of both the antennae and the foretarsi reduced oviposition even further to 5.2% of controls; discrimination, now judged by very few masses, fell to 67%.

Decrease in egg laying following antennectomy could be due to factors other than olfactory deprivation; for example, ablation may cause trauma resulting in reduced oviposition. Accordingly, we attempted to neutralize the sensory function of antennae by coating them with shellac or silicone rubber. The results of this treatment were similar to, although not as extreme as, those in response to complete antennectomy: oviposition was reduced markedly

TABLE I

Effects of antennectomy and antennal coating on oviposition by C. lacinia. *Environmental conditions for testing: A, controlled environment; B, greenhouse, C, outdoors. DI = discrimination index. Oviposition reduced quantitatively by antennal ablations (or coating) but discrimination not affected*

	Ablation	No. subsegments remaining	No. ♀♀	Oviposition: No. egg masses laid on host	on non-host	per ♀♀	% of control	DI
A	Entire	0	50	5	0	0.10	7	1.00
	None	34	50	56	15	1.42	—	0.79
B	Entire	0	20	4	0	0.20	13	1.00
	None (coated)	34	20	12	1	0.65	42	0.92
	None	34	20	31	0	1.55	—	1.00
C	Entire	0	27	4	1	0.19	10	0.80
	Club and ½ shank	14	11	2	0	0.18	10	1.00
	Club only	20	13	17	1	1.38	75	0.94
	None	34	31	57	0	1.84	—	1.00

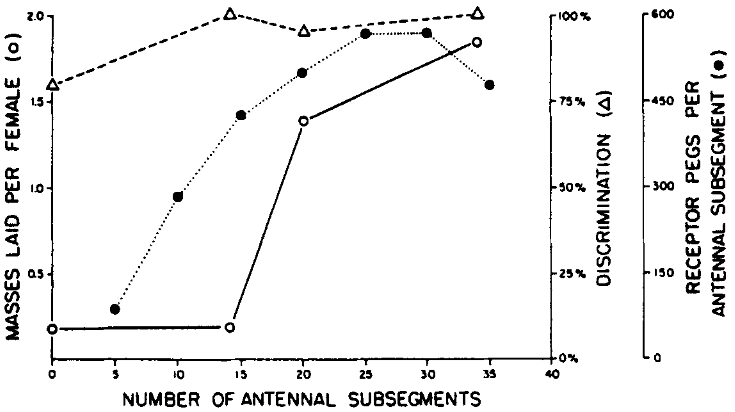

Fig. 1. Effect of antennal ablation on oviposition by *C. lacinia*. Oviposition (masses laid/♀) correlates with number of thin-walled receptors remaining after ablation. Graph of receptor pegs per antennal segment adapted from a study of the queen butterfly (*Danaus gilippus*) antenna (Myers, 1969).

while discrimination remained high (Table I).

Another likely effect of antennectomy is the disruption of the function of the Johnston organ, believed important in flight control (Geweche & Schlegel, 1970). Coating the antenna changes its mass and, therefore, may also affect its operation. Within the confines of the ovipositional cages, however, all experimentals appeared to behave the same as the controls; consequently, it is unlikely that the Johnston organ is directly required for oviposition.

Partial antennal ablations identified those segments necessary for control of egg laying. Antennae were severed at: 1) the base of the club, 2) halfway between the club and the antennal base, and 3) at the base. These ablations left 20, 14 and 0 antennal subsegments, respectively. The number of masses laid is a function of the number of antennal subsegments remaining, with those on the club (the distal 15) being especially important (Fig. 1). Myers (1968) reports that the distal subsegments have the highest density of receptors. Therefore, the probable determinant of decreased oviposition is the quantitative loss of antennal olfactory receptors. Just as in complete antennectomy, partial ablation had no effect on discrimination (Table I).

The role of the palps and foretarsal receptors in oviposition. The palps of *C. lacinia* each have a flask-shaped pit in which are located many setae. The possibility that these are receptors involved in oviposition was tested by bilateral ablation of the palps of 20 ♀♀. This operation reduced egg laying to 0.85 masses per ♀ (63% of normal controls) but did not impair discriminations (DI = 0.94).

The drumming behavior of ♀ butterflies coupled with the persistence of discriminatory ability after antennectomy and palpectomy

TABLE II

Effects of foretarsal ablations on oviposition by Chlosyne lacinia *with intact antennae. Discrimination greatly reduced after foretarsal ablation only in controlled environment chamber*

	Type	Ablation	No. ♀♀	Oviposition: No. egg masses on host	on non-host	on other[1]	per ♀	% of control	DI
A.	Exp.	Both foretarsi	64	34	32	2	1.06	79	0.50
	Exp.	Foretarsal tips	60	34	30	8	1.20	90	0.47
	Control	One foretarsus	30	34	1	4	1.30	97	0.87
	Control	None	61	68	5	9	1.34	—	0.83
B.	Exp.	Both foretarsi	20	20	0	0	1.00	65	1.00
	Exp.	Foretarsal tips	20	20	4	0	1.20	77	0.83
	Control	One foretarsus	20	17	1	0	0.90	58	0.94
	Control	None	20	31	0	0	1.55	—	1.00

[1] Cage, clay pots, and feeding sponge.

strongly implicates the foretarsi in host identification. To test this hypothesis, 2 experiments utilizing partial ablations of the foretarsi were performed in each of the three environments: 1) ablation at midfemur, removing all receptors from the forelegs, and 2) ablation of the distal foretarsal segment, removing the terminal spines and clustered receptors as well as the dorsal pit. To control for trauma induced by the operation itself, a unilateral ablation removing one foretarsus at midfemur was performed.

The results of this experiment (Table II) clearly show that the foretarsi are crucial for discrimination in the controlled environment chamber: bilateral ablations of either the entire foretarsi or just the terminal segments of foretarsi abolished discrimination entirely (DI = 0.50, 0.47). Statistical comparisons show that pooled experimental animals differ significantly (P = 0.02) from pooled controls. This outcome depended on environment, however, since identical ablation experiments performed in the greenhouse showed virtually no effects (DI = 1.0, 0.83). Preliminary outdoor experiments showed results similar to those performed in the greenhouse.

The possibility that light quality might have been a factor accounting for these differences was investigated by repeating the foretarsal ablation experiment in the controlled environment chamber but substituting special fluorescent lamps having emission spectra close to that of sunlight. The results were similar to those of the controlled environment chamber with plant-gro lamps: animals lacking foretarsi discriminated less well (DI = 0.63) than those with their forelegs intact (DI = 1.00).

Electrophysiology of foretarsal receptors. The above behavioral tests imply the presence of contact chemoreceptors. To confirm this, clustered foretarsal setae were individually examined for chemosensory activity using electrophysiological techniques. Typical insect chemosensory responses were obtained. Several spike sizes are discernable suggesting a more complicated response to NaCl than in the blowfly labellar receptors (Gillary, 1966). Classical adaptation is evident, and increasing concentrations of NaCl elicited an increased rate of discharge. Although the variability of the data is high, the mean responses describe a classical dose-response curve (Fig. 2).

Responses of these receptors to hot water plant extracts were also recorded. Although there were obvious differences among records from different plant extracts, spike counts re-

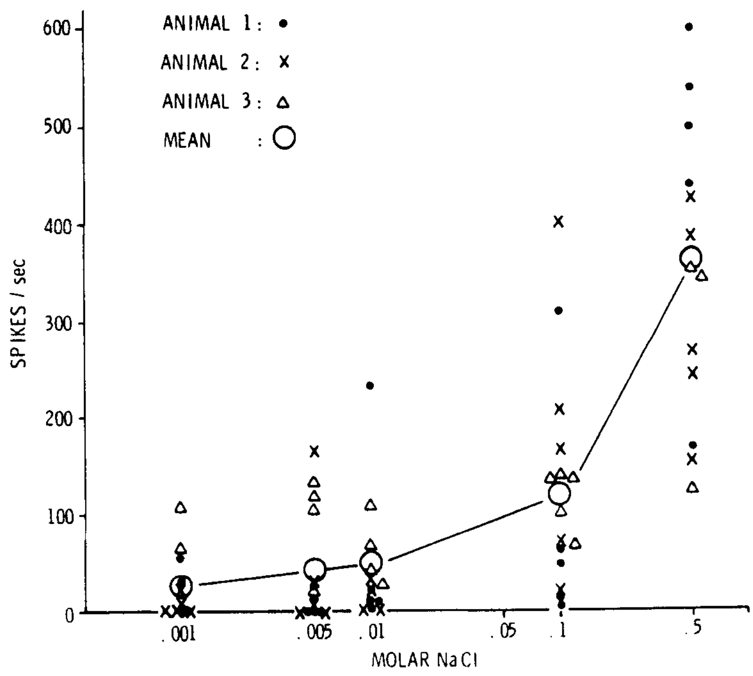

Fig. 2. Dose-response curve for foretarsal sensilla to NaCl. Ordinate represents average spike frequency for first half-second of stimulation. Data recorded electrophysiologically from individual uniporous trichoid sensilla from 3 different preparations.

vealed no simple quantitative differences between responses to host and non-host extracts.

DISCUSSION

The sensory organs involved in oviposition. The electrophysiological results showing positive responses and classical adaptation to stimuli as well as typical dose-response curves to salt confirm that the clustered foretarsal setae are chemosensory. Hot water extracts of leaves always elicited activity from several receptor cells, although no consistent differences could be discerned between the host and non-host groups. However, since many chemicals that uniquely characterize plant groups are non-polar (Alston & Turner, 1963), they were excluded by our recording technique which requires water solubility. More sophisticated techniques, such as sidewall recording, may be necessary to study non-aqueous extracts.

A second type of receptor that may also be involved in oviposition is a smaller paired sensillum located on the dorsolateral surfaces of the foretarsi and tibia (Calvert, 1974). Electrophysiological recordings demonstrated that these were also chemosensory, but further characterization was not done.

The antennae have long been known to be chemosensory organs of great sensitivity, and our study demonstrated that they are of paramount importance in oviposition. These findings are in contrast with work on other butterflies (*Danaus gilippus bernice* Cramer; Myers, 1969; *Papilio protener demetrius* Cramer; Ichinose & Honda, 1978; *Pieris brassicae* L.; Ma & Schoonhoven, 1973) in which the presence or absence of the antennae made no observable difference in ovipositional quantity.

Other chemosensory systems also may be involved in oviposition and discrimination. The dorsal pit organs of the foretarsi described by Calvert (1974) and the flask-shaped pits on the palps (see Wigglesworth, 1972) are probably olfactory since they cannot be brought directly into contact with the leaf surface. In contrast, setae located on the ovipositor are used only after the oviposition process has begun and therefore probably function only as mechanoreceptors used in positioning the eggs within the cluster (David & Gardiner, 1962; Traynier, 1979).

Chemoreceptors located on the ambulatory tarsi may be used in oviposition. We unfortunately were unable to test these because both ablation and coating techniques interfered with the operation of the tarsal claws used by ♀♀ to hold onto the leaf while ovipositing. Another commonly used technique, inactivation of the receptors by acid, also interfered with ambulation.

Roles of receptors in the discrimination of plants. Specific roles of each receptor group can theoretically be assessed by ablation of individual organs. The removal of the antennae, however, greatly reduced oviposition, and thus it is difficult to accurately assess the role of the antennal receptors in host discrimination.

Ablation of the foretarsi clearly abolished discrimination in one environment, the controlled environment chamber. Comparing conditions here with other environments may suggest which specific features of host plants act as cues for the butterfly. The controlled environment chamber differs from greenhouse and outdoor conditions in three principal ways: light quality, wind patterns and diurnal temperature fluctuations.

The plant-gro fluorescent lights used in the indoor chamber are relatively deficient in green, a color expected to be important for ovipositing insects (Ilse, 1937). However, repetition of these experiments using fluorescent lights having spectral distribution curves close to sunlight yielded similar results. Thus light quality *per se* does not account for these differences.

Air circulation in the controlled environment chamber provided by a humidifier fan was tested with a smoke generator and found to be continually turbulent. This situation differs greatly from field conditions, which are generally characterized by alternating periods of gusting wind and calm air, and from greenhouse conditions where air flow was uniform and unidirectional. Perhaps a greater reliance is placed on contact chemoreceptors of the foretarsi when turbulent wind conditions disrupt normal host-odor release patterns.

Another variable expected in the field is the diurnal fluctuation of both air and leaf temperatures which vary according to the amount of radiation received (Kimball & Hand, 1936). Such thermal fluctuations are likely to affect both the production and release of host volatiles (Adams & Hagerman, 1977). The fluorescent lights in the controlled environment chamber do not engender as high leaf surface temperatures as does Texas sunlight. Accordingly, the quantity of host volatiles in the controlled environment chamber would be less than that released by plants in outdoor cages or greenhouse. If foretarsal ablation forced animals to depend on their olfactory organs, absence of host volatiles in the controlled environment chamber could explain the lack of discrimination. This interpretation suggests that the drumming behavior may be an adaptation to provide gravid ♀♀ with accurate host information on cool or cloudy days. Such a mechanism would be especially important during prolonged periods of inclement weather, since on the average, temperate butterflies have only 4—9 days in which to oviposit (Stamp, 1980).

Release of oviposition. Host discrimination and ovipositional release appear to be separate functions mediated by different sense organs. The antennae are clearly involved in the release of oviposition, since antennectomy causes a drastic reduction in the number of eggs laid (Table I). The antennae and/or other olfactory organs also provide information for discrimination, since ♀♀ can discriminate well in the absence of foretarsi (Table II, greenhouse). This concept was also supported by the results of 2 additional experiments: 1) ablation of foretarsi did not lower discrimination appreciably in outdoor cages; and 2) oviposition occurred on non-hosts in a host odor stream in preference to non-hosts in a non-host odor stream (Calvert, 1975).

In contrast with the antennae, the foretarsi do not appear to control release of egg deposition, since ♀♀ deprived of their foretarsi maintained near normal oviposition levels. However, such animals failed to discriminate in the controlled environment chamber where olfactory cues were lacking or confusing (Table II). Presumably, then, the main function of the foretarsi is to provide information for discrimination, which becomes crucial when the antennae are rendered less effective by a decrease in host volatiles or by a confusing mixture of host and non-host volatiles.

The appearance of the palpal pit is similar to the shallower antennal pits. Their recessed position prevents direct contact with the surface. Thus, by inference, we presume these are receptors with an olfactory function (see Wigglesworth, 1972). Removal of the palps resulted in responses similar to but less drastic than antennal ablations tested in the same environment (outdoors): egg laying was reduced, but discrimination was normal (Calvert, 1975). Thus, we tentatively conclude that the palps contribute to the animal's olfactory analytical system.

Host location by butterflies. Searching for oviposition sites involves a series of behavioral events each of which is guided by visual, olfactory or gustatory stimuli. Visual and olfactory cues are the only ones that can act over distances. Vision may only serve a host-locating animal in a general way by enabling it to distinguish broad plant categories to which the host belongs (Kennedy *et al.*, 1961; but also see Gilbert, 1974, and Rauscher, 1978). Since leaf hue is about the same for all plants (about 550 nm), color vision alone cannot provide cues sufficiently specific for host discrimination (Moericke, 1969). Leaves may differ in tint or intensity, but so far only one insect has been shown to exploit this difference (Moericke, 1969).

Olfactory cues are more likely to yield specific host information, since odor plumes may be traced upwind and become the basis for preliminary landing decisions (Yamamoto, *et al.*, 1969). However, wind patterns are variable and adjacent non-hosts may present confusing odors, perhaps even masking those of the host (Atsatt & O'Dowd, 1976). Some fail-safe mechanism giving reliable close range information is needed for ovipositing ♀♀ to verify their hosts.

Such a mechanism may be provided by drumming and associated antenna-dipping behavior where sensory information could be obtained by mechanoreception, gustation and olfaction. It is unlikely that tactile cues are specific enough for host discrimination since, among plants in the habitat of *C. lacinia*, variety in leaf surface features is lacking and densities of the most prominent feature, trichomes, overlap considerably (Calvert, 1975). Olfaction and gustation, however, play important roles in host discrimination and in releasing oviposition behavior. Moreover, tasting or smelling at close range the chemicals released by drumming the leaf surface would not be subject to uncertainties introduced by varying winds and complex plant associations typical of lepidopteran habitats.

Sensory back-up systems for critical behavioral tasks have evolved in numerous animal groups (Gould, 1980). In insects, given that the consequences of ovipositional mistakes are likely to be starvation of the newly hatched larvae, the behaviors leading to host discrimination would certainly be considered critical. In *C. lacinia*, drumming behavior may provide sensory information which, although apparently redundant in some circumstances, becomes critical for host discrimination in less than optimal environmental conditions.

We thank R. Barth, L. Gilbert, J. Larimer and R. Neck for discussions and H. Hagedorn, E. Städler, J. Frazier, V. Dethier and R. Prokopy for criticism. B. Bradley suggested the use of discrimination indices. We also thank G. Bush for the use of the greenhouse and the Brackenridge Field Station Research Committee for the use of this research station. Supported by U.S.P.H.S. Physiology and Biophysics Training Grant 5TOIGM00836 and P.H.S. Grants NS-10760 and NB-08251.

RÉSUMÉ

Influence sur la ponte de Chlosyne lacinia *Geyer (Lep. Nymphalidae) des structures sensorielles et du comportement précédant la ponte*

Le rôle des antennes et des tarses antérieurs sur la ponte et la sélection des hôtes a été étudié chez *Chlosyne lacinia*, papillon nymphalidé aux pontes groupées, dont le comportement avant la ponte comporte un tambourinage et un picotage antennaire. L'ablation intégrale des antennes réduit brutalement la ponte, une antennotectomie partielle la reduit proportionnellement au nombre de récepteurs antennaires éliminés. Les ablations antennaires n'affectent pas significativement la discrimination entre plantes — hôtes ou non. L'ablation des tarses antérieurs supprime la discrimination en pièce climatisée, mais non en serre ou en cages á l'extérieur. Cette différence peut être expliquée par une libération réduite de substances volatiles dans les chambres climatisées avec des surfaces foliaires plus froides ou par la turbulence permanente de l'air qui y était provoquée par les ventilateurs des humidificateurs. Des techniques électrophysiologiques ont été utilisées pour déceler l'activité chimiosensorielle des setae des tarses antérieurs. Nous concluons que des récepteurs chimiques de contact des tarses antérieurs sont utilisés pendant le tambourinage pour contrôler l'hôte dans des conditions écologiques où l'olfaction est inutilisable.

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Accepted: July 9, 1982