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CONTACT CHEMORECEPTION GUIDES OVIPOSITION OF TWO LAURACEAE-SPECIALIZED SWALLOWTAIL BUTTERFLIES (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT.– Females of *Papilio troilus* Linnaeus and *Papilio palamedes* Drury (Lepidoptera: Papilionidae), two closely related swallowtail butterflies, oviposit almost exclusively on a few woody plant species in the family Lauraceae. While geographic patterns of preference differ among Lauraceae species, the butterflies rarely oviposit on any plant species outside the Lauraceae.The role of host plant chemistry in stimulating oviposition was assessed by extracting the preferred host foliage of the respective butterfly species, spraying the extracts and fractions on various substrates, and assessing oviposition relative to controls. *P. troilus* and *P. palamedes* were stimulated to oviposit on filter paper or non-host leaves sprayed with polar extracts of their primary host plants, indicating clearly that leaf chemistry, detectable as contact chemosensory cues, plays a significant role in their oviposition choices. Dependence on chemical oviposition elicitors found only in the foliage of the host plants may explain the behavioral fidelity to Lauraceae shown by these two oligophagous butterflies.

KEY WORDS: behavior, Florida, Michigan, Nearctic, North America, Ohio, oviposition behavior, *Papilio*.

The swallowtail butterflies, *Papilio palamedes* Drury and *P. troilus* Linnaeus, recognize a very restricted range of plant taxa as hosts, ovipositing exclusively on a few species within the Lauraceae. In the United States, *P. palamedes* inhabits the eastern coastal states from southern Virginia south through Florida and west toward Texas and Mexico, closely corresponding to the geographic distribution of red bay (*Persea borbonia* (L.) Spreng.), its predominant host in the field (Scriber 1996). The range of *P. troilus* includes that of spicebush (*Lindera benzoin* (L.) Blume) and sassafras *(Sassafras albidum* (Nutt.) Nees) (Lauraceae), ranging from Canada to Florida east of the Mississippi River and occurring in sympatry with *P. palamedes* in southern Florida (Lederhouse *et al.,* 1992). *P. troilus* utilizes only red bay in southern Florida, outside the habitat of spicebush and sassafras (Nitao *et al.,* 1991). Results of laboratory oviposition bioassays conform to patterns of host use in the field. The two specialist species accurately select lauraceous foliage (88-90%) when placed in a 7-choice array with leaves of 6 non-host species in small bioassay containers (Frankfater, 1996). Only a few eggs were placed on the other 6 plant species (Rosaceae, Oleaceae, Rutaceae, Magnoliaceae, Rhamnaceae, and Salicaceae). *P. palamedes* and *P. troilus* also exhibit differential preferences among lauraceous host species. In bioassays with leaves from 3 lauraceous species, *P. palamedes* females from Florida and Georgia deposit the majority of their eggs on red bay, and oviposit to a lesser extent on spicebush and sassafras. *P. troilus* females from Michigan, Ohio, and Georgia oviposit mainly on spicebush and sassafras, and place fewer eggs on red bay. However, the Florida populations prefer red bay (Fig. 1).

While habitat, host height, leaf shape, leaf color, and chemical volatile odors may play roles in most ovipositing butterflies (Rausher, 1978; Saxena and Goyal, 1978; Miller and Strickler, 1984; Renwick and Chew, 1994; Renwick and Huang, 1994) the final and most critical step for host acceptance usually involves contact (tactile and surface chemical) receptors (Degen and Städler, 1998), especially for butterflies in the family Papilionidae (Feeny *et al.*, 1983, 1988, 1989; Nishida and Fukami, 1989; Honda, 1986, 1990; Oshugi *et al.*, 1991; Papaj *et al.*, 1992; Sachdev-Gupta *et al.*, 1993; Scriber, 1993; Feeny, 1995; Nishida, 1995; Haribal *et al.*, 1998).

The ratios of chemical stimulants and deterrents found in foliage determine the range of plant species accepted for oviposition by *Papilio and Pieris* species (Huang and Renwick 1993; Renwick and Huang, 1994; Honda and Hayashi, 1995). In papilionids, mixtures of stimulant compounds found within host plants act in combination to synergistically elicit oviposition (Ohsugi *et al.*, 1985; Feeny *et al.*, 1988; Nishida and Fukami, 1989; Honda, 1990; Sachdev-Gupta *et al.*, 1993; Nishida 1995).

A physiological dependence on a few compounds exclusive to the family Lauraceae for oviposition stimulus may underlie the accurate host recognition of *P. troilus* and *P. palamedes* both in the field and in multi-choice bioassay arenas in the lab. Extracts of spicebush and red bay, the respective favorite host plants of *P. troilus* and *P. palamedes*, were bioassayed to determine if contact oviposition chemical stimulants play a significant role in host acceptance by females of these two oligophagous species. *Sassafras albidum* and *Cinnamomum camphora* are two other Lauraceous hosts which are "intermediate" in suitability for both *Papilio* species (Nitao *et al.*, 1991) and were not analyzed here.

MATERIALS AND METHODS

General bioassay procedure

Field-caught or hand paired, lab-reared females were stored at 18°C and fed once every other day until their use in the bioassay. Each bioassay arena consisted of one round, transparent plastic container with top (26cm in diameter x 9cm) lined with a paper towel at the bottom. Oviposition substrates, consisting of either filter paper triangles or non-host tulip tree (*Liriodendron tulipifera* L., Magnoliaceae) leaves treated with host extracts, were placed along the sides of the container equally spaced from each other. The petioles of the leaves were inserted into waterpics to maintain leaf turgor. A single female occupied each bioassay arena, where she encountered all treatments and the control substrate simultaneously.

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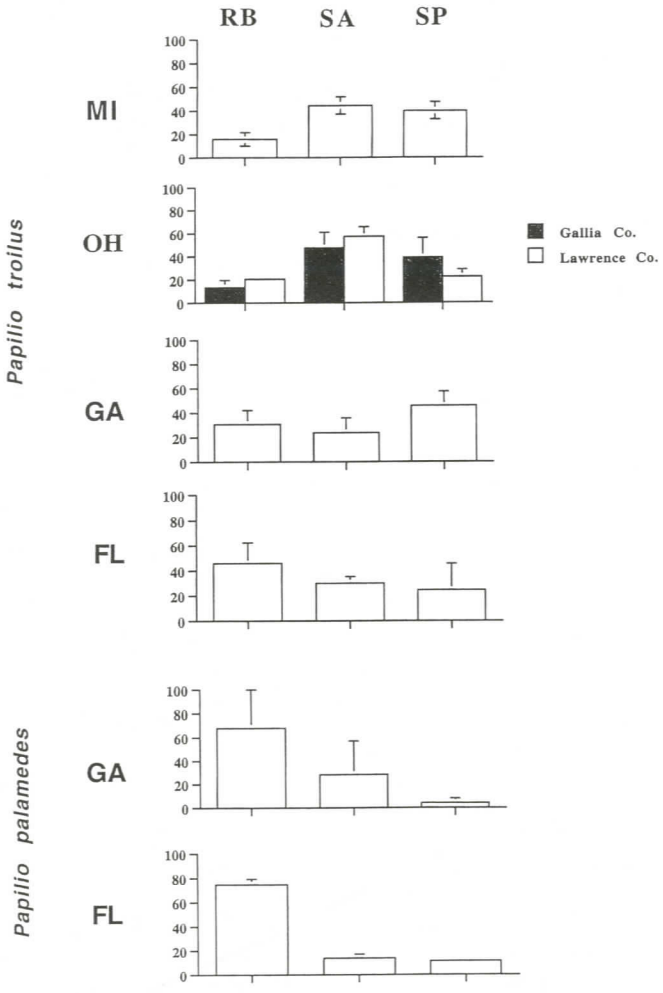

Fig. 1. Percentage of total eggs (mean ± S.E.) in 3-choice arenas laid by *Papilio troilus* from Michigan (St. Joseph Co.; n = 17 females), Ohio (Gallia, Lawrence; n = 28 females), Georgia (Echols Co.; n = 7 females), and Florida (Highland Co.; n = 6 females) compared to *Papilio palamedes* from Georgia (Echols Co.; n=3 females) and Florida (Highlands Co.; n = 10 females). The 3 choices were red bay (*Persea borbonia*; RB), sassafras (*Sassafras albidum*, SA), spicebush (*Lindera benzoin*, SP), all of the Lauraceae family Scriber et al, published). In Highlands County, Florida, the only natural host available is red bay, while all other populations have only sassafras and spicebush, with no red bay.

Bioassay containers were stacked on turntables that rotated once every six minutes and were illuminated on one side with incandescent lights (see Scriber, 1993). Once a day, egg counts on the oviposition substrates were tallied and fresh treatments and controls were supplied. Eggs laid greater than 2.5cm away from a substrate (the approximate distance between a female's foretarsi and curled ovipositor), or equal distances between two treatments, were scored as "container." Females were fed a 20% honey solution once daily. Females were allowed to oviposit for several days, and analysis was performed on arcsine transformed percentages of the total eggs laid on each substrate.

Extraction and fractionation of Spicebush

In 1994, fresh, intact spicebush leaves (130.7 grams) collected from Kalamazoo County, Michigan were extracted for one minute with chloroform (3x), then with methanol (3x) in an extraction column. The procedure yielded 0.8g of chloroform extract and 8.3g of methanol extract.

A modified extraction procedure was used in 1995. Freeze-dried, ground spicebush leaves (120.5g) collected from Gallia County, Ohio were extracted sequentially with 3 solvents. The leaf powder was extracted first with 700ml of hexane for 5 minutes, then soaked (> 6 hours, 2x) in 700ml of hexane. The procedure was repeated with ethyl acetate and methanol. The residues were dried *in vacuo* at 40°C. Subsequent procedures focused on the methanol extract (20.3g), since preliminary experiments revealed this extract to have ovipositional activity. An aliquot (10.2g) of the methanol extract was redissolved in 200ml of 20% methanol in a flask during agitation with a stir bar. The solution was extracted (3x) with 50ml of ethyl acetate, distributing 8.0g of material into the aqueous phase and 2.1g into the ethyl acetate phase. The ethyl acetate-soluble material was dried under a vacuum at 40°C, and the aqueous phase was stored frozen at 20°C until use in the bioassays.

Extraction and fractionation of Red Bay

In 1995, 72.9g of freeze-dried, milled red bay leaves collected from Highland County, Florida were extracted with ca. 400ml of each solvent, following the protocol for the 1995 extraction of spicebush. The procedure yielded 16.4g of vacuum-dried methanol extract. The crude methanol extract (5.7g) was partitioned between water and ethyl acetate as above, distributing 1.1 and 4.6g into the organic-phase and aqueous-phase, respectively.

An additional 56.3g of the red bay leaf powder stored at –80°C was extracted later in the summer to give 13.7g of methanol extract. A portion of this material (6.9g) was partitioned as above between ethyl acetate and water, yielding 1.6 and 5.3g of material, respectively.

4-choice filter paper bioassay with 1994 Spicebush extract

A leaf area meter was used to measure the average surface area of 65 freshly picked spicebush leaves weighing a total of 22.4 grams. Aliquots of each extract from 1994 (average g extract/cm^2) were redissolved in their original extraction solvent and pipetted onto filter paper triangles of known surface area. The solvent was allowed to evaporate from the paper strips before their inclusion in the bioassay. Four filter paper triangles, treated with either the methanol extract, the chloroform extract, both extracts, or untreated were placed in each bioassay arena.

5-choice filter paper bioassay with Spicebush leaf

Using spicebush extracts and fractions of leaf samples from 1995, gram leaf equivalents (average gram extract/leaf, hereafter abbreviated GLE) of the crude methanol extract and the water fraction were sprayed evenly onto both sides of filter paper triangles using a chromatographic sprayer. Approximately four times the GLE of the ethyl acetate fraction was misted onto the filter paper triangles due to a calculation error. However, this mistake did not significantly alter the results of the bioassay (see Fig. 4A). Within one oviposition chamber, each female could contact all 5 oviposition substrates: 3 filter paper triangles (coated respectively with the crude methanol extract, the ethyl acetate fraction and the water fraction) an untreated filter paper triangle, and a spicebush leaf with its petiole inserted into an aquapic to maintain leaf turgor.

3-choice and 5-choice bioassays using non-host leaves as substrates

GLE of the crude extracts and fractions were sprayed separately onto both sides of tulip tree leaves using a chromatographic sprayer. Tulip tree leaves were chosen as a substrate because it is not a host plant of *P. troilus* or *P. palamedes* but it was thought that recognition of a leaf surface would enhance the general activity of oviposition on the treatment choices. The 3-choice leaf bioassay with *P. troilus* consisted of a tulip tree leaf treated with the 1994 methanol extract of spicebush, an untreated tulip leaf, and a spicebush leaf. In the 5-choice bioassay, oviposition preference of

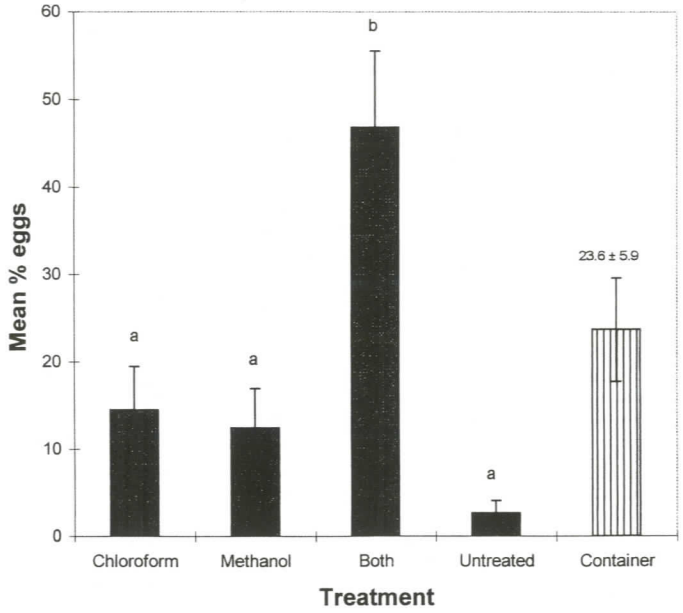

Fig. 2. Percentage of eggs (mean ± S.E.) laid by *Papilio troilus* females (n = 6) on each of 4 choices with spicebush extracts: filter paper triangles coated with methanol extract (methanol), chloroform extract (chloroform) a combination of both extracts (both) and an untreated filter paper triangle (untreated). Extracts were made from fresh spicebush leaves. Significant differences between means ($p < 0.01$) are shown for arcsine transformed percentages and indicated by differences in letter.

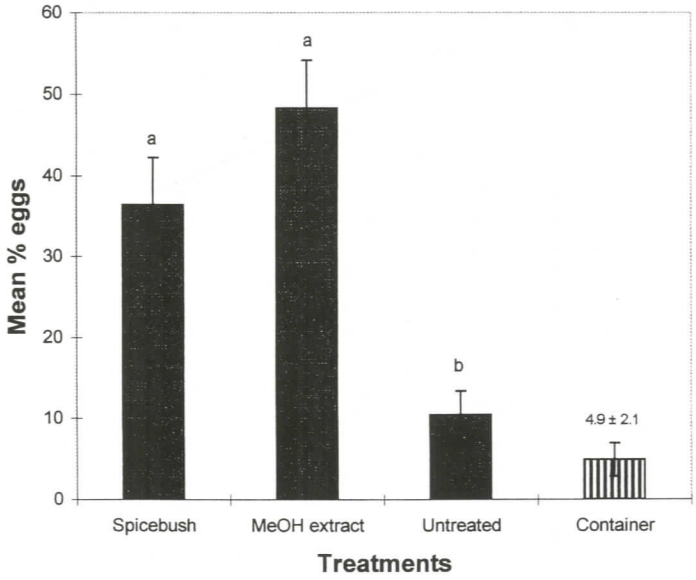

Fig. 3. Percentage of (mean ± S.E.) laid by *Papilio troilus* females (n = 10) on each of three choices: an untreated spicebush leaf, a tulip tree leaf coated with the methanol extract of spicebush and an untreated tulip tree leaf. Significant differences between means ($p < 0.01$) are indicated by different letters.

P. troilus was tested on the 1995 crude methanol extract, the ethyl acetate and water fractions and untreated tulip tree and spicebush leaves. In the case of *P. palamedes*, red bay extracts and fractions were used, and 1 or 2 red bay leaves collected from plants in the greenhouse served as the positive control instead of spicebush.

Statistical analysis

The percentage of eggs laid by individual females on each treatment throughout the duration of the bioassay was calculated. The percentages were arcsine transformed prior to their analysis to normalize the variances. A standard two-way analysis of variance (ANOVA) for unreplicated data was performed, with treatments and butterflies as the main effects (Sokal and Rohlf, 1981). The term "unreplicated" refers to the fact that only 1 butterfly occupied each block, or bioassay arena. If treatment was found to be significant, a one-way ANOVA was performed on the arcsine transformed percentages, excluding the "container" category to maintain independence between treatments. In this apparatus, females fly only on the side nearest the light source. Each leaf passes by the female for one minute during which a choice must be made; the single sequence continues with only one leaf at at time encountered by the female. As such, these are a sequence of no-choice studies with decision to lay an egg basically independent of the other leaves. Specific significant differences between treatments could then be characterized with the Student-Newman-Keuls test (SuperANOVA, 1993).

RESULTS

In the 4-choice bioassay with *P. troilus* (Fig. 2), two-way ANOVA showed significant differences between treatments (F_4= 6.60, p = 0.0015), but not butterflies (F_9= 0.01, p = 1.0). Filter-paper triangles coated with the combined chloroform + methanol extracts had high ovipositional activity, receiving 46% of all eggs laid, significantly more than the control and the other two treatments according to a one-way ANOVA ($p < 0.01$, Fig. 2). Filter paper triangles coated with either the methanol or chloroform extract alone were not found to be significantly different from the control. Twenty-four percent of the eggs were included in the "container" category.

The 3-choice leaf bioassay (Fig. 3) demonstrated the effect of the cues from the oviposition substrate on ovipositional selectivity. Only 5% of the eggs were laid off of the intended substrates on the sides and bottoms of the assay chambers. In the 2-way ANOVA, just the methanol extract treatment category was found to be significant (F_2 = 14.051, $p < 0.0001$). A 1-way ANOVA revealed that *P. troilus* females laid significantly more eggs on tulip tree leaves treated with the methanol extract (48%) and intact spicebush leaves (36%) than tulip tree leaves sprayed with methanol solvent only ($p < 0.01$).

In the presence of an intact spicebush leaf, *P. troilus* females laid negligible numbers of eggs on filter paper triangles sprayed with spicebush extracts in the 5-choice assay (Fig. 4A). 89% of the eggs were laid on the spicebush leaf, while significantly fewer (9%) were laid on the other filter paper substrates together ($p < 0.01$, 1-way ANOVA). In contrast, tulip tree leaves sprayed with spicebush extracts proved more stimulatory than both the tulip tree leaf control and the spicebush leaf itself (Fig. 4B). Only 10% of the eggs were placed on spicebush compared to 30% on leaves containing the crude methanol extract, 30% on leaves treated with the ethyl acetate fraction, 18% on leaves treated with the aqueous fraction and 12% on the untreated tulip tree leaves. A one-way ANOVA revealed that the crude methanol extract and the ethyl acetate fraction received significantly more eggs than did the untreated spicebush and tulip tree leaves ($p < 0.05$).

In the case of *P. palamedes* as well, tulip tree leaves sprayed with the crude red bay extracts received more eggs than red bay leaves (Fig. 5). Only the crude methanol extract was found to be significantly different from the untreated red bay and tulip tree controls by a one-way ANOVA ($p < 0.01$). In both *P. troilus* and *P. palamedes* tulip tree assays, the butterflies laid comparable percentages of eggs on the untreated tulip tree leaves and their preferred host leaf, and laid eggs with greatest frequency on tulip

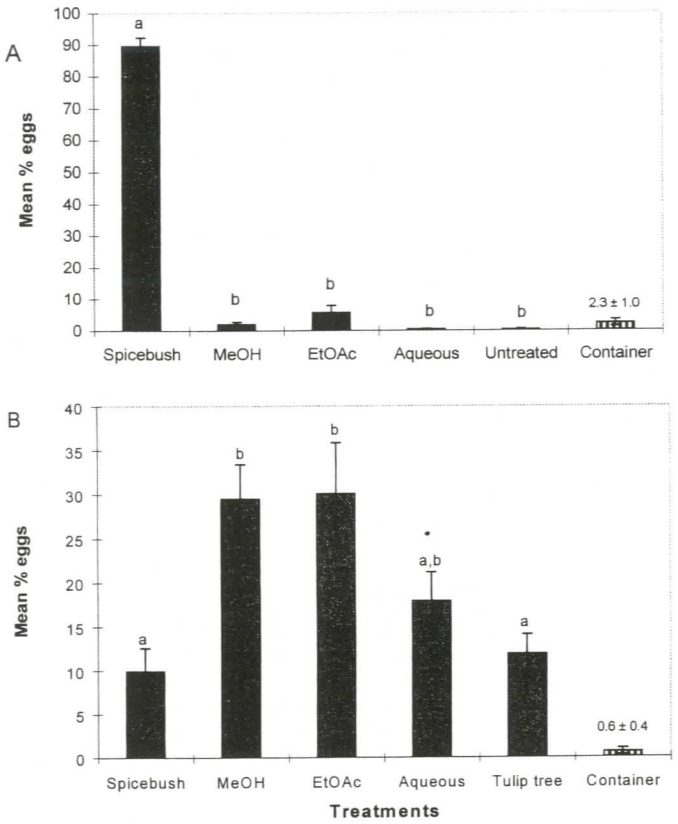

Fig. 4. Percentage of eggs (mean ± S.E.) laid by *Papilio troilus* females on each of 5 choices of spicebush extracts: a spicebush leaf, substrate sprayed with crude methanol extract (MeOH), substrate sprayed with the ethyl acetate fraction (EtOAc), substrate sprayed with the aqueous fraction (Aqueous) and an untreated substrate. Significant differences between means ($p < 0.05$) are shown for arcsine transformed percentages and indicated by letter. A. The substrates are filter paper triangles (n = 32 females). B. The substrates are tulip tree leaves (n = 16 females).

tree leaves coated with host extracts. The results of all the bioassays demonstrate that host plant chemicals stimulate oviposition by *P. troilus* and *P. palamedes*. We did not continue the bioassays with subfractions, nor did we attempt to identify any of the stimulants.

DISCUSSION

Our rotating single choice, sequential oviposition arena allowed us to assess various phytochemical extracts as cues for contact chemosensory preference evaluations. In these arenas, differences in visual (color/shape) cues would be difficult to discern, as would any key volatile odors. Our extracts were also of entire leaves, not just the surface waxes. Nonetheless, these results indicate that certain extracts were very effective when applied to filter paper and to other non-host leaves as a substrate.

Filter paper sprayed with both chloroform and methanol extracts was more attractive to *Papilio troilus* than either extract or untreated filter paper (Fig. 2). Methanol extracts of spicebush sprayed on tulip tree (a toxic non-host; Scriber *et al.*, 1991) attracted more oviposition than the unsprayed spicebush (host) leaf (Fig. 4B). The same was true for *P. palamedes* with methanol extracts of red bay on tulip tree substrate compared to the red bay leaf itself (Fig. 5). However, spicebush leaves were preferred over all extracts when presented on paper as a substrate (Fig. 4A).

However, chemical cues are not solely responsible for host acceptance. In the *P. troilus* four-choice filter paper bioassay (Fig. 2), a significant percentage of eggs were distributed around the

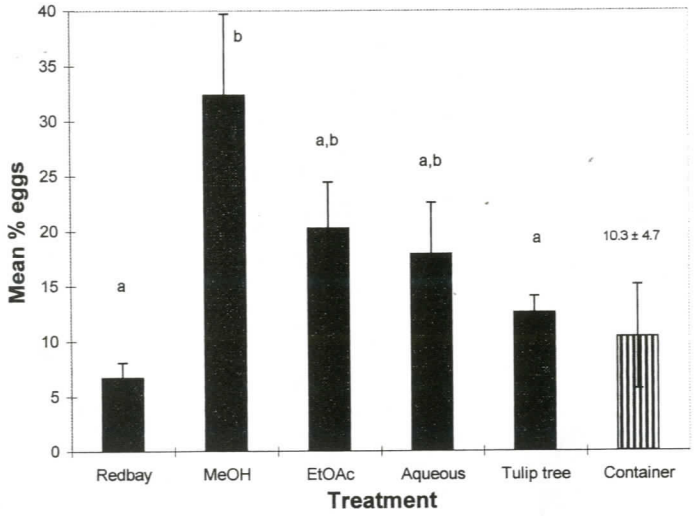

Fig. 5. Percentage of eggs (mean ± S.E.) laid by *Papilio palamedes* females (n = 9) on each of 5 choices with red bay extracts: an untreated red bay leaf, a tulip tree leaf sprayed with methanol extract, a tulip tree leaf sprayed with the ethyl acetate fraction, a tulip tree leaf sprayed with the aqueous fraction, and an untreated tulip tree leaf. Significant differences between means ($p < 0.05$) are shown for arcsine transformed percentages and indicated by letter.

bioassay arena, away from the filter paper substrates. One explanation is that the filter paper triangles lack cues necessary for their complete recognition by the butterflies as a host surface. The absence of such cues in combination with the physiological need to oviposit and stimulation by the leaf extracts may account for the seemingly indiscriminate dispersion of some eggs. Off-substrate oviposition declined substantially in the 3-choice and 5-choice all-leaf assays, most likely due to the perception of general leaf cues such as color, moisture, texture and odor that distinguish leaf tissue from paper strips (Fig. 3, 4B and 5). A comparison of the two 5-choice bioassays with *P. troilus* (Fig. 3) dramatically demonstrates the importance of physical cues in host recognition. In the presence of an intact spicebush leaf, *P. troilus* females laid negligible amounts of eggs on extract-treated filter paper. However, when sprayed onto the surface of tulip tree leaves, *P. troilus* females showed a statistically significant preference for the leaves treated with the methanol and ethyl acetate extracts.

Feeny *et al.* (1989) also demonstrated that non-host volatiles can deter oviposition. Nevertheless, the tulip tree leaves (a non-host) had no adverse effect on oviposition in our bioassays. Both *Papilio* species oviposited a significant number of eggs on tulip tree leaves sprayed with polar extracts of their host plant. In fact, in the five-choice leaf assays, the untreated tulip tree leaf and the host leaf received roughly equal percentages of eggs. Saturation of the air by volatiles from host and non-host leaves within the confines of the plastic containers may have negated the role of odor in orienting a butterfly to one particular leaf.

The hesitation of *P. troilus* to oviposit on the extract treated paper in the four-choice bioassay (Fig. 2) and five-choice assays (Fig. 4A) may be explained by a lack of moisture. Water vapor itself can act as an oviposition stimulant. For example, Shorey (1964) noted that *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae) laid very few eggs on dry filter paper discs. However, moistening the discs with cotton wicks results in a 10 fold increase in the number of eggs laid on the filter paper. Moisture may also facilitate detection of chemical stimulants. *Etiella zinckenella* Treitschke (Lepidoptera: Pyralidae) gave a strong oviposition response to polar extracts of soybean leaves applied to the gauze surrounding a moist substrate. However, the same set-up with a dry substrate did not

elicit such a large difference between the treatment and the control (Hattori, 1988). Although the filter paper triangles were misted with distilled water prior to their placement in our four-choice assay, the large amount of heat generated by the incandescent lights may have quickly dried them.

A combination of visual, tactile, volatile and contact chemical cues greatly increases oviposition in comparison with any cue by itself (Saxena and Goyal, 1978; Traynier, 1986; Feeny *et al.*, 1989). In our bioassay set-up, a real leaf surface was preferred to filter paper triangles sprayed with aqueous extracts, despite their green color and chemical stimuli. Miller and Strickler (1984) suggest a model in which the integration of stimuli from a variety of sources determines the suitability of a substrate for oviposition. Their "rolling fulcrum" model is simlar to Traynier's hypothesis (1986) that butterflies prefer to oviposit on substrates with an "average" of acceptable visual and chemical cues.

An idiosyncracy of the bioassay was that the tulip tree control leaf received as many eggs as did the host leaf in the 5-choice assays (Fig. 4B and 5). This phenomenon may reflect the greater continuous leaf surface area of the tulip tree leaf, or "carry-over" stimulation from the extract treated surfaces onto the adjacent leaf. An element of learning may have been involved if the butterflies may have come to associate the host chemistry with the tulip leaf surface. Additional bioassay errors may have resulted from the effects of the solvent on the tulip tree leaves. However, in other studies (Frankfater, 1996) no significant differences between untreated and solvent treated leaves were detected.

Although several factors are responsible for the recognition of a substrate as a host, as evidenced by the results here, leaf chemistry is a critical component in the stimulation of oviposition by butterflies (Kolb and Scherer, 1982). Reliance on compounds unique to particular plants may maintain host preferences in butterflies and limit host shifts to chemically similar groups of plants (Nishida and Fukami, 1989; Feeny, 1991; Sachdev-Gupta, 1993; Feeny, 1995). It is possible that some of the same phytochemicals found to be stimulants here, may deter oviposition in the generalist butterfly, *Papilio glaucus*, which avoids red bay extracts during oviposition (Frankfater and Scriber, 1999).

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