Journal of the Lepidopterists' Society
62(2), 2008, 84-88

DIFFERENTIAL ANTENNAL SENSITIVITIES OF THE GENERALIST BUTTERFLIES *PAPILIO GLAUCUS* AND *P. CANADENSIS* TO HOST PLANT AND NON-HOST PLANT EXTRACTS

R. J. MERCADER

Department of Entomology, Michigan State University, East Lansing, MI 48824, USA; email: mercade2@msu.edu,

L. L. STELINSKI

Entomology and Nematology Department, University of Florida, Citrus Research and Education Center,
700 Experiment Station Road, Lake Alfred, FL 33850, USA,

AND

J. M. SCRIBER

Department of Entomology, Michigan State University, East Lansing, MI 48824, USA.

ABSTRACT. It is likely that olfaction is used by some generalist insect species as a pre-alighting cue to ameliorate the costs of foraging for suitable hosts. In which case, significantly higher antennal sensitivity would be expected to the volatiles of preferred over less or non-preferred host plants. To test this hypothesis, antennal sensitivity was measured by recording electroantennogram (EAG) responses from intact antennae of the generalists *Papilio glaucus* L. and *P. canadensis* R & J (Papilionidae) to methanolic leaf extracts of primary, secondary, and non-host plants. EAGs recorded from antennae of *P. glaucus* were approximately four fold higher than those of *P. canadensis* in response to extracts of its most suitable host plant, *Liriodendron tulipifera* (Magnoliaceae). Likewise, EAG responses of *P. canandensis* to its preferred host, *Populus tremuloides* (Salicaceae), were significantly higher than those of *P. glaucus*. In addition, *P. glaucus* exhibited significantly higher (approximately three fold) EAG responses to its preferred host, *L. tulipifera*, than to its less-preferred hosts, *Ptelea trifoliata*, *Sassafras albidum*, and *Lindera benzoin*. The results from this study indicate a significant divergence in the olfactory system of two closely related generalist butterfly species, including a strong specialization in the olfactory system of *P. glaucus*.

Additional key words: Electroantennogram, olfaction, oviposition, decision-making, host selection.

For insects with larvae that develop on a single host plant, female ovipositional choice determines larval habitat and therefore the likelihood of larval survival. However, a clear correlation between adult ovipositional preference and host suitability for larval growth has not been found in many systems (reviewed in Mayhew 1997), and 'mistakes' in which eggs are laid on plants toxic to the larvae are fairly common (Straatman 1962; Wiklund 1975; Chew 1977; Berenbaum 1981; Larsson & Ekbom 1995; Renwick 2002; Graves & Shapiro 2003). Such 'mistakes' are believed to be rare for phytochemically specialized species, but generalists, such as *Papilio glaucus* L. and *P. canadensis* R & J (Papilionidae), are known to regularly place a small fraction of their eggs on hosts toxic to their larvae in natural habitats (Brower 1958, 1959) and in controlled environments despite the presence of a suitable alternative (Scriber *et al*. 1991; Scriber 1993). In contrast, specialist herbivores may fail to oviposit on readily available suitable hosts; for example, *Papilio palamedes*' geographic range is determined by female ovipositional preference and not the availability of hosts suitable for larval development (Lederhouse *et al*. 1992). One hypothesis that has been proposed to explain this observation and the higher abundance of specialist insects is that an increase in error rate should be associated with an increase in polyphagy (Levins & MacArthur 1969). In recent years this idea has been updated in terms of neural limitations to include a prolonged decision-making time along with an increased error rate as costs of polyphagy (Bernays 2001; Janz 2003).

Despite the common assertion that olfaction is an important sensory modality for orientation to host plants (Renwick & Chew 1994; Dicke 2000; Finch & Collier 2000), the importance of olfactory cues for oviposition-site location in day-flying butterflies has received relatively little attention compared with moths (reviewed in Hansson 1995; Honda 1995, but see Feeny *et al*. 1989; van Loon *et al*. 1992; Baur & Feeny 1995; Kroutov *et al*. 1999). In addition, the role of olfactory cues in butterfly host plant searching and acceptance behavior has received little attention relative to visual and/or contact cues (e.g. Rausher 1978; Stanton 1982; Scherer & Kolb 1987; Grossmueller & Lederhouse 1985; Thompson & Pellmyr 1991; Honda 1995; Weiss 1997; Schoonhoven *et al*. 1998).

Olfactory cues may play an important role in long and short-range searching behavior of pre-alighting generalist butterflies increasing their efficiency. Baur & Feeny (1995) found electroantennogram (EAG) evidence for evolutionary lability in the peripheral

olfactory system of three specialist butterflies, *Papilio* polyxenes, *P. machaon hippocrates*, and *P. troilus*. If the peripheral olfactory system is labile, it may allow for adaptations in generalist species that allow for a functionally specialized behavior in areas where a primary host is abundant, while maintaining the flexibility to accept alternate hosts in areas where the primary host(s) are rare or not present. If olfactory cues are used to reduce decision-making time in generalist species, significantly higher sensitivity would be expected in the peripheral nervous system to primary hosts over less preferred hosts.

We tested this hypothesis for the polyphagous *P. glaucus* by comparing its antennal sensitivity by EAG recordings with that of its sibling species, *P. canadensis*, to extracts of preferred, secondary, and non-host plants. These two sister species can readily produce fertile hybrid offspring (e.g. Scriber 1998); *P. canadensis* males prefer *P. glaucus* females (Deering & Scriber 2002), and until recently, they were considered the same species (Hagen *et al*. 1991). However, despite their similarities they exhibit significant differences in host plant use. In particular, tulip tree, *Liriodendron tulipifera* (Magnoliaceae), the preferred host of *P. glaucus*, is toxic to *P. canadensis* larvae, while quaking aspen, *Populus tremuloides* (Salicaceae), the preferred host of *P. canadensis*, is toxic to *P. glaucus*. For each species, antennal sensitivity was measured by recording EAG responses to plant extracts of four hosts and one non-host of *P. glaucus*, which included tulip tree and quaking aspen.

Materials and Methods

Insect source. Butterflies used in EAG studies were reared from eggs laid by wild-caught females on their natural host plants. *P. canadensis* females were collected from the first flight in the Battenkill River Valley area at the New York/Vermont border, U.S.A. and the larvae were reared to pupae in the field on sleeved tree branches of black cherry, *Prunus serotina* (Rosaceae). *P. glaucus* females were collected in Lancaster Co. in southeastern Pennsylvania, U.S.A. and were also field-reared on black cherry. After eclosion, butterflies were fed a honey-water solution and stored at 4° C for a maximum of 6 days until they were tested. By using adults that had not encountered any hosts prior to our assays and were reared on the same common host we prevented any influence due to adult or larval induction of preference (reviewed in Mercader & Scriber 2005).

Plant extracts. Leaves of tulip tree, L. *tulipifera* (Magnoliaceae), quaking aspen, *P. tremuloides* (Salicaceae), hop tree, *Ptelea trifoliata* (Rutaceae), sassafras, *Sassafras albidum* (Lauraceae), and spicebush, *Lindera benzoin* (Lauraceae) were collected from trees growing in Ingham Co. Michigan, U.S.A. in areas known to be pesticide free. For simplicity, hereafter hosts will be referred to by their common names. The detailed protocol for preparing plant extracts was described by Gökçe *et al*. (2005). In brief, dried and ground plant materials (10 g samples) were treated with 100 ml of methanol for 24 h. Thereafter, the suspensions were filtered through two layers of cheesecloth and the resulting extracts were stored until use in glass containers wrapped in aluminum foil in the dark at 4° C.

Electroantennograms (EAGs). The EAG apparatus and test protocols were a slight modification of those described in detail by Stelinski *et al*. (2003). The odor stimuli used were the plant extracts described above, methanol as a negative control, and hexanal (Aldrich Chemical Co., Milwaukee, WI, U.S.A., > 98 % pure) dissolved in hexane (Aldrich) as a positive control. Hexanal was used as a standard positive control given that synthetic green leaf volatiles are known to elicit EAG responses in *Papilio* species (Bauer & Feeny 1995). Two milligrams of each plant extract, hexanal solution, and methanol or hexane solvents alone (20 µL total solution) were pipetted onto 1.4 × 0.5 cm strips of Whatman No. 1 filter paper. These were aged for 5 min in a fume hood to allow for solvent evaporation. Subsequently, strips treated with extract or volatile treatments were inserted into glass Pasteur pipettes. EAG measurements were recorded as the maximum amplitude of depolarization elicited by 1 mL puffs of air through EAG-cartridges directed over antennae of live butterfly preparations. The time interval to expel 1 mL of stimulus odor or clean air was ca. 120 ms (Stelinski *et al*. 2003). Plant-extract or chemical stimuli were delivered through one arm of a glass Y-tube (each arm 2 cm in length, base 1 cm long, and 0.5 cm diameter) positioned approximately 5 mm from the antenna as carbon-filtered and humidified air was delivered at 50 mL/min into the second arm and onto the preparation via Tygon tubing.

Male and female butterflies of each species and sex were 2–6 d post-eclosion when used for EAG assays. Butterflies were mounted on 5.0 cm diameter plastic Petri dishes with a clay strip (30 × 5 mm) placed over their wings and thorax. EAG recordings were conducted by removing the terminal tip of the club (< 0.5 mm) of the antenna used for recording with fine scissors, and the recording electrode was positioned directly over the severed end. The reference electrode was inserted into the head near the base of the antenna. EAGs were performed ca. 30 s following mounting of butterflies and terminated at most 2 min later. For each plant extract

tested, EAGs were recorded from 8–10 insects of each sex and species. Plant-extract stimulations were presented to individual butterflies in random order, and control stimulations (filter paper impregnated with 20 µL of hexane or methanol) were delivered prior to each plant-extract stimulus presentation.

Statistical analyses. Between-species, pairwise comparisons of EAG responses were performed separately for tulip tree and quaking aspen on female responses using Mann-Whitney U tests with a Bonferroni corrected significance level of $\alpha < 0.05$. Within species, EAG responses for *P. canadensis* were log transformed and *P. glaucus* responses were square-root transformed to normalize the distributions and homogenize variance. Data were analyzed as repeated measures analysis of variance with individual butterfly as the subject, using Proc Mixed in the SAS System (SAS Institute 2000). The model included odor stimulus and sex as explanatory variables. Pair mean separations were performed for *P. canadensis* and *P. glaucus* using Tukey's multiple comparisons test.

RESULTS

EAG between species comparisons. There were significant differences between EAG responses of *P. canadensis* ($\chi^2 = 15.6$, df = 2, $P < 0.001$) and *P. glaucus* ($\chi^2 = 11.3$, df = 2, $P = 0.003$) to the extracts of tulip tree and quaking aspen (Fig. 1). The magnitude of EAG responses of *P. glaucus* was significantly greater to extracts of tulip tree than those of *P. canadensis*. In contrast, the magnitude of EAGs elicited by quaking aspen extracts was significantly higher for *P. canadensis* than *P. glaucus*.

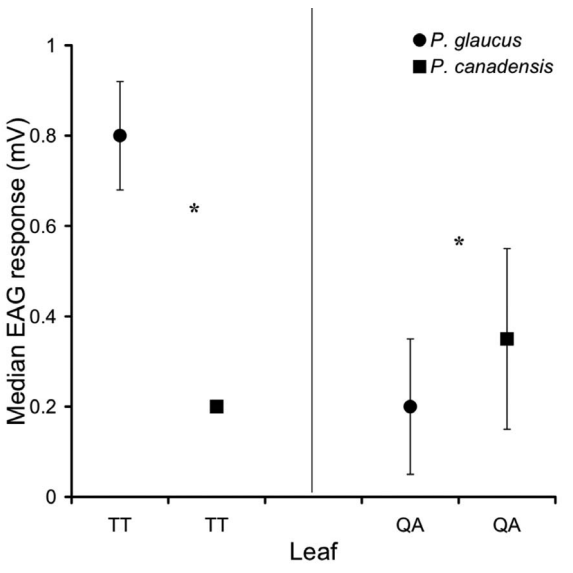

Fig. 1. Median EAG responses of *P. glaucus* and *P. canadensis* females to the extracts of tulip tree TT (*Liriodendron tulipifera*) and quaking aspen QA (*Populus tremuloides*). Bars around the medians represent the inter-quartile ranges (*P. canadensis* inter-quartile range for tulip tree is smaller than size of square). Pair-wise differences were analyzed for each extract using the Mann-Whitney U tests. Values within extract with an * had a significant difference at Bonferroni corrected $\alpha < 0.05$.

EAG within species comparisons. Within-species odor stimuli had a significant effect for *P. glaucus* ($F = 50.1$, df=6,102, $P < 0.0001$), and *P. canadensis* ($F = 24.67$, df = 6,108, $P < 0.0001$). There was no significant sex-by-odor stimulus interaction for *P. glaucus* or *P. canadensis*; therefore, male and female responses were combined for analysis of pair-wise differences (Tables 1

Table 1. Mean EAG responses ± SE of male and female *P. glaucus*. Data for males and females were combined for analysis given that there was no significant sex by odor stimulus interaction.

	Mean ± SE EAG antennal response (mV) to plant extracts				
Odor sources	Males	N	Females	N	P < 0.05
Methanol	0.07 ± 0.01	8	0.09 ± 0.02	10	c*
Hexanal	0.70 ± 0.06	8	0.60 ± 0.09	10	a
Tulip Tree	0.85 ± 0.07	8	0.87 ± 0.07	10	a
Quaking Aspen	0.26 ± 0.07	8	0.19 ± 0.04	10	b
Sassafras	0.23 ± 0.05	8	0.22 ± 0.04	10	b
Spicebush	0.23 ± 0.04	8	0.30 ± 0.04	10	b
Hop Tree	0.25 ± 0.04	8	0.28 ± 0.07	10	b

*Significant differences in antennal responses to odorant stimuli are indicated by different lowercase letters (P < 0.05, Tukey's HSD).

Table 2. Mean EAG responses ± SE of male and female *P. canadensis*. Data for males and females were combined for analysis given that there was no significant sex by odor stimulus interaction.

	Mean ± SE EAG antennal response (mV) to plant extracts				
Odor sources	Males	N	Females	N	P < 0.05
Methanol	0.14 ± 0.03	10	0.09 ± 0.02	9	d*
Hexanal	0.57 ± 0.07	10	0.60 ± 0.09	9	a
Tulip Tree	0.21 ± 0.03	10	0.24 ± 0.03	9	c
Quaking Aspen	0.43 ± 0.07	10	0.37 ± 0.05	9	a
Sassafras	0.30 ± 0.06	10	0.46 ± 0.09	9	abc
Spicebush	0.35 ± 0.05	10	0.41 ± 0.04	9	ab
Hop Tree	0.28 ± 0.05	10	0.29 ± 0.06	9	bc

*Significant differences in antennal responses to odorant stimuli are indicated by different lowercase letters (P < 0.05, Tukey's HSD).

and 2). *P. glaucus* exhibited higher EAG responses to its preferred host, tulip tree, than to less-preferred hosts, hop tree, sassafras, and spicebush, and the non-host quaking aspen (Table 1). Responses to tulip tree were similar to those elicited by the hexanal positive control (Table 1). Likewise, *P. canadensis* exhibited a significantly higher EAG response to its preferred host, quaking aspen, than to hop tree or tulip tree (Table 2). Once again, responses to the preferred host were not different from those elicited by the synthetic standard (Table 2). However, EAGs elicited by two of the non-hosts, sassafras and spicebush, were not significantly different from those elicited by quaking aspen for *P. canadensis*. There was no difference between responses to methanol versus hexane solvents alone; hence, data are not shown for the latter negative control.

Discussion

Antennal sensitivity of *P. glaucus* was approximately three-fold higher to extracts of the preferred host, tulip tree, than to any other extract tested (Table 1). Conversely, tulip tree extract elicited a weaker antennal response from *P. canadensis* than the others tested (Table 2). Furthermore, EAGs recorded from *P. canadensis* to extracts of this species' preferred host plant, quaking aspen, were greater than those from *P. glaucus* (Fig. 1). These results agree with the prediction that peripheral sensitivity to primary hosts should be greater than to less preferred hosts in generalist butterfly species if olfactory cues play a role in host finding behavior. It is notable that species-specific responses were recorded to preferred host plants despite the use of extracts of dried leaves in the current study, which may have limited our assay to higher molecular weight volatiles. This suggests that these butterfly species may use host-plant volatiles, at least as short-range cues, while foraging for suitable host plants, which agrees with field observations of *P. glaucus* females hovering, but not landing, on non-hosts while searching for oviposition sites (R. J. M. personal observations).

Although *P. glaucus* is a highly polyphagous swallowtail species, females exhibit a distinct ovipositional preference for tulip tree throughout their range (Scriber *et al*. 1991; Mercader & Scriber 2005), even in populations where this host plant does not occur (Bossart & Scriber 1995). Congruently, antennal responses to tulip tree were approximately three times greater than to another major host (hop tree), two secondary hosts (sassafras and spicebush), and a non-host (quaking aspen). Although the EAG technique cannot distinguish between attractive versus deterrent olfactory stimuli, the heightened antennal sensitivities recorded in this study corresponded well with known host plant preferences of both species.

It is important to note that although greater EAG responses were observed for females of *P. canadensis* for its most common host quaking aspen than all other hosts tested, these were not significantly different than those for the marginal host sassafras and non-host spicebush (Table 2). This lower specificity in *P. canadensis* relative to *P. glaucus* is not unique to the olfactory system. In ovipositional arenas that primarily test contact chemoreception, *P. canadensis* females have a significantly lower specificity than *P. glaucus*, including a high acceptance rate for the non-host tulip tree (Scriber *et al*. 1991; Mercader & Scriber 2007). This lower specificity in *P. canadensis* is likely to be due to the absence of plants in the Lauraceae (e.g. sassafras and spicebush), Magnoliaceae (e.g. tulip tree), and Rutaceae (e.g. hop tree) where *P. canadensis* occurs, greatly reducing the selection pressure for higher specificity.

Interestingly the divergence in antennal sensitivity between *P. glaucus* and *P. canadensis* was observed in both males and females (Tables 1 and 2). As males do not oviposit and these species do not mate on host plants, divergence in sensitivity to host plant odors does not have any clear advantage for the males of these two species. This similarity in the antennal sensitivities of males and females in both species may reflect a developmental similarity between males and females (with no adaptive function in males) or serve an unknown function.

Heightened antennal sensitivity of *P. glaucus* to tulip tree relative to the other host extracts tested lends support to the hypothesis that olfactory cues may be used to reduce decision-making time during host-plant selection in this species. Pre-alighting cues are more likely involved in maximizing rates of oviposition than in host acceptance behavior (Thompson & Pellmyr 1991); therefore, it is likely that olfactory cues may be used to maximize *P. glaucus*' rate of landing on tulip tree wherever this preferred host is present. Furthermore, the higher sensitivity of *P. canadensis* to odors of quaking aspen relative to the other less-preferred plant species evaluated here adds further support to the hypothesis that host-plant location may be, in part, mediated by chemical signals in these two generalist, sister butterfly species. Further laboratory and field behavioral assays will need to be conducted to confirm this hypothesis.

Acknowledgements

We would like to thank William Houtz and Howard Romack for providing adult butterflies and/or pupae. Earlier drafts of the

manuscript were significantly improved by comments from Cesar Rodriguez-Saona and Rufus Isaacs. This study was supported in part by MAES project #01644.

LITERATURE CITED

BAUR, R. & P. FEENY. 1995. Comparative electrophysiological analysis of plant odor perception in females of three *Papilio* species. Chemoecology 5/6: 26–36.

BERENBAUM, M. R. 1981. An oviposition "mistake" by *Papilio glaucus* (Papilionidae). J. Lepid. Soc. 35:75.

BERNAYS, E. A. 2001. Neural limitations in phytophagous insects: Implications for diet breadth and evolution of host affiliation. Ann. Rev. Entomol. 46: 703–727.

BOSSART, J. L. & J. M. SCRIBER. 1995. Maintenance of ecologically significant genetic variation in the tiger swallowtail butterfly through differential selection and gene flow. Evolution 49: 1163–1171.

BROWER, L. P. 1958. Larval foodplant specificity in butterflies of the *Papilio glaucus* group. Lepid. News 12: 103–114.

_____. 1959. Speciation in butterflies of the *Papilio glaucus* group. II. Ecological relationships and interspecific sexual behavior. Evolution 13: 212–228.

CHEW, F. S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution 31: 568–579.

DEERING, M. D. & J. M. SCRIBER. 2002. Field bioassays show heterospecific mating preference asymmetry between hybridizing North American *Papilio* butterfly species (Lepidoptera: Papilionidae). J. Ethol. 20: 25–33.

DICKE, M. 2000. Chemical ecology of host-plant selection by herbivorous arthropods: a multitrophic perspective. Biochem. Syst. Ecol. 28: 601–617.

FEENY, P., E. STADLER, I. AHMAN, & M. CARTER. 1989. Effects of plant odor on oviposition by the black swallowtail butterfly, *Papilio polyxenes* (Lepidoptera, Papilionidae). J. Insect Behav. 2: 803–827.

FINCH, S. & R. H. COLLIER. 2000. Host-plant selection by insects—a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. Entomol. Exp. Appl. 96: 91–102.

GÖKÇE, A. L., L. L. STELINSKI & M. E. WHALON. 2005. Behavioral and electrophysiological responses of leafroller moths to selected plant extracts. Environ. Entomol. 34: 1426–1432.

GRAVES, S. D. & A. M. SHAPIRO. 2003. Exotics as host plants of the California butterfly fauna. Biol. Conserv. 110: 413–433.

GROSSMUELLER, D. W. & R. C. LEDERHOUSE. 1985. Oviposition site selection - An aid to rapid growth and development in the tiger swallowtail butterfly, *Papilio glaucus*. Oecologia 66: 68–73.

HAGEN, R. H., R. C. LEDERHOUSE, J. L. BOSSART & J. M. SCRIBER. 1991. *Papilio glaucus* and *P. canadensis* are distinct species. J. Lepid. Soc. 45: 245–258.

HANSSON, B. S. 1995. Olfaction in Lepidoptera. Experientia 51: 1003–1027.

HONDA, K. 1995. Chemical basis of differential oviposition by lepidopterous insects. Arch. Insect. Biochem. 30: 1–23.

JANZ, N. 2003. The cost of polyphagy: oviposition decision time vs. error rate in a butterfly. Oikos 100: 493–496.

KROUTOV, V., M. S. MAYER & T. C. EMMEL. 1999. Olfactory conditioning of the butterfly *Agraulis vanillae* (L.) (Lepidoptera, Nymphalidae) to floral but not host-plant odors. J. Insect Behav. 12: 833–843.

LARSSON, S. & B. EKBOM. 1995. Oviposition mistakes in herbivorous insects—Confusion or a step towards a new host giant. Oikos 72: 155–160.

LEDERHOUSE, R. C., M. P. AYRES, J. K. NITAO & J. M. SCRIBER. 1992. Differential use of Lauraceous hosts by swallowtail butterflies, *Papilio troilus* and *P. palamedes* (Papilionidae). Oikos 63: 244–252.

LEVINS, R. & R. MACARTHUR. 1969. An hypothesis to explain the incidence of monophagy. Ecology 50: 910–911.

Mayhew, P. J. 1997. Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79: 417–428.

MERCADER, R. J. & J. M. SCRIBER. 2005. Phenotypic plasticity of host selection in adult tiger swallowtails; *Papilio glaucus* (L.), pp. 25–57. *In* Ananthakrishnan, T. .N. & D. Whitman (eds.), Insects and phenotypic plasticity. Science Publishers, Enfield.

_____. 2007. Diversification of host use in two polyphagous butterflies: differences in oviposition specificity or host rank hierarchy? Entomol Exp. Appl. 125: 89–101.

RAUSHER, M. D. 1978. Search image for leaf shape in a butterfly. Science 200: 1071–1073.

RENWICK, J. A. A. 2002. The chemical world of crucivores: lures, treats and traps. Entomol. Exp. Appl. 104: 35–42.

_____. & F. S. Chew. 1994. Oviposition behavior in Lepidoptera. Ann. Rev. Entomol. 39: 377–400.

SAS INSTITUTE. 2000. SAS/STAT User's Guide, version 6, 4th ed., vol. 1. SAS Institute, Cary, NC.

SCHERER, C. & G. KOLB. 1987. Behavioral experiments on the visual processing of color stimuli in *Pieris brassicae* L. (Lepidoptera). J. Comp. Physiol. A 160: 645–656.

SCHOONHOVEN, L. M., T. JERMY & J. A. VANLOON. 1998. Insect-plant biology: from physiology to evolution. New York: Chapman & Hall.

SCRIBER, J. M. 1993. Absence of behavioral induction in oviposition preference of *Papilio glaucus* (Lepidoptera, Papilionidae). Great Lakes Entomol. 26: 81–95.

_____. 1998. Inheritance of diagnostic larval traits for interspecific hybrids of *Papilio canadensis* and *P. glaucus* (Lepidoptera: Papilionidae). Great Lakes Entomol. 31: 113–123.

_____., B. L. Giebink & D. Snider. 1991. Reciprocal latitudinal clines in oviposition behavior of *Papilio glaucus* and *P. canadensis* across the Great Lakes hybrid zone: possible sex-linkage of oviposition preferences. Oecologia 87: 360– 368.

STANTON, M. L. 1982. Searching in a patchy environment—foodplant selection by *Colias eriphyle* butterflies. Ecology 63: 839–853.

STELINSKI, L. L., J. R. MILLER & L. J. GUT. 2003. Presence of long-lasting peripheral adaptation in the obliquebanded leafroller, *Choristoneura rosaceana* and absence of such adaptation in the redbanded leafroller, *Argyrotaenia velutinana*. J. Chem. Ecol. 29: 405–856.

STRAATMAAN, R. 1962. Notes on certain Lepidoptera ovipositing on plants which are toxic to their larvae. J. Lepid. Soc. 16: 99–103.

THOMPSON, J. N. & O. PELLMYR. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. Ann. Rev. Entomol. 36: 65–89.

VANLOON, J. J. A., W. H. FRENTZ & F. A. VANEEUWIJK. 1992. Electroantennogram responses to plant volatiles in two species of *Pieris* butterflies. Entomol. Exp. Appl. 62: 253–260.

WEISS, M. R. 1997. Innate colour preferences and flexible colour learning in the pipevine swallowtail. Anim. Behav. 53: 1043–1052.

WIKLUND, C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. Oecologia 18: 185–197.

Received for publication 3 January 2007; revised and accepted 5 December 2007.