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SUITABILITY OF FOUR FAMILIES OF FLORIDA "BAY" SPECIES FOR *PAPILIO PALAMEDES* AND *P. GLAUCUS* (PAPILIONIDAE)

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ABSTRACT. We tested the suitability of four Florida "bay" plant species for larval growth and adult oviposition preferences for two swallowtail butterfly species, *P. palamedes* and *P. glaucus*. Much confusion exists about the host plant records for these butterflies in the literature. We confirmed that of the four bay species tested, only red bay (*Persea borbonia*) of the Lauraceae was suitable to support larval survival and growth of *P. palamedes*. All *P. palamedes* larvae offered sweetbay (*Magnolia virginiana* of the Magnoliaceae), Loblolly bay (*Gordonia lasianthus* of the Theaceae) or Southern Bayberry (*Myrica cerifera* of the Myricaceae) died as neonates. Conversely, only sweet bay (*Magnolia*) was suitable for supporting survival of neonate *P. glaucus* larvae, with red bay, loblolly bay and bayberry unacceptable or toxic. Oviposition preferences (individually assessed in a revolving four-choice arena) were strongly in favor of the most suitable host for each species: sweet bay received 93.9% of the total *P. glaucus* eggs and red bay received 54.2% of the total *P. palamedes* eggs. The generally low level of adaptation of the *Lauraceae* specialized spicebush swallowtail, *Papilo troilus*, to red bay was evident in that all nine Florida females refused to oviposit on any of the four "bays" (including red bay).

Additional key words: herbivore-plant interactions, tiger swallowtail butterfly, palamedes swallowtail, spicebush swallowtail, Lauraceae, Magnoliaceae, Theaceae, Myricaceae.

Largely because of its distinctive plant species and geographic isolation as a peninsula, Florida harbors some unique and rare butterfly and moth species (Minnow & Emmel 1992; Emmel 1995). The phytochemical constraints and ecological opportunities affecting host selection and use by various Lepidoptera (Feeny 1995) are of general interest. Some of these unique biochemical, physiological, behavioral and ecological adaptations of Lepidoptera to Florida's local host plants have been documented for the sweet bay silkmoth, *Callosamia securifera* (Peigler 1976, Scriber 1983, Johnson et al. 1996) and three different species of swallowtail butterflies (Scriber 1986, Nitao et al. 1991, Scriber et al. 1991, 1995, Lederhouse et al. 1992, Bossart & Scriber 1995a, 1995b, Frankfater & Scriber 1999a, 1999b). We have examined population fluctuations and the relative densities of *Papilio palamedes, P. troilus*, and *P. glaucus* in central Florida hammocks and bay forests for the past decade (Scriber et al. 1998a). Field observations and lab studies suggest close affinities in preference for either Magnoliaceae or Lauraceae, but not both.

Nonetheless, one of the most confusing examples of uncertainty in host plant records for Lepidoptera exists for *Papilio troilus, P. palamedes*, and *P. glaucus*. Early food plant references for *Papilio* species in the literature are especially unclear about the Florida hosts since the use of the term "bay" (Mitchell & Zim 1964, Scriber 1984) could refer to several species in four different families: 1) Red bay (*Persea borbonia* (L.) Spreng) of the Lauraceae family, 2) Sweet bay or white bay (*Magnolia virginiana* (L.) of the Magnoliaceae family, 3) Loblolly Bay (*Gordonia lasianthus* (L.) Ellis) of the Theaceae family, 4) or Southern Bayberry (*Myrica cerifera* L.) of the Myricaceae family. For example, it has been stated that "*Papilio palamedes*. . . larvae feed on magnolias in the Bay Tree hammocks of the Everglades" (Young 1955). While loblolly bay occurs throughout Highlands County and in each Florida county north of Lake Okeechobee and into Georgia; red bay, sweet bay, and southern bayberry occur in every county of Florida including the southern ones down to the Keys (Little 1978, Nelson 1994).

In a study of latitudinal and geographic variation in host plant records for the 560+ species of swallowtail butterflies, Scriber (1973, 1984) lists numerous citations that report both the Magnoliaceae and Lauraceae families as host plants for the *Papilio troilus, P. palamedes*, and *P. glaucus* butterfly species. No specific records of bayberry (or other Myricaceae) nor *Gordonia* (or other Theaceae) were listed as hosts or foods for these *Papilio*. However, since all four "bay" species frequently coexist in swamps, hammocks and floodplain forests of southern Florida, we were inter-

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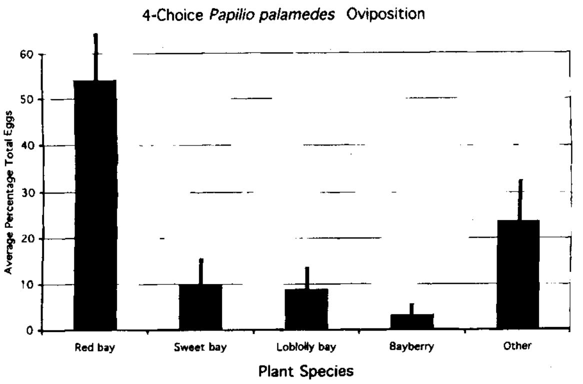

FIG. 1. The 4-choice oviposition preferences (mean ± SE) of eight Florida *P. palamedes* females on four "bay" species or "other" (on paper lining or plastic arena) (red bay, Lauraceae; sweet bay, Magnoliaceae; loblolly bay, Theaceae; southern bayberry, Myricaceae). The average eggs per female was 45 ± 16 (SE).

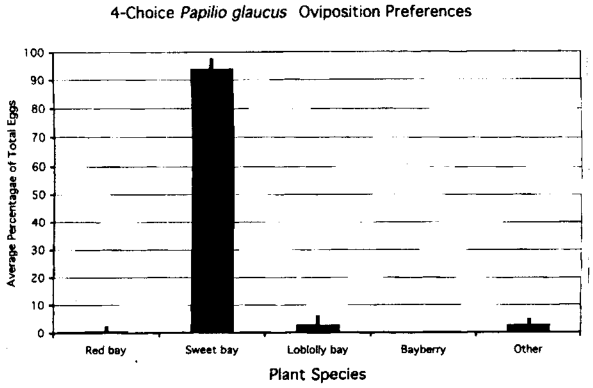

FIG. 2. The 4-choice oviposition preferences (mean ± SE) of five Florida *Papilio glaucus* females on four "bay" species (see Fig. 1). The average total eggs per females was 84 ± 36 (SE).

ested in determining which of these four were used (or capable of being used) for oviposition and/or for larval food. We conducted our multichoice oviposition and larval survival and growth studies in Highlands County, Florida, at the Archbold Biological Station and some bioassays were conducted with material sent to Michigan State University.

Clarification of uncertain adult oviposition and larval food plant records is critically important for understanding the relationships between insects and plants in ecological and evolutionary time (Ehrlich & Raven 1964, Feeny 1995). A procedure for reporting host plants or food plant observations was provided by Shields et al. (1969), and they explained how misidentification of either the insect or plant species can lead to errors that get transmitted in textbooks, guidebooks, and other scientific literature for decades. In our case, it has been suspected that *P. palamedes* only feeds on members of Lauraceae and not on members of Magnoliaceae (Brooks 1962, Scriber 1986); however sweet bay (*Magnolia virginiana*, previously described as *Magnolia glauca*) or Magnoliaceae is listed as hosts for *P. palamedes* by numerous authors (Jordan 1907, Young 1955, Klots 1958, Forbes 1960, Ehrlich & Ehrlich 1961, Kimball 1965, Harris 1972, Tietz 1972, Tyler 1975, Pyle 1981, Okano 1983, Beutelspacher-Baights & Howe 1984, Opler & Krizek 1984, Pyle 1997). While still other authors do not list sweet bay magnolia as a host for *P. palamedes* they do list it as a host for *P. troilus* (Scudder 1889, Shapiro 1974, Howe 1975, Scott 1986, Tilden & Smith 1986), which is also very unlikely (Scriber 1986, Scriber et al. 1991, Nitao et al. 1992).

Our study was conducted with *P. palamedes* and *P. glaucus* in order to determine both the adult female oviposition preferences in 4-choice arenas and the neonate larval survival abilities of both of these swallowtail butterfly species in no-choice bioassays with four "bay" species of Highlands County, Florida. While we intended to include *Papilio troilus* larvae in these studies, we were not successful in obtaining oviposition from the females (n = 9) we did secure.

METHODS

Adult females of *Papilio palamedes*, *P. troilus*, and *P. glaucus* captured in Florida (Highlands, Levy and Columbia Counties) were set up in 4-choice oviposition arenas to assess host preferences via contact chemoreception. The arenas are round plastic boxes that revolve 10 times per hour on a mechanized platform in front of incandescent lights. Leaves of each bay species were supported in water-filled floral aquapics and draped along the side and bottom of the dish as described by Scriber (1993). The four bay species, *Persea borbonia* (red bay = RB), *Magnolia virginiana* (sweet bay = SB), *Gordonia lasianthus* (loblolly bay = LB), and *Myrica cerifera* (southern bayberry = BB), were collected from the area west of Istokpoga Lake near the city of Lake Placid, Florida. The oviposition arenas were inside the invertebrate biology laboratory of Mark Deyrup at the Archbold Biological Station. Herbarium vouchers of these plant species have been deposited in the Michigan State University research collection (JMS).

Each day, eggs were collected and the number of eggs placed on each "bay" by individual females was recorded as were the few eggs sometimes placed on the side of the plastic dish. Adult females were fed each day (with the exception of two periods of 48-hour intervals over our four week study period). Some eggs of *P. palamedes* and *P. glaucus* were sent by overnight express mail with leaves of the bay species to our laboratory at Michigan State University. When received, *the eggs were immediately placed in a growth chamber set at 26° and 18 L: 6D photoperiod.* The leaves were placed in refrigeration at about 4°C in order to maintain their freshness. Subsequent shipments of leaves were sent via overnight mail, and put under refrigeration. A majority of these eggs and neonate larvae of *Papilio* were maintained in Florida at the Archbold Biological Station (at room temperature) for parallel and simultaneous bioassays (n = 70 *P. palamedes* and n = 140 *P. glaucus*). Eggs were checked at least twice a day so that neonates could be placed on leaves within hours of eclosion at each location. 150 × 25 mm petri dishes were set up with a circle of paper towel in the bottom and with an aquapic filled with water in which to place the leaves to prevent them from drying out. The maternal source from which the larvae came was recorded for each bioassay treatment. When larvae hatched, they were allocated equally among the four types of bay leaves, three larvae per dish. Larvae were gently placed on the leaves using a camelhair brush. All work surfaces and the camelhair brush used were cleaned with a 5% bleach/95% water solution before and after uses. Larvae were kept in the same growth chamber and were monitored daily to determine survival through the first instar. Survivors were reared to pupation on their host plant treatment.

RESULTS

It was absolutely clear that three of the "bay" species (sweet bay, loblolly bay and bayberry) were unsuitable for larvae of *P. palamedes*. All *P. palamedes* larvae placed on these hosts died with little or no eating and no frass production within a few days during the first larval instar stage, while survival and growth was very good on red bay, (*Persea borbonia*). The red bay survival for the neonates of six different families at Michigan State University was: 100%, 100%, 80%, 60%, 44% and 14% (n = 3, 2, 10, 5, 16, and 7 respectively). Similar results were obtained with sibling *P. palamedes* larvae from one mother larva bioassayed on each of the four treatment plant species in Florida at the Archbold Biological Station: 37 of 40 neonates reached the second instar on red bay and all neonates on the other 3 "bay" species died (n = 10 larvae each) without evidence of eating or feces.

In contrast, *Papilio glaucus* neonates all died (with no eating or frass) on red bay as well as on loblolly bay and bayberry. Sweet bay (*Magnolia virginiana*) was the only suitable host for these tiger swallowtail larvae in the Florida studies. All larvae on red bay (n = 16), loblolly bay (n = 16), and bayberry (n = 16) refused to eat and died, whereas 77 of 94 larvae (82%) survived to the second instar on sweet bay. Similarly, the *smaller subset of eggs shipped overnight to Michigan* had a 50% larval survival on sweetbay and 0% survival on each of the other species.

The 4-choice oviposition preferences of the adult females of *P. palamedes* favored red bay over the other 3 "bays" in 7 of 8 females that laid more than 10 eggs. The other female *palamedes* oviposited on the dish or paper lining more than all of the four "bay" choices together. A total of sixteen other females of *P. palamedes* laid fewer than 10 eggs each in their four-choice arenas and were excluded from analyses.

In contrast, five adult females of *Papilio glaucus* selected the sweet bay (the only suitable larval host) for the majority of their oviposition choices in the 4-choice arena (four of these selected SB for more than 93% of their eggs). A total of 28 other female *P. glaucus* laid fewer than 10 eggs.

All females (n = 9) of the Florida *P. troilus* refused to lay any eggs in the 4-choice oviposition arenas (five from Highlands County in the south and two each from Levy County and Columbia County in the north). While we were unable to bioassay *P. troilus* larval survival on the four "bay" species in this study, it was of interest that those females of the spicebush swallowtail all refused to lay any eggs, even with the (Lauraceae) red bay presented as one of the choices.

DISCUSSION

It was clear that not even sympatric Florida populations of the *palamedes* swallowtail butterfly could survive on three of the four "bays" of Florida: only red bay of the Lauraceae supported larval survival and growth. Neither sweet bay (Magnoliaceae), loblolly bay (Theaceae), nor southern bayberry (Myricaceae) were eaten in no-choice bioassays and all neonate larvae tested from six different families died. It has been shown previously that sweet bay was toxic to *P. palamedes* larvae (Scriber 1986) due to toxic neolignans from *Magnolia virginiana* leaves (Nitao et al. 1992) but nothing is known about the specific deterrent/toxin mechanisms for loblolly bay nor Southern bayberry.

It was also observed that larvae of Florida tiger swallowtail butterflies, *P. glaucus,* could not survive the neonate (first instar) stage on any of the "bays" other than *Magnolia virginiana* (sweet bay) of the Magnoliaceae. All larvae died on (and refused to even eat) leaves of red bay, loblolly bay, and southern bayberry in no-choice bioassays. The toxicity of red bay to *P. glaucus* was suggested earlier (Scriber 1986) but the phytochemical cause is still not known for this plant or the other two bay species bioassayed here. It is unusual that larvae of this polyphagous species refused to even nibble on the leaves since it is known that neonates often eat small trenches in the edge of toxic plants from many families (Hagen 1986, Scriber 1988, Scriber et al. 1991, Scriber et al. 1999).

Oviposition preferences of these two different *Papilio* were generally for the bay species that was the only suitable host (red bay for *P. palamedes*, and sweet bay for *P. glaucus*). The few scattered eggs on other plants is not surprising, perhaps because the experimental 4-choice oviposition arenas do not provide enough space to prevent co-mingling of volatile chemicals (e.g., stimulants and deterrents). Contact chemosensory stimulations are the key cues used by Lauraceae-specialized *Papilio* (Carter & Feeny 1999, Carter et al. 1999, Frankfater & Scriber 2001) and the deterrents in the Lauraceae (red bay) for *Papilio glaucus* females (Frankfater & Scriber 1999). These strong tarsal contact and oviposition stimulation/deterrency reactions to red bay phytochemicals could explain the dominant patterns of single host recognition and preference in our arenas. Adult preference and larval performance in these four bay species seem to be clearly related for both *P. palamedes* and *P. glaucus* for host or non-host. However, there are many ecological reasons why such a physiological and behavioral "preference/performance" correlation (whether or not genetically based) might not always be expected within a species (Thompson & Pellmyr 1991, Thompson 1995, Bossart & Scriber 1999). For example, Florida populations of *P. glaucus* survive better and grow faster than Georgia, Ohio, and Michigan populations on sweet bay, which reflects significant differences in behavioral and physiological adaptations of local populations (Scriber 1986, Scriber et al. 1991). It is interesting that, despite ecologically significant divergence among *P. glaucus* populations of these four states, no detectable genetic divergence in allozyme frequencies were observed (Bossart & Scriber 1995b).

The fact that *P. troilus* females refused to lay any eggs in the 4-choice oviposition arenas (even on red bay) is interesting, since most *palamedes* females did. In southern Florida, the only Lauraceous host plant for *P. troilus* appears to be red bay, *Persea borbonia*. However, throughout their geographic range north of Gainesville, *P. troilus* females prefer sassafras (*Sassafras albidum*) or spicebush (*Lindera benzoin*). Local larval adaptation of southern Florida *P. troilus* populations to red bay, their only host species in Highlands County, has been demonstrated to have a genetic basis (Nitao et al. 1991, Nitao 1995). Five of the nine *P. troilus* females were from Highlands County (four were from the north). Perhaps the recognition of red bay in the 4-choice oviposition array is less well developed for *P. troilus* in general compared to *P. palamedes*, especially since this is the case for larval survival and growth on red bay (Scriber et al. 1991, Lederhouse et al. 1992, Nitao 1995). Larval survival on red bay was 77% for *P. palamedes* (n = 30 families, 562 larvae) and only 47% for *P. troilus* (8 families, 119 larvae) while larval survival on spicebush is basically reversed; 28% for *P. palamedes* (20 families, 165 larvae) and 86% for *P. troilus* (7 families, 156 larvae; Scriber et al. 1991). For two other Lauraceae species, larval survival on sassafras (78% and 79%) and camphor tree (52% and 50%) is basically the same for *P. palamedes* and *P. troilus*, respectively.

Despite their close co-occurrence in Florida swamps, wetlands, hammocks, and forests, the four "bay" species from four different plant families analyzed in our studies are clearly recognized as host and non-hosts for *P. palamedes* and *P. glaucus*. Only red bay is a host for *P. palamedes* and only sweet (white) bay as a host for *P. glaucus*. When early literature records are incorrect, mistakes can be passed on from one to another (Shields et al. 1969). We believe this issue has largely been clarified for Florida "bays" (Young 1955, Mitchell & Zim 1964, Scriber 1984) by our oviposition and larval bioassays here.

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