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FOODPLANT PROCESSING ADAPTATIONS IN FOUR *HYALOPHORA* SPECIES (LEPIDOPTERA: SATURNIIDAE): REGIONAL AND TAXONOMIC SPECIALIZATION

J. Mark Scriber[1] and Eric Grabstein[2]

ABSTRACT

To determine whether local populations of four *Hyalophora* species (Lepidoptera: Saturniidae) had improved survival or were physiologically adapted for rapid and/or efficient growth on their local hosts, a series of larval feeding studies were conducted using gravimetric techniques on several host plant species. Significantly better survival and growth performances were observed for *H. columbia* (a tamarack specialist) on its host, *Larix laricina*. Similarly, *H. gloveri* had the best growth performance on *Elaeagnus angustifolia* (its favorite) as did certain sympatric populations of *H. cecropia* on black cherry, *Prunus serotina*. *Hyalophora gloveri* and *H. columbia* are largely sympatric with *Betula papyrifera* and perform better than their allopatric congeners *H. cecropia* in the east and *H. euryalus* in the west. While survival of the tamarack specialist was poor, all three of the other North American *Hyalophora* species survived and grew very well on choke cherry, *Prunus virginiana*, which is sympatric with all four *Hyalophora* species. The extent to which these are genetically based adaptations is not known, nor are the specific mechanisms of biochemical adaptation involved in these differential performances of larvae.

Dethier (1954) predicted that monophagous species should utilize their host more efficiently than polyphagous species. Hypotheses regarding the evolution of feeding specialization usually assume there is a cost to adaptation, with an implied trade-off principal that "a jack of all trades is master of none" (see Futuyma and Moreno 1988 for a review). Scriber and Feeny (1979) empirically tested this hypothesis using butterfly (Papilionidae) and silkmoth (Saturniidae) species. Variability in plant nutritional and allelochemical content with various plant species and regional variation in insect feeding preferences were found to be major problems in assessing these physiological and toxicological "costs". Comparisons of congeners with different degrees of specialization, but with a shared host plant proved to be a better test of the hypothesis, since nutritional/allelochemical variability are minimized (Scriber 1984). One of the best tests of the feeding specialization hypothesis (that larval performance will be better on local host plant favorites that populations have adapted to, than on hosts used elsewhere) appears to be possible with a comparison of larval performance of the giant silkmoth family (Saturniidae). For this study we chose the widespread, but endemic North American silkmoth genus *Hyalophora* with its four largely parapatrically distributed species (*cecropia*, *euryalus*, *gloveri*, and *columbia*; Fig. 1).

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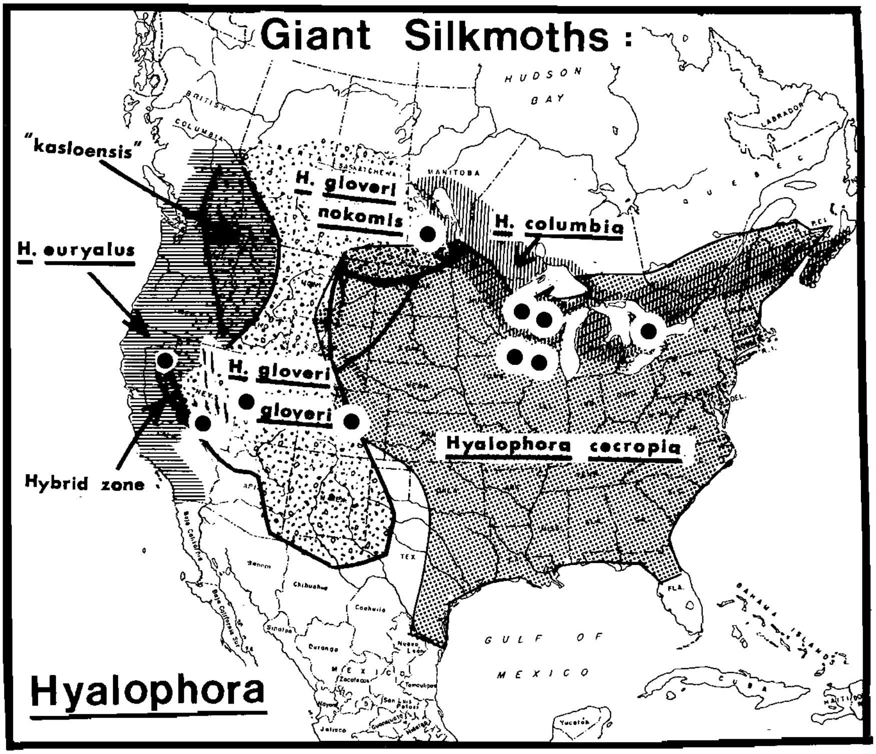

Figure 1. Geographic ranges of the North American *Hyalophora*. Distribution records are from Sweadner (1937), McGugan (1958), Ferguson (1972), Collins (1973, 1984), Kohalmi and Moens (1975), Ferge (1983), Tuttle (1985). Dots indicate the geographic locations of specimens used in studies reported here.

The widespread eastern species *Hyalophora cecropia* (L.) is polyphagous, capable of feeding on at least 88 different species of plants from 20 families of angiosperms including introduced ornamentals (Waldbauer and Sternburg 1967, Scarbrough et al. 1974). The most common natural hosts are geologically old families, the Rosaceae, Salicaceae, and Aceraceae (Ferguson 1972). The two western species *H. gloveri* (Strecker) and *H. euryalus* (Boisduval) prefer the Rhamnaceae (*Ceanothus* and *Rhamnus* spp.) and Ericaceae (*Arctostaphylos* and *Arbutus*), members of the geologically more recent Madro-Tertiary flora (Alexrod 1977, Collins 1984). These plants are important members of sclerophyll chaparral and scrub communities in the California Coast Ranges and Sierra Nevada and are adapted to a climate of winter rains and summer drought; the range of *H. euryalus* is nearly congruent with the broad extent of these plant communities. While *H. gloveri* includes manzanita and other *Arctostaphylos spp.* (Ericaceae) as hosts in Arizona and *Ceanothus velutinus* (Rhamnaceae) in the Great Basin and Rocky Mts., its principal hosts are *Salix* spp. (Salicaceae) and *Prunus* spp. and *Purshia tridentata* (Rosaceae) (Collins 1984). Northern populations of *H. gloveri* occupying recently deglaciated terrain are more specialized feeders. In the northern plains *H. gloveri nokomis* prefers buffalo berry

(*Shepherdia argentea* Pursh), silverberry (*Elaeagnus commutata*), and the introduced Russian olive (*Elaeagnus angustifolia*), all in the Elaeagnaceae (Collins 1973).

The primarily Canadian form *H. columbia* (Smith) inhabits acid bogs and is a specialist on the conifer tamarack (*Larix laricina*). Although *H. columbia* is commonly treated as a separate species, Kohalmi and Moens (1975) and Collins (1973) describe intergradient populations in nature, and female hybrids between columbia and nominate gloveri are fully fertile. In northern Wisconsin, *H. columbia* and *H. cecropia* are sympatric and fly at the same time of the season, however due to various behavioral prezygotic isolating mechanisms there appears to be a low incidence of hybridization (Ferge 1983, Tuttle 1985).

Our objective in this study was to determine whether there is evidence that local foodplant specialization has an associated component of improved larval survival, growth rate, and/or efficiency. To conduct the study, we obtained specimens of all four *Hyalophora* silkmoth species and proceeded with controlled environment feeding experiments on selected foodplant species, including: black cherry, *Prunus serotina*, and choke cherry, *P. virginiana* (Rosaceae), paper birch, *Betula papyrifera* (Betulaceae), Russian olive, *Elaeagnus angustifolia* (Elaeagnaceae), and tamarack, *Larix laricina* (Pinaceae).

METHODS AND MATERIALS

Breeding stock was collected in the wild as cocoons or obtained from breeders who could verify its regional source (Fig. 1). Interpopulational and interspecific hybrids were obtained by laboratory cage mating and with funnel traps in the field which were baited with virgin *Hyalophora* females. Mated females were placed in paper bags to oviposit. Clusters of ova were cut out and placed in 10 cm diameter plastic petri dishes. Small twigs of host plant were maintained in "aquapics" placed in the petri dishes and changed at 1 to 3 day intervals, at which time larvae were censused for survival and stage of growth.

For penultimate instar feeding studies, *Hyalophora* larvae of each species were reared from neonate stages through to the penultimate instar en masse on the particular foodplant to be used in feeding experiments. These groups of individuals were kept in an environmental chamber set at 16 hr photo-: 8 hr scotophase, and at 23.5°C and 19.5°C during the photo- and scotophase, respectively. The relative humidity in the chamber was roughly 60% and 90% during the photo- and scotophase, respectively.

At the beginning of the penultimate stadium, larvae were placed individually in 150 × 25 mm plastic petri dishes with moist filter paper to maintain humidity. Petri dishes were kept in an environmental chamber under the same conditions described for rearing. Sample larvae were weighed at the beginning of the penultimate stadium, frozen, lyophilized and then weighed again (dry). The percentage of dry biomass was determined for each larva.

Foodplant leaves were excised from branches (collected the previous day and stored in water at ca. 5–10°C) immediately before use, weighed and placed by their petioles in Aquapics® to maintain their turgidity (Scriber 1977). Sample aliquots of leaves were taken from each branch for later determinations of percentage dry weights. Fresh leaves were presented at approximately 48 hr intervals; uneaten food was collected, dried and weighed. The food consumption of each larva for the whole penultimate stadium was estimated by standard gravimetric techniques (Waldbauer 1968).

Nutritional indices were calculated based upon dry weight (biomass) of leaves, feces, and larvae. The mean larval weight during the stadium ($\bar{B}$) was estimated by measuring the the initial plus final weight and dividing by 2. Indices of larval performance are reported as in Scriber and Slansky (1981).

RESULTS

While all four *Hyalophora* species survived well in the early instar stages on the two cherry species (black cherry and choke cherry), penultimate instar consumption rates and efficiencies of conversion of plant tissue into insect biomass were significantly different among species and populations. On black cherry, larvae of the tamarack feeding specialist (*H. columbia*) did not survive to the feeding study and *H. gloveri* larvae from a Utah population grew at a significantly lower rate than eastern *H. cecropia* larvae (Table 1). Larvae of *H. euryalis* from California grew significantly slower than *H. cecropia* from Wisconsin, but were only slightly slower than *H. cecropia* from Colorado (Table 1). Of all populations, the fastest growing and most efficient (E.C.I.) were those of Wisconsin *H. cecropia* which are also the only populations of *cecropia* tested that are sympatric with the black cherry host plant. Slower and less efficient growth of Colorado *H. cecropia* compared to Wisconsin *H. cecropia* suggest that interpopulation as well as interspecific physiological adaptations exist.

Nearly all *H. columbia* larvae died on choke cherry, *P. virginiana*, as with black cherry, before reaching the penultimate instar feeding experiment (Table 2). Unlike the case with black cherry, on choke cherry all of the other *Hyalophora* species grew at the same rate, with some trade-offs in consumption rates and efficiencies (Table 2). Unlike black cherry, the geographic range of choke cherry extends across almost all of Canada and the northern half of the United States and is sympatric in certain locations with all four species of *Hyalophora* in this study. It should be noted that choke cherry of California has been considered taxonomically distinct and is sometimes called *Prunus demissa*. Whether or not the identical growth rates of the various *Hyalophora* species reflect similar physiological adaptations evolved due to local use of choke cherry by their populations in areas of sympatry is unclear (since local preferences are poorly documented). However, it would appear that Rosaceae is a generally suitable host plant family for the group, with *H. columbia* as a possible exception.

Another host plant that has considerable geographic overlap with the *Hyalophora* group is paper birch, *Betula papyrifera*, with a range across Canada at least as extensive as is that of *Prunus virginiana*. Paper birch extends from New England south into the Smoky Mts. and across the Great Lakes states and essentially all of Canada into Alaska. It does not extend south throughout the Rockies nor does it occur in California. Nonetheless, larvae of *H. euryalis* from California and *H. gloveri* from Utah grew as fast and as efficiently on this plant as did the Wisconsin *H. cecropia* (Table 3). We were unable to test *H. columbia* larvae on this plant, but hybrid *columbia* × *gloveri* larvae grow at an extremely rapid rate (195 mg g^{-1} day^{-1}). It would be especially valuable to bioassay *H. gloveri* from Canada, where the extensive use of paper birch is perhaps most likely. In fact, *Hyalophora* eggs were collected on paper birch in the putative hybrid zone between *gloveri* and *columbia* in the Riding Mts. of Manitoba (J. M. Scriber personal observation), however too few were found for experimental feeding studies.

In the heart of the range of *H. gloveri*, Elaeagnaceae are the primary host plants (Ferguson 1972, Collins 1973). One of these host plant species, Russian olive (*Elaeagnus angstifolia*), was bioassayed with all four *Hyalophora* species to see if differential adaptations may be evident in growth of their larvae. All of the *H. columbia* died before or during the penultimate instar while feeding on *E. angustifolia* (Scriber and Collins, unpublished data). All *H. euryalis* also died in the neonate (first instar) stage and no feeding experiments were possible. Both *H. gloveri* and *H. cecropia*

Table 1. Utilization of black cherry, *Prunus serotina* by penultimate instar larvae of four *Hyalophora* species.

Hyalophora species		(n)	Consumption Rate (RCR) mg/day/g	(AD) %	Efficiency (ECD) %	(ECI) %	Growth Rate (RGR) mg/day/g
H. euralis[1]		(4)	859 ± 36 b	34.3 ± 1.0 ab	45.1 ± 1.2 a	15.5 ± 0.2 abc	133 ± 7 c
H. gloveri[2]	(UT)	(5)	645 ± 33 b	33.4 ± 0.9 ab	43.1 ± 3.0 a	14.3 ± 0.9 bc	92 ± 5 d
	(UT)	(4)	688 ± 40 b	32.4 ± 0.9 b	42.3 ± 3.2 a	13.6 ± 0.7 bc	91 ± 6 d
H. cecropia[3]	(CO)	(8)	988 ± 37 ab	36.8 ± 1.8 ab	39.0 ± 1.6 a	14.1 ± 0.1 bc	140 ± 5 c
	(CO)	(6)	993 ± 64 ab	42.0 ± 2.2 a	38.9 ± 1.8 a	16.2 ± 0.4 abc	160 ± 9 bc
	(CO)	(5)	943 ± 38 ab	33.8 ± 1.4 ab	47.0 ± 1.6 a	15.8 ± 0.5 abc	150 ± 8 c
	(WI)	(5)	1088 ± 33 a	43.0 ± 0.6 a	41.7 ± 2.0 a	17.9 ± 0.9 ab	194 ± 5 ab
	(WI)	(14)	1043 ± 39 a	42.4 ± 1.0 a	46.7 ± 2.2 a	19.5 ± 0.5 a	202 ± 6 a
H. cecropia[4] × *H. columbia*		(9)	1255 ± 146 a	30.8 ± 3.2 b	48.0 ± 8.0 a	13.2 ± 1.5 c	150 ± 8 a
H. columbia[5]		(all died)	–	–			(all died in earlier instars)
(LSD)[6]			(390)	(9.9)	(21.1) n.s.	(4.3)	(38)

[1] *H. euryalis* from California (Nevada Co.l)

[2] *H. gloveri* two source female from K. Thorne (Utah).

[3] *H. cecropia* three source females from Colorado (outside the natural range of black cherry); two source females from Madison, WI which use black cherry as one of the natural host plants.

[4] *H. cecropia* from S. Stone (Colorado); *H. columbia* from D. Robacker (Price Co., WI).

[5] *H. columbia* from L. Ferge (Oneida Co., WI).

[6] n.s. = no significant differences between the means.

Significant differences between the means are indicated (P = 0.05 via Tukey's test for unequal sample sizes).

Table 2. Utilization of choke cherry (*Prunus virginiana*) may penultimate instar larvae of *Hyalophora* species. Data are presented as a mean ± SE (see methods for procedures).

Insect taxa	(n)	Consumption Rate (RCR) mg/day/g	(AD) %	Efficiency (ECD) %	(ECI) %	Growth Rate (RGR) mg/day/g
H. euryalus[1]	(3)	734 ± 31 b	37.2 ± 1.4 a	44.7 ± 2.8 b	16.6 ± 0.7 a	121 ± 7 a
H. gloveri[2]	(3)	896 ± 84 a	26.8 ± 0.9 b	45.1 ± 0.8 b	12.8 ± 0.3 c	109 ± 12 a
H. cecropia[3]	(8)	680 ± 22 b	27.6 ± 0.6 b	54.0 ± 1.3 a	14.9 ± 0.2 b	101 ± 2 a
H. columbia[4]						(all but one died earlier)
(L.S.D.)		(162)	(3.5)	(6.9)	(1.5)	(23) n.s.

[1] From California (Nevada Co.). The choke cherry used by *gloveri* and *euryalus* in nature is *P. demissa*, now considered a separate species from *virginiana*.

[2] From K. Thorne (Utah).

[3] From Wisconsin (Dane Co.)

[4] From Wisconsin (Lincoln Co.)

Precise counts of the initial number of neonate larvae were not made in this study; however replication is less than the desired ten 4th s = instar larvae because too few survived to reach this penultimate instar feeding experiment stage.

Significant differences between the means are indicated (P = 0.05) via Tukey's test for unequal samp.le sizes (Winer 1962, Snedecor and Cochran 1967).

Table 3. Utilization of paper birch, *Betula papyrifera*, by various *Hyalophora* species. Data are presented as a mean ± SE.

Insect species	(n)	Consumption Rate (RCR) mg/day/g	(AD) %	Efficiency (ECD) %	(ECI) %	Growth Rate (RGR) mg/day/g
H. euryalus[1]	(4)	963 ± 67 b	36.1 ± 3.1 a	36.2 ± 4.3 b	13.0 ± 1.8 a	128 ± 24 ab
H. gloveri[2]	(2)	1432 ± 62 a	34.3 ± 2.2 a	24.1 ± 2.4 b	8.2 ± 0.3 a	117 ± 1 b
H. cecropia[3]	(8)	833 ± 51 b	27.2 ± 0.8 a	63.6 ± 2.2 a	17.3 ± 0.5 a	147 ± 9 ab
H. columbia[4] × *H. gloveri*	(2)	1646 ± 04 a	33.6 ± 0.1 a	35.1 ± 1.8 b	11.8 ± 0.6 a	195 ± 10 a
(L.S.D.)		(274)	(12.5) n.s.	(26.4)	(9.6) n.s.	(68)

[1] From California (Nevada Co.).

[2] Utah *gloveri* × Panamint Mts. *gloveri* CA.

[3] From Wisconsin (Dane Co.)

[4] From Wisconsin (Lincoln Co.)

[5] n.s. = no significant differences between means.

Significant differences between the means are indicated (P = 0.05, Tukey's test for unequal sample sizes).

survived and grew to pupation on this plant. *Hyalophora gloveri*, the species normally using Elaeagnaceae as host plants, grew at nearly twice the rate (146 mg g^{-1} day^{-1}) of the generalist (70 mg g^{-1} day^{-1}; Table 4). Only occasionally (where used as ornamentals) might *H. cecropia* encounter and use Russian olive. *Elaeagnus commutata* or *Shepherdia canadensis* (which extends to south Michigan) could be used by *cecropia*, but no reports exist. This difference in growth rate was due to both greater efficiencies and faster consumption by *H. cecropia* (Table 4), and it would appear that differential adaptations (behavioral, physiological, and toxicological) exist among the four North American *Hyalophora* species with regard to *Elaeagnus angustifolia.*

The larch feeding specialist, *Hyalophora columbia* survived and grew exceptionally well on eastern larch, *Larix laricina* (Fig. 2). In fact, consumption rates of *Larix* by *H. columbia* were faster than any other *Hyalophora* species on any foodplant (Tables 1–5). Also, their growth rate was as fast as *H. cecropia* on black cherry, and these represent the fastest growth rates reported for any *Hyalophora* on any host plant species (Table 5). While 1st instar survival on tamarack is excellent for all four species of *Hyalophora* (77%–100%, M. Collins and J.M. Scriber unpublished), none of the larvae in our lab except *H. columbia* survived to the penultimate instar feeding experiments here.

DISCUSSION

Differential survival and growth on a particular plant species by different species of Lepidoptera could be expected if different adaptations (behavioral, physiological and toxicological) have evolved. This study, using the four North American species of giant silkmoths (*Hyalophora cecropia, H. euryalis, H. gloveri*, and *H. columbia*), illustrates that differential survival and performance does occur in certain cases. However, it is important to note that survival and growth of larvae from widely scattered localities in laboratory feeding experiments may not perfectly reflect adaptations of the species as a whole, or even the adaptations of the source population under their natural (outdoor) conditions (see Scriber 1983, 1984).

While black cherry and choke cherry (*P. serotina* and *P. virginiana* of the Rosaceae) are generally suitable for survival and growth of *Hyalophora*, there appear to exist interspecific differences, and intraspecific (interpopulation) differences that might reflect local adaptations (Tables 1 and 2). Similarly, paper birch (*Betula papyrifera*) of the Betulaceae appears generally suitable to various *Hyalophora* species, although comparable growth is achieved differently by different species. For example, *H. gloveri* consumes paper birch rapidly but metabolically are inefficient in processing the leaves compared to *H. cecropia* larvae that consume slowly (Table 3). *Hyalophora euryalus* is intermediate in both consumption rate and efficiency (Table 3).

The differential adaptations of *H. gloveri* to *Elaeagnus angustifolia* appear quite prominent. Toxic to neonate larvae of *H. euryalus* and unsuitable for development of *H. columbia*, Russian olive also extracts a cost in *H. cecropia* that halves its growth rate compared to *H. gloveri* (Table 4). This appears to represent a significant divergence in host plant adaptations, and may reflect significant underlying phytochemical bases of the interspecific antibiosis observed with *Hyalophora*.

While the tamarack feeding specialist grows extremely well on tamarack, other *Hyalophora* can also survive and grow relatively well as early instars on this plant (M. Collins and J.M. Scriber, unpublished). The degree to which the tamarack feeding abilities are shared by other *Hyalophora* deserves additional study.

The determination of whether the differences observed in these feeding studies have a genetic basis awaits a series of hybridization and backcross studies as has been done for other Lepidoptera (Peigler 1977, Thompson 1988a, Scriber et al.

Table 4. Nutritional indices of penultimate instar larvae of *H. gloveri* and *H. cecropia* fed Russian olive, *Elaeagnus angustifolia*.

	(n)	Consumption Rate (RCR) mg/day/g	(AD) %	Efficiency (ECD) %	(ECI) %	Growth Rate (RGR) mg/day/g
H. gloveri[1]	(5)	892 ± 60 a	31.3 ± 0.8 a	52.8 ± 2.1 a	16.5 ± 0.6 a	146 ± 07 a
H. cecropia[2]	(11)	585 ± 31 b	28.9 ± 0.8 a	47.0 ± 2.1 a	13.6 ± 0.8 b	79 ± 05 b
H. columbia[3]	(0)	–	–			All died
H. euryalis[4]	(0)	–	–			All died

[1] From K. Thorne (Utah).
[2] From Wisconsin (Dane County).
[3] From Ontario. All larvae died before or during (n = 4) the penultimate (4th) instar.
[4] From California. All larvae died in the first instar (see also Table 1).

Significant differences indicates F-test (P = 0.05)

Table 5. Utilization of eastern larch (tamarack), *Larix laricina*, by *Hyalophora columbia*. Data are presented as a mean ± SE.

	(n)	Consumption Rate (RCR) mg/day/g	(AD) %	Efficiency (ECD) %	(ECI) %	Growth Rate (RGR) mg/day/g
H. columbia[1]	(6)	1471 ± 72	42.7 ± 2.9	31.0 ± 3.6	12.7 ± 0.9	185 ± 09

[1] Original cocoons from Les Kohalmi (Ontario, CANADA).

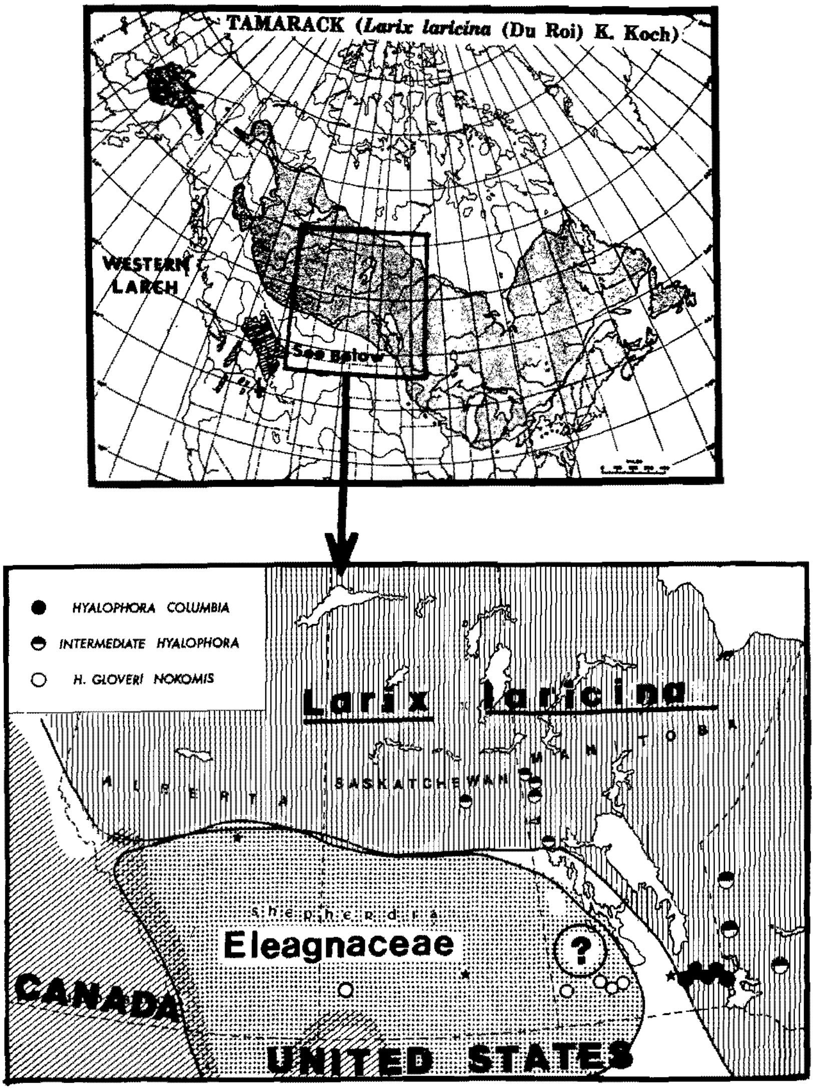

Figure 2. The geographic distribution of tamarack, *Larix laricina*, and *Shepherdia* (Elaeagneaceae) with *Hyalophora* collection sites (adapted from Harlow and Harrar 1949, Collins 1973, Kohalmi and Moens 1975). Question mark indicates Riding Mountains site of *Hyalophora* egg collection on paper birch, *Betula papyifera* (JMS).

1989, Thompson 1990). It is also unknown for any *Hyalophora* species whether physiological adaptation to particular host plants is also paralleled by more specific choices in host plant selection by ovipositing females (i.e., a preference/

performance correlation; Thompson 1988b). The importance of these adaptations in host choice and host use abilities for interpretation of the geographic distribution of *Hyalophora* is of major significance. It would be of considerable interest to know whether the inability to survive and grow rapidly and/or efficiently on specific plants is a consequence or a cause of feeding specialization. Such uncertainties about cause and effect of feeding specialization might be best resolved by additional and extensive comparisons of interpopulation and intrapopulation variation in growth performance than by interspecific comparisons. Generalist species such as *H. cecropia* provide a uniquely suited opportunity to pursue such questions.

The common assumption that specialists evolve from generalists may be true most of the time, but is likely not to be true in certain cases. In North America, for example, the polyphagous tiger swallowtail, *Papilio glaucus* (Papilionidae) is felt to have evolved from Lauraceae, Magnoliaceae, and/or Rutaceae specialists (Miller 1987, Scriber et al. 1991, Hagen and Scriber 1991). In a similar case, it is likely that the polyphagous North American moth *Antheraea polyphemus* (Cramer) (Saturniidae) is derived from an Asian oak-feeding (Fagaceae) specialized form similar to *A. pernyi* (Guerin) and is thought to have migrated from Eurasia via the Bering land bridge during the Miocene (Ferguson 1972, Michener 1952). The North American saturniids *Actias luna* Linn. and *Antheraea polyphemus* closely resemble their Asian congeners and are evidence of this migration, while the genus *Hyalophora* appears to have evolved originally as a polyphagous Nearctic endemic (Collins, pers. comm) and *H. columbia* has become specialized.

This polyphagy of *H. cecropia* (and of the tiger swallowtail butterfly, *Papilio glaucus*) suggests a long association with the species-rich flora of the southeastern U.S., which includes many plant species with Asian affinities (Graham, 1964). Thus the present distribution of *H. cecropia* and its polyphagy in association with "ancient" hosts are evidence that *H. cecropia* may be more closely related to the progenitor of modern *Hyalophora* than are its western congeners (M. Collins, pers. comm.). A similar, and strikingly parallel host range pattern is evident with the *Papilio glaucus* group (Dethier 1954, Scriber 1988, Hagen and Scriber 1991). Furthermore, the southeastern forest flora, or at least important elements of it, appear to have survived the pleistocene glaciation more or less intact in refugia (Watts 1980, Davis 1981, Solomon and Webb 1985) which makes it plausible that *cecropia* as a taxon may have occurred prior to this event. Intraspecific adaptations to host plants, with the individual variation in oviposition choice and larval host use carefully monitored will help determine the genetic basis of these phenotypic responses. Such studies may help resolve these speculations about the relationships of insect phylogeny and host plant affiliations.

In summary, it does appear that improved physiological and toxicological performance may be the result of adaptations evolved on local hosts in the case of *H. columbia* on its primary host (tamarack) and for *H. gloveri* on its primary host (*Elaeagnus*), and possibly for certain *H. cecropia* populations on their locally preferred host (*Prunus serotina*). We do not know the extent to which these improved performances are genetically based.

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