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While food plants of many species of sphinx moth larvae are well known, food plants of the adults are not. Many observations of the feeding habits of adult sphinx moths undoubtedly have been made, but much of the information is probably resting in the field notebooks and memories of the observers.

To my knowledge no summary of known feeding information has been presented previously for American Sphingidae. A rather thorough list of food plants for adult European sphinx moths has been published by Wahlgren (1941). This list also includes other moth families as well and it can be a useful reference for many workers.

For the most part I have restricted the present paper to sphinx moths of the eastern United States, but it has not been possible to include all of these as no information was uncovered for some species. The dearth of observations of our Western species makes such restriction necessary and, while unfortunate, unavoidable at the present time.

Data for this study were compiled from personal information based on many years of observing and collecting sphinx moths, from questionnaires sent to other workers in the field, and from published information. Several appropriate references to Sphingidae feeding on carrion have been included, although this literature has not been searched exhaustively.

ANNOTATED LIST OF FOOD PLANTS

In the following list feeding times (FT) are indicated as (D) diurnal, (C) crepuscular, and (N) nocturnal. Average proboscis length (PL) is given in millimeters. In several cases these data are not available. Flowers visited by the moths (their nectar presumably was used as food) are indicated as food source (FS).

SPHINGINAE

Most insects of this subfamily have a moderate to extremely well-developed proboscis and well-developed sucking pump and proboscis extension muscles. Despite complete morphological feeding capability, however, many species do not seem to be as active feeders as many feeding species in other subfamilies. Some species have degenerate feeding apparatus and do not feed as adults.

Manduca sexta (Johansson)

FS: *Lonicera japonica* (Japanese honeysuckle), *Calonyction aculeata* (moonflower), *Petunia hybrida* (petunia). FT: C, N. PL: 80.0 mm.

Manduca quinquemaculata (Haworth)

FS: *Lonicera japonica, Petunia hybrida, Saponaria officinalis* (bouncing bet), *Phlox* sp. (phlox), *Nicotiana* sp. (tobacco). FT: C, N. PL: 90.0 mm.

I have several times observed *M. sexta* and *M. quinquemaculata* feeding at honeysuckle well after dark, apparently later than most other evening feeding species. In some remarkable photographs, Tillet (1966) shows some feeding attitudes of *M. sexta* at moonflowers.

Dolba hylaeus (Drury)

FS: *Saponaria officinalis*. FT: Probably C. PL: 32.0 mm.

Ceratomia amyntor (Hübner), *Ceratomia undulosa* (Walker), *Ceratomia catalpae* (Boisduval)

No feeding observations for moths of the genus *Ceratomia* have been made. Fleming (1968) demonstrated the morphological incapability of *C. undulosa* and *C. catalpae* to feed. The proboscis is reduced to lengths of 9.8 mm. and 4.4 mm. respectively, and the proboscis extensor musculature is considerably reduced in both insects as compared to feeding species. The sucking pump, too, is reduced. The proboscis length in *C. amyntor* is 12.0 mm. While this is still long enough to form a functional sucking tube, it is noteworthy that it is shorter than that possessed by any feeding species within my knowledge. Other representatives of this subfamily have reduced feeding parts and probably they have lost feeding ability. Included here are *Lapara bombycoides* Walker (PL: 3.5 mm.) and *Isogramma hageni* (Grote), among others.

Sphinx eremitus (Hübner)

FS: *Lonicera japonica, Petunia hybrida, Saponaria officinalis, Catalpa speciosa* (catalpa). FT: C. PL: 39.0 mm.

Sphinx chersis (Hübner)

FS: *Lonicera japonica, Saponaria officinalis*. FT: C. PL: 46.0 mm.

Sphinx kalmiae (J. E. Smith)

FS: *Lonicera japonica, Saponaria officinalis*. FT: C. PL: 40.0 mm.
Platt (1969) caught this insect in a hanging bait trap using bait consisting of a mixture of stale beer, brown sugar, unsulfured blackstrap molasses, and fermenting fruit.

Sphinx drupiferarum (J. E. Smith)

FS: *Lonicera japonica*. FT: C. PL: 44.0 mm.
Smith (1943) reports this species fairly common at fruit blossoms during April and May in Kansas.

Sphinx gordius Cramer

FS: *Saponaria officinalis*. FT: Probably C.

Sphinx luscitiosa Clemens

No feeding observations were uncovered for this species but I suspect that it should be looked for around plants that are visited by other members of its genus.

Sphinx perelegans Hy. Edwards

Essig (1926) reports that: "The moths visit flowers of the evening primroses and rhododendron . . ."

Sphinx sequoia Boisduval

Essig (1926) states: "The moths frequent the flowers of wild cherry and buckeye."

SMERINTHINAE

Smerinthus geminatus Say, *Smerinthus cerisyi* (Kirby), *Paonias excaecata* (J. E. Smith), *Paonias myops* (J. E. Smith), *Cressonia juglandis* (J. E. Smith), *Pachysphinx modesta* (Harris).

Apparently no known feeding observations for North American moths of this subfamily have been made. Morphological investigations by Fleming (1968) suggest that the insects are not capable of any feeding activity. The proboscis is reduced, depending on species, to lengths ranging from 2.5 to 5 mm -- too short to be of much use. Also the proboscis extensor muscles have been reduced to only one pair. Three pairs are present in all feeding sphinx moths examined by Fleming. Schmitt (1938) points out that the minimum number of proboscis extensor muscles for feeding members of any lepidopteran family he examined is two pairs. Rothschild and Jordan (1903) state that the proboscis of the moths of the neotropical genus *Protambulyx* is not particularly reduced and remains functional. Knuth (1895) considered, erroneously, *Smerinthus ocellatus* (Linnaeus) to be a feeding species.

MACROGLOSSINAE

Feeding observations have been recorded for only a few species, most of them in the genus *Haemorrhagia* (=*Hemaris*). Members of that genus prove to be very active feeders indeed. These moths possess highly developed morphological features associated with feeding, although the proboscis is not particularly long.

Erinnyis ello (Linnaeus)

FS: *Saponaria officinalis*.

Haemorrhagia thysbe (Fabricius)

FS: *Lonicera japonica, Cirsium muticum* (swamp thistle), *Cirsium* sp. (other thistle), *Monarda fistulosa* (beebalm, wild bergamot), *Trifolium pratense* (red clover), *Syringa vulgaris* (lilac), *Saponaria officinalis, Phlox* sp., *Philadelphus coronarius* (mock orange), *Pontederia cordata* (pickerelweed), *Vicia* sp. (vetch), *Symphoricarpos albus* (snowberry), *Vaccinium* sp. (cranberry and blueberry genus), *Ledum groenlandicum* (Labrador tea), *Hieracium aurantiacum* (orange hawkweed), *Asclepias syriaca* (common milkweed). FT: D, but may feed well into the evening until sundown. PL: 19.4 mm.

Haemorrhagia gracilis Grote & Robinson

FS: *Phlox* sp., *Pontederia cordata, Rubus* sp. (blackberry and raspberry genus), *Taraxacum officinale* (dandelion), *Hieracium aurantiacum*. FT: D. PL: 14.0 mm.

Haemorrhagia diffinis (Boisduval)

FS: *Lonicera* sp., *Diervilla lonicera* (bush honeysuckle), *Phlox* sp., *Cirsium* sp., *Monarda fistulosa, Trifolium pratense, Syringa vulgaris, Philadelphus coronarius, Pontederia cordata, Symphoricarpos albus, Vaccinium* sp., *Ledum groenlandicum, Hieracium aurantiacum, Asclepias syriaca, Viola canadensis* (Canada violet). FT: D. PL: 17.0 mm.

Smith (1943) indicates that these insects: " . . . visit flowers, particularly fruit and wild currant blossoms."

Haemorrhagia senta Strecker

Holland (1903) notes the insect: " . . . frequenting the blossoms of *Lupinus*."

PHILAMPELINAE

Insects of this subfamily usually have moderate to well-developed musculature associated with sucking and proboscis extension. Some of the species are active feeders.

Pholus satellitia pandorus (Hübner)

FS: *Petunia hybrida, Saponaria officinalis, Phlox* sp., *Philadelphus coronarius, Lychnis alba* (white campion). FT: C. PL: 34.5 mm.

M. C. Nielsen (personal communication) has attracted this species to beer and molasses bait.

Pholus achemon (Drury)

FS: *Lonicera japonica*, *Petunia hybrida, Phlox* sp., *Philadelphus coronarius*. FT: C.

Essig (1926) records observations of this species: " . . . visiting flowers of evening primroses, rhododendrons, and petunias."

Feeding information for other members of the genus *Pholus* was not uncovered. I have observed *P. fasciatus* (Sulzer) on the wing in Louisiana but have never seen it visit flowers. Morphological feeding mechanisms of this species are probably similar to *P. s. pandorus* and one would expect similarity of feeding habits as well.

Ampeloeca versicolor (Harris)

No definite recorded plant visitations were found for this species, but W. E. Sieker (personal communication) reports that he has attracted it and the following species while "sugaring."

Ampeloeca myron (Cramer)

FS: *Lonicera japonica, Lychnis alba.* FT: C. PL: 14.7 mm.

Darapsa pholus (Cramer)

FS: *Lonicera japonica, Lychnis alba.* FT: C. PL: 22.0 mm.

M. C. Nielsen, R. W. Holzman, and W. E. Sieker (personal communication) indicate that they have attracted this species to bait. Nielsen used beer and molasses. Sieker and Holzman did not specify the type of bait. Platt (1969) found the insect commonly in the bait trap previously mentioned under *S. kalmiae.*

Sphecodina abbotti (Swainson)

FS: *Syringa vulgaris, Viburnum carlesi*. FT: C. PL: 19.5 mm.

On one occasion I saw an individual of this species visit an unidentified species of *Lonicera* (honeysuckle). The moth poised itself over one or two blossoms for a few seconds and then flew off. I was not able to tell whether or not it actually fed. Since this, and the next species, fly rather early in the season comparatively few plants that would satisfy their feeding needs are available to them.

J. P. Donahue (personal communication) collected *S. abbotti* at human feces. Reed (1958) found the species feeding on dog carcasses in advanced decay.

Deidamia inscriptum (Harris)

FS: *Syringa vulgaris, Phlox* sp. FT: C. PL: 12.2 mm.

Amphion nessus (Cramer)

FS: *Syringa vulgaris, Geranium robertianum* (herbrobert), *Kolkwitzia amabilis* (beauty bush), *Philadelphus coronarius, Phlox* sp. FT: D, especially on cloudy afternoons, and C.

PL: 16.0 mm.

Platt (1969) has taken this insect at the bait trap mentioned under *S. kalmiae* above. Payne and King (1969) observed the species feeding at soupy pig carrion, and Reed (1958) reports it at dog carcasses in advanced decay.

Proserpinus flavofasciata (Walker)

FS: *Taraxacum officinale.*

Holland (1903) states: "It is found in very early summer hovering over flowers." FT: D.

CHOEROCAMPINAE

Members of this subfamily have a moderately developed proboscis. Head musculature associated with feeding in *Celerio lineata* (Fabricius) is very well-developed. I have not had the opportunity to examine the cranial muscles of any other representatives of the subfamily, but I suspect internal examination of some other species would reveal the pattern indicated in *C. lineata*.

Xylophanes tersa (Linnaeus)

FS: *Lonicera* sp.

This insect, which is at times common in southern United States, probably sips nectar from a variety of plants, despite the single definite record indicated.

Celerio lineata (Fabricius)

FS: *Lonicera japonica, Petunia hybrida, Phlox* sp., *Saponaria officinalis, Syringa vulgaris, Cirsium* sp., *Trifolium pratense.* FT: C, D. PL: 37.0 mm.

Essig (1926) states: "The moths appear at dusk and visit columbines, honeysuckle, moonvine, Jimpson weed, larkspurs, petunias, and many other flowers."

Wahlgren (1941) reports the European *C. l. livornica* (Esper) at *Lonicera caprifolium.*

Celerio galli intermedia (Kirby)

FS: *Saponaria officinalis.*

Wahlgren (1941) reports the European *C. galli* (Rottemburg) at *Centaurea scabiosa*, *Lonicera periclymenum*, *L. caprifolium, Echium vulgare, Lavandula spica,* and *Syringa* sp.

MODE OF FEEDING

Close observation of the mode of feeding of adult sphinx moths has been neglected and could be a fruitful field of investigation. Very little may be found in the literature concerning it. In the past most individuals interested in Sphingidae have concerned themselves with the taxonomy of the group, or have been collectors who swept up the sphingid prizes and placed them in orderly rows in cabinets. Such individuals seldom took the time to watch their prey's activity.

The following account, superficial though it is, may be of some interest. The observations were made in Van Buren County, Michigan, on 5 June 1969. A small patch of garden phlox was under observation on a rather cool (55°- 60°F.) evening in hopes that it would be visited by sphinx moths. At 8:05 PM. EST a single *A. nessus* flew to the phlox patch. As it approached to a distance of about 5 cm. from a blossom the moth extended its proboscis and directed it to the center of a flower. The insect hovered as the proboscis was thrust into the flower. The prothoracic legs, well spread apart, usually but not always came in contact with the flower and probably helped steady the insect as it fed. The mesothoracic legs were

spread outward and downward from the body and seldom made contact with the petals. The metathoracic legs were held close to the body along its lateroventral surface. As the insect fed it made at least two, and never more than three, plunges of the head and proboscis into the center of the flower. The proboscis was then withdrawn and the moth flew to another blossom. At a flight distance from the blossoms of up to two meters the insect held its proboscis only partly coiled. I attempted to determine the number of individual flower visits but lost count after about 20. The flowers were white and various shades of red and lavender. I did not observe any preference for one color over another.

At 8:20 PM three more moths of the same species joined the first. All followed the same general feeding pattern. One extremely large individual always touched the petals with four feet; another would sometimes use three feet. On one occasion one of the insects came to rest on a flower for about two seconds. By 8:30 PM all but one moth had left.

DISCUSSION

The data presented in this study are not complete enough to indicate preferences for specific food plants by each species of sphinx moth, but it would be misleading to suggest that specific preferences do not exist. Apparently the range of food plants for feeding species of sphinx moths is broad for some species and narrow for others. Good reasons for this situation are not presently available.

Obviously any species is morphologically limited to certain plants according to the length of the proboscis. A moth with a tongue length in the 15 to 20 mm. range would have difficulty in extracting nectar from a flower with a throat much deeper. Thus while a long-tongued species like *M. sexta* might be successful at a lily, a species like *D. myron* would not. Such conditions would allow long-tongued species to have a wider variety of food plants than short-tongued species. Interestingly enough, those of the moths observed with proboscis lengths of over 50 mm. did not show a wide variety in their choice of food plant. One very long-tongued moth, *Herse cingulata* (Fabricius), a relatively common species in the South, has not been included on the list since its feeding habits were not observed.

Besides morphological restrictions inherent in some species there are certainly behavioral limitations as well. Simply stated, a moth of a given species could feed at a given flower but it does not. This of course suggests the matter of attraction to food plants, but how a moth finds its way to its nectarian feast is a question that is not yet answered.

Knoll (1927) demonstrated that several European twilight-flying sphinx moths could find flowers by sight alone. But as Wahlgren (1941) points out, it is not known what role odor plays. One of the apparently "favorite" plants of crepuscular sphinx moths, *Lonicera japonica,* presents a pleasant and far reaching odor to humans. Yet a moth's reaction to this odor cannot be gauged similarly. It may be noteworthy that crepuscular-feeding sphinx moths are usually attracted to flowers relatively light in color and stronger than average in aroma. It would be foolish to suggest that smell does not play a role in attraction.

Moths attracted to bait almost certainly find their way there through olfactory stimuli. The odors created by most baits are identical or very similar to odors encountered by a given species for thousands of years and hence may be programmed into the moth's behavior and be effective in rendering a certain response. The appearance of some baits and, of course, bait traps are not common in nature and moths have probably not had time to become attracted to them by simply visual stimuli.

It is quite possible that the penetrating aroma of certain flowers attracts moths at considerable distances and as they fly nearer the aroma producing plant, visual sensations take over as behavior-controlling agents and aid the moth in orientating itself in an advantageous feeding position over the flower.

The recorded variety of food plants is greatest for the day-flying moths of the genus *Haemorrhagia*. This may however be because the moths are diurnal in habit and thus are more frequently observed. For many of the evening-flying species, the range of food plants is probably greater than indicated. Some of these moths are not particularly abundant, and are less apt to be seen at their time of flight. Several species of the genus *Sphinx* fall into this group. Of the approximately three dozen kinds of plants recorded for all moth species in this study, *Lonicera japonica*, *Saponaria officinalis*, and *Phlox* sp. stand out as favorites for feeding sphinx moths.

Several species of sphinx moths have lost their feeding capabilities. In our geographic area these include members of the subfamily Smerinthinae and members of the genus *Ceratomia* and the genus *Lapara* of the Sphinginae. The lack of feeding ability may be viewed as an evolutionary "mixed blessing." If the adult insect has eliminated its need for feeding, it has eliminated certain associated risks, but the life-span may be shortened so much that mate-finding may be jeopardized. (Feeding might play a secondary role in mate-location in some Lepidoptera since potential mates are brought together at the feeding site, although this has not been demonstrated with sphinx moths.) Although the evidence is slim, some sphinx moths which apparently feed less often than others may ultimately dispense with feeding altogether. The behavioral trend to feed less frequently indicates a shift into a new niche and possibly morphological changes follow.

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