

# Hairstreaks (and Other Insects)

## Feeding at Galls, Honeydew, Extrafloral Nectaries, Sugar Bait, Cars, and Other Routine Substrates

DAVID L. WAGNER AND BENEDICT L. GAGLIARDI

**T**he northern oak hairstreak (*Satyrrium favonius ontario* (W. H. Edwards)) is one of the most infrequently encountered resident butterflies in New England; only three adults were seen over the five-year course of the Connecticut Butterfly Atlas project (O'Donnell et al. 2007). Shapiro (1974) considered it one of the rarest northeastern butterflies, and (as often quoted elsewhere in the butterfly literature) Holland (1931) regarded the northern oak hairstreak to be so infrequent that he wondered if the butterfly might be a re-occurring aberration of a more common hairstreak. Its scarcity is mysterious in that its host, oak, is one of the most abundant plant genera in the East. Its congener, the striped hairstreak (*Satyrrium liparops* (Le Conte)) is infrequently

encountered in New England; most reports are of adults nectaring at milkweed blossoms in late June and July. However, its late instars are among the most common lepidopteran larvae on apple and highbush blueberry (*Vaccinium corymbosum* L.) in early June. In spring 2013, we found numerous striped hairstreak larvae while beating blueberry for immatures of Henry's elfin butterfly (*Callophrys henrici* (Grote & Robinson)); five to eight *S. liparops* caterpillars were found on every highbush blueberry that was sampled along a woodland path in Salem, Connecticut. The same path and adjacent yard yielded only two striped hairstreak adult sightings over the course of the next six weeks despite repeated and targeted visits to view the butterfly.

Here, we suggest an explanation for the relative scarcity of these hairstreaks; offer a prospective essay on the importance of non-floral sugar resources (NFSRs) to these two *Satyrrium* (as well as additional hairstreaks, multitudes of moths, and hordes of other insects); and end with a brief exploration of the possibility that non-nectar resources have not received their due as a source of food for a broad array of insects, and that NFSRs could be the primary source of carbohydrates for greater numbers of adult Holometabola than flowers. By extension, honeydew-secreting aphids, mealy bugs, leafhoppers, treehoppers, scales, and whiteflies may be underappreciated keystone taxa in forests, barrens, deserts, and other communities where the availability of nectar is often limited.

Our inquiry began in late June of 2013 on Great Blue Hill, south of Boston, when we observed 15 adult *Satyrrium*



Fig. 1. Edward's hairstreak (*Satyrrium edwardsii* (Grote & Robinson)) male feeding at pip gall on Great Blue Hill, Canton, Massachusetts (photo courtesy of Bruce DeGraaf).

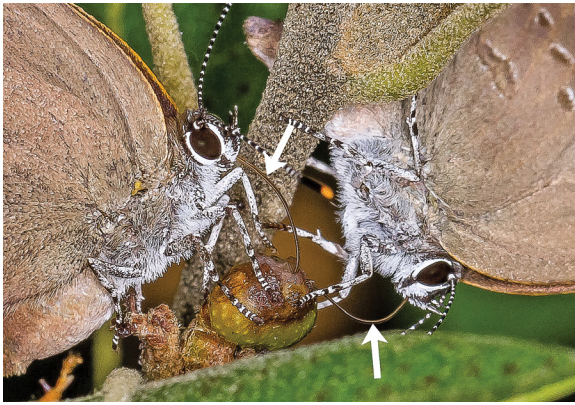


Fig. 2. Edward's hairstreak and banded hairstreak (*Satyrium calanus* (Hübner)) females at same gall (photo courtesy of Bruce DeGraaf).

hairstreaks representing three species feeding at cynipid wasp galls (Figs. 1-3). Over the course of 2013 and 2014, we observed more than 45 *Satyrium* hairstreaks feeding at pip galls on scrub oak (*Quercus ilicifolia* Wangenh.). We failed to realize the potential significance of our observations until recently, as more and more reports of non-nectar feeding by hairstreaks and other insects began to accumulate, inspiring our thesis that non-floral resources are routinely exploited and that flower feeding, while frequently observed, could be the exceptional behavior for some hairstreaks and other insects.

The oak pip galls on Great Blue Hill were those of a *Callirhytis* wasp (likely *Callirhytis perditor* Bassett). *Callirhytis* is one of few cynipid genera known to induce the exudation of sugary solutions over the surface of their galls (Fig. 3). The exudates attract ants, which collectively protect the developing wasp larva from attack by parasitoids and inquilines that might otherwise gain entry into the gall (Weld 1959, Washburn 1984, Inouye and Agrawal 2004). To the best of our knowledge, this paper constitutes the first report for gall-feeding by New World butterflies.

The only sighting of a live northern oak hairstreak made by Dr. David Wright, a renowned hairstreak enthusiast, over the course of his lifetime was a female that he found probing its proboscis over the hood of his car at 7:45 a.m. one June morning (Fig. 4). We suspect that the animal was feeding on hemipteran honeydew, which is well known to collect on surfaces under and in the vicinity of oaks in summer (Sumner and Buck 2003, Swiecki and Bernhardt 2006, Jesse 2010). While online and other extension resources suggest that aphids are principally responsible, we suspect that the rich fauna of treehoppers (Membracidae) on eastern oaks is also a contributor of honeydew from late spring into summer (see below). Other plants host hemipterans that produce honeydew, sometimes in abundance; tuliptree (*Liriodendron tulipifera* L.) as well as hickory and pecan (both *Carya*) commonly host hemipterans that produce copious honeydew. The

Fig. 4. Female oak hairstreak probing hood of car early in morning. Apex of the short proboscis is just visible behind right pro-femur; the shadow between the first two pairs of legs is that of the proboscis. Lansdale, PA (photo courtesy of David Wright).



Fig. 3. Honeydew-secreting acorn pip gall of *Callirhytis cf. balanacea* Weld (Family Cynipidae) on black oak (*Quercus velutina* Lam.). Note: this a different species of gall than that in Figs. 1 and 2 but serves to illustrate the surface exudates common to *Callirhytis* galls (photo and identification courtesy of Charley Eiseman).

ubiquity of honeydew in eastern forests is sometimes made evident by blooms of sooty molds (*Antennariella*, *Aureobasidium*, *Limacinula*, *Capnodium*, *Cladosporium*, *Scorias*, and others).

In barrens, where flowers are often scarce, hairstreaks on rare occasions are attracted to and feed on the fermenting sugary baits used by lepidopterists to collect moths (D. Schweitzer, personal communication). Schweitzer also has seen the juniper hairstreak (*Callophrys gryneus* (Hübner)) and red-banded hairstreak (*Calycoptis cecrops* (F.)) feeding at extrafloral nectaries on the bases of immature trumpet vine (*Campsis radicans* (L.) Seem) seedpods in southern New Jersey.

Given these observations, it is our guess that much of the relative scarcity of the oak and striped hairstreaks is more apparent than real—it is simply a matter of detection (Gagliardi and Wagner 2014, in prep.). The oak hairstreak has been thought to be a canopy dweller (e.g., O'Donnell et al. 2007, Schweitzer et al. 2011)—a butterfly that selects and holds its territories and conducts its





courtships in the canopy, out of human view. Honeydew and gall feeding would allow the butterfly to function almost entirely at the tops of one of its host, white oak (*Quercus alba* L.) (Gagliardi and Wagner 2014, in prep.). Likewise, the striped hairstreak seeks out and defends its mating stations high in vegetation. Both butterflies do visit flowers; we have visitation records for >80 northern oak hairstreak sightings on 12 flower species, and more than this for the striped hairstreak. The issue is one of primacy; we believe that nectar is a secondary resource, one that has special importance on hot days when liquid may be even more important than a source of sugar, or after hard rains that have washed NFSRs away.

### Principal Resources: Who, When, and What

Principal honeydew producers include aphids (Aphididae); scales, mealy bugs, and kin (Coccoidea); leafhoppers (Cicadellidae); and treehoppers (Membracidae). In the Northeast, oak-feeding taxa that appear to be primarily responsible for honeydew production include aphids and a diverse array of treehoppers. Internet resources and extension bulletins lay much of the blame for nuisance honeydew on aphids of the genus *Myzocallis*. Matt Wallace, a treehopper specialist at East Stroudsburg University, thinks membracids are also contributing. He has found membracids in enormous numbers on various oak species from late May into early July at his study sites in eastern Pennsylvania (Wallace 2008, Wallace and Maloney 2010). Frost (1957) reported more than 6,000 membracids coming to lights in early July in central Pennsylvania; Medler and Smith (1960) collected more than 200,000 treehoppers in light traps over a five-day period in early June in Wisconsin. There are nearly 100 species of treehoppers in the eastern U.S. that are oak feeders; two tribes, the Smiliini (e.g., *Cyrtolobus* and *Ophiderma*) and Telamonini (e.g., *Glossonotus* and *Telamona*), are especially diverse. Presumably, the more abundant nymphal stage produces most of the honeydew.

Only a few genera of cynipids (e.g., *Callirhytis* and *Disholcaspis*) are known to induce the exudation of sugary substances over the surface of their gall. Both are large genera with many species on oaks in the Northeast.

Scales are also important honeydew producers. Oak-feeding scales of widespread occurrence and abundance in eastern woodlands and forests include *Parthenolecanium quercifex* (Fitch) and *Melanaspis obscura* (Comstock) (M. Raupp, personal communication, but see also Swiecki and Bernhardt 2006). The source of most honeydew on tuliptree is the scale *Toumeyella liriodendri* (Gmelin) (Sadof 2012).

Honeydew production (availability) varies seasonally. *Callirhytis* galls only secrete sugar for the brief period when the cynipid larva is actively growing. Peak release for membracids is in June and July in the Northeast. The seasonal peaks for honeydew secretion by hemipterans and cynipids include the flight periods of all six of New England's *Satyrium* hairstreaks (O'Donnell et al. 2007, Gagliardi and Wagner 2014, in prep., Stichter 2014). Regardless of the season, its availability can be greatly diminished by drenching rains.

While the sugars in both nectar and non-floral resources are used to power metabolism, nutritionally they are scarcely equivalent, with NFSRs likely to be much more heterogeneous. Baits, by design, are fermenting concoctions, replete with yeasts and bacteria. The nutritional content of cynipid gall exudates has not been studied. Honeydew is sugar-laden excrement—a by-product of phloem-feeding hemipterans, mostly free of any nitrogenous compounds, which have been gleaned by the digestive tract of the producers. Nectar is something of a polar opposite, being manufactured and packaged by angiosperms for the purpose of attracting and benefiting their insect, bird, mammalian, and even reptilian (gecko) pollinators. Given that honeydew is regarded as a hemipteran waste product, it is hardly surprising that it would be found to be nutritionally inferior to nectar (Wäckers 2000, Wäckers et al. 2008). However, because honeydews serve as substrates for sooty molds, yeasts, and bacteria and likely contain solutes from the surfaces upon which they fall, there is substantial possibility for honeydews to be highly variable nutritionally, especially over the vertical and horizontal heterogeneity of an oak woodland.

### Non-Satyrium Hairstreaks and Related Lycaenids

The picture we paint for *Satyrium* hairstreaks applies more broadly. Early hairstreaks (*Erora laeta* (W.H. Edwards)) are seen far less frequently at flowers than they should be if nectar were their principal source of carbohydrates, and this is especially true of the males, which are greatly outnumbered by females in collections. The white-M hairstreak (*Parrhasius m-album* (Boisduval & Leconte)), another canopy dweller (Schweitzer et al. 2011: 21), is rarely, if ever, seen nectaring in the spring in the Northeast; it is occasional at flowers through its summer and fall generations. Perhaps the butterfly is simply numerically rare in the spring and not so by summer's end, and perhaps not.



Fig. 5. Colorado hairstreak *Hypaurotis crysalus* (W. H. Edwards) feeding at *Callirhytis* pip gall on *Quercus rugosa* Née, growing downslope from the butterfly's host oak and preferred perching and mating station, *Quercus gambellii* Nutt. Mt. Lemmon, Arizona (photo courtesy of Ken Kertell).

At The Nature Conservancy's Manumuskin Preserve in South Jersey, red-banded hairstreaks (*C. cecrops*) are among the most frequently seen butterflies; summer nectar is virtually absent in this ultraxeric barren, except for the exotic *Centaurea maculosa* Lam., which no hairstreaks visit along the sand roads (D. Schweitzer, personal communication).

Two North American thecline hairstreaks are essentially never seen at flowers: Colorado hairstreak (*Hypaurotis crysalis*) and golden hairstreak (*Habrodais grunus* (Boisduval)). *Hypaurotis* was recently documented feeding at cynipid pip galls by Ken Kertell (Fig. 5), an association that may prove to be the primary source of NFSRs for this insect. The harvester (*Feniseca tarquinius* (F.)), a mile-tine lycaenid, is occasionally seen feeding at honeydew (Scott 1986, Fig. 6), but is more likely to be encountered imbibing fluids from dung or sap flows.

### What Might This Explain?

If non-nectar sugar consumption is practiced routinely (and in some cases, exclusively) by hairstreaks and other Lepidoptera, such behaviors could explain a number of puzzling entomological phenomena. It could account for the unreliable appearance of oak, striped, and other hairstreaks at flowers, across days, and across years. Hard rains and fluctuations in hemipteran and cynipid populations would lower availability of NFSRs, and as alternative resources diminish, frequency of flower visitation would be expected to increase. In the Northeast, *Satyrrium* hairstreaks are noteworthy among butterflies for having “good” years (Holliday 1993, O'Donnell 2007; D. Schweitzer and D. Wright, personal communication), i.e., those years when many can be seen nectaring at flowers such as milkweed and sumac blossoms.

Good hairstreak years could coincide with diminished honeydew availability or, conversely, be a response to generous NFSR availability in the previous season. Honeydew feeding might explain the seemingly unpredictable week-to-week performance of bait trapping for moths (see discussion in Wagner et al. 2011: 20-21), why baiting is often ineffective in the vicinity of tuliptrees, and why the efficacy of baiting for forest noctuids drops off



Fig. 6. Harvester feeding at alder woolly aphid (*Prociphilus tessellatus* (Fitch)) honeydew (photo courtesy of Frank Model).



Fig. 7. *Euclystis proba* (Schaus) (Noctuidae: Calpinae) feeding at honeydew secreted by *Enchophora sanguinea* Distant (Fulgoroidea) at La Selva Biological Station, Costa Rica (photo courtesy Piotr Naskrecki).

precipitously in the spring after red maple has finished flowering (D. Schweitzer, personal communication). As noted, honeydew production by membracids, many cynipids, and other taxa peaks in spring and early summer and falls off thereafter. The availability of NFSRs might be the reason why the white-M hairstreak is not seen at flowers in the spring, but is a regular flower visitor in the summer and fall.

Also relevant is the fact that before eastern forests were cut and fragmented by American Indians and later colonists, nectar availability may have been much scarcer<sup>1</sup>—forest-dwelling *Satyrrium* and other insects must have had non-floral options available to them.

### Looking Beyond Lycaenid Butterflies

It is difficult to know the importance of honeydew and other non-nectar resources to insects because such resources are typically dispersed, ubiquitous, and more cryptic than flowers. Figures 7 and 8 show two moths feeding at honeydew. Table 1 lists taxa that have been commonly reported feeding at honeydew. Perhaps thousands, if not the majority, of ants, flies (Downes and Dahlem 1987, Marshall 2012), and parasitic wasps (Wäckers et al. 2008)—all keystone taxa in shaping the global population dynamics of insects (Hölldobler and Wilson 1990, Strydom and Eubanks 2007)—are honeydew feeders. Other important lineages of honeydew feeders include lacewings; erbid, noctuid, and nolid moths; and non-parasitic wasps (Table 1). Several groups of predaceous insects also feed

<sup>1</sup> It is hard to know the significance that American chestnut (*Castanea dentata* (Marsh.) Borkh.) had in eastern forests historically—it bloomed in June when many *Satyrrium* are on the wing. Basswood (*Tilia americana*) can be a prolific nectar source for woodland Lepidoptera and other insects wherever it grows.



**Table 1. Commonly reported honeydew feeders. Named subordinate taxa (indented) are those of great diversity or ecological significance. A comprehensive listing for many entomophagous insects relevant to biological control is given in Wäckers et al. (2008).**

Taxon	Comments	Documentation/References
<b>Diptera</b>		
Diptera, many lineages, from all suborders	Steve Marshall (2012) routinely sprays a honey water solution onto leaves so he can photograph a diversity of adult flies, and writes of “great gatherings”	Downes and Dahlem 1987, Marshall, 2012
Calypterata	muscoïd and related flies commonly observed at honeydew; given morphology of the mouthparts it is our belief (and evidently that of Steve Marshall 2012) that honeydew is a primary nutritional source for this lineage	
Tachinidae	of major importance in population regulation of other insects; honeydew thought to be primary diet of adult tachinids; honey water used by Monty Wood to collect Tachinidae throughout most of his career	Marshall 2012, Legner 2014
<b>Lepidoptera</b>		
Noctuoidea	generally regarded to be infrequent; likely sporadically practiced by Erebidæ and Noctuidæ, but Allan 1937, 1945 suggested honeydew was a primary carbohydrate resource for Noctuoidea	Allan 1937, 1945; Scoble 1992: 22, Leverton 2001, Sansum 2013
Nolidae	two species in this paper, Figs. 8, 10; some species notoriously scarce at light and bait, e.g., <i>Nycteola</i> may prove to be honeydew feeders	two species in this paper, Figs. 8, 10
Lycaenidae	generally uncommon to rare, but practiced by many Miletinae; some theclini (e.g., <i>Hypaurotis</i> ); many Eumaeini (e.g., <i>Satyrium</i> )	Fiedler 1993; this paper
Pyraloidea	<i>Cryptolabes</i> (“The Honeydew Moth”)	Wysoki et al. 1975
Yponomeutidae	<i>Yponomeuta</i> will feed at aphid clusters	Thorpe 1928
<b>Hymenoptera</b>		
	many lineages within virtually all family-level taxa are honeydew collectors, especially ants, ichneumonoids; many bees collect honeydew when abundant or when nectar resources are scarce	
Chalcidoidea	presumably widespread; <i>Eretmocerus eremicus</i> Rose and Zolnerowich, 1997	Hagenbucher et al. 2014
Ichneumonoidea	many species depend on honeydew even though it has been shown to have less nutritional value than other sugar sources.	Elliott et al. 1987; England and Evans 1997; Lee et al. 2004; Short and Steinbauer 2004; Faria et al. 2008; Hopkinson et al. 2013; Rusch et al. 2013
Other parasitic micro-hymenoptera, esp. Cynipoidea, and Procrupoidea		Jervis et al. 1993; Rivero and Casas 1999
Vespoidea	often preferred by <i>Vespula</i> wasps when they are abundant.	Krombein 1951; Moller and Tilley 1989; Beggs 2001; Wäckers et al. 2008; Gardener-Gee and Beggs 2013
Formicidae		Way 1963; Beattie 1985; Strysky and Eubanks 2007; Wäckers et al. 2008
Apoidea		Moller and Tilley 1989
<b>Other Orders</b>		
Neuroptera	green and brown lacewings well known to be attracted to and feed at honeydew; also visited by Mantispidae, and Sisyridae (which are sister to other extant Neuroptera); likely widespread across order	Keeler 1978; Bugg 1987; Canard 2001; Lundgren 2009; additional references in Wäckers et al. 2008: Table 1
Coleoptera		references below from Wäckers et al. 2008: Table 1
Anthribidae		Zoebelein 1956
Cantharidae		Zoebelein 1956
Coccinellidae		Pemperton and Vandenberg 1993

on honeydew (reviewed by Wäckers et al. 2008, also Table 1). Even known flower feeders such as flower flies, bees, and sand wasps are also known to collect honeydew.

Here too, in part, could be the partial basis of the broad attraction potency of yellow pan traps used to collect parasitic Hymenoptera. Yellowed plants and tissues may have high populations of sucking insects, which could

yield a source of sugar. Furthermore, the catches in pan traps are certainly not limited to the lineages of wasps that are parasitizing hemipterans or taxa attracted to and feeding at yellow flowers. To the contrary, the catches include a taxonomic array of lepidopterans, dipterans, and hymenoptera that are not known to feed at flowers or the honeydew producers.



Fig. 8. *Platynota near obliqua* Wlsm. (Tortricidae) to left and *Elaeognatha argyritis* Hampson (Nolidae) feeding at same site as Fig. 7 (photo courtesy Piotr Naskrecki).



Fig. 9. Second image of *Euclystis* feeding directly from terminus of the plant hopper (photo courtesy Piotr Naskrecki).



Fig. 10. *Eligma narcissus* (Cramer) (Family Nolidae) feeding at *Kalidasa nigromaculata* (Gray) (Family Fulgoridae) honeydew in Vietnam (photo courtesy of Tim McCabe).

### Musings on the Ecological Importance of NFSRs

While most entomologists are well aware of non-floral sugar resources, and generally understand that they are important (e.g., Downes and Dahlem 1987, Strysky and Eubanks 2007, Wäckers et al. 2008, Marshall 2012), their ecological value is, at best, poorly known. Except in the case of ants, there are no studies that have evaluated their importance across taxa in native ecosystems. Strysky and Eubanks (2007) provided a compelling case for hemipteran-ant mutualisms as a keystone interaction that affects the fitness of plants hosting honeydew-producing hemipterans, as well as the abundance and distribution of proximate arthropod communities, especially herbivores feeding on plants with elevated ant activity. Our assessment is broader in ecological and taxonomic scope, for both hemipterans and ants; it would include all honeydew-producing Hemiptera and all ants that feed at honeydew, either directly from hemipterans or from scattered understory sources.

Our knowledge of butterfly literature indicates that NFSRs are underappreciated in *Satyrinum* and hairstreaks more generally. Table 2 contrasts the number of citations we found for floral versus non-floral resources: three of our searches for NFSRs retrieved only 5% or less of the citations obtained for coordinate floral resources. A core thesis of this essay is that the disparities exemplified in

Table 2 are likely to be lopsided relative to the actual numbers of individual insects using NFSRs and the numbers of insect species that get their primary sugar resources from NFSRs, and thus likely underestimate the ecological significance of NFSRs in nature.

There are reasons why this might be the case. Flowers are generally conspicuous and concentrate activity at point sources (i.e., in the vicinity of the pollen or pistils). Honeydew and other NFSRs are dispersed spatially, often occur in trace amounts that are not readily noticeable to the human eye, are available both at ground level and in canopies out of view, and allow for feeding at any time of day or night. The volumetric difference between flower nectar and NFSRs has an additional detection consequence. Larger, easily observed insects have greater energy requirements and must seek out larger sugar resources such as flowers, fruits, and tree wounds. Smaller insects require less energy, such that honeydew and other NFSRs have a greater chance of satisfying their energy requirements, and so these insects and their feeding behaviors are less obvious. We might even have it backwards: what if sugar acquisition from honeydew, galls, extrafloral nectaries, exudates from ergot-infested seed heads, direct collection from scales and other hemipterans, tree wounds, and other sources represents the more general case, and nectaring at flowers is the exception



**Table 2. Floral versus non-floral sugar resources. Results from a Scopus search conducted on 22 December 2014. Results include the number of publications returned for all years. The right column indicates the % NFSRs hits relative to number obtained from the flower-related search terms.**

Search Terms	Scopus Citations	Search Terms	Scopus Citations
"nectar feeding" or "nectar-feeding"	471	"honeydew feeding" or "honeydew-feeding"	21 (4%)
"flower feeding" or "flower-feeding"	83	"honeydew feeding" or "honeydew-feeding"	21 (25%)
"flower resource" or "flower resources"	80	"nonfloral resource" or "non-floral resource" or "non floral resource" or "nonfloral resources" or "non-floral resources" or "non floral resources"	4 (5%)
"floral visitation" or "floral visitations" or "flower visitation" or "flower visitations"	314	"honeydew visitation" or "honeydew visitations"	0

for insects? After all, the latter often requires rather specialized mouthparts.

### Acknowledgments

This paper grew from a status survey for the oak hair-streak provided by the Massachusetts Natural Heritage and Endangered Species Program (NHESP Contract No. HERIT-13-05). We thank Carolyn Mills for assistance with the literature searches. The images that capture much of our story were supplied by Piotr Naskrecki, Bruce DeGraff, Ken Kertell, David Wright, and Charley Eiseman. Friends and colleagues who provided unpublished observations that gained relevance and importance over the course of our study include Richard Boscoe, Rich Cech, Rich Chyinski, Michael Gates, Tom Henry, Stuart McKamey, Noble Proctor, Michael Raupp, Robert Robbins, Dale Schweitzer, Matt Wallace, Reginald Webster, and David Wright. Earlier drafts of the paper were read by Chris Maier, Steve Marshall, Robert Robbins, Carl Schaefer, Dale Schweitzer, Mike Singer, Mike Thomas, Katie Todd, and Matt Wallace. Identifications were supplied by John Brown (tortricid), Geert Goemans (fulgorid), Tim McCabe (nolid), and Piotr Naskrecki (individuals in his images). Additional support for our study was provided by a State Wildlife grant and USFS Co-Op Agreement 14-CA-11420004-138 to DLW.

### Literature Cited

Downes, W.L., and G.A. Dahlem. 1987. Keys to the evolution of Diptera: role of Homoptera. *Environ. Entomol.* 16: 847-854.

Frost, S.W. 1957. More about Membracidae at lights. *Entomol. News* 68: 77-78.

Gagliardi, B.L., and D.L. Wagner 2014. An ecological and status assessment of the oak hairstreak (*Satyrium favonius ontario*) in the Northeast. Unpublished Technical Report submitted the Massachusetts Natural Heritage and Endangered Species Program (NHESP).

Gagliardi, B.L., and D.L. Wagner 2014. Biology, climate niche, and conservation status of the oak hairstreak (*Satyrium favonius ontario*) in the Northeast. *Ann. Entomol. Soc. Am.* In prep.

Holliday, K. 1993. A hairstreak experience. *News Lep. Soc.* 2: 59-61.

Holland, W.J. 1931. The butterfly book. Revised edition. Doubleday, Doran, Garden City, NY.

Hölldobler, B., and E.O. Wilson. 1990. The ants. Belknap Press, Cambridge, MA.

Inouye, B.D., and A.A. Agrawal. 2004. Ant mutualists alter

the composition and attack rate of the parasitoid community for the gall wasp *Disholcaspis eldoradensis* (Cynipidae). *Ecol. Entomol.* 29: 692-696.

Jesse, L. 2010. Shade tree aphids and honeydew. *Horticulture and Home Pest News*. Iowa State University: <http://www.ipm.iastate.edu/ipm/hortnews/2010/5-26/aphids.html>. Accessed January 2015.

Marshall, S. 2012. Flies: the natural history and diversity of diptera. Firefly Books, Richmond Hill, Ontario.

Medler, J.T., and P.W. Smith. 1960. Membracidae attracted to black light. *J. Econ. Entomol.* 53: 173-174.

Naskrecki, P., and K. Nishida. 2007. Novel tritrophic interactions in lantern bugs (Insecta: Auchenorrhyncha: Fulgoroidea). *Nat. Hist.* 41: 2397-2402.

O'Donnell, J.E., L.F. Gall, and D.L. Wagner (eds.). 2007. The Connecticut butterfly atlas. Connecticut Department of Environmental Protection, Hartford, CT.

Sadof, C. 2012. Sap-sucking bugs make a mess of Indiana's state tree. *Purdue Extension Bulletin*. <http://www.ppdl.purdue.edu/ppdl/hot12/5-23.html>. Accessed: December 2014.

Schweitzer, D.F., M.C. Minno, and D.L. Wagner. 2011. Rare, declining, and poorly known butterflies and moths (Lepidoptera) of forests and woodlands in the eastern United States. U.S. Forest Service, Forest Health Technology Enterprise Team, FHTET-2011-01. USDA Forest Service, Morgantown, WV.

Scott, J.A. 1986. The butterflies of North America, a natural history and field guide. Stanford University Press, Stanford, CA.

Shapiro, A.M. 1974. Butterflies and skippers of New York State. *Search.* 4: 1-60.

Styrsky, J.D., and M.D. Eubanks. 2007. Ecological consequences of interactions between ants and honeydew-producing insects. *Proc. Biol. Sci.* 274: 151-164.

Stichter, S. 2014. The butterflies of Massachusetts. <http://www.butterfliesofmassachusetts.net/index.htm>. Accessed December 2014.

Sumner, D.A., and F.H. Buck, Jr. 2003. Exotic pests and diseases: biology and economics for biosecurity. Iowa State Press, Ames, Iowa.

Swiecki, T.J., and E.A. Bernhardt. 2006. A field guide to insects and disease of California oaks. USDA General Technical Report PSW-GTR-197. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Dept. of Ag.

Wäckers, F. 2000. Do oligosaccharides reduce the suitability of honeydew for predators and parasitoids? A further facet to the function of insect-synthesized honeydew sugars. *Oikos.* 90: 197-201.

Wäckers, F.L., P.C.J. van Rijn, and G.E. Heimpel. 2008. Honeydew as a food source for natural enemies: making the best of a bad meal? *Biol. Control.* 45: 176-184.

- Wagner, D.L., D.F. Schweitzer, J.B. Sullivan, and R.C. Reardon. 2011. *Owlet caterpillars of eastern North America*. Princeton University Press, Princeton, NJ.
- Wallace, M.S. 2008. Occurrence of treehoppers (Hemiptera: Membracidae: Smiliinae) on oaks in Delaware Water Gap National Recreation Area, 2004-2006. *J. Insect Sci.* 8: 1-16.
- Wallace, M.S., and S.M. Maloney. 2010. Treehopper (Hemiptera: Membracidae) biodiversity and seasonal abundance in the Pocono till barrens, Long Pond, Pennsylvania. *Proc. Entomol. Soc. Wash.* 112: 281-294.
- Washburn, J.O. 1984. Mutualism between a cynipid gall wasp and ants. *Ecology.* 65: 654-656.
- Weld, L.H. 1957. *Cynipid galls of the eastern United States*. Privately printed, Ann Arbor, MI.
- Table 2 References**
- Allan, P.B.M. 1937. *A moth-hunter's gossip*. Watkins and Doncaster, London.
- Allan, P.B.M. [as An Old Moth-Hunter]. 1945. Honey-dew. *Entomologist's Record and Journal of Variation.* 57: 93-97.
- Beattie, A.J. 1985. *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, Cambridge, UK.
- Beggs, J. 2001. The ecological consequences of social wasps (*Vespa* spp.) invading an ecosystem that has an abundant carbohydrate source. *Biol. Conserv.* 99: 17-28.
- Bugg, R.L. 1987. Observations on insects associated with a nectar-bearing Chilean tree, *Quillaja saponaria* Molina (Rosaceae). *Pan-Pacific Entomologist*, 63: 60-64.
- Canard, M. 2001. Natural food and feeding habits of lacewings, pp. 116-129. *In* P.K. McEwen, T.R. New, and A.E. Whittington (Eds.). *Lacewings in the crop environment*. Cambridge University Press, Cambridge, UK.
- Downes, W.L., and G.A. Dahlem. 1987. Keys to the evolution of Diptera: role of Homoptera. *Environ. Entomol.* 16: 847-854.
- Elliott, N.C., G.A. Simmons, and F.J. Sapiro. 1987. Honeydew and wildflowers as food for the parasites *Glypta fumiferanae* (Hymenoptera: Ichneumonidae) and *Apanteles fumiferanae* (Hymenoptera: Braconidae). *J. Kans. Entomol. Soc.* 60: 25-29.
- England, S., and E.W. Evans. 1997. Effects of pea aphid (Homoptera: Aphididae) honeydew on longevity and fecundity of the alfalfa weevil (Coleoptera: Curculionidae) parasitoid *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae). *Enviro. Entomol.* 26: 1437-1441.
- Faria, C.A., F.L. Wäckers, and T.C.J. Turlings. 2008. The nutritional value of aphid honeydew for non-aphid parasitoids. *Basic Appl. Ecol.* 9: 286-297.
- Fiedler, K. 1993. The remarkable life history of two Malaysian lycaenid butterflies. *Nature Malaysiana.* 18: 35-43.
- Gardener-Gee, R. and J. Beggs. 2013. Invasive wasps, not birds, dominate in a temperate honeydew system. *Austral. Ecol.* 38: 346-354.
- Hagenbucher, S., F.L. Wäckers, and J. Romeis. 2014. Aphid honeydew quality as a food source for parasitoids is maintained in Bt cotton. *PLoS ONE.* 9: e107806.
- Hopkinson, J.E., M.P. Zalucki and A.H. David. 2013. Honeydew as a source of nutrition for *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae): effect of adult diet on lifespan and egg load. *J. Entomol.* 52: 14-19.
- Jervis, M.A., N.A.C. Kidd, M.G. Fitton, T. Huddleston, and H.A. Dawah. 1993. Flower-visiting by hymenopteran parasitoids. *J. Nat. Hist.* 27: 67-105.
- Keeler, K.H. 1978. Insects feeding at extrafloral nectaries of *Ipomoea carnea* (Convolvulaceae). *Entomol. News* 89: 163-168.
- Krombein, K.V. 1951. Wasp visitors of tulip-tree honeydew at Dunn Loring, Virginia. *Ann. Entomol. Soc. Am.* 44: 141-143.
- Lee, J.C., G.E. Heimpel, and G.L. Leibe. 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomologia Experimentalis et Applicata.* 111: 189-199.
- Leverton, R. 2001. *Enjoying moths*. Poyser, London.
- Legner, E.F. 2014. Tachinidae. Discoveries in Natural History 2014. Tachinidae. <http://www.faculty.ucr.edu/~legner/identify/tachinid.htm>. Accessed December 2014.
- Lundgren, J.G. 2009. *Relationships of natural enemies and non-prey foods*. Springer, New York, NY.
- Marshall, S. 2012. *Flies: the natural history and diversity of Diptera*. Firefly Books, Richmond Hill, Ontario.
- Moller, H., and J.A.V. Tilley. 1989. Beech honeydew: seasonal variation and use by wasps, honey bees, and other insects. *N. Z. J. Zool.* 16: 289-302.
- Pemberton, R.W., and N.J. Vandenberg. 1993. Extrafloral nectar feeding by ladybird beetles (Coleoptera, Coccinellidae). *Proc. Entomol. Soc. Wash.* 95: 139-151.
- Rivero, A., and J. Casas. 1999. Incorporating physiology into parasitoid behavioral ecology: the allocation of nutritional resources. *Res. Popul. Ecol.* 41: 39-45.
- Rusch, A., S. Suchail, M. Valantin-Morison, J. Sarthou, and J. Roger-Estrade. 2013. Nutritional state of the pollen beetle parasitoid *Tersilochus heterocerus* foraging in the field. *BioControl* 58: 17-26.
- Sansum, P. 2013. Honeydew feeding in adult Noctuidae and Erebidae - some observations and note on differing modes of access. *J. Res. Lepid.* 46: 75-80.
- Scoble, M.J. 1992. *The Lepidoptera: form, function, and diversity*. Oxford University Press/Natural History Museum, London.
- Short, M.W., and M.J. Steinbauer. 2004. Floral nectar versus honeydew as food for wasp parasitoids: implications for pest management in eucalypt plantations. *Australian Forestry* 67: 199-203.
- Styrsky, J.D., and M.D. Eubanks. 2007. Ecological consequences of interactions between ants and honeydew-producing insects. *Proc. Biol. Sci.* 274: 151-164.
- Thorpe, W.H. 1928. Note of *Hyponomeuta cognatella* Hübn. feeding on the honey-dew of *Aphis rumicis* Linn. *Entomologist's Monthly Magazine* 64: 46.
- Wäckers, F.L., P.C.J. van Rijn, and G.E. Heimpel. 2008. Honeydew as a food source for natural enemies: making the best of a bad meal? *Biol. Control* 45: 176-184.
- Way, M.J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annu. Rev. Entomol.* 8: 307-344.
- Wysoki, M., Y. Izhar, E. Gurevitz, E. Swirski, and S. Greenberg. 1975. Control of the honeydew moth, *Cryptoblabes gnidiella* Mill. (Lepidoptera: Phycitidae) with *Bacillus thuringiensis* Berliner in avocado plantations. *Phytoparasitica* 3: 103-111.
- Zoebelein, G. 1956. Der Honigtau als Nahrung der Insekten. *Z. Angew. Entomol.* 38: 369-416.

David L. Wagner is an insect biosystematist with research interests in lepidopteran taxonomy and phylogeny, their caterpillars, insect-plant relationships, tri-trophic interactions, and invertebrate conservation. He can be reached at the Center for Conservation and Biodiversity, University of Connecticut, Storrs, Connecticut 06269, E-mail: david.wagner@uconn.edu.

Benedict L. Gagliardi is a master's student interested in the systematics and life histories of North American smoky moths (Zygaenidae), their mimicry complexes, and the conservation of Lepidoptera.

DOI: 10.1093/ae/tmv045