Respite from a Rogue: Northern Hardwood Forests as A Refuge for Giant Silk Moths Threatened by Non-Target Biological Control

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(1). Parasitism of giant silk moths by the exotic biological control agent is low in the northern forest and has declined dramatically throughout the northeast in other forest types.
(2). This provides a cautious ray of optimism for the conservation of these iconic threatened insects

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http://www.nsrcforest.org

Project Summary

(350-400 words; written for a non-technical audience)

The goal of this project was to determine if northern hardwood forests offer refuge to native giant silk moths (Saturniidae) from a parasitic fly, *Compsilura concinnata*, introduced for biological control of gypsy moth a century ago. The decline of these iconic species has been linked to high parasitism from *Compsilura*. Several species of increasingly rare silk moths are still relatively common in parts of the Adirondack Park. We hypothesized that the transition from oak dominated forests of southern New England and NY to northern hardwoods may limit *Compsilura*, either directly through habitat preference or indirectly because gypsy moths, a non-native species, persist at higher population densities in forests with a high oak component relative to maple-beech forests.

To evaluate the central goal, we focused on three objectives:

(1) Quantify parasitism of silk moths by *Compsilura* across an oak cover gradient in the Adirondack Park.

(2) Assess other forest metrics, sources of mortality, and the abundance of gypsy moth as covariates of silk moth parasitism.

(3) Compare parasitism of silk moths at a regional scale using oak dominated forest sites in four eastern states (VA, PA, MA, NY) and our data from northern hardwood forests.

To assess parasitism, we used experimental 'sentinel' populations where laboratory reared larvae are placed in natural habitat at known locations, left *in situ* for a defined period of time, and then retrieved and reared in captivity. These larvae are then used to estimate percent parasitism. Other sources of mortality were assessed using exclusion cages as well as deployment and retrieval of realistic artificial 'dummy' larvae that record bird, small mammal, and invertebrate predation attempts.

Parasitism across 16 sites in the Adirondacks was low (~17%) but variable (0-71%). Surprisingly, there was no relationship between *Compsilura* parasitism of silk moths and basal area oak or any other forest cover metric. Gypsy moth populations were very low across the Adirondack Park and had no influence on *Compsilura* parasitism. Importantly from a conservation perspective, we found that parasitism of silk moth larvae across four states was far below what was recorded 15-20 years ago, suggesting that the impact of this fly may be diminishing. Thus, low levels of parasitism in northern hardwood forests do not appear to be a function of these ecosystems but rather, reflect this unprecedented reduction in the impact of this generalist parasitoid throughout the Northeast. Although declines in the population density and impacts of long established and widespread introduced species have been recorded, this trajectory is not common. With respect to *Compsilura*, the underlying driver in their regional decline in abundance is not known.

Background and Justification

- Giant silk moths are among the most iconic native insects, renowned for their size and beauty
- Across New England and lower NY State, many once common giant silk moth species have declined or even been extirpated (Fig. 1) along with a suite of other summer feeding, medium-to large bodied moths in other taxa[1].
- The decline in several species of silk moth has been linked to parasitism caused by a generalist parasitoid, *Compsilura concinnata*, a tachinid fly introduced to control gypsy moth a century ago (Fig. 2)[2,3].
- While the fly had little impact on the target species, it now attacks the caterpillars of ~200 species of native butterflies and moths (Fig. 3)[4].

Fig 1. Regal moth – a giant silk moth now extirpated from New York

Fig. 2. *C. concinnata* was first released in 1906 in Massachusetts

Fig 3. The large caterpillars of silk moths such as this Cecropia are particularly vulnerable as they have a long development time and feed in exposed locations

Background and Justification

- *Compsilura* is an extreme generalist even within its native range and has multiple generations annually, only one of which aligns with gypsy moth.
  - Higher populations of gypsy moth may increase *Compsilura* populations, in turn increasing the impact on non-target species such as silk moths.
  - Higher densities of gypsy moth are associated with oak dominated forests.
- Collections and monitoring suggest that several species of silk moths are still relatively abundant in the Adirondack Park (ADKP) and imperial moth which has disappeared from most of NY state, is still present.
  - ADKP is characterized by a transition from oak-dominated forests typical of southern New England and downstate New York to maple-beech dominated northern hardwood forests.
  - Some experimental data that includes sites in and around ADKP suggests that the impact of *C. concinnata* on silk moths may be lower than in Massachusetts.

Fig. 4. (a) Top to bottom: Cecropia, Luna, and Polyphemus are all relatively abundant in the Adirondack Park. (b) Imperial moth

Objectives

Overarching hypothesis is that *Compsilura* parasitism of silk moths is lower in northern hardwood forests because the reduction/absence of oaks restricts densities of gypsy moth

(1) Quantify parasitism of silk moths by *Compsilura* across an oak cover gradient in the Adirondack Park.

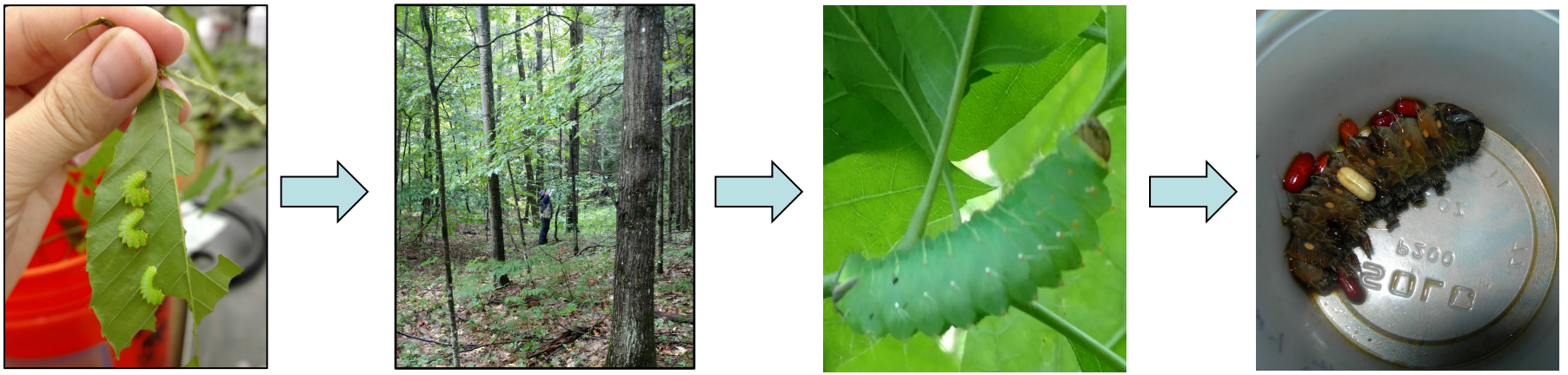
(2) Assess other forest metrics and the abundance of gypsy moth as covariates of silk moth parasitism. Quantify other mortality factors.

(3) Compare parasitism of silk moths at fine (stand) and medium (regional) scale with from oak dominated forests in four states (VA, PA, MA, NY) where gypsy moth outbreaks have occurred frequently in the past several decades.

Fig. 5. (a) *Compsilura* adult, (b) parasitized giant silk moth larvae, (c) multiple *Compsilura* larvae emerging from the giant silk moth caterpillar in (b).

Methods

- We assessed parasitism using experimentally established sentinel populations, consistent with earlier studies, in order to facilitate comparison.
  - Sentinel populations were created by rearing caterpillars in the lab and then placing them in the field for 5-6 days at low population densities to simulate natural conditions.
  - Larvae retrieved at the end of exposure period and reared individually. All sources of mortality recorded. Parasitism estimated as a percentage of the retrieved larvae.
- For consistency, we used a single species of silk moth in all studies, *Antheraea polyphemus* (Polyphemus moth).



Larvae reared from eggs under laboratory conditions until they reach the appropriate size.

Larvae placed on designated saplings spaced at minimum distances of >60m in plots for 5-6 days

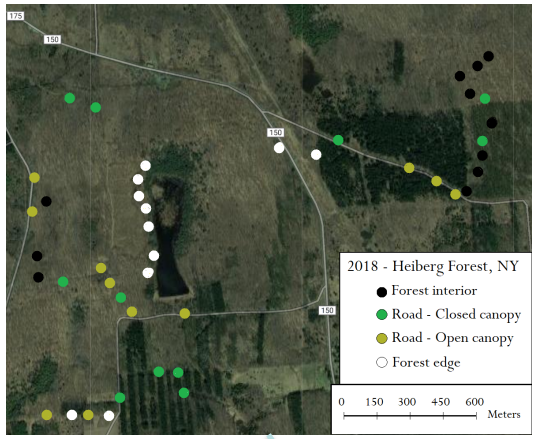
Saplings searched, all remaining caterpillars returned to lab for rearing.

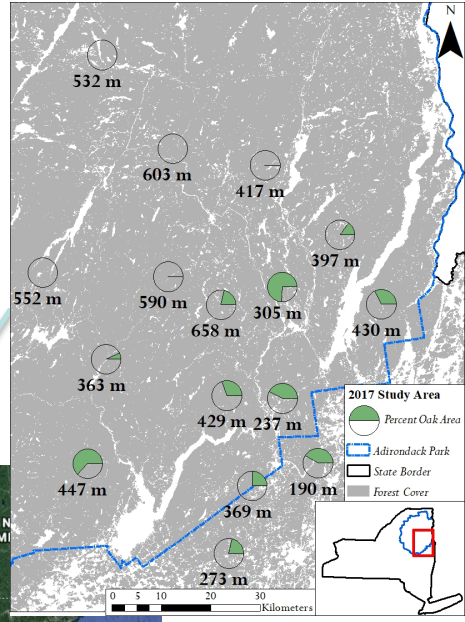
Reared until death or successful pupation. Parasitism determined.

Fig. 6. Sequence in the protocol **for** sentinel population establishment for assessing parasitism of giant silk moths

Study Sites

- We used digital inventory maps and ground-truthing to select a series of plots.
- *ADKP study* – 16 sites, 10 beech saplings / site
  - 3 caterpillars per tree
  - One control tree with caged caterpillars
  - Trees separated by > 60 and sites by at least 6km
  - 15 plasticine dummy larvae in each plot to assess bird predation
- *Regional Study* – 13 sites (3 each in MA, NY, VA, 4 in PA)
  - Protocol as above.
  - Oak saplings used for sentinels
- *Fine Scale Study*
  - Individual beech saplings selected in one of four habitats (Forest edge, forest interior, path - open canopy, path closed canopy)





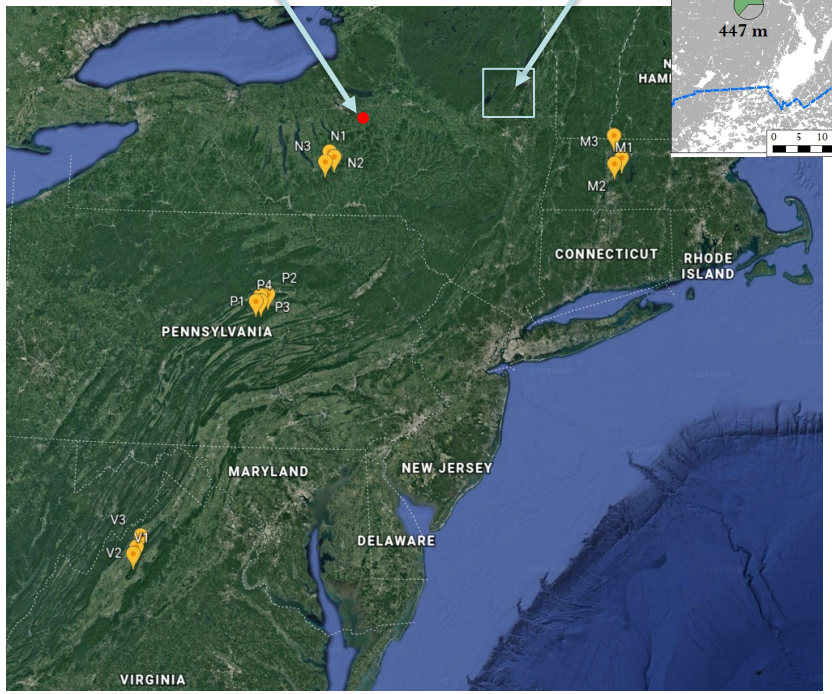


Fig. 7. Location of sites and plots. In 2017, 16 plots were intensively sampled in the southeastern Adirondack Park in oak transitional, and northern hardwood forest types (Basal area % shown in green with elevation asl). In 2018, plots were located in oak dominated forests in four states as well as on a fine scale in the northern hardwood cover type at Heiberg Forest in central NY.

2017 Adirondack Park Study

- In the ADKP, parasitism ranged from 0-71%, with a mean of 17% (Fig. 8) but there was no correlation with any forest variable (Table 1)
- Gypsy moth density was so low (16 larvae total) that analysis was not possible. Overall, these gypsy moth had 37.5% *Compsilura* parasitism. Abundance of forest tent caterpillar (FTC), a common species in our plots, was not correlated with silk moth parasitism.
- We did find a positive correlation with altitude, but this is likely due to collinearity with another factor such as temperature or forest composition.

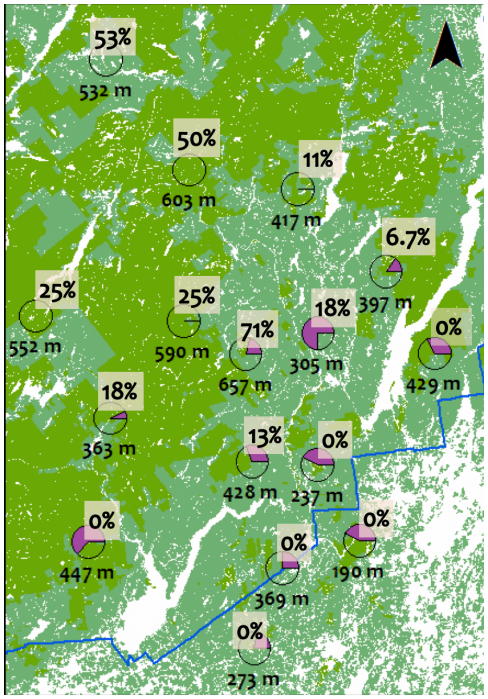


Fig. 8. Parasitism of Polyphemus sentinel larvae in each Adirondack Park plot (purple = % oak basal area).

Table 1. Significant predictors of parasitism of sentinel Polyphemus larvae by C. concinnata and their coefficients as determined by least absolute shrinkage and selection operator (LASSO) regression analysis. Italicized predictors explained significant portions of the variance in logit-transformed parasitism across all sites in a linear model [latitude ($F_{1,12}$ = 29.07, p < 0.001); degree days ($F_{1,12}$ = 11.21, p < 0.01); elevation ($F_{1,12}$ = 2.475, p = 0.142)].

Predictor	Coefficient
Latitude	0.93957
Longitude	·
Elevation (m)	0.00291
Aspect	·
Degree days	-0.00405
Total FTC (1/m2)	·
Oak basal area (m2)	·
Understory stem density (m2)	·
Canopy tree diversity (D)	·
Intercept	-43.1204

Take Home: Overall, parasitism is low in the Adirondack Park but contrary to our hypothesis, it is not driven by oak prevalence or gypsy moth abundance

Regional Comparison

- Surprisingly low levels of parasitism across 13 plots in four states (Fig. 9), ranging from 0% in four PA plots to a high of 26.7% in one MA plot.
- As with the ADKP study, accumulated degree-days and elevation had a significant effect on parasitism (Table 2), perhaps linked to the seasonal emergence and activity patterns of the parasitoid.
- Only modest 'predation' (4% by birds) occurred to our plasticine dummy caterpillars across our studies. These attacks were correlated with 'disappearance' of living sentinel caterpillars ($F_{1,12} = 5.96$, $p = 0.03$)

Fig. 10. Plasticine 'dummy' caterpillar with evidence of a bird strike (triangular beak imprint)

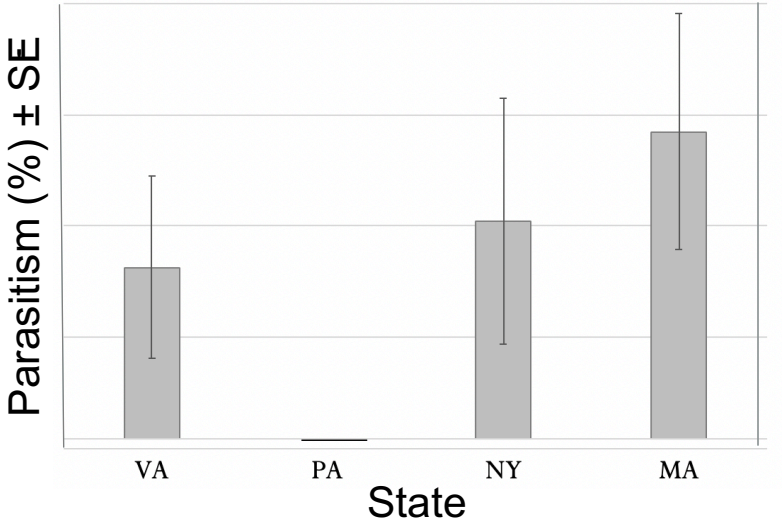


Fig. 9. *Compsilura* parasitism of sentinel larvae across four states. Published papers show that silk moth parasitism in MA, VA, and NY was significantly higher 15-25 years ago than we showed in this study.

Table 2. Significant predictors of parasitism of sentinel Polyphemus larvae by *C. concinnata* and their coefficients as determined by least absolute shrinkage and selection operator (LASSO) regression analysis of 13 sites across four states in 2018. Italicized predictors explained significant portions of the variance in logit-transformed *Compsilura* parasitism across all sites in a linear model.

Predictor	Coefficient	$F_{1,6}$	p-value
Latitude	-0.99893	1.847	0.223
Longitude	*0.67208*	*10.12*	*0.019*
Elevation (m)	*0.01189*	*7.000*	*0.038*
Degree days	*0.21673*	*22.11*	*0.003*
Oak basal area (m^2)	0.14555	1.522	0.263
Canopy tree diversity (D)	-0.11245	2.728	0.150
Intercept	74.60695		

Fine Scale Study

- At a fine scale (individual trees at one site; Fig. 11) there was a trend toward lower parasitism on edge/open canopy trees but no statistical difference among habitats (Fig. 12).
- Studies have shown that parasitism of several different Lepidoptera species by *Compsilura* increases in forests with distance from edge[5,6], our study shows a similar pattern.
- Parasitism levels in this study was similar to the ADKP study in 2017 and southern tier sites in the 2018 multi-state study suggesting that our sentinel approach is robust and likely reflects real patterns.

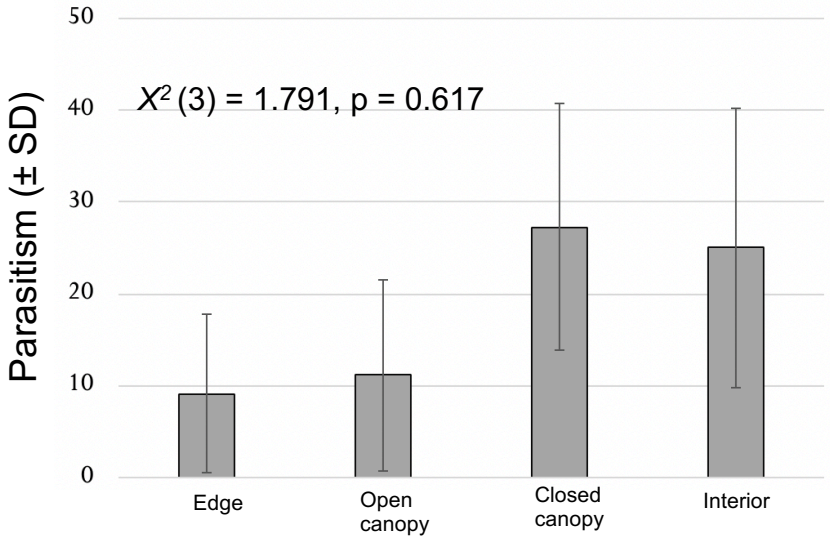


Fig. 12. *Compsilura* parasitism of silk moth larvae in edge and interior habitats on understory beech saplings at Heiberg Forest

Fig. 11. Undergraduate Emma Livingstone retrieving a sentinel larva (see arrow) after 6 days at Heiberg Forest. These large caterpillars are relatively sessile, and remain largely motionless during the day, feeding and moving short distances at night.

Project Outcomes

- The most important outcome of this project is that parasitism levels everywhere are relatively low, and this was true at all spatial scales examined (Fig. 13).
- Our project has documented an unprecedented regional collapse in the impact of this parasitoid, which, if sustained, is a critical result for the conservation of Lepidoptera, given the large impact and broad host range of this parasitoid.

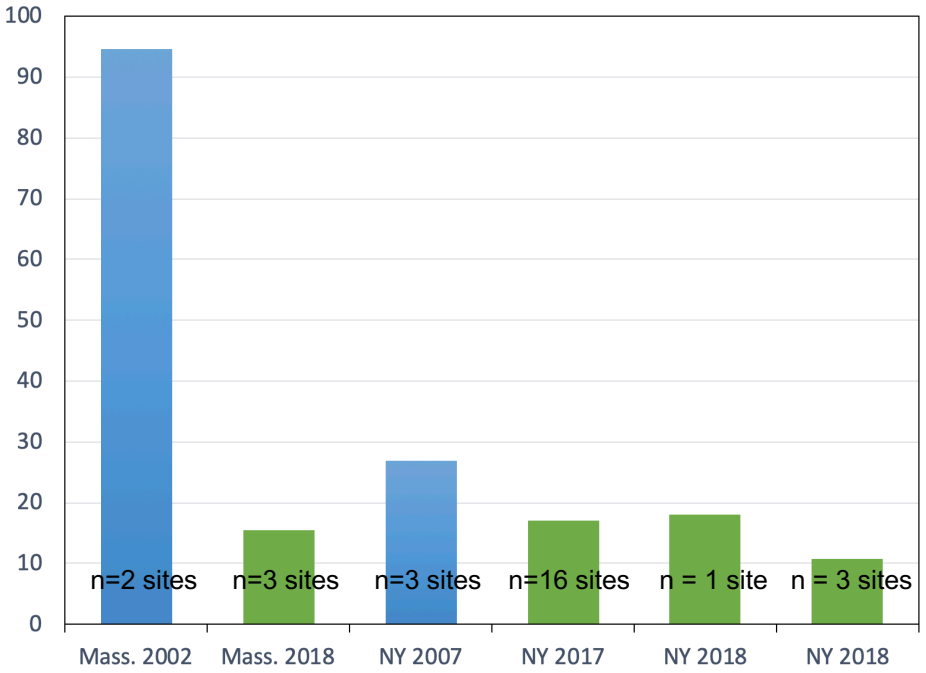
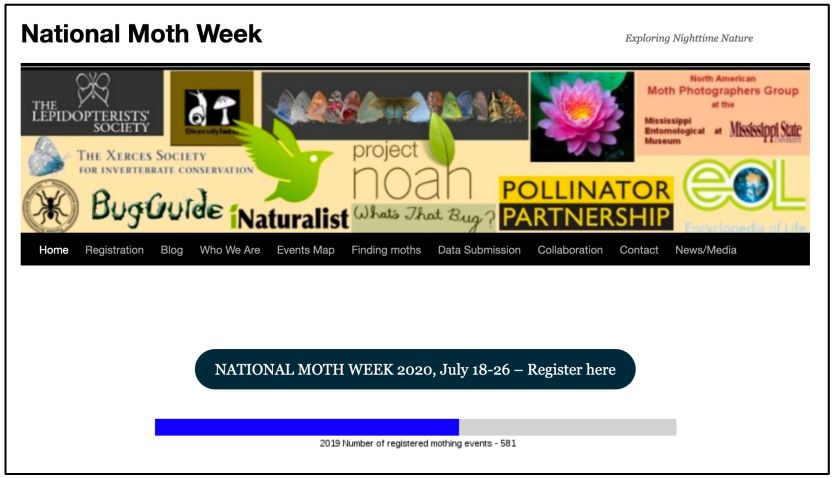


Fig. 13. Parasitism (%) of Polyphemus sentinel caterpillars in Parry (2009) and this study. Data encompasses the ADKP study (Fig. 8), MA and NY from the multi state comparison in Fig. 9. and the Heiberg Forest fine scale study (Fig. 12).

- Published and unpublished data indicate that high parasitism was still occurring in giant silk moths and other lepidopteran taxa through the mid-2000's in Massachusetts, eastern NY, and VA.
- Unclear if the lower levels of parasitism in central and northern NY in the mid/late 2000's were the norm or an indication that parasitism was already declining.
- Given the importance of native caterpillars in the structure and function of forest ecosystems, this has very positive implications for conservation

Outreach

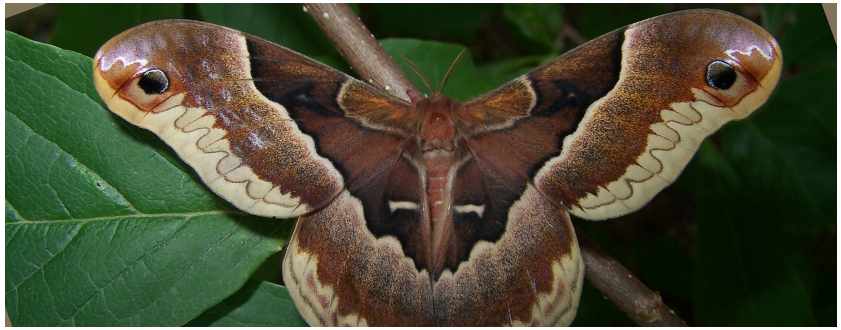
- Doctoral student Rea Manderino (funded by this NSRC grant) engaged a variety of professional and lay audiences throughout this project and focused on increasing public awareness about the importance of invertebrates in maintaining ecosystem health
- She leveraged our NSRC funds to get awards from the Grober Foundation and Sussman Foundation that were used to develop an outreach focus to the project.



  - Grober Foundation Award: she engaged freshman students in a field-based class at Cranberry Lake focused on insect conservation.
  - The Sussman Foundation Award: used to forge a linkage with the non-profit Caterpillar Lab <https://www.thecaterpillarlab.org/> in New Hampshire, an organization dedicated to educational programs that raise public awareness of the importance of insects, especially moths and butterflies in functioning ecosystems.
  - Rea is a co-founder of the fairly popular Facebook site **Relax. I'm an Entomologist** and has used that social media platform to advance insect conservation including this project.
- We participated in National Moth Week <http://nationalmothweek.org/> and Rea ran the insect portion of an ESF sponsored Bioblitz at Redwood, NY.

Implications and Applications in the Northern Forest Region

- Contrary to our original hypothesis, Northern Hardwood forests are not a refuge for silk moths because of the low or absent oak component or their poor quality for gypsy moth.
- We suspect, but can not prove, that northern hardwood forests may have nurtured healthy giant silk moth populations for some other reason (e.g., low light pollution, unfragmented forests with a relatively low human footprint, little or no history of DDT spraying).
- Our unprecedented documentation of an ongoing, region-wide collapse in the importance of an exotic generalist parasitoid has broad implications that encompass not just the northern forest but northeastern forest ecosystems in general.
- Given their importance in the diets of other threatened organisms like bats and birds such as the whip-o-will, formal monitoring of exemplar giant silk moth taxa may be prudent.



Future Directions

- We unfortunately have a very long data gap on population trends for giant silk moths in eastern North America with little empirical data from 1930 until the late 1990's. This includes the critical 1960's when amateur lepidopterists first started to describe the precipitous decline and increasing rarity of a number of silk moth taxa.
- The population dynamics of *Compsilura* are poorly described, either spatially or temporally, thus it is premature to view the decline in this species as evidence for a new equilibrium. Because we lack any long term data, we could be observing natural fluctuations in the amplitude of its populations.
- The absence of regional gypsy moth outbreaks in the northeast for more than 30 years likely has played a role because local population densities of *Compsilura* are influenced by this insect. The large outbreak of gypsy moth in southern New England 2016-2018 may provide insight into the complex relationship between *Compsilura*, gypsy moth, and alternative host species such as giant silk moths.
- Continued monitoring, especially in quantitative ways, of silk moth populations and periodic assessment of parasitism levels may provide evidence of recovery if their decline was largely attributable to *Compsilura* or suggest alternative hypotheses for understanding the general decline in this group.

List of Products

Manuscripts (Peer-reviwed)

Manderino, R., P.C. Tobin and D. Parry. Environmental drivers of native giant silk moth parasitism by a rogue biological control agent. Manuscript *in prep* for Ecology. Planned submission April 2020.

Other publications

Manderino, R. 2018. Giant Silk Moths in Northeast Forests. The New York Forest Owner. 56: 23-27

Dissertations.

Rea Manderino. Re-evaluating *Compsilura concinnata* as the causative agent in giant silk moth decline. SUNY-ESF. Defense scheduled, August 2020.

Undergraduate Theses

Emma Livingston. 2018. Forest cover composition and parasitism of giant silk moth parasitism by *Compsilura concinnata*

Chapin Czarnecky. The role of ultraviolet coloration in the giant silk moth *Antheraea polyphemus* and predation by birds

Emily Booth. 2020 (expected). The parasitoid community of native caterpillars in the Adirondacks relative to population density of the exotic competitor, *Compsilura concinnata*.

Presentations

Invited

Manderino, R, and D Parry. Re-evaluating the *Compsilura* hypothesis for explaining declines of native giant silk moths (Saturniidae). **Entomological Society of America**, ESA, ESC, and ESBC Joint Annual Meeting. Vancouver, BC, Canada. November 13, 2018.

Contributed

Manderino, R, P Tobin, and D Parry. Spatially variable parasitism of giant silk moth (Saturniidae) by the rogue biological control agent, *Compsilura concinnata*, across a forest compositional gradient. **Ecological Society of America**, 103rd Annual Meeting. New Orleans, LA. August 10, 2018.

Czarnecki, C, R Manderino, D Hanley, and D Parry. Ultraviolet Coloration of Caterpillars and Avian Predation. **Ecological Society of America**, 103rd Annual Meeting. New Orleans, LA. August 9, 2018.

Manderino, R, P Tobin, and D Parry**.** Northern Hardwood Forests as a Refuge for Giant Silk Moths Threatened by Non-Target Biological Control. **International Congress of Entomology,** ICE 25th Quadrennial Meeting. Orlando, FL. Sept. 30, 2016.