

# Caterpillar Chemical Defense and Parasitoid Success: *Cotesia congregata* Parasitism of *Ceratomia catalpae*

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Received: 9 March 2010 / Revised: 22 July 2010 / Accepted: 25 July 2010 / Published online: 4 August 2010  
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**Abstract** Sequestration of plant compounds by herbivorous insects as a defense against predators is well documented; however, few studies have examined the effectiveness of sequestration as a defense against parasitoids. One assumption of the “nasty host” hypothesis is that sequestration of plant defense compounds is deleterious to parasitoid development. We tested this hypothesis with larvae of the sequestering sphingid *Ceratomia catalpae*, which is heavily parasitized by the endoparasitoid *Cotesia congregata*, despite sequestering high concentrations of the iridoid glycoside catalpol from their catalpa host plants. We collected *C. catalpae* and catalpa leaves from six populations in the Eastern US, and allowed any *C. congregata* to emerge in the lab. Leaf iridoid glycosides and caterpillar iridoid glycosides were quantified, and we examined associations between sequestered caterpillar iridoid glycosides and *C. congregata* performance. Caterpillar iridoid glycosides were not associated with *C. congregata* field parasitism or number of offspring produced. Although wasp survival was over 90% in all populations, there was a slight negative relationship between caterpillar iridoid glycosides

and wasp survival. Iridoid glycosides were present in caterpillars at levels that are deterrent to a variety of vertebrate and invertebrate predators. Thus, our results support the alternative hypothesis that unpalatable, chemically defended hosts are “safe havens” for endoparasitoids. Future trials examining the importance of catalpol sequestration to potential natural enemies of *C. congregata* and *C. catalpae* are necessary to strengthen this conclusion.

**Key Words** Catalpa · Catalpol · Catalpa sphinx · Endoparasitoid · Iridoid glycosides · Nasty host hypothesis · Sequestration · Hymenoptera · Braconidae · Lepidoptera · Sphingidae

## Introduction

The ability of herbivorous insects to sequester defensive compounds from their host plants has evolved in specialist and generalist species in at least four orders (Duffey, 1980; Bowers, 1990, 1993; Nishida, 2002; Opitz and Müller, 2009). Chemical defenses are among the most effective defenses of herbivores against natural enemies (Dyer and Gentry, 1999), and anti-predator defense likely is a major factor in the evolution of sequestration (Bowers, 1992). Endoparasitoids are another significant biotic source of mortality, but little is known about chemical defenses against these enemies. Endoparasitoids are insects that develop as larvae inside other insects, typically resulting in the death of the host (Godfray, 1994; Quicke, 1997). Because endoparasitoids spend their entire larval life inside the host, possible negative effects of sequestered compounds may be more pronounced for endoparasitoids than for predators. One hypothesis that assumes a negative effect of sequestration on endoparasitoids is the “nasty host”

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hypothesis (Gauld et al., 1992, 1994), which posits that tropical parasitoids are not more diverse because sequestering hosts are more toxic and thus less available to parasitoids. Indirect support for this component of the nasty host hypothesis comes from studies that show a negative relationship between levels of sequestered host defensive compounds and parasitoid success (Campbell and Duffey, 1979; McDougall et al., 1988; Sime, 2002; Nieminen et al., 2003; Singer and Stireman, 2003; Lampert et al., 2008).

We used larvae of the catalpa sphinx, *Ceratomia catalpae* Boisduval (Lepidoptera: Sphingidae), and its parasitoid, *Cotesia congregata* Say (Hymenoptera: Braconidae), to test some assumptions of the nasty host hypothesis. The catalpa sphinx specializes on species of *Catalpa* (Bignoniaceae) (Baerg, 1935; Bowers, 2003), which contain the iridoid glycosides catalpol and catalposide (Nayar and Fraenkel, 1963; von Poser et al., 2000), terpenoids that are unpalatable to a range of generalist herbivores (Bowers, 1991). However, these compounds are used as feeding stimulants by catalpa sphinx larvae (Nayar and Fraenkel, 1963), which also sequester them for their own chemical defense (Bowers and Puttick, 1986; Bowers, 2003). Catalpa sphinx larvae hydrolyze catalposide to catalpol before sequestration, and caterpillar catalpol concentrations (5–20% total dry weight) can be several times higher than catalpa leaf iridoid concentrations (2–5% dry weight) (Bowers and Puttick, 1986; Bowers, 2003). Most of the iridoid glycosides are stored in the hemolymph, which contains approximately 50% dry weight catalpol (Bowers, 2003). Further, larvae regurgitate onto potential predators to repel them, and this regurgitant contains iridoid glycosides (Bowers, 2003).

The gregarious koinobiont parasitoid, *Cotesia congregata*, is the major parasitoid of catalpa sphinx larvae in the Eastern U.S. (Baerg, 1935; Ness, 2003a, b). *Cotesia congregata* generally are restricted to larvae of Sphingidae as hosts; however, Krombein et al. (1979) list only 15 sphingid species as hosts and also list *Trichoplusia ni* (Noctuidae) as a host. In laboratory experiments, *Hyles lineata* (Sphingidae) also was shown to be a permissive host, *Pachysphinx occidentalis* was a refractory host, showing complete encapsulation, and *Sphinx vashti* was considered semi-permissive, showing some encapsulation (Harwood et al., 1998). In another experiment, *T. ni* was a semi-permissive host (Beckage and Tan, 2002). *Cotesia congregata* attacks its hosts during the 2nd through the 4th instars by rapidly injecting eggs. Larvae develop in the hemocoel, bathed in and eating hemolymph, over approximately 2 weeks, then exit through the host cuticle, and pupate inside silken cocoons attached to the host. *Cotesia congregata* successfully parasitize catalpa sphinx larvae despite catalpol sequestration by this host.

The effects of sequestered iridoid glycosides on predators are well documented. Checkerspot butterflies that sequester

these compounds induce vomiting in birds that eat them (Bowers, 1980, 1981), and invertebrate predators will reject or perform poorly when offered caterpillars sequestering iridoid glycosides (de la Fuente et al., 1994/1995; Dyer and Bowers, 1996; Camara, 1997; Strohmeyer et al., 1998; Theodoratus and Bowers, 1999; Rayor and Munson, 2002). There is mixed evidence that sequestered iridoids harm parasitoids. The specialist braconid, *Cotesia melitaearum*, grew faster when developing in caterpillar hosts (*Melitaea cinxia*, Nymphalidae) with higher levels of iridoid glycosides, and development of the generalist ichneumonid, *Hyposoter horticola*, was not affected by levels of iridoid glycosides in the host (Harvey et al., 2005). In contrast, a field survey found that *M. cinxia* feeding on *Plantago lanceolata* (Plantaginaceae) plants that were low in iridoids were more likely to be parasitized than larvae feeding on high iridoid glycoside containing plants (Nieminen et al., 2003).

In this study, we tested one assumption of the nasty host hypothesis by examining the effects of catalpol sequestration by catalpa sphinx larvae on the performance of its parasitoid *Cotesia congregata*. We examined the leaf chemistry of several populations of catalpa trees across the Eastern United States, and tested for correlations with sequestered iridoids in catalpa sphinx larvae from those populations. We then determined whether different levels of average sequestration at a site were related to differences in parasitism success and performance of *C. congregata*. In this system, one assumption based on the nasty host hypothesis is that increased catalpol sequestration is associated with decreased parasitoid success.

## Methods and Materials

**Collections** Sixty-seven separate sites with *Catalpa bignonioides* were located and surveyed throughout the Eastern U.S., ranging from Southern New Jersey to Western North Carolina, from 14–19 August, 2007. Most stands were individuals or small groups of trees in residential or public lots. Six of the stands were attacked by catalpa sphinx larvae, and catalpa sphinx larvae parasitized by *Cotesia congregata* (as determined by the presence of emerged cocoons) were found at all locations except for Cape May Co., New Jersey (Table 1).

Each population was sampled according to the following protocol. All catalpa sphinx larvae within reach (~2.8 m) were removed from trees along with the leaves upon which they fed. Larvae were a combination of 3rd, 4th, and 5th instars (~20%, 64%, and 16%, respectively) during these collections. Leaves and larvae were placed in 1 l plastic Ziploc® boxes and stored in a cooler until they could be processed in the laboratory at the University of Colorado, Boulder. Additional catalpa sphinx larvae were shipped in late August from a

**Table 1** Sites with *Catalpa bignonioides* from which catalpa sphinx (*Ceratomia catalpae*) larvae were collected

	Site	Latitude	Longitude	Trees	<i>C. congregata</i>
1	Cumberland Co., VA	37°42'44.38"	78°10'43.14"	~30	Present
2	Johnston Co., NC	35°41'18.24"	78°23'53.07"	10	Present
3	Patrick Co., VA	36°37'37.37"	80°07'40.92"	1	Present
4	Botetourt Co., VA	37°37'01.84"	79°58'09.69"	3	Present
5	Adams Co., PA	39°47'05.63"	77°16'04.47"	10	Present
6	Cape May Co., NJ	39°14'39.43"	74°50'58.30"	15	Absent

collection made at the Clemson University Experimental Forest (Pickens Co., South Carolina).

**Plant and Insect Chemistry** Upon arrival in Colorado, a subset of five to ten unparasitized larvae from each population were starved for 8 h, weighed, and frozen at  $-80^{\circ}\text{C}$  for chemical analysis with gas chromatography [extraction protocol and instrument setup followed those described previously by Bowers (2003)]. The remaining larvae were removed from leaves, placed in a growth chamber set to  $25^{\circ}\text{C}$  with a 16:8 h, L:D photoperiod, and maintained on washed *C. bignonioides* leaves collected from the University of Colorado campus until either pupation or parasitoid emergence. The damaged leaves on which caterpillars had been collected were washed with distilled water to remove caterpillar frass, pooled by population, oven-dried at  $50^{\circ}\text{C}$ , then ground into a fine powder for chemical analysis. Leaves from the Pickens Co., South Carolina, population arrived almost entirely eaten and were not included in the chemical analysis. We extracted iridoids from a 50 mg subsample of the leaf powder from each population and quantified catalpol and catalposide. Iridoid extraction methods and instrument setup were the same for leaves and caterpillars.

Leaf iridoid glycoside amounts (mg) were divided by the weight of the extracted sample to obtain a percentage dry weight of catalpol and catalposide for each population. Because leaf samples were pooled, we could not statistically compare the iridoid glycoside concentrations of leaves among populations. To estimate caterpillar iridoid glycoside concentrations on a dry weight basis, we used a conversion factor (D.W./F.W. = 0.1193,  $r^2 > 0.98$ ) obtained from a separate set of 30 starved 4th and 5th-instar *Manduca sexta* larvae that were killed, weighed, dried, and weighed again. We applied this conversion factor to the wet weight of the catalpa sphinx larvae to calculate larval dry weight to allow direct comparisons with leaf iridoid concentrations. We did not have sufficient numbers of catalpa sphinx larvae to obtain fresh-dry weight conversions from this species. Larval catalpol concentration was compared among six populations using analysis of variance (ANOVA) (SPSS version

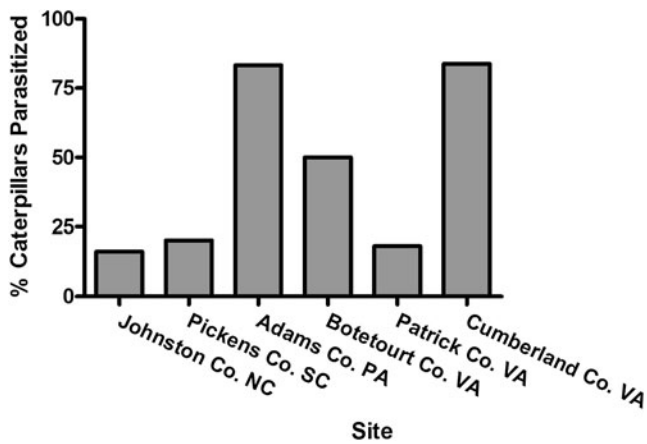
9.0). Populations were treated as a random factor. We then used linear regression to determine whether sequestered iridoids were dependent on leaf chemistry.

**Parasitism by *Cotesia congregata* and Caterpillar Sequestration-Parasitoid Relationships.** When *C. congregata* cocoons appeared on the remaining larvae, larvae were isolated in individual plastic cups to allow parasitoid adults to develop. Any adult *C. congregata* were anesthetized and removed, while any hyperparasitoids of *C. congregata* were killed and preserved for voucher specimens. After all *C. congregata* and their hyperparasitoids had emerged, catalpa sphinx larvae were killed by freezing and then dissected to examine them for the presence of parasitoid larvae. Any cocoons that did not yield adults were dissected to identify the occupant (*C. congregata* or hyperparasitoid). We added the total number of dead *C. congregata* larvae inside catalpa sphinx hosts to the number of cocoons to calculate total parasitoid clutch size, and divided the number of *Cotesia* cocoons by total clutch size to determine the proportion that survived until pupation. Average total clutch size and arcsine-square root transformed mortality were compared among populations, treating population as a random factor, using 1-way ANOVA. Parasitism level was calculated as the number of parasitized catalpa sphinx divided by the total number of larvae collected at each site and compared among populations using a  $\chi^2$  test.

## Results

**Insect Collections and Parasitoid Success** We collected over 500 individual catalpa sphinx larvae from seven populations. Trees typically were heavily attacked by dozens to hundreds of larvae, often to the point of defoliation. Approximately one-third of the larvae collected were parasitized by *C. congregata*, which were absent only at the Cape May Co., New Jersey site.

Levels of parasitism by *C. congregata* varied five-fold among populations, ranging from 15% to 80% ( $\chi^2 = 182.51$ ,  $P < 0.001$ ) (Fig. 1). The average total parasitoid clutch size (adults + larvae dead inside catalpa sphinx host) among all sites was  $24.52 \pm 1.69$  individuals per

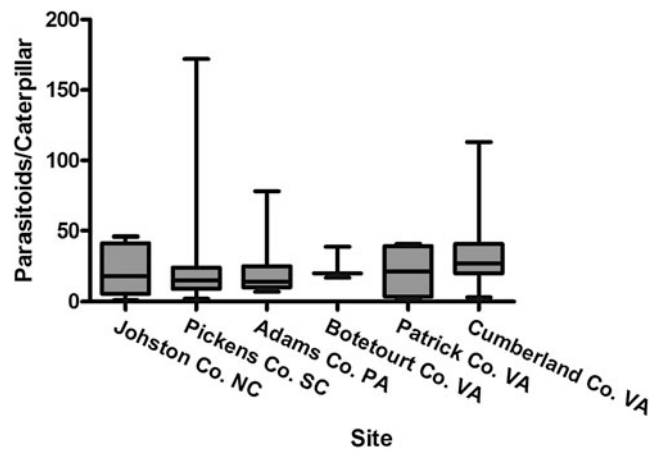


**Fig. 1** *Cotesia congregata* parasitism levels for six populations of catalpa sphinx larvae (*Ceratomia catalpae*)

brood with a median of 21, which did not differ significantly among the surveyed populations ( $F_{5,164}=1.79$ ,  $P=0.12$ ) (Fig. 2). Clutch size varied widely from 1 to 172. Only 11 broods contained over 100 individuals. Within-brood survivorship was over 90% for all populations, and it varied significantly among populations ( $F_{5,164}=3.33$ ,  $P=0.007$ ). This result was driven by the results from the Cumberland Co., Virginia, population (the only population to have catalpa sphinx larvae that contained over ten dead parasitoid larvae); if this population is excluded from analysis, parasitoid survivorship to pupation did not significantly vary among the other populations ( $F_{4,82}=1.35$ ,  $P=0.26$ ).

Hyperparasitoids were found only in *C. congregata* from parasitized catalpa sphinx larvae collected from the Adams Co., Pennsylvania, and Cumberland Co., Virginia sites. At least one hyperparasitoid individual emerged from 16% of *Cotesia* broods from the Adams Co. population and 6% of those from the Cumberland Co. population. Hyperparasitoid species included those that attacked larval stages [e.g., *Mesochorus* sp. (Ichneumonidae) (Baur and Yeargan, 1994)] and pupal stages (e.g., *Hypopteromalus* (Pteromalidae) (Gaines and Kok, 1999) of *Cotesia*).

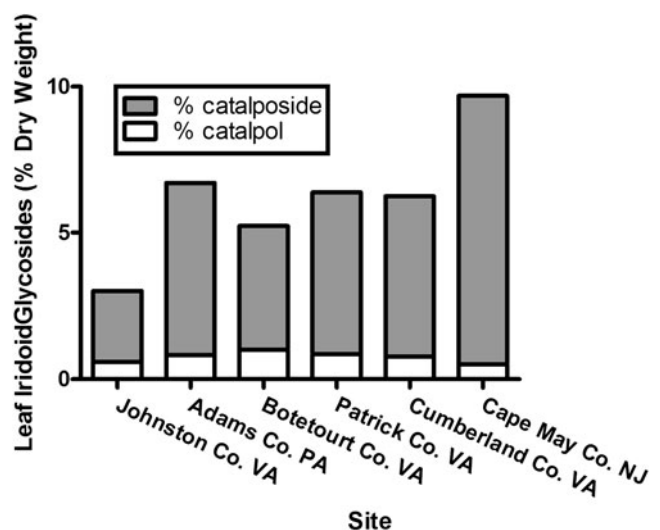
**Plant and Caterpillar Chemistry** Iridoid glycoside concentrations in catalpa leaves varied over 3-fold, ranging from 3–10% dry weight depending on the population (Fig. 3). Leaves contained much higher concentrations of catalposide than its precursor catalpol (Fig. 3). Caterpillar iridoid glycoside concentrations also varied among populations ( $F_{5,29}=5.63$ ,  $P=0.001$ ), ranging from 6.5% to 22.5% dry weight catalpol (mean:  $13.04\% \pm 0.87$ ). Larvae from populations with higher concentrations of leaf iridoids tended to sequester higher concentrations of catalpol, although this was only marginally significant



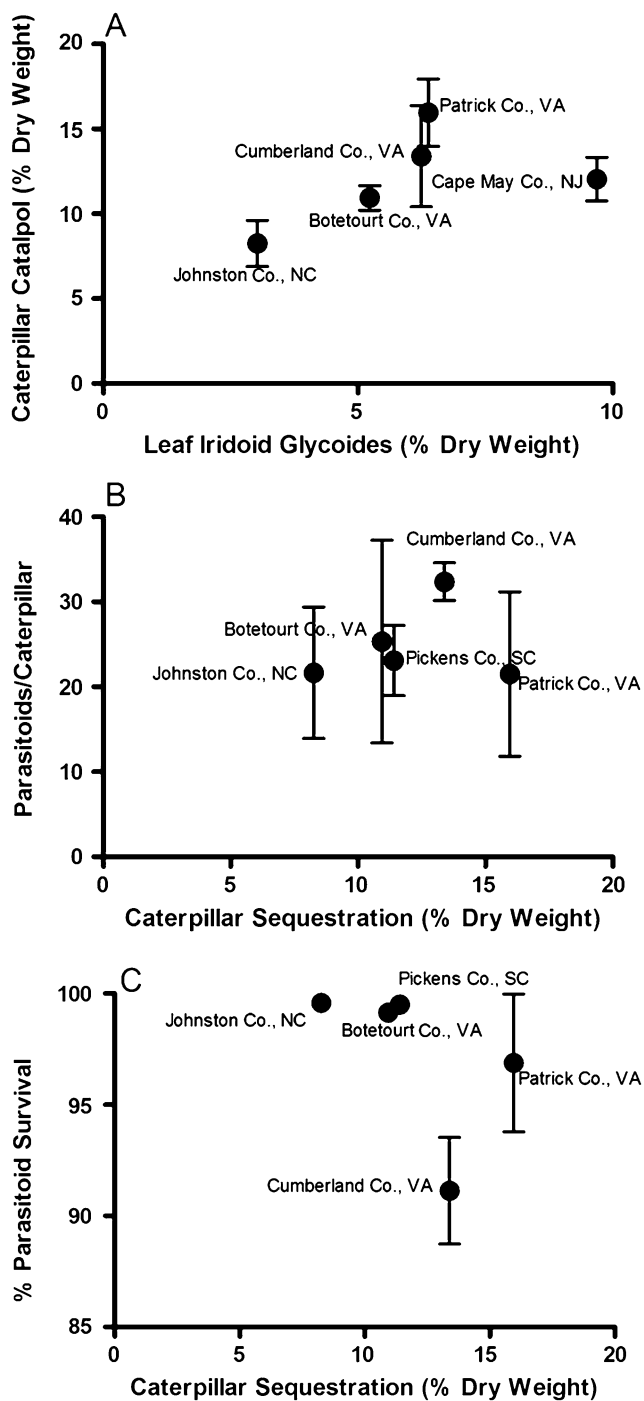
**Fig. 2** Comparison of *Cotesia congregata* total clutch size among populations. Lines within boxes represent medians, box margins represent 25th and 75th percentiles, and whiskers represent the extreme low and high values

( $r^2=0.20$ ,  $P=0.09$ ; caterpillar catalpol =  $0.55 \times \text{leaf iridoids} + 8.63$ ) (Fig. 4a).

**Caterpillar Chemistry and Parasitoid Fitness Responses** - There was a weak positive but not significant relationship between sequestration and total clutch size of *C. congregata* in each population ( $r^2=0.04$ ,  $P=0.09$ ) (Fig. 4b). Within-brood survivorship was over 90% for all broods and decreased as caterpillar sequestration increased ( $r^2=0.29$ ,  $P=0.03$ ), when all broods were considered (Fig. 4c). Again, this relationship was driven by results from the Cumberland Co., Virginia population. If this population is excluded, there is no negative relationship between brood survivorship and sequestration ( $r^2=0.85$ ,  $P=0.07$ ).



**Fig. 3** Iridoid glycoside content of *Catalpa bignonioides* leaves from five sites in the Eastern U.S. Bars represent amounts detected in samples pooled from one to ten trees



**Fig. 4** Relationship between **a** *Catalpa* iridoid glycosides and caterpillar sequestration by catalpa sphinx (*Ceratomia catalpae*). **b** *Catalpa* iridoid glycosides and *Cotesia congregata* total clutch size, and **c** *Catalpa* iridoid glycosides and *Cotesia congregata* percentage of larvae surviving to adulthood

## Discussion

The nasty host hypothesis assumes a deleterious effect of host sequestered plant toxins on insect parasitoids (Gauld et al., 1992, 1994). Catalpa sphinx caterpillar sequestration

did not appear to negatively affect its endoparasitoid *Cotesia congregata*. Parasitoid survival was high (over 90%), total clutch size did not vary significantly among the six populations, and populations with high average levels of caterpillar sequestration were heavily parasitized by *C. congregata*. These results agree with other studies that demonstrate that caterpillar sequestration by catalpa sphinx larvae does not deter successful parasitism by *C. congregata* (Bowers, 2003; Crocker, 2008). Catalpa sphinx larvae are exposed, gregarious feeders (Baerg, 1935), which is characteristic of many unpalatable, chemically-defended herbivores (Bowers, 1992). As such, they are apparent to parasitoids such as *C. congregata*. This caterpillar host species may appear more attractive to female *C. congregata* than other sphingid hosts that are less apparent, particularly if there are no fitness consequences to developing inside this sequestering species.

Our data do not support the component of the nasty host hypothesis that posits that chemically defended hosts are unsuitable to parasitoids (Gauld et al., 1992, 1994). Instead, parasitism levels and clutch size tended to increase in populations of caterpillars that were more chemically defended. There was an overall decrease in larval *C. congregata* survival as average caterpillar chemistry increased; however, the significance of this effect was heavily influenced by seven out of 83 parasitoid broods collected from a single population. Parasitoid survival was not negatively affected by chemistry if these broods, which were the only broods out of almost 200 with 10 or more dead larvae, were not considered.

A potential explanation for our results is that sequestering herbivores are “safe havens” for developing endoparasitoids (Dyer and Gentry, 1999; Gentry and Dyer, 2002; Smilanich et al., 2009). According to this hypothesis, parasitoids that develop inside chemically defended hosts receive fitness benefits in that they are protected from their own natural enemies, including hyperparasitoids and predators of the host. This hypothesis is supported by studies in which parasitoids perform better when reared from more toxic individuals of a single host species (Zvereva and Rank, 2003; Harvey et al., 2005). Large scale surveys of parasitoid incidence have shown that chemically defended insects typically have high levels of parasitism in the field (Cornell and Hawkins, 1995; Gentry and Dyer, 2002).

Sequestering catalpa sphinx larvae provide a safe haven for developing *C. congregata* parasitoids if these sequestering caterpillar hosts are protected from natural enemies such as caterpillar predators and hyperparasitoids of *C. congregata*. The importance of caterpillar sequestration as a predator deterrent for both catalpa sphinx and emerged *C. congregata* pupae remains unknown. Caterpillar sequestration is a deterrent to ants (Dyer, 1995; Dyer and Bowers, 1996), as well as to

a variety of other predators (de la Fuente et al., 1994/1995; Theodoratus and Bowers, 1999; Rayor and Munson, 2002). Ants are major antagonists of catalpa sphinx larvae in the Eastern US and can repel larvae from entire trees (Ness, 2003a, b). Ants may act as an important selective agent for catalpol sequestration, and high catalpol levels may allow catalpa sphinx larvae to avoid ant harassment.

The presence of hyperparasitoids would suggest catalpa sphinx larvae may not be completely safe havens for primary parasitoids. Hyperparasitoids successfully developed from *C. congregata* cocoons in two different populations. Catalpol is sequestered by *C. congregata* (Bowers, 2003). It is currently unknown whether hyperparasitoid development is adversely affected by catalpol sequestered by *C. congregata*, and how such fourth trophic level effects might vary among different hyperparasitoid taxa. In another study, *Mesochorus* sp. (Ichneumonidae) (*Mesochorus* was the most common hyperparasitoid genus reared in this study) adults contained small amounts of catalpol when reared from parasitoids of sequestering checkerspot caterpillars, thus indicating that hyperparasitoids do consume catalpol (Reudler Talsma, 2007). If hyperparasitoids are unaffected by the relatively low levels of iridoid glycosides sequestered by *C. congregata*, then the warningly colored catalpa sphinx larvae could provide a strong visual cue for hyperparasitoid host location.

Although our results did not reveal any strong negative relationships between caterpillar chemical defense and parasitoid success, future study is needed to determine whether catalpol might be intrinsically toxic to developing *C. congregata* larvae or any other parasitoid species. Catalpol acts as a feeding deterrent to non-adapted insects (Bowers and Puttick, 1988), and *C. congregata* larvae may lack catalpol-sensitive gustatory receptors. However, there are also post-consumption toxic effects of catalpol on several herbivore species (Bowers and Puttick, 1988, 1989). Catalpol exposure and consumption may have more subtle effects on *C. congregata*, such as prolonged development time; measuring this was not possible with host larvae parasitized in the field.

Further study is necessary to determine the ecological importance of the safe haven hypothesis. In particular, field studies that closely examine the palatability of chemically defended host species to generalist predators are needed to evaluate whether their parasitoids are less prone to attack by predators. In addition, the potential of hyperparasitism deterrence by developing inside chemically defended hosts deserves consideration. Controlled lab experiments that manipulate dietary catalpol and catalpol sequestration of parasitized catalpa sphinx larvae would provide further evidence that *C. congregata* are not negatively affected by catalpol sequestration. Finally, the role of chemical defense in determining parasitoid host choice deserves future study.

The safe haven hypothesis predicts that parasitoids may prefer unpalatable hosts, and this preference for chemically defended hosts would provide strong support for the adaptive use of hosts unpalatable to natural enemies.

**Acknowledgements** We thank Karen Kester and Vanessa Crocker, Department of Biology, Virginia Commonwealth University; Richard Olsen, USDA-ARS, Washington DC, and the U.S. National Arboretum; and Clyde Sorenson, Department of Entomology, NC State University for advice on catalpa sphinx locations and Laura McLoud for shipping caterpillars from Clemson, SC. Ellen Brown of the Reynolds Homestead Historical Site, Ernest and Fred Tyson, and David Pace permitted collections on private property. Richard Olsen, Carolina Quintero, Susan Whitehead, and two anonymous reviewers provided useful comments on the manuscript. This study was funded by NSF grant DEB 0614883 to MDB and LAD.

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