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Ecological dissociation and re-association with a superior competitor alters host selection behavior in a parasitoid wasp

Dhaval K. Vyas¹ · Jeffrey A. Harvey^{2,3} · Ryan L. Paul¹ · George E. Heimpel⁴ · Paul J. Ode¹

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Abstract

Interspecific competition for limited resources can drive ecological specialization and trait expression. Organisms released from intense competition may exploit a broader range of resources, but if reunited with stronger competitors, survivorship may depend on foraging behaviors that reduce competition. We compared the host selection behavior of the parasitoid *Cotesia glomerata* from two North American populations that differ in their association with *Cotesia rubecula*, a superior competitor. Both parasitoids originate from Europe and attack the imported cabbageworm (a.k.a. small cabbage white) *Pieris rapae*, but *C. glomerata* was introduced into North America almost a century before *C. rubecula*. After re-association in North America, *C. rubecula* has displaced *C. glomerata* in several regions, but not in other regions. Host selection was measured in female *C. glomerata* from Maryland (MD) where it coexists with *C. rubecula*, and in conspecifics from Colorado (CO) where *C. rubecula* is absent. Unparasitized and *C. rubecula*-parasitized *P. rapae* hosts were used in choice tests to examine whether *C. glomerata* host selection behavior differed based on the population's association history with *C. rubecula*. We found that *C. glomerata* from MD had a higher likelihood of avoiding hosts parasitized by *C. rubecula* (and thus avoiding competition) than did wasps from CO. The ability of *C. glomerata* to avoid hosts parasitized by *C. rubecula* may facilitate coexistence in MD; whereas, the lack of discrimination in CO populations of *C. glomerata* naïve to *C. rubecula* could contribute to the displacement of *C. glomerata* were *C. rubecula* to enter the same habitat.

Keywords Competition · Foraging behavior · *Cotesia glomerata* · *Cotesia rubecula* · *Pieris rapae*

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Enemy-free space plays a significant role in the evolutionary ecology of species, but most enemy-free space studies focus on trophic interactions (e.g., predator–prey, parasitoid–host). We know little about how a species is affected after escaping from interspecific competitors. This research is one of the few that shows behavioral changes in a weaker competitor following separation from its stronger competitor. These results enhance our understanding of how species may change when communities experience disruptions to established ecological relationships.

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✉ Dhaval K. Vyas
Dhaval.Vyas@colostate.edu

¹ Graduate Degree Program in Ecology and Department of Bioagricultural Sciences and Pest Management, Colorado State University, 1177 Campus Delivery, Fort Collins, CO 80523-1177, USA

² Netherlands Institute of Ecology, Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands

Introduction

Interspecific interactions are well-known to influence the foraging decisions of individuals (e.g., predation—Milinski and Heller 1978; Brown et al. 1988; Kohler and McPeck 1989; competition—Willis 1966; Inouye 1978). In species with broad geographic ranges, foraging behaviors are expected to covary with the community structure of consumers, competitors, and/or resources (e.g., prey for predators, plants for herbivores). Changes in community structure might be expected to select for altered foraging behaviors

³ Section Animal Ecology, Department of Ecological Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

⁴ Department of Entomology, University of Minnesota, 1980 Folwell Avenue, St. Paul, MN 55108, USA

when a species expands its range and becomes dissociated from its historical community. Such dissociation can result in relaxed selection for behaviors that had previously mitigated the effects of predation or competition (Coss 1999; Lahti et al. 2012).

When asymmetric competition exists between two species that exploit the same resource, weaker competitors can co-exist with competitively superior species by altering their foraging behaviors, typically by recognizing and avoiding the particular resources or foraging habitats used by the stronger competitor. Studies of interspecific competition in a wide range of taxa show that avoidance of a shared foraging habitat is common in communities where two or more competing species have strongly overlapping niches (e.g., mammals: Grassel et al. 2015; birds: Björklund et al. 2016; fish: Britton et al. 2018; insects: Janssen et al. 1995; Murdoch et al. 1996; Tamò et al. 2006; Chailleux et al. 2014). However, it is unclear how these avoidance mechanisms may change when weaker competitors have been dissociated from a stronger competitor for many generations.

Interspecific competition is a significant component of the community ecology of insect parasitoids, including many species of parasitic wasps. Parasitoids are insects whose larvae develop in, or on, the bodies of other insects, whereas the adults are free living (Godfray 1994). In nature, some host individuals are often attacked by two or more parasitoid species (i.e., multiparasitism) (Price 1972; Ueno 1999; Harvey et al. 2013), creating conditions in which there may be intense competition for host resources. Within a multiparasitized host, immature endoparasitoids (species whose larvae develop inside their insect host) employ various means of excluding competitors, such as physical attack, physiological suppression, and/or resource competition (Harvey et al. 2013). Given the severe costs (typically death) of multiparasitism for the loser, the weaker parasitoid competitor will benefit from avoiding hosts previously parasitized by a stronger competitor. Avoidance of multiparasitism has been documented in several host–parasitoid systems (Fisher 1961; van Dijken et al. 1992; Gauthier et al. 1999; Tamò et al. 2006), yet little is known about the short-term changes in avoidance behaviors under conditions of dissociation from, and subsequent re-association with, superior competitors. Such events are likely commonplace in both natural range expansions as well as intentional introductions for biological control programs. Avoidance behaviors may be reduced, or even lost, if a weaker competitor exists in competitor-free space for a number of generations.

Here, we compare the effects of interspecific competition on the host selection decisions of *Cotesia glomerata* females from populations that have a history of interaction with a stronger competitor, *Cotesia rubecula* (both Hymenoptera: Braconidae), with *C. glomerata* females that have been dissociated from *C. rubecula*. When *C. glomerata* and *C.*

rubecula parasitize the same host, *C. rubecula* usually kills eggs or larvae of *C. glomerata* (Laing and Corrigan 1987). Both parasitoids are originally from Europe, where coexistence in the same field sites is largely mediated by their use of different host species; *C. rubecula* is a specialist on *Pieris rapae* (Lepidoptera: Pieridae) and *C. glomerata* predominantly attacks *Pieris brassicae* and only rarely attacks *P. rapae* (Geervliet et al. 2000). In North America, *C. glomerata* was introduced intentionally as a biological control agent against *P. rapae* in the 1880s and rapidly spread throughout much of the continent (Clausen 1978). On the other hand, *C. rubecula* was first discovered in British Columbia in the early 1960s, possibly as an unassisted introduction, and was subsequently redistributed as a biological control agent to several locations in the upper Midwest and New England (US) (Wilkinson 1966; McDonald and Kok 1992; van Driesche and Nunn 2002; Wold-Burkness et al. 2005). *Cotesia glomerata* have at least two generations per year (Laing and Levin 1982; Fei et al. 2014); therefore, prior to the arrival of *C. rubecula*, North American *C. glomerata* lived without *C. rubecula* for an approximate minimum of 160 generations. *Cotesia glomerata* continues to live without *C. rubecula* in some parts of North America where it has undergone at least an additional 100 generations since the two species were last in contact.

Pieris brassicae is absent in North America, forcing *C. rubecula* and *C. glomerata* to rely on *P. rapae* as the primary host species. While the two parasitoids exhibited considerable geographic overlap in the years after the establishment of *C. rubecula* in North America, *C. rubecula* has competitively displaced *C. glomerata* in many of these locations (Biever 1992; Herlihy et al. 2012). Nevertheless, there are areas in North America where *C. glomerata* and *C. rubecula* currently coexist using the same host species (e.g., Maryland and Delaware, US), as well as areas where *C. rubecula* has never occurred and *C. glomerata* continues to exist without any significant competition for *P. rapae* hosts (e.g., Colorado, US). Therefore, it is conceivable that Colorado populations of *C. glomerata* have lived in competitor-free space possibly long enough to have lost the ability to detect and avoid hosts previously parasitized by *C. rubecula*. Failure by female *C. glomerata* to avoid hosts parasitized by *C. rubecula* could lead to displacement of *C. glomerata* by *C. rubecula* if the two species are re-associated (Herlihy et al. 2012); conversely, avoidance of hosts parasitized by *C. rubecula* may permit coexistence of these two parasitoids.

In this study, we compared the avoidance behaviors of two North American *C. glomerata* populations, each with different histories of association with *C. rubecula*. Specifically, we tested the hypothesis that the long-term dissociation from *C. rubecula* has led to relaxed selection on the ability of *C. glomerata* to avoid hosts already parasitized by its stronger competitor. We predicted that Maryland (MD)

C. glomerata would avoid hosts previously parasitized by *C. rubecula*, whereas Colorado (CO) *C. glomerata* would fail to discriminate between unparasitized hosts and hosts previously attacked by *C. rubecula*. We also explored whether the time elapsed since parasitism by *C. rubecula* influenced the foraging decisions of MD and CO female *C. glomerata*. Some parasitoids can successfully attack a previously parasitized host as long as the subsequent attack occurs within a safe period (Ueno 1999; de Moraes and Mescher 2005; Magdaraog et al. 2013). A *C. rubecula* egg usually hatches 48 h after oviposition and the first instar larva uses its sharp mandibles to kill con- and heterospecific larvae (Laing and Corrigan 1987). Second, and subsequent, instars of *C. rubecula* lack enlarged, sharp mandibles. We expected that *C. glomerata* females from the MD population would be more likely than CO *C. glomerata* to avoid hosts that were parasitized by *C. rubecula* less than 24 h earlier, because upon hatching, *C. glomerata* larvae would be exposed to the killing morph of *C. rubecula* in these hosts. Finally, if *C. glomerata* attacks hosts previously parasitized by *C. rubecula*, then they should lay smaller clutch sizes to reduce fitness losses from larval competition with *C. rubecula*.

Methods

Insects

Cotesia glomerata and *C. rubecula* both prefer to oviposit in first and second instars of caterpillars in the family Pieridae (Brodeur and Geervliet 1992; Gols et al. 2019). *Cotesia rubecula* lays one egg per attack, whereas *C. glomerata* can lay 20–50 eggs per attack. The *C. rubecula* larva usually emerges from its host in the host's penultimate (fourth) instar, whereas *C. glomerata* larvae emerge from the host's final (fifth) instar. *Cotesia* larvae complete development by egressing from their host and pupating within a single white cocoon in the case of *C. rubecula* or a group of yellow cocoons in the case of *C. glomerata*.

Cotesia glomerata colonies were initiated from field-collected broods from Colorado State University's Agricultural Research and Education Center (CSU ARDEC; GPS: 40.652703, -104.994627) and an organic farm in Maryland (Glade Link Farms, GPS: 39.569801, -77.285140). The *C. glomerata* colony initiated from Colorado-collected material was maintained separately from the colony initiated from Maryland-collected material. Field-collected *C. glomerata* broods were housed in 946-ml clear plastic cups that were placed in environmental control chambers set to a 16L:8D photoperiod and 25 °C until adult wasps emerged. Adult wasps were provided with a 10% honey–water solution and kept in 946-ml plastic cups in the chambers set to a 16L:8D photoperiod and 20 °C. *Cotesia rubecula* colonies

were started from field-collected cocoons at sites near the University of Minnesota in St. Paul, MN, USA. Cocoons were reared individually in 2 ml plastic centrifuge tubes and adults were reared at the same conditions as *C. glomerata*. *Pieris rapae* colonies were initiated with approximately 20 pupae that were collected from CSU ARDEC. They were reared in insect cages in the greenhouse at a 16L:8D photoperiod at 20–25 °C. Adult butterflies oviposited onto live collard plants (*Brassica oleracea*) grown in 10-cm-wide pots.

Cotesia rubecula is absent in Colorado, but it co-occurs, often in the same host individuals (i.e., multiparasitism), with *C. glomerata* in Maryland. In order to determine the level of multiparasitism in the field, *P. rapae* caterpillars were collected in 2017 from varieties of cabbage (*Brassica oleracea*) at five different organic farms (Calvert Farm [GPS: 39.712712, - 75.984629], Calvert's Gift Farm [GPS: 39.584793, - 76.738527], Flying Plow [GPS: 39.692704, - 76.089965], Gorman Farm I [GPS: 39.148985, - 76.866518] and Gorman Farm II [GPS: 39.185325, -76.951153]) in Maryland from May to September in 2017. We collected and dissected a total of 751 caterpillars from across the 5 instars (L1–L5): 83 L1, 300 L2, 141 L3, 147 L4 and 80 L5. The farms in Maryland were located throughout the state with a minimum separation of 13.5 km. At each farm, 20–50 plants per variety were selected and each leaf was inspected for caterpillars. If a farm was visited more than once, a different row or plot of the same cabbage variety was selected to prevent repeated sampling of plants. A total of 1063 plants were surveyed for caterpillars.

Field-collected caterpillars were dissected to assess whether immature *C. glomerata* and/or *C. rubecula* were present. *Cotesia rubecula* eggs are distinguished from *C. glomerata* because *C. rubecula* eggs occur in fewer numbers (<5) and are approximately twice the size of *C. glomerata* eggs. Only *C. rubecula* larvae possess large sclerotized-mandibles and a caudal appendage. At times (28/751), the parasitoid eggs were encapsulated, which occurs when the host's immune cells surround and impair parasitoid egg development (Nappi 1975). When encapsulated eggs were observed, we were able to accurately distinguish the species of parasitoid by counting the number of eggs (> 5 for *C. glomerata*) and size of the egg, characteristics that remain observable even 3–5 days following encapsulation (Brodeur and Vet 1995; DKV and JAH pers. observation).

Experimental design

Choice tests were conducted to compare the host selection behavior of female *C. glomerata* from Colorado with females from Maryland (which are currently associated with *C. rubecula*) when presented with unparasitized caterpillars

and caterpillars previously parasitized by *C. rubecula*. Each host individual was in the second instar because this stage is readily attacked by both *Cotesia* species (Brodeur and Geervliet 1992). Previously parasitized hosts were attacked by *C. rubecula* either <0.5 h, 24 h, 48 h, or 72 h prior to exposure to *C. glomerata*, allowing us to determine whether *C. glomerata* host preference was affected by the time since parasitism by *C. rubecula* (and hence, developmental stage of *C. rubecula*).

Prior to the start of each choice test, each female *C. glomerata* was ‘primed’ (to increase her responsiveness to hosts in choice tests; Fatouros et al. 2005) by exposing her to a collard leaf previously damaged by a *P. rapae* larva for 10 min in a 60-mm petri dish. Choice tests involved placing a mated, primed female *C. glomerata* with no prior oviposition experience in an arena containing an unparasitized *P. rapae* caterpillar and a caterpillar previously parasitized by *C. rubecula*. The unparasitized and *C. rubecula*-parasitized caterpillars were placed on separate collard leaves in the choice test arena prior to the introduction of the *C. glomerata* female. The collard leaves with the caterpillars were cut from the plant and the leaf petioles were placed individually in 37-ml plastic cups filled with water to prevent wilting. The cups were color-coded with a marker to indicate which leaf held the unparasitized or *C. rubecula*-parasitized caterpillar. Arenas consisted of a 946-ml clear plastic cylinder, into which the test *C. glomerata* female was introduced above and away from the pair of leaves on which the caterpillars were feeding. Once the female ceased grooming and began to walk towards the leaves, we observed foraging behaviors for 15 min.

We recorded the following observations in each choice test: the first leaf (with unparasitized or *C. rubecula*-parasitized larva) on which foraging behavior was observed, first host attacked (unparasitized or *C. rubecula*-parasitized), time to attack (s), attack duration (s), and clutch size (number of eggs). Host-searching behavior was defined as either repeated contact of the distal end of the female’s abdomen or her antennae with the surface of the leaf. An attack was defined as the insertion of the ovipositor into the host while the female assumed a stationary posture with wings spread and legs elevated off the substrate. Attacks ended when the female began moving and retracted her ovipositor from the host. After an attack, the *C. glomerata* female was removed and the arena containing the host caterpillars was placed in an incubator set at a 16L:8D photoperiod and 20 °C for 48 h to allow the parasitoid eggs to hatch. Forty-eight hours after a choice test, each caterpillar was dissected to verify the presence of and count the number of eggs or larvae from both *Cotesia* species. If a host caterpillar exposed to *C. rubecula* lacked a *C. rubecula* egg or larva, that choice test was excluded from the analyses as this would have meant that the foraging *C. glomerata* had been mistakenly

presented with two unparasitized hosts. Each choice test ended after a female completed oviposition or if 15 min elapsed without a female contacting either leaf. Five CO *C. glomerata* and three MD *C. glomerata* failed to contact the leaf or to attack either host; these choice tests were discarded and repeated with new females.

A total of 18 choice tests were performed per time interval for a total of 72 replicates for CO *C. glomerata* and 72 replicates for MD *C. glomerata*. Separate female *C. glomerata* were used for each choice test. Therefore, a total of 72 CO *C. glomerata*, 72 MD *C. glomerata*, 144 caterpillars parasitized by *C. rubecula* and 144 unparasitized caterpillars were used in this study. Multiple choice tests were completed in a day, which was treated as a block (see below).

Analyses

We analyzed our data with three statistical models. First, host preference (unparasitized, *C. rubecula*-parasitized) was treated as a binary response and analyzed using a multiple logistic regression with *C. glomerata* population (CO, MD), time interval since parasitism by *C. rubecula* (<0.5, 24, 48, or 72 h), and their interaction term as explanatory variables. Time interval was considered as an ordinal variable. Second, time to attack (s), attack duration (s), and clutch size (number of eggs) were treated as continuous response variables and were each analyzed using separate two-way ANOVA with parasitism status (unparasitized or *C. rubecula*-parasitized) of host and *C. glomerata* population (CO or MD) as explanatory variables. Third, we were also interested in assessing whether these three response variables were affected by the time since parasitism by *C. rubecula*. For this final model, unparasitized hosts were excluded because they were not attacked by *C. rubecula* and obviously lacked a time interval between attack by *C. rubecula* and exposure to *C. glomerata*. Time to attack, attack duration, and clutch size were each analyzed using separate two-way ANOVAs with time since oviposition by *C. rubecula* and *C. glomerata* population treated as explanatory variables. The relationship between attack duration and clutch size was measured using Pearson correlation after log transformation of attack duration to decrease skew. Five females that attacked a host but failed to lay eggs were omitted from this analysis (CO unparasitized = 1; CO *C. rubecula*-parasitized = 1; MD *C. rubecula*-parasitized = 3). Blocks were the different dates on which sets of choice test experiments were performed and block was treated as a random effect in the regression analyses. Response variables were unaffected by the block term in any of the analyses; therefore, statistical models were rerun without the blocking variable and these results are presented. A two-tailed exact binomial test, with function `binom.test` in RStudio version 1.0.136 (R Development Core Team 2008), was used to compare the observed and expected

probabilities of multiparasitism found in field-collected caterpillars. JMP version 12.0.1 (SAS Institute) was used for all other analyses. All means are presented as means with standard errors (mean ± SE) and all statistical analyses were tested at a significance level of $\alpha = 0.05$.

Results

Multiparasitism was rarely observed in field-collected *P. rapae* caterpillars from Maryland with 10% (74/751) containing both *C. glomerata* and *C. rubecula*. Of the 751 *P. rapae* collected, 310 (41%) were attacked by *C. glomerata* and 153 (20%) were attacked by *C. rubecula*. Based on these values, randomly searching wasps in a patch of 100 hosts were expected to multiparasitize 8% [95% CI: 7%, 12%] of these hosts, which was slightly below the observed value of 10% ($p = 0.08$) (Fig. 1).

Cotesia glomerata females from Colorado were 2.1 times [95% CI: 1.1, 4.0] more likely to attack hosts that were previously parasitized by *C. rubecula* than were *C. glomerata* females from Maryland (Fig. 2; likelihood ratio $\chi^2 = 4.73$, $df = 1$, $p = 0.03$). The time interval between parasitism by *C. rubecula* and encounter by *C. glomerata* had no influence on the likelihood of attacking *C. rubecula*-parasitized hosts by either CO or MD *C. glomerata* (CO: likelihood ratio— $\chi^2 = 3.41$, $df = 3$, $p = 0.33$; MD: likelihood ratio— $\chi^2 = 3.42$, $df = 3$, $p = 0.33$). With time interval held constant, *C. glomerata* females from MD were significantly more likely to choose unparasitized hosts over hosts previously parasitized by *C. rubecula* (likelihood ratio— χ^2 goodness-of-fit test = 4.55, $df = 1$, $p = 0.03$), whereas *C. glomerata* females from CO failed to show a preference for

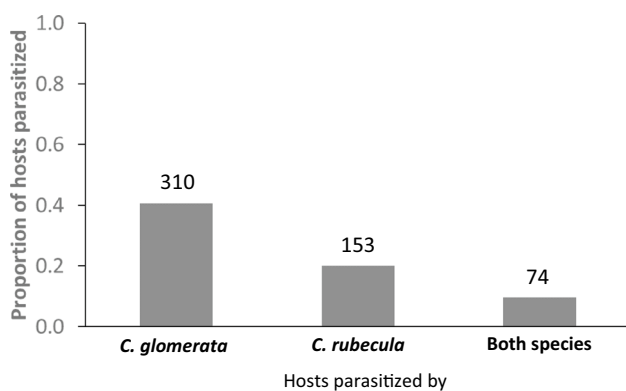


Fig. 1 The proportion of field-collected *Pieris rapae* ($n = 751$) that were parasitized by *Cotesia glomerata*, *C. rubecula*, and by both *Cotesia* species (i.e., multiparasitized) in MD. The values above the bars are the number of *P. rapae* parasitized for each parasitism category. A binomial test indicated that the observed probability of multiparasitized hosts was above the expected value from wasps foraging randomly (0.08 [95% CI: 0.07, 0.12])

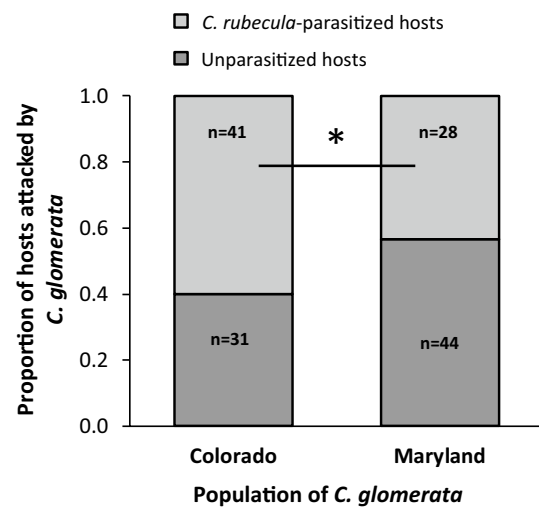


Fig. 2 The proportion of unparasitized hosts and hosts parasitized by *Cotesia rubecula* that were attacked by Colorado (CO) and Maryland (MD) *C. glomerata* in a choice test ($n = 72$ females for each population). The numbers inside the graphs indicate how many females attacked each type of host. The asterisk indicates significant differences between the CO and MD *C. glomerata* when attacking each type of host

unparasitized hosts over those previously parasitized by *C. rubecula* (likelihood ratio— χ^2 goodness-of-fit test = 1.39, $df = 1$, $p = 0.24$). Taken together, these findings indicate that *C. glomerata* from Colorado are less likely to avoid against hosts previously parasitized by *C. rubecula* than are *C. glomerata* from Maryland.

Overall, 133 out of 144 (92.3%) *C. glomerata* attacked the host that was on the leaf first contacted by the female. The remaining 11 trials consisted of either *C. glomerata* females first contacting an unparasitized host followed by an attack of a parasitized host ($n = 7$) or the opposite ($n = 4$). When a *C. glomerata* first contacted an unparasitized host and ignored it to attack a *C. rubecula* parasitized host, six out of seven (85.7%) trials involved a CO *C. glomerata*. In three of the four (75%) trials where a *C. glomerata* first contacted a parasitized host, but then attacked the unparasitized host, the *C. glomerata* were from MD.

Once a female *C. glomerata* initiated rapid antennal and/or abdominal contact with the leaf in pursuit of a host, the mean time to attack an unparasitized or *C. rubecula*-parasitized host was independent of the population origin of *C. glomerata* (CO vs. MD: 305.4 ± 27.2 s vs. 322.1 ± 28.8 s; $F_{1,140} = 0.15$, $p = 0.70$) or parasitism state of the host (unparasitized vs. *C. rubecula*-parasitized: 311.4 ± 29.0 s vs. 315.8 ± 27.1 s; $F_{1,140} = 0.002$, $p = 0.97$). When *C. glomerata* females from Colorado and Maryland attacked hosts previously parasitized by *C. rubecula*, the time to attack was similar for both populations (CO vs. MD: 310.5 ± 34.1 s vs. 312.8 ± 52.1 s; $F_{1,61} = 0.02$, $p = 0.89$)

and was unaffected by the time since parasitism by *C. rubecula* (<0.5 h = 401.8 ± 91.5 s, 24 h = 241.1 ± 39.3 s, 48 h = 304.6 ± 49.5 s, 72 h = 334.9 ± 61.6 s; $F_{3,61} = 1.51$, $p = 0.22$).

After a host was found, the time a female spent attacking was independent of population (CO vs. MD: 67.1 ± 8.6 s vs. 52.75 ± 5.9 s; $F_{1,140} = 1.49$, $p = 0.22$) and the parasitism status of the host (unparasitized vs. *C. rubecula*-parasitized: 66.1 ± 8.8 s vs. 54.3 ± 5.9 s; $F_{1,140} = 1.10$, $p = 0.35$). When attacking hosts that were previously parasitized by *C. rubecula*, there were no significant differences in oviposition duration between population (CO vs. MD: 74.8 ± 13.1 s vs. 53.4 ± 10.2 s; $F_{1,61} = 1.45$, $p = 0.23$) or time interval since *C. rubecula* attack (<0.5 h = 97.1 ± 29.4 s, 24 h = 48.9 ± 12.3 s, 48 h = 54.6 ± 11.8 s, 72 h = 75.5 ± 19.5 s; $F_{3,61} = 0.92$, $p = 0.43$).

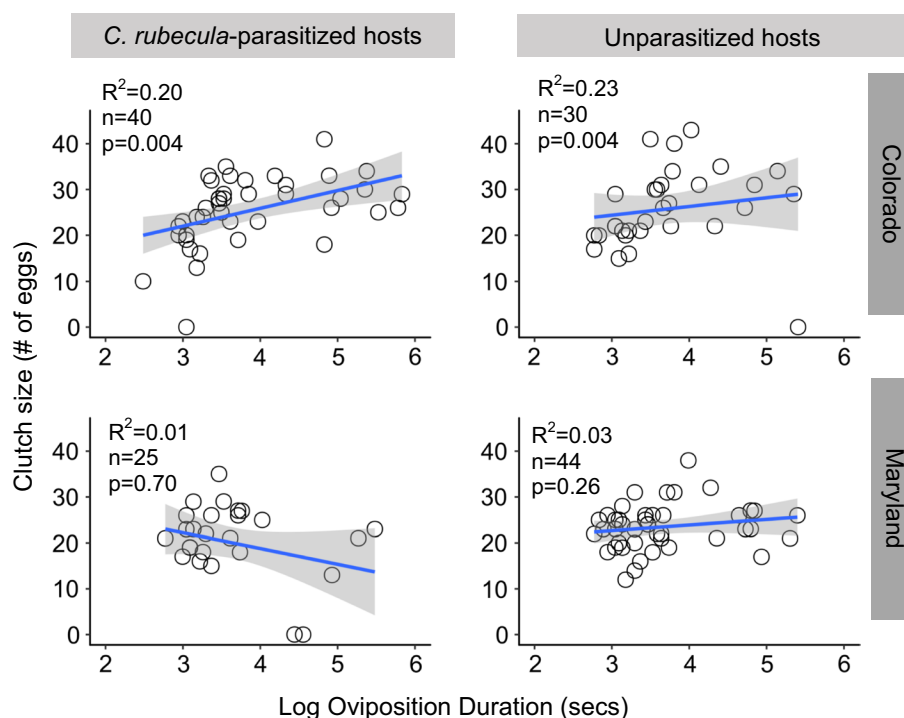
For both unparasitized and *C. rubecula*-parasitized hosts, we found a weak positive relationship between attack duration and clutch size for only *C. glomerata* from CO (Fig. 3; unparasitized hosts: $r = 0.52$, $n = 30$, $p = 0.004$; *C. rubecula*-parasitized hosts: $r = 0.45$, $n = 40$, $p = 0.004$). There was no relationship between the time it took female *C. glomerata* from MD to oviposit and the size of their clutches (Fig. 3). Female *C. glomerata* from MD and CO laid similar clutch sizes in unparasitized hosts and hosts previously parasitized by *C. rubecula* (CO unparasitized vs. parasitized: 26.63 ± 1.35 eggs vs. 26.02 ± 1.02 eggs; MD unparasitized vs. parasitized: 24.20 ± 1.04 vs. 23.40 ± 1.38 eggs; $F_{3,135} = 1.48$, $p = 0.22$). After controlling for the parasitism status of the hosts, CO *C. glomerata* had larger clutch sizes

than did MD *C. glomerata* (CO vs. MD: 26.29 ± 0.82 eggs vs. 23.91 ± 0.83 eggs; $F_{1,135} = 4.43$, $p = 0.04$). When wasps attacked *C. rubecula* parasitized hosts, clutch size was independent of population ($F_{1,57} = 2.40$, $p = 0.13$) or the length of time since parasitism by *C. rubecula* (<0.5 h = 23.9 ± 1.3 eggs, 24 h = 24.2 ± 1.8 eggs, 48 h = 22.9 ± 2.7 eggs, 72 h = 23.3 ± 2.1 eggs; $F_{3,57} = 0.33$, $p = 0.81$). Clutch sizes ranged from 12 to 56 eggs; five females (two from CO and three from MD) attacked a host without laying any eggs, so these females were excluded from these analyses.

Discussion

Foraging parasitoids are capable of avoiding oviposition in hosts previously parasitized by conspecific females (van Alphen and Visser 1990; Godfray 1994) and can even detect herbivore-induced volatiles at long distances to avoid hosts parasitized by a stronger competitor (Janssen et al. 1995; Tamò et al. 2006). While other studies have found between-population variability in the ability to avoid hosts attacked by conspecifics (van Baaren and Boivin 1998; Goubault et al. 2004), to our knowledge this is the first study to compare the ability of different populations to discriminate against hosts parasitized by heterospecifics. Our results support the hypothesis that host selection behavior of North American populations of *C. glomerata* differs based on whether they have become re-associated with *C. rubecula*. *Cotesia glomerata* females from CO, where *C. rubecula* is absent, appear to lack the ability to discriminate between unparasitized

Fig. 3 The relationship between the log of oviposition duration and the number of *Cotesia glomerata* eggs observed in unparasitized and *C. rubecula*-parasitized hosts attacked by Colorado and Maryland *C. glomerata*. The shaded area around the line is the 95% CI



hosts and those previously parasitized by *C. rubecula*. *Cotesia glomerata* experience high mortality if attacking a host parasitized by *C. rubecula* (Laing and Corrigan 1987); thus, *C. rubecula* should exert strong directional selection favoring avoidance behavior in *C. glomerata* females from MD towards hosts previously parasitized by *C. rubecula*. In Europe, where both parasitoids and *P. rapae* originate, the two *Cotesia* species coexist because they almost exclusively use different host species: *C. rubecula* attacks only *P. rapae* and *C. glomerata* predominately attacks *P. brassicae* and only rarely attacks *P. rapae* (Geervliet et al. 2000).

That *C. glomerata* from MD were significantly less likely to multiparasitize a host than were *C. glomerata* from CO, yet females from both locations almost always oviposit in the first host examined by antennal contact and laid similar clutch sizes, suggests that host discrimination in MD females may occur well before the host is physically encountered. Parasitoids, including *C. glomerata* and *C. rubecula* (Geervliet et al. 1998; Fatouros et al. 2005; Poelman et al. 2011), are well-known to respond to herbivore-induced plant volatiles (Geervliet et al. 1998; Baldwin et al. 2002; Dicke and Baldwin 2010; Gols 2014). Geervliet et al. (2000) used a wind tunnel study to show that *C. glomerata* females avoid patches of *P. rapae* hosts that are nearby *C. rubecula*. Indeed, parasitoid species identity is known to alter herbivore-induced plant volatile profiles (Poelman et al. 2011). For instance, *Brassica oleracea* plants attacked by unparasitized *P. rapae* caterpillars, *C. rubecula*-parasitized caterpillars, and *C. glomerata*-parasitized caterpillars all differ in their volatile profiles (Poelman et al. 2012; Zhu et al. 2014). These volatile profiles are, in turn, differentially attractive to hyperparasitoids (Poelman et al. 2012) and, presumably, used as cues by MD *C. glomerata* females to assess whether a host is unparasitized, parasitized by a heterospecific competitor, or parasitized by a conspecific. When given a choice between plants fed upon by unparasitized *Pieris* caterpillars or ones parasitized by *C. rubecula* (multiparasitism) or *C. glomerata* (superparasitism), *C. glomerata* uses competitor-related cues to avoid plants with parasitized hosts (multiparasitism—Geervliet et al. 2000; superparasitism—Fatouros et al. 2005).

Previous studies with *P. rapae* as a host have found that mated and unmated *C. glomerata* reduce clutch size and attack duration when superparasitizing hosts (Kusano and Kitano 1974; Ikawa and Suzuki 1982; Tagawa 1992). Interestingly, we found that once an attack was initiated, neither CO nor MD *C. glomerata* females adjusted their clutch sizes regardless of the time elapsed between when the host was parasitized by *C. rubecula* and subsequently encountered by *C. glomerata*. It is likely that female *C. glomerata* in our study failed to adjust clutch sizes in response to the presence of *C. rubecula* because *C. rubecula* causes 100% mortality of immature *C. glomerata* regardless of the number of eggs

laid. Under these conditions, there would be no selection for altered clutch sizes since variation in clutch size fails to increase survivorship.

Where *C. glomerata* and *C. rubecula* co-occur in North America, at least four possible mechanisms may be responsible for their coexistence. First, as was the focus of this study, *C. glomerata* may have experienced strong selection pressure to avoid attacking hosts already parasitized by *C. rubecula* as seems to be the case with our MD study population. To further support the idea that multiparasitism avoidance may influence the coexistence between *C. glomerata* and *C. rubecula*, our dissections of field-collected *P. rapae* hosts in MD suggest that multiparasitism is infrequently observed. It was not possible to know the order of attack for these multiparasitized hosts; but as *C. rubecula* is known to accept hosts parasitized by *C. glomerata* (Laing and Corrigan 1987), these multiparasitized hosts could be a product of *C. rubecula* attacking after *C. glomerata*. Our reliance on dissections may have underestimated the multiparasitism, so subsequent studies should consider using molecular tools (e.g., species-specific genetic markers) with a higher sensitivity for detecting the presence of both *Cotesia* species within a host.

Second, *C. glomerata* foraging behaviors might undergo selection to be more efficient when competing with *C. rubecula*. Specialized parasitoids, such as *C. rubecula*, tend to be more efficient than generalist parasitoids when foraging for hosts (Vet et al. 1993; Cortesero et al. 1997; Wang and Keller 2002). *Cotesia rubecula* can attack more caterpillars in the same amount of time as can *C. glomerata* because *C. rubecula* attacks are at least ten times faster than *C. glomerata* (pers. observation DKV and RP). *Cotesia rubecula*, a specialist on *P. rapae*, has evolved a foraging strategy suited for the solitary host distributions of *P. rapae*, whereas *C. glomerata* foraging behaviors were likely adapted for the clustered distributions of *P. brassicae* (Le Masurier and Waage 1993; Wiskerke and Vet 1994; Vos et al. 1998). However, the change in the primary host of North American populations of *C. glomerata* may have selected for a foraging strategy similar to *C. rubecula* (Wiskerke and Vet 1994; Vos et al. 1998). When searching for hosts, North American *C. glomerata* search more plants and spend less time searching per plant than European *C. glomerata*. Since the foraging strategies of North American *C. glomerata* likely have changed to help it survive on a less preferred host, these foraging behaviors may also undergo further change to enable coexistence with a stronger competitor. If foraging efficiency is variable across *C. glomerata* populations, then the more efficient populations might be able to avoid competitive displacement once *C. rubecula* enters the habitat.

Third, *C. glomerata* populations may persist if alternative host species are present. Whereas *C. rubecula* is an extreme specialist on *P. rapae* (Brodeur et al. 1996), *C. glomerata*

has a broader host range including several North American pierid species, such as the green-veined white *P. napi*, the checkered white *Pontia protodice*, and the western white *Pontia occidentalis* (Laing and Levin 1982; Benson et al. 2003; van Driesche et al. 2004; Herlihy et al. 2012; DV pers. observation). If these alternate host populations are sufficiently high, *C. glomerata* may be able to persist even in the face of intense competition with *C. rubecula* for *P. rapae*.

Finally, attacks from shared enemies may reduce the competitive advantage of *C. rubecula* over *C. glomerata* if *C. rubecula* are preferentially attacked (Kaser and Ode 2016; Weis et al. 2016). Both *Cotesia* species are attacked by similar hyperparasitoid species in North America (McDonald and Kok 1991), but *C. rubecula* is larger (Ikawa and Okabe 1985; Geervliet and Brodeur 1992; Brodeur et al. 1998; Harvey et al. 1999) and can offer greater host resources per cocoon for the hyperparasitoid offspring. If its larger size makes the solitary *C. rubecula* more vulnerable than *C. glomerata* to hyperparasitoid attacks, then differential mortality from these attacks may enable *C. glomerata* to coexist with *C. rubecula*. Even if both *Cotesia* species are similarly preferred by hyperparasitoids, the gregarious nature of the *C. glomerata* brood allows some cocoons to escape hyperparasitism (Gaines and Kok 1999), whereas the solitary *C. rubecula* lacks this advantage. Mortality from hyperparasitoid attacks is suspected to limit the range of *C. rubecula* in North America (McDonald and Kok 1992; Gaines and Kok 1999), therefore this top-down factor could be significant for mediating competitive interactions between the two *Cotesia* species.

The relative importance of these four non-exclusive explanations is unknown and requires further research with additional *C. glomerata* populations. These parasitoid communities could be operating under different evolutionary pressures across a broad geographical landscape, creating a mosaic of communities in which different North American populations of *C. glomerata* exist (Thompson 1994). Across taxa, separation from important heterospecifics (e.g., predators, pathogens, and pollinators) is known to alter behaviors that are important for mediating interspecific interactions. Studies on predator-free space show that relaxed selection can attenuate a wide range of behaviors, including visual (Coss 1999), acoustic (Fullard et al. 2007) and olfactory recognition of predators (Cousyn et al. 2001). Just as recognition of predators weakens in predator-free space, so should recognition of stronger competitors in competitor-free space.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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